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Inhibitory Effects of Water Deficit on Maize Leaf Elongation[1]

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ABSTRACT

The growth rate of maize leaves has been investigated for plants grown in pots in controlled conditions and subjected to slow drying over a period of days. The elongation of leaves experiencing water deficit was inhibited primarily during the afternoon. No decrease in the turgor of the growing cells could be detected at that time. Solute concentration in the growing cells increased in tissue experiencing water deficit, but this was shown to occur after the growth rate had fallen. Calculations of the rate of solute accumulation necessary to maintain these concentrations indicated that the rate was less in slowly growing than in rapidly growing cells. The growing tissue of well-watered leaves excreted protons into the apoplastic space, but this acidification decreased in tissue exposed to water deficit. The pH of the apoplastic space correlated with the growth rate of the tissue. *In vitro* acidification of isolated, frozen-thawed tissue, maintained under constant tension, increased wall extensibility. The results suggest that one role of proton excretion may be to promote wall-loosening events necessary for cell enlargement, and that inhibition of this process may have reduced growth rate in leaves exposed to water deficit.

The elongation rate of cereal leaves is quite sensitive to plant water status. Small reductions in the water potential of the root medium immediately decrease the growth rate of maize (1) and barley (22) leaves. Similarly, increased evaporative demand immediately slows the growth rate of wheat leaves (8). Longer term experiments in which plants are subjected to soil drying also demonstrate a close relationship between growth rate and leaf water potential (3, 20, 25). Although it might be assumed that lowered water potential acts to reduce growth rate of cereal leaves by decreasing cell turgor, efforts to demonstrate this have not been successful. On the contrary, it has been found that growing cells in cereal leaves respond to low water potentials by lowering solute potential and in this way maintaining cell turgor (22, 25). These results suggest that some other factor besides turgor is limiting leaf elongation at low water potential.

Recent work on the cellular regulation of dicotyledonous leaf expansion has shown that the growth of etiolated leaves is restricted by cell wall stiffness (31). Illumination of primary bean leaves stimulated the rate of cell enlargement by causing the cells to acidify the cell wall space. This acidification resulted in wall loosening and allowed growth rate to increase. As a consequence, leaf turgor actually decreased (32). In this case, no changes in other cellular parameters regulating cell enlargement (hydraulic conductivity or wall yield threshold) were detected.

The present study proceeds from the work of Michelena and Boyer (25), in which maize plants grown in pots were allowed to dehydrate over a period of days. In an effort to determine the cause of the decreased growth rate caused by water deficit, we asked two types of questions. First, was the high solute concentration which developed in drying leaves in itself inhibitory to leaf growth? Second, did cell wall extensibility change? The ability of growing cells to acidify their apoplastic space was determined, and the effect of the acidification on wall extensibility was measured. While the results do not provide a mechanism for the inhibition of growth, they suggest that an important effect of low water potentials is to impair the ability of growing cells to excrete acid, and that acidification may be involved in the regulation of cell elongation for monocotyledonous leaves.

MATERIALS AND METHODS

Plant Material. Maize (*Zea mays* L. variety Mol7 × B73, Illinois Seed Foundation) plants were grown individually in pots containing a mixture of soil, peat, perlite, and sand (3:1:1:1). The plants were maintained in a controlled environment chamber providing a 14-h photoperiod, daytime irradiance of 800 μmol m^{-2} s^{-1} PAR (cool-white fluorescent bulbs), 30/20°C day/night temperatures, and 65–95% RH. Tissue samples were generally taken 20 to 40 mm for the base of the fifth leaf when this leaf was 35 to 50 cm long. At this stage, the ligule was still within the elongating region, and all samples were of blade and not sheath tissue. Preliminary experiments showed that leaf growth rate was constant for well-watered plants until the ligule passed through the elongating region, at which time growth rate declined. Plants were watered daily until the fifth leaf was 25 to 30 cm long, after which water was withheld from experimental plants.

Measurement of Growth Rate, Water Potentials, and Osmotic Potentials. The rate of leaf elongation was determined either by measuring leaf length with a meterstick over relatively long periods of time, or by attaching a leaf to a position transducer and measuring the change in output over shorter times. Water and solute potentials were determined on isolated leaf pieces as described previously (25). Briefly, plants were cut off at the base and immediately placed into a humid chamber. The fifth leaf was separated from the rest of the shoot, and sections were cut from the elongating region (except as specified), excluding the midvein. Samples were quickly loaded into psychrometer chambers, and measurements of potentials were made by the isopiestic technique (5). Turgor was calculated from the difference between the water and osmotic potentials determined for the same piece of tissue.

Calculations of the Rate of Solute Accumulation. The osmotic potential of the growing region was determined before and after 4 h of growth during midday, and converted to concentration by the proportionality 40 mmol bar^{-1}. The change in cell volume over the growth period was calculated from the measured length of the epidermal cells between veins (Fig. 1), and average values of width (20 μm) and thickness (15 μm). It was assumed that the average cell length in each sample (taken 20 to 40 mm from the

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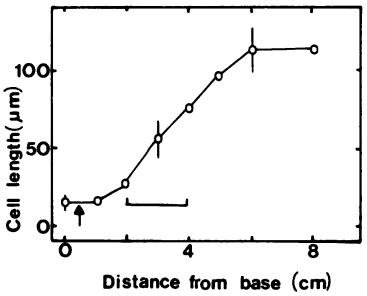

FIG. 1. Epidermal cell lengths in the growing region of the fifth leaf. Length of cells between veins on three well-watered leaves were measured; SE is indicated (n = 10). The arrow denotes the position of the ligule; samples were taken between 2 to 4 cm.

leaf base) was initially the same as that of cells 30 mm from the base, and that the profile of cell lengths down the stem was identical for all treatments. The average cell length 4 h later was determined from the growth rate by positioning on Figure 1. Solute content per cell was calculated from concentration and volume, and the rate of accumulation of solutes was determined by subtracting the initial from the final solute content, and expressing the result on an hourly basis.

Measurement of Wall Extensibility and Acidification. Cell wall extensibility was determined by the Instron technique (10, 31). Leaf pieces were cut 5 mm wide, excluding the midvein, boiled for 2 min in methanol, then stored in methanol until use. For testing on the Instron TM-S extensiometer, stored leaf pieces were rehydrated, placed between clamps 5 mm apart, and stretched twice to a load of 20 g. The clamps separated at 2 mm min^{-1}, and per cent plastic (or irreversible) extension was calculated from the difference between the slopes of the first and second extensions. No significant difference could be measured in the dry weight per unit area of the tissue. Therefore, the data are presented as per section, and not corrected for area exposed to the load.

The capacity of cell walls to extend in the presence of acid was determined by placing frozen-thawed leaf strips under 10 g constant tension and measuring extension over time with a position transducer before and after strips were acidified (31). The strips were first surrounded by neutral buffer, 10 mM K-phosphate (pH 7.0) until the initial extension was complete (30 min). Then the buffer was replaced by 10 mM K-phosphate-citrate (pH 4.5). In some cases, the cuticle was very lightly abraded with emery powder before the section was cut.

The ability of the growing cells to acidify the apoplastic space was determined by placing leaf pieces, or in some cases intact plants with the outer four leaves removed, into a humid chamber, and lowering a combination pH electrode (Ingold No. 14043, Ingold Electrodes, Inc., Andover, MA) into a 0.1 ml drop of 1 mM K-phosphate-citrate (pH 6.0) directly on the surface of the elongating tissue. The cuticle was not abraded, because experiments described above indicated that it provided only a very slight barrier to proton movement which at most would delay the detection of the change in surface pH by a few minutes.

RESULTS

Timing of Osmotic Adjustment Relative to Inhibition of Growth. In the previous study of Michelena and Boyer (25), measurements of growth were made over long periods of time with the result that it was not possible to determine whether changes in growth rate were the cause or the result of the accumulation of solutes in the growing cells. To test these possibilities, continuous measurements of leaf growth rate were made and the water status of the growing region was sampled frequently in similar plants experiencing progressively lower

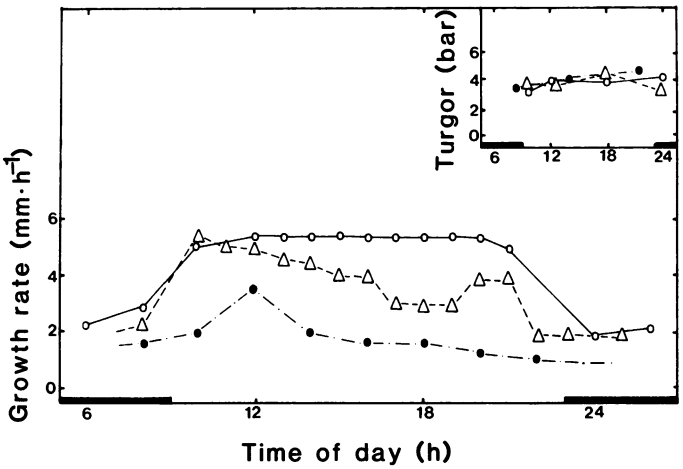

FIG. 2. Diurnal growth rate and turgor of leaves experiencing varying degrees of water deficit. Leaf elongation was measured by position transducer; growth rate calculated at points indicated. The data shown are for three individual leaves on plants of the same age which had not been watered for 1 (○), 3 (△), or 5 (●) days. Each plant was one in a batch of ten of which the rest were sampled for data presented in Figures 3, 4, and 6. Variation (SE, n = 10) in growth rate, as determined by hand measurements, ranged from 0.5 to 0.2 mm h^{-1} for rapidly and slowly growing leaves, respectively. Turgor values are calculated from data presented in Figure 3. This diurnal run was repeated two times with similar results.

water potentials.

The leaves grew faster during the day than during the night (Fig. 2), perhaps because the days were warm (30°C), and the nights cool (20°). This has also been reported for rice (14) and wheat (8). The inhibition of growth caused by withholding soil water occurred primarily during the latter part of the day. There was little diurnal variation in water or osmotic potentials in elongating tissue of well-watered plants (Fig. 3). However, in plants experiencing significant water deficit (5 d), both water and osmotic potentials began to decrease over the diurnal period. As a result, the turgor did not vary, either diurnally or with progressive water deficit (inset, Fig. 2). These results confirm the conclusion presented previously (22, 25) that growth is apparently not limited by lack of turgor during the early stages of water deficit in elongating regions of leaves of grass species.

The inhibition of growth that first appeared during the latter half of the 3rd d was not associated with osmotic adjustment since the osmotic potential measured at this time of day had not declined (Fig. 4). Therefore, the inhibition of growth preceded the change in osmotic potential.

The osmotic potential of cells depends on the rate of solute uptake and use. Because cells enlarge in the growing region, changes in osmotic potential also can be associated with changes in the volume of water in the cells. We calculated the rate of increase in solute content necessary to account for the observed osmotic potentials by measuring the osmotic potential before and after a given time, and correcting the values for changes in cell size (32). During midday, growth rate differed for plants experiencing varying degrees of water deficit (Fig. 2) such that the increase in cell volume in 4 h for well-watered tissue (65%) was larger than that of the drier tissue (−3 d, 29%; −5 d, 6%) (Table I). However, despite the differences in the rate at which water entered these cells, the osmotic concentration of the cells did not change significantly except for the driest tissue. As a result, the solutes necessary to maintain the osmotic potential must have accumulated more slowly in the cells at low water potentials than at high water potentials. This is shown by the rate of change in solute content calculated in Table I, in which

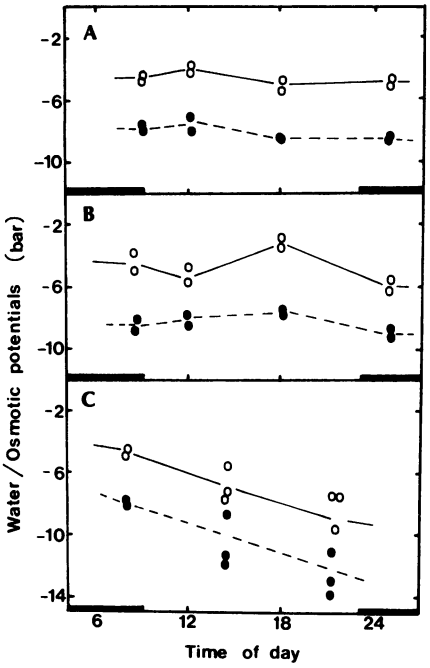

FIG. 3. Diurnal water and osmotic potentials of the growing region. Data are shown for plants which had not been watered for 1 (A), 3 (B), or 5 (C) days. Each point represents an individual sample from which both water (O——O) and osmotic (●- - -●) potentials were determined. The results were qualitatively similar for three replicate experiments.

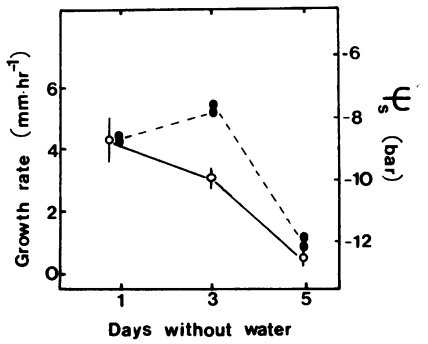

FIG. 4. Relationship between growth rate and osmotic potential. Osmotic potentials (●- - -●) were from midday samples shown in Figure 3. Growth rates (O——O) were measured by meter stick over the 4-h time period prior to sampling (SE indicated, $n = 4$).

well-watered cells accumulated solutes faster than those cells experiencing low water potentials (1.8 and 2.1 times faster than cells in plants 3 and 5 d without water, respectively). The calculations support the idea that osmotic adjustment was not due to an increased rate of solute accumulation, but rather to decreased rate of water uptake. In fact, it appears that the rate of solute accumulation was decreased by water deficit.

Changes in Apoplast Acidification. The surface pH of tissue from the elongating region of well-watered leaves was slightly less than pH 6.0 when the tissue was maintained in the dark (Fig. 5). Illumination of the tissue caused the leaf surface to be acidified after an initial increase in surface pH lasting 30 to 60 min. Whether the change in surface pH was due to increased light intensity, or the small increase in tissue temperature caused by the lamp (3°C) is not known. The surface pH of leaf tissue from plants at low water potentials was initially higher (pH 6.3) than that from well-watered plants (pH 5.9), and responded to illumination more slowly than did the control tissue (Fig. 5). After 2 h, the surface pH of well-watered tissue was always more acidic than that of the samples from leaves exposed to low water potentials (Fig. 6). Furthermore, the decreased pH obtained after 2 h was directly correlated with growth rate of the tissue before it was sampled.

Acidification, *in vitro*, of isolated cell walls placed under constant tension caused the walls to become more extensible (Fig. 7). This response occurred immediately for leaf strips which had been lightly abraded to puncture the cuticle, a barrier to proton movement in some stem tissue (16). A similar response was observed after a slight delay (5 min) for tissue with unabraded cuticle, indicating that the cuticle is actually very thin in this tissue.

This demonstration showing that acidification of isolated walls under tension increased wall extensibility (Fig. 7), in conjunction with the results correlating growth rate with wall acidification (Figs. 5, 6), suggests that the more acidic cell walls of well-watered tissue should be more extensible than those of tissue at lower water potential when measured by the Instron technique. Measurements of wall extensibility consistently showed a slight but not significant difference between well-watered and drier tissue (Table II).

DISCUSSION

Many tissues adjust osmotically in response to desiccation treatment (30). As a result, turgor is partially or completely maintained in these tissues. On the other hand, growth often is inhibited even though turgor maintenance is complete, especially in stem and leaf tissue (23, 25). In roots, growth may be rapid under these conditions and it has been suggested that osmotic adjustment does in fact maintain growth of root tissue (17, 29). The fact that turgor maintenance does not maintain growth in leaf tissue presents the very interesting question of what factor besides turgor is inhibiting growth during conditions of low water potential.

The data presented here (Figs. 2–4; Table I) reaffirm previous findings (25) that turgor in the growing cells of maize leaves is maintained throughout the diurnal period, and that osmotic adjustment occurs in those cells as low water potentials develop. The accumulation of solutes which must occur to lower the osmotic potential takes place after the growth rate begins to decrease. This suggests that increased solute concentration in itself cannot be the cause of growth inhibition in this tissue. Furthermore, it was calculated that the rate of accumulation decreased as the rate of cell enlargement decreased. In this case, accumulation included effects of changes in rates of uptake, use, and also dilution of solutes by water absorption. We have no information which will allow us to separate the effects of these processes. However, the osmotic adjustment that occurred despite decreased rates of accumulation can most simply be explained by decreased water absorption followed by a decreased rate of solute uptake. This hypothesis is similar to that recently drawn from results with soybean stems (24) at low water potentials and from wheat leaves treated with increasing NaCl, where decreased water uptake was accompanied by subsequently decreased salt uptake (15).

For many tissues, it has been demonstrated that increased rates of growth are often due to acidification of the apoplastic space (12, 26, 31). The acidification is necessary for growth to occur, and its effect is to cause loosening of the cell walls. Recently, the geotropic curvature of dicotyledonous stems has also been attributed to asymmetric acidification which causes one side of the stem to grow faster than the other (27, 33). Data presented here suggest that the growth of monocotyledonous leaves may also be occurring by the acid-growth mechanism. Growing cells normally acidified the apoplastic space (Fig. 5), and isolated cell walls from the growing region became more extensible under

Table I. *Calculation of the Rate of Solute Accumulation Necessary to Account for Cell Osmotic Potential in Growing Cells during Midday*

Growth rate was varied by withholding water. Cell lengths were taken from Figure 1, initial values at 30 mm from the leaf base. Cell volumes were calculated using average dimensions of 15 μm (depth), 20 μm (width), and lengths indicated. Osmotic concentration was calculated from osmotic potential (Ψ_s) by conversion factor 40 mmol bar^{-1}. SE (n) indicated.

Time Without Water	Growth Rate	Cell Length	Cell Volume	Osmotic Concn.	Solutes/Cell	Rate of Solute Accumulation to Account for Change in Osmotic Concn.
d	*mm* h^{-1}	*μm*	*pl*	*mmol* l^{-1}	*pmol*	*pmol* h^{-1} *cell*$^{-1}$
Initial						
1		58	17	330 ± 20 (4)	5.6	
3				330 ± 8 (6)	5.6	
5				340 ± 12 (4)	5.7	
After 4 h						
1	4.1 ± 0.4 (7)	94	28	340 ± 16 (4)	9.5	0.97
3	2.8 ± 0.3 (8)	76	22	350 ± 20 (6)	7.7	0.52
5	0.5 ± 0.1 (9)	60	18	420 ± 20 (5)	7.5	0.45

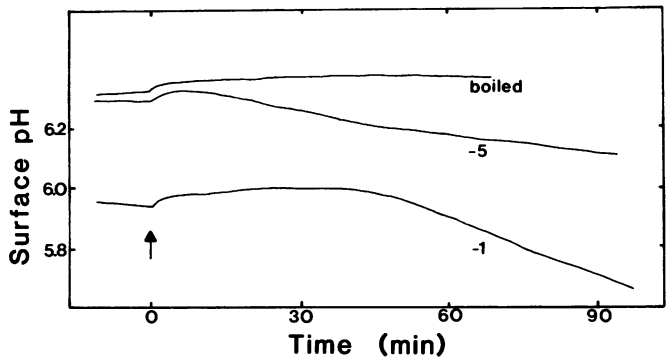

FIG. 5. Leaf surface acidification by tissue sections, from the elongating region, exposed to light. Surface pH was measured with a combination pH electrode lowered into 0.1 ml of 1 mM K-phosphate-citrate (pH 6.0) directly on a leaf section placed on wet filter paper in humid container. Traces are shown for live sections cut from leaves having been without water for 1 or 5 d (growth rates 5.0 and 1.3 mm h^{-1}, respectively). The arrow denotes onset of illumination. A boiled leaf section was used as control. The surface pH of well-watered tissue maintained in the dark did not change more than 0.1 pH unit over 2 h.

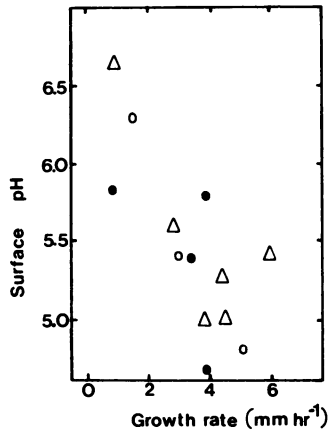

FIG. 6. Correlation between leaf surface pH and growth rate. Growth rates of leaves were measured during midday for leaves experiencing various degrees of water deficit. Leaf pieces (Δ, O) or leaves on intact plants (●) were placed under the pH electrode as described in Figure 5, and surface pH was recorded after 2 h illumination. The different symbols represent plants from three experiments, each point representing a single determination.

constant stress when they were acidified (Fig. 7). Water deficit limited the rate at which acidification occurred, and growth rate was correlated with the pH of the walls (Fig. 6). Not only do these results suggest that growth of maize leaf cells is mediated by proton excretion, but they also indicate that an important effect of water deficit is to impair this acidification process. Similar results have been reported for oat coleoptiles in which inhibition of growth by incubation in mannitol solutions was accompanied by decreased proton excretion (11, 21).

It may be possible to account for the decreased acidification in tissue experiencing water deficit on the basis of feedback inhibition of a solute uptake mechanism, which is one of the possibilities suggested by the calculations in Table I. If a majority of the solutes accumulated in the growing cells are taken up from the apoplast, it is possible that decreased solute uptake might be accompanied by decreased proton excretion, as many transport mechanisms are proton driven (19, 28). This would mean that the decreasing ability of leaf tissue to acidify the apoplast as shown (Fig. 6) could be an indirect result of decreased solute transport. Alternatively, decreased proton transport may have been the primary act, and solute transport a result of the decreased proton transport.

It has been suggested previously that in similar situations an undetectably small drop of turgor may, in fact, be the cause of growth inhibition (22, 24, 25). Such a small drop would be important if the yield threshold of the cell walls were close to the turgor existing in the cells. For example, sunflower leaves have been shown to need at least 6.5 bars of turgor to grow, but normally had several bars in excess of this critical value (2). This situation has also been proposed to exist in growing coleoptile cells (9, 18). This would suggest that turgor pressure could fluctuate over a range of several bars with a corresponding fluctuation in growth rate, and that growth would not stop until several bars of turgor had been lost. If, however, yield threshold in growing maize leaf cells exists within 0.5 bar of the turgor maintained in the cells, a drop in turgor of 0.5 bars would completely inhibit growth, but be undetectable by the techniques used here.Therefore, it is possible that a small drop in turgor is, in fact, the initial event that results in decreased growth of leaves experiencing low water potentials.

It is possible that the psychrometric measurements of water potential and turgor in excised leaf tissue are in error due to wall relaxation in the absence of water uptake by the growing cells. Direct (pressure probe) measurements of turgor in pea stems (13) have shown that 1.5 to 2.0 bar pressure is lost upon excision. If

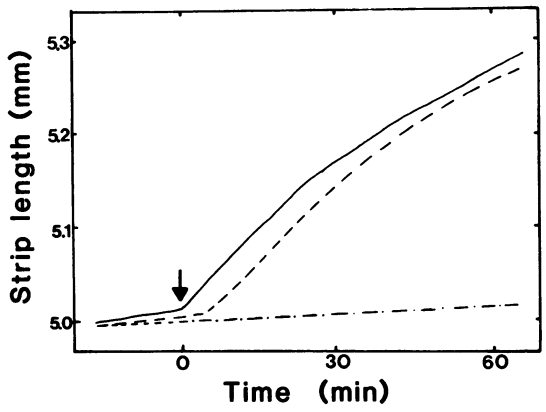

FIG. 7. Acid-induced extension isolated cell walls. Leaf strips were cut from the growing region of well-watered leaves, frozen-thawed, and placed under 10 g constant tension. Change in length was measured by position transducer while the pH of the incubation medium 10 mM K-phosphate, was changed from 7.0 to 4.5 (at arrow). Traces are representative of abraded (——) and unabraded (- - -) tissue, and tissue maintained at pH 7 (-·-).

Table II. *Cell Wall Extensibility*

Tissue was tested with an Instron tensiometer as described in "Materials and Methods". SE (*n*) is indicated.

Time Without Water	Growth Rate	Plastic Extension/ 10 g Load
d	*mm h*$^{-1}$	%
1	4.6 ± 0.2 (5)	2.9 ± 0.1 (9)
3	2.7 ± 0.1 (5)	2.7 ± 0.1 (10)
5	1.1 ± 0.3 (5)	2.4 ± 0.1 (10)

this also occurs when growing corn leaf tissue is excised, the calculations of turgor (Fig. 2) would be underestimated especially at higher growth rates, and growth rate might be correlated with changes in turgor. Because the growing cells of corn leaves are embedded in sheathes of older leaves, it is not possible to make psychrometric measurements on intact tissue. Comparisons of water potentials measured psychrometrically in intact and excised sunflower leaf (2, 4) and soybean stem (6, 7) tissue have not shown a discrepancy between intact and excised tissues, suggesting that wall relaxation is smaller than the variability in the comparisons (about 1 bar), and that turgor does not change much in excised tissue of these species. In these experiments we have assumed that little or no wall relaxation occurs in excised corn leaf tissue until otherwise demonstrated. Until precise measurements of both turgor and yield threshold can be made in growing corn leaf tissue, the primary cause of the inhibition of growth by water deficit will remain unclear. However, the results presented here demonstrate a strong correlation between growth rate and acidification of cell walls of corn leaves, and suggest that decreased wall extensibility may be associated with the inhibition of growth.

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