THE EFFECT OF LOCALIZED PRESSURE ON THE GROWTH OF THE MAIZE RADICLE

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Summary

When radicles of *Zea mays* (L.) are compressed they elongate less rapidly. In this experiment different regions of the radicle were compressed to localize the effects of the stress.

Compressing the apex at 1 kg/sq cm reduced growth much more than compressing a length of fully enlarged tissue. The most striking change in compressed apices was a reduction in the rate of elongation, and this is attributed chiefly to a change in the shape assumed by cells enlarging under stress.

A mechanical load of 3 kg/sq cm caused browning and loss of turgor when applied to fully enlarged tissue, but this did not occur when the tissue enlarged and matured under stress.

I. Introduction

When roots penetrate finely structured layers of soil or clods, the apices are subjected to mechanical stress. The magnitude of the stresses may be large: the pressure required to extend the root channel is of the order of 10 kg/sq cm even in soils of modest strength (Barley, Farrell, and Greacen 1965). Surprisingly little is known, however, about the effects of mechanical stress on root growth.

Earlier experiments have been concerned both with the statics and dynamics of root growth. In experiments with maize, *Zea mays* (L.), Pfeffer (1893) found that a resistance of 12 kg/sq cm, acting on the maximum cross-section, prevented elongation of the radicle. Gill and Miller (1956) and Barley (1962), who also worked with maize, showed that the rate of elongation of the radicle decreased with each increment in the confining pressure.

The decrease in growth observed in previous experiments may have been caused either by mechanical stress acting directly on the growth of the apex, or by interference with translocation to the apex. Whether only one or both of these causes operated was unknown, so in the present experiment the application of pressure has been restricted to certain parts of the radicle.

II. Methods

Radicles of maize 40 mm in length, selected 96 hr after wetting the seed, were treated in the following ways:

A: Control radicles were grown without mechanical restraint.

B: A 1-cm length of fully enlarged tissue, initially 10–20 mm from the tip, was compressed.

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C: The cap and meristem (terminal 2–3 mm) of the radicle were compressed at the start of the experiment, and further growth occurred under load.

Pressures of 1, 2, and 3 kg/sq cm were applied via a thin flexible diaphragm with a modified form of the apparatus described by Barley (1962). Reference should be made to the 1962 paper for a description of the basic apparatus and method. The pressure was built up to the required value over a period of 1–2 min. Radicles were introduced into the pressure cells through inlet holes (see Fig. 1). The inlets were lined with moist blotting-paper. In treatments A and C the radicles protruded 2–3 mm onto the porous plate at the start of the experiment. In treatment B the radicles protruded 20 mm onto the porous plate.

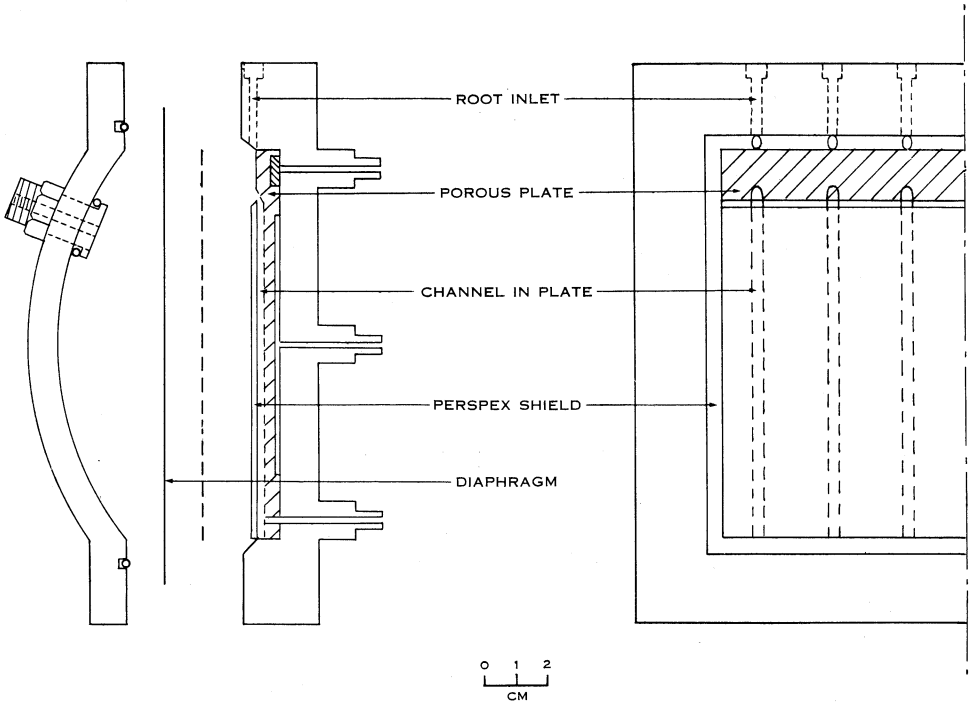

Fig. 1.—The modified pressure cell. Details of the original cell are given by Barley (1962).

In treatment B the porous plates on which the radicles were grown were modified by forming 3-mm diameter semicircular channels in each plate. Each channel ran from the apex of the radicle to the bottom edge of the porous plate (see Fig. 1). At the start of the experiment the apical 1 cm of the radicle was placed in this channel, which was then covered with a 1·5-mm thick Perspex shield. This shield prevented the diaphragm from bearing on the apex or on any part of the radicle which subsequently grew in the channel, but allowed the mechanical load to operate on the proximal part of the radicle.

The seed, the base of the radicle, and the other seminal roots were grown in perlite. An aqueous solution containing 5 mM $CaSO_4$ and 5 mM K_2SO_4 was used to wet the perlite and the porous plate. The plants were normally grown in the dark.

Observations were made during the experiment through the Perspex cover of the pressure cell with a filtered light of wavelength 0·48–0·62 mμ. After growth for 48 hr at 20°C the plants were harvested, and the increase in length (l) and the dry weight (w) of the section of length l were determined. The volume of the freshly severed lengths of radicle was found by immersing each length for 15 sec in water and measuring displacement. Anatomical data were obtained at ×150 with an eyepiece graticule, using 10 μ longitudinal and transverse sections cut from freshly harvested radicles with a hand-microtome.

III. Results

Mean values of l and w are given in Table 1. Data on cell size and number are given in Table 2 for controls and for tissue that elongated under stress (treatment C).

Table 1

GROWTH WITHIN THE PRESSURE CELL WHEN DIFFERENT REGIONS OF THE MAIZE RADICLE WERE COMPRESSED WITH A MECHANICAL LOAD OF 1 KG/SQ CM

Results are expressed as mean values ± standard errors of the mean

Treatment	Region Compressed	Increase in Length, l (cm)	Dry Weight, w, of Section of Length, l (mg)	w/l (mg/cm)
A	Nil (control)	8·6±0·20	6·0±0·24	0·70±0·023
B	1-cm length of fully enlarged tissue	6·7±0·21	4·3±0·24	0·63±0·026
C	Apical meristem and subsequent growth within the cell	1·7±0·09	2·4±0·13	1·40±0·066

Control radicles (treatment A) elongated at a constant rate of 1·8 mm/hr. When a pressure of 1 kg/sq cm was applied to a 1-cm length of fully enlarged tissue (treatment B) the radicles continued to elongate without any time lag at 80% of the rate of the control. The width of the compressed 1-cm length did not change during the experiment, and the width and dry weight per unit length of the new growth differed little from that of the control. When a pressure of 1 kg/sq cm was applied to the meristem, and the radicles took up the load as they grew (treatment C), elongation proceeded at a greatly reduced and continuously decreasing rate. A few radicles elongated for 2–4 mm within the inlet tube, pushing the seed higher into the perlite. This portion of the elongation growth was not included in the data given in Table 1. The compressed radicles (treatment C) were wider than the controls, the change in width being associated with an increase in width of the fully enlarged cortical cells—see Table 2. Although the increased width entailed an increase in dry weight per unit length, the absolute gain in dry weight of the tissue within the pressure cell was much below that of the control. Radicle volume behaved similarly to dry weight, and dry weight per unit volume of tissue did not differ significantly between treatments (mean 0·099 g/cm^3; S.E. 0·0046 g/cm^3).

Pressures of 3 and 4 kg/sq cm bruised the fully enlarged tissue from 1–2 cm behind the tip in treatment B. The damaged tissue turned brown and lost turgor. Elongation ceased and was not resumed during the 48-hr experiment. The more elevated pressures did not cause any visible tissue damage in treatment C, where pressure was intially confined to the meristem, and the cells elongated and matured while subject to stress.

TABLE 2

EFFECT OF COMPRESSION OF MAIZE RADICLES DURING GROWTH ON THE NUMBER, SIZE, AND SHAPE OF FULLY ENLARGED CORTICAL CELLS

Measurements were made 10 mm behind the apex. Results are expressed as mean values ± standard errors of the mean

Treatment	Pressure Applied (kg/sq cm)	No. of Files of Cortical Cells	Cortical Cell Length, s (μ)	Cortical Cell Diameters, d		$10^5 \times$ Calculated Volume, v* (μ^3)
				Major Axis, d_1 (μ)	Minor Axis, d_2 (μ)	
A	0	484±20·1	223±7·0	35·3±0·8		2·19
C	1·0	569±19·7	72±3·3	77·5±4·4	48·3±2·8	2·12

* $v_A \simeq \pi d^2 s/4$; $v_C \simeq \pi d_1 d_2 s/4$.

IV. DISCUSSION

Except when high pressures were applied to a length of fully enlarged root, causing visible tissue damage, stress mainly affected elongation growth in the apical region of cell division and enlargement.

It would have been desirable to confine the stress to the apex in treatment C, leaving the proximal tissue unstressed throughout the experiment. However, this would have been difficult to do experimentally, as the stress would have had to be progressively relieved during growth. The early stages of treatment C correspond to the desired kind of loading, as the proximal part of the radicle is at first within the inlet tube. The initial response of the radicles stressed in this way (no lag period, marked reduction in elongation rate) has been noted.

The reduction in the rate of elongation of the stressed apices is most readily explained by a change in cell shape in response to stress. As the pressure exerted by the root along its longitudinal axis exceeds the radial pressure transmitted by the diaphragm (Barley 1962), a shear stress would have been superimposed on the tissue stress within the radicle after application of the load. The decrease in length of the cortical cells in treatment C (−68%) compared with the control accounted for most of the reduction in radicle elongation (−80%). An increase in cell number across the width of the radicle—see Table 2—made a minor contribution to the change in shape. The increase probably involved displacement of meristematic cells from their original files as described by Hottes (1929). Changes in shape similar to those observed in the experiment are known to be produced in nature when roots force their way through strong soils (Barley 1963; Barley, Farrell, and Greacen 1965).

It has previously been found that even a small shear stress causes an irreversible change in the shape assumed by bean [*Vicia faba* var. *minor* (Beck)] epicotyls during elongation growth (Sedgley and Barley 1963). In the experiment with bean epicotyls the small (0·5 kg/sq cm) axial load changed the shape assumed during growth without reducing growth in volume or dry weight. In treatment C of the present experiment, where a compressive stress of 1 kg/sq cm operated on the principal axes of the maize radicle, the growth in volume and dry weight within the pressure cell was only 40% that of the control. As final cell volume was not reduced by the compression (see Table 2), a decreased rate of cell division or rate of cell enlargement must have been associated with the reduction in volumetric growth of the radicle. Although cell division cannot have limited the rate of elongation when the stress was first applied, as a store of recently divided cells was available for enlargement, cell division may have become important later in the experiment. It is known that the rate of cell division rapidly declines when the radicle is mechanically impeded from enlarging (Hallbauer 1911). A reduction in the transient elastic component of cell enlargement may also be expected if the cells behave as osmometers with imperfectly elastic walls (Barley 1962).

Finally, interference with translocation needs to be considered. In treatment B translocation into the tissue within the pressure cell was reduced when a length of fully enlarged tissue was compressed—the gain in dry weight within the pressure cell being 28% below that of the control at a pressure of 1 kg/sq cm. This is of ecological interest, as the older parts of roots are sometimes compressed by the swelling action of wetting clay. There may be much less interference with translocation when the tissue is allowed to enlarge and mature under stress. Moreover, at 1 kg/sq cm the radicles elongated much more rapidly in treatment B than in treatment C, and the effect of stressing fully enlarged tissue on elongation was relatively minor.

V. Acknowledgment

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VI. References

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