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The influence of mechanical impedance on the growth of maize roots

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Key words Cell wall structure Ethylene Maize Mechanical impedance Root growth

Summary Maize roots were grown between 1 mm glass beads on which a pressure of 40 kPa was applied. The roots were supplied with a constant flow of aerated nutrient solution. Compared with roots grown in a nutrient solution, the impeded crown roots showed a reduction in length of about 75%, whereas the diameter was about 50% increased.

These changes in root morphology have been attributed to changes in cell wall structure of the cortex cells, which also occur as a result of the influence of ethylene.

It is suggested that ethylene acts as an intermediate factor in the effect of mechanical impedance on root growth.

Introduction

Under field conditions availability of water and ions is often limiting plant growth[12], so that the development of an extensive root system is commonly considered as a prerequisite for optimal crop growth. In the field, however, soil conditions are often sub-optimum for root growth. The mechanical resistance of the soil can be an important factor limiting root growth. The increasing use of heavier agricultural machinery together with a decreasing intensity of soil cultivation can result in a greater compaction of the soil. The way in which mechanical impedance restricts root growth is however not completely understood.

The maximal pressure that can be exerted by roots (root growth pressure) is correlated with the osmotic potential of the plant tissue[15,15] and amounts to about 900–1300 kPa.

Growth is an irreversible (plastic) extension of the cell wall under the influence of the hydrostatic pressure of the cell content.

$$P = \pi + \psi \tag{1}$$

Where
P = the hydrostatic pressure within the cell (turgor pressure);
π = the osmotic potential of the cell contents;
ψ = the water potential of the cell.

When the cell does not grow, the forces that counteract the extension of the cell wall and the turgor pressure are in equilibrium.

$$P = W + B + M \tag{2}$$

Where
W = the pressure exerted by the wall on the cell contents (wall pressure);

B = the pressure exerted by surrounding tissue (tissue pressure);
M = the mechanical resistance of the root environment.
The mechanical behaviour of the cell wall depends on its yield value (W_0). If the wall pressure (W) is smaller than W_0, the wall is reversibly extended. If the wall pressure exceeds W_0, the wall extends plastically with a growth rate V.

$$V = (W - W_0)/\eta \tag{3}$$

Where
V = the growth rate of the cell wall in a certain derection;
η = the viscosity of the cell wall in the growth direction.
From (2) and (3) it follows:

$$V = (P - B - M - W_0)/\eta \tag{4}$$

From (4) it can be concluded that the growth rate of a root can be influenced in different ways. Increase of the mechanical impedance of the root environment (M) leads to a decrease in root growth rate (V).

From experiments about the effect of mechanical impedance on root growth it appears that resistances much smaller than the root growth pressure induce significant reduction of root growth. In barley for instance a mechanical resistance of 50 kPa results in a growth reduction of 80%[7,13]. The growth rate is practically independent of the applied impedance between 100 kPa and the value of 'root growth pressure'[4].

This disproportionate effect of low resistances makes it unlikely that a mechanical resistance exerted on the root retards the root growth directly.

Another observation supporting this statement is that the reduction in growth is only in axial extension while lateral expansion is generally increased[2,18], although the exerted resistance is working in axial as well as radial direction.

The shape of a plant cell is mainly determined by its cell wall structure: growth in lateral and axial direction depends on the orientation of cellulose microfibrils in the cell wall[16,17].

Because the shape of the parenchyma cells of the root cortex is strongly influenced by mechanical impedance, the influence of mechanical impedance on the cell wall structure has been studied.

Material and methods

a. Growing conditions

To overcome uncertainties in the study of the response of roots to varying mechanical impedance the method adopted was similar to that described by Gill and Miller[5], Barley[1] and Goss[7]. Roots were grown between small glass beads (ballotini) to which external pressure could be applied and between which an aerated nutrient solution was circulated. The diameter of the ballotini was 1 mm, giving a pore diameter of 160 µm.

Two, three weeks old maize plants, from which the seminal roots had been removed were placed with their still unbranched crown roots each in a perspex box (l × b × h = 10 × 10 × 15 cm).

The shoots of the plants were fitted in an opening at the top side of the box using a closed-cell rubber stopper. Two opposite walls of each box contained an inlet and an outlet, while a third wall of one box had a circular opening (∅ 7 cm) in which a PVC membrane was mounted. Over the membrane a funnel shaped, water tight, cover was mounted. Pressure could be exerted on the membrane by means of a water column. After mounting the plants, this box was filled completely with ballotini and the other one with nutrient solution. Both boxes were connected with rubber tubes and a small plunger-type pump circulated the nutrient solution through both boxes. After 14 days the plants were harvested.

Because the relative great distance between two opposite side walls it was possible that the pressure exerted upon the roots was not equal throughout the box.

The pressure in various parts of the ballotini box was measured by imbedding the lower end of a glass capillary on which a small rubber balloon was mounted (∅ 5 mm) between the ballotini. The balloon and the capillary were filled with water and the water level was visible in the capillary end that protruded above the top side of the ballotini box. On the membrane a pressure of 40 kPa was applied, by which the small balloon was compressed. The balloon could be expanded by applying air pressure

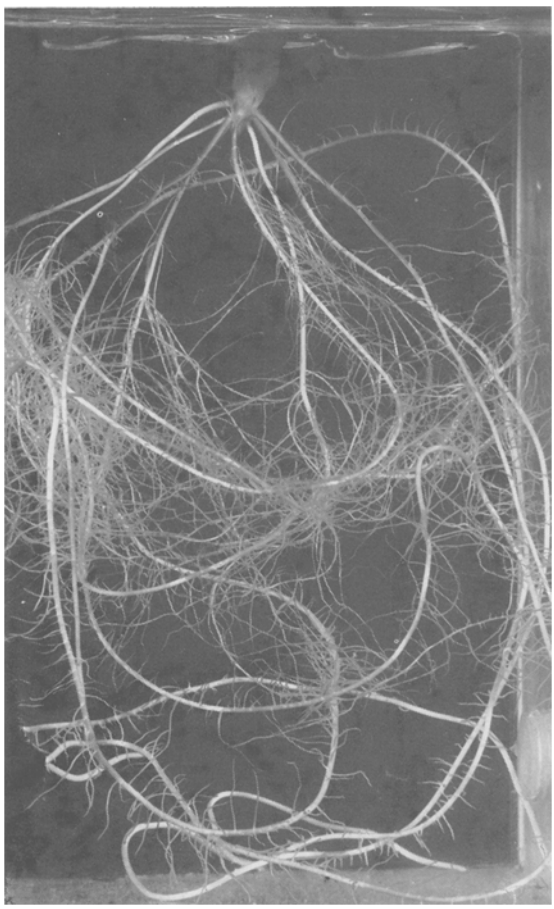

Fig. 1. Crown roots of a maize plant grown 14 days in a nutrient solution.

at the top side of the capillary. The pressure required to expand the balloon was closely similar to the pressure that had been applied to the membrane, so the membrane pressure is a valid estimate of the pressure experienced by the roots in all positions in the ballotini box.

b. Measurement of the cell wall structure

After harvest of the plants, the roots were immersed in a fixative containing formalin 40%: propionic acid: alcohol 70% = 5:5:90. After dehydration 1 cm long pieces of the crown roots were embedded in paraplast. Longitudinal microtome sections were made of a thickness about the diameter of one cortex cell, so that a great number of double walls, composed of the cell walls of two adjacent cells could be studied in face view.

The orientation of microfibrils in a cell wall was studied using its dichroic properties after staining with zinc chloride-iodine. The phenomenon of dichroism results from the relative absorption of polarized light dependant on the position of the absorbing object in relation to the direction of vibration of the light. In solution iodine has no orientation, but when these molecules are absorbed to orientated structures, such as cellulose microfibrils of a cell wall, they become oriented with respect to these structures and towards the swinging direction of the polarized light in such a way that the direction of maximum absorption is parallel to the longitudinal axis of the microfibrils. When the

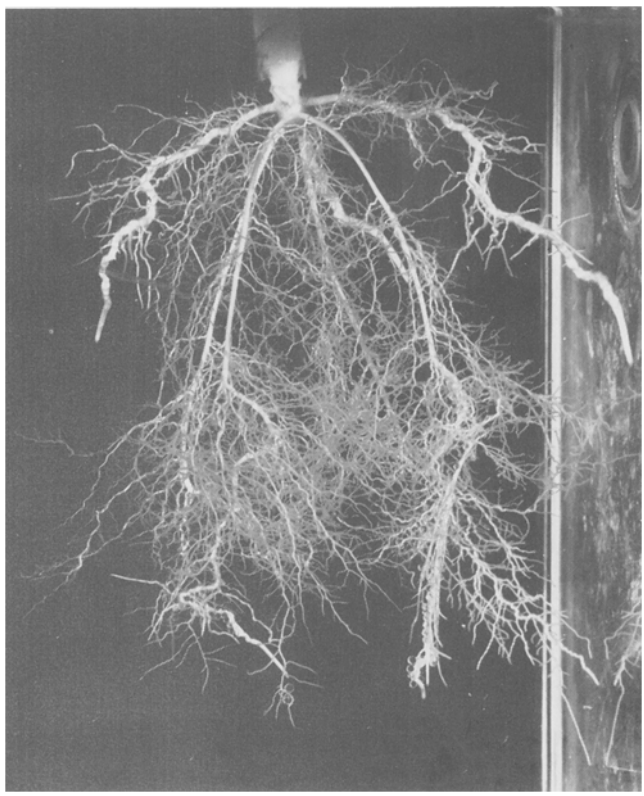

Fig. 2. Crown roots of a maize plant grown between ballotini. Parts of the oldest crown roots that have developed in a nutrient solution and when 5 cm long embedded between ballotini, are visible as straight thin main axes. The roots grown in the ballotini bed are curved and have an increased diameter. The laterals are unimpeded.

Fig. 3. Cell walls of root cortex cells, grown in a nutrient solution, stained with zinc-chloride iodine and observed in polarized light vibrating transverse to the cell axis. Transverse microfibrils are visible as indicated by the transverse pit openings.

microfibrils are oriented perpendicular to the vibration direction of the polarized light, then the microfibrils are transparent.

New cellulose microfibrils are deposited on the inside of the cell wall. In case of parenchyma cells this deposition is, as a rule, perpendicular to the long axis of the cell, which is parallel to the axis of the root. When in a cell wall microfibril layers with a different orientation are present, those layers can be observed separately, after staining with zinc chloride-iodine, in polarized light vibrating parallel to one of the microfibril directions[16,17]. A condition is however that not too many microfibril directions must occur and that in each direction a sufficient number of microfibrils must be present.

Results

Figures 1 and 2 show root systems grown respectively in nutrient solution and between 1 mm ballotini at an applied pressure of 40 kPa.

The crown roots grown between ballotini show about 75% decrease in length and about 50% increase in diameter as compared with those grown in a nutrient solution. Furthermore, branching is stimulated on impeded roots: there are more laterals, which are longer and show secondary and tertiary branching. Clearly the growth of laterals is not inhibited by ballotini of this size. The total weight of the

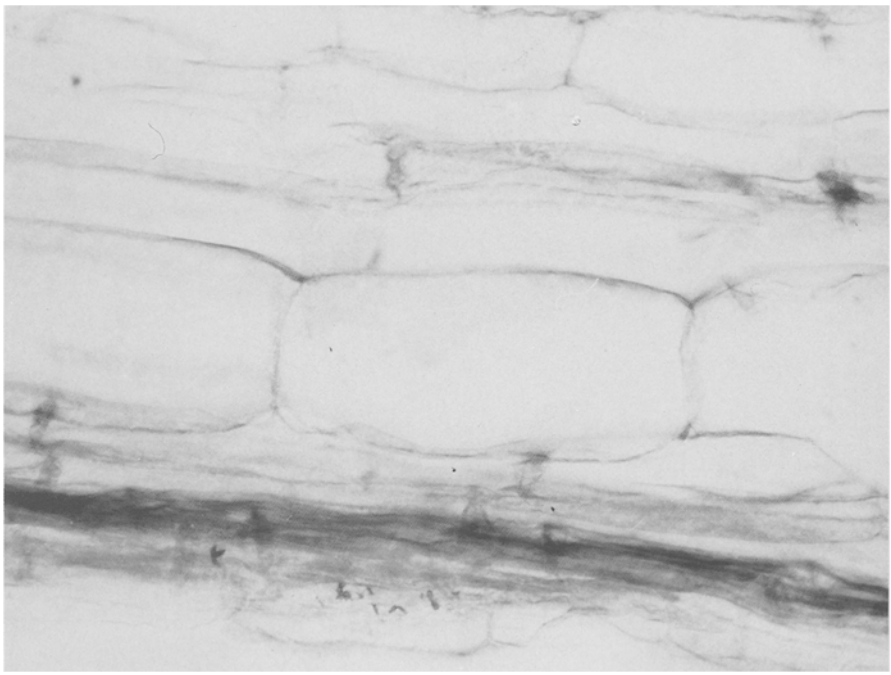

Fig. 4. The same object as Fig. 3, but observed in polarized light vibrating parallel to the cell axis. The cell walls are transparent, indicating that no longitudinal microfibrils are present.

root system in ballotini is less than roots grown in nutrient solution, while shoot growth is hardly inhibited.

Figures 3 and 4 show cell walls of full-grown cortex cells of a crown root grown in a nutrient solution. Both pictures show an identical part of the same microtome section. Fig. 3 shows a cell wall stained with zinc chloride-iodine and photographed in polarized light vibrating perpendicular to the cell axis, in figure 4 the plane of polarization is parallel to the cell axis. Only in Fig. 3 the cell walls are clearly visible from which it can be concluded that mainly transverse microfibrils are present in cell walls of roots grown in nutrient solution. This is confirmed by the presence of transversely oriented pit openings in the cell wall.

Figures 5 and 6 show cell walls of parenchyma cells of roots grown between ballotini. Again both pictures are of the same section photographed in polarized light vibrating respectively perpendicular and parallel to the long axis of the cell. In the first place there is a striking change in cell shape: the cells grown between ballotini are much shorter, but their diameter is increased compared with cells grown in nutrient solution, resulting in about the same cell volume. From Fig. 5 it can be concluded that transverse microfibrils are present, but after turning the polarizer 90° it shows that also longitudinal microfibrils are present (Fig. 6).

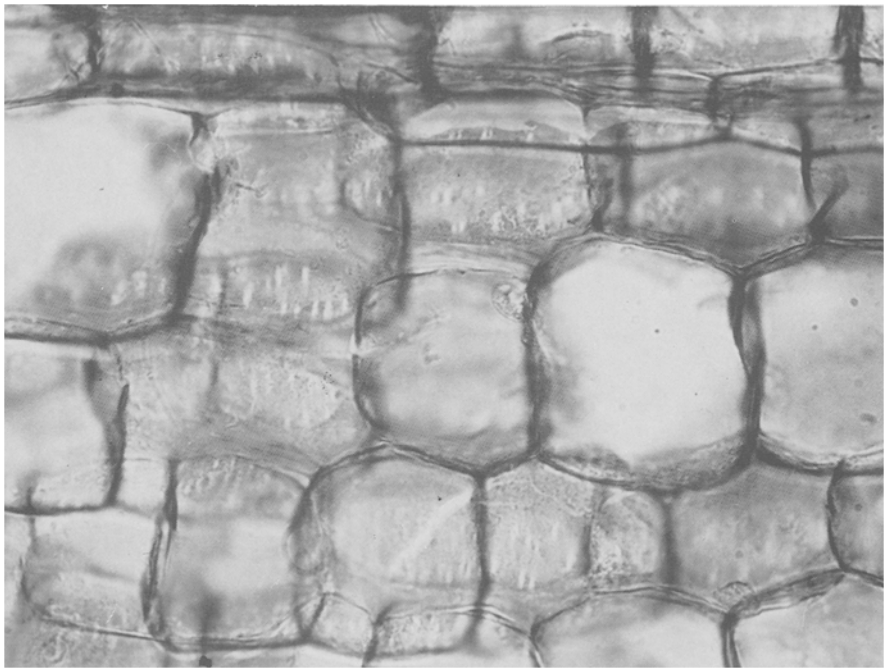

Fig. 5. Cell walls of root cortex cells, grown between ballotini stained with zinc-chloride iodine and observed in polarized light vibrating transverse to the cell axis. Transverse microfibrils are visible.

Discussion

The cell wall structure is an important factor determining the shape of a growing cell. Transverse microfibrils inhibit lateral growth, resulting in longitudinal growth. Longitudinal microfibrils inhibit axial growth in favour of lateral growth. Deposition of cellulose microfibrils parallel to the cell axis under the influence of a mechanical resistance applied to the root can be considered as the main cause of inhibition of root growth, while by the same cause lateral growth of the root is promoted. This lateral growth mainly occurs in the outer cell layers of the root cortex, which is in agreement with observation of Wilson, Robards and Goss[18]. The innermost cell layers experience a considerable wall pressure (see formula 2) from the outer cell layers so that in spite of the presence of longitudinal microfibrils lateral growth does not occur. Cellulose microfibrils in the primary wall of cortex cells are as a rule deposited transverse to the long axis of the cell. Deposition of microfibrils in longitudinal direction does as far as known only occur under the influence of ethylene[11,14] or under the influence of high concentrations of indole-3-acetic acid (IAA) in the presence of 2% sucrose[17] a condition by which ethylene production is induced[3,9].

A second observation that is important in this context is that when plants are

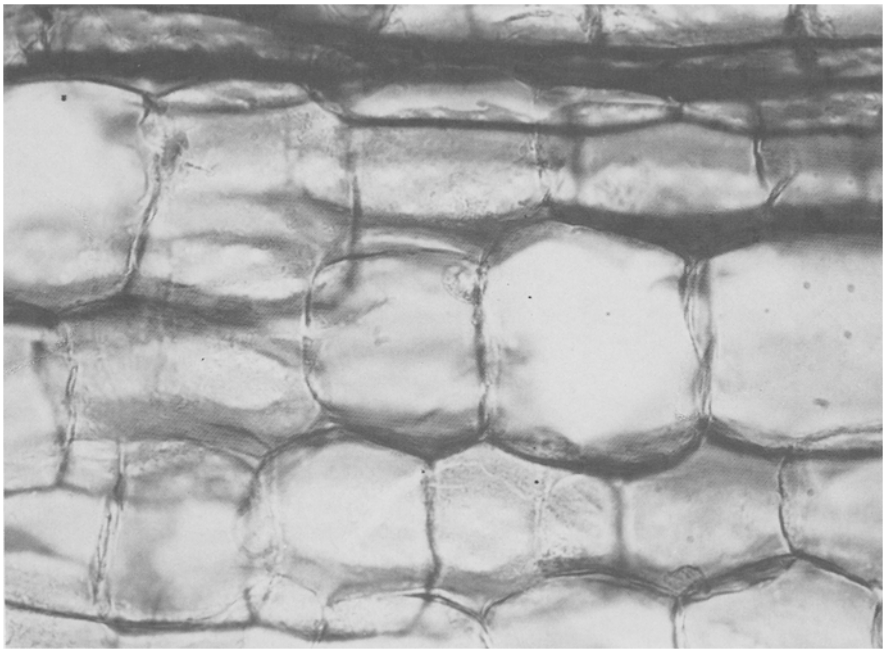

Fig. 6. The same object as Fig. 5, but observed in polarized light vibrating parallel to the cell axis. Part of the polarized light is absorbed, indicating that also longitudinal microfibrils are present.

exposed to physical stress (mechanical impedance) they start to produce ethylene. This is estiblished at growing stems[6] as well as at roots[8].

From the observations mentioned above the conclusion seems justifiable that roots that are under the influence mechanical resistance during growth become shorter and thicker than roots grown in a nutrient solution, because under the influence of ethylene, cellulose microfibrils in the parenchyma cell walls are deposited axially. A direct influence of mechanical impedance smaller than 100 kPa on extension growth of roots seems unlikely.

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