

Soil Compaction and Plant Root Growth [and Discussion]

D. R. P. Hettiaratchi, M. J. Goss, J. A. Harris, P. H. Nye and K. A. Smith

Phil. Trans. R. Soc. Lond. B 1990 **329**, 343-355

doi: 10.1098/rstb.1990.0175

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Soil compaction and plant root growth

D. R. P. HETTIARATCHI

Department of Agricultural and Environmental Science, University of Newcastle upon Tyne, U.K.

SUMMARY

Plant roots are subjected to mechanical impedance when soil pore space cannot accommodate the extending root system. The paper examines briefly the theoretical aspects of the combined effects of stress and moisture history in modifying both the pore space available for root growth and soil strength that limits the ability of roots to deform the soil.

A root extension model that requires cyclic changes in root apex geometry to overcome pore space confinement is described. Cells in the growth zone of roots are analysed as pressurized thin-walled structures of simple geometrical shape made of a polymeric elastomer reinforced by a network of symmetrical inextensible fibrils. Such structures exhibit somewhat unexpected but unique changes in shape governed by both fibril arrangement and contact stresses acting on the external surfaces.

A simplified model of a root apex can be constructed from these structural units and the behaviour of this model lends support to the proposed variable root apex geometry routine evolved by roots to penetrate compact soils. This analysis highlights the crucial role played by physical factors in the growth processes of roots and the disparate models described provide the basis for the development of a comprehensive quantitative model of root proliferation.

1. INTRODUCTION

All agricultural activity depends, either directly or indirectly, on the performance of the subterranean parts of plants. Soil compaction is a form of mechanical pollution which has a profound influence on root function and must therefore have far-reaching consequences on agricultural production. A major obstacle to understanding this problem is the enormous complexity of the many interactions plant roots make with their environment, the soil. The development of quantitative models, which describe root growth, is only one element in the compliment of techniques currently available for investigating plant root growth and this paper attempts to present some of the mathematical models developed to describe the more important physical interactions between plant roots and soil.

Figure 1 shows the main subject areas involved in the modelling process. The paper deals with topics only directly connected with the generation of mechanical impedance to root growth and how plant roots respond to this restraint. To make any headway in this activity it is essential to simplify the basic problems. The soil medium, for example, has to be dealt with as a granular continuum and no allowance is made for the existence of cracks and earthworm channels.

2. MECHANICAL CONFINEMENT

When the pore space dimensions in a soil continuum are large enough to accommodate the root axes and its laterals the growth of the root system is not subject to any mechanical impedance. The problem arises mainly

when the meristematic region of a root system has to physically displace or deform the soil medium to grow.

The comprehension of the entire process of root growth devolves around the following three factors connected with this deformation process: (a) the mechanics of soil pore space change, this controls the space available for the root to extend; (b) the stresses generated in the soil because of any deformations imposed by the root, and (c) the influence of these stresses on the living biological material of the growing root. In examining these it is necessary to simplify the problem by assuming that the availability of water, nutrients and oxygen are not limiting.

3. MECHANICAL BEHAVIOUR OF SOIL

Both the stress and moisture history of the soil determine the degree of mechanical confinement experienced by a root growing in it. In simple terms the stress history determines pore space geometry (relevant to §2(a) above) and the moisture history controls the stress-deformation characteristics (see §2(b) above). The different disciplines involved in understanding these interactions are set out in figure 1 and only a brief exposition of the critical state and micro-structural models will be dealt with here.

(a) *Micro-structural model*

A particular moisture content of a soil can be reached either by (i) a process of drying out (drainage or evaporation) or wetting (irrigation or rainfall) without any physical disturbance or (ii) when the dry mineral constituents are physically mixed with the

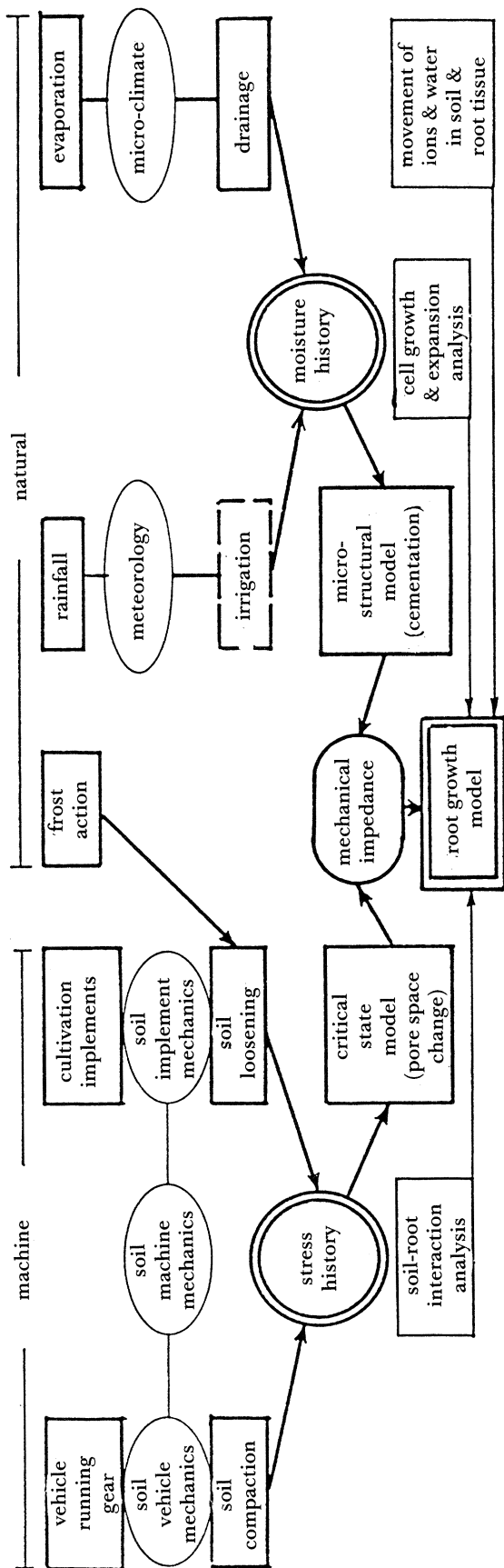


Figure 1. Structural arrangement of general root growth model. Elliptical compartments enclose major disciplines involved in the analysis.

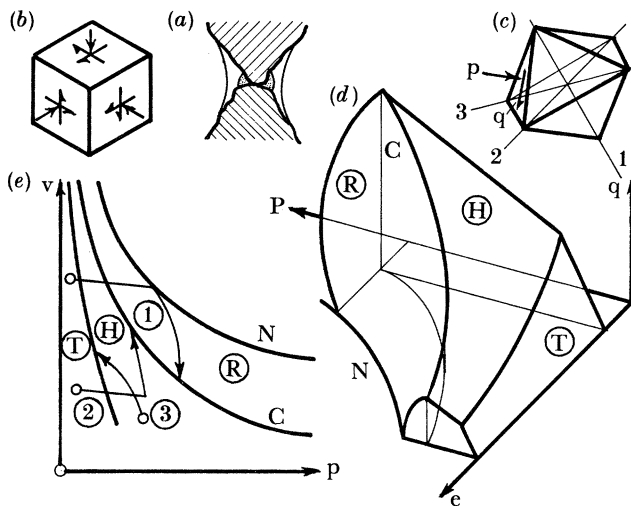


Figure 2. (a) Microstructural model. (b) General state of stress on a soil element. (c) Octahedral stresses equivalent to (b). (d) Critical state space. (e) Projection of critical state space on isotropic e - p plane.

necessary water. In either event the physical condition of the soil, at identical moisture status, is different. In the former case (cemented state) strong bonds formed between the coarser mineral particles present (well developed in the dried out soil) whereas in the latter (remoulded state) the main bonds between the mineral particles are predominantly moisture films (figure 2a).

In a real field situation there could exist an infinite range of combinations of these two conditions. The main reason for this choice is that both these states can be reproduced consistently under laboratory conditions. The mathematical model that describes the strength characteristics of these soils has been described by Hettiaratchi *et al.* (1985) and Hettiaratchi (1987). In this context it is only necessary to consider these two models simply as states that control root growth by virtue of their strength characteristics and hence their resistance to deformation. In the cemented form the inter-particle bonds have chemical encrustations (see figure 2a) and is the stronger of the two states.

(b) Critical state model

The soil, conditioned by its moisture history, has to be viewed from the standpoint of (i) pore space change brought about by engineering activities (compaction and cultivations) and natural events such as frost action and (ii) the resistance to deformation by growing roots.

The Cambridge critical state model (Roscoe *et al.* 1958) provides the basic framework for describing the mechanical behaviour of saturated soils. These concepts have been extended to partly saturated soils (Liang 1985; Hatibu 1987; Hettiaratchi 1987) that is the moisture state of particular interest in root growth modelling. This model prescribes the way the pore space of a given soil (quantified by its void ratio e) alters with applied stresses.

The precise description of the stress acting on the soil is, however, less straightforward. The elementary cube of soil shown in figure 2b shows the general state of

stress. This cube can be replaced by the regular octahedron shown in figure 2*c*. It is always possible to orient its three axes (labelled 1, 2 and 3) such that all the eight normal stresses (p) acting on each face are the same and simultaneously all the eight shear stresses (q) on each face are of equal magnitude. Note that p represents an equal all-round pressure similar to that acting on a body submerged in a dense liquid and q is a system of shear stresses.

In the three-dimensional orthogonal coordinate system shown in figure 2*c* two of the axes can be used to represent the stress components p and q and the remaining axis the pore space (e) available for accommodating roots. The critical state model identifies certain state boundary surfaces (labelled R, H and T in figure 2*d*) within the p - q - e space outside of which combinations of p , q and e cannot exist. Values of p , q and e falling within these state boundaries develop only recoverable or elastic deformations while those traversing the surfaces generate permanent plastic deformations. The shape of these surfaces are unique to a given soil at a specified moisture content and moisture history and once these are established experimentally the mechanical behaviour of the soil is completely delineated.

The boundary junction C (the critical state line) represents the combinations of p , q and e at the point of failure of the soil. The junction curve N represents the path traced by the soils undergoing permanent deformation when compressed by equal all-round pressures (note $q = 0$) and is referred to as the normal consolidation line.

4. PORE SPACE CHANGE

The models described in §3 can be used to investigate how soil pore space is altered by engineering operations in the field. Pore space as represented by the void ratio e is only an indirect measure of the availability of space within the soil matrix to accommodate the root system. The actual geometry of the voids and their distribution are the main factors determining mechanical impedance and these are difficult to relate to a single parameter such as void ratio e . The particle size distribution of the soil influences this relation but for the present the actual magnitude of e will be used as a guide to the degree of mechanical impedance a soil will offer to a growing root system.

Space precludes a detailed analysis of the critical state model and how pore space changes can be traced for different field operations (see for example Hettiaratchi *et al.* (1980); Hettiaratchi (1989)). Combinations of p , q and e (a state path) that follow the R surface to failure on the critical state line (trace 1 on figure 2*e*) invariably induce a reduction in e and hence increase the likelihood of mechanical impedance to roots. This models the compaction induced by the interaction of tractor running gear with the soil. A state path traversing the H surface has an opposite effect (trace 2 on figure 2*e*) and there is an increase in e , showing soil loosening with a consequent decrease in mechanical impedance. These state paths represent cultivation operations. Frost action induces (negative)

tensile stresses within the soil and would tend to reduce any (positive) compaction stresses in the soil (trace 3 on figure 2*e*).

The excitement of having a model that is able to interpret all pore space changes taking place in a soil has to be tempered somewhat by the fact that in practice the experimental determination of the state space parameters is fraught with considerable complications. For instance, even in the simplest case these parameters must be found for a range of moisture contents for both re-moulded and cemented states. The experimental work is involved, tedious and time consuming (see Liang 1985; Hatibu 1987; Bhuyan 1988). In addition to this there is the considerable problem of determining what p and q are for a given tillage tool or tractor wheel.

5. RESPONSE TO MECHANICAL IMPEDANCE

As part of the simplifying process it is necessary to examine the response of roots to mechanical impedance under controlled laboratory conditions. In these investigations it is necessary to keep factors affecting root growth, such as temperature, soil aeration, moisture content, nutrient supply and above-ground light levels at a constant optimal level and record root growth as a function of mechanical impedance only.

The apparatus developed at Newcastle for these fundamental investigations used a modified triaxial apparatus that is commonly used in estimating soil strength. As shown in figure 3*a* the root environment is a right circular cylinder ($\phi 38 \text{ mm} \times 76 \text{ mm}$) whose side walls consist of a thin rubber membrane A. The lower end of the cylinder is closed and has tappings (B, C) for aeration of the sample and the supply of a nutrient solution. The upper end has a collar D to allow the shoot to grow out of the rooting medium E. A number of such 'triaxial rhizometers' are used to replicate the experimental runs and all of these are contained in a constant temperature cabinet with provision for light-

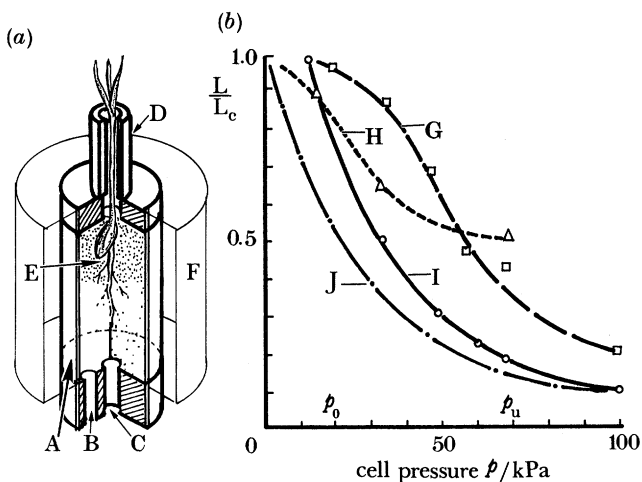


Figure 3. (a) Details of Newcastle 'triaxial rhizometer'. (b) Results from rhizometer experiments: G, barley in a sandy loam; H, rice in clay; I, barley in glass beads; J, barley in glass beads (after Goss 1977); L, root length; L_c , root length of control ($p = 0$).

ing from above. The degree of mechanical confinement is controlled by the hydrostatic pressure p of the water in the annular jacket F. Details of this apparatus and the experimental work have been described by Abdalla *et al.* (1969). Similar investigations were conducted in Australia (Barley 1962, 1963) and at Letcombe (Goss 1977).

A summary of the experimental results obtained from these fundamental investigations is shown in figure 3*b*. Hydrostatic confining pressures of $p = p_o$ of 20–30 kPa are readily overcome by the roots, but extension is almost completely arrested at an upper limit of $p = p_u$ of ca. 70 kPa. In the intervening pressure range ($p_o < p < p_u$) roots grow with considerable attenuation in length coupled with a corresponding increase in root diameter and typically, confining pressures of the order of 50 kPa will reduce root length by 50%. These findings pose two important questions: (a) what is the significance of the confining pressures? and (b) why is the root diameter larger in the confined roots?

(a) Confining pressure

If the rooting medium E in the Newcastle triaxial rhizometer were a fluid then it is evident that the pressure acting on the root surface will be identical to the cell pressure p . When the medium is a granular material this condition no longer holds. The applied hydraulic pressure is analogous to the hydrostatic pressure p discussed in §3*b*. It has been shown (see Abdalla *et al.* 1969) that a change in this pressure is tantamount to an alteration in the strength characteristics of the soil and is indeed an artificial way of introducing the effects of the inter-particle bonding in the microstructural model (§3*a*) into the rooting medium. The geometry of the pore volume can be controlled by employing a rooting medium of uniform glass beads of appropriate diameter. Richards & Greacen 1986 investigated this effect by replacing the root with a fluid filled flexible tube and they measured the pressure deformation characteristics of the tube at different values of p .

These experiments clearly show the influence of p in altering the elastic and plastic stress deformation characteristics of the medium. The precise nature of these alterations would, of course, depend on the particulate nature of the medium. A simple calculation for a sandy loam soil (see figure 3 in Abdalla *et al.* (1969) shows that a 50% reduction in root length results from an eightfold increase in elastic strength (corresponding to a 50 kPa confining stress).

(b) Root swelling

The swelling of roots subjected to mechanical confinement was carefully documented and a possible explanation for this behaviour was advanced two decades ago (Abdalla *et al.* 1969). In this hypothesis the swelling of confined roots is a crucial step in the way roots have evolved a strategy for overcoming the effects of mechanical confinement. A resolution of the mech-

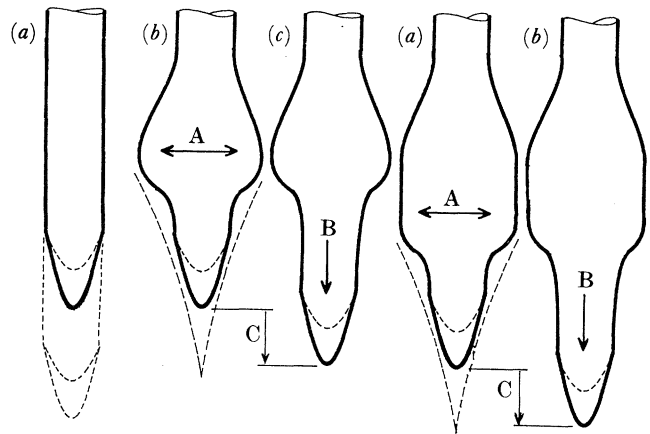


Figure 4. Steps in the 'variable apex geometry' root extension model. (a) Axial extension arrested by soil in root cap zone; (b) Radial expansion of region behind root tip weakening soil in root cap zone; (c) Axial extension resumed; A, radial growth mode; B, axial growth mode; C, root extension increment.

anics of this behaviour is central to any understanding of root growth in compact soils.

The main steps in the growth cycle in this hypothesis are re-iterated here:

- (i) axial elongation of the root is prevented by the strength of the soil in the neighbourhood of the root cap (i.e. $p > p_u$);
- (ii) the elongation zone of the root alters its normal growth direction from axial (which is inhibited) to radial;
- (iii) radial thickening helps to relieve the arresting stresses at the root cap (effectively bringing $p < p_u$);
- (iv) normal axial growth of the elongation zone resumes until the root cap enters the zone of soil where $p > p_u$;
- (v) the cycle of steps resumes from (ii).

This hypothesis is shown in figure 4 and it will be readily seen that a root extending in a soil having an equivalent p in the range $p_o < p < p_u$ will continue to grow with an increase in root diameter. When $p < p_o$ or when the pore space is larger than the normal root apex diameter growth will proceed uninhibited. However, root growth will be arrested when $p > p_u$ in which case step (ii) cannot take place or, if this were feasible, the effect of (iii) in reducing p becomes ineffectual.

(c) Growth model prerequisites

The validity of this physical model for root growth devolves on acceptable explanations of the following three factors: (i) how is it possible for the growth polarization of the elongating zone of a root to continue in a radial mode when the axial mode is arrested, after all, the soil in the neighbourhood of the root cap and that surrounding the elongation zone are of comparable strength (no spatial variation of p); (ii) does a radial expansion just above the root cap help to reduce the strength of the soil in the root cap zone? and (iii) what mechanism, if any, governs the change in growth polarization from axial to radial. These questions will be dealt with in the following sections.

6. STRESS ANALYSIS

(a) Growth polarity

Ladanyi (1963) employed the expansion of a spherical cavity in a soil as the basis for calculating the bearing capacity of deep piles. A similar analysis was carried out by Greacen *et al.* (1968) for modelling penetrometer performance. The advance of the root cap into the soil correlates closely with these punch-indentation problems and mobilises a three-dimensional spherical deformation of the soil surrounding the root cap. The radial expansion of the root elongation zone is akin to a two-dimensional expansion of an infinite cylinder in the soil just behind the root cap. A comprehensive analysis of the contact stresses generated by both these types of deformation was carried out by Nguyen (1977).

The results obtained by Nguyen by using both an elastic-plastic model (after Vesic 1972) and a critical state model with deformations in the brittle and ductile domains (zones under surfaces H and R, respectively in figure 2*d*) are summarised in figure 5*a*. It is clear from this data that the contact stress (p_c) generated in the course of a cylindrical expansion of the extension zone is always smaller than the stress p_s mobilized in a spherical expansion associated with the indentation of the root cap through the soil. The ratio $r = p_s : p_c$ depends on the soil type and is sensitive to the angle of friction of the soil. Greacen *et al.* (1968) found $r = 5$ for frictional soils and Nguyen (1977) deduced that typical values of r ranged from 1.3 (for a frictionless cohesive soil) to 2.5 (for a frictional soil with a high modulus of rigidity). It can be shown by simple elastic theory (Abdalla *et al.* 1969) that r has a minimum value of 1.5 and a comparable elastic-plastic analysis (Hettiaratchi

et al. 1973) showed that $p_s = 1.16p_c + 0.19c$, where c is the soil cohesion.

An experimental verification of these theories was carried out in two soil types by Hettiaratchi *et al.* (1973). A specially modified probe was used in these tests and values of $r = 2$ for a sandy loam and $r = 5$ for a coarse sand were obtained (see figure 5*b*). It is clear from all the available evidence that when the elongation zone is unable to advance the root cap in an axial direction the root apex is still capable of expanding in a cylindrical mode because the mobilized contact stresses in the former growth step is always greater than those for the latter. This discussion provides the answer to requirement 5*c* (i) of the growth model.

(b) Stress interaction

The radial expansion of the elongation zone is representative of a symmetrical radial expansion of the end of a finite cylinder in the soil. It is evident that the soil at the end of the cylinder will be displaced radially outwards developing an equivalent tensile stress in the soil thus reducing the ambient value of p . Referring to figure 2*e* the critical state model predicts that the state path for this case will be directed towards the T surface (trace 3) and the soil will ultimately fail by tensile cracking. Thus the radial enlargement tends to alleviate the constraints to the axial extension of the root cap.

This stress relief effect has also been shown by a two-dimensional photo-elastic analysis of a simple model of the soil continuum (Hettiaratchi *et al.* 1973). A finite element analysis carried out by Richards *et al.* (1986) also lends firm support to these findings. Mechanical probes designed to simulate the radial and axial expansion modes have been tested (Hettiaratchi *et al.* 1973; Nguyen 1977) and the tips of these scale model roots were loaded to the point where their axial extension was just arrested. On operating the radial expansion zone the tip advanced freely in an axial direction and figure 5*c* shows how the axial (or punch) contact pressure falls off dramatically. These theoretical and experimental investigations provide conclusive evidence of the way the radial expansion of the root extension zone can assist the root tip to advance into a soil that it could not penetrate on its own. This provides the evidence for sustaining requirement 5*c* (ii).

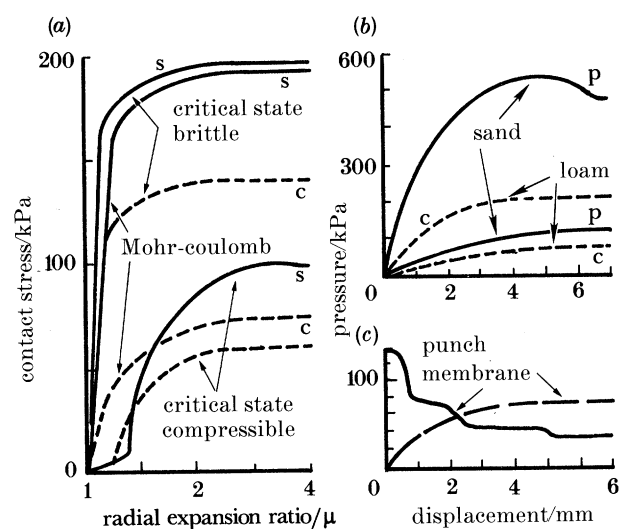


Figure 5. (a) Theoretical predictions for contact stresses in punch indentation (spherical expansion) and radial deformation (cylindrical expansion) by using Mohr-Coulomb and critical state models; S, punch indentation; C, radial expansion (after Nguyen 1977). (b) Experimental contact stresses using a variable geometry penetrometer; P, punch indentation; C, radial expansion. (c) Influence of a radial expansion (membrane) on punch indentation (punch) contact pressure (after Hettiaratchi *et al.* (1973)).

7. CHANGES IN ROOT APEX GEOMETRY

(a) A simple mechanical analogy

The micrograph in figure 6*a* is a typical cross section of a root apex and figure 6*b* shows its mechanical analogue. The root cap A is merely the 'nose cone' of a miniature thrust-boring tunnelling machine. It is subject to considerable wear and tear due to abrasion as it is forced through its hostile surrounds and to compensate for this its skin is renewed from new cells which originate from the distal surface B of the quiescent centre C of the apical meristem. The root cap is thrust into the soil by the change in length of the cells in the elongation zone D of the root. The thrust F is taken up partially on the numerous root hairs

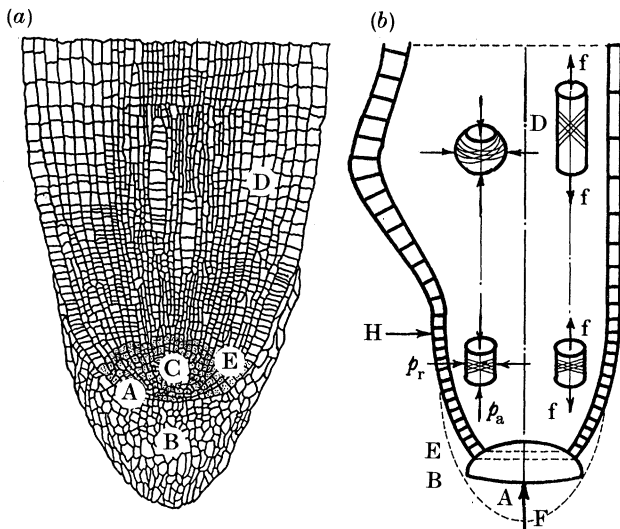


Figure 6. (a) Typical micrograph trace of the longitudinal section of a root apex. (b) Mechanical analogue of root apex. Right half section, normal growth; left half section, influence of mechanical impedance.

anchoring the rear of the thruster section D of the root to the soil. This reduces the unsupported length of the slender axially loaded section of the root and counteracts any tendency to buckle.

The force F driving the root cap into the soil is made up of the individual forces f generated by the elongating cells in zone D. These cells are organized in the form of a series-parallel array of 'hydraulic jacks'. The parallel units of this configuration (radial rows) increase the force capacity and the series units (longitudinal files) provide the long stroke required for root elongation. Once the individual 'jacks' in this system have fully extended a fresh supply of retracted jacks are advanced, towards the elongation zone D, from the domed basal surface E of the quiescent centre.

Root growth is a combination of cell division in the meristem above the quiescent centre followed by cell expansion. The former is the source of fresh retracted 'jacks' and the latter constitutes the actuation phase of these jacks. The energy for extending each 'jack' comes from photosynthates used to re-concentrate the vacuolar fluid that is diluted after each extension (see §6b). The axial stress component p_a acting on the cells in zones E and D of the root is induced by the force F and any radial forces acting on the root epidermis will generate the radial stress component p_r .

(b) Simple cell growth model

The present discussion is primarily concerned with the behaviour of parenchymatous cells of the root although the basic analytical techniques may be applicable to cells in the plant as a whole. These root cells are hollow thin walled structures made up of strong polymeric substances and subjected to high internal pressure. The question is, 'how do such structures change shape and increase in size in an ordered fashion?' The current concept held by plant physiologists is that the wall of the cell, stretched by internal hydrostatic pressure, changes its shape by

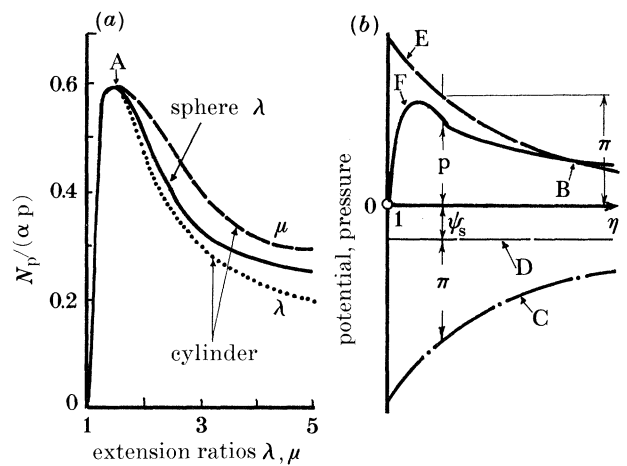


Figure 7. (a) Non-dimensional pressure-deformation characteristics of thin-walled inflatable spheres and cylinders made of polymeric elastomers. Note the pressure number N_p is proportional to internal pressure (see notation). (b) Water relations of plant cells. A, point of dimensional instability; B, end of water inflow; C, cell vacuolar fluid potential; D, soil matric potential; E, cell potential; F, cell pressure volume characteristic (turgor).

loosening of the walls (see, for example Cosgrove 1986). Some of the hypotheses on wall stretching require the intervention of plant hormones (see, for example Taiz (1984); Cleland (1971)).

The present model is based on the way axially symmetric membrane structures, made of non-linear polymeric elastomers, alter their shape during hydrostatic inflation. The unique nature of the characteristics of these structures has been used to develop a theory for the growth of highly vacuolated plant cells (Hettiaratchi *et al.* 1974). The pressure extension characteristics of spherical and cylindrical cells obtained from this analysis are shown in figure 7a. These are presented in non-dimensional form and are independent of the absolute values of initial cell size and the strain energy modulus of the cell wall material and thus represents a general solution. The cell pressure number N_p can simply be considered as being directly proportional to the turgor pressure p in the cell. All dimensional changes are represented as extension ratios (η , λ and μ) and each is the ratio of the current value of the dimension to its initial value. Thus unit values represent no change, values greater than unity indicate an increase and values less than unity, up to zero, is a contraction.

These pressure-volume characteristics show a distinct instability at the point A (figure 7a). The pressure in the cells increases as a result of osmotic influx of water and when it reaches point A dimensional instability ensues with a consequent large increase in cell size and this constitutes the growth step of the cell. This increase in cell size is independent of any biochemical intervention from the cell protoplasm and is a purely physical-dimensional change that arises as a result of the very nature of the pressure-volume characteristics. Clearly this process requires a critical pressure p_c to be exceeded before membrane instability takes place and this is in accordance with observations on cell growth (Cleland 1971).

The well-known water relations of plant cells shown in figure 7*b* trace the influx of water driving the growth phase. Dilution of the vacuolar contents terminates cell extension at point B in figure 7*b*. The cell protoplasm concentrates the vacuolar sap from photosynthates transferred via the phloem and at the same time deposits fresh wall material on the inside of the expanded cell. The cyclic growth steps are then repeated until primary growth ceases when the grown wall material has raised p_c above that of the osmotic potential of the cell contents. In this event the cell cannot reach its instability point to initiate the next extension cycle and growth ceases.

The rate of growth of the cell in this model depends on: (i) the rate of inflow of water into the cell, and (ii) the time taken for osmoregulation. The model explains the effect of water stress, temperature and the control exerted by plant growth hormones and poisons on cell growth rates. All these factors influence either one or both of the rate processes (i) and (ii) above. This model also predicts the characteristic non-linear growth rate frequently observed in the development of plant structures. However, this simple membrane model ignores two important matters of detail. First it takes no account of how the shape of the extending cell is controlled and secondly the external boundaries of the cell are assumed to be stress free.

(c) Influence of wall microfibrils

The microfibrils found in plant cell walls are relatively inextensible and hence impart directional properties to the cell wall and play a vital part in controlling the way the cell shape alters during growth. The influence of these microfibrils on the behaviour of inflatable structures has been modelled (Hettiaratchi *et al.* 1978; Wu *et al.* 1988).

The presence of microfibrils in the simple membrane model discussed in §7*a* has been dealt with by introducing two pairs of regular helices of opposite hand running at an angle α with the longitudinal axis of the cylindrical cell (Hettiaratchi *et al.* 1978). How these microfibrils control the way a cylindrical cell alters its shape is shown in figure 8*a*. It will be seen from this simplified analysis that a radial expansion of the cell must be accompanied by an axial contraction and an increase in fibril angle and vice versa. The volume variation associated with these linear dimensional changes depends on the initial fibril angle α and reaches a maximum value when the fibril angles approaches the critical value

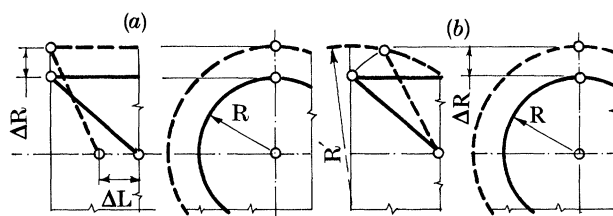


Figure 8. (a) Influence of inextensible microfibrils on radial and axial extension ratios. Cylinder remains a cylinder on expansion. (b) Cell surface deformations when axial extension is fixed. Cell surface barrels outwards. Surface has additional curvature R' .

$\alpha_c = \cos^{-1}(1/\sqrt{3}) = 54.74^\circ$. The extension ratio limit λ_m for an initial fibril angle α can be calculated from $\lambda_m^2 = 1/(3 \cos^2 \alpha)$. A summary of these geometrical changes are set out in table 1 (details in Hettiaratchi *et al.* (1987)).

When the axial extension is arrested volume increase can still proceed by radial expansion. However, as shown in figure 8*b* this imposes an additional degree of curvature R' at right angles to the cylindrical surface and this requires the cylinder walls to barrel outwards. This effectively alters the growth polarity from axial to radial and fulfils the requirement 5*c*(iii).

The effect of the microfibrils on the pressure deformation characteristics is shown in figure 9. From the limited selection of curves in this diagram (for details see Hettiaratchi *et al.* (1978)) it will be noticed

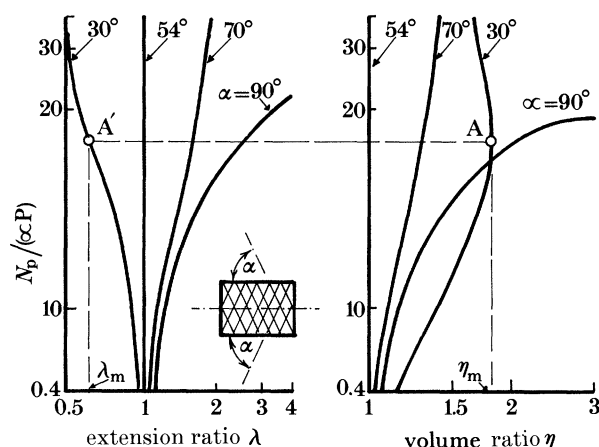


Figure 9. Non-dimensional pressure-deformation characteristics of reinforced thin-walled inflatable cylinders made of polymeric elastomers. Fibril reinforcement consists of a single layer of two symmetrical helices.

Table 1. Influence of microfibril orientation on cell geometry

range	fibril angle α	axial extension change $\Delta\lambda$	radial extension change $\Delta\mu$	volume change $\Delta\eta$	extension limit for peak volume λ
1	90°	+	-	+	infinite
2	$\alpha_c < \alpha < 90^\circ$	+	-	+	decreases with α
3	α_c	0	0	0	$\lambda = \mu = 1$
4	$0 < \alpha < \alpha_c$	-	+	+	decreases with α

Table 2. Influence of hydrostatic contact stresses on cell surfaces

range	fibril angle	hydrostatic contact stress h_v	equivalent fibril angle α_v
1	$\alpha_c < \alpha < 90^\circ$	$p_h < p$	$\alpha_v < \alpha_c$
2	$0 < \alpha < \alpha_c$	$p_h < p$	$\alpha_v > \alpha_c$
3	all	$p_h = p$	$\alpha_v = \alpha_c$
4	all	$p_h = 0$	(no change)

that, for example, when the fibril angle $\alpha = 30^\circ$ the cell volume peaks at point A ($\eta = \eta_m$) and the cell has contracted axially to A' ($\lambda = \lambda_m$). In the present context a plant cell cannot decrease in volume without efflux of vacuolar fluid (plasmolysis). Since this is not possible under normal circumstances points A and A' represent the limit of the expansion of the cell. When α approaches 90° the magnitude of λ_m is very large and the cell can extend to many times its original length with steady volume increase before this limit is reached. The extension limit λ_m decreases very rapidly as initial fibril angle α reduces from 90° (see equation in §7c).

(d) Influence of boundary stresses

The influence of boundary stresses p_a and p_r (see figure 6b) on the behaviour of the reinforced cell have been examined in outline (Hettiaratchi *et al.* 1978). When $p_a = p_r = p_h$ the reinforced cell is subjected to an equivalent hydrostatic pressure of magnitude p_h . The performance curves are similar to those shown in figure 9 except that the cell with an initial fibril angle of α behaves like a cell with the virtual angle α_v . These trends are set out in table 2.

The two remaining possibilities are for $p_a < p_r$ and $p_a > p_r$ and these inequalities depend on the relative magnitudes of the external contact forces H and F in figure 6b. The cell performance curves are much the same as those set out in table 2 so long as neither of the pressures p_a or p_r equals the cell turgor pressure p . When $p_a = p$ cell extension in the axial direction is arrested. As discussed in §7c this requires the cell to barrel outwards and growth with volume increase is confined to increments in the radial direction. When $p_r = p$ then radial enlargement is arrested and as shown in figure 8a axial extension with cell volume increase would continue with accompanying radial contraction. Now since p_r acts in the same direction as the radial contraction this situation would enhance the axial growth. A summary of the influence of microfibril arrangement and external contact stresses on the way inflated structures behave is given in figure 10.

It is interesting to note that some of the effects of inextensible reinforcement on the behaviour of the structures just discussed has found many practical engineering applications. For example, hydraulic hose is manufactured with the reinforcing outer braid laid at the neutral angle of 54° (range 3, table 1). This ensures that the hose does not thrash around because of length changes during intermittent pressure changes. The fact that a reinforced cylinder can be distorted

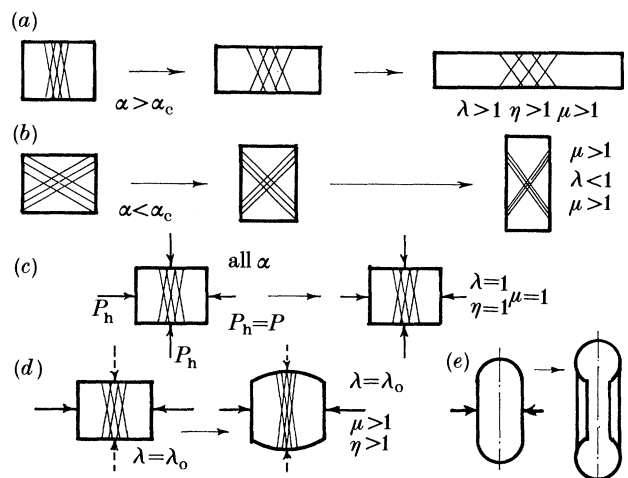


Figure 10. Schematic representations of the behaviour of fibril reinforced cells (a) Fibril arrangement for cell extension. (b) Fibril arrangement for cell contraction. (c) Hydrostatic contact pressure arrests growth. (d) Case (a) with axial extension arrested. (e) Enforced axial contraction. Cell surface becomes toroidal (manufacturing technique for tyres).

into a barrel shape is used in the manufacture of motorcar tyres. As shown in figure 10e (a further progression from figure 10d) the ends of the cylindrical mould when inflated and forced together distorts into the familiar toroidal shape of the tyre. In the plant kingdom this action involves growth polarity change from axial to radial!

(e) Change in growth polarity of root apex

The microfibril orientation and the external loads applied to the cell have been shown to control the shape of the growing cell. It is evident that axial confinement will change the growth polarity of the elongating cells to a radial direction ($p_a = p$, $p_r < p$, see §6a). The effect of this change in root apex shape is shown diagrammatically in the left half of figure 6b. The increase in radial growth stops when the cell has reached its peak volume with $\alpha = \alpha_c$. If the stress interaction on the surrounding soil helps to relieve the axial confinement then extension will resume (see §6b). When radial growth cannot accomplish this or if the external stresses reach a hydrostatic confining state ($p_a = p_r = p$) all growth of the root will cease because cell volume cannot increase ($\eta = 1$).

The discussion in this section provides the theoretical explanation for the mechanism of growth polarity change set out as proviso (iii) in §5c. The reorganization of the apical growth patterns is shown to take place as a result of the interaction of external physical constraints on the dimensional performance characteristics of the reinforced cells.

8. ROOT GROWTH BIOMECHANICS

It is perhaps pertinent to examine the theoretical framework developed so far in relation to the wealth of experimental evidence currently available on the

cellular behaviour of growing plant roots. It would be impossible to review all the accumulated pool of valuable knowledge and reference is made to only a few recent publications.

(a) Influence of fibril arrangement

Consider first the design strategy of root parenchyma cells. Unlike growth at the shoot apex these cells are required to provide the forces necessary for soil penetration by the root cap. Range 1 of table 1 and figure 10*a* show that the optimum microfibril angle for unconstrained cell extension is 90° (transverse fibrils). With this arrangement the cell can in theory extend indefinitely. With a fibril angle of say 80° the cell can extend up to nearly three times its original length with a radial contraction to 0.8 of its original diameter (see figure 4 in Hettiaratchi *et al.* (1978)). Extension cannot proceed beyond this because it entails a decrease in cell volume and the fibril angle would have decreased from 80° to the critical value of 54.74°.

Veen (1982) found transverse microfibril orientation in unimpeded maize roots. An identical observation in inner walls of pea root cells was made by Hogetsu (1986) and his work also shows that the transverse fibrillar arrangement in cells at the distal boundary of the elongation zone (2 mm from the root tip) alter to an oblique orientation at the basal limit of the elongation zone (5–7 mm from the apex). Taking rough measurements from the electron micrographs published (Hogetsu 1986, figure 2*c, d*) the fibril angle at end of extension is around 40° (expected value 54°).

The original 'multi-net growth' pattern proposed by Roelofsen (1965) for the growth of cotton hairs is an early theory which traces the change in fibril angles from its newly laid transverse orientation to an oblique one as extension progresses and is in accordance with the tenets of the present discussions. However, current theory has not advanced far enough to deal with cell walls composed of several layers of fibrils, each laid at a different angle.

(b) Influence of external stresses

Veen's investigations on maize roots show that for impeded roots typical dimensional changes in the cortical cells are around $\lambda = 0.75$ and $\mu = 1.5$ ($\eta = 1.69$). The cells have contracted marginally (this contradicts the theory as it requires $p_a > p$ and $\alpha < 54^\circ$ (or both)), expanded radially and increased in volume. Polariscope observations on treated cells show that in the stressed cells both transverse and 'longitudinal' fibrils are present although no measurements were made as to the precise angles made by the longitudinal fibrils.

The data shown in table 3 has been extracted from the detailed and painstaking experimental work described by Wilson *et al.* (1977). The root dimensions of the 4th and 5th row of the cortical cells at 3 mm and 12 mm from the root tip (taken from their figures 12, 13 and 14) are used as the initial and fully extended states, respectively. It will be seen that for an applied boundary pressure of 20 MPa the cell extension is

Table 3. Root cell proportions from Wilson *et al.* 1977

(C, control; I, impeded; *, calculated value.)

dimension	state	distance from root apex		
		3 mm	12 mm	ratio
diameter	C	37	42	1.14
(μm)	I	50	58	1.16
length	C	137	200	1.46
(μm)	I	135	154	1.14
volume	C	150	325	2.17
($\mu\text{m}^3 \times 10^3$)	C	147*	277*	1.89*
	I	270	410	1.52

virtually inhibited ($\lambda = 1.14$ compared with $\lambda = 1.46$ for the control) and the cell diameter has increased to $\mu = 2.32$. An unexpected finding is that the cell diameter has also increased in the control although this is not to the same extent as in the impeded root.

If it is assumed that the cells have all extended to the limit ($\lambda = \lambda_m$) then it is possible to calculate the initial fibril angle and these turn out to be around 67° for the control and 60° for the impeded root. Note that the impeded root with external contact stresses gives a smaller calculated virtual fibril angle α_v than the unimpeded cells and is as set out in table 2. The experimental cell volumes show that the impeded root has assimilated less water than the unimpeded root that could possibly be a result of external contact stresses reducing the fibril angle to a lower virtual angle. Another interesting finding is that the 3rd row of cortical cells showed hardly any change in diameter and a possible explanation is that by virtue of its position the stresses p_r and p_a exerted on its boundaries by neighbouring rows of cells have reached the limiting value of p and growth will be arrested (see figure 10*c*).

(c) Root swelling and growth hormones

The analysis presented so far has attributed the swelling of impeded roots to purely physical factors. Ethylene at very low concentrations is known to inhibit root extension and induce lateral swelling (see, for example Jackson *et al.* 1981). This presents the possibility that endogenous ethylene controls the growth of impeded roots and the associated change in root geometry is not a consequence of physical confinement. Moss *et al.* (1988) have shown that the suppression of ethylene by inhibitors (norbornadiene and amino-ethoxy-vinyl-glycine) in roots failed to reverse the effects of impedance and these observations would rule out this role for ethylene. A possible explanation for the swelling of the root apex is that ethylene disrupts the highly organized deposition of the microfibrils in the cell wall and thus removes the control for ordered axial extension of the appropriate root cells as discussed earlier.

9. CONCLUDING REMARKS

The paper has attempted to spin together the twin strands of soil machine mechanics and cellular bio-

mechanics to formulate the basic elements of a unified quantitative model describing the growth of plant roots in compact soils. Changes brought about by natural causes and engineering field operations to the soil pore space available for accommodating plant roots can be traced in critical state space. Soil strength is governed by the microstructural nature of the soil skeleton and influences both the proportions of the critical state boundaries and the response of the soil to deformation by growing roots. It has been shown that a 'variable apex geometry' cyclic growth routine enables plant roots to penetrate compact soil. This growth mode results in thickened roots and a corresponding reduction in root length, typically 50% for an eightfold increase in soil elastic strength. Evidence, both experimental and theoretical, has been presented in support of the three basic criteria required for the operation of this soil penetration model. The analysis of the structural mechanics of fibril reinforced thin-walled cells has highlighted how cells can continue to increase in volume when subjected to external stresses and provides a possible explanation for continued growth under mechanical confinement. Admittedly the analyses presented have been carried out by treating the soil as an isotropic granular continuum and plant cells as simple regular geometrical structures.

Although the overall performance of the individual components of the growth model in explaining most observed behaviour appears to be adequate there are many facets of the problem that are as yet not completely understood or explained. These estimates are frustrated by the difficulty in quantifying the stress components generated by the interaction of machine elements with the soil. Yet again in the biomechanical model, how are all the unstable growth extension steps in the cellular community synchronized? Without this the symplastic pathways between the cells will be disrupted as the individual walls slide past each other shearing off the plasmodesmata connections. Some evidence of this behaviour is apparent from the nastic movements observed during growth. These characteristic movements are a manifestation of asynchronous timing of wall extension events in the growing cell population.

In a field situation the attenuation of root length because of compaction may not result in a corresponding loss in crop yield and brings into focus the need to integrate the proposed model with a partitioning model (see Johnson *et al.* (1987)). Other modelling techniques (see, for example, Andrew (1987); Rose (1987)) may have an important supporting role to play in the further development of the present model. There is however the danger that such a wide ranging model may become almost as complicated as the real system itself.

Penetrometers with conical indenters of fixed proportions are frequently used to assess mechanical impedance to root growth. It has been shown that the apex of live roots change shape systematically when penetrating compact soil and fixed penetrometers are unable to reproduce this action. The cone index of such penetrometers seriously overestimate the actual root stresses (a factor of four was found by Eavis (1967)).

Such penetrometers are sensitive to soil strength and hence some correlation to root growth is possible. It would appear that improved variable geometry penetrometer techniques would have to be developed for a more precise assessment of root length attenuation.

The disparate models for various aspects controlling root growth presented cannot by themselves be considered as constituting a comprehensive mathematical description of soil-root interactions. However, it would appear that the major components of a general root extension model are now in place and careful experimental evaluation of many aspects of these would be required before a coherent and reliable predictive tool is evolved. The paper has highlighted the crucial role of a physical dimension in some plant physiological processes and the way ahead provides an exciting and challenging inter-disciplinary endeavour for engineers and scientists interested in this fascinating field.

I record my gratitude to both Dr A. R. Reece, for stimulating my interest in plant biomechanics and to Professor D. J. Greenwood for his encouragement and support that have helped me to sustain this interest.

REFERENCES

- Abdalla, A. M., Hettiaratchi, D. R. P. & Reece, A. R. 1969 The mechanics of root growth in granular media. *J. agric. Engng Res.* **14**, 236–248.
- Andrew, S. P. S. 1987 A mathematical model of root exploration and of grain fill with particular reference to winter wheat. *Fert. Res.* **11**, 267–281.
- Barley, K. P. 1962 The effects of mechanical stress on the growth of roots. *J. exp. Bot.* **13**, 95–110.
- Barley, K. P. 1963 The influence of soil strength on growth of roots. *Soil Sci.* **96**, 175–180.
- Bhuiyan, M. A. S. 1988 The mechanical behaviour of stabilised soils. Ph.D. thesis, University of Newcastle upon Tyne.
- Cleland, R. E. 1971 Cell wall extension. *Ann. Rev. Plant Physiol.* **22**, 197–222.
- Cosgrove, D. 1986 Biophysical control of plant cell growth. *Ann. Rev. Pl. Physiol.* **37**, 377–405.
- Eavis, B. W. 1967 Mechanical impedance and root growth. *Proc. agric. Engng Symp. Inst. Agric. Engng.* No. 4/F/39.
- Goss, M. J. 1977 Effects of mechanical impedance on root growth in barley (*Hordeum vulgare*). I. Effects on elongation & branching of seminal root axis. *J. exp. Bot.* **28**, 96–111.
- Greacen, E. L., Farrell, D. A. & Cockroft, B. 1968 Soil resistance to metal probes and plant roots. *Trans. 9th Int. Cong. Soil Sci.* **1**, 769–779.
- Hatibu, N. 1987 The mechanical behaviour of brittle agricultural soils. Ph.D. thesis, University of Newcastle upon Tyne.
- Hettiaratchi, D. R. P. 1987 A critical state soil mechanics model for agricultural soils. *Soil use Manag.* **3**, 94–105.
- Hettiaratchi, D. R. P. 1989 Critical state soil-machine mechanics. *Proc. Nordiske Jordbruksforskeres Forening Seminar No.* 165, 53–68. Oslo, Norway.
- Hettiaratchi, D. R. P. & Ferguson, C. A. 1973 Stress deformation behaviour of soil in root growth mechanics. *J. agric. Engng Res.* **18**, 309–320.
- Hettiaratchi, D. R. P. & O'Callaghan, J. R. 1974 A membrane model of plant cell extension. *J. theor. Biol.* **45**, 459–465.

- Hettiaratchi, D. R. P. & O'Callaghan, J. R. 1978 Structural mechanics of plant cells. *J. theor. Biol.* **74**, 235–257.
- Hettiaratchi, D. R. P. & O'Callaghan, J. R. 1980 Mechanical behaviour of agricultural soils. *J. agric. Engng Res.* **25**, 239–259.
- Hettiaratchi, D. R. P. & O'Callaghan, J. R. 1985 The mechanical behaviour of unsaturated soils. *Proc. Int. Conf. Soil Dynamics, Auburn U.S.A.* **2**, 266–281.
- Hogetsu, T. 1986 Orientation of wall microfibrils deposition in root cells of *Pisum sativum* L. var Alaska. *Pl. Cell Physiol.* **27**, 947–951.
- Jackson, M. B., Drew, M. C. & Giffard, S. C. 1981 Effects of applying ethylene to the root system of *Zea mays* on growth and nutrient concentration in relation to flooding tolerance. *Physiologia Pl.* **52**, 23–28.
- Johnson, I. R. & Thornley, J. H. M. 1987 A model of shoot: root partitioning with optimal growth. *Ann Bot.* **60**, 133–142.
- Ladanyi, B. 1963 Expansion of a cavity in saturated clay medium. *J. Soil Mech. Fdn Div., ASCE* **90** (SM4), 127–161.
- Liang, Y. 1985 Mohr-Coulomb parameters & soil indentation tests. Ph.D. thesis, University of Newcastle upon Tyne.
- Moss, G. I., Hall, K. C. & Jackson, M. B. 1988 Ethylene and the response of roots of maize (*Zea mays*) to physical impedance. *New Phytol.* **109**, 303–311.
- Nguyen, P. T. 1977 Mechanics of soil deformation in relation to root growth. Ph.D. thesis, University of Newcastle upon Tyne.
- Richards, B. G. & Greacen, E. L. 1986 Mechanical stresses in an elongating cylindrical root analogue in granular media. *Aust. J. Soil Res.* **24**, 393–404.
- Roelofsen, P. A. 1965 Ultrastructure of the wall in growing cells and its relation to the direction of growth. *Adv. bot. Res.* **2**, 69–149.
- Roscoe, K. H., Schofield, A. N. & Wroth, C. P. 1958 On the yielding of soils. *Geotechnique* **8**, 22–53.
- Rose, D. A. 1983 The description of the growth of root systems. *Pl. Soil* **75**, 404–415.
- Taiz, L. 1984 Plant cell expansion: regulation of cell wall mechanical properties. *Ann. Rev. Pl. Physiol.* **35**, 585–657.
- Veen, B. W. 1982 The influence of mechanical impedance on the growth of maize roots. *Pl. Soil* **66**, 101–109.
- Vesic, A. S. 1972 Expansion of cavities in infinite soil mass. *J. Soil Mech. Fdn Div., ASCE* **99**(SM3), 265–289.
- Wilson, A. J., Robards, A. W. & Goss, M. J. 1977 Effects of mechanical impedance on root growth in barley, *Hordeum vulgare* L. II effects of cell development in seminal roots. *J. exp. Bot.* **28**, 1216–1227.
- Wu, H., Spence, R. D. & Sharpe, P. J. H. 1988 Plant cell wall elasticity II: polymer elastic properties of the microfibrils.

ABBREVIATIONS AND SYMBOLS USED IN THE TEXT

- e void ratio of soil (space available for accommodating roots).
- N_p non-dimensional turgor pressure number. $N_p = p/[C(r^* - 1)]$, where C is the strain energy modulus of the cell wall material and r^* is the ratio of the external radius of the cell to its internal radius (see Hettiaratchi *et al.* 1978).
- p octahedral normal stress; cell turgor pressure; contact stress on outside of cell surface.

- q octahedral shear stress.
- α fibril angle with longitudinal direction of cell.
- η volumetric extension ratio (current cell volume/initial cell volume).
- λ axial extension ratio (current cell length/initial length).
- μ radial (diametral, circumferential) extension ratio (current cell radius/initial cell radius).

Discussion

M. J. Goss (*The Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen, U.K.*). In Dr Hettiaratchi's model, which provides a physical description of cell and root growth, if the stress confining the root is removed the rate of extension will immediately increase. This in fact does not happen (Goss & Russell 1980), but the roots elongate at a reduced rate until cells formed in the absence of stress begin to expand. Dr Hettiaratchi also appears to have concluded that the orientation of cellulose microfibrils within the cell wall changes as a result of the growth rather than their orientation being determined as they are laid down, which would be the conclusion from the experimental findings I quoted.

Reference

- Goss, M. J. & Russell, R. S. 1980 *J. exp. Bot.* **31**, 577–588.

D. R. P. HETTIARATCHI. The time lag between release of confining stress and resumption of root extension pointed out by Dr Goss is entirely compatible with the physical model described. Consider the scenario when the confining stress has virtually arrested axial root growth. The model predicts that in this condition a significant number (if not all) of the cells in the elongating zone of a root tip would have changed their growth polarity from axial to radial. These cells have arisen in the meristematic region with the microfibrils orientated transversely (see, for example Hogetsu (1986); Veen (1982)). As explained in §7 (*c, d*), the only way fully vacuolated cells in this mode can grow is by a change in geometry involving radial expansion associated with an increase in cell volume. During this process the transverse microfibrils ($\alpha = 90^\circ$) alter their inclination to a smaller value ($\alpha < 90^\circ$) and expansion will cease when the cell reaches its critical volume-change ratio appropriate to its initial fibril angle (see figure 9). At this point the microfibril inclination of these cells would have decreased to a value near 54° .

If at this stage the confining stress is released, then extension cannot resume immediately simply because there are no vacuolated cells programmed for axial extension (i.e. with $\alpha = 90^\circ$) in the elongation zone. Most of the cells that would normally contribute to axial extension have adverse fibrillar angles for axial extension. However, if the confining stress has not injured the meristematic region, cell division will recommence and cells with transverse fibrillar orientation will progress from the meristem and axial extension will re-start.

Additionally, the inner layers of the radially polarized cell walls may be at the stage where fresh transverse fibrils can be deposited (i.e. before lignification has set in). If the volumetric extension limit in these cells has not been reached some of these cells could revert partially to axial extension. The time lag of days cited by Dr Goss is probably an appropriate period for both mitotic and other biochemical activity to re-establish the full compliment of the next generation of cells programmed for axial extension. Thus normal axial extension rate can be regained only very gradually after the removal of confinement. The actual time lag to reach normal extension rates would depend on the level of confinement and the resulting degree of change imposed on the fibrillar arrangement of cells in the elongation zone.

It should be recalled that in the growth model proposed, the rate of influx of water into the extending cells is a crucial factor controlling cell extension (see §7(b)). The response to contact stimulus described in the paper (Goss & Russell 1980) can be explained on this basis. It is well known that the geotropic response is lost when a root is decapped. This fact provides strong evidence that the root cap is the organ that has central hormonal control of the necessary differential growth rates of the extending cells on diametrically opposite sides of a root. In all probability the chemical (auxin) responsible for this control traverses basipetally along the stele (that is at a more advanced stage of development in this region when compared with the cortex) to the appropriate site in the elongation zone. This chemical signal then either enhances the permeability of the walls of the cells on the side that will eventually form the outer radius of curvature of the root or alternatively inhibits influx rates on the cells on the opposite side. This response provides the differential growth rates required by a guidance system for 'steering' the root growth away from the axial direction. In the present context a reduction of flow rate is the more likely action. When the root cap is compressed symmetrically (as in the experiment referred to) the stimulation would signal a reduction of the water influx rate of all the elongating cells (not just on one side as would be the case when it is deflected asymmetrically by gravity) thus attenuating the overall axial extension rate. The model shows that growth rate reduction due to contact stimuli can be accounted for purely as an indirect effect of the chemical geotropic response signals emanating from the root cap.

J. A. HARRIS (*Environment and Industry Research Unit, Polytechnic of East London, Romford Road, U.K.*). In view of the changes occurring in plant cell wall architecture and composition during radial expansion of root cells in compacted cells, is there likely to be an increase in resistance to infection by potential mycorrhizal symbionts? If so, this could further exacerbate the problems in soils reinstated after civil engineering operations that tend to be both compacted and low in mycorrhizal inoculum potential. I would welcome your comments on this please.

D. R. P. HETTIARATCHI. Dr Harris has raised a pertinent point regarding the effect of mechanical impedance on root growth that the paper has not dealt with directly. The changes taking place in a stressed root are more likely to influence endotrophic mycorrhiza because their hyphae have to invade the intercellular space and even penetrate the walls of the root cells.

Two aspects of the behaviour predicted by the model are thus relevant to this question. In the first place the inter-cellular regions at the ends of the root cells will be under compressive loading and if the cells have polarized into the radial growth phase then the side walls too will be under compression. Under these conditions the fungal hyphae may have difficulty in invading the interior of the root as these filaments too will have to overcome considerable mechanical confinement. The hyphae may, however, be still capable of entering the root via root hair cells or in regions closer to the meristem where radial growth polarization is not significant and thus entry is not restricted along the longitudinal wall spaces lying on the epidermis of the root. Once the hyphae have entered the root by these routes they will still be faced with the problems of invading the apoplast which is under compression.

The second consideration concerns the changes in fibrillar arrangement and its effect on the invasion of the fungus into the root cells. If the hyphae have overcome the confinement of the apoplast then changes in fibril arrangement of the walls themselves cannot provide a higher resistance to penetration than that encountered in an unstressed cell. The general conclusion therefore is that mechanically confined roots will be more resistant to invasion and will prove to be an inhospitable host for the endotrophic mycorrhiza. Dr Harris' conjecture that there could be a reduction in the contribution made by symbiotic mycorrhiza in plants growing in reinstated compact soils would appear to be correct.

P. H. NYE (*Department of Plant Sciences, University of Oxford, U.K.*). We can now predict the uptake of nutrients by a plant from a given soil quite accurately if we know how its roots are distributed. What can soil mechanics experts tell us about the way root patterns will develop?

D. R. P. HETTIARATCHI. The question raised by Professor Nye highlights the disparity in the state of development between transport models and root growth models, the latter being still way behind the former. The paper has dealt with the two individual mathematical models that quantify changes in pore space (critical state model) and the mechanics of root extension within the available pore space (biomechanical model). The next logical step is to conflate these into a unified model that should have the capacity to predict the extension of a single root axis as a function of the relevant soil properties. However, even this model takes no account of (i) the initiation of laterals; (ii) the way plants partition resources between root and shoot (see §9); (iii) the spatial variation of the relevant parameters in the soil, and (iv) the transport of moisture and nutrients to the root. Evidently all

these factors control the development of root distribution patterns and must be built into the model.

Soil mechanics theory can make a small contribution to (i). A mechanical reason for the initiation of lateral roots has been advanced by Goss & Russell† (1980). They have shown that lateral roots usually break out from the pericycle at sites where the root surface is subjected to a tensile stretching. This results primarily from the buckling of the root and arises when the soil support is inadequate to restrain the bending of the root. This situation could be included in the unified model, but would require a deviation from the basic assumption that the soil is an isotropic continuum.

The influence of the moisture regime in the soil is taken care of in the biomechanical model in that any water stress will result in growth attenuation. Once again these effects can be included only if the spatial variation of these factors can be mapped. In general it would appear that a comprehensive root branching model must await advances in the incorporation of the four points set out earlier into the present model that deals with the growth of a single root axis under ideal and greatly simplified conditions.

Reference

Goss, M. J. & Russell, R. S. 1980 *J. exp. Bot.* **31**, 577–588.

K. A. SMITH. (*Edinburgh School of Agriculture, U.K.*). Dr Hettiaratchi has put forward an explanation of how an individual root axis responds to, and overcomes, resistance to extensive growth. However, I wonder how we can go beyond this to predict the quantitative effects on the size and shape of the root system. A major factor may be the occurrence of remote effects, for example, if the extension of a root axis is inhibited this generally stimulates the growth of lateral roots, and the quantitative effects may vary between species and varieties. I'd like to have comments on this aspect.

D. R. P. HETTIARATCHI. Some of the points raised by Dr Smith have been dealt with in the answer to Professor Nye's question. The paper has dealt with two

basic components of a root growth model which, as Dr Smith correctly points out, only deals with the extension of a single root axis. There is no doubt that the remote effects mentioned by Dr Smith will govern the development of the root system as a whole and the present model has not addressed this problem nor has it taken into account the influence of partitioning of resources between root and shoot (see §9). The complete model for the development of the entire root system will have to take into account the spatial variation of moisture, nutrient, pore space and the presence of pre-existing cracks and earthworm holes. To build these parameters into an overall model it would be necessary to develop sub-models that can quantify these variations and it would appear that at our current state of knowledge these models have not yet been perfected.

The model for the extension of individual root axes is probably not species dependent in that basic mechanisms operating in the model are common to all subterranean roots (e.g. fibril arrangement, peak turgor pressure, cell-wall permeability and root architecture). However the development of the entire root system is clearly species dependent and could quite possibly differ between varieties of the same plant. This would therefore be an additional factor to take into account in building a model to predict the development of root systems. The present indications are that such a model would be too complicated to construct. What the present model can predict is the performance of individual parts of the system. It could, for example, predict whether the root axes can extend and if it can, the rate at which it will do this and the influence localized parameters (soil pore space, moisture and nutrient availability etc.) will have on this process. If, as pointed out by Dr Smith, inhibition of root extension stimulates break out of laterals then the model can be applied to ascertain whether these laterals could proliferate through the soil. The model is only a clear starting point and can thus give only very general indications as to whether a root system will propagate but, unfortunately, it cannot predict how the overall system will develop.