Effects of Magnesium Deficiency on the Photosynthesis and Respiration of Leaves of Sugar Beet

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ABSTRACT

The effects of Mg deficiency on the photosynthesis and respiration of sugar beets (Beta vulgaris L. cv. F58-554H1) were studied by withholding Mg from the culture solution and by following changes in CO₂ and water vapor exchange of attached leaves. Leaf blade Mg concentration decreased from about 1200 to less than 200 meq kg⁻¹ dry matter without change in the rate of photosynthetic CO₂ uptake per unit leaf area, while from 200 to 50 meq kg⁻¹ the rate decreased to one-third. Rates of respiratory evolution of CO₂ into CO₂-free air responded to Mg like those of photosynthetic CO₂ uptake, the rates decreasing to one-half, below 200 meq kg⁻¹. Respiratory CO₂ evolution in the dark increased almost 2-fold in low Mg leaves. Magnesium deficiency had less effect on leaf (mainly stomatal) diffusion resistance (rₛ) than on mesophyll resistance (rₘ); in Mg-deficient plants rₘ increased from 2.9 to 7.1 sec cm⁻¹, whereas rₛ became significantly greater than the control value only in the most severe instances of Mg deficiency.

Magnesium is required by a large number of enzymes involved in energy transfer, particularly those utilizing ATP (2). It is a constituent of the Chl molecule and is required for the normal structural development of the chloroplast (4, 11), as well as other organelles such as the mitochondrion (5). Thus, it is to be expected that Mg deficiency would have damaging effects on photosynthesis and respiration. This has been shown for both processes in spinach (1), and for photosynthesis in maize (6). Magnesium deficiency has a pronounced effect on sugar beet plants, causing chlorosis, yellowing, scorching of the interveinal tissues of the leaf blade, and eventually, necrosis (13). In the present investigation, our objective was to assess the effects of Mg deficiency on the photosynthetic and respiratory CO₂ exchange of sugar beet leaves and to determine whether Mg has any effect on leaf CO₂ uptake attributable to changes in stomatal diffusion resistance.

MATERIALS AND METHODS

Details of the procedures followed in the culture of plants, in the determination of gas exchange parameters of individual attached leaves, and in the estimation of the contents of leaf minerals, are as described in earlier papers (8 to 10). The culture solution employed to obtain Mg deficient plants contained, in mmole/l, 2.5 Ca(NO₃)₂·4 H₂O, 0.5 KH₂PO₄, 2.5 KNO₃, 1.0 K₂SO₄, and 0.5 NaCl, and, in mg/l, 0.25 B, 0.25 Mn, 0.025 Zn, 0.01 Cu, and 0.005 Mo. Iron was added as ferric-sodium ethylene diamine tetraacetate complex to give 2.5 mg of Fe/l. The culture solution for the control plants was the same except for 1 mmole of MgSO₄/1 which was added in place of the K₂SO₄.

The gas-exchange measurements were begun at Mg cutoff, 28 days from planting, at which time three control plants were supplied with the complete culture solution and eight plants with the culture solution containing no added Mg. Measurements were made on control plants at the beginning and end of each period of deficiency.

In addition to the information concerning gas-diffusion resistances, provided in earlier work (8, 9), we wish to make the following points. Assuming a cuticular resistance to water vapor of at least 10 sec cm⁻¹, the leaf diffusion resistance (rₛ), which includes cuticular and stomatal diffusion resistances, would differ from stomatal diffusion resistance by about 2% (for low values of rₛ). As the cuticular resistance may well have been much higher than 10 sec cm⁻¹, the leaf diffusion resistance probably approximates to the stomatal diffusion resistance in most instances referred to below, excepting possibly the highest values or rₛ. The boundary layer resistance for CO₂, rₛ, was found to be 0.2 sec cm⁻¹ for most leaves.

RESULTS

The Mg concentrations in the leaf decreased rapidly after cutoff, reaching the critical level of 80 meq kg⁻¹ of dry matter after 9 days, and remaining constant thereafter (Fig. 1). Visible symptoms of Mg deficiency did not appear until 12 days after cutoff; the recently matured leaves showed interveinal chlorosis, but the experiment was terminated before any necrosis developed. The concentration of Mg in control leaves also decreased, from 1230 to 710 meq kg⁻¹ in the blade. This was almost certainly attributable to an inadequate supply of Mg, the demand of these fast-growing plants outstripping supply even though the culture solutions were changed three times a week. Despite this, leaf Mg concentration was sufficiently high to prevent visible deficiency symptoms or changes in photosynthetic or respiratory performance.

Depletion of leaf Mg, as a result of withholding Mg from the culture solution, probably led to a slight increase in Ca uptake by the plant, since the Ca concentration of the leaf blade and petiole showed increases during the 1st week (Fig. 1). By the end of the 2nd week the Ca concentration in the leaf blade had decreased to about 200 meq kg⁻¹, a value considerably below that of the control blade, while in the petiole it had de-
FIG. 1. Effects of withholding Mg from the culture solution on the concentrations of Mg and Ca in the leaf blade and petiole with time after cutoff.

Increased to about 300 meq kg⁻¹, about the same as the control. The concentrations of K in the leaf blade at the 5th and 7th days from cutoff were 1664 and 1541 meq kg⁻¹, respectively, which were somewhat higher than the control values of about 1300 meq kg⁻¹. Thus, it appeared that the leaf initially absorbed Ca and possibly K as substitute cations for Mg, a phenomenon which has recently been reported in maize (3). The concentrations of other cations in the leaf blade or petiole, including Cu, Fe, Mn, Na, and Zn, did not change significantly with time after Mg cutoff.

After Mg cutoff, the rates of photosynthetic CO₂ uptake in normal and O₂-free air, F and F*, respectively, apparently increased during the first week, then decreased rapidly during the next 10 days to about one-third of the control rates (Fig. 2A). Most of the decrease in photosynthetic rates which occurred after the first week was due to increased mesophyll resistance (r_m and r_m*) (Fig. 2D). Leaf (mainly stomatal) diffusion resistance, r_l, increased after the first week but only became significantly greater than the control in the most severe instances of Mg deficiency (Fig. 2C). Even at the end of the experiment when r_l reached its maximum value, the proportion of the total resistance to CO₂ attributable to r_l, i.e., r_l/(r_l + r_m + r_m*) was only 15% in Mg-deficient leaves compared to the normal value of about 13% in control leaves.

Respiratory CO₂ evolution into CO₂-free air in the light (R_l) decreased almost linearly with time after Mg cutoff, while dark respiration (R_d) apparently increased (Fig. 2B). The in-

FIG. 2. Effects of Mg deficiency on various leaf gas exchange parameters with time after cut-off. A: Changes in rate of photosynthetic CO₂ uptake in O₂-free air, F*, and in normal air (21% O₂), F; B: changes in rates of respiratory CO₂ evolution in the light, R_l, and dark, R_d; C: changes in leaf diffusion resistance for water vapor, r_l; D: changes in CO₂ mesophyll resistance in O₂-free air, r_m*, and in normal air, r_m. The data for F, F* and r_l were determined at 50 mw cm⁻² visible radiation, 25 °C, and at an ambient CO₂ concentration of 300 ng cm⁻².

FIG. 3. Relationship of the rate of photosynthetic CO₂ uptake, F, and of photosynthetic evolution of CO₂ into CO₂-free air, R_l, with the Mg concentration of the leaf blade [data obtained from three different experiments (C, D, E)].
increase in $R_o$ in low Mg leaves appeared to take place in the first week after cutoff; $R_o$ increased from 2.3 to 4.0 ng of CO$_2$ cm$^{-2}$ sec$^{-1}$, and this rate was maintained subsequently while the rate for the control leaf decreased slightly over the experimental period. $R_o$ of the low Mg leaves decreased to about one half that of the control leaf over the period of deficiency.

**DISCUSSION**

There were apparent increases in the rates of photosynthetic CO$_2$ uptake per unit area, F and F*, after Mg cutoff (Fig. 2A); F and F* of Mg-deficient plants attained maxima of 81 and 189 ng of CO$_2$ cm$^{-2}$ sec$^{-1}$, respectively. These maximal values are about two standard deviations higher than the mean values for 10 control leaves, 71 and 165 ng of CO$_2$ cm$^{-2}$ sec$^{-1}$, with standard deviations of $\pm$5 and $\pm$22 ng cm$^{-2}$ sec$^{-1}$, respectively. However, such increases in F and F* with time after Mg cutoff may occur in control as well as Mg deficient plants. One possible explanation for the increases may be that the nutrition and therefore photosynthetic performance of the plant may have been improved by replenishing the culture solutions, exclusive of Mg, at Mg cutoff.

We believe that the relationship of photosynthetic rate with leaf-Mg concentration follows that illustrated in Figure 3, i.e., that the rate increased with leaf Mg from 50 up to about 200 meq kg$^{-1}$, and that from 200 to 1200 meq kg$^{-1}$ the photosynthetic rate remained fairly constant. Rates of photorespiratory CO$_2$ evolution into CO$_2$-free air followed a similar relationship with leaf Mg (Fig. 3). Thus the leaf was able to sustain normal photosynthetic and photorespiratory activities at Mg concentrations down to as low as 20% of those of the control leaf.

Peaslee and Moss (6) found that rates of photosynthesis in maize were diminished by Mg deficiency only after chlorosis became evident, and concluded that low Mg affected photosynthesis through an effect on Chl formation. In sugar beet, chlorosis was not evident until 5 days after photosynthetic rates decreased. Peaslee and Moss (6) also observed that photosynthetic rates were closely related to the Mg concentration of the leaf tissue and obtained a critical concentration of 200 $\mu$g of Mg/g fresh weight. Assuming an approximate dry weight-fresh weight ratio of 10% and converting to milliequiv-<ref>lents, this yields a figure of 165 meq of Mg kg$^{-1}$ dry weight for the critical concentration for photosynthesis compared to 150 meq kg$^{-1}$ for sugar beets (Fig. 3). The critical concentration for sugar beet growth, in terms of plant dry matter accumulation, is about 80 meq kg$^{-1}$ (12), somewhat lower than that for photosynthesis.

Dark respiration increased as leaves became more Mg deficient. Magnesium deficiency might be expected to cause some derangement of the respiratory processes since Mg is required for enzymes of glycolysis, the pentose phosphate pathway, and the tricarboxylic acid cycle (7).

The effect of Mg deficiency on photosynthesis was predominately through increased mesophyll resistance; $r_o$ and $r_e$ increased continually until the termination of the experiment. Stomata were very little affected by Mg deficiency until the 15th or 16th day as indicated by $r_d$ which changed little until that time. In the case of the most Mg-deficient plant (16 days after cutoff), the increase in total resistance (i.e. the resistance to CO$_2$ movement from the atmosphere to the intracellular site of photosynthesis) attributable to Mg deficiency was 5.5 sec$^{-1}$ of this increase, 84% was due to an increase in $r_o$ and only 16% to an increase in $r_d$.

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**LITERATURE CITED**


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