Plant Physiol. (1990) 93, 222–230
0032-0889/90/93/0222/09/$01.00/0

Received for publication December 6, 1989
and in revised form January 15, 1990

Biophysics of the Inhibition of the Growth of Maize Roots by Lowered Temperature[1]

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ABSTRACT

Roots of hydroponically grown maize (*Zea mays* cv LG11) have a greatly reduced growth rate at 5°C (0.02 millimeters per hour) compared with those at 20°C (1.2 millimeters per hour). Various physical parameters of roots growing at each temperature were compared. Turgor pressure of cells in the elongation zone increased from 0.59 ± 0.05 megapascal at 20°C to 0.82 ± 0.04 megapascal after 70 hours at 5°C; thus, growth rate was not limited by decreased pressure. On cooling, tissue plasticity (measured by Instron/tensiometer) decreased slowly over 70 hours. On rewarming to 20°C from 5°C, growth rate, turgor pressure, and tissue plasticity all returned concertedly to their original values over a period of days. However, immediately following cooling growth rate dropped rapidly from 1.8 to 0.12 millimeters per hour in 30 minutes but turgor pressure and tissue Instron plasticity remained unchanged. A plot of turgor pressure against growth rate indicated that, following cooling from 30 to 15°C, the *in vivo* wall extensibility of the tissue was reduced by 75%. Yield threshold was unchanged. Cells whose expansion was arrested in the long-term cold treatment do not resume growth. Root growth recovers by the expansion of cells newly produced by the meristem. Cessation of extension growth is an effect on the individual expanding cell. Growth recovery is not a reverse of this effect but requires the generation of fresh cells.

The basis of the decrease of plant growth at low temperatures is of interest both for its economic implications and for the opportunities it provides for the study of the biochemical and biophysical mechanism of cell expansion (29). Studies of the responses of plants to low temperature have tended to concentrate either on the mechanism of injury (either by chilling or by freezing [18]) or on the effect of temperature on cell division within the meristem (1, 7). As emphasized by Green (11), tissue extension is a function of cell expansion alone. Therefore, to understand growth limitation by temperature the phenomenon must be studied in the context of the single expanding cell. Recent technical developments, such as the simultaneous application of pressure probe (13) and convenient methods for analysis of cell wall properties (4), have begun to provide information about the biophysical properties of growing tissues at cellular resolution within the extension zone. Root tissue has proved to be ideal for this type of study. The expanding cells are amenable to pressure probe analysis and the growing zone can be accurately described (21, 22).

It is becoming increasingly apparent that the physical properties of the cell wall, rather than turgor pressure changes, are responsible for growth rate changes in many of these systems (8, 28). This study extends this approach to the reduction in the growth of maize roots by low temperatures (2).

The experimental design is similar to that of previous studies into the cause of altered elongation in cereal roots (21, 23). If water transport into the expanding cells is not limiting, their expansion can be considered in the framework of the equation (19, 24):

$$r = \phi(P - Y) \quad (1)$$

where r = growth rate, ϕ = wall extensibility, P = turgor pressure, and Y = yield stress threshold.

A combination of pressure probe and growth rate measurement was used to examine the relative contributions of these parameters to the changes in root growth rate following a reduction in root temperature. Tissue plasticity was measured using the Instron/tensiometer as a further test and additionally to further examine the relationship between *in vivo* wall extensibility and *in vitro* plasticity.

Since changes in cell wall properties and/or turgor pressure will be reflected in an altered longitudinal distribution of cell length (11, 23) this was analyzed and provided additional information as to the microscopic location of the elemental growth points. The biophysical changes measured in this and similar studies have their bases in discrete biochemical events that are of considerable current interest. Detailed description of the time course and the precise location of these biophysical changes with temperature should provide clues as to which biochemical processes would reward further study.

MATERIALS AND METHODS

Plant Material

Maize (*Zea mays* cv LG11) seedlings were grown under hydroponic conditions as previously described (2). During both growth rate and turgor pressure measurements, nutrient solution at the appropriate temperature was continuously pumped past the root.

[1] Financial support from the Science and Engineering Research Council (GR/E 36227) is gratefully acknowledged (J. P.).

Measurement of Root Growth Rate

Long-term (hours) root elongation rate was measured by recording the length of 30 roots after an appropriate time period using a ruler.

Short-term (minutes) root elongation rate was measured by direct microscopic observation of the position of the root tip in a specially constructed growth chamber (23) in which changes in root length were recorded by means of an eyepiece graticule. Changes in length could be detected with precision down to approximately 3 μm in 1 min.

A thermocouple within the chamber recorded the temperature of the solution bathing the root. In addition to influencing plant growth, a temperature shift in the circulating solution caused an expansion or contraction of the growth chamber. Growth rate (Fig. 1a) was therefore calculated as the difference between the apparent growth rate (Fig. 1b) and the movement of the chamber lid to which the base of the root was anchored (Fig. 1c).

Measurement of Turgor Pressure

Turgor pressure was measured between 3 to 8 mm from the tip of the root cap (which encompasses the zone of maximum cell expansion) using the pressure probe technique (13). Epidermal and cortical cells were sampled along the root radius. The depth of the probe tip (and, hence, the location of the cell being measured) in the root was measured by means of a linear voltage displacement transducer attached to the micromanipulator on which the probe was mounted (22).

It was noted that contact of the root tip with any surface resulted in a reduction in growth rate. Thus, it proved impossible to measure growth rate and turgor pressure simultaneously in the same root using current techniques since achieving the latter required holding the root in a Perspex holder (13, 21) to allow penetration by the probe. Two lines of evidence justify the assumption that turgor pressure is unchanged (at least over short periods) by this treatment. Turgor pressure remains constant over long periods of time once the roots are positioned in the Perspex holder and turgor pressure measurements of roots in the holder are consistent with the osmotic pressure of the apical region of control roots (data not shown).

Measurement of Tissue Plasticity

Wall properties were measured using an Instron-type tensiometer (4, 31). Root tips were excised directly into boiling methanol (and boiled for 2 min) and rehydrated in distilled water prior to measurement. Tissue was fixed between the rubber-faced tensiometer clamps (set at 8 mm apart) and a

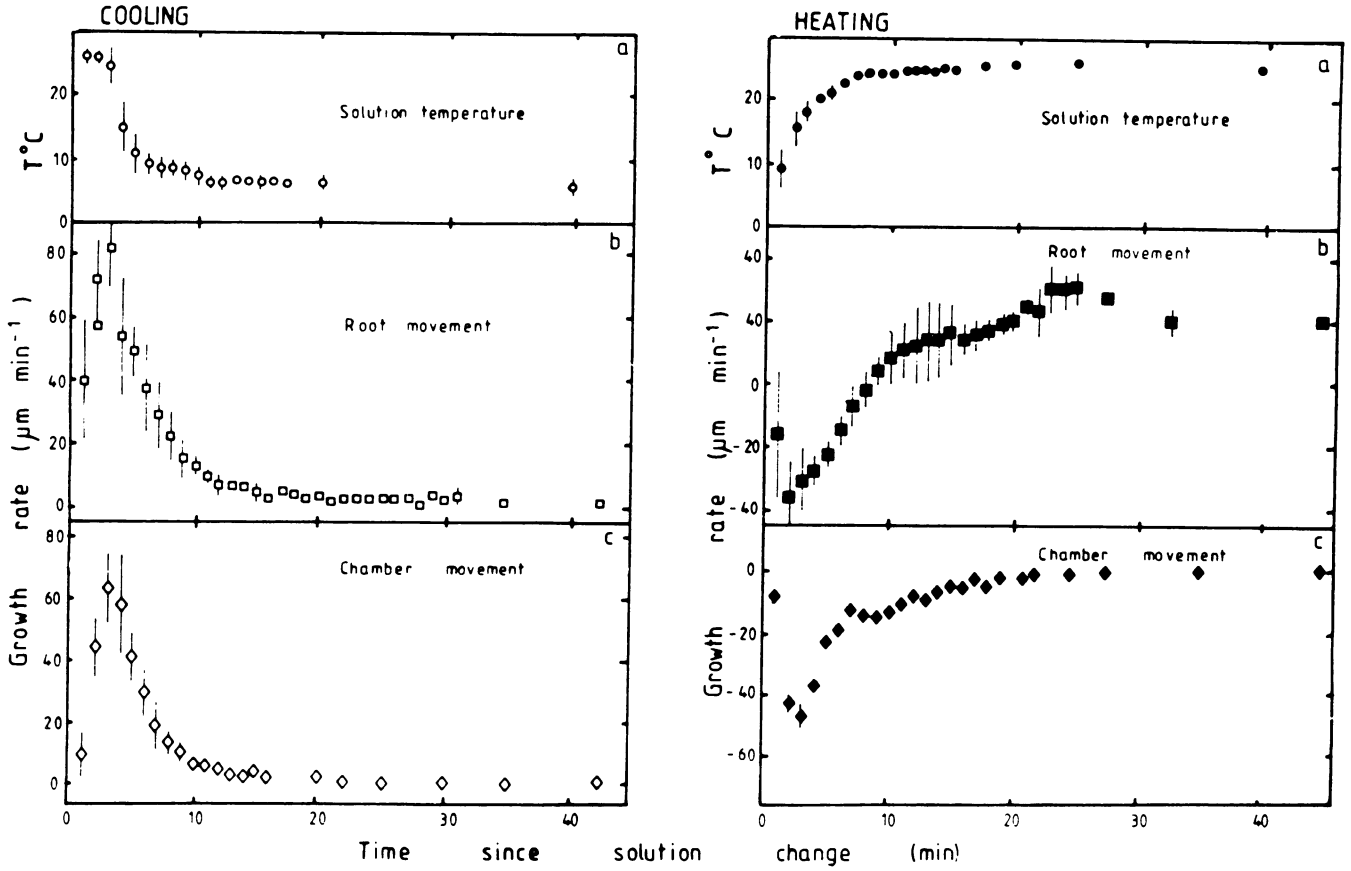

Figure 1. Change in solution bathing temperature (a) with consequent movement of root (b) and chamber (c) during the shift. Each point represents the mean of 7 measurements (±SD).

good grip was ensured by dusting the clamps with a little diatomaceous earth. The apical 2 to 10 mm from the root cap base of tissue were measured.Tissue was extended twice to 0.118 N (12 g) stress at a load application rate of 2.3 mm min^{-1} and plasticity was calculated from the difference in the slope of the linear portion of the two load/extension curves. The second plastic extension was subtracted from the first (plastic plus elastic) to give both plastic and elastic extensibilities.

Estimation of Yield Stress Threshold and *In Vivo* Wall Extensibility

The yield stress threshold (Y) and wall *in vivo* extensibility (ϕ) were measured directly from plots of growth rate as a function of turgor pressure (6, 8) according to Equation 1.

RESULTS

Long-Term Consequence of Changes in Temperature on Growth

Maize roots growing at 20°C showed a constant increase in length over the 10-d experimental period with an average rate of 1.2 mm h^{-1} (20 μm min^{-1}, Fig. 2a). In marked contrast, roots held at 5°C for the same period of time extended at a rate of only some 0.02 mm h^{-1} (Fig. 2a).

Following the 10-d period at 5°C the roots were transferred to fresh solution at 20°C. Increase in root length initially continued to be slow but, following a marked lag phase, growth rate became comparable with that of roots growing at 20°C throughout (Fig. 2b). After 100 h of the recovery phase, root elongation rate was fully restored at 1.4 mm h^{-1} (Fig. 2b).

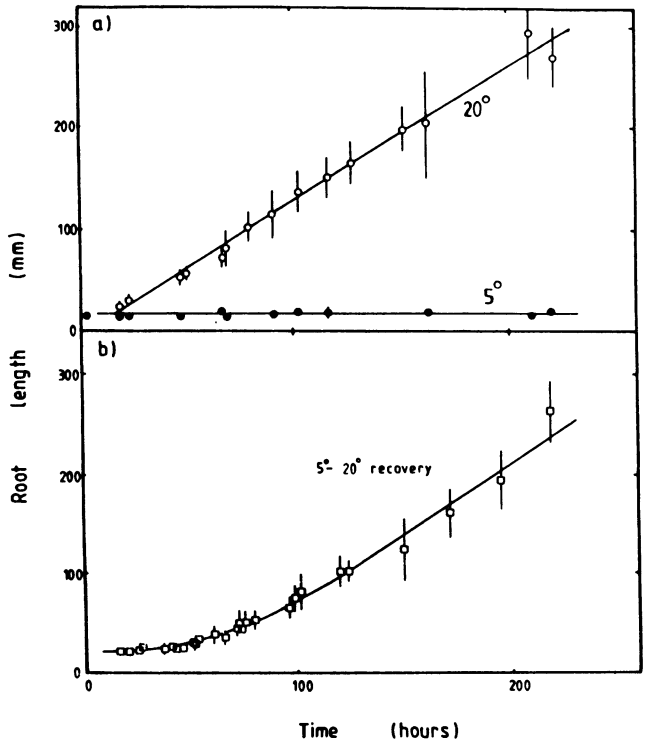

Figure 2. Root length as a function of time for maize roots growing under different temperature regimes. Each point represents mean of 30 measurements (±SD). (a) Roots growing at 5°C (●) or 20°C (○); (b) roots growing at 20°C following 10 d at 5°C (□).

Long-Term Consequence of Changes in Temperature on Turgor Pressure

Root cells growing at 20°C had constant turgor pressure within the tip region over the 10-d experimental period. The average pressure of cells between 3 and 8 mm from the tip of the root cap was 0.59 ± 0.05 MPa (n = 210) (Fig. 3a). In contrast, turgor pressure within the same region of roots growing at 5°C increased during the first 70 h of the experiment, thereafter remaining constant (Fig. 3a). Between 70 and 240 h turgor pressure 3 to 8 mm from the tip of the root cap was 0.82 ± 0.04 MPa (n = 170; Fig. 3a), an increase of over 0.2 MPa in comparison to the roots at 20°C. Turgor pressure returned to control (20°C) values during the recovery phase following return to 20°C (Fig. 2b).

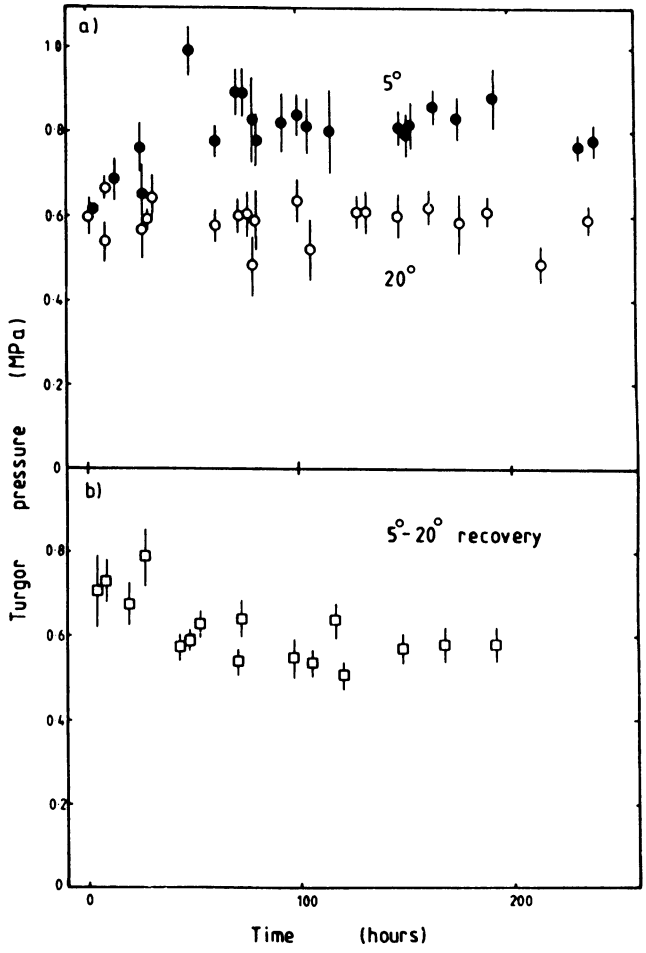

Figure 3. Turgor pressure as a function of time of epidermal and sub-epidermal cells 2 to 8 mm from the RCB of roots grown under different temperature regimes. Each point represents the means of at least 10 measurements (±SD). (a) Roots growing at 5°C (●) or 20°C (○); (b) roots growing at 20° following 10 d at 5°C (□).

Turgor pressure was normally measured in epidermal and subepidermal cells. To ensure that there were no changes in the turgor pressure of other cells within the tissue that could account for the observed pattern of growth rate reduction, this parameter was measured after 150 h at 20 and 5°C along a radius within the growing zone. It was constant across the cortex (Fig. 4) at approximately 0.6 MPa in roots grown at 20°C and 0.8 MPa in roots grown at 5°C.

Long-Term Consequence of Changes in Temperature on Cell Wall Properties

The Instron plasticity of the terminal 2 to 10 mm of the root remained constant over the 10-d period at 20°C (Fig. 5a). In contrast, during the 5°C incubation Instron plasticity declined from 1.9% to about 0.2% (Fig. 5a).

Following transfer from 5 to 20°C, the Instron plasticity of the same region increased from its initially low value (Fig. 5a) to about 3% after 240 h (Fig. 5b). Instron plasticity increased gradually during the 5 to 20°C transfer recovery period, reaching values comparable those of roots grown at 20°C after 100 h.

Short-Term Consequence of Changes in Temperature on Growth

A series of experiments was performed in which the events during the minutes following a sudden temperature drop from 25 to 6°C were studied. (The temperatures used in the short-term experiments are slightly different from those used in the long-term study because the roots were studied in different experimental equipment.)

Lowering the temperature of the solution bathing the root from 25 to 6°C resulted in a rapid decline in growth rate from an initial value of around 30 $\mu m h^{-1}$ to only 2 $\mu m\ h^{-1}$ after 30 mins at 6°C (Fig. 6a).

Following 50 min at 6°C, the temperature of the solution bathing the root was increased rapidly to 25°C.Root elongation rate increased from its initial low value to rates comparable with roots growing at 25°C within 25 min of the temperature change (Fig. 6b). There was no lag phase for this recovery.

Short-Term Consequence of Changes in Temperature on Turgor Pressure and Cell Wall Properties

In a separate experiment the turgor pressure and instantaneous volumetric elastic moduli using the pressure probe ϵ_i (13) of cells within the growing zone was measured at 25°C and following a 20 min period at 6°C (Table I). Turgor pressure at 25°C was 0.64 ± 0.08 MPa (n = 19) and 0.60 ± 0.08 MPa (n = 22) at 6°C. ϵ_i appeared equally unaffected by the short-term temperature treatment being 3.7 ± 2.0 MPa at 25°C and 4.2 ± 2.3 MPa at the lower temperature.

Correspondingly, there was no change in the Instron plasticity (measured at 20°C) of the terminal 2 to 10 mm of the root following a 50 min incubation at 5°C (Table II). Instron plasticity was 1.8% when measured at either 20 or 5°C. Very similar results were obtained when the tensiometric measurements were performed at 5°C. Instron tissue plasticity was 1.9 ± 0.6 (n = 20) for the 20°C treated roots measured at 5°C and 2.0 ± 0.5 (n = 15) for those incubated at 5°C and measured at the same temperature. No changes in elasticity were noted for tissue grown at 20 or 5°C and measured at 20 or 5°C (Table II). Thus, it would appear that in the short term none of the measured parameters could account for the reduction in root growth.

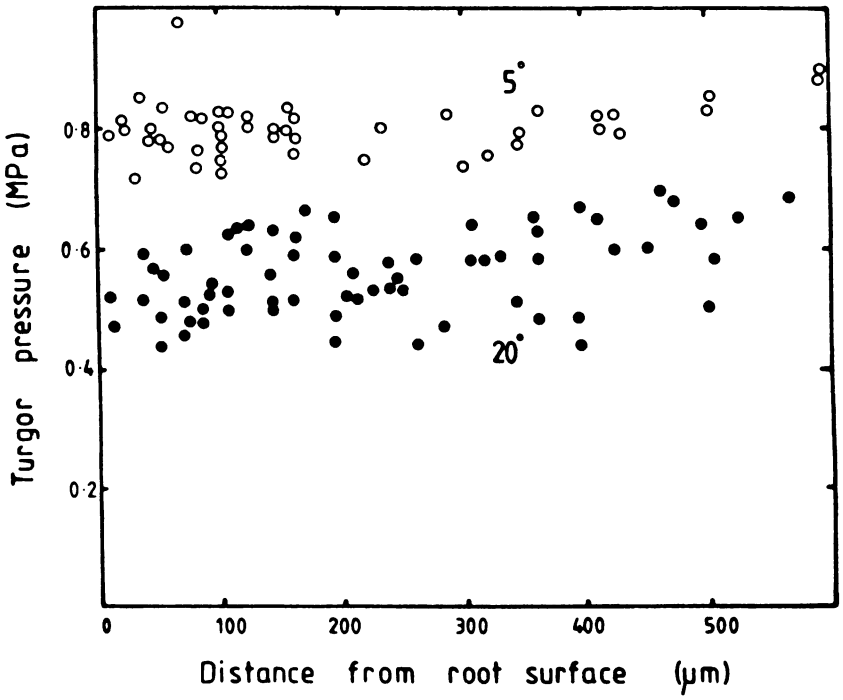

Figure 4. Turgor pressure profiles across the root diameter between 2 to 8 mm from the RCB following 150 h at either 5°C (○) or 20°C (●). Each point represents the pressure of a single cell.

Yield Threshold (Y) and *in Vivo* Cell Wall Extensibility (ϕ)

Y and ϕ were measured using the principle previously used by Cleland (6) in which growth rate was determined at a series of different turgor pressures to ascertain if an alteration in one of these parameters could account for the reduction in growth rate. Because the technique requires that the tissue is growing measurably it was not possible to perform such measurements at the low temperatures used previously (5 or 6°C) since root elongation rate at these temperatures was very low. Accordingly, 30 and 15°C were chosen as the convenient high and low temperatures to be compared.

Root growth rate was measured during a short-term (<15 min) incubation in various concentrations of mannitol at both 30 and 15°C. In a parallel experiment, turgor pressure of cells in the growing zone of the root was measured using the pressure probe. A plot of root elongation rate against the appropriate cell turgor pressure gave a line with slope ϕ and intercept Y for roots at 30 and 15°C as predicted from Equation 1 (Fig. 7).

Rapidly changing the temperature of the solution bathing the root from 30 to 15°C did not significantly alter Y from 0.22 MPa at 30°C to 0.24 MPa at 15°C. However, ϕ decreased dramatically from 152 μm min^{-1} MPa^{-1} at 30°C to 37 μm min^{-1} MPa^{-1} at 15°C. Thus, the reduction in root elongation following a temperature step-down was associated with a reduction in ϕ.

Table I. *Relationship between Turgor Pressure, Cell Volume, and Volumetric Elastic Modules (ϵ_i) ± SD following Short-Term Incubation (5–50 min) at 20 or 5°C*

Treatment	Turgor Pressure	Number cells	Cell Volume (pL)	ϵ_i
°C	*MPa*		*MPa*	
20	0.64 ± 0.08	19	139 ± 77	3.7 ± 2.0
5	0.60 ± 0.08	22	195 ± 110	4.2 ± 2.3

Table II. *Instron Tissue Plasticity and Elasticity (% Extension/0.118 N (12 g) load^{-1}), of Methanol-Killed Root Tips 2–8 mm from rCB) following Incubation of Live Roots for 50 Min at 20 or 5°C*

Measurements were performed at 20 or 5°C. The number of observations ± SD, are shown in brackets.

Tissue	Extensibility measured at					
	20°C			5°C		
	Elastic	Plastic	(*n*)	Elastic	Plastic	(*n*)
20°C grown roots	4.6 ± 0.7	1.8 ± 0.6	(18)	4.0 ± 0.9	1.9 ± 0.6	(20)
5°C grown roots	4.4 ± 0.5	1.8 ± 0.4	(17)	4.4 ± 0.6	2.0 ± 0.5	(15)

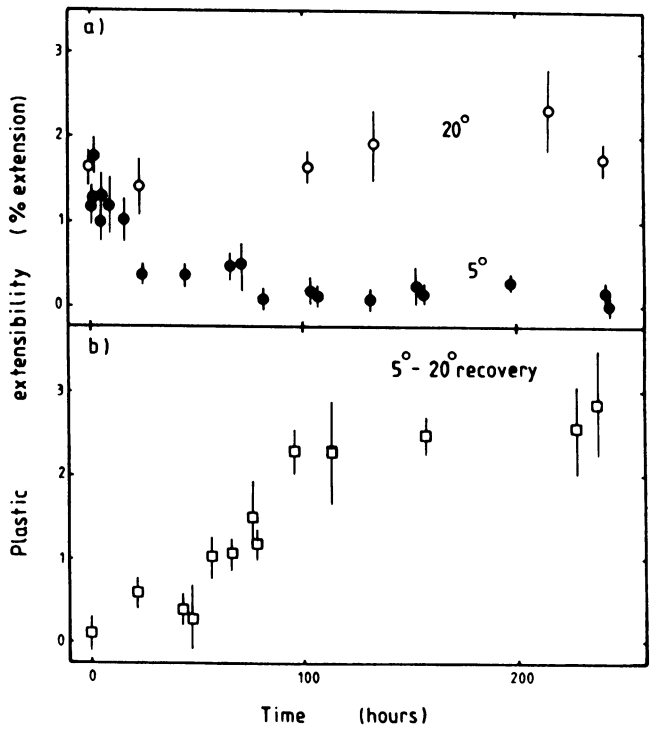

Figure 5. Instron plasticity (% extension/0.118 N (12 g) load^{-1}) of methanol-killed tips (2–8 mm from RCB) as a function of time for roots growing under different temperature regimes. Each point represents mean of 10 measurements ±SD. (a) Roots growing at 5°C (●) or 20°C (○); (b) roots growing at 20° following 10 d at 5°C (□).

Effects of Temperature on Longitudinal Distribution of Cell Length

Cell expansion is the result of turgor pressure expanding the cell against the resistance of the cell wall. At the observed constant turgor pressure the observed change in ϕ would be expected to alter the longitudinal pattern of cell-length distribution. Accordingly, cell lengths were measured at different distances from the RCB[2] in roots growing at 20°C, 5°C or recovering at 20°C after 10 d at 5°C.

Figure 8a shows a typical pattern of cell-length distribution in a root growing at 20°C. Cell length was constant at about 10 μm over a region extending to about 1 mm from the RCB. After this point, cell length started to increase, reaching a maximum of about 175 μm at 7 mm from the RCB. In roots grown for 10 d at 5°C a different pattern was observed (a typical distribution from one root is shown in Fig. 8b). There was a zone of only shallow increase in cell length away from the RCB proximal to which cell length increased more rapidly. This resulted in a zone of shorter cells (51 ± 3.0 μm) extending away from the RCB at the root tip. The average length of this zone was 3.1 ± 0.3 mm (n = 9) which roughly corresponded to the amount of root extension which occurred during the 10 d at 5°C.

Figure 8c illustrates a typical distribution of cell lengths following 2 d recovery at 20°C after a 10 d period at 5°C. Cell length was constant at around 10 μm over the apical 0.9 mm. An increase commenced after this point, reaching a maximum of around 140 μm at about 4 mm from the RCB. There was a plateau of constant cell length between 4 to 6 mm from the RCB then it declined resulting in a region of shorter cells between 6 to 12 mm from RCB. After 12 mm from the RCB cell length increased in a control root growing at 20°C throughout. After 5 d recovery, the pattern of cell length

[2] Abbreviation: RCB, root cap base.

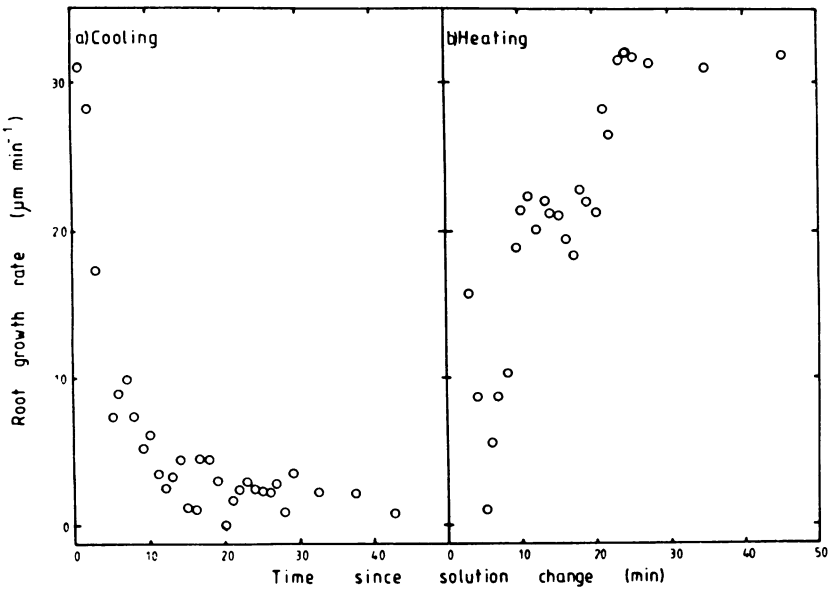

Figure 6. Response of root growth to short term temperature changes. Each point calculated from data in Figure 1. (a) Cooling root from 25 to 6°C; (b) warming root from 6 to 25°C.

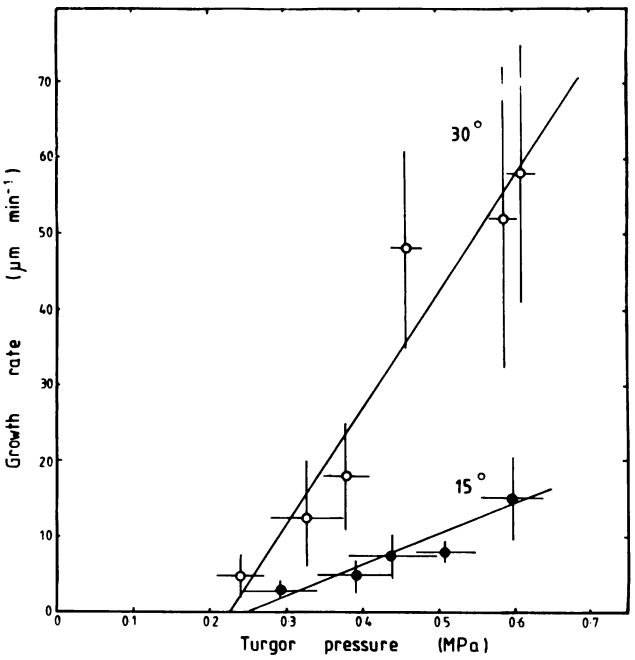

Figure 7. Root growth rate as a function of turgor pressure of the growing zone (2–8 mm from the RCB) of maize roots growing at two different temperatures following short term incubation (<15 min) in various concentrations of mannitol. Growth rate: each point mean of between 8 to 22 measurements ±SD. Turgor pressure: each point mean of between 30 to 50 measurements (±SD).

distribution over the initial 10 mm from the RCB was identical with that of a 20°C control root (Fig. 8d).

DISCUSSION

The reduction in root elongation rate as a consequence of long-term exposure to low temperature was associated with an *increased* turgor pressure within the tip of the *slow* growing roots, thus eliminating this parameter as the basis of the growth reduction and therefore implication changes in wall properties (8, 19, 29). In addition, a decrease in the Instron measured tissue plasticity of the growing zone of the root was measured over the same time period. During the recovery phase at 20°C following 10 d at 5°C, root elongation rate and Instron plasticity of the root tip both recovered at generally similar rates. Studies on other systems have noted such changes in Instron plasticity associated with reduced elongation rate (30). For example, the reduced rates of wheat root growth following exposure to solutions of different ionic composition (21) and following excision of the tip (23) correlated with decreases in Instron plasticity as measured with the Instron tensiometer.

In contrast, transfer from high to low temperature caused a rapid decrease in root growth rate but only a more gradual decrease in the tissue Instron plasticity suggesting that this measure may not be a valid estimate of ϕ from Equation 1. The lack of correspondence in time between changes in root elongation rate and Instron plasticity in this study is important since such Instron plasticity has often been considered to be an indication of ϕ, the *in vivo* wall extensibility (5). One possible explanation of a similar mismatch has been offered by Cleland (5) who proposed that the measurement of plasticity by the Instron tensiometer may represent the wall properties of the immediate past rather than that of the current state of the wall. This implies that there will be a lag phase between any alteration of ϕ *in vivo* and a change in Instron plasticity. Such a difference was noted between the time courses of the decline in root elongation rate and the decline in root Instron plasticity following excision (23) which would support such a hypothesis. In the present study no decline in Instron measured plasticity was detected within 60 min of the reduction in growth rate so that such a lag phase would have to exceed this period. In *Avena* coleoptiles the length of the lag period was 60 to 90 min (5) but it was shorter in those of

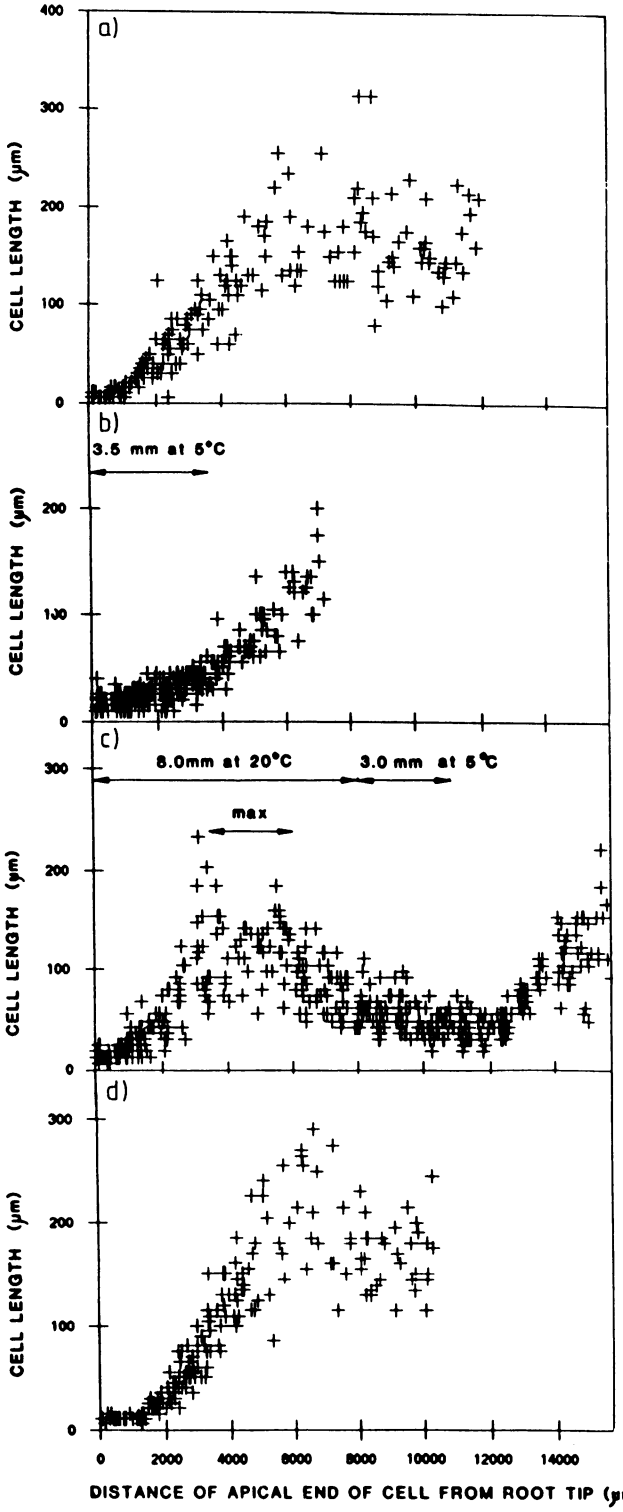

Figure 8. Pattern of cell lengths at the tips of maize roots grown under different temperature regimes. (a) Control grown at 20°C; (b) roots grown for 10 d at 5°C; (c) roots grown for 10 d at 5°C followed by 2 d at 20°C; (d) the same treatment as in (c), but with an additional 3 d of recovery at 20°C. (Distances were measured from RCB to the apical end of each cell.)

maize (17). It seems likely that the decline in the Instron plasticity of the root during the long-term incubation at 5°C may be unrelated to *in vivo* changes in wall properties responsible for the reduction in root elongation rate that occur immediately within the cell wall. This implies that plasticity of methanol-killed tissue measured with the Instron/tensiometer technique is unrelated to ϕ and Y of living tissue.

Evidence for a change in wall properties on changing temperature *was* found when ϕ and y were measured from plots of growth rate as a function of turgor pressure following osmotic manipulation of the tissue. Whereas Y was unchanged. ϕ (the *in vivo* wall extensibility) was lowered following temperature reduction. Changes in ϕ have been correlated with alterations in growth rates in other systems (27).

Interestingly, gibberellin-modulated changes in growth rate of pea stems have also been reported to be mediated by changes in wall properties unrelated to any significant changes in Instron plasticity (10). The contrasting good correlation between root tip Instron plasticity following methanol extraction and root growth during the recovery phase could be explained by the necessity for the recovery of cell division to supply new cells to the expanding zone (2) rather than the recovery of expansion by partially expanded cells. Thus, on the one hand growth diminution by low temperature is an effect on the cells expanding at the moment of temperature decrease, while on the other during growth rate recovery new cells for expansion must be produced. This is supported by examination of the details of cell length distribution.

We propose that after transfer from 20°C to 5°C the reduction in ϕ severely reduces cell expansion and effectively freezes the pattern of cell length present before the temperature shock. Some cell expansion does occur at 5°C, albeit much reduced, which accounts for the small amount of growth observed at the lower temperature. On transfer of 20°C, the small cells do not recommence expansion as can be seen by the 'notch' of small cells in the cell length profile between 8 and 12.5 mm from the base of the root cap after 2 d of recovery (Fig. 8c). The cells in the 'floor' of the notch represent those cells that left the apical region (0–1 mm) during the 10 d period at 5°C and whose expansion was severely reduced by the cold treatment. On reexposure to 20°C during the recovery period these cells did not resume expansion. This observation is in sharp contrast to the behavior of maize leaf cells that show a temporary accelerated growth rate after rewarming expanding cells from 5 to 28°C (16). The general behavior, also, is in marked contrast to the observations of Pahlavanian and Silk (20) who indicate that over the temperature range of 16 to 29°C mature cell length is probably independent of temperature. Most of the cells distal of the notch were all produced by cell division after the return transfer to 20°C. Cells in the zone 6 to 8 mm from the cap base in the root shown in Fig. 8c did not expand to the mature cell length characteristic of the control (20°C grown) tissue. This occurred only after the root had made more than 2 mm of new growth.

A similar reduction in cell expansion was noted following the excision of wheat roots (23) when, similar to the present study, the unexpanded cells could not be induced to continue expansion. (Although, in contrast to the present study, in that system root elongation could not be restored).

A further feature of note is the time course of behavior of turgor pressure on cooling the roots; 24 h after the diminution of growth rate the pressure in the expanding cells has increased by some 0.1 MPa (Fig. 3a). It would be thought that any growth-induced water potential gradients at the control temperature would have been dissipated over this period. The pressure, however, continues to increase for a further 30 to 40 h reaching values 0.3 MPa above that of the control. Radial water flows across the root would predict relaxation of water potential gradients several orders of magnitude faster than this (14). Because of this we feel it unlikely that the bulk of these turgor changes represents a recovery of turgor pressure due to loss of growth-induced water potential gradients which are, in any case, thought to be small in maize roots (26). Water potential gradients were also found to be small in a study of growing pea stems (9) in which inhibition of growth by low temperature resulted in a slight decrease in turgor pressure and the water potential gradient was calculated to be no greater than 0.05 MPa.

This result is also of significance in consideration of the rate of solute import to the root tip. Local solute concentration is a balance between local deposition rates (synthesis plus transport) and local dilution (growth and metabolism) (25). Since turgor pressure remains constant in the growing zone of the control roots (20°C) these factors must be in equilibrium. On transfer to 5°C this equilibrium is disturbed since growth is slowed to a larger extent than is the local solute deposition rate. This is reflected in an increase in the turgor pressure. After 50 h at the lower temperature an equilibrium is restored and pressure becomes constant with time. This suggests the possibility of a negative feedback onto the solute flux from the turgor pressure of the tip cells. Turgor controlled solute fluxes have been documented in several tissues (*e.g.* sugar beet, 32). Alternatively, the equilibrium achieved may be due to a nonspecific but concentration-dependent leakage of a solute of solutes out of the cells. Roots are known to leak carbohydrate into their medium (12) and that this leakage can be stimulated by chilling (3). Increases in the turgor pressure of roots following growth rate reduction have been noted previously (15, 23)

This study provides two pieces of information that may be of use in directing future investigations of the biochemistry of cell expansion. First, it highlights two zones of a root following recovery from a period at low temperature in which the size, shape, and—presumably—orientation of wall polymers will be identical, one of which is growing while the other is not. These are the zones of expansion 1 to 4 mm from the RCB and the 'frozen' zone eg the cells in the zone 12 to 15.5 mm from the RCB in Figure 8c. Comparison of the detailed biochemistry of the two zones should provide information on the long-term changes occurring in the cell wall at low temperature. Second, knowledge of the biochemical changes occurring in the growing cells following a short period at low temperature may provide information about the nature of the observed change in ϕ responsible for the reduced growth rate.

ACKNOWLEDGMENTS

We are grateful for stimulating discussion with Prof. Gareth Wyn Jones and for the technical help of Mr. Gwynfor Williams.

LITERATURE CITED

1. **Barlow PW** (1987) The cellular organization of roots and its response to the physical environment. *In* PJ Gregory, JV Lake, DA Rose, eds, Root Development and Function. Cambridge University Press, Cambridge, pp 1–26
2. **Barlow PW, Adam JS** (1990) The response of the primary root meristem of *Zea mays* L. to a period of cold. J Exp Bot (in press)
3. **Christiansen MN, Carns HR, Slyter DJ** (1970) Stimulation of solute loss from radicles of *Gossypium hirsutum* L. by chilling, anaerobiosis and low pH. Plant Physiol **46:** 53–56
4. **Cleland RE** (1967) Extensibility of isolated cell walls: measurement and changes during cell elongation. Planta **74:** 197–209
5. **Cleland RE** (1984) The Instron technique as a measure of immediate past wall extensibility. Planta **160:** 514–520
6. **Cleland RE** (1986) The role of hormones in wall loosening and plant growth. Aust J Plant Physiol **13:** 93–103
7. **Clowes FAL** (1976) The root apex. *In* MM Yeoman, ed, Cell Division in Higher Plants. Academic Press, London, pp 253–284
8. **Cosgrove DJ** (1986) Biophysical control of plant cell growth. Annu Rev Plant Physiol **37:** 377–405
9. **Cosgrove DJ, Cleland RE** (1983) Osmotic properties of pea stem internodes in relation to growth and auxin action. Plant Physiol **72:** 332–338
10. **Cosgrove DJ, Sovonick-Danford SA** (1989) Mechanism of gibberellin-dependant stem elongation in peas. Plant Physiol **89:** 184–191
11. **Green PB** (1976) Growth and cell pattern formation on an axis: critique of concepts, terminology and modes of study. Bot Gaz **137:** 187–202
12. **Haller T, Stolp H** (1985) Quantitative estimation of root exudation of maize plants. Plant Soil **86:** 207–216
13. **Hüsken D, Zimmermann U, Steudle E** (1978) Pressure probe technique for measuring water relations of cells in higher plants. Plant Physiol **61:** 158–163
14. **Jones H, Leigh RA, Tomos AD, Wyn Jones RG** (1983) Water-relation parameters of epidermal and cortical cells in the primary root of *Triticum aestivum* L. Planta **158:** 230–236
15. **Jones H, Leigh RA, Tomos AD, Wyn Jones RG** (1988) Abscisic acid and wheat root growth: effect on turgor pressure, solute content and membrane hydraulic conductivity. Planta **170:** 257–262
16. **Kleinendorst A** (1975) An explosion of leaf growth after stress conditions. Neth J Agric Sci **23:** 139–144
17. **Kutschera U, Schopfer P** (1986) *In-vivo* measurement of cell-wall extensibility in maize coleoptiles: effect of auxin and abscisic acid. Planta **169:** 437–447
18. **Levitt J** (1980) Responses of plants to environmental stress, Ed 2, Vol 1. Chilling, Freezing and High Temperature Stresses. Academic Press, New York
19. **Lockhart JA** (1965) An analysis of irreversible plant cell elongation. J Theor Biol **8:** 264–275
20. **Pahlavanian AM, Silk WK** (1988) Effect of temperature on spatial and temporal aspects of growth in the primary maize root. Plant Physiol **87:** 529–532
21. **Pritchard J, Tomos AD, Wyn Jones RG** (1987) Control of growth rate in wheat seedling roots. I Effects of ions. J Exp Bot **38:** 948–959
22. **Pritchard J, Williams G, Wyn Jones RG, Tomos AD** (1989) Radial turgor pressure profiles in growing and mature zones of wheat roots—modification of the pressure probe. J Exp Bot **40:** 567–571
23. **Pritchard J, Wyn Jones RG, Tomos AD** (1988) Control of wheat root growth. The effects of excision on growth, wall rheology and root anatomy. Planta **176:** 399–405
24. **Ray PM, Green PB, Cleland RE** (1972) Role of turgor in plant cell growth. Nature **239:** 163–164
25. **Silk WK, Hsiao TC, Diedenhofen U, Matson C** (1986) Spatial distribution of potassium, solutes and their deposition rates in

the growth zone of the primary corn root. Plant Physiol **82:** 853–858

26. **Silk WK, Wagner KK** (1980) Growth sustaining water potential distributions in the primary corn root. Plant Physiol **66:** 858–863
27. **Taylor G, Davies WJ** (1986) Yield turgor of growing leaves of *Betula* and *Acer*. New Phytol **104:** 347–353
28. **Thomas A, Tomos AD, Stoddart JL, Thomas H, Pollock, CJ** (1989) Cell expansion rate, temperature and turgor pressure in growing *Lolium temulentum* leaves. New Phytol **112:** 1–5
29. **Tomos AD** (1985) The physical limitations of leaf cell expansion. *In* NR Baker, WJ Davies, CK Ong, eds, Control of Leaf Growth. Society of Experimental Biology Seminar Series, Vol 27. Cambridge University Press, Cambridge, pp 1–33
30. **Van Volkenburgh E, Cleland RE** (1986) Wall yield threshold and effective turgor in growing bean leaves. Planta **167:** 37–43
31. **Van Volkenburgh E, Hunt S, Davies WJ** (1983) A simple instrument for measuring cell-wall extensibility. Ann Bot **51:** 669–672
32. **Wyse RE, Zamski E, Tomos AD** (1986) Turgor regulation of sucrose transport in sugar beet tap root tissue. Plant Physiol **81:** 478–481