GENERATION OF SOIL STRUCTURE BY PLANT ROOTS

Thesis submitted for the degree of
Doctor of Philosophy
in
The University of Adelaide
Faculty of Agricultural and Natural Resource Sciences

by

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April 1993

This thesis is dedicated to the memory of my parents, ***Albert and Selina.***

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ABSTRACT

The work reported in this thesis was carried out to study the processes involved in the generation and/or modification of soil structure by plant roots. Two aspects of root activities considered to be important in generation of soil structure were studied: firstly, the formation of biopores as roots penetrate the soil and secondly, the formation of aggregates by roots. Plant species were compared for the ability of their roots to influence these processes.

(i) Penetration of roots into strong soil

Plant roots cannot be expected to ameliorate soil if they cannot penetrate the soil. The first step in the project was to develop techniques for identifying species with the desired properties for penetration. To this end, two laboratory methods were developed. The methods applied either mechanical or osmotic stress to the roots. The mechanical stress method involved growing seedlings of dicotyledonous and monocotyledonous species in compression chambers. The chambers were filled with fine siliceous sand at 0.2 kg kg^{-1} water content and subjected to forces which produced an external mechanical stress on the roots of 1.14 MPa. In the osmotic stress method, the seedlings were grown in the same sand which was wetted with solutions of poly (ethylene glycol) to give osmotic potentials of 0.0, -0.25, -0.5 and -1.0 MPa. In both methods, plants were fed with nutrient solution and responses of the roots (elongation and diameter) to the stresses were measured.

The results showed that both methods of stress significantly reduced the elongation and increased the diameter of roots compared with those plants grown in unstressed conditions. Differences in both elongation and diameter were observed among the species. Generally, the roots of dicotyledons (with large diameters) elongated more under stress than monocotyledons (with small diameters). There were positive correlations between root diameter and elongation over all the species grown under stressed conditions. This finding lead to the hypothesis that the tendency of the roots to thicken under stress might influence their ability to penetrate strong soil. This hypothesis was investigated in a field study which also tested the accuracy of the laboratory methods in predicting field perfomance of roots.

The field study involved eight species which were selected with the two methods of stress described above. The plants were grown in micro-plots (2 x 2 m) on a red-brown earth which had a compact and strong subsoil (mean penetrometer resistance 3.0 MPa, bulk density 1.8 Mg m^{-3} at 0.81 times the

plastic limit) at the 0.1-0.3 m depth. Soil tilled to a depth of 0.3 m to reduce mechanical resistance was sown with the same species to serve as a control. Root penetration and density in the soils were measured by the core-break method. Results showed that the strong subsoil reduced the elongation of roots and that diameters of root tips were larger than those from uncompacted soil. A higher proportion of thicker roots (mostly dicotyledonous species) penetrated the strong soil layer than thinner roots (mostly monocotyledons). This result is consistent with theories on mechanics of root growth in strong media. Root diameter affects the mode of soil deformation and maximum pressures exerted on the soil by the root. A comparison of the two methods of stressing the roots showed that the method involving mechanical stress was a better predictor of the field performance of roots than that involving osmotic stress.

The influence of root growth on the physical properties of the soils was investigated by measuring sorptivity to water, size, stability and tensile strength of aggregates collected from the soils. The results showed that the water sorptivity of soils which had been planted to dicotyledonous species were generally higher than those with monocotyledons. This was attributed to bigger biopores which the roots of the dicotyledonous species might have made through the compact subsoil. Species varied in their effects on other properties of the soil. Ryegrass for example, was good at stabilising aggregates but was not good at penetration. Safflower, on the other hand, was good at penetrating compacted soil but was not good at stabilising aggregates. It was concluded that a programme aimed at improving soil structure by plant roots should involve a matching combination of species with different abilities and that breeding programmes should aim at producing species with a combination of the desired characteristics. This work has lead to the development of simple, and rapid techniques of screening large numbers of species for the ability of their roots to penetrate strong soil.

(ii) Formation of aggregates by plant roots

Laboratory studies were undertaken to study the mechanisms and processes of aggregation by plant roots in soils with different degraded structural conditions. In the first experiment, roots of three species (pea, ryegrass and wheat) were grown through 15 wetting and drying cycles in two soils whose macro structure was destroyed by crushing. The soils were a swelling black earth (67% clay) and a non-swelling red-brown earth (19% clay). Measurements of aggregation and properties of aggregates (2-4 mm) showed that the amount of clay in a soil, the degree of wetting and drying and root

length density all had significant influences on the sizes of the aggregates formed, and on their tensile strength and stability. It was concluded that cracking of soil and compression of aggregates by stresses generated as a result of water extraction by plant roots were the main mechanisms responsible for the formation and strength of aggregates in homogenised soils.

The other experiment in this series was done by growing the three species through beds of coarse artificial aggregates (18-21 mm). The aggregates were made from the surface soil of the red-brown earth and were mechanically strengthened by adding 1% poly (vinyl alcohol). Plants were grown through 15 wetting and drying cycles. Results showed that ryegrass significantly increased the proportion of smaller sized aggregates (< 18 mm) more than pea and wheat. This was mainly done through breakdown of the large aggregates by roots which had penetrated the coarse aggregates. The presence of roots in the aggregates had physically strengthened them compared with the control soil. Wetting and drying cycles produced stronger aggregates than soil which was kept wet continuously.

The findings from this work have shown that plant species differ in the ability of their roots to penetrate compacted soils. The two laboratory screening techniques developed in the study were in good agreement with results of field penetration test. The techniques could assist in identfying and selecting species with greatest potential for use as biological ploughs. Biopores which remain after the roots have decayed can have significant influence on the movement of water through the compact soil layer.

STATEMENT

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

SIGNED: DATE: 3rd May, 1993

ACKNOWLEDGEMENTS

I would like to thank my supervisors, Dr A M Alston (Department of Soil Science, Waite Agricultural Research Institute, University of Adelaide), Dr J M Kirby (CSIRO Division of Soils, Canberra) and Dr A R Dexter (Silsoe Research Institute, Silsoe, UK) for their helpful discussion and direction in all aspects of my research program.

I thank Mr P T Brown (Department of Soil Science) who produced most of the diagrams for this thesis. He also provided me invaluable computer assistance and help in the laboratory throughout my program. Thanks also go to Ms L Giles (Biometry Section) who helped in the analyses of the data for different sections of the thesis. The photographs in this thesis were taken by Mr A Dunbar and Ms J Groom (ETU, University of Adelaide) to whom I am indebted.

I am grateful to the following people and organisations who supplied me with seeds: Mr R S Norton, Dr R Knight and Mr S Khan (Waite Agricultural Research Institute); Hodder and Tolley Pty Ltd of Toowoomba, Queensland; Ms S Greenhalgh of the Agricultural Research Centre, Trangie, New South Wales; and Mr R E Holloway of the South Australian Department of Primary Industries. I would also like to thank Mr T W Ellis (Department of Agricultral Technology, University of Adelaide) for allowing me to use his experimental site for some of my study. He also assisted me in the field. I particularly acknowledge his help in operating the gantry during the extraction of cores for root penetration measurements. Mr C T Hignett (CSIRO Division of Soils, Adelaide) helped in the measurement of root length densities and also supplied me with root sampling frames for the field measurements.

I wish to thank Dr B P Naidu (Department of Crop Protection, University of Adelaide) for his help in measuring the osmotic potential of the poly (ethylene glycol) solutions used in my research. I also thank many other people in the University for the help they gave me in one way or another, in particular, Dr R S Murray, Dr G K McDonald, Dr C D Grant, Mr C Rivers, Mr E Mapfumo, Mr S Sedaghatpour and Mrs J Ditchfield.

I am grateful to the Australian International Development Assistance Bureau (AIDAB) for financial support in a form of a scholarship which enabled me to study in Australia. I also thank the University of Malawi for granting study leave.

I would like to offer special gratitude to my wife Ellen and children (Dalitso, Fenji and Robert) for their patience and support during the entire study period.

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PUBLICATIONS FROM THE THESIS

(a) Refereed articles

1. Materechera S A, Dexter A R and Alston A M 1991 Penetration of very strong soil by seedling roots of different plant species. *Plant and Soil* **135,** 21-31.

2. Materechera S A , Dexter A R and Alston A M 1992 Formation of aggregates by plant roots in homogenised soils. *Plant and Soil* **142,** 21-31.

3. Materechera S A, Dexter A R, Alston A M and Kirby J M 1992 Growth of seedling roots in response to external osmotic stress by polyethylene glycol 20,000. *Plant and Soil* **143,** 85-91.

4. Materechera S A, Alston A M, Kirby J M and Dexter A R 1992 Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil* **144,** 297-30.

5. Materechera S A, Alston A M, Kirby J M and Dexter A R 1993 Field evaluation of laboratory techniques for predicting the ability of roots to penetrate strong soil and of the influence of roots on water sorptivity. *Plant and Soil* **149,** 149-158.

Submitted

6. Materechera S A, Kirby J M, Alston A M, and Dexter A R 1993 Modification of soil aggregation by roots growing through beds of coarse aggregates. *Plant and Soil* (Submitted).

(b) Conference poster

7. Materechera S A, Alston A M and Kirby J M 1992 Penetration of compact sub-soil by plant roots. Poster presented at the 5th Australian National Soil Science Conference, Adelade, Australia, 19-23 April, 1992.

SECTION 1

Introduction

Soil structure is an important property of soil because it influences not only the physical conditions (aeration, heat and water economy, and soil mechanical impedance) but also microbial decomposition of organic matter and availability of plant nutrients (Hamblin, 1985). The importance of soil structure is not only in relation to agricultural production but it also controls aspects of pollution and energy requirements for tillage among other factors. Soil structure has been characterised as the major indirect and direct physical factor affecting the soil environment and limiting the productivity of soils (Russell, 1971). However, evidence from many parts of the world shows that soil structure and its stability are becoming increasingly less favourable for crop growth (*e.g.* Boels *et al.*, 1982; Lal and Stewart, 1990). The consequences of this for crop production and for the environment in general can be catastrophic.

The fundamental problem in management of soil structure is concerned with the creation and stabilisation of structural features (Dexter, 1989). Development and adoption of viable management systems capable of regenerating and improving the structure of degraded soils are now urgently required. Different physical, chemical and biological processes are responsible for the formation and stabilisation of the different structural units. Plant roots are among the most important factors that play major roles in modifying soil structure. Generation of soil structure in soil can be influenced by two aspects of root growth. Firstly, the formation of continuous vertically oriented pores as the roots penetrate the soil would be of major importance for both drainage and crop growth. Secondly, the interactions of roots and soil can influence aggregation of the soil. While the roles of plant roots in creating various soil structural features has long been realised, the mechanisms involved have not been fully understood or quantified.

The trend towards use of heavier farm and tillage equipment and vehicular traffic on agricultural land has increased not only the severity, but also the depth to which soil compaction occurs (Håkansson, 1982; Håkansson *et al.*, 1987). Compaction of soil below the normal depth of tillage is of increasing concern because of its persistence and effects on plant growth and yield (Gaultney *et al.*, 1982; Johnson *et al.*, 1990; Logsdon *et al.*, 1992; Oussible *et al.*, 1992; Voorhees, 1992; Voorhees *et al.*, 1986). The causes and effects of mechanical resistance in the subsoil have been well documented. What is

required now are ways of alleviating subsoil compaction with minimum cost. The use of plant species whose roots have superior ability to penetrate strong soil is an attractive approach (Dexter, 1991; Elkins, *et al.*, 1977; Goss, 1987). The idea is to produce channels through the strong soil by using roots. When the roots that have penetrated subsequently decay, they leave behind biopores. These biopores may be important for improving the structure of soil for drainage and the growth of subsequent crops. This phenomenon has been referred to colloquially as "biological ploughing" (Elkins, 1985; Heinonen, 1986; Henderson, 1989).

Although various researchers have investigated root penetration in strong soils, little work has been done to compare the ability of different plant species to penetrate soils of very high strength. Root elongation at high strengths, although slow, can be important for soil reclamation and ameliorative purposes. To use plant roots for creating biopores in strong soil however requires an understanding of the mechanisms which roots use to penetrate soils with high mechanical impedance. The understanding of the mechanisms might lead to the introduction of methods for rapid screening of species for the ability of their roots to penetrate strong soil. Apart from showing that the process of biological tillage does occur, there is need to establish the specific beneficial effects of this process on the soil.

The roles of plant roots in the formation of aggregates, although known broadly, has not been quantitatively described. There is need to understand the processes of soil aggregate formation by plant roots in soils of different initial degraded conditions. In this way, a better understanding of the dynamics of structural change in soils can be gained. Information on these aspects of regenerating soil structure is crucial if we are to be able to use and develop the activities of roots to improve soils.

The series of experiments reported in this thesis was designed to answer some specific questions relating to the generation and/or modification of soil structure by plant roots under different soil and climatic conditions. The general objectives of the study were to obtain a detailed quantitative understanding of the processes of soil structure generation by plant roots in different soil types and to compare the ameliorative ability of different plant species on structure. The specific objectives were:

1. to investigate the mechanisms of root penetration in strong soil and develop simple laboratory methods for screening and selecting plants for the ability of their roots to penetrate strong soil,

2. to compare the abilities of roots of different plant species to penetrate and ameliorate compact sub-soil in the field, and

3. to study the processes involved in the formation of soil aggregates by plant roots in soils with different initial degraded conditions.

SECTION 2

Literature Review

2.1 Introduction

The literature reviewed in this section forms the background for the studies undertaken in this thesis. The review outlines the general aspects of root growth which have influence on soil structure. To understand how roots generate soil structure we need to know what soil structure is, the ways it develops, how roots grow in soil and why sometimes they do not, and how roots influence structure. Each of these topics will be considered in turn in this section.

2.2 Definition and characterisation of soil structure

The term soil structure has several meanings in the agronomic, engineering, soil mechanics and soil science literature. Consequently, definitions of what constitutes soil structure are numerous and can sometimes be vague. It appears (Table 2.1) that any definition considers three aspects: the size distribution of primary particles, their spatial arrangement into aggregates of various sizes and the voids that result, and the stability of the aggregated state. The definition of Dexter (1988a) accommodates the many different aspects of soil structure which exist at many different size scales in the soil (Fig. 2.1). The advantage of this definition is that it is valid for the arrangement of colloidal clay particles in a floccule, for the arrangement of clods in a tilled soil, for the array of root and earthworm channels in an untilled stratum of the soil, and for the variability of soil strength in a compacted layer. This is an all-embracing definition of soil structure and will be used in this thesis.

Hadas (1987) considered the development of a conceptual framework that emphasizes the hierarchical nature of soil structure. In this concept, the lowest hierarchical order is the combination of single mineral particles such as a floccule or domain of clay plates. The next hierarchical order is larger compound particles such as clusters of domains. The next hierarchical order is when a number of clusters are combined into microaggregates, and so on as illustrated in Fig. 2.2. Although not all of these hierarchical orders exist in all soils, "good" soil structure is described as one where all the hierarchical orders are well-developed and stable (Dexter, 1988a). This concept is a powerful one and is consistent with the view of micro-aggregates as the units from which

clods in arable soils are built (Oades and Waters, 1991). This concept of soil structure helps us to gain additional insights on the importance of soil structure and its relation with other physical factors, tillage, organic matter and root growth.

Table 2.1 Some definitions of soil structure obtained from literature.

Brewer and Sleeman (1960):
The physical constitution of a soil material as expressed by the size, shape, arrangement and degree of development of the primary soil particles and voids into naturally or artificially formed structural units.
Dexter (1988a):
The spatial heterogeneity of the different components or properties of the soil.
Hillel (1980):
The arrangement and organisation of the particles in the soil.
Marshall (1962):
The arrangement of the soil particles and of the pore space between them. It includes the size, shape and arrangement of the aggregates formed when primary particles are clustered together into larger separable units.
Soil Survey Staff (1975):
The aggregation of primary soil particles into compound particles or clusters of primary particles which are separated from adjoining aggregates by surfaces of weakness.

As stated previously, the range in sizes of the features involved in soil structural hierarchy is large. This means that a wide range of methods exist for measuring and interpreting data on soil structure (Letey, 1991). The method used depends mostly on the purpose and relevance of the measured parameters to the investigation. The different methods of measuring soil structure have been presented in several publications (*e.g.* Brewer and Sleeman, 1988; Dexter, 1988a; Larionov, 1982) and will not be further reviewed here. We now turn our attention to the ways soil structure develops.

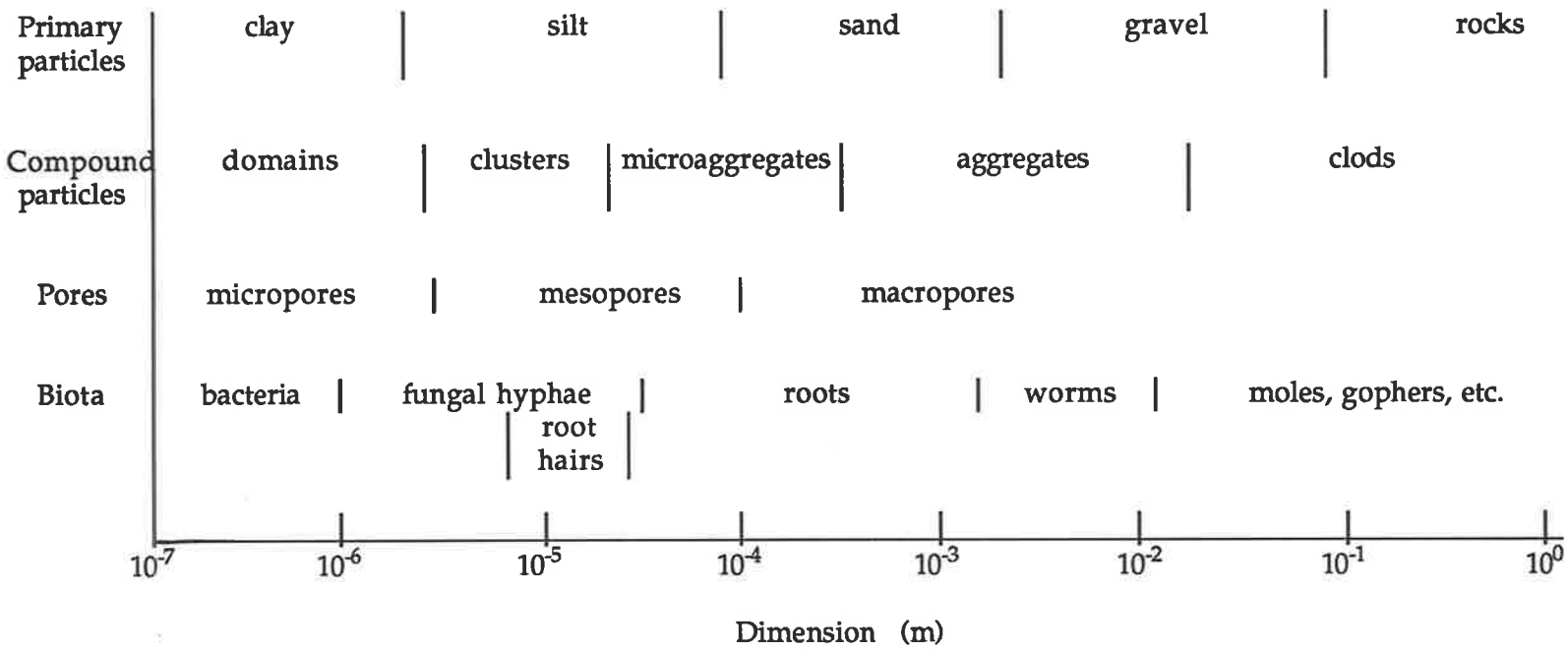


Fig. 2.1 Approximate dimensions or typical diameters of common soil structural features. Some primary particles and pores may be two orders of magnitude smaller than shown (re-drawn from Dexter, 1988a).

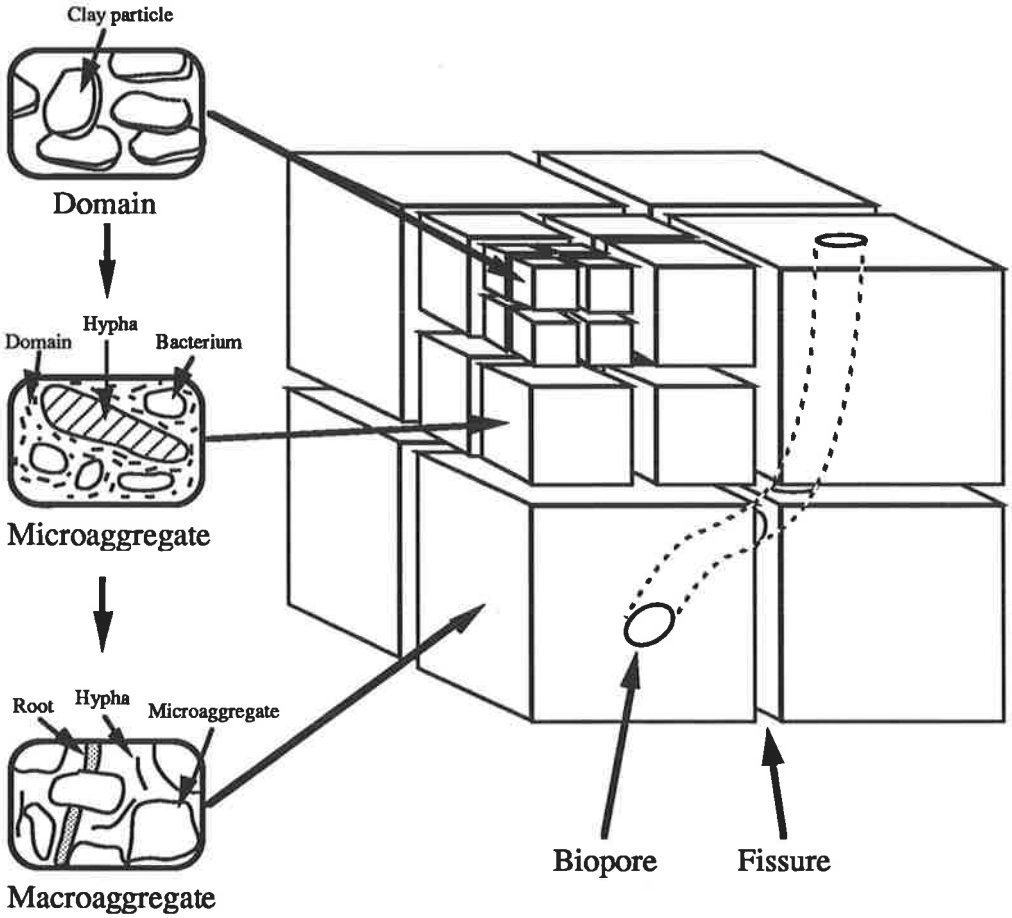


Fig. 2.2 Diagramatic representation of the hierarchical organisation of soil particles and soil structural elements (re-drawn from the cover of the *Aust. J. Soil Res.*, Vol. **29** (6), 1991.

2.2.1 *Formation of Soil Structure*

In agricultural soils, structural features of a given size order may be produced either by the combination of structural elements of lower hierarchical order or by the fragmentation of structural elements of higher hierarchical order. These have been referred to as 'combination' and 'fragmentation' processes respectively (Dexter, 1988a). Different factors are responsible for creating soil structure through these processes. However, since the interest in this thesis is on the roles of plant roots in influencing these processes, only those processes which are affected by plant roots will be reviewed. In the past, much attention has been given to the study of the biological roles of roots in the stabilisation of soil structure (*e.g.* Allison, 1968; Harris *et al.*, 1966; Martin *et al.*, 1955). Somewhat less attention seems to have

been given to the physical roles of roots in the creation of structure. Before discussing the roles of plant roots in creating soil structure, it is worthwhile to review the general characteristics and functions of plant roots.

2.3 Plant roots

2.3.1 *Characteristics of plant roots*

Although variable in size, the general structure of root apices is broadly similar in all flowering plants (Russell, 1977). A typical structure of a growing root tip is shown diagramatically in Fig. 2.3.

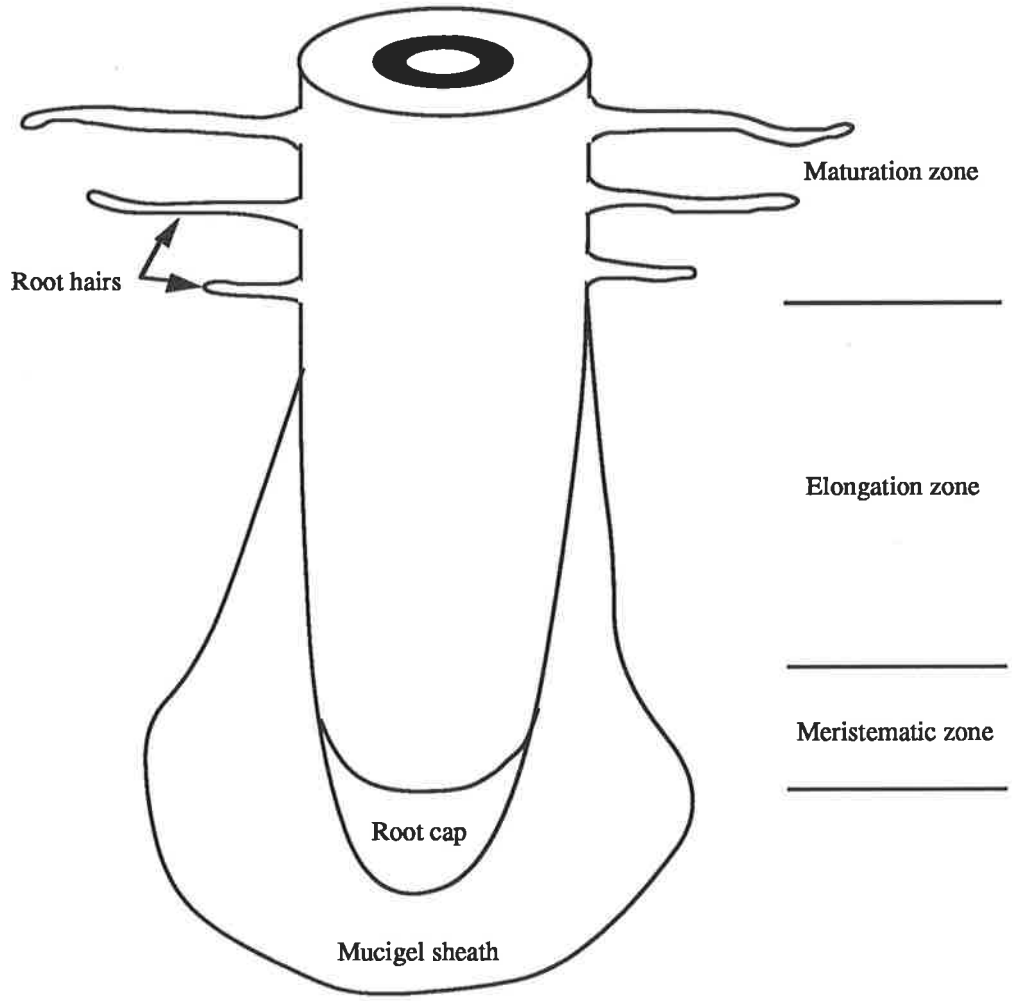


Fig. 2.3. Diagramatic longitudinal section of apical zone of a plant root. Not drawn to scale. (adapted from Russell, 1977).

In the apical meristem, cell division occurs both away from and towards the base of the root giving rise respectively to the root cap and to new root cells. A gelatinous non-cellular material, the mucilage, surrounds the root

and especially the cap. The cells formed in the apical meristem, from which the new tissues of the root itself develop, elongate and differentiate. Behind the region of elongation, the root is covered by root hairs. These originate as protuberances from epidermal cells. The root hairs appear a few millimeters behind the root apex and help in anchoring young roots in the soil. Root hairs enhance the uptake of those nutrients which have relatively low mobility in soils (Drew and Nye, 1969; Itoh and Barber, 1983; Misra *et al.*, 1988a).

2.3.2 *Functions of roots*

Roots perform a variety of functions for the plant. Roots absorb the water and nutrients required to satisfy the plant's demand. Water absorption by roots can lead to the soil undergoing several series of wetting and drying cycles during a season. The roots also provide anchorage to keep the plant from being washed or blown away or being toppled by wind and water. Anchorage is also necessary for the shoot to emerge through soil crusts or for roots to force a path through the soil.

Fleshy roots especially of dicotyledonous plants such as sugar beet, radish and turnip serve as storage reservoirs for starches, sugars and proteins in their pith or cortex. Another important role of roots is the release (both active and passive) of organic and inorganic materials from roots into the soil. The release of these materials may occur through a variety of mechanisms including secretion, leakage, autolysis and the sloughing of cells from the root (Barber and Martin, 1976). Carbohydrates, such as polysaccharides, released by plant roots are important materials as they are the main agents for stabilising soil aggregates (Habib *et al.*, 1990; Tisdall and Oades, 1979).

2.3.3 *Classification of root systems*

Root systems are classified as fibrous-rooted or tap-rooted, depending upon the size and number of the individual roots as well as their origin (Klepper, 1987). Monocotyledonous plants, such as cereals and grasses, tend to have fibrous root systems and dicotyledonous plants, such as legumes, tend to have taprooted systems. In fibrous root systems, seminal roots develop from the germinated seed. When the growth of the seminal roots is underway, adventitious or nodal roots develop from from the basal nodes of the stem. Lateral roots develop from both the seminal and adventitious roots. In taprooted plants on the other hand, the radicle emerges from the seed and develops into a primary root that is positively geotropic. Subordinate branches (secondary roots) arise from the primary roots and explore the soil to the sides of the primary root. A diagramatic illustration of the differences in

the structure of the two root systems is given in Fig. 2.4. For a detailed discussion on the origin, branching and distribution of root systems, Klepper (1987; 1992) should be consulted.

Roots have also been classified according to their diameter by Böhm (1979) as follows; very fine (< 0.5 mm), fine (0.5 to 2 mm), small (2 to 5 mm), medium (5 to 10 mm), large (10 to 20 mm) and very large (> 20 mm).

2.3.4 *Mechanical properties of roots*

The mechanical properties of roots are important when considering mechanical impedance and the mechanisms of root growth through compact soils. These will now be outlined briefly here.

Root tensile strength. Abe and Iwamato (1986) reported that the tensile strength of living roots of *Cryptomeria japonica*, increased with root diameter. Gliński and Lipiec (1990) quoted the tensile strength for grass roots to be 3 to 10 MPa and that of forest tree roots to be 10 to 70 MPa.

Root growth pressure. Roots are capable of exerting pressure both in the axial and radial directions. The measurement of maximum axial and radial root growth pressures dates back to Pfeffer in 1893 (Gill and Bolt, 1955). Since then the principles upon which the measurement techniques are based have not changed much although the techniques themselves have improved (Misra *et al.*, 1986a). Table 2.2 summarises the data on maximum root growth pressures available from literature.

Misra *et al.* (1986a) have shown that the pressure which a root can exert is dependent on its diameter. The size dependency of root pressure would reduce the ability of smaller compared with larger diameter roots to penetrate soil. It would also provide a mechanism whereby roots could gain additional benefit from radial enlargement in soil of high strength. This aspect of root growth is investigated and discussed in Section 4.0.

Root buckling stress. When a root is stressed axially, it may buckle. The buckling stress is defined as the maximum stress which a root can resist without buckling (Whiteley *et al.*, 1982). The forces required to buckle root tips growing across air gaps were measured by Whiteley *et al.* (1982). The buckling stress decreased as the size of the air gap increased, but attempts to predict the buckling stress from the elastic modulus of the tip were only partly successful. In general, buckling will limit root penetration into a soil aggregate if the buckling stress is smaller than the maximum presssure that a root can exert.

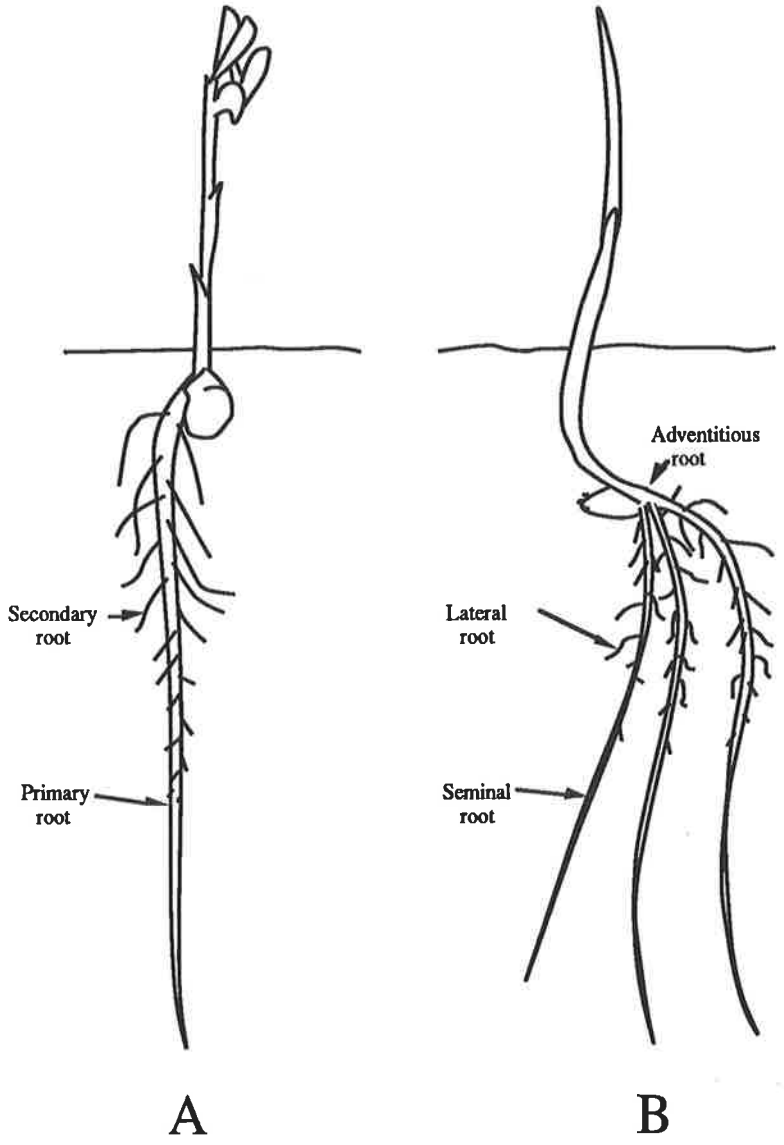


Fig. 2.4 The essential structures of (A) dicotyledonous and (B) monocotyledonous root systems (re-drawn from Bekendam and Grob, 1979).

Elasticity of root tips. Whiteley and Dexter (1981a) characterised root elasticity of 16 crop species using Young's modulus (the ratio between stress or applied pressure and the resulting linear deformation). The response was non-linear. Two parameters α and β, which account for the non-linearity were used to interpret the results. Values of the effective moduli ranged between 5 and 100 MPa for fully turgid roots. The parameter α ranged from 3.2 to 1.4 and β ranged from 1.1 to 0.7 showing that there were significant inter-species differences in the elastic properties of roots. Environmental factors

such as soil water potential and nutrition had significant influences on the elasticity of roots.

Table 2.2 Maximum axial and radial root growth pressures reported in literature.

Reference	Plant species used	Pressure	Range pressure (kPa)	Mean Pressure (kPa)
Pfeffer (1893, cited by * below)	*Faba vulgaris*	axial	704-1936	1082
Gill & Bolt (1955)*	*Faba vulgaris*	radial	390-611	509
	Zea mays	axial	953-2494	1451
	Zea mays	radial	n/a	659
	Vicia sativa	axial	826-1333	1080
Taylor & Ratliff (1969)	*Pisum sativum*	axial	600-2600	1300
	Gossypium hirsutum	axial	600-1600	940
	Arachis hypogea	axial	500-2000	1150
Eavis *et al.* (1969)	*Pisum sativum*	axial	700-1600	290
	Gossypium hirsutum	axial	400-1300	888
Aggarwal & Prihar (1975)	*Cicer arietinum*	axial	n/a	450
	Zea mays	axial	n/a	1090
Misra *et al.* (1986a)	*Pisum sativum*	axial	n/a	497
		radial	n/a	900
	Gossypium hirsutum	axial	n/a	289
	Helianthus annuus	axial	n/a	238

n/a = data not available

The mechanical properties of roots discussed above have been used to produce a stochastic model for the behaviour of root tips in structured soils (*e.g.* Dexter, 1978; Hewitt and Dexter, 1979). These models have provided useful information on the effect of soil structure and strength on root environment and behaviour. The properties may also be important in explaining the differences in the abilities of roots of different plant species to penetrate strong soil as discussed in Section 2.6.4.

2.4 Root growth

Geometrically, the root system is a set of filaments, the length of which is increased by the elongation and branching of its components. A simulation model of the growth of the root system was described by Lungley (1973). The rate of root growth varies widely among species and soil conditions. The

growth rate also depends on the type of roots within a given plant (Kramer, 1983).

2.4.1 Mechanics of root growth

Growth of a root is a consequence of the production of new cells by the apical meristem and from cell enlargement. Turgor pressure drives cell enlargement and hence elongation of the root. A plant root has been considered as a collection of cells each acting as an ideal osmometer. Simple models have been proposed to describe the physical parameters that regulate the expansion of cells in roots. These models consider the expansion of a cell as a yielding of the cell wall under the action of tensile stresses in the cell wall. Thus, elasticity of individual cell walls have been studied from the point of view of cell growth (Cleland, 1971; Green *et al.*, 1971; Heyn, 1940; Lockhart, 1965). Green *et al.* (1971) have expressed the rate of volumetric growth of a plant cell (R) as

$$R = \varphi (P - Y) \qquad [2.1]$$

where φ is the wall extensibility, P is the turgor pressure and Y is a yield threshold. According to this formula, growth rate is a function of a stress (turgor pressure) and the rheological properties of the cell wall. However, for the case of a root tip growing through soil, cell growth is also affected by the physical environment and this becomes particularly important where soil water potential and the mechanical resistance of the soil to deformation become rate controlling factors. In this case, the hydrostatic (turgor) pressure, P, within the cell vacuole is opposed by the wall pressure, W, and the pressure applied externally by the soil, σ_n, which arises as a reaction of the soil to deformation by the root. The pressure balance at the cell wall may thus be written as

$$P + W + \sigma_n = 0 \qquad [2.2]$$

The relationship between the rate of root elongation and wall pressure has therefore been expressed by Greacen and Oh (1972) as

$$R = m\ (W - W_c) \qquad [2.3]$$

where m is the extensibility of the cell wall material of the root and W_c is the threshold value of wall stress for cell elongation. This equation was used in

the model of Dexter (1987b), who expressed the rate of root elongation (R) by considering the cell wall pressure as a balance between the total internal water potential ($|\Psi_i|$) and the total external water potential of the cell ($|\Psi_o|$)

$$R = m\,(|\Psi_i| - |\Psi_o| - W_c - \sigma_n) \qquad [2.4]$$

where R is the elongation of a single cell. The elongation is applicable to the concerted efforts of all cells in the elongation zone. For elongating cells, σ_n denotes the pressure required for soil deformation.

Greacen and Oh (1972) have found that the relationship of Equation 2.3 held true regardless of whether W was limited by the confining pressure of the soil (σ_n) or by the soil water potential (Ψ_o). This led them to test the osmoregulating efficiency of pea roots against the total water potential and mechanical resistance of soil. The term osmoregulation refers to adjustments of the internal osmotic potential of the plant cell contents. They found that osmoregulation in pea roots was 100% efficient against water potential down to -1500 kPa, but was only 70% efficient against external mechanical stress on roots. They proposed that the model of Equation 2.3 may describe a mechanism which controls growth and distribution of roots in the soil.

In contrast, Russell and Goss (1974) and Goss (1977) have argued that the elongation rate of roots is so sensitive to very low pressures applied to soil in triaxial cells in which the roots are growing, that a simple physical model is not feasible, and that hormonal control is involved. Richards and Greacen (1986), Hettiaratchi (1990) and Bengough and Mullins (1990b) have countered by pointing out that the resistance actually experienced by such roots is much greater than that applied to the cell, so that a physical model of root growth into strong soil may not be ruled out by the apparent sensitivity of the roots to small confining pressures.

2.4.2 *Root growth in homogenous media*

A plant root extending through a homogeneous soil medium must deform or displace the soil to create the cavity in which to grow. In a rigid soil matrix, the diameter of a root determines the maximum pore size through which a root can grow. In a study of root growth through porous sinters, Wiersum (1957) concluded that elongating roots were unable to decrease in thickness to penetrate small rigid pores. In contrast, Scholefield and Hall (1985) reported that roots of grasses were capable of penetrating pores much smaller than their nominal thickness. This capability was thought to be limited by the size of the root cap and stele. Constricted root tips elongated at a

slower rate but could grow down long capillaries if adequately aerated. Similar findings were reported by Aubertin and Kardos (1965), who found that maize (*Zea mays*) roots did have some ability to squeeze through the necks of rigid pores smaller than the diameter of the roots and to enlarge subsequently into 'pore cavities'. It is possible that root constriction could be a mechanism by which roots of some plants can penetrate soils with high strength.

2.4.3 Root growth in structured soil

The soil profile is heterogeneous and shows strength discontinuities especially between the aggregated seedbed of the tilled layer and the hard or compacted layer beneath (Dexter, 1986a). A feature of tilled soil most likely to affect an elongationg root is an interface between macro-pores and soil aggregates (Dexter, 1986b; Ehlers *et al.*, 1983; Hewitt and Dexter, 1984; Whiteley and Dexter, 1984a). These authors found that it is common to find a preferential growth of roots on the clod surface rather than within the clod.

Whiteley and Dexter (1983) found that roots are able to elongate more rapidly in cracks narrower than the root diameter than through undisturbed clods without cracks, provided that the crack was not oriented at an oblique angle to the preferred geotropic direction. Cracks are usually formed by desiccation during dry periods or during growth of a crop. The crack patterns can be modified by drying of soil by plant roots when they absorb water from the soil (Johnson, 1962).

Dexter (1978) and Hewitt and Dexter (1979) proposed an improved model of root growth in structured soil. They examined the growth of roots of maize, sorghum and soyabean through beds of spherical aggregates. They also investigated the effects of aggregate size and strength on the spread or distribution of roots. A combination of a statistical model for soil structure with a statistical model of penetration behaviour of a root at a void/aggregate interface was introduced. It was found that the behaviour of a root at such an interface is dependent on the previous history of the root in its passage through the soil and that the smaller the aggregate size, the greater was the nutrient availability per unit length of root. More information on the penetration behaviour of roots in aggregates has been incorporated into this model by Misra *et al.* (1988b)

In addition to interfaces between macropores and solid surfaces, there can also be interfaces between soil zones of differing strength (Dexter and Hewitt, 1978). This is a common feature in soils with macrostructure and is associated with plough sole development in cultivated soils. Roots which encounter a sharp discontinuity in soil strength at the seedbed-subsoil

interface, they have several behavioural options, as shown in Fig. 2.5. The number of roots penetrating the subsoil below the seedbed have been shown to depend on the maximum pressures the roots can exert, the angle of interception of roots with the surface, the strength of the subsoil and the mechanical properties of the roots (*e.g.* Dexter, 1986abc; Gardner and Danielson, 1964; Greacen *et al.*, 1969; Taylor and Gardner, 1960). Most of these studies have been conducted under artificial conditions *i.e.* using wax, glassbeads, sand or remoulded soils. Reactions of roots to each of these conditions would differ substantially from most field situations because glassbeads and sand are largely incompressible and are frictional (non-cohesive) materials in which low applied pressures can completely arrest root elongation.

Most soils pose some mechanical impedance to root growth. According to Barley and Greacen (1967), mechanical impedance is experienced to varying degrees by virtually all roots growing through soil. We will now focus our attention to the causes and effects of mechanical impedance on root growth.

2.5 Soil mechanical impedance

2.5.1 Definition and causes

Mechanical impedance refers to the resistance offered by the soil matrix to deformation by a growing root, thus permitting root elongation only to the extent to which the root pressure exceeds the mechanical impedance (Bennie, 1991). Regions of high mechanical resistance in the soil can arise as a natural soil feature, or can be caused by compaction by heavy farm machinery or by the formation of plough pans (Barnes *et al.*, 1971; Bennie and Krynauw, 1985). Compaction usually reduces the volume of large pores in the soil and may restrict root growth because of increased mechanical resistance and/or poor aeration. Compact soils of high strength may thus limit root growth and crop yields (Taylor and Brar, 1991; Rosenberg and Willets, 1962).

The best indirect method of estimating resistance to root growth through soil involves measuring soil resistance to a metal probe or penetrometer. Theoretical aspects of soil resistance to penetrometers and plant roots will now be considered.

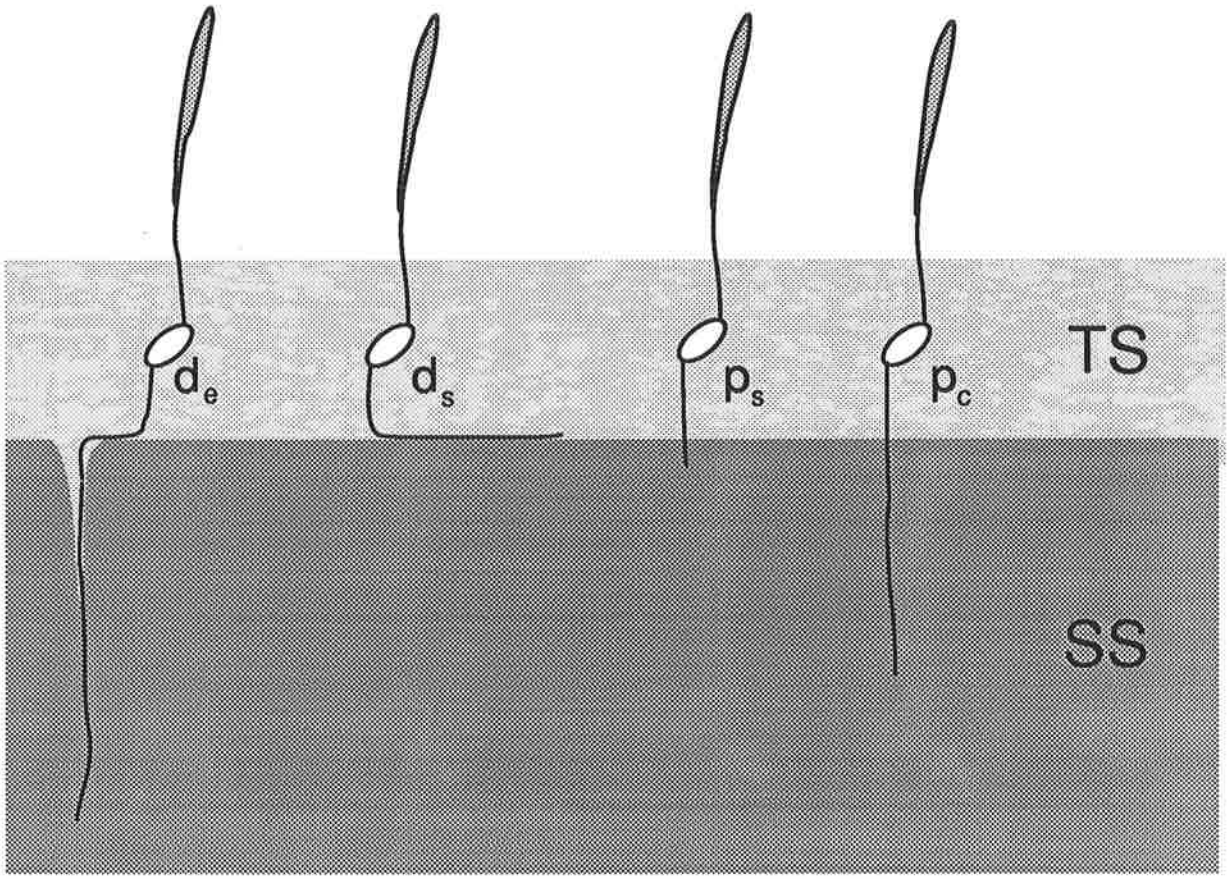


Fig. 2.5. Schematic illustration of possible behaviour of roots encountering a strong untilled subsoil layer, **SS**, after growing through a loose tilled seed-bed, **TS**. The roots can either be deflected or penetrate the layer. Those deflected may grow horizontally along the interface between the layers until they find some path of low resistance and enter the subsoil through this path, $\mathbf{d_e}$, or may dry and cease elongation, $\mathbf{d_s}$. Those penetrating will either continue elongating in the same direction but at reduced rate, $\mathbf{p_c}$, or elongate short distance into the layer and almost cease further elongation, $\mathbf{p_s}$.

2.5.2 *Penetration of soil by metal probes and plant roots*

Penetrometry theory

During penetration of soil by a metal probe or a plant root, the volume of the probe or root is accommodated by the formation of cavities (Barley, 1968; Dexter, 1987a). These cavities are similar to those observed in studies of deep foundations (Meyerhof, 1961) and of piles (Nishida, 1961). Thus the theory of penetration of a rigid probe into soil involves the calculation of the pressures required to expand cylindrical and spherical cavities in the soil. Cavity expansion theories (Greacen *et al.*, 1968; Farrell and Greacen, 1966) consider that there are two zones of soil deformation; an inner plastic (*i.e.* irrecoverable deformation) zone near the penetrometer or root, and an elastic (*i.e* recoverable deformation) zone outside this.

Within the plastic zone the soil is in a state of failure. The stresses within this zone therefore depend on the failure strength of the soil. In other words, the stresses are governed by cohesion and friction. Within the elastic zone the soil has not failed, and the stresses are dependent upon the elastic stiffness of the soil. Most agricultural soils have strength properties strongly related to water content and density (*e.g.* Kirby, 1989). Thus, cohesion in particular will increase with decreasing water content and increasing density. The elastic stiffness will increase dramatically with decreasing water content and increasing density. Thus, the predicted cavity pressure for both spherical and cylindrical cavities is a function of soil mechanical properties, and will increase with decreasing water content and increasing density.

Based on the theory proposed by Farrell and Greacen (1966) and Greacen *et al.* (1968) the total point resistance (Q_p) to a blunt probe or root can be estimated as

$$Q_p = \sigma_n (1 + \tan\phi \cot \alpha) \qquad [2.5]$$

where $\tan\phi$ is the coefficient of soil-probe friction, α is the included semiangle of the cone and σ_n is the stress acting normally to the cone surface.

From observations using x-radiography (Greacen *et al.*, 1967; Greacen *et al.*, 1968) and time lapse photography (Cockroft *et al.*, 1969), it was evident that blunt probes (α=30°) and root tips tend to induce in the soil spherical and cylindrical straining modes respectively.

Vesic (1972) used essentially the same solution procedures as Farrell and Greacen (1966) and Greacen *et al.* (1968) to solve the spherical and cylindrical cavity expansion. The analysis also considered the case where the soil is undrained and an excess pore water pressure develops. It is clear from these

theories that it is possible to calculate the force required to push into soil a penetrometer tip of a certain geometry if the properties of the soil are known. One would use the properties of the soil to calculate the cavity expansion pressure and then use the Equation of Greacen *et al.* (1968) (*i.e.* Equation 2.5) to estimate total point resistance.

The preceding section shows that the penetration of a metal probe or plant root can be significantly influenced by soil mechanical properties. Soil texture and minerology may also influence the penetration of soil by probes and roots, due to their effects on soil strength (Bennie, 1991). However most of the theories described above have not been used much in studies of practical agriculture because, firstly, their application requires accurate estimates of mechanical properties which are time consuming and need expensive equipment; and secondly the theories are not applicable to heterogenous soils. For practical reasons, more rapid empirical methods are normally needed and thus penetrometers have been commonly used.

2.5.3 Comparison of penetrometer and root resistances in soil

The ideal way to determine the relationship between penetrometer resistance and root resistance is to measure both independently in the same soil. However, because of experimental difficulties in measuring root resistance, relatively few such studies have been made (Bengough and Mullins, 1991; Eavis, 1967; Misra *et al.*, 1986b; Stolzy and Barley, 1968; Whiteley *et al.*, 1981). The results of all these studies indicate that penetrometers experience a resistance between two and eight times greater than roots (see Table 2.3 for reasons).

Further indirect evidence of this difference comes from comparing studies of root elongation rate and penetrometer resistance with measurements of the maximum pressures that roots can exert. Critical values of penetrometer resistance at which root elongation ceases are in the 0.8-5.0 MPa range, depending on the soil and crop (Greacen *et al.*, 1969). Maximum axial pressures a root can exert vary between about 0.24 and 1.45 MPa, depending on the species, but are mostly in the range 0.9-1.3 MPa (Misra *et al.*, 1986a). It is clear that penetrometers experience greater resistance than plant roots when penetrating the same soil and many reasons have been suggested to explain this discrepancy. These reasons are summarised in Table 2.3.

The preceeding discussion suggests that the pressure of the bulk aggregated soil, measured with a rigid penetrometer probe, can be a poor and variable indicator of the mechanical impedance to root growth in aggregated soils. These differences between penetrometers and roots have resulted in the

expression of much doubt as to the usefulness of penetrometers. Despite their limitations however, penetrometers do provide useful measures of soil to which root growth may be referred (Bengough, 1991; Bradford, 1980). As Dexter (1987a) has pointed out, 'penetrometry with all its limitations will continue to be used for a long time to come in estimating the soil resistance to root penetration'.

Table 2.3 Main differences between plant roots and penetrometers.

Characteristic	Roots	Penetrometers
Diameter	Generally 0.1-2.0 mm	Generally 0.1-20.0 mm
Shape	Approximately paraboloid but may expand radially if mechanically impeded	Usually conical
Friction	Unknown; probably small due to mucilage secretion and cells sloughing off root	Considerabe friction on probe tip and on shaft
Penetration rate	< 1 mm h^{-1}	Often > 1 mm min^{-1}
Flexibility	Can follow cracks or planes of weakness through the soil	Rigidly mounted; follow a linear path through the soil
Water uptake	Extract water from the soil as they grow and causes local changes in pore water potential	Do not extract water

Adapted from Bengough (1991)

2.5.4 *Effect of probe/root diameter on penetration*

Existing experimental evidence on the effects of probe or root diameter on resistance to penetration is based almost entirely on penetrometer measurements and is often contradictory (Table 2.4). However it would appear from the table that the penetrometer pressure is dependent on the probe diameter when the probe diameter is commensurate with that of the root. When the particle size is similar to the probe, the probe would have to move a whole soil particle aside thus causing more soil deformation in relation to its size than when the particles are much smaller than the probe (Whiteley and Dexter, 1981b).

Table 2.4 Studies in which resistance to probes of different diameters was measured[a].

Reference	Soil	Probe diameter (mm)	Probe type (semiangle)	Greatest pressure for penetration required by
Dexter & Tanner (1973)	Field soil (various textures)	10,20,30,40	sphere	smallest probe
Barley *et al.* (1965)	Remoulded sandy loam	1.0,2.0,3.0	conical (30°)	no difference
Gooderham (1973) cited by * below	-	1.0,2.0	-	smallest probe
Bradford (1980)	undisturbed	3.8,5.1	conical (30°)	no difference
Whiteley *et al.* (1981)*	Undisturbed clods and remoulded cores of sandy loam	1.0,1.25,1.5 1.75,2.0	conical (30°)	no difference
Whiteley & Dexter (1981b)	Remoulded (various textures)	1.0,1.25,1.5 1.75,2.0	conical (30°)	smallest probe
Bengough (1988)	Undisturbed cores of sandy loam	0.5,1.0	conical (30°)	smallest probe

[a] Adapted from Table 2 of Bengough and Mullins (1990b).

Richards and Greacen (1986) and Greacen (1986) in their theoretical model of cavity expansion in granular media imply that thin roots may deform the soil elastically thereby encountering less resistance than thicker roots which cause plastic deformation. However, the limited studies of several different plant species available to date do not indicate that roots of smaller diameter are relatively less mechanically impeded by soil or by ballotini (Gooderham, 1973; Goss, 1977). We know however that penetrometers cannot mimic root growth. In contrast to roots, which can grow around objects that offer high resistance to displacement, a small probe may have to displace soil particles of a diameter comparable to the probe resulting in its experiencing greater resistance. There is need for more investigation on the penetration of strong soil by plant roots of different sizes.

In summary, the literature reviewed in the preceding sections shows that the penetrability of soils by roots and penetrometer probes can be affected by several factors. These include; presence of paths of low mechanical resistance such as continuous biopores (created by root and soil fauna); porosity and bulk density of the soil; water content of soil; texture, overburden pressure, degree of confinement and aggregate size and macrostructure. Following this discussion of the factors influencing the penetration of soil by roots and probes, we will now proceed to discuss the effects of mechanical impedance on the growth of roots.

2.6 Effects of mechanical impedance on root growth

2.6.1 Root elongation, distribution and branching

Root growth is limited by high mechanical impedance, poor soil aeration and inadequate water supply all of which interact making it difficult to distinguish unequivocally among their effects. For this reason, many studies on the effect of mechanical impedance on root growth have been concerned with the behaviour of roots grown in remoulded soils in which effects of high soil strength can be separated from other factors. It has been shown in many studies that root elongation rate decreases approximately exponentially with increase in soil strength and/or penetrometer pressure irrespective of the plant used. There are many reports in the literature on this subject and extensive reviews are available (*e.g.* Barley and Greacen, 1967; Bengough and Mullins, 1990b; Bennie, 1991; Gliński and Lipiec, 1990; Russell, 1977; Russell and Goss, 1974; Taylor, 1971; Taylor *et al.*, 1972).

The depth, thickness and mechanical resistance of the root-impeding soil layer can influence the distribution of roots in the soil profile (Bennie, 1991). If the root-impeding layers are near the surface, they will slow the downward root growth, which will finally result in a shallower rooting depth (Bennie and Botha, 1986). Furthermore, when the mechanical impedance is high enough to prevent root growth, the total root system will be restricted to the upper part of the profile (Boone and Veen, 1982). Greater lateral root formation has also been shown to occur in roots grown in soil with high mechanical impedance (Goss and Russell, 1980; Goss, 1977; Schuurman, 1965).

2.6.2 Root morphology

When root growth is impeded due to high soil strength, the roots are known to have shorter, thicker and more irregularly shaped tips (Abdalla *et al.*, 1969; Barley, 1976; Goss and Russell, 1980; Taylor, 1974b). These changes in the external root morphology are normally so prominent that they can be

used to identify the presence of high soil strength (Bennie, 1991). The increase in diameter of mechanically impeded roots has been attributed to an enlargement of the cortex in which cells become shorter in longitudinal direction and wider in transverse, while the cell volume is unaffected (Atwell, 1988; Barley, 1976).

Mechanical impedence may also cause changes in the cell structure of the endodermis and pericycle. Prihar *et al.* (1975) found an elaborate production of sclerified cells in the cortical and vascular tissues of maize and soyabeans. According to Prihar *et al.* (1975), such cells may reflect traits developed in such roots to resist forces and prevent deformation in internal cells. Whatever is the explanation for this behaviour, the phenomenon of radial thickening of mechanically impeded roots is of particular interest to the work reported in this thesis because Abdalla *et al.* (1969) have hypothesized that thickening may relieve the constraint at the root tip, thereby permitting further elongation into the strong medium. This hypothesis will now be reviewed.

2.6.3 *Hypothesis of Abdalla et al. for root penetration in strong granular medium*

Abdalla *et al.* (1969) constructed a model for the mechanics of root growth in strong granular medium by considering the deformation of a cylinder of soil in front of the root tip (Fig. 2.6). The model predicts that for any given strain, less stress is required to deform the soil radially than axially. Further, experiments were performed in which a penetrometer with sides capable of radial expansion (by inflation of a rubber membrane) was placed under a static load in a container of sand. Inflation of the membrane resulted in the probe penetrating to a greater depth. The authors inferred from this work that radial swelling of roots may reduce resistance to elongation by a root.

Support for this hypothesis comes from the experiment of Hettiaratchi and Ferguson (1973) who used a special penetrometer which could be expanded cylindrically to look at the two limiting conditions of the hypothesis. They showed that radial expansion induced a reduction of stress ahead of the simulated root tip. Similarly Graf and Cooke (1980) used a finite-element model to predict that the radial expansion of impeded root tips could reduce the axial stress on the root cap: they assumed a low coefficient of root-soil friction and that the soil behaved as a homogeneous linear elastic medium.

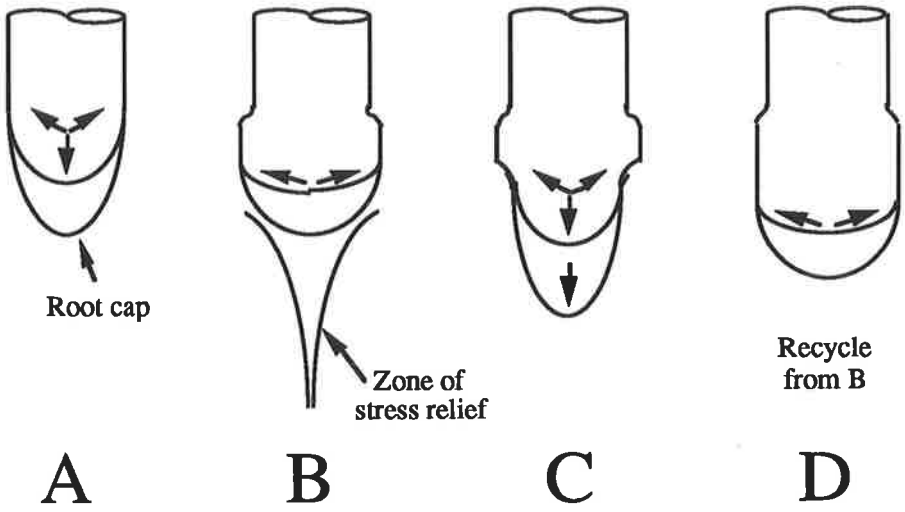


Fig. 2.6 Schematic representation of the model of Abdalla *et al.* for the mechanics of root penetration in a granular continuum (re-drawn from Abdalla *et al.*, 1969).

The sequence of events in a root during high confining stress may be described as follows. (A) On the application of the confining stress, axial elongation of the root tip is inhibited. The meristematic region then grows radially. (B) The radial thickening then helps to relieve the stress at the root tip (by creating a crack). (C) the root tip then overcomes the reduced axial stress and the meristem once again elongates longitudinally until the root tip reaches a zone in which the stress regime would again inhibit axial elongation. This is so because the relief of stress due to (B) would be expected to reduce exponentially from the tip downwards. (D) The cycle is repeated from (B) and the root therefore proceeds to grow with a thickened section. It should be mentioned here that there is no evidence so far to show that the sequence of events follows this order.

A zone of stress relief caused by radial enlargement of a root was also predicted by Richards and Greacen (1986), and by Hettiaratchi and O'Callaghan (1974) and Hettiaratchi (1990). All these studies found that there was a zone of stress relief caused by radial thickening. It has been suggested by Hettiaratchi and Ferguson (1973) that the relieving of stress at the root tip might enable a root to grow through dense soils more than it would by uniform growth. The importance of this mechanism for soil penetration by plant roots has not yet been fully investigated.

The literature reviewed above suggest that stress relief may occur at the tip of roots which have thickened radially while growing in strong medium. The stress relief at the tip of the root could be a possible mechanism which

enables plant roots to grow through strong soil. This review will now consider differences that exist in the ability of roots of plant species to penetrate strong soil.

2.6.4 Differences among plant species in penetrating strong soil

There are conflicting views regarding the abilities of different plant species to overcome mechanical impedance. Elkins *et al.* (1977) reported that roots of Pensacola bahia grass (*Paspalum notatum* cv Flugge) were able to penetrate compacted soil layers that restricted growth of cotton roots. They suggested that the fibrous sheath beneath the epidermis in the roots of bahiagrass gave them rigidity and enabled them to penetrate dense soil. A cotton crop grown after the bahiagrass was able to grow into the channels made by the roots of the bahiagrass with consequent increased water uptake and growth.

Whiteley and Dexter (1981b) indicated that the ability of roots to penetrate a compact soil increased with increasing diameter. Taylor and Gardner (1960) on the other hand could not find differences between the penetrating ability of legumes (diameter 1.8 mm) and that of non-legumes (diameter 0.55 mm). Bennie and Burger (1981) did not find any differences in the penetration by maize, wheat, cotton, and peanuts, into a compacted layer of a loam soil. They concluded that the relative decrease in rooting length, rooting density, or the number of roots entering a compacted layer is the same for most plant species. They suggested that the differences observed among plant species are merely functions of their abilities to produce roots in uncompacted soil. In this case, plants with many fine roots will have a higher probability of finding sites of lower mechanical impedance than plants with few roots.

The review so far indicates that there are conflicting views regarding differences in abilities of roots to penetrate strong soil. One important factor which influences any difference in root penetrability is the genetic differences which exist among species.

2.7 Mechanisms for development of soil structure by plant roots

Although the exact mechanisms of structure formation by plant roots have not been fully established, let alone quantified, the explanation of the influence of root systems on aggregation will now be discussed.

2.7.1 *Drying of soil*

Plant roots are the most effective way of drying a soil down to the depth of rooting. Drying of soil in the vicinity of the root systems as water is absorbed by the roots and the resulting shrinkage of soil seems to be the major mechanism for creating structure in soils (Dexter, 1988a; Russell, 1971). Wet soils, providing they contain some clay, will shrink as they become drier. Shrinkage forms fracture surfaces which produce cracks or channels through the body of the soil. The drying action of the roots is very important in the formation of such cracks. The cracks may constitute the initial faces of soil aggregates (Grant and Dexter, 1986; White, 1966). Cracking of soil resulting from shrinkage can also help to disrupt compact layers and permit further exploration of the soil by plant roots.

Wetting of the dry soil can result in the breakdown of the larger aggregates or clods into finer soil aggregates. Breakdown is caused by the combined effects of differential swelling and pressure build-up in entrapped air which can cause mechanical failure of the aggregate (Dettman, 1958; Emerson, 1977; Grant and Dexter, 1989; 1990). The process can result in complete slaking of the soil into separate micro-aggregates typically < 250 μm, or there may be partial slaking or mellowing (Utomo and Dexter, 1981b). In the latter case, arrays of micro-cracks are formed throughout the soil mass and make the soil weaker and more friable (McKenzie and Dexter, 1985).

The importance of wetting and drying cycles on soil aggregation has been well documented (Horn and Dexter, 1989; Kolodny and Neal, 1941). It is possible that the increase in aggregation under grass based-pastures which has been known for a long time (*e.g.* Low, 1955; Uhland, 1949) may be largely a consequence of the effect of high densities of grass roots on the hydrology of the soil. As water is taken up by the roots, the water potential decreases. The change in water potential, will increase the compactness of the soil through its effect on the effective stress (Barley, 1968). The role of effective stresses in compacting soil is covered in Section 4.3.4 of this thesis.

2.7.2 *Formation of channels*

When a root penetrates into soil with no pre-existing macro-structure, it produces a biopore. This is done by deformation of the soil mainly by cylindrical expansion. The volume occupied by the root is accompanied by loss of an equal volume of pore space from the surrounding soil (Dexter, 1987b). Thus the soil around a root can be compacted to some extent for a distance in the order of the root diameter beyond the surface. Several researchers have shown increases in the bulk density of the soil next to roots

(*e.g.* Cockroft *et al.*, 1969; Greacen *et al.*, 1968; Guidi *et al.*, 1985) which has been attributed to compaction by pressure of the roots.

The importance of root growth on channel formation was shown by Barley (1954) who, found that the permeability of a non-aggregated sandy loam soil free of organic matter fell after maize was sown. When the roots began to grow some pores were blocked and others were eliminated. Later, the permeability of the soil increased (although not to its original volume) as the roots began to decay. The biopores formed by one crop may also provide channels for deep rooting of a following crop (*e.g.* Ehlers *et al.*, 1983; Elkins *et al.*, 1977; Jakobsen and Dexter, 1988; Wang *et al.*, 1986; Wiersum, 1967).

2.7.3 *Enmeshment*

Enmeshment means provision of mechanical support for the soil matrix by roots. It is a function of the extension of root and the formation of root hairs leading to new improved anchorage of the plant and greater capacity to exploit water and nutrient resources. Structure in the soil can be modified or created by enmeshment. The effectiveness of the roots is dependent on them limiting the movement of particles or aggregates and so restricting mobilisation by wind and rain. Waldron (1977) and Waldron and Dakessian (1982) showed that plants such as pine, oak, lucerne and a range of grasses increase the shearing resistance of soil. Similarly, Willatt and Sulistyaningsih (1990) found that the root system of rice increased both shearing resistance and bearing capacity of a loamy soil in East Java, Indonesia.

Roots and fungal hyphae, particularly those of vesicular-arbuscular mycorrhizal (VAM) are important binding agents of soil microaggregates (< 0.25 mm diameter) into macroaggregates (> 0.25 mm diameter) (Tisdall and Oades, 1982). The roots and hyphae form an extensive network within each aggregate and particles of clay stick firmly to them, by mucilage or polysaccharide. Although the individual hyphae are not strong, the combined strength of all hyphae and fine roots hold particles more or less equally in all directions so that aggregates do not slake when wetted quickly (Miller and Jastrow, 1990).

2.7.4 *Biological activity*

A root in the soil releases organic matter which varies from simple organic molecules to cells and tissues that are sloughed in the process of growth. The materials released from roots include exudates, secretions, mucilages and lysates (Rovira *et al.*, 1970). These substances are the substrates for the microbial flora, and material for cementing soil aggregates. The

amount and nature of substrate produced in roots depends on the plant species. For example, lucerne and ryegrass improve structural stability of soil by increasing polysacchrides in the rhizosphere (Goss and Reid, 1981; Reid and Goss, 1980; Tisdall and Oades, 1979). The increase in aggregate stability by maize, soyabean and wheat roots observed by Monroe and Kladivko (1987) was attributed to the physical entanglement of aggregates by roots and to the increased production of root exudates resulting from root growth. Maize roots, on the other hand, decreased the stability of soil structure by chelating iron and aluminum, thus destroying chemical bonds with organic matter (Goss and Reid, 1979).

2.8 Concluding remarks

It is evident from the foregoing discussion that plant roots can have significant influences in the formation of biopores and aggregates, and also on the stabilisation of the aggregated structures. The effectiveness of different plant species in generating aspects of soil structure is related to the morphology and activity of the root system. As considerable inter species differences exist in root characteristics, there is scope for utilising some species to improve the structure of damaged soils. To do this, however, we need to understand the mechanisms involved in the amelioration of soil structure by plant roots in different soils and climates. A better understanding of the mechanisms and root properties involved in the processes will not only contribute to knowledge but may provide a means of improving soils for plant growth.

SECTION 3

Response of Roots to Mechanical Impedance

3.1 Introduction

Soil compaction and the resulting resistance to elongation of roots in the strong soil has been widely identified as a factor which retards root growth and in many cases reduces crop yields (see Section 2.5). Ways of alleviating the effects of compaction with minimum cost are required. One possible approach is to use plant species whose roots have superior ability to penetrate strong soil. It may be inferred from some theories of soil mechanics (see Section 2.6.3) that the radial thickening of roots growing under mechanical stress can increase their penetration into strong medium. The aim of the work reported in this section was to test the response of roots of different plant species to mechanical stress. The hypothesis being examined was that the tendency of roots to thicken provides an indication of their ability to penetrate strong soil. This could lead to the development of a method for screening large numbers of species for the ability of their roots to penetrate strong soil in the field.

3.2 Materials and methods

3.2.1 Plant species

Twenty-two plant species were selected to cover a broad range of plant material for comparison. The names of the species and their seed weights are presented in Table 3.1. Seed weight was measured by weighing 100 seeds. Seeds of each species were germinated in trays containing moist vermiculite. When the primary root length of the seedlings reached between 15 and 30 mm, their lengths were measured and the seedlings were planted, one to a growth apparatus.

3.2.2 Growth apparatus

A sideview of the apparatus used for growing seedlings is shown in Fig. 3.1. An open-topped cylindrical brass compression chamber 70 mm diameter by 63 mm high with removable base was used. Each chamber was filled with 270 g of oven-dried siliceous sandy soil known as Young Sand (Richards and Greacen, 1986). The sand has well-rounded grains of about 150 μm diameter. The distribution of particle sizes for the sand is presented in Fig. 3.2. It has a low compressibility and a high friction angle (Richards and Greacen, 1986). A

Table 3.1 Plant species and their seed weights.

Plant Species				Seed weight[a] (g/100 seeds)
Code	Common Name	Scientific Name	Cultivar	
Monocotyledons				
A	Barley	*Hordeum vulgare*	Galleon	3.85 (0.055)[b]
B	Maize	*Zea mays*	Hy 740	39.90 (0.098)
C	Oats	*Avena sativa*	Dolphin	3.10 (0.084)
D	Rice	*Oryza sativa*	Inga	2.57 (0.025)
E	Sorghum	*Sorghum bicolor*	Super sweet	2.79 (0.045)
F	Rhodesgrass	*Chloris gayana*	Katambora	0.04 (0.001)
G	Ryegrass	*Lolium rigidum*	Wimmera	0.24 (0.004)
H	Wheat	*Triticum aestivum*	Kite	3.68 (0.015)
Dicotyledons				
I	Cotton	*Gossypium hirsutum*	Delta Pine 90	9.53 (0.058)
J	Faba bean	*Vicia faba*	Fiord	40.10 (0.110)
K	Lincoln weed	*Diplotaxis tenuifolia*	-	0.04 (0.001)
L	Leucaena	*Leucaena leucocephala*	Cunningham	5.34 (0.046)
M	Lucerne	*Medicago sativa*	Hunter River	0.23 (0.002)
N	Lupin	*Lupinus angustifolius*	Gungurru	14.80 (0.116)
O	Medic	*Medicago scutelatar*	Sava	1.47 (0.049)
P	Oil radish	*Raphanus oleifera*	Siletta	1.47 (0.029)
Q	Pea	*Pisum sativum*	Greenfeast	23.90 (0.187)
R	Pigeon pea	*Cajanus cajan*	Quantum	9.10 (0.095)
S	Safflower	*Carthamus tinctorius*	Gilla	3.90 (0.022)
T	Soyabean	*Glycine max*	Davis	20.60 (0.123)
U	Sunflower	*Helianthus annuus*	Hysun 44	7.16 (0.055)
V	Vetch	*Vicia sativa*	Languedoc	6.59 (0.662)

[a] mean of ten replicates

[b] numbers in parenthesis are standard errors.

water retention characteristic of the sand is presented in Fig. 3.3. For the water potentials, samples of sand were drained from saturation on "porosity 4" sintered glass funnels set at the different potentials (0 to 0.01 MPa) over the range of the water contents which was used in the growing of the plants. Gravimetric water content, W, of each sample was determined after drainage had stopped.

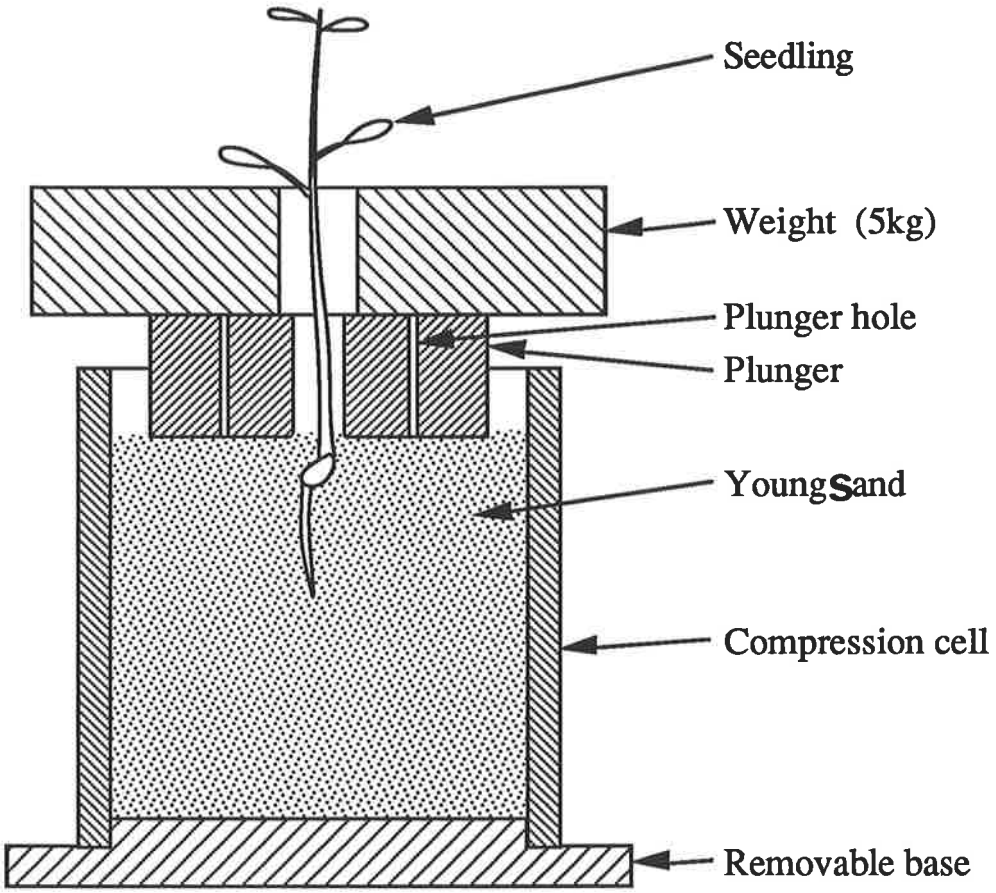


Fig. 3.1 A cross sectional view of the apparatus used for growing seedlings.

The dry bulk density of the sand in the chambers ranged from 1.32 to 1.37 Mg m^{-3} (mean 1.35 ± 0.01) and the total porosity was around 0.49 $m^3 m^{-3}$. An intact seedling was planted in the centre of the chamber at a depth of about 3 mm into the sand. When any damage to roots was observed during transfer, the seedling was discarded. The sand was then moistened to a water content of approximately 0.20 kg kg^{-1} (-3.5 kPa) with a mixture of nutrient solution and de-ionised water. This water content was found to give adequate

aeration in the sand. The nutrient solution was modified from that of Johnson *et al.* (1957). It was used at one-tenth concentration by mixing 10 cm^3 of the full strength nutrient solution with 90 cm^3 water. The diluted solution contained 7.23 m*M* NO_3^-, 2.5 m*M* Ca^{2+}, 1.0 m*M* Mg^{2+}, 3.0 m*M* K^+, 0.65 m*M* $HPO_4^{2-} + H_2PO_4^-$ and 1.0 m*M* SO_4^{2-}.

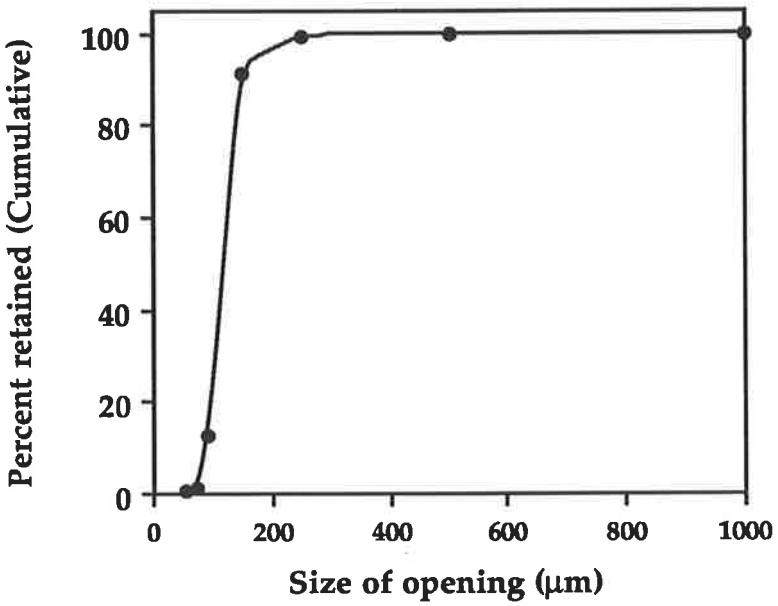


Fig. 3.2 Particle size distribution of Young Sand.

A plunger of 600.9 g weight was placed on top of the sand and used to support a 5.0 kg weight. The principle behind the use of the weight and the way it was determined are described later. The plunger had two holes of 3.0 mm diameter which were used to make penetrometer measurements. The combined mass of the weight and plunger applied a vertical pressure of 14.2 kPa to the sand.

Another seedling, which served as a control, was grown in a 300 mm deep plastic container of vermiculite. Each seedling was supplied with 20 cm^3 of nutrient solution and the vermiculite was kept moist throughout the growing period by watering with de-ionised water. The pH of the vermicullite measured at the end of the growth period ranged from 6.70 to 7.32 (mean 7.23).

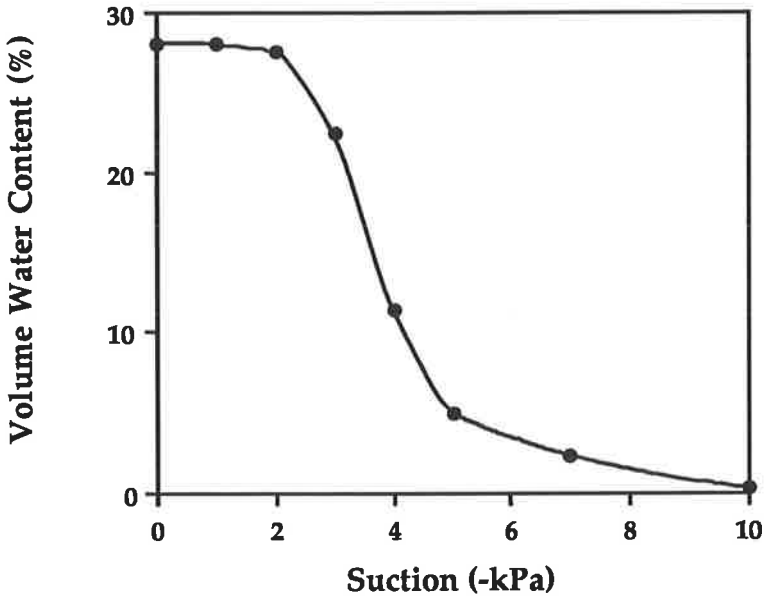


Fig. 3.3 A water retention characteristic of Young Sand.

Determination of weight

To determine the weight which would produce a penetrometer resistance in excess of 4.0 MPa in Young Sand, four compression chambers were filled with the sand and wetted to field capacity (Ψ=–4.5 kPa). The chambers were subjected to different weights of 0, 2.27, 4.55 and 6.82 kg and left to stand in a growth cabinet. The penetrometer resistance of the sand in each chamber was measured after 10 days. It was determined from the results (Fig. 3.4) that a weight of 5 kg would in addition to the weight of the plunger produce the required resistance in the compression chambers. This weight was used on all chambers during the growth of the seedlings as shown in Fig. 3.5.

3.2.3 Growth conditions

All plants were kept in a growth cabinet where the photoperiod was 12 h. A bank of fluorescent light tubes supplied an irradiance of 125 μmol m^{-2} s^{-1} at plant level. Light intensity was measured by a Lambda Photometer model L1-185A. The day/night air temperatures were 20°/16°C respectively. All plants were grown for a period of ten days. Ten replicates were grown for each species.

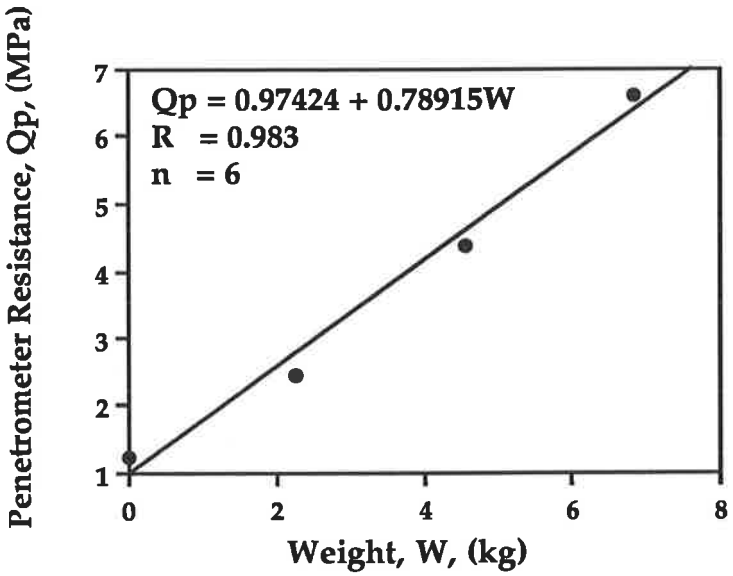


Fig. 3.4 Relationship between weight (W) and penetrometer resistance (Q_p) of Young Sand at a water content of 0.20 kg kg^{-1}.

3.2.4 *Measurements after plant growth*

Penetrometer resistance (Q_p).

Penetrometer resistance was used as a measure of soil strength. A steel probe having a cone diameter, d_p, of 2.0 mm and semi-angle of 30° was driven into the sand through plunger holes at a rate of 3 mm min^{-1} in the growth apparatus using a loading frame (Fig. 3.6). The probe passed through a slot made in one of the weights. The force on the tip of the probe was measured as a dial reading on a proving ring, and was converted to a penetration force, F(N) using the following calibration

$$F(N)=0.8687\,D - 4.163*10^{-4}\,D^2 + 3.17*10^{-7}\,D^3 \qquad [3.1]$$

where D is the dial reading on the proving ring. The depth of penetration when the force was measured was 32 mm (16 d_p) which was similar to the depth at which root elongation was occurring. This was also the depth where constant maximum penetrometer resistance occurred in all the chambers (Fig. 3.7). Penetrometer resistance was calculated from the penetrometer force as

$$Q_p = 4F/\pi d_p^2, \quad MPa \qquad [3.2]$$

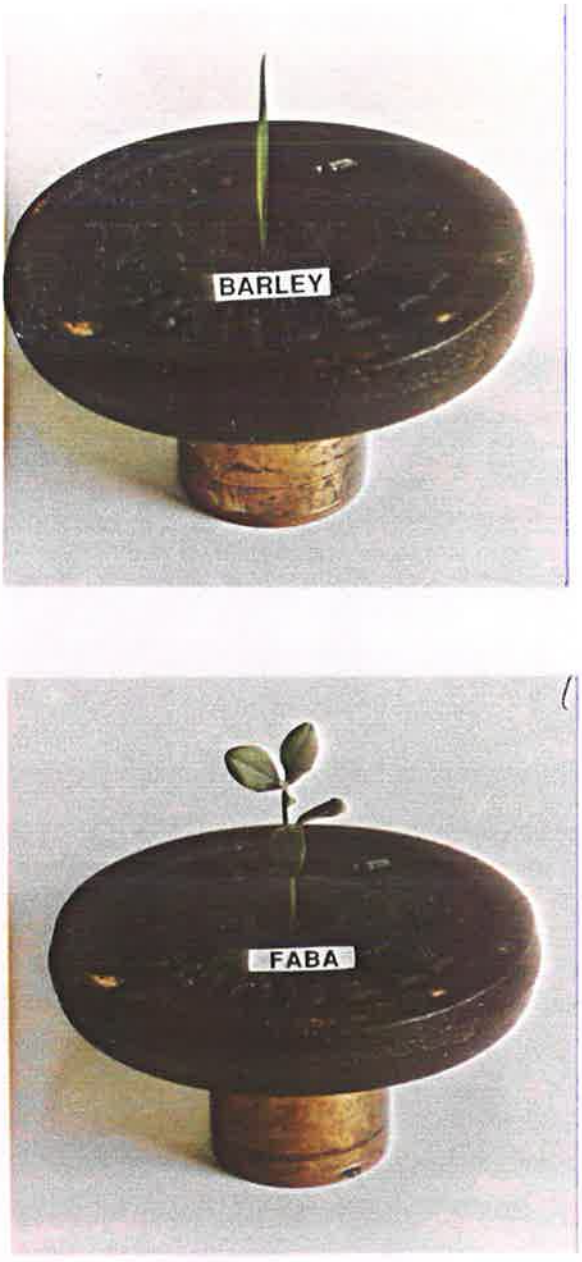


Fig. 3.5 Plant species growing under mechanical stress.

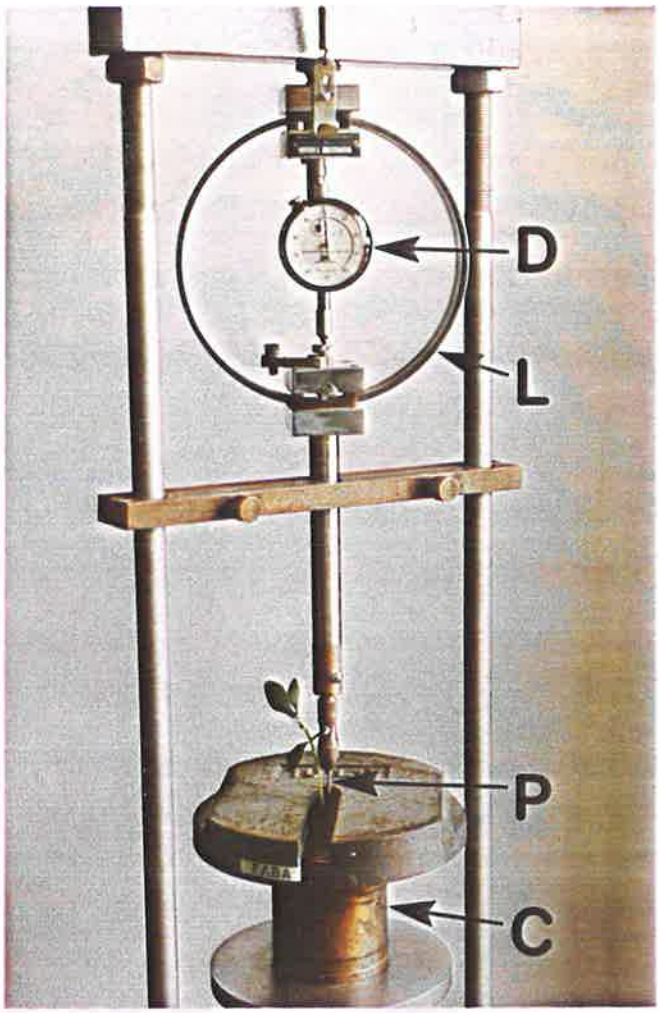


Fig. 3.6 Measuring penetrometer resistance in the compression cell (C) using a penetrometer probe (P) on a loading frame. Penetrometer force is read on a dial gauge (D) in a load ring (L).

Four measurements were made in each chamber by rotating the plunger and the mean was used in calculating the penetrometer resistance. Q_P was the only indicator of resistance faced by the root tips during growth.

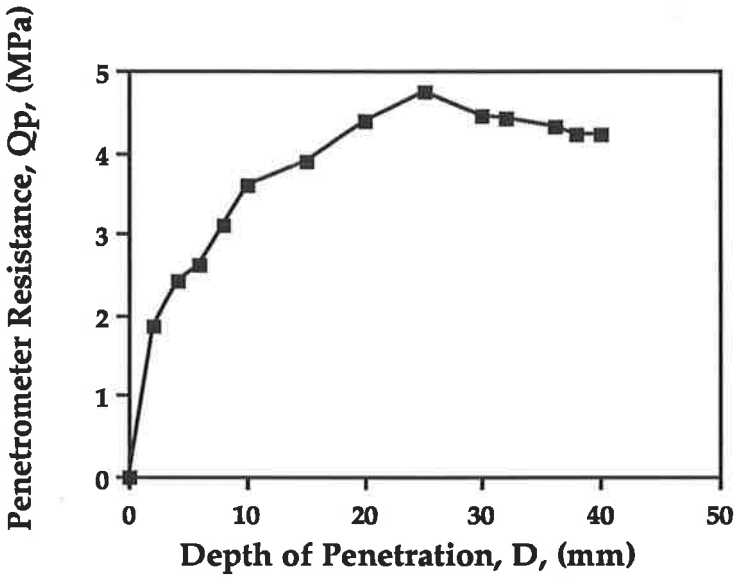


Fig. 3.7 Effect of depth of penetration (D) on penetrometer resistance (Q_P) of Young Sand in the compression cells.

Water content

Immediately after penetrometer measurements were made, the weight and plunger were removed and the seedling was carefully removed from the opened chamber. Samples of sand were collected from each chamber for the determination of gravimetric water content and pH.

Root length and diameter

The lengths of the primary/seminal roots of plants from both compression chambers and vermiculite containers were measured with a ruler. Root diameters were measured at distances (X) of 1.0, 3.0 and 5.0 mm from the tip using a calibrated travelling microscope. Distortion (change of shape) of the root tips by mechanical stress was evident in most dicotyledonous species. Monocotyledonous species had less distortions. However, since the diameters of the dicotyledonous species were large, this did not cause problem in the measurements.

Comparison between species

To compare the abilities of the different seedling roots to penetrate strong soil, the elongation and diameter of roots of the stressed plants were expressed relative to those of the control plants, *i.e.* as relative root elongation (RRE) and relative root diameter (RRD). These were calculated by using the length and diameter of the control plants (0 MPa penetrometer resistance) as references and expressing the values (length and diameter) of the stressed plants as fractions of the reference values (Bennie and Burger, 1981). The elongations and diameters of the stressed plants relative to those of the unstressed plants are thus given by RRE = E_s/E_c and RRD = d_s/d_c where E_s and E_c are the elongations of roots of the stressed and unstressed plants respectively, and d_s and d_c are the diameters of roots of the stressed and unstressed plants respectively.

Plant species were ranked using RRE and RRD as ranking characteristics. Spearman rank correlation coefficients, r_s, (Gibbons, 1974) were used to test the goodness of agreement between the ranked pairs of attributes for a set of n individuals. The statistic (r_s) is given by:

$$r_s = 1 - \frac{6\sum_{i=1}^{n} D_i^2}{n(n^2-1)} \qquad [4.3]$$

where n is the number of paired observations (x_i, y_i) and D_i is the rank (x_i) -rank (y_i). An r_s of 1 indicates complete agreement in order of the ranks while an r_s of -1 indicates complete agreement in the opposite order of the ranks.

3.2.5 Analyses of data

All data were subjected to standard analysis of variance with the Genstat 5 program (Genstat 5 Committee, 1987) on a VAX computer. Results presented here are means of ten replicates.

3.3 Results

3.3.1 Water content and penetrometer resistance of Young Sand

It was important to maintain uniform conditions (water and strength) in the sand during the growth of the seedlings. This was achieved. Table 3.2 shows that the water content of the sand was maintained around 0.20 kg kg^{-1} (mean 0.198 kg kg^{-1}) for all the species. This resulted in a similar close range in the penetrometer resistance of the sand (mean 4.24 MPa). Because of the

narrow range in water content of the sand, the penetrometer resistance was not significantly affected by water content (correlation coefficient -0.107). Thus, it was reasonable to assume that the roots of the different plant species were subjected to similar strength during growth period.

Table 3.2 Penetrometer resistance (Q_p) and gravimetric water content (W) of Young Sand during the plant growth period.

Plant Species	Q_p (MPa)	CV %	W (kg kg^{-1})	CV %
Barley	4.28 (0.043)[a]	13.6	0.195 (0.02)	6.4
Maize	4.21 (0.048)	15.2	0.198 (0.03)	8.7
Oats	4.23 (0.035)	11.1	0.196 (0.03)	8.2
Rice	4.21 (0.035)	11.4	0.199 (0.02)	5.7
Sorghum	4.28 (0.083)	18.4	0.196 (0.02)	6.4
Rhodesgrass	4.26 (0.072)	20.8	0.197 (0.03)	10.3
Ryegrass	4.22 (0.052)	16.4	0.199 (0.02)	7.5
Wheat	4.14 (0.070)	22.3	0.199 (0.03)	8.6
Cotton	4.23 (0.035)	11.2	0.196 (0.02)	6.8
Faba bean	4.28 (0.043)	13.7	0.207 (0.03)	9.0
Lincoln weed	4.28 (0.062)	19.8	0.199 (0.02)	5.6
Leucaena	4.24 (0.045)	14.4	0.196 (0.03)	7.9
Lucerne	4.26 (0.056)	17.8	0.199 (0.02)	7.4
Lupin	4.23 (0.047)	15.1	0.202 (0.03)	7.9
Medic	4.26 (0.046)	14.5	0.200 (0.01)	4.4
Oil radish	4.28 (0.070)	20.2	0.197 (0.02)	6.6
Pea	4.21 (0.035)	11.4	0.199 (0.03)	10.4
Pigeon pea	4.19 (0.080)	20.3	0.199 (0.03)	7.9
Safflower	4.23 (0.057)	18.2	0.207 (0.03)	9.2
Soyabean	4.21 (0.058)	18.3	0.199 (0.02)	5.2
Sunflower	4.26 (0.046)	14.6	0.196 (0.03)	8.1
Vetch	4.25 (0.043)	14.6	0.198 (0.03)	8.2
Mean	4.24 (0.035)	16.1	0.199 (0.03)	7.6

[a] Numbers in brackets indicate standard error of mean

CV = coefficient of variation

3.3.2 Root elongation and diameters as affected by mechanical stress

The roots of all species investigated in the study were very sensitive to soil strength in terms of elongation (Table 3.3). A mean penetrometer resistance of 4.2 MPa in the sand in the compression chambers reduced root elongation of the stressed plants by over 90% (mean 94 %) compared with the unstressed controls. However, in the strong sand, elongation of the roots of

dicotyledon species was slightly higher (mean 5.4 mm) than that of the monocotyledons (mean 3.4 mm).

Table 3.3 Root elongation of mechanically stressed (S) and control (C) plants after 10 days of growth.

Plant species	Root elongation (mm)		% Reduction by stress
	S	C	
Monocotyledons			
Barley	3.1 (0.04)[a]	124.6 (0.76)	97.5
Maize	4.4 (0.06)	106.7 (0.72)	95.9
Oats	3.2 (0.05)	114.2 (1.14)	97.2
Rice	3.1 (0.02)	60.2 (0.15)	94.9
Sorghum	3.4 (0.02)	63.8 (0.15)	94.7
Rhodesgrass	2.5 (0.05)	60.6 (0.36)	95.9
Ryegrass	3.0 (0.02)	68.2 (0.28)	95.6
Wheat	4.1 (0.04)	120.7 (0.82)	96.6
Dicotyledons			
Cotton	4.5 (0.02)	68.0 (0.20)	93.4
Faba bean	6.8 (0.03)	98.7 (0.74)	93.1
Lincoln weed	2.7 (0.04)	59.8 (0.25)	95.5
Leucaena	5.2 (0.05)	66.9 (0.22)	92.2
Lucerne	4.3 (0.03)	75.9 (0.31)	94.3
Lupin	7.1 (0.06)	69.4 (0.27)	87.8
Medic	4.5 (0.03)	62.4 (0.22)	92.8
Oil radish	4.9 (0.04)	88.3 (0.60)	94.5
Pea	7.0 (0.04)	104.6 (0.85)	93.3
Pigeon pea	4.6 (0.06)	72.7 (0.20)	93.7
Safflower	5.6 (0.05)	94.5 (0.67)	94.1
Soyabean	5.7 (0.06)	81.5 (0.41)	93.0
Sunflower	6.4 (0.05)	105.3 (0.68)	93.9
Vetch	6.5 (0.04)	112.7 (0.38)	94.2

[a] Numbers in parenthesis are the standard error of mean.

In addition to the effects on root extension, soil strength also had significant effects on the size of the root tips. In general, high soil strength caused the cells of the root apex to expand radially *i.e.* the diameter of the root was bigger at all the three distances from the root tip compared with the control plants (Table 3.4). The diameters of the roots of all the species increased with soil strength, but the increase in the dicotyledons was much

Table 3.4 Root diameter measured at three distances, X (mm), from the tip in mechanically stressed (S) and control (C) plants after 10 days of growth.

Plant species	Root diameter (mm)					
	X=1.0		X=3.0		X=5.0	
	S	C	S	C	S	C
Monocotyledons						
Barley	0.74 (0.05)[a]	0.46 (0.03)	0.85 (0.03)	0.51 (0.09)	0.70 (0.03)	0.50 (0.03)
Maize	1.37 (0.08)	0.81 (0.02)	1.47 (0.02)	0.87 (0.03)	1.32 (0.09)	0.89 (0.03)
Oats	0.87 (0.07)	0.52 (0.03)	0.87 (0.07)	0.54 (0.03)	0.76 (0.07)	0.55 (0.04)
Rice	0.57 (0.01)	0.37 (0.01)	0.54 (0.03)	0.41 (0.01)	0.51 (0.02)	0.43* (0.02)
Sorghum	0.77 (0.03)	0.53 (0.02)	0.83 (0.04)	0.58 (0.02)	0.75 (0.04)	0.61 (0.02)
Rhodesgrass	0.24 (0.02)	0.13 (0.01)	0.27 (0.01)	0.18 (0.01)	0.26 (0.01)	0.17 (0.01)
Ryegrass	0.30 (0.02)	0.19 (0.01)	0.38 (0.01)	0.23 (0.03)	0.39 (0.03)	0.25 (0.01)
Wheat	0.80 (0.03)	0.49 (0.02)	0.83 (0.04)	0.56 (0.02)	0.74 (0.04)	0.50 (0.02)
Dicotyledons						
Cotton	0.91 (0.07)	0.55 (0.03)	1.23 (0.08)	0.67 (0.03)	1.14 (0.06)	0.69 (0.01)
Faba bean	1.83 (0.17)	0.86 (0.04)	2.21 (0.15)	0.96 (0.05)	2.18 (0.21)	1.04 (0.04)
Lincoln weed	0.24 (0.02)	0.13 (0.01)	0.27 (0.01)	0.16 (0.01)	0.27 (0.01)	0.17 (0.01)
Leucaena	0.87 (0.08)	0.49 (0.03)	0.95 (0.06)	0.55 (0.03)	0.90 (0.05)	0.56 (0.01)
Lucerne	0.67 (0.03)	0.40 (0.02)	0.77 (0.04)	0.43 (0.02)	0.70 (0.04)	0.46 (0.02)
Lupin	1.58 (0.05)	0.84 (0.03)	2.02 (0.05)	1.00 (0.05)	1.82 (0.08)	1.09 (0.08)
Medic	0.77 (0.04)	0.40 (0.02)	0.91 (0.05)	0.43 (0.02)	0.86 (0.04)	0.45 (0.02)
Oil radish	0.72 (0.05)	0.33 (0.02)	0.84 (0.06)	0.37 (0.02)	0.76 (0.04)	0.39 (0.01)
Pea	1.41 (0.09)	0.73 (0.02)	1.68 (0.10)	0.77 (0.02)	1.77 (0.12)	0.83 (0.02)
Pigeon pea	1.02 (0.06)	0.61** (0.04)	1.02 (0.05)	0.68 (0.04)	1.06 (0.05)	0.69 (0.03)
Safflower	1.10 (0.12)	0.51 (0.02)	0.96 (0.06)	0.54 (0.03)	0.86 (0.05)	0.55 (0.03)
Soyabean	1.39 (0.06)	0.78 (0.03)	1.77 (0.07)	0.89 (0.06)	1.54 (0.10)	0.98** (0.08)
Sunflower	0.82 (0.06)	0.48 (0.01)	1.06 (0.09)	0.53 (0.02)	0.91 (0.07)	0.54 (0.02)
Vetch	1.23 (0.09)	0.70 (0.04)	1.41 (0.10)	0.76 (0.03)	1.28 (0.07)	0.82 (0.03)

[a] Numbers in parenthesis indicate standard error of the mean. For all values of X, the means for S and C were all significantly different ($p \leq 0.001$) by the LSD test, except for those indicated by * ($p \leq 0.05$) and ** ($p \leq 0.01$)

greater (mean 86%) than that in the monocotyledonous species (mean 41%). Root tips of plants grown in the control (C) and stressed (S) environments are shown in Plate 1.

According to Greacen (1986), the zone of elongation of an impeded root extends from the meristem to almost 5.0 mm from the extreme tip of the root, with the zone of maximum elongation rate lying between 1.5 and 2.5 mm from the tip. To establish which of the three distances *i.e.* 1.0 mm (X1), 3.0 mm (X2) and 5.0 mm (X3) had thickened the most due to mechanical stress, an analysis of variance of the differences between the two distances (X2-X1) and (X3-X2) was done. The results (Table 3.5) show that there were significant differences in the thickening of roots at the three distances for all the species except pea, pigeon pea and safflower.

The general trend emerging from this analysis is that for those species where the difference between the two distances (*i.e.* X2-X1 and X3-X2) is significant, it is the (X2-X1) distance which has the higher mean. This implies that the diameter at 3.0 mm was bigger than at 1.0 mm from the tip of the root. In many cases, the difference between X3 and X2 (*i.e.* X3-X2) is negative, again implying a larger root diameter at 3.0 mm than at 5.0 mm from the tip. It is interesting to note at this stage that there were positive correlations between root elongation and root diameters of stressed plants at all three distances. The correlation coefficients between root elongation and diameter at X2 being higher (0.65) than those for X1 (0.57) and X3 (0.59).

3.3.3 Comparisons between plant species

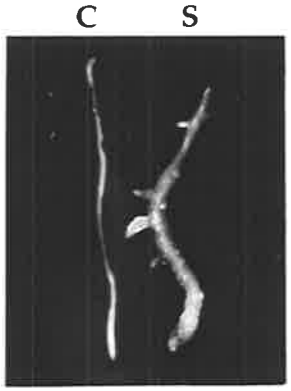
The results of RRE and RRD are presented in Table 3.6. There is a wide variation among the species in both RRE and RRD. It is evident from these results that there is a difference in the RRE and RRD of monocotyledonous and dicotyledonous species - those for dicotyledons being higher than those of monocotyledons. For example, the mean RRE for monocotyledons is 0.04 (range 0.025-0.054) while that of dicotyledons is 0.07 (range 0.045-0.105). A similar observation is made for RRD at all three distances. A further point of interest in this comparison are the positive correlations between RRE and RRD which were 0.63, 0.71 and 0.68 for X1, X2 and X3 respectively.

The size of the seed did not seem to have much influence on the thickening or the penetrating ability of roots of any species. The correlations between seed weights and RRE and RRD were very low, both overall and within species. The mean correlation coefficients for all the species combined were 0.026, 0.014, 0.025 and 0.011 for the correlations between seed weight and

Plate 3.1 Root tips of some species after growing in control (C) and stressed (S) environments. Notice the uncharacteristic proliferation of first-and second-order lateral roots close to the tip of the pea root.

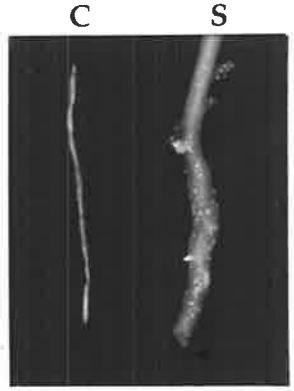
Dicotyledons

Leucaena



Medic

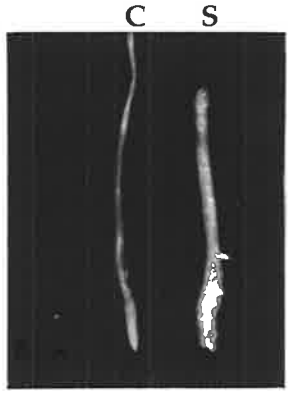
Pea



Soya bean

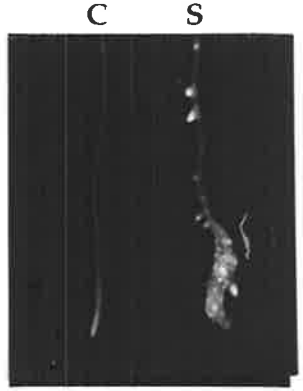
Monocotyledons

Barley



Maize

Oats



Wheat

RRE and RRD at 1.0, 3.0 and 5.0 mm from the tip respectively. This suggests that the ability of root systems to thicken and penetrate strong media is a genetic characteristic and does not necessarily depend on the size of the seed.

Table 3.5 Differences in the diameters of roots of stressed plants measured at distances X1 (1 mm), X2 (3 mm) and X3 (5 mm) from the tip.

Plant species	Distance		Significance level
	X2-X1	X3-X2	
Monocotyledons			
Barley	0.116	-0.148	*
Maize	1.000	-0.153	*
Oats	-0.004	-0.129	***
Rice	0.028	-0.083	***
Sorghum	0.061	-0.074	**
Rhodesgrass	0.025	-0.003	***
Ryegrass	0.079	0.006	*
Wheat	0.035	-0.092	**
Dicotyledons			
Cotton	0.312	-0.088	**
Faba bean	0.384	-0.025	*
Lincoln weed	0.021	0.003	***
Leucaena	0.076	-0.050	*
Lucerne	0.099	-0.073	***
Lupin	0.431	-0.193	***
Medic	0.139	-0.051	**
Oil radish	0.120	-0.079	***
Pea	0.274	0.081	ns
Pigeon pea	-0.004	0.036	ns
Safflower	-0.143	-0.101	ns
Soyabean	0.375	-0.222	***
Sunflower	0.184	-0.093	*
Vetch	0.183	-0.124	***

Significant differences between the two distances are given as * ($p \leq 0.05$), ** ($p \leq 0.01$), *** ($p \leq 0.001$); ns = not significant.

3.3.4 Ranking of plant species

Since this study was concerned with selection of plant species based on the penetrating ability and thickening of the roots, a ranking of the species was done using both RRE and RRD as ranking characteristics (Table 3.7). Spearman's rank correlation coefficients (r_s) were calculated to test the agreement between the two ranking characteristics. There was a significant positive rank correlation ($r_s = 0.79$, $p \leq 0.05$) between RRD and RRE. This

Table 3.6 Relative root elongation (RRE) and relative root diameter (RRD) of the plant species.

Plant species	RRE	RRD[a]			
		X=1 mm	X=3 mm	X=5 mm	Mean
Monocotyledons					
Barley	0.025 (0.003)[b]	1.74 (0.26)	1.73 (0.21)	1.43 (0.08)	1.35
Maize	0.044 (0.007)	1.71 (0.10)	1.70 (0.10)	1.49 (0.10)	1.63
Oats	0.029 (0.004)	1.71 (0.16)	1.66 (0.14)	1.38 (0.12)	1.42
Rice	0.052 (0.004)	1.55 (0.06)	1.48 (0.09)	1.20 (0.06)	1.38
Sorghum	0.054 (0.004)	1.47 (0.05)	1.43 (0.07)	1.24 (0.05)	1.39
Rhodesgrass	0.041 (0.007)	1.79 (0.10)	1.56 (0.13)	1.61 (0.14)	1.33
Ryegrass	0.045 (0.004)	1.60 (0.09)	1.69 (0.11)	1.58 (0.12)	1.55
Wheat	0.035 (0.004)	1.63 (0.07)	1.50 (0.09)	1.47 (0.06)	1.41
Dicotyledons					
Cotton	0.067 (0.004)	1.69 (0.14)	1.85 (0.11)	1.67 (0.11)	1.70
Faba bean	0.073 (0.007)	2.19 (0.29)	2.38 (0.25)	2.14 (0.23)	2.18
Lincoln weed	0.045 (0.006)	1.98 (0.20)	1.72 (0.11)	1.61 (0.11)	1.53
Leucaena	0.078 (0.007)	1.82 (0.16)	1.75 (0.11)	1.60 (0.12)	1.72
Lucerne	0.057 (0.004)	1.70 (0.10)	1.80 (0.11)	1.54 (0.12)	1.74
Lupin	0.105 (0.010)	1.92 (0.11)	2.05 (0.11)	1.72 (0.14)	1.85
Medic	0.072 (0.003)	1.95 (0.09)	2.12 (0.10)	1.93 (0.11)	1.98
Oil radish	0.059 (0.007)	2.16 (0.13)	2.28 (0.19)	1.93 (0.08)	2.03
Pea	0.069 (0.005)	1.96 (0.13)	2.19 (0.12)	2.11 (0.11)	2.08
Pigeon pea	0.063 (0.008)	1.71 (0.10)	1.54 (0.09)	1.56 (0.11)	1.83
Safflower	0.065 (0.010)	2.19 (0.25)	1.82 (0.14)	1.60 (0.12)	1.83
Soyabean	0.071 (0.008)	1.83 (0.12)	2.07 (0.14)	1.66 (0.17)	1.89
Sunflower	0.065 (0.008)	1.71 (0.11)	1.91 (0.15)	1.72 (0.14)	1.88
Vetch	0.058 (0.003)	1.76 (0.13)	1.86 (0.09)	1.58 (0.08)	1.79

[a] RRD was measured at distances X (mm) from the tip.

[b] Numbers in parenthesis indicate standard error of means.

indicates that there is a good agreement in the order of the ranks or the different characteristics used in the ranking of the species. It can be seen that dicotyledonous species generally occupy top ranks *i.e.* they had higher RRE than monocotyledons. A similar trend is apparent in the RRD where the top ranks are occupied by dicotyledons and the bottom by monocotyledons. There is however some interchanging of positions among species in the rankings for RRE and RRD, which may suggest that the tendency of roots to thicken is perhaps only a rough guide to the ability of roots to penetrate strong soils.

Table 3.7 Ranking of plant species using RRE and RRD as rank characteristics.

	Rank characteristic	
Position	RRE	RRD
1	Lupin	Faba bean
2	Leucaena	Pea
3	Medic	Oil radish
4	Faba bean	Medic
5	Soyabean	Soyabean
6	Pea	Sunflower
7	Cotton	Lupin
8	Pigeon pea	Pigeon pea
9	Sunflower	Safflower
10	Safflower	Vetch
11	Vetch	Lucerne
12	Lucerne	Leucaena
13	Oil radish	Cotton
14	Sorghum	Maize
15	Rice	Ryegrass
16	Lincoln weed	Lincoln weed
17	Ryegrass	Oats
18	Maize	Wheat
19	Rhodesgrass	Sorghum
20	Wheat	Rice
21	Oats	Barley
22	Barley	Rhodesgrass

Figs. 3.8 and 3.9 present pairwise comparisons of all the species based on RRE and RRD (at 3 mm from the tip). The comparisons in each figure are divided into three parts *viz*: within monocotyledons (light shaded); between monocotyledons and dicotyledons (unshaded) and within dicotyledons (dark shaded). The general observation from Fig. 3.8 is that there are more significant differences in the RRE of roots when dicotyledons are compared

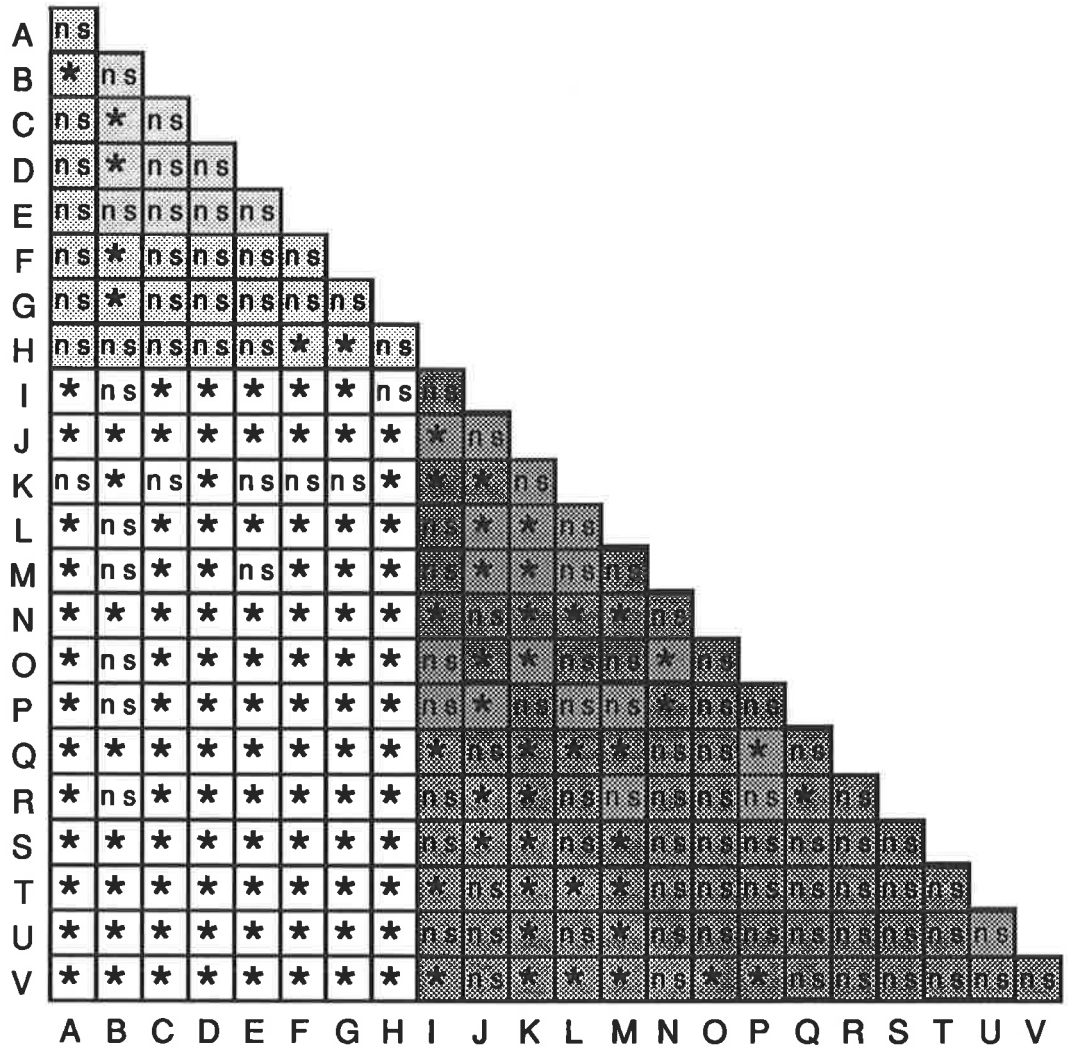


Fig. 3.8 Comparison of pairs of means for RRE of the plant species. * = significant difference ($p \leq 0.05$) by the LSD test; ns = not significant. Species codes are given in Table 3.1.

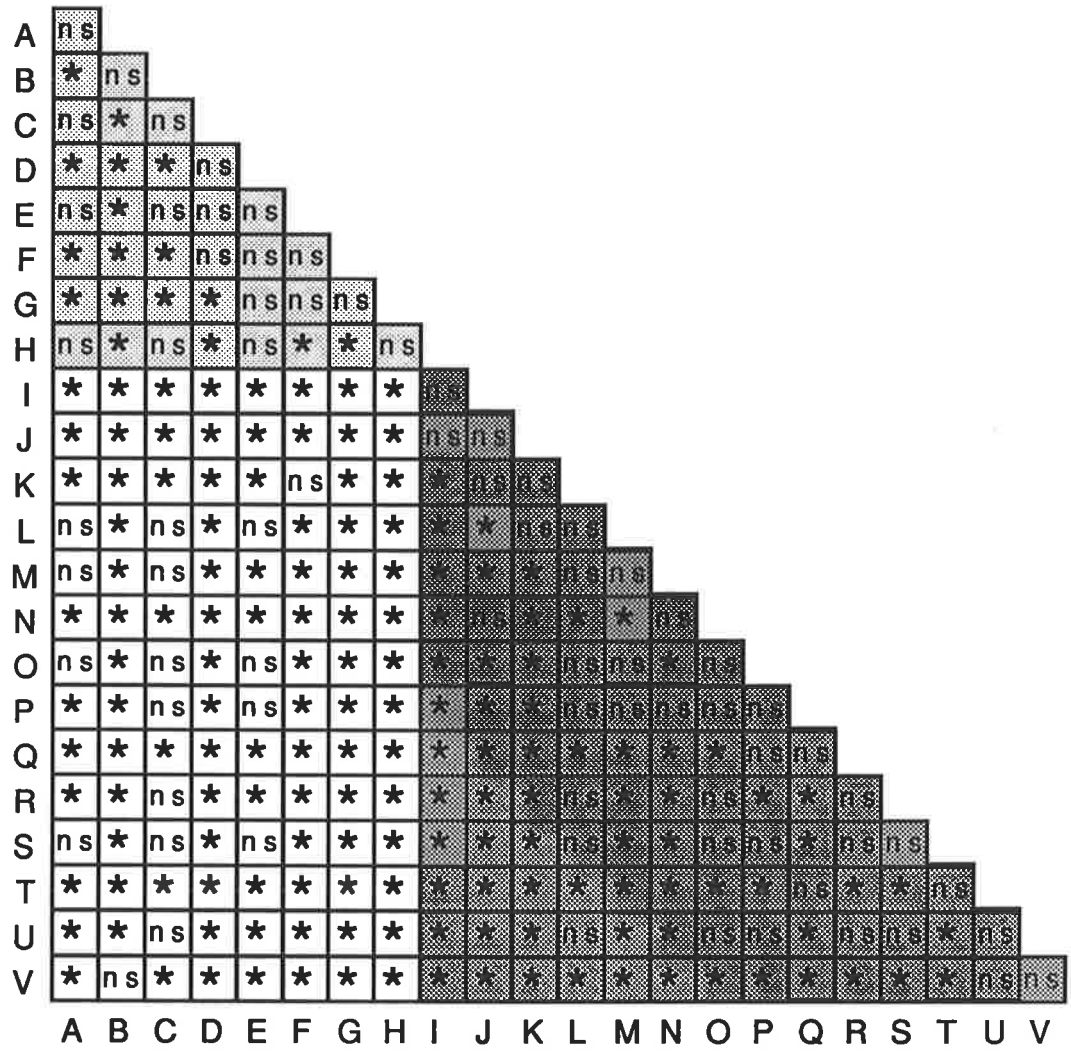


Fig. 3.9 Comparison of pairs of means for RRD of the plant species measured 3.0 mm from the tip. * =significant difference ($p \leq 0.05$) by the LSD test; ns = not significant. Species codes are given in Table 3.1.

with monocotyledons while there are fewer differences in the pairs when comparisons are made within the same species classification (*i.e* monocotyledons *v* monocotyledons or dicotyledons *v* dicotyledons). For example, there are 80%, 12% and 63% pairs of means which are not significantly different in the dark shaded, unshaded and light shaded areas respectively. A similar trend is evident in Fig. 3.9. In this comparison however, there are more differences between the means in each of the three areas.

3.4 Discussion

The rates of elongation of the unstressed control roots grown in vermiculite in this study ($6.0 \leq$ rate ≤ 12; mean 8.5 mm day^{-1}) are generally lower than those reported elsewhere. For example, Cahn *et al.* (1989) reported growth rates ranging from 2.8 to 83 mm day^{-1} in maize (*Zea mays* cv. Cornell 25) grown in minirhizotrons in a greenhouse at temperatures ranging from 25°C to 30°C and an irradiance of 200 µmol m^{-2} s^{-1}. The slow rates of growth in this study could be due to the low irradiance (125 µmol m^{-2} s^{-1}) and temperature (20°C) in the growth cabinet. However, the results have shown that mechanical stress (in the form of soil strength) on the root tips of the different species caused a remarkable reduction in the elongation of the roots and also caused the roots to increase in diameter. This form of response by roots to mechanical stress has widely been observed by other authors (*e.g.* Abdalla *et al.*, 1969; Atwell, 1988; Bengough and Mullins, 1991; Goss and Drew, 1972; Taylor and Burnett, 1964).

The increase in root diameter behind the apex has as yet not been adequately explained. Some suggestions have been made *e.g.* by Atwell (1988), Atwell and Newsome (1990), Barley (1962) and Greacen (1986), who attribute the increase to enlargement of the cortex. According to these authors, the cells become shorter in the longitudinal direction but remain wide in the traverse (see Section 2.6.2). The enlargement of the cortex is thought to be a consequence of both the increase in the diameter of the outer cells, and an increase in the number of cells per unit length of root (Bengough and Mullins, 1990b). Some authors (*e.g.* Kays *et al.*, 1974; Veen, 1982) have suggested that the plant hormone, ethylene may be responsible for the changed shape of impeded roots because it has a similar effect on the shape when applied to unimpeded roots. It is beyond the scope of this thesis to examine in detail the physiological causes of this swelling. What is important to note here are the large differences among the roots of plant species in their abilities to thicken when under stress.

The reduction in rate of root elongation in strong soil has been attributed to both a decrease in the rate of cell division in the meristem and a decrease in cell length (Eavis, 1967). Taylor (1980) has explained the reduction in elongation of roots in strong soil using basic principles of mechanical impedance as follows: plant roots elongate when the turgor pressure inside new cells is sufficient to overcome the constraint of the cell walls and any external constraint caused by the surrounding soil matrix. The difference between turgor pressure and pressure on cell wall, defined as 'root growth pressure' by Gill and Bolt (1955) must be greater than the impedance acting upon the cross-section of the root if the root is to elongate. Misra *et al.* (1986a) have reported wide variations in the maximum growth pressures which roots of different plant species can exert. They also reported that the maximum growth pressure exerted by the roots increased as the root diameter increased according to the relationship:

$$P_a = 242\, d_r^{0.94} \qquad [3.4]$$

where P_a was the maximum axial root growth pressure (kPa) and d_r was the root diameter (mm).

This finding is noteworthy because the results reported in this section show that dicotyledonous species were able to elongate in the strong medium more than monocotyledons. Although root growth pressures were not measured here, it could be inferred from Equation (3.4) that roots of most of the dicotyledons would have exerted more axial growth pressure on the sand than those of monocotyledons because of differences in root diameters. The wide variation between the species offers considerable opportunity for genetic selection and screening of species and cultivars for use in special soil management programs. For example, plant species with roots which are fine and expand least radially, *e.g.* ryegrass, may perform better under uncompacted soil conditions while plants with thicker roots and greater ability to penetrate strong soil can be used to perforate compact layers and create easily accessible pathways for roots of the succeeding crop. If similar results from this experiment can be found in the field, the technique can be useful for screening species for the ability of their roots to penetrate strong soil.

Of further interest are the high correlations between elongation and root diameter. These findings support the idea behind the theory of the mechanics of root penetration in strong soils suggested by Abdalla *et al.* (1969). Abdalla *et al.* (1969) showed that thickening of the root cap reduces soil strength ahead of

the root tip thus allowing elongation to proceed until the root cap is impeded again. Hettiaratchi and Ferguson (1973) concluded from a theoretical analysis that the thickening of root tips in mechanically impeded roots might enable a root to grow through dense soils five times stronger than is possible by uniform growth. As Elkins (1985) has observed, root characteristics are heritable, so that it could be possible through plant breeding and/or genetic engineering to develop root systems with improved capability for altering soil physical conditions. The work reported here could assist in the task of identifying species with such genetic potential.

The results from this study should enable us to select species with the greatest potential for inclusion in field studies aimed at assessing the actual ability of roots to penetrate strong soils. However, the method used in this section although simple, was rather tedious and time consuming. A potentially simpler and more rapid technique of stressing plants with an osmoticum was investigated. This experiment is reported in the next section.

SECTION 4

Growth of Plant Roots in Response to Osmotic Stress

4.1 Introduction

It was postulated in Section 3.0 that the ability of plant roots to thicken when under mechanical stress could be an indicator of their ability to penetrate strong soil and could be useful in screening species for this purpose. The method used, although simple, was rather laborious and time consuming. Another potential technique of screening species for this purpose was therefore investigated. It involved the application of osmotic stress to the roots of the plants by using solutions of poly (ethylene glycol) (PEG).

The water potential of the medium surrounding roots has successfully been controlled by use of PEG *e.g.* Jackson (1962); Janes (1961); Trizek (1985); Lagerwerff *et al.* (1961); Williams and Shaykewich (1969). Plants growing against osmotic stress induced by PEGs not only have reduced root elongation rates (Coutts, 1982; Kawasaki *et al.*, 1983; Michel and ElSharkawi, 1970), but their roots also increase in diameter (*e.g.* Kaufmann, 1968; Ciamporova and Luxova, 1976; Zekri and Parsons, 1990). This observation is of fundamental interest here because similar effects occur in soils with high mechanical strength (see Sections 3.3.2 and 3.4). It is possible that PEG could also be used for the purpose of selecting species for the ability of their roots to penetrate strong soil.

The first objective of the study reported in this section was to compare the growth of seedling roots of ten selected plant species in PEG solutions of different osmotic potentials. The second objective was to find how the previously determined effects of mechanical stress on root growth (Section 3.0) compare with those of osmotic stress. If responses to osmotic stress can be satisfactorily related to mechanical stress, then osmotic stress could be used as an alternative method to screen plant species for the ability of their roots to penetrate compact soils.

4.2 Materials and methods

4.2.1 Experimental treatments

The treatments consisted of the application of four osmotic potentials (0.0, -0.25, -0.5 and -1.0 MPa) around the roots of seedlings of ten plant species The species used were monocotyledons (barley, oats, rhodesgrass, ryegrass and wheat) and dicotyledons (faba bean, lupin, lucerne, pea and safflower). Scientific

and cultivar names of these species have been presented in Table 3.1. The species were selected to include equal numbers of both monocotyledons and dicotyledons. The experiment was replicated 10 times.

4.2.2 *Preparation of osmotic solutions*

The osmotic solutions were prepared from pharmaceutical grade PEG (molecular weight= 20,000) supplied by Sigma Chemical Company. To find the quantities of PEG required for a given osmotic potential, a series of concentrations were prepared by dissolving various amounts of PEG in nutrient solution and measuring their potentials (Table 4.1). Water potential was measured with a Wescor Psychrometer model HP 115 at 24.5° C. The nutrient solution was the No. 1 Hoagland solution (Hoagland and Arnon, 1950) diluted ten times. Full strength solution was composed of 1 m*M* KH_2PO_4, 5 m*M* KNO_3, 5 m*M* $Ca(NO_3)_2$, 2 m*M* $MgSO_4$, 1m*M* Fe-EDTA and 1 m*M* trace elements (Mn, Zn, Mo, Cu, B). The concentrations of PEG needed to obtain the four potentials were obtained from Figure 4.1 and were respectively 0.0, 0.10, 0.20 and 0.30 kg PEG L^{-1} solution. The pH of the PEG solutions were adjusted to pH 6.2 with 0.01*M* KOH.

Table 4.1 Measured osmotic potential of PEG solutions.

Solution number	PEG concentration (kg L^{-1})	Osmotic potential (MPa)					
		1	2	3	4	Mean	s.e.
1	0.00	0.000	0.000	0.000	0.000	0.000	0.00
2	0.02	-0.023	-0.020	-0.019	-0.021	-0.021	-0.01
3	0.05	-0.065	-0.060	-0.066	-0.058	-0.062	-0.01
4	0.10	-0.280	-0.250	-0.230	-0.210	-0.243	-0.03
5	0.15	-0.350	-0.380	-0.360	-0.370	-0.365	-0.01
6	0.20	-0.500	-0.520	-0.570	-0.550	-0.535	-0.03
7	0.25	-0.730	-0.680	-0.760	-0.700	-0.718	-0.04
8	0.27	-0.960	-0.930	-1.000	-1.020	-0.978	-0.04
9	0.30	-1.260	-1.330	-1.360	-1.320	-1.318	-0.04
10	0.35	-1.520	-1.580	-1.440	-1.550	-1.523	-0.06

s.e. = standard error of the mean

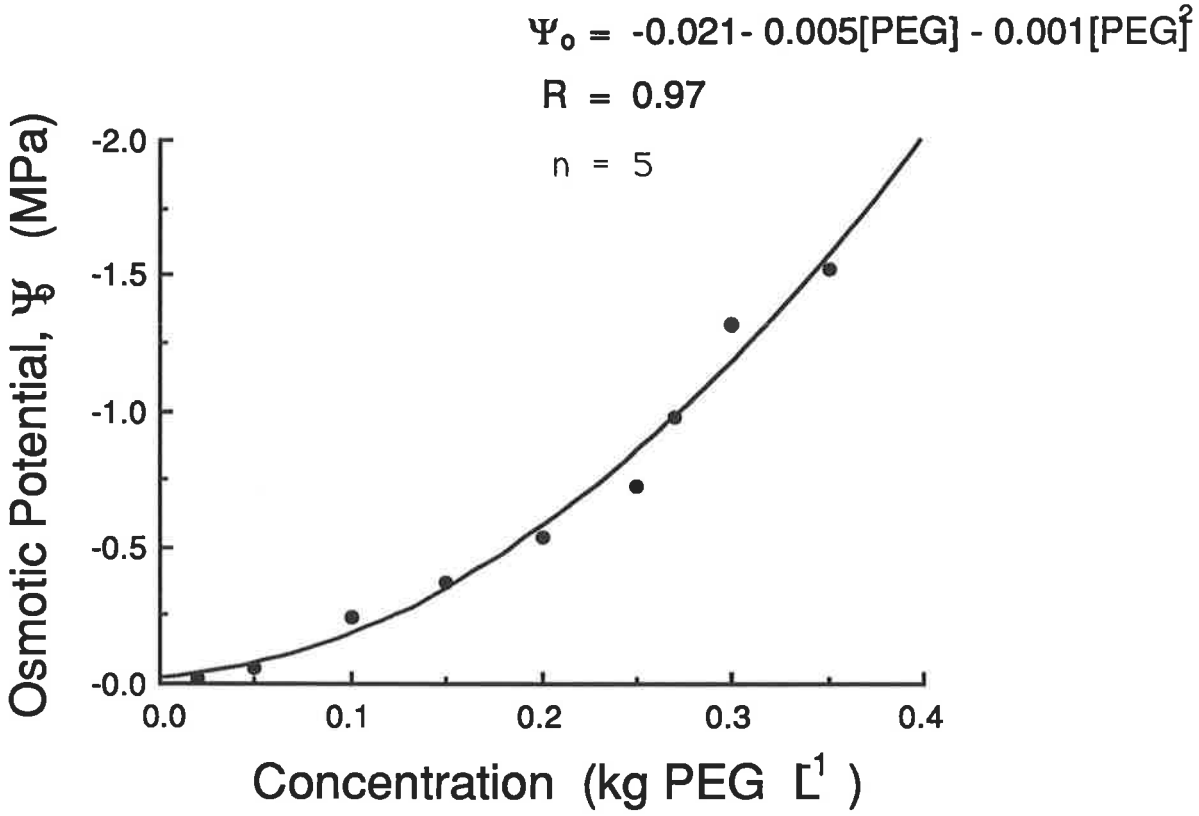


Fig. 4.1 The relationship between concentration of PEG 20,000 and osmotic potential (Ψ_o).

4.2.3 *Growth apparatus*

"Porosity 3" sintered glass funnels (10 cm diameter) were used. The base of each funnel was connected to one end of flexible plastic tubing and the other end was set at a height of 25 cm from the sintered glass to give a suction as shown in Figure 4.2. The four solutions were added to separate funnels through the plastic tubing. The sand in each funnel was packed to a bulk density of 1.25 Mg m^{-3} by pouring weighed, air-dried sand and packing it to predetermined volumes by gently tapping the sides of the funnel. The depth of sand in the funnels was 60 mm. This is the same sand which was used in Section 3.0 (see Section 3.2.2 for its properties).

The tops of the funnels were covered with polythene film to reduce evaporation and the sand was wetted by PEG solution until equilibration was achieved. The water in the sand was considered to be at equilibrium when the wetting front reached the top of the sand columns. This took about 3 to 4 days. The suctions in the -0.5 and -1.0 MPa funnels were reduced to 20 cm to speed the wetting process. After equilibration however, a head of 25 cm was maintained on

all funnels. This enabled the water content of the sand to be kept close to field capacity (0.20 kg kg^{-1}) during the period of growth. It also assured good aeration in the sand.

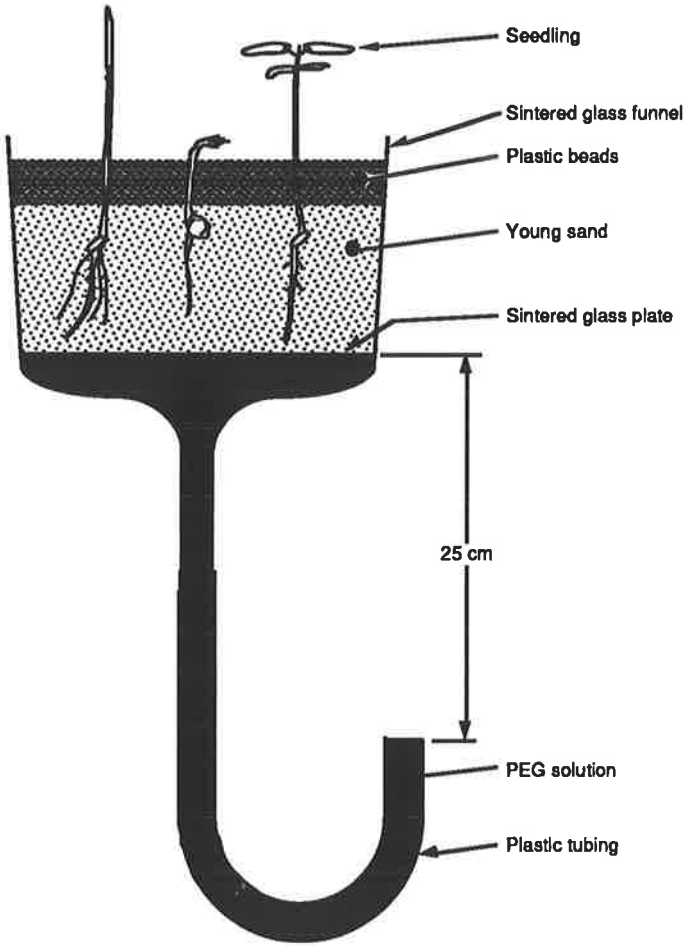


Fig. 4.2 Apparatus used to grow the seedlings.

Although the total water potential (Ψ_t) in the sand is composed of the PEG, matric and nutrients components (*i.e.* $\Psi_t = \Psi_{peg} + \Psi_{matric} + \Psi_{nutrients}$), the effect of the matric and nutrients potentials is considered negligible compared with the range of PEG potentials applied. This is because the Ψ_{matric} is 25 cm water which is equal to -0.0025 MPa, and the $\Psi_{nutrients}$ is considered negligible because of the very dilute solutions used.

4.2.4 Preparation of seedlings for growth

Seeds were germinated in moist vermiculite. When the roots were about 10-15 mm long, their lengths were measured and the seedlings transplanted in each of the four sintered glass funnels containing the wet sand. Only strong, straight

and undamaged roots were selected. A seedling was planted by poking a hole in the sand with a wire and placing the seedling root in the centre of the hole. The seedling was firmly anchored in position by pressing the sand around it. When all plant species were transplanted, the sand was covered with a layer (about 1.0 cm) of black plastic beads to reduce evaporative losses.

4.2.5 Growth conditions

The seedlings were grown for 48 h in a room in which the temperature was 25 ± 1°C. Relative humidity was not controlled and varied between 50% and 70%. Light intensity of 120 μmol m^{-2} s^{-1} was supplied continuously during the growth period by four tungsten filament bulbs above the plants. Figure 4.3 shows the plants growing in the growth apparatus.

After growth, the sand was removed from the funnels and seedlings were recovered. Samples of sand were collected for the determinations of pH and gravimetric water content. pH was determined in a 1:5 soil:water suspension using a glass calomel electrode. The roots were washed free of sand and their lengths and diameters measured. Root elongation was calculated as the difference between the initial and final lengths of the root. Root diameter was measured to ± 10 μm at distances of 1, 3 and 5 mm from the tip using a calibrated microscope eyepiece. The values reported here are the means of the three measurements. The apparatus was washed clean before new sand was added for the next replicate.

4.2.6 Analyses of data

Data were analysed with the Genstat 5 program (Genstat 5 Committee, 1987) on a VAX computer. The LSD test was used to separate means. To compare the species, relative root elongation (RRE) and relative root diameter (RRD) were calculated as described in Section 3.2.4.

4.3 Results

4.3.1 Water content and pH of Young Sand

The water content and pH of the sand at the end of the experiment are given in Table 4.2. Water contents (W) of the sand at the four osmotic potentials during the experiment were in the range 0.21 ≤ W ≤ 0.26 kg kg^{-1} (mean 0.24 kg kg^{-1}). There were no significant differences ($p < 0.05$) in the water contents at the different potentials. The pH of the sand measured at the end of each growth period was in the range 5.9 ≤ pH ≤ 6.3 (mean 6.1) and the differences were not significant ($p \leq 0.05$). The calculated air-filled porosities (f_a) of the sand at

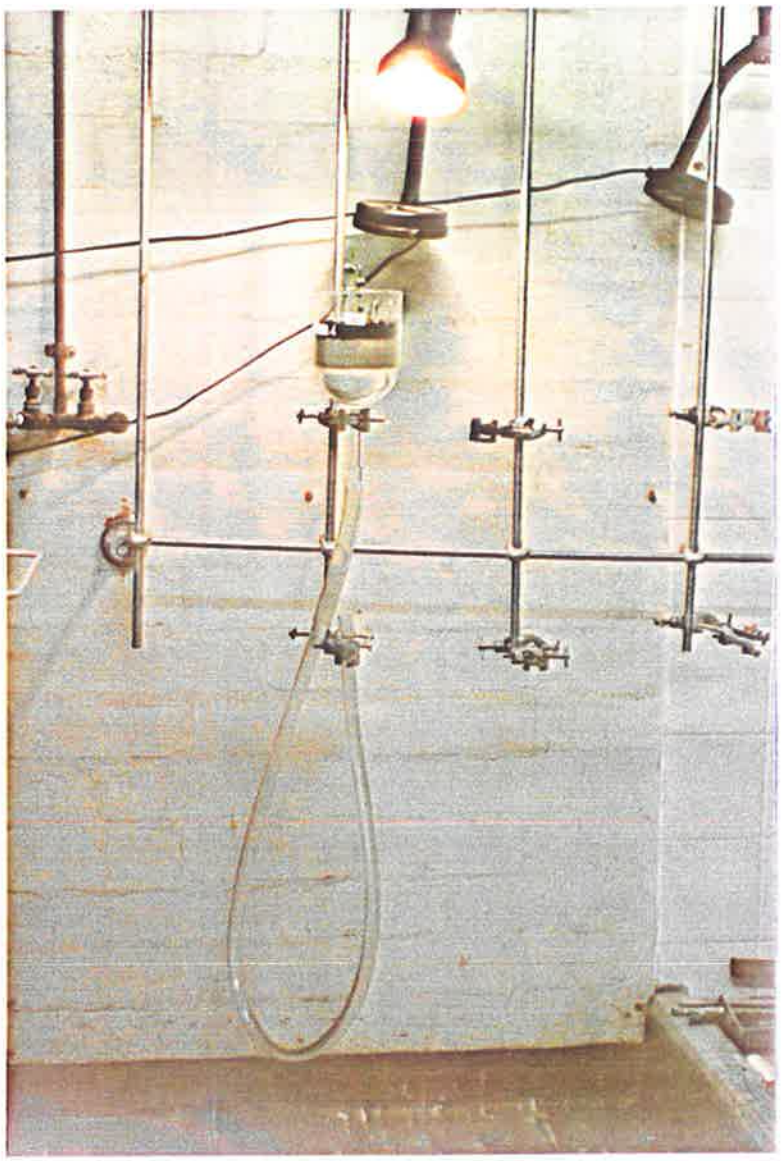


Fig. 4.3 Plant species growing under osmotic stress.

Table 4.2 Gravimetric water content (W) and pH of Young Sand at different osmotic potentials (MPa) measured at the end of each growth period.

Replicate No.	W					pH				
	0.0	-0.1	-0.25	-1.0	*Mean* ± s.e.	0.0	-0.10	-0.25	-1.0	*Mean* ± s.e.
1	0.257	0.236	0.254	0.256	0.251±.01	6.2	6.3	6.1	5.9	6.13±.15
2	0.243	0.258	0.228	0.240	0.242±.02	6.1	5.9	6.0	6.1	6.03±.08
3	0.250	0.227	0.247	0.245	0.240±.04	6.2	6.2	6.3	6.2	6.23±.05
4	0.263	0.248	0.236	0.226	0.243±.01	6.0	6.0	6.1	6.1	6.05±.05
5	0.238	0.233	0.254	0.230	0.239±.09	6.0	5.9	5.9	5.9	5.93±.04
6	0.255	0.250	0.239	0.261	0.251±.01	6.1	5.9	6.2	6.1	6.08±.11
7	0.260	0.246	0.253	0.239	0.250±.03	6.2	6.3	6.2	6.3	6.25±.05
8	0.245	0.231	0.261	0.241	0.245±.01	6.0	6.0	5.9	6.1	5.98±.04
9	0.227	0.258	0.242	0.223	0.238±.01	6.2	6.1	6.1	5.9	6.07±.11
10	0.259	0.222	0.249	0.210	0.235±.02	6.1	6.0	6.2	6.1	6.10±.07
Mean	0.255	0.241	0.246	0.237		6.1	6.1	6.1	6.1	
±s.e.	0.01	0.02	0.01	0.01		0.08	0.15	0.13	0.14	

s.e. = standard error

different osmotic potentials were also similar and in the range 14% ≤ f_a ≤ 19% (mean 17%). These figures are important because growth of roots could be influenced differently by deviation in the value of any one of these properties.

4.3.2 Root elongation

Elongation of roots of all plant species was significantly reduced by decreasing osmotic potential (Table 4.3). There are interesting trends in the response of the different species to osmotic potential. Generally, monocotyledonous species were less affected than dicotyledonous species by stress at lower levels of -0.25 and -0.5 MPa while at -1.0 MPa it was the opposite. This is clearly reflected when RRE is considered (Fig. 4.4). The average RRE for monocotyledons at -0.25 and -0.5 MPa potentials were 0.48 and 0.20 while those of dicotyledons were 0.37 and 0.15 respectively. However, at -1.0 MPa the RRE for monocotyledons is 0.02 while that of dicotyledons is 0.05. There are also clear differences among the species within the broad classifications of monocotyledons and dicotyledons.

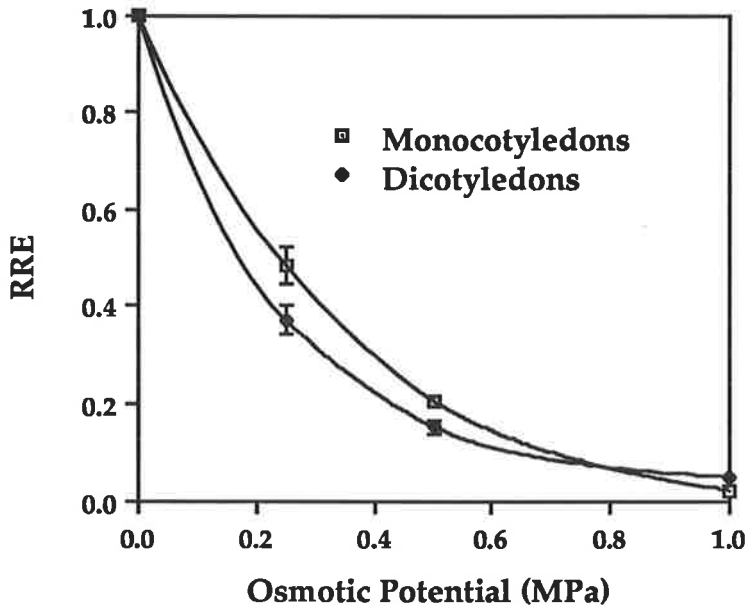


Fig. 4.4 Influence of osmotic potential on RRE of monocotyledonous and dicotyledonous species. Bars are standard errors of means.

Table 4.3 Effect of osmotic potential on root elongation and relative root elongation of the species. Values are means ± standard error.

Plant species	Root elongation (mm)						Relative root elongation			
	Osmotic potential (MPa)				LSD		Osmotic potential (MPa)			
	0.0	-0.25	-0.50	-1.00	$P \leq 0.01$	$P \leq 0.001$	0.0	-0.25	-0.50	-1.00*
Monocotyledons										
Barley	48.2±2.4	24.1±1.6	8.3±0.8	0.70±0.1	5.4	7.1	1.0	0.50	0.17	0.015a
Oats	48.8±2.1	20.9±1.5	9.6±0.5	1.00±0.1	6.7	9.6	1.0	0.43	0.20	0.021c
Rhodesgrass	26.7±1.3	12.3±1.0	6.2±0.4	0.46±0.0	3.1	4.1	1.0	0.46	0.23	0.017b
Ryegrass	29.8±0.9	15.3±1.1	5.8±0.5	0.53±0.0	2.9	3.8	1.0	0.51	0.20	0.018b
Wheat	44.7±2.0	23.1±1.7	10.1±0.9	0.75±0.1	5.8	7.6	1.0	0.52	0.23	0.017b
Mean	39.6	19.1	8.0	0.69			1.0	0.48	0.20	0.017
Dicotyledons										
Faba bean	32.9±1.7	9.6±0.5	5.7±0.4	2.1±0.2	3.3	4.3	1.0	0.29	0.17	0.064f
Lucerne	28.3±1.1	12.0±0.8	4.8±0.3	1.3±0.2	2.5	3.3	1.0	0.42	0.17	0.046d
Lupin	49.5±1.9	18.7±0.7	6.9±0.6	2.2±0.1	4.1	5.4	1.0	0.38	0.14	0.044d
Pea	32.1±1.6	14.3±1.1	5.9±0.5	1.8±0.2	3.6	4.7	1.0	0.46	0.18	0.056e
Safflower	35.5±2.2	10.9±0.7	3.7±0.4	1.2±0.2	5.4	7.1	1.0	0.31	0.10	0.034c
Mean	35.7	13.1	5.4	1.7			1.0	0.37	0.15	0.048

*Means within this column with the same letter are not significantly different ($p \leq 0.05$) by the Tukey's test.

4.3.3 *Root diameter*

The responses of root diameters to osmotic stress are presented in Table 4.4. The responses for all the species can clearly be divided into two regions. In the first, diameters increase with increasing stress and the second in which diameters decrease with increasing stress. It is interesting to note that the point of inflection after which diameters start to decrease seem to occur at the same potential (-0.25 MPa) for most of the species.

There are also differences between the species (Fig. 4.5). Generally the monocotyledons (with smaller diameters) thickened more than dicotyledons at -0.25 and -0.5 MPa while at -1.0 MPa, dicotyledons have bigger RRD than the monocotyledons. There were no visible symptoms of PEG toxicity on the plants except that roots in some of the treatments looked weak and started to wilt.

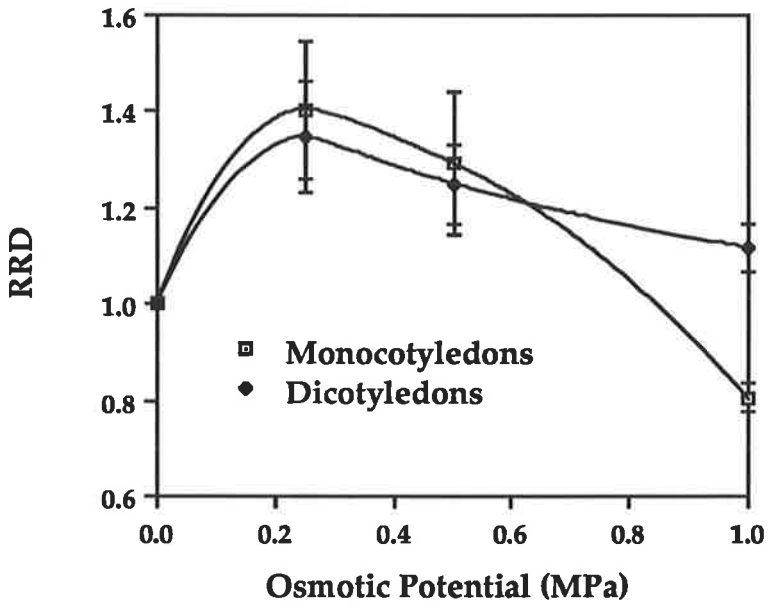


Fig. 4.5 Influence of osmotic potential on RRD of monocotyledonous and dicotyledonous species. Bars are standard errors of means.

4.3.4 *Ranking of species*

Plant species were ranked according to RRE and RRD at the different stress levels (Table 4.5). There is a consistent trend in the results for both RRE and RRD. In both cases, monocotyledonous species are on top ranks at potentials of -0.25 and -0.50 MPa. However, at the potential of -1.0 MPa, it is the opposite. The reason for this change is not known. However, since our interest is to screen species with ability to penetrate soils of high strength, the lowest potential

Table 4.4 Effect of osmotic potential on root diameter and relative root diameter of the species. Values are means ± standard error.

Plant species	Root diameter (mm)						Relative root diameter			
	Osmotic potential (MPa)				LSD		Osmotic potential (MPa)			
	0.0	-0.25	-0.50	-1.00	$P \leq 0.01$	$P \leq 0.001$	0.0	-0.25	-0.50	-1.00
Monocotyledons										
Barley	0.51±.03	0.73±.04	0.71±.03	0.40±.01	0.12	0.18	1.0	1.43	1.39	0.78a
Oats	0.59±.02	0.83±.04	0.75±.04	0.47±.01	0.13	0.18	1.0	1.41	1.27	0.80b
Rhodesgrass	0.23±.01	0.37±.02	0.33±.01	0.19±.00	0.05	0.07	1.0	1.61	1.43	0.83b
Ryegrass	0.37±.01	0.45±.01	0.39±.01	0.31±.02	0.08	0.11	1.0	1.22	1.05	0.84b
Wheat	0.53±.12	0.71±.02	0.70±.14	0.41±.09	0.12	0.16	1.0	1.34	1.32	0.77a
Mean	0.45	0.62	0.58	0.36			1.0	1.40	1.29	0.80
Dicotyledons										
Faba bean	1.27±.03	1.75±.07	1.58±.05	1.48±.05	0.16	0.21	1.0	1.38	1.24	1.17c
Lucerne	0.44±.02	0.65±.06	0.59±.03	0.46±.02	0.19	0.25	1.0	1.48	1.34	1.05d
Lupin	1.09±.03	1.43±.01	1.41±.02	1.26±.02	0.13	0.20	1.0	1.31	1.29	1.16c
Pea	1.30±.04	1.52±.04	1.45±.03	1.46±.06	0.16	0.21	1.0	1.17	1.12	1.12e
Safflower	0.68±.03	0.95±.03	0.86±.02	0.74±.05	0.19	0.25	1.0	1.39	1.26	1.08d
Mean	0.96	1.26	1.18	1.08			1.0	1.35	1.25	1.12

Means within this column with the same letter are not significantly different ($p \leq 0.05$) by the Tukey's test.

Table 4.5 Ranking of plant species using RRE and RRD at different osmotic potentials.

Rank position	Osmotic potential (MPa)					
	-0.25		-0.50		-1.0	
	RRE	RRD	RRE	RRD	RRE	RRD
1	Wheat	Rhodesgrass	Rhodesgrass	Rhodesgrass	Faba bean	Faba bean
2	Ryegrass	Lucerne	Wheat	Barley	Pea	Lupin
3	Barley	Barley	Ryegrass	Lucerne	Lucerne	Pea
4	Rhodesgrass	Oats	Oats	Wheat	Lupin	Safflower
5	Pea	Safflower	Pea	Lupin	Safflower	Lucerne
6	Oats	Faba bean	Faba bean	Oats	Oats	Ryegrass
7	Lucerne	Wheat	Lucerne	Safflower	Ryegrass	Rhodesgrass
8	Lupin	Lupin	Barley	Faba bean	Wheat	Oats
9	Safflower	Ryegrass	Lupin	Pea	Rhodesgrass	Barley
10	Faba bean	Pea	Safflower	Ryegrass	Barley	Wheat

(*i.e.* -1.0 MPa) seems to be the most appropriate way of performing this surrogate compaction screening test. The species were thus ranked based on their RRE and RRD at -1.0 MPa and their response at this potential was compared with the rankings of responses of the same plants to mechanical stress (Table 4.6). There was a significant positive Spearman's rank correlation coefficient of 0.90 ($p \leq 0.001$) between RRE and RRD. This shows that there is good agreement in the order of ranking for the two characteristics. In both rankings, dicotyledonous species occupy the top positions while monocotyledons are in lower positions.

Table 4.6 Comparison of the rankings of RRE and RRD for osmotic and mechanical stresses.

Rank Position	Osmotic stress[a]		Mechanical stress	
	RRE	RRD	RRE	RRD
1	Faba bean	Faba bean	Lupin	Pea
2	Pea	Lupin	Pea	Lupin
3	Lucerne	Pea	Faba bean	Safflower
4	Lupin	Safflower	Safflower	Lucerne
5	Safflower	Lucerne	Lucerne	Faba bean
6	Oats	Ryegrass	Ryegrass	Ryegrass
7	Ryegrass	Rhodesgrass	Rhodesgrass	Oats
8	Rhodesgrass	Oats	Wheat	Wheat
9	Wheat	Wheat	Oats	Barley
10	Barley	Barley	Barley	Rhodesgrass

[a] at -1.0 MPa potential

4.3.5 Comparison of osmotic and mechanical stresses

The mechanical stress used in Section 3.0 was a penetrometer resistance of 4.2 MPa and using the appropriate empirical equation (17) of Dexter (1987b):

$$\sigma / \sigma_{max} = 1 - e^{-\alpha Qp} \qquad [4.1]$$

where Q_p is 4.2 MPa, σ_{max} is assumed to be 1.3 MPa and α is 0.5 MPa^{-1}, this corresponds to an external mechanical stress, σ, on the roots of approximately 1.14 MPa. The magnitude of the responses of roots are different for the two methods. This could be a consequence of a number of factors which differed between the two experimental procedures. These include the degree and length

of time the stresses were applied to the roots. In spite of this, however, the two methods can be compared through correlation of the rankings of the characteristics, RRE and RRD. The correlation coefficients were: 0.79*, 0.78*, 0.82** and 0.95** for RRE_m *v* RRE_o, RRE_m *v* RRD_o, RRD_m *v* RRE_o and RRD_m *v* RRD_o respectively. The subscripts *m* and *o* stand for mechanical and osmotic stresses respectively. The asterisks * and ** mean significance at $p \leq 0.01$ and $p \leq 0.001$ respectively. There is a good agreement in the rankings of the species by the two methods.

4.4 Discussion

The results presented here clearly show that the osmotic potential of the root environment has a significant influence on both the elongation and diameter of roots of all species tested. Elongation of roots was reduced by increasing osmotic stress. This was an expected result as similar observations have been made by several other investigators (*e.g.* Kaufmann, 1968; Lawlor, 1969;1973; Michel and ElSharkawi, 1970; Newman, 1966b).

The observation made in this study, that elongation of roots was reduced critically at potentials near -1.0 MPa, is consistent with the results of Kirkegaard *et al.* (1992) who found a zone of optimum radicle growth in pigeon pea to be between -0.01 and -0.5 MPa matric potential and a critical matric potential close to wilting point (-1.5 MPa) in three soils from Queensland, Australia. At this critical potential, the elongation dropped very significantly. Mirreh and Ketcheson (1973) also found that the growth of maize roots was reduced by 50 percent as matric potential decreased from -0.1 to -0.8 MPa in soil having negligible strength. The model of root growth described by Dexter (1987b) however proposes a constant linear decline in root elongation as water potential is reduced from 0 to -1.6 MPa.

The swelling of the roots at an osmotic potential of -0.25 is presumably a typical growth response of roots to stress. Similarly, the reduction in the diameters of the roots at higher osmotic stresses (-0.5 and -1.0 MPa) is interesting. Whiteley and Dexter (1981a) found that osmotic stress of -1.5 MPa by PEG molecular weight = 20,000 resulted in shrinkage of the root diameters by 35-40% in wheat and pea and by more than 50% in safflower. They explained these effects as being a direct result of changes in turgor pressure of the root cells. They described the point of inflection at which root diameters start to decrease as the point of 'limiting plasmolysis'. This is the point at which the roots lose their rigidity and the diameter of the root begin to decrease significantly (Lockhart, 1965). It should be mentioned here that there was no such reduction in diameter of roots in the compaction test reported in Section 3.

The increases in diameter of roots observed at lower potentials (-0.25 and -0.5 MPa) are similar to those observed in roots grown under mechanical stress. However, it is not clear whether the mechanisms responsible for the increase in root diameter at these potentials are the same or not. Elucidation of the mechanisms responsible for these physiological responses are beyond the scope of this thesis. The important observation here is that the two methods of stressing plants produced radial thickening of the roots. Abdalla *et al.* (1969) and Barley (1963) have proposed that this growth behaviour could be responsible for the ability of roots to penetrate compact soils. Since the osmotic effects of PEG on root growth used in this experiment gave results which agree closely with those obtained for the same species grown under mechanical stress in Section 3.0, the practical significance of this finding is that osmotic stress by PEG could be used as an easier and more rapid method for screening and selecting plant species for the ability of their roots to thicken under stress. The results of the work reported in Sections 3.0 and 4.0 made it possible to select some species for investigating whether plants do benefit from thick roots when penetrating strong soils. The next Section reports a study in which the ability of roots of selected plant species to penetrate strong soil was investigated in the field.

SECTION 5

Field Evaluation of Laboratory Techniques for Predicting the Ability of Plant Roots to Penetrate Strong Soil

5.1 Introduction

It has already been mentioned in Section 1.0 that compaction of soil below the depth of normal tillage (subsoil compaction) by heavy axle loads is an increasing concern because of its persistence and consequent detrimental effects on crop yields. Alleviation of subsoil compaction by mechanical means is expensive and natural ameliorative forces such as wet/dry, freeze/thaw cycles and biological activity have limited effects in this layer (Blake *et al.*, 1976; Voorhees, 1983). The use of plant roots with superior ability to penetrate the strong subsoil layer may offer a viable alternative to deep tilling by heavy machinery.

In Sections 3.0 and 4.0 of this thesis, two laboratory methods of screening plant species for the ability of their roots to penetrate strong soil were developed. The objective of the work reported in this section was to evaluate the penetration of compact soil by roots of plants selected by use of the two techniques, and to compare the accuracy of the two methods in predicting the penetration of roots in the field.

5.2 Materials and methods

5.2.1 Site, location and soil descriptions

The study was conducted at Roseworthy (lat. 35° 30'S, long. 138°40'E) which is located about 40 km north east of Adelaide, South Australia. The site has a Mediterranean climate with cool, wet winters (June to August) and warm, dry summers (December to March). The average annual rainfall is 450 mm most of which falls during the winter and early spring months. The area supports mixed farming practices and is dominated by cereal/legume-based pasture rotations. This site was chosen because it has been under intensive cultivation with conventional tillage equipment for over 50 years and a compact layer had developed below the tilled layer, between about 0.1 and 0.2 m depth (Fig. 5.1a). The flat terrain of the site made it ideal for this study.

The soil is a member of the red-brown earths and is classified as a Dr 2.43 (Northcote, 1979) or as a Calcic Rhodoxeralf (Soil Survey Staff, 1975). The surface soil is a well drained fine sandy loam. Some properties of the soil are given in

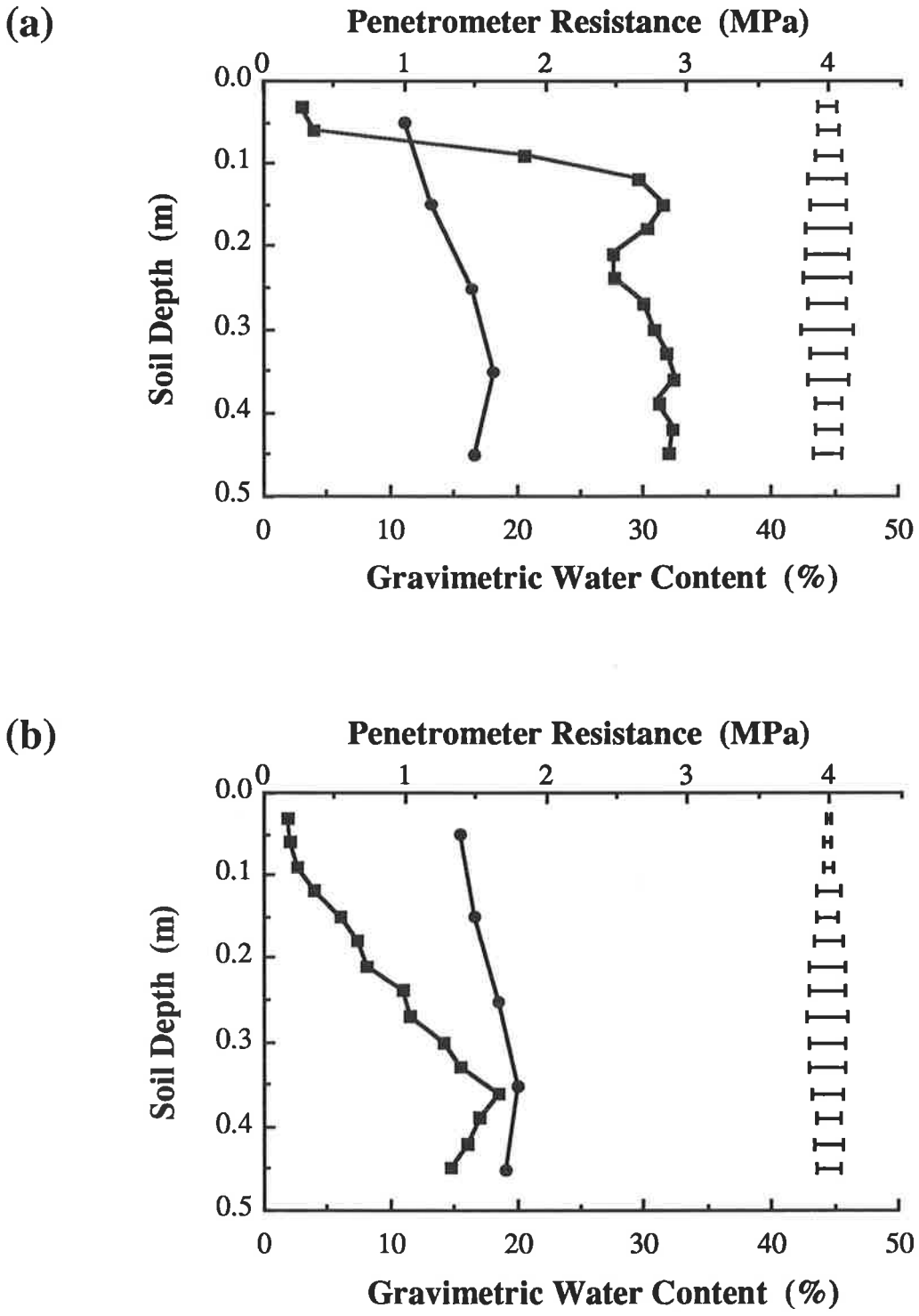


Fig. 5.1 Penetrometer resitance (■) and gravimetric water content (●) for the compacted (a) and uncompacted (b) plots at the time of first sampling of the roots. Bars are standard errors of means (n = 180) for penetrometer resistance.

Table 5.1. The liquid limit was determined by the fall-cone method (Campbell, 1975) and the plastic limit by the rolling of a thread of soil (British Standards Association, 1967).

Table 5.1 Some properties of the red-brown earth used in the field experiment.

	Depth (m)		
Property	0-0.1	0.1-0.2	0.2-0.3
Particle size distribution (% w/w)			
2000-60	80.6	30.6	47.1
60-2	17.9	65.1	32.0
< 2 μm	1.5	4.3	20.9
Water content (kg kg^{-1})			
Plastic Limit	0.19	0.16	0.20
Liquid Limit	0.29	0.27	0.36
pH (1:2.5 soil:water)	7.32	7.78	8.06
Organic carbon (%)	1.73	0.94	0.71
Bulk density (Mg m^{-3})			
Compacted	1.16	1.57	1.43
Uncompacted	1.14	1.25	1.32

5.2.2 Experimental design and treatments

A split plot design was used with each treatment replicated four times in a randomised block layout. The main plots (20 x 10 m) were the two compaction treatments located about 10 m apart. The sub-plots were four blocks each 20 m x 2 m with a 0.5 m buffer between them. Each sub-plot was divided into nine plots 2 m in length where the nine treatments were randomised. Treatments consisted of eight plant species (barley, faba bean, lupin, oats, pea, ryegrass, safflower, wheat) and a non-planted control. The cultivars are the same as those used previously (see Table 3.1). Species were selected from both the top and bottom ends of the rankings of RRE and RRD for the two methods (*i.e.* mechanical and osmotic stress methods) for comparison.

The soil in the uncompacted treatment was deep tilled (in June 1990) to a depth of 300 mm with a Chamberlain John Deere 4280 tractor towing a John Shearer 14 tyne trashworker with narrow points (Ellis, 1990). This reduced the strength of the soil beneath the tilled layer (Fig. 5.1b).

5.2.3 *Management of plots*

The soil was ploughed and rotary cultivated to a depth of 0.1 m in May 1991. Before they were sown, all plots were sprayed with trifluralin (350 g active ingredient ha^{-1}) as a standard pre-sowing, knockdown herbicide. All subsequent weedings were done by hand. Diammonium phosphate (19:20:0) fertiliser was broadcast onto each plot at a rate of 200 kg ha^{-1} and was thoroughly mixed into the ploughed layer by raking. All plots were sown immediately after the first rains in June 1991. Seeds were sown by broadcasting evenly on the flat seedbed at a rate of 120 seeds per plot. Thinning was done after germination to leave 100 plants per plot. The same plant population was used for all the species.

5.2.4 *Root measurements*

Measurements of root growth into the profile were made at two stages of crop growth.

Seedling stage

This stage is defined as that between emergence and 5 weeks after emergence of plants. In most of the species, this was the time when the root system had one, two or three seminal roots. Roots were excavated at this stage to study the effect of root diameter on the behaviour of the seminal roots at the interface between the tilled layer and the strong compacted subsoil. It was hypothesized that the behaviour of roots at this interface would have a large influence on the subsequent penetration and distribution of roots in the strong layer.

Excavation of roots was started when they reached the compacted layer. Roots were sampled using the modified monolith method of Nelson and Allmaras (1969). An open-ended stainless steel frame of 200 x 100 x 100 mm was used to extract the soil monolith. The frame was driven into the soil with a rubber mallet until the top was flush with the soil surface. The undisturbed monolith was extracted with the root system intact by digging around the frame with a knife. Each monolith contained five or six plants. Two monoliths were extracted from each plot.

Counting of roots was done by using a modification of the needleboard technique described by Schuurman and Goedewaagen (1971). A piece of plywood 15 mm thick and measuring 200 x 100 mm with wire needles placed at 50 mm intervals along the board was prepared. The needles were 100 mm long. The board was pressed into the soil on the side of the soil monolith after removing the sampling frame. This held the roots intact in their vertical position. The top loose soil was then carefully scrapped away with a knife. In this way, the

number of roots reaching and penetrating the compact layer could be counted. Percentage penetration was computed by dividing the number of roots that penetrated the compacted layer by the total number of roots that reached the layer and multiplying by 100. Roots of 40 plants were counted for each species.

After the roots had been counted, the remaining soil was washed out by soaking in water and two primary (seminal) roots from each plant were collected at random and their diameters measured. Root diameter was measured with a calibrated microscope eyepiece at distances of 1, 3 and 5 mm from the tip. The values reported are the means (± standard deviation) of the three measurements. A total of 80 roots were measured for each species.

To compare the sensitivity of the different roots to thicken under mechanical stress, relative root diameters (RRD) were computed. This was done by expressing the mean diameters of roots from compacted plots relative to those from uncompacted plots *i.e.* RRD = d_c/d_r where d_c and d_r are the mean diameters of the roots from compacted and uncompacted plots respectively.

Penetrometer resistance was measured immediately after root sampling in each plot. This was done using a Bush recording penetrometer (Anderson *et al.*, 1980) at 0.03 m depth increments to 0.45 m. The penetrometer had a cone base diameter of 12.6 mm and an included tip angle of 30°. Five penetrometer probings were taken in randomly chosen spots of each plot. Fig. 5.2 shows the penetrometer in use in the field.

On the same day that the roots were collected, undisturbed soil cores were taken from all the plots in metal rings (76 mm diameter by 76 mm length) for the determination of bulk density, from a location close to the penetrometer probings. Two cores were taken at each 0.1 m depth increment down to 0.3 m. Water content was determined gravimetrically from samples collected sequentially at 0.1 m depths down the profile. Penetrometer resistance and gravimetric water contents were measured again in the profile at two other times during the growing season (in August and November 1991). This was done to monitor the variation in soil strength down the profile during the growing season.

Maturity stage

This stage is defined as the time after the species had stopped growing *i.e.* at harvest. Plants were harvested in November 1991. At that time, roots were sampled to determine the depth to which they had penetrated into the profile. Sampling tubes 10 cm in diameter were hydraulically driven into the soil to a

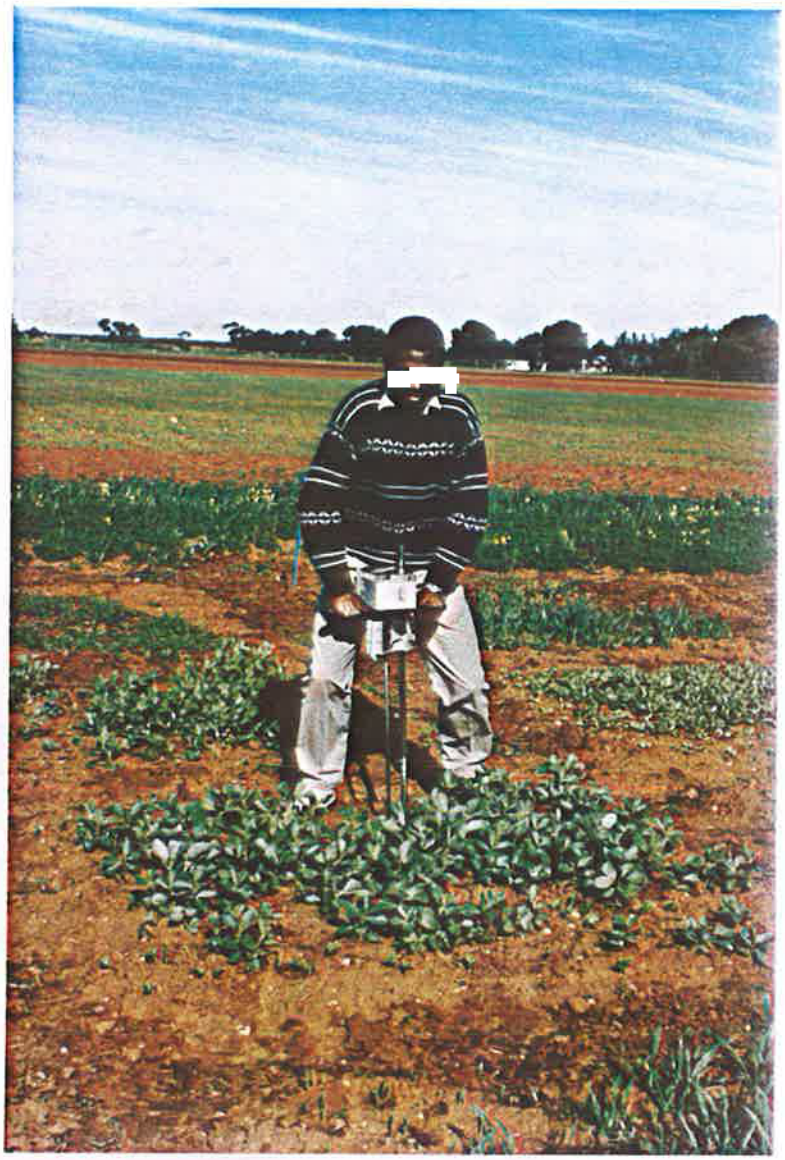


Fig. 5.2 Measuring penetrometer resistance using the Bush recording penetrometer.

depth of 2 m by a prototype gantry supplied by John Shearer Ltd. (Fig. 5.3). The sampling tube was placed on top of a single plant. The soil core was carefully removed from the tube by pushing with a metal rod. The soil was cut into 10 cm segments. Each segment was then broken in the middle to reveal a cross section. The numbers of fresh roots, observable with the naked eye were counted on both faces. The simplicity of this 'core-break' method allowed rapid sampling and counting of roots (Bennie *et al.*, 1987; Drew and Saker, 1980). Two cores were extracted from each plot.

Root count (number) at each depth were used as a measure of rooting density. The number of roots in the 0.0-0.1 m depth was considered to be 100 percent and the numbers found at other depths were expressed as proportions of these and multiplied by 100 to obtain the values (%) of rooting density reported in this section Thus, the values of rooting density for the layers below 0-0.1 m indicate the percentage of roots which penetrated to or beyond that depth. Relative root density (RDR) was calculated to test the hypothesis that the differences in the ability of the various species to penetrate the compacted soil was related to their rooting density under unrestricted conditions of growth (*i.e.* uncompacted soil). This was done by expressing the root density in each depth of the compacted soil as proportion of those of the same species in the uncompacted soil *i.e.* RDR = d_c/d_d where d_c and d_d are the root densities in the depths of the compacted and uncompacted soils respectively.

The accuracy of the two screening methods in predicting the field performance of roots was tested by examining the agreement in the rankings of the species with respect to RRE, RRD (from laboratory tests) and RDR (from the field test). This was done by using Spearman's rank correlation coefficients as described in Section 3.2.4.

5.2.5 Analyses of data

Data were analysed with Genstat 5 (Genstat 5 Committee, 1987) on a Vax computer. Tukey's t-test was used to compare means. Species were ranked based on the root diameter, RRD, percent penetration and RDR.

5.3. Results

5.3.1 Seedling stage

The results of measurements of root diameter and percent penetration are presented in Table 5.2. Root diameters of the plants grown in the compacted soil were thicker than those from uncompacted soil. There are significant ($p \leq 0.05$) differences in the percent penetration of roots of the different species. Species

Fig. 5.3 Extracting soil cores using a sampling tube (ST) mounted on a gantry.

Table 5.2 Root penetration and diameter for the plant species at the seedling stage.

Plant Species	Total roots			Root diameter[a] (mm)		
	Counted[b]	Penetrated	% Penetration[c]	Compacted	Uncompacted	RRD[d]
Barley	226	81	35.7a	0.43±0.08	0.36±0.05	1.19
Faba bean	206	118	57.3c	1.52±0.27	0.81±0.16	1.88
Lupin	245	144	58.8c	1.47±0.19	0.83±0.12	1.79
Oats	168	71	42.2b	0.54±0.08	0.40±0.08	1.35
Pea	219	129	58.9c	1.28±0.15	0.71±0.12	1.80
Ryegrass	326	102	30.1a	0.23±0.04	0.18±0.04	1.28
Safflower	207	126	60.8c	0.93±0.16	0.50±0.10	1.86
Wheat	250	61	33.4a	0.46±0.07	0.39±0.06	1.21

[a] Numbers are means ± standard error.

[b] Refers to number of roots reaching the layer with the highest penetrometer resistance

[c] Means within this column with the same letter do not differ significantly ($p \leq 0.05$) by the Tukey's test.

[d] Relative root diameter

with bigger diameters tended to have greater penetration than those with smaller diameters. Dicotyledonous species had larger diameters and RRD than monocotyledons. There were also differences among the species in both RRD and percent penetration. The significance ($\rho \leq 0.05$) correlation between diameter of roots in compacted soil and penetration was 0.67 and that between RRD and penetration was 0.71.

Rank positions of the species are presented in Table 5.3. Species with higher RRD and root diameters were in the top positions of the rankings while those with smaller diameters and RRDs ranked lower. There was good agreement in the order of the ranks for the three characteristics. The Spearman's rank correlation coefficients were 0.88, 0.74 and 0.86 for root diameter *v* RRD, root diameter *v* percent penetration and RRD *v* percent penetration respectively. All correlations were signicant ($p < 0.001$).

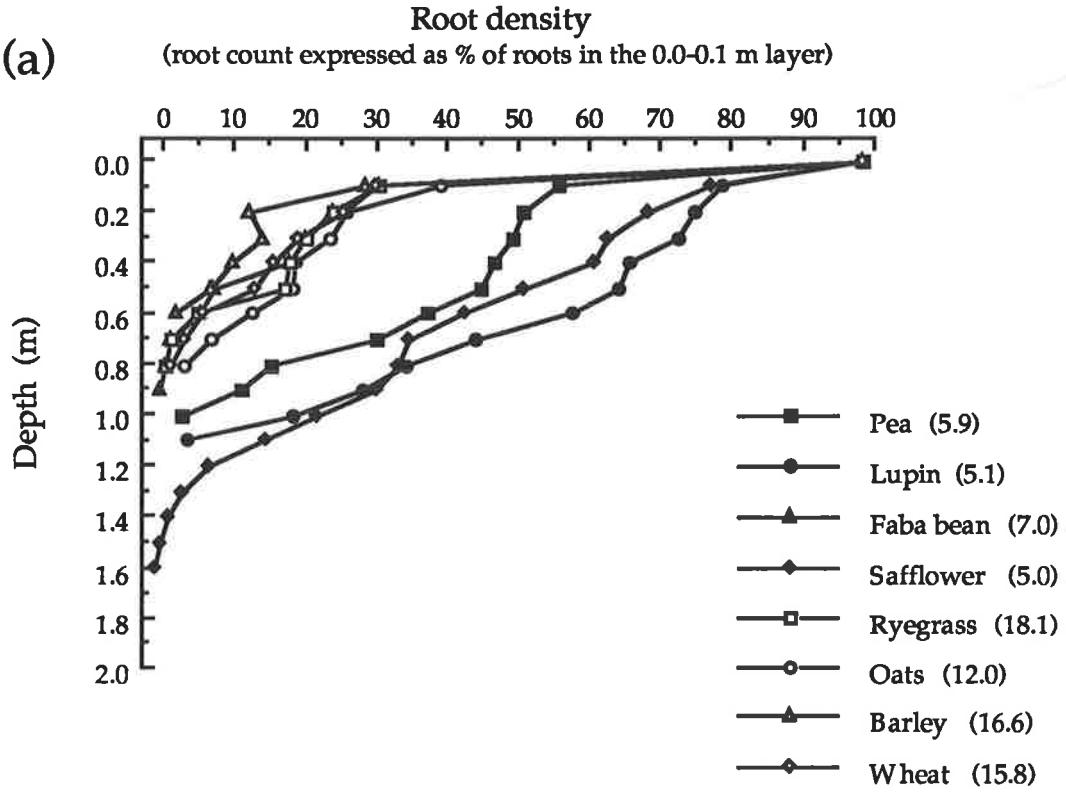
Table 5.3 Ranking of plant species at the seedling stage according to root diameter in the compacted soil, relative root diameter (RRD) and percent penetration.

Position	Ranking characteristic		
	Root diameter	RRD	Percent penetration
1	Faba bean	Faba bean	Safflower
2	Lupin	Safflower	Pea
3	Pea	Pea	Lupin
4	Safflower	Lupin	Faba bean
5	Oats	Oats	Oats
6	Wheat	Barley	Barley
7	Barley	Wheat	Wheat
8	Ryegrass	Ryegrass	Ryegrass

5.3.2 *Maturity stage*

Depth of root penetration and root density of the plants in the compacted and uncompacted soils are presented in Fig. 5.4. The densities of roots of all species in the 0.1-0.3 m depth of the uncompacted soil were higher (mean 86.9%) than those of the compacted soil (mean 45.9%). This means that there was a higher percentage of roots from the surface layer which penetrated to or beyond this depth in the uncompacted than compacted soils. The higher penetration of roots in the uncompacted soil is an obvious result of reduced penetration resistance in this soil compared with the compacted soil.

In the compacted soil, roots of dicotyledonous species except faba bean generally penetrated deeper into the profile than monocotyledons. The maximum



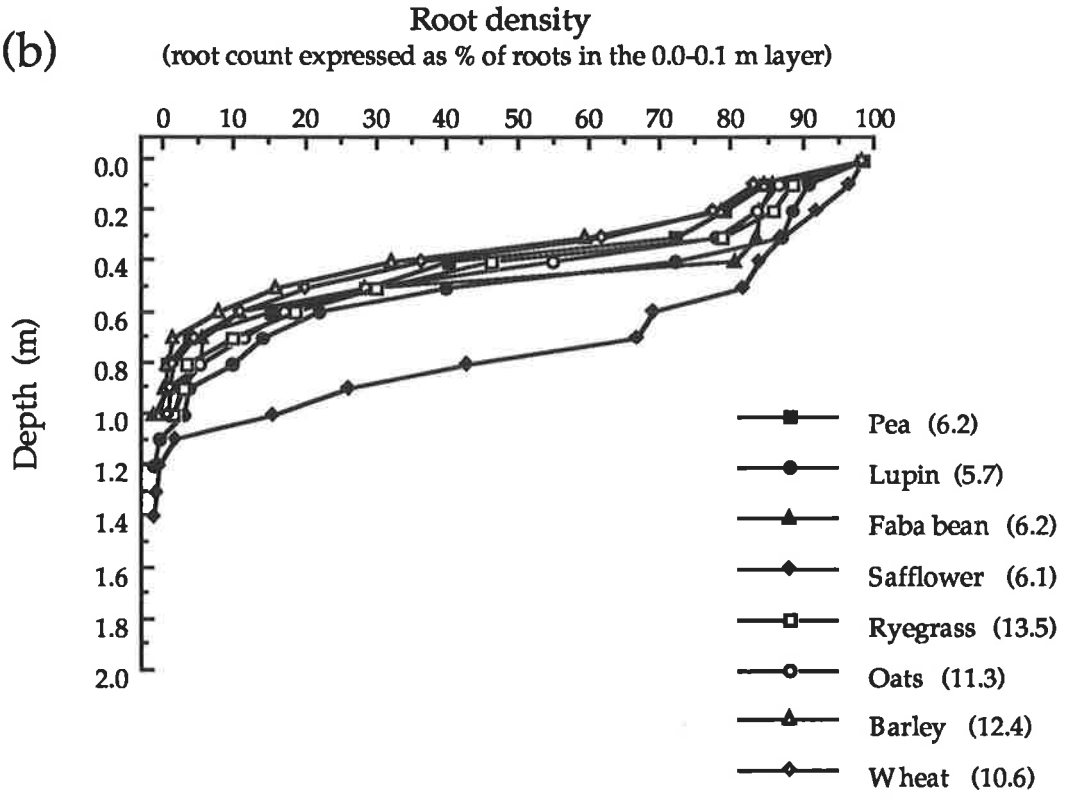


Fig 5.4 Root density (root counts in each layer expressed as % of roots in the 0.0-0.1 m layer) in the profiles of the compacted (a) and uncompacted (b) soils at maturity. Numbers in parenthesis are the mean (n=16) counts of roots in the surface (0.0-0.1 m) layer for each species.

depths to which roots had penetrated this soil were 1.5 m for the dicotyledonous species and 0.90 m for the monocotyledons. A higher proportion of roots from the top layer in dicotyledons penetrated through the layer with the highest penetrometer resistance (0.1-0.30 m) than in monocotyledons. The average rooting densities were 28.3% and 63.4% for monocotyledons and dicotyledons respectively. Lupin and safflower had the highest rooting densities to depth among dicotyledonous species, while oats and wheat were highest among monocotyledons.

The RDRs of the species are presented for each depth in Table 5.4. The RDR for most species decreased in compact layer (0.1-0.3 m), and increased again below about 0.5 m for most species. The lower RDR values in the top 0.5 m show that there was a higher proportion of roots penetrating this depth in the uncompacted than compacted soil. This could be a direct effect of the reduced resistance experienced by the roots in the uncompacted soil. The results indicate that a higher proportion of roots of dicotyledonous species than monocotyledons penetrated the compacted soil and that there were differences between the species within the groups. Lupin and safflower had the highest RDRs among the dicotyledons, while oats and wheat were top among the monocotyledons.

Table 5.4. Relative root densities (RDR)[a] of the species at different depths.

Depth (m)	RDR							
	Faba bean	Lupin	Pea	Safflower	Barley	Oats	Ryegrass	Wheat
0.0-0.1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
0.1-0.2	0.36	0.87	0.66	0.80	0.35	0.46	0.35	0.37
0.2-0.3	0.30	0.85	0.65	0.75	0.17	0.29	0.29	0.34
0.3-0.4	0.25	0.84	0.69	0.72	0.26	0.34	0.27	0.33
0.4-0.5	0.24	0.91	1.16	0.73	0.34	0.35	0.40	0.45
0.5-0.6	0.29	1.59	1.54	0.63	0.48	0.66	0.59	0.67
0.6-0.7	0.54	2.54	2.34	0.62	0.38	0.76	0.32	0.57
0.7-0.8	0.37	2.92	5.75	0.53	np	0.63	0.24	0.80
0.8-0.9	0.26	3.15	7.04	0.78	np	0.64	0.40	0.78
0.9-1.0	0.57	5.71	np	1.13	np	np	np	np
1.0-1.1	np	4.30	np	1.35	np	np	np	np
1.1-1.2	np	3.77	np	4.71	np	np	np	np
1.2-1.3	np	np	np	6.67	np	np	np	np
1.3-1.4	np	np	np	5.71	np	np	np	np
1.4-1.5	np	np	np	10.5	np	np	np	np

[a] Root density in compacted soil as proportion of that in soil uncompacted soil
np =roots of the species did not penetrate to this depth.

5.3.3 *Comparison of the laboratory techiques*

A summary of the rankings of the species for RRE, RRD (from laboratory tests) and RDR (from field) is presented in Table 5.5. The results show that the dicotyledonous species (except faba bean) had consistently higher rankings in all the tests than monocotyledonous species. There is however interchanging of the rank positions for the species in the different tests. This suggests that the characteristics RRE and RDR are only a rough guide to the actual ability of the roots to penetrate strong soil. Correlation coefficients of rankings of the species for RRE, RRD and RDR were 0.53*, 0.74**, 0.51* and 0.67** for RRD$_o$ v RDR, RRD$_m$ v RDR, RRE$_o$ v RDR and RRE$_m$ v RDR respectively. The subscripts o and m stand for osmotic and mechanical stresses respectively and significance levels are given as * ($p \leq 0.05$) and ** ($p \leq 0.01$).

5.3.4 *Variation of penetrometer resistance with soil water content*

The extent to which the layer with the highest penetrometer resistance in the compacted soil restricted root elongation and growth during the growing season depended on soil water conditions of the soil profiles at different times of the year. Fig. 5.5 shows the variations in the penetration resistance in the soil profiles in August and November 1991. The figure shows that the strength of the soil in both soils was reduced by higher water content in August 1991 but was high again in November 1991 when the soil water content was low. The implication of such variation in soil strength during the growing season is that it could mirror the effects of resistance offered by the soil during the early stages of growth - a sort of "compensatory growth" behaviour. A compact soil layer may restrict seminal roots early in the season when the profile is not thoroughly wet, but be soft enough for the penetration of nodal or lateral roots later in the season.

5.4 Discussion

5.4.1 *Seedling stage*

In the laboratory study reported in Sections 3 of this thesis, it was shown that the roots of all the species thickened (increased in diameter) in response to high mechanical impedance in the soil. The magnitudes of the swelling were smaller in the field study than in the laboratory. This difference is attributed to the higher soil strength used in the laboratory and to small scale variations in soil strength which exist in the field, and which roots may be able to exploit. It is interesting to note that the roots which had greater thickening also had a higher percentage penetration into the compacted layer. There are three mechanisms by which the root thickening may aid the penetration into the strong soil. These are

Table 5.5. A comparative summary of the rankings of the species based on RRE, RRD (from the laboratory tests) and RDR (from the field test).

Rank position	Laboratory				Field
	Mechanical stress		Osmotic stress		Root penetration
	RRE	RRD	RRE	RRD	RDR[a]
1	Lupin	Pea	Faba bean	Faba bean	Lupin
2	Pea	Lupin	Pea	Lupin	Safflower
3	Faba bean	Safflower	Lupin	Pea	Pea
4	Safflower	Faba bean	Safflower	Safflower	Oats
5	Ryegrass	Ryegrass	Oats	Ryegrass	Wheat
6	Wheat	Oats	Ryegrass	Oats	Faba bean
7	Oats	Wheat	Wheat	Wheat	Ryegrass
8	Barley	Barley	Barley	Barley	Barley

[a]ranking based on mean RDR of the species in thelayer with the highest penetrometer resistance (0.1-0.3 m depth) layer.

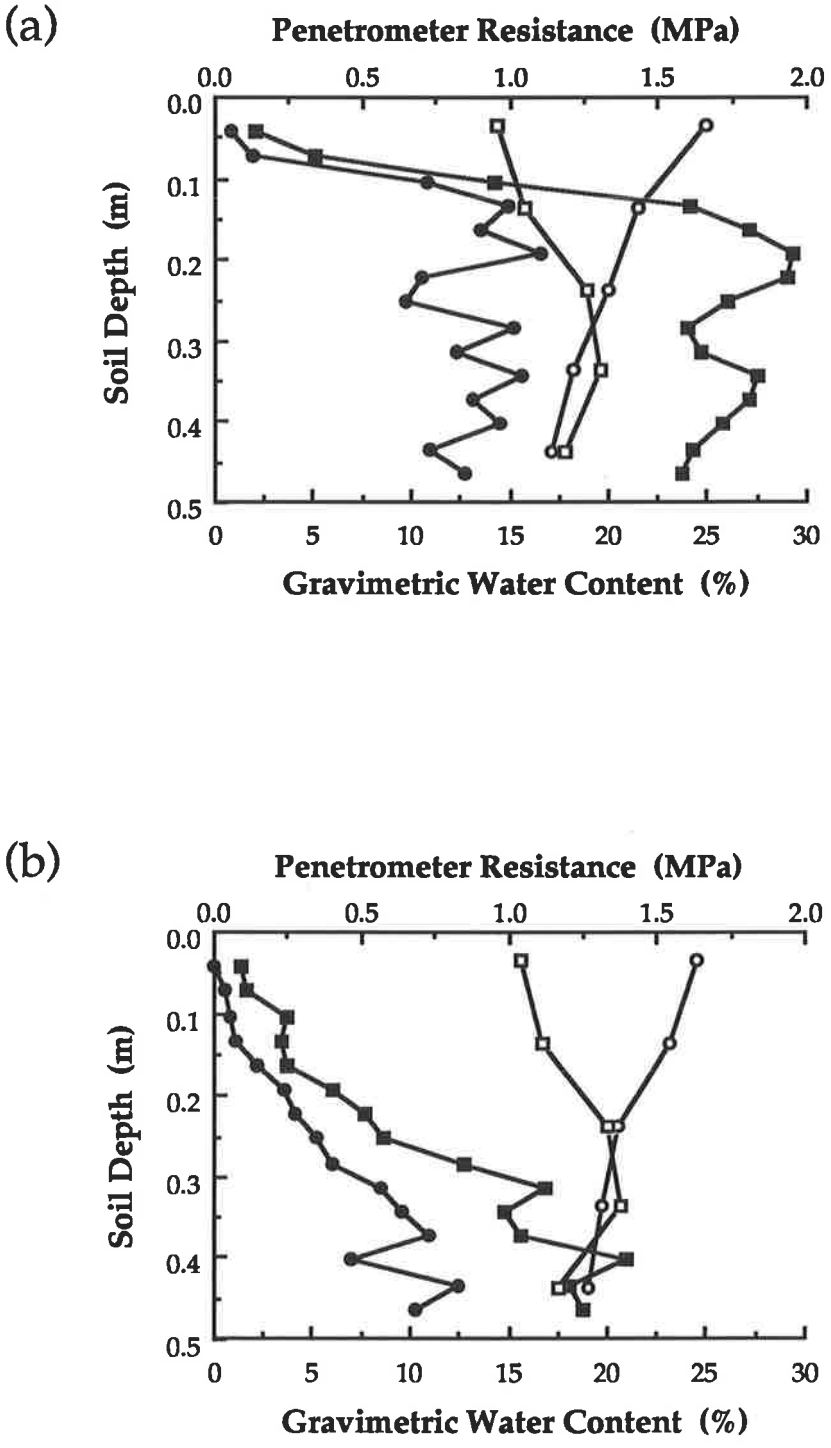


Fig. 5.5 Penetrometer resistance (dark symbols) and gravimetric water content (light symbols) for the compacted (a) and uncompacted (b) plots measured in August (squares) and November (circles) 1992.

the greater resistance of thicker roots to bending, the higher axial pressures exerted by thicker roots, and the stress relief at a root tip caused by thickening. The effects are inter-related but it is logical here to discuss them one by one.

(a) The ability of roots to penetrate a macroscopically structured soil may depend on the elastic properties of the roots (Whiteley and Dexter, 1981a). These properties include the resistance of the root to buckling, which is related to root diameter. The roots with bigger diameters (mostly dicotyledons) would be expected to be more resistant to buckling than those with thinner roots (mostly monocotyledons). This would make the dicotyledonous species more able to penetrate the strong soil than the monocotyledons.

(b) When a root tip is confined axially, it may exert a considerable amount of force in the axial direction (Gill and Bolt, 1955). Misra *et al.* (1986a) showed that the maximum axial root growth pressures which roots can exert are highly dependent on root diameter as discussed in Section 3.0 (see Equation 3.2).

(c) Radial expansion of a root causes a relief of stress, and consequent weakening of soil ahead of the root tip (Abdalla *et al.*, 1969; Barley, 1962; Hettiaratchi, 1990; Hettiaratchi and Ferguson, 1973; Richards and Greacen, 1986). Barley and Greacen (1967) suggested that this could result in tensile failure ahead of the tip. However, it is not necessary for tensile failure to occur for this mechanism to reduce the axial pressure required for root penetration.

It is not possible to discriminate amongst these effects as mechanisms for the observations in this study, that thicker roots expanded more in the strong soil and penetrated more succesfully. The thicker roots of the dicotyledons would presumably have been less prone to buckling and more able to develop the higher pressures necessary to penetrate the harder soil. These roots also expanded radially to a greater extent (*i.e.* had higher RRD values) than the roots of the monocotyledons. They would therefore have benefited from the stress relief of root thickening more than the roots of the monocotyledons.

The extent to which differences in root morphology might have influenced the results of this study is not known but it is possible that the roots of the species with higher penetration could possess some physiological characteristic which increases their ability to penetrate. These properties are discussed in more detail in Section 9.

The results discussed so far were collected at the beginning of the growing season when the plants were young and the soil was still relatively dry (water content less than plastic limit) and very strong (mean penetrometer resistance 3.0 MPa). It was not possible at this stage to say whether the observed effects of root diameters on penetration would influence the subsequent depth of penetration and distribution of the roots. Roots may have additional strategies for entering

the subsoil in the wetter part of the season. Dexter (1986c), for example, suggested that in very wet conditions a root tip might sense a hole at some distance (because of high oxygen concentration in the hole) and change its direction of growth towards the hole. The results obtained at the seedling stage seem to confirm the theoretical predictions that root diameter may have a significant influence on the penetration of roots into strong soil. The significance of the finding is that the result relates not to the controlled and artificial conditions commonly used in most previous studies, but to the heterogeneous soil conditions which occur in the field.

5.4.2 Maturity stage

In terms of the absolute numbers of roots in the 0.0-0.1 m layer (Fig. 5.4), lupin, safflower and pea had more roots in the uncompacted soil than in the compacted soil whereas the other species had more roots in the compacted soil. Species which did not penetrate more into the compact layer had more roots in the surface layer. The implication is that roots of those species that were less well able to penetrate the layer with the highest penetrometer resistance were near the surface.

Lupin, pea and safflower also a had higher proportion of roots in the compacted soil below 0.3 m than in the same depth of the uncompacted soil (hence higher RDRs). The implication might be that having successfully penetrated through compact soil, the roots of these species were then effective at exploiting subsoil resources below the compacted layer. In the uncompacted soil, the plants did not so exploit the resources, presumably because they had no need. This could be a case of compensatory growth when plants with part of their roots growing in unfavourable environments may produce more roots in the more favourable part of the soil than others where conditions are favourable throughout. The other five species (barley, faba bean, oats, ryegrass and wheat) did less well at penetrating the strong layer, and had a smaller proportion of roots below 0.3 m in the compacted soil than in the uncompacted soil.

As noted above, the number of roots which the plant had in the uncompacted soil did not seem to have influenced the penetration of the roots. Species which had large numbers of roots in the top (surface) layer did not have higher penetration through the compact layer. For example faba bean (dicotyledon) and ryegrass (monocotyledon) had the highest numbers of roots in the surface layer of the uncompacted soil but did not have the highest proportions of roots penetrating through the layer with the highest resistance. On the contrary, they had the lowest RDRs. This observation is in contrast with the conclusion of Bennie and Burger (1981) who found from a pot experiment that the

ability of the roots to penetrate strong soil was related to the numbers of roots a plant has in unrestricted conditions. In light of the findings from this study, it is suggested that the ability of roots to penetrate strong soil would be influenced by root numbers only if the soil in which they are growing has an abundance of cracks and pores. In this case, the species with large numbers of roots (mostly monocotyledons) would have a statistical advantage over those with fewer roots (dicotyledons) with regard to entry into these paths of low resistance.

The soil in this study was non-swelling and did not crack on drying. Moreover, it did not have many visible pores. Thus, it is likely that penetration of roots would have been influenced more by mechanisms other than entry of roots into existing channels. Findings reported earlier (see Section 5.4.1) suggest that root diameters could have significant influence on the ability of roots to penetrate strong soil. This has been related to the ability of the roots with bigger diameters to deform the soil more effectively than those with smaller diameters.

The possible effects of the root sampling procedure on RDRs need to be mentioned here. Taking samples directly underneath the plant may have overestimated root development for tap-rooted dicotyledons and underestimated that of monocotyledons particularly in the 0.0-0.1 m layer. The plant root densities directly underneath the plants of monocotyledonous species can be low due to the orientation of nodal roots (van Noordwijk *et al.*, 1985). However, as counting was made on roots which were vertically oriented to the breakage face of the core, the error caused by the sampling procedure would have been small.

5.4.3 Ability of the two laboratory techniques to predict the penetration of roots in the field

A comparison of RRE and RRD as predictors of field performance of roots (Section 5.3.3) showed that the laboratory method involving mechanical stress had significantly higher ($p < 0.05$) correlations with field penetration for both RRE and RRD than that involving osmotic stress. The better agreement in the rankings of the field result with mechanical stress method could be due to similarity in conditions under which the roots grew in the two situations. It could also be related to the efficiency of the plant roots to osmoregulate in the two stress conditions. Greacen and Oh (1972) found that pea roots osmoregulated 100% against total soil water potential down to -1.5 MPa potential while they osmoregulated by 70% efficiency against mechanical resistance (see Section 2.4.1). The results from this work however suggest that the method involving mechanical stress is more suitable for screening species for field performance of their roots. In both methods however, RRD had higher correlations with the field

penetration than RRE. This would suggest that RRD is a better indicator of the ability of roots to penetrate strong soil than RRE.

5.5 Concluding remarks

The results of this study show that species differ in the ability of their roots to penetrate strong soil. The two laboratory screening techniques were in good agreement with the results of the field test. Dicotyledonous species seemed to be better in general than monocotyledons at penetrating the layer with the highest penetrometer resistance. It is not known whether these differences in penetration also affected the physical properties of the soils. The next step in the study was therefore to investigate the changes in soil physical and hydraulic properties after growth of the plants. The results of these investigations are reported in the next section.

SECTION 6

Influence of Roots on the Physical and Hydraulic properties of a Red-brown Earth

6.1 Introduction

The objective of the work reported in this section was to study the changes in selected soil physical properties induced by roots. The properties investigated included a) cloddiness of soil, b) aggregate stability, c) aggregate tensile strength and d) water sorptivity of soil. These properties were chosen because they can give a good indication of the structural condition of the soil at the time of measurement and also because they could be measured easily within the time available for the study.

6.2 Materials and methods

6.2.1 Experimental treatments and design

Eight plant species and two soil treatments (compacted and uncompacted) were used. Details of the field site, soil, treatments, design and management of plots have already been given in Sections 5.2.1 and 5.2.2.

6.2.2 Soil aggregate-size distribution (ASD)

The distribution of aggregate sizes was determined by the method of Kemper and Rosenau (1986). Samples for this analysis were collected in March 1992. Soil was cut away with a shovel at depths of 0-0.1, 0.1-0.2, 0.2-0.3, 0.3-0.4 m into a cloth bag. The soil was air-dried before sieving to determine aggregate size distribution. ASD was determined by dry sieving air-dried samples on a stack of sieves with openings of 16, 8, 4, 2 mm. A mechanical sieve shaker rotating at 30 rpm was used for three minutes to separate the aggregates into different size fractions (> 16, 16-8, 8-4, and 4-2 mm). After sieving, the fractions were weighed and calculated as proportions of the whole mass of the sample. Three replications were sieved for each depth. The results are expressed as the percentage of the soil > 8 mm diameter. This limit was chosen because it is difficult to maintain a uniform sowing depth with seedbeds consisting of aggregates larger than this size (Braunack, 1978).

6.2.3 Aggregate stability (AS)

The stability of aggregates (2.0-4.0 mm in diameter) in water was determined using initially air-dry aggregates in the wet-sieving technique (Yoder,

Oven-dried aggregates were used to remove the variation in water content between treatments. As tensile strength is much dependent on soil water content it was only by drying the aggregates that the treatments could be compared.

1936). The equivalent of 20 g of oven-dried aggregates was placed in the uppermost sieve of a set of 4 with openings 2.0, 1.0, 0.5 and 0.25 mm diameter. Oven-dry weights were calculated using water correction factors determined from sub-samples of each air-dry soil. The sieves containing the air-dry aggregates were then immersed in water. The water level was adjusted so that the aggregates on the upper sieve were just submerged at the highest point of oscillation. The sieve stack was oscillated through an amplitude of 3.5 cm at a rate of 25 min^{-1} for 3 minutes. Aggregate stability was expressed as the proportion of the > 2.0 mm fraction stable to the wet sieving treatment (Williams *et al.*, 1966).

6.2.4 *Aggregate tensile strength (ATS)*

Tensile strength was determined on aggregates of 8-16 mm size range by an indirect tension (crushing) test (Dexter, 1988b). Fifty aggregates from each treatment and depth were dried in the oven at 105°C for 24 h and cooled in a desiccator before being crushed. Each of the aggregates was crushed by a vertical force applied between two flat horizontal plates on a loading frame (Fig. 6.1). Tensile strength (kPa), was calculated for each aggregate using the equation

$$Y = 0.576\ F/d^2 \qquad [6.1]$$

where F is the force (N) required to fracture the aggregate and d is the 'effective spherical diameter' (in m) of each aggregate calculated as

$$d = \underline{d}\,(M_o/M_a)^{0.33} \qquad [6.2]$$

where $\underline{d}$ is the mean sieving diameter (0.012 m), M_o is the mass (kg) of the individual aggregate, and M_a is the mean mass (kg) of the twenty aggregates in the batch (Dexter and Kroesbergen, 1985).

6.2.5 *Water sorptivity of soils (S_o)*

Sorptivity was used as a quick and easy method to measure a field hydraulic property of the soil to indicate treatment-induced changes in the ability of the soil to absorb water. Sorptivity is useful not only as a component of the infiltration equation, but also as an indicator of soil structure (Walker and Chong, 1986; White and Sully, 1987). It is in the latter sense that the measurements are used in this paper. Disc permeameters do not disturb the surface soil and the flow of water through macropores can be controlled. Measurements were made in autumn (April 1992) when the soil was very dry. This was five months after plants were harvested and by this time, most of the roots had decayed to leave

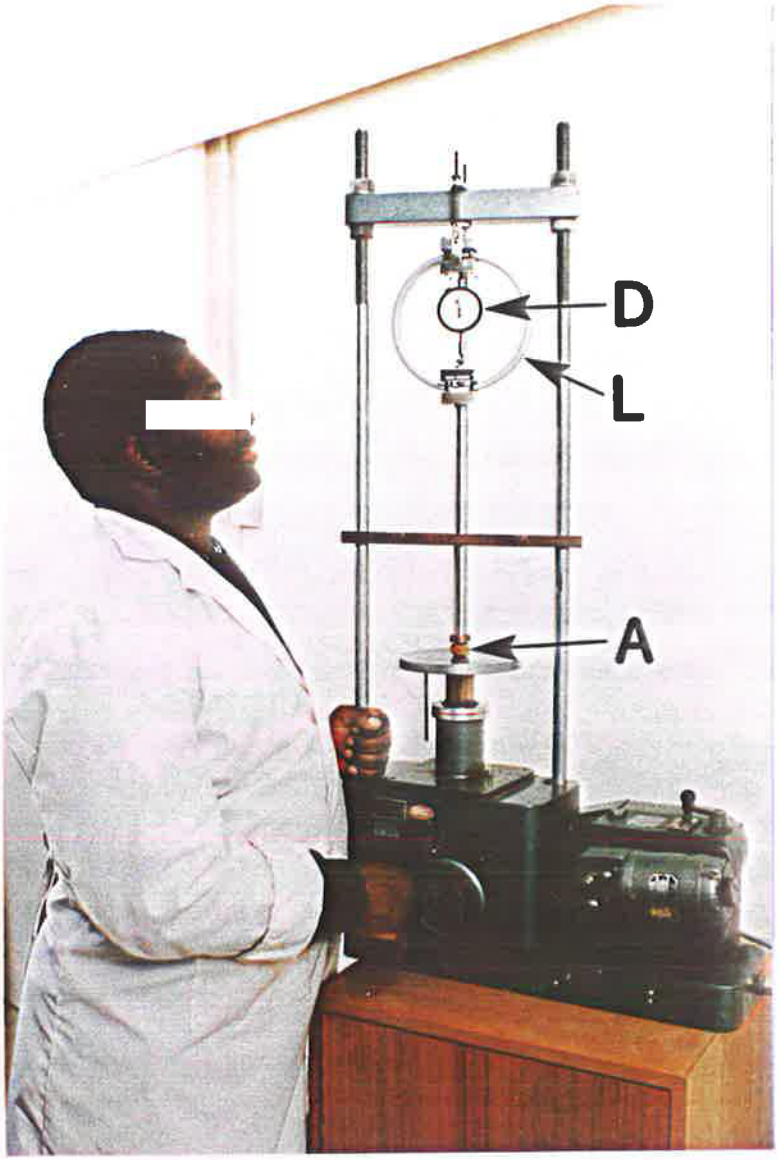


Fig. 6.1 Crushing an aggregate (A) between two flat parallel surfaces on a loading frame. Crushing force is measured by a dial gauge (D) in a load ring (L).

the biopores. Measurements were made at randomly selected positions in each plot under ponded conditions (0.05 kPa) and at a water supply pressure of - 0.1 kPa, which is equivalent to a nominal pore size of 3 mm. Thus, only pores of nominal diameter 3 mm or less contributed to the flow of water (Perroux and White, 1988). Sorptivity was calculated from the early time data of cumulative infiltration measured at depths of 0.0-0.1, 0.1-0.2, 0.2-0.3 and 0.3-0.4 m.

An area about 200 mm^2 was cleaned by clipping any vegetation down as low as possible and removing any large stones visible at the surface. The ring was inserted about 5 mm into the soil and the permeameter was set level on the ring. If the surface was not flat, the ring was filled with some fine river sand as a contact material between the bottom of the permeameter and the surface. The sand was smoothed by drawing a steel blade across the top of the ring. The permeameter reservoir was filled with water and the permeameter was repositioned on the ring. Infiltration was recorded at predetermined times (t) of 0.001, 0.003, 0.004, 0.006, 0.007, 0.008, 0.017, 0.042, 0.083, 0.117, 0.167, 0.250, 0.417, 0.500 and 1 h. Fig. 6.2 shows the disc permeameter in use during the measurements of infiltration.

Cumulative infiltration (Q) at any time was the total amount of water that had gone into the soil at time (t) divided by the cross sectional area (πr^2) of the disc and was calculated as

$$Q/\pi r^2 = (SR\text{-}SR_i)(RC)/\pi r^2 \qquad [6.3]$$

where SR is the scale reading on the disc reservoir at the time of measurement, SR_i is the initial scale reading, and RC is the reservoir calibration. Sorptivity was calculated by determimng the slope of the straight line portion of the cumulative infiltration ($Q/\pi r^2$) against square root of time ($t^{-0.5}$) graph (CSIRO, 1988). Two measurements were made at each depth for each treatment in both the compacted and uncompacted soils.

6.2.6 *Analyses of data*

Data were analysed by the Genstat 5 program as described in Section 5.2.5.

6.3 Results

A summary of the analyses of variance for the soil properties investigated is presented in Table 6.1. The results show that there were significant interactions (species x depth) for all the properties in both the compact and uncompacted soils. This implies that the influence of root growth of the different species on soil

Fig. 6.2 Measuring sorptivity of water using a disc permeameter.

properties differed with depth. The plots of the interactions for the different properties will be presented.

Table 6.1. Summary of analyses of variance for the different soil properties of the compacted and uncompacted plots.

Source of variation	df	Compacted Soil				Uncompacted Soil			
		ASD	AS	S_o	ATS	ASD	AS	S_o	ATS
Species	8	***	**	***	**	***	***	***	*
Depth	1	**	***	***	**	***	*	***	*
Species x Depth	8	***	***	**	*	***	*	*	*

significance given by * ($p \leq 0.05$), ** ($p \leq 0.01$), *** ($p \leq 0.001$)
ASD = Aggregate size distribution; AS = Aggregate stability; S_o = Sorptivity; ATS = Aggregate tensile strength.

The distribution of aggregates sizes of the soil after growth of plants are presented in Fig 6.3. The soil in the uncompacted plots had lower percentage of coarse (> 8 mm) aggregates at all depths and species. This could be due to the deep tillage operation, which could have reduced the size of the aggregates. In the compact soil, plots which had plants in them had significantly ($p \leq 0.01$) fewer coarse aggregates in the top three layers than for the control. A general observation is that soils with monocotyledonous species had lower percentages of coarse aggregates in the 0.1-0.3 m depth than soil with dicotyledons.

Results for the stability of aggregates in water are presented in Fig. 6.4. The stabilities of aggregates in the two soils were not very different, although the aggregates of soil from the compacted plots were slightly more stable than those from the uncompacted plots. In both cases, the planted soil had higher stability of aggregates than unplanted soil presumably due to the presence of roots. Aggregates from soils planted with monocotyledonous species were more stable than those from soil planted with dicotyledonous species.

Tensile strength of the aggregates (8-16 mm) at different depths is presented in Fig. 6.5. Generally, aggregates in the surface (0.0-0.1 m) layer of both soils had lower tensile strength than those in the 0.1-0.2 m and 0.2-0.3 m depths. The increase in strength of the surface aggregates could be due to higher clay content in the latter layers compared with the surface layer. In the 0.3-0.4 m depth however, the ATS is lower than that of the aggregates from 0.1-0.2 m and 0.2-0.3

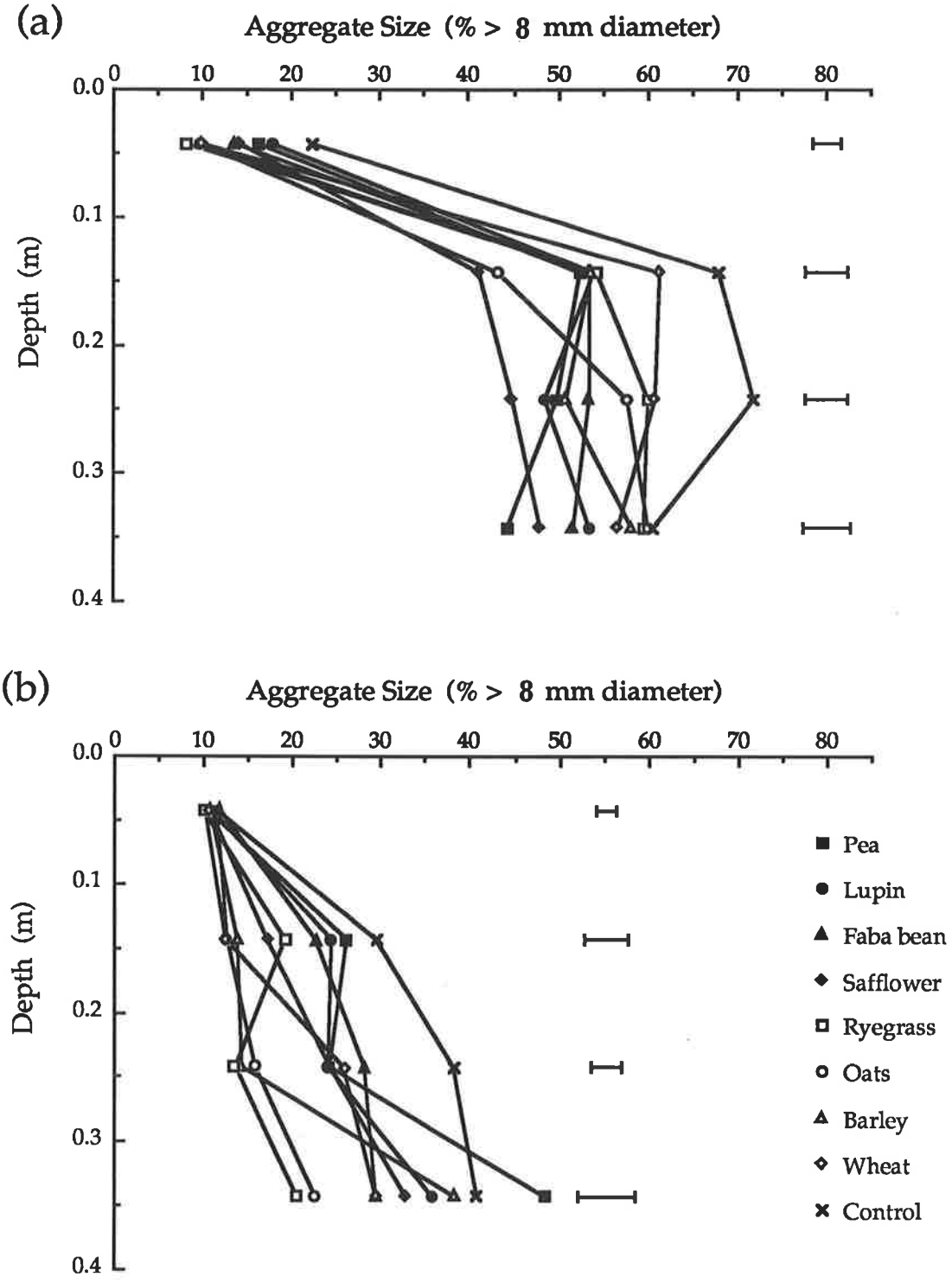


Fig 6.3 Effect of plant species on size distribution of aggregates (% > 8 mm) at different depths for the compacted (a) and uncompacted (b) soils. Bars are LSD ($p \leq 0.05$) for each depth.

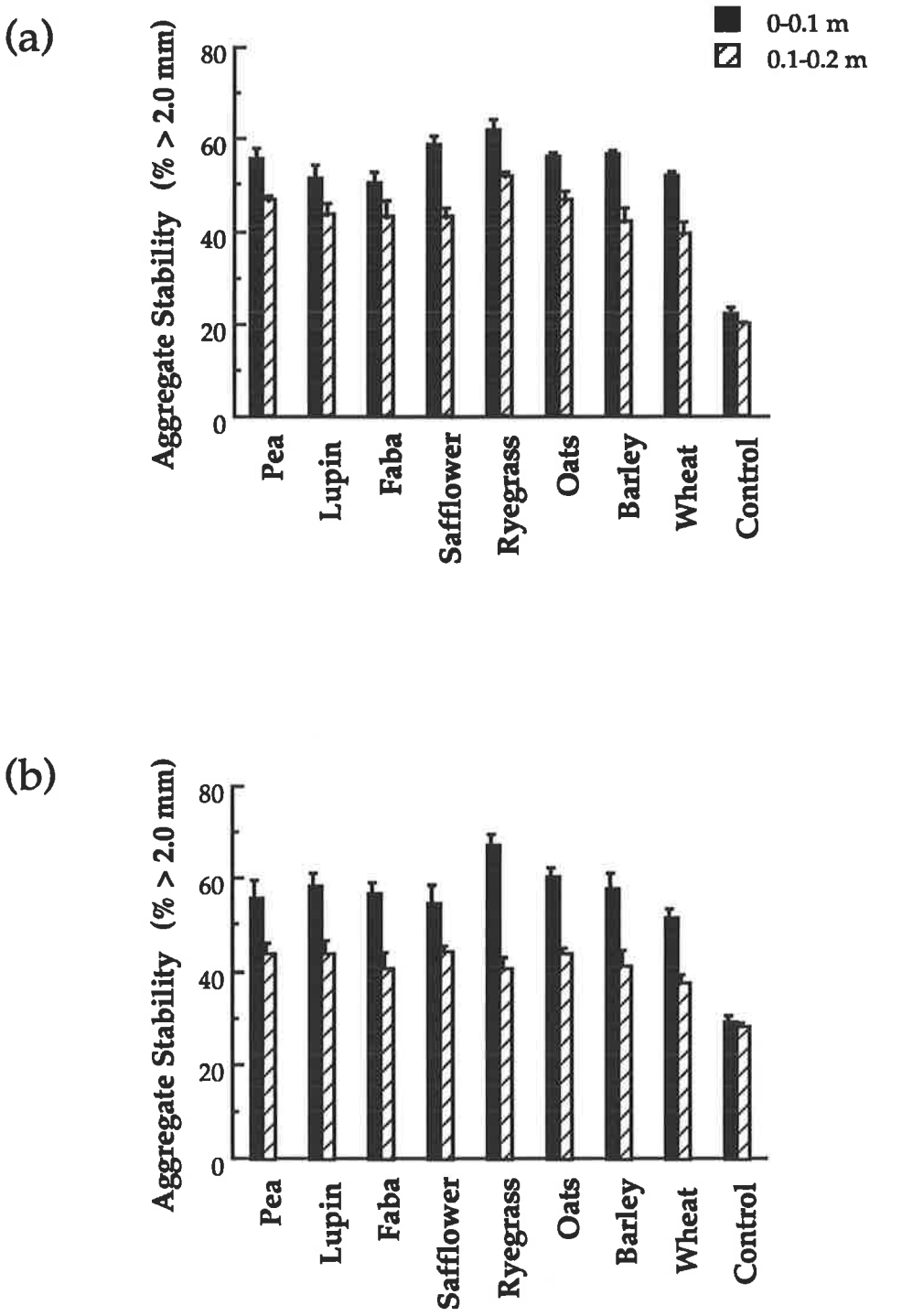


Fig 6.4 Effect of plant species on stability of aggregates in water (% > 2 mm) for the compacted (a) and uncompacted (b) soils at two depths. Bars are standard errors of means (n=16).

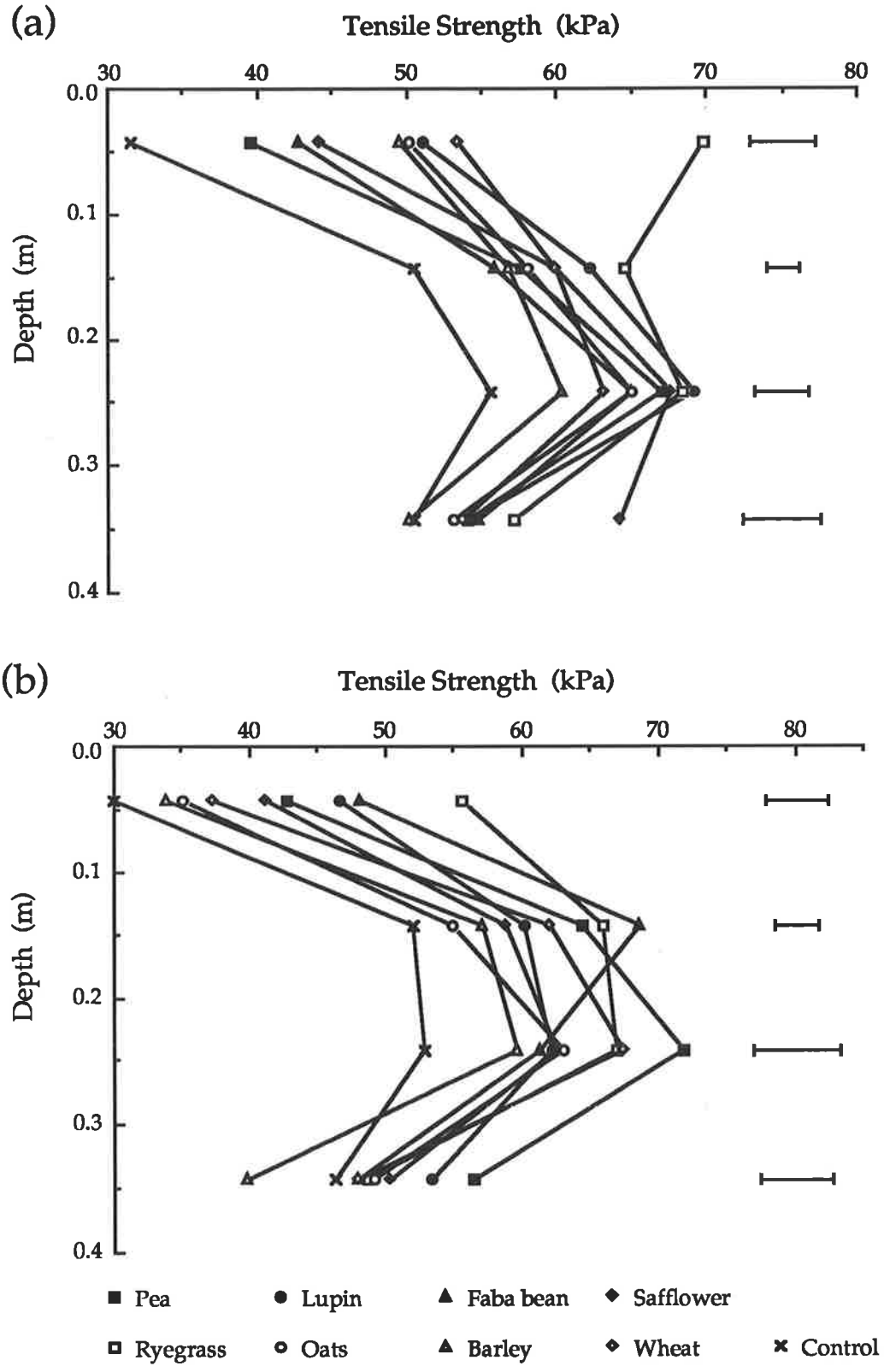


Fig. 6.5 Effect of plant species on tensile strength of aggregates (8-16 mm) at different depths for the compacted (a) and uncompacted (b) soils. Bars are LSD ($p \leq 0.05$) for each depth.

m depths. This reduction in strength of aggregates in the 0.3-0.4 m depth could be due to presence of a carbonate layer in this depth which could have made the aggregates weaker. The effect of the species is evident in both soils. Aggregates from planted soil were stronger than those from soil which had no plants. Ryegrass had the highest ATS in the surface layer, possibly as a result of its having the highest root density in this layer.

Water sorptivities of soils from the plots measured six months after harvest, are presented in Fig. 6.6. The values were generally greater in the uncompacted than compacted soils, presumably due to the deep tilling operation making the soil more porous. Soils with plants had higher sorptivities than those without plants presumably due to biopores left by the roots of the plants. The sorptivities of water through the compacted soil layer were generally higher in plots which had been planted with dicotyledonous species than with monocotyledons. Soils which were planted with safflower and oats had the highest sorptivities in the compact layer among dicotyledonous and monocotyledonous species respectively. The sorptivities in the uncompacted soil did not differ much with species. The variation in water content of the soils at the time of measuring sorptivity is presented in Table 6.2. Analysis of variance showed that soil water content did not differ significantly between compacted and uncompacted soils nor between planted and non-planted soil. There were, however, significant ($p \leq 0.05$) differences in the water content of the soils at different depths.

Table 6.2. Water content (kg kg^{-1}) of the soil subjected to the different treatments, at the time of sorptivity measurements.

Depth (m)	Compacted soil			Uncompacted soil		
	Planted	Non-planted		Planted	Non-planted	
			Mean			Mean
0.0-0.1	0.068±.003	0.071±.006	(0.070)a	0.066±.002	0.065±.004	(0.066)a
0.1-0.2	0.076±.006	0.083±.004	(0.080)a	0.069±.005	0.072±.006	(0.071)a
0.2-0.3	0.093±.005	0.097±.006	(0.095)b	0.085±.006	0.089±.007	(0.087)b
0.3-0.4	0.124±.002	0.115±.003	(0.120)c	0.101±.003	0.116±.002	(0.109)c
Mean	0.090	0.092		0.080	0.086	

Values are means (n=36) ± standard error for the four replicates. Numbers in parenthesis are the means for each depth. Means within a column followed by the same letter are not significantly different ($p \leq 0.05$) by the Tukey's test.

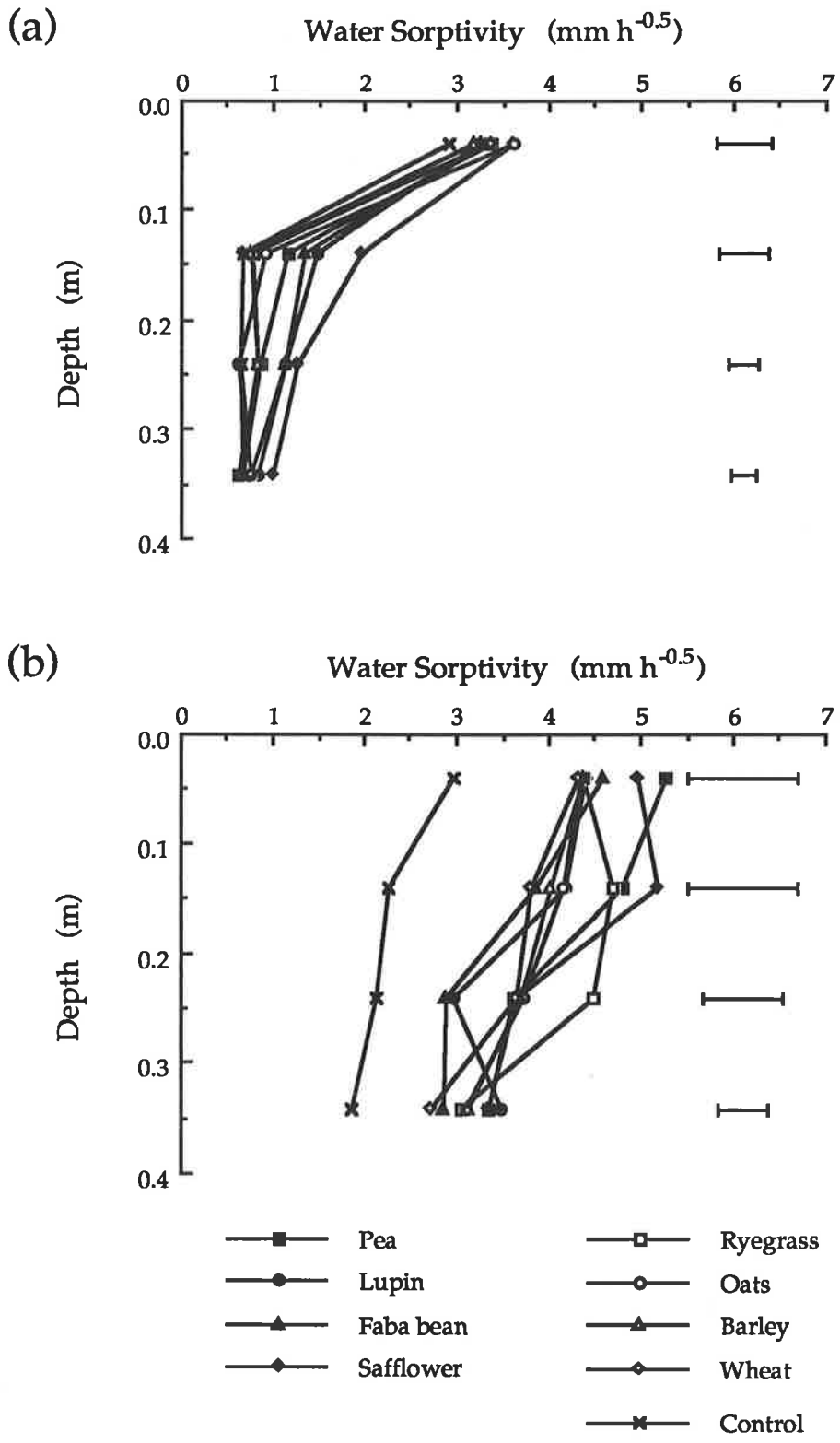


Fig. 6.6 Effect of plant species on sorptivity of water in the soils at different depths for the compacted (a) and uncompacted (b) soils. Bars are LSDs ($p \leq 0.05$) for each depth.

6.4 Discussion

Root growth increased the infiltration of water in both the compacted and uncompacted soils. Although no measurements were made of number or size of pores in the soil, the formation of channels by roots is considered to be the main factor responsible for the higher water sorptivity in soils which had plants compared with unplanted soil.

The results of this study show dicotyledons to be better at improving the infiltration of water through compacted soil than monocotyledons. In the compacted soil, growth of dicotyledonous species (with bigger roots) resulted in greater sorptivities than was the case for monocotyledons which in turn produced greater sorptivities than in the soil in which no plants had been grown. The greatest sorptivities in the compact soil were from plots in which safflower and lupins had been grown. The plots with pea were little different from the plots sown with monocotyledons.

Although sorptivity is influenced much by the antecedent water content of the soil, this is not considered to be the main reason for the differences observed between the plots with plants and those without plants. Table 6.2 shows that the water content of the soil subjected to the two treatments did not differ significantly at the time when sorptivity was measured. Earthworms would not have contributed much to the formation of channels because there was no earthworm activity detected in the 0.1-0.3 m depth during the growing period. Pits were dug by hand to 300 mm depth in each plot at the middle of the growing season and only few earthworms were found in the surface layer (0-0.1 m). The higher sorptivities of the soils with dicotyledons compared with those planted with monocotyledons is presumably a result of bigger biopores created by the roots of the dicotyledonous species. Although diameters of the resulting biopores were not measured, it is logical to expect that the biopores left by safflower roots for example (mean diameter 1.45±.14 mm) would be bigger than those left by ryegrass (mean diameter 0.22±.07 mm). Other authors (Barley, 1954; Beven and German, 1982; Gish and Jury, 1983; Meek *et al.*, 1992) have also found that plant roots were important in regard to water flow through the soil.

It can be estimated from the proportions of roots penetrating the compact layer and the planting density that the roots of safflower would leave about 100 biopores per m^2 while ryegrass would leave about 160 per m^2. However, despite the fewer biopores safflower produced higher infiltration of water through the compact layer. This is consistent with the above explanation that the higher sorptivities associated with the safflower could be due to the size of the biopores created by its roots.

As dicotyledonous species are normally grown at lower densities than the fine-seeded grasses, it seems that there will be few such pores created per unit area of ground. It may be worthwhile planting these species at densities of several hundred per m^2 to increase the number of pores for penetration of roots for subsequent crops. However it is unlikely, especially under dryland conditions, that deep rooted species which do not have a commercial return in their own right could be justfied economically and grown solely for their beneficial effects on soil structure. Future comparisons will need to consider the use of 'economic optimum' planting densities for each species.

It is noteworthy that the channels formed by roots were able to influence water movement through the soil five months after harvesting the crops. This implies that the channels were stable to any pressure that might have been applied to the soil during sampling. This is consistent with the finding of Blackwell *et al.* (1990) who demonstrated that channels formed by lucerne roots can be very stable at diameter > 4 mm under externally-applied mechanical stresses of up to 200 kPa. Although the diameters of pores we are dealing with here are much smaller than those of Blackwell *et al.*, their data give an indication of just how stable can be the biopores formed by plant roots.

It is interesting to note that soil properties were affected differently by different species. Ryegrass, for example, was good at stabilising aggregates but was not good at penetrating strong subsoil, while safflower was very good at penetrating the strong subsoil but was poor at stabilising aggregates. Although the present experiment cannot identify the exact mechanism(s) responsible for the high stability of soil aggregates in ryegrass, it is likely that the mechanisms could include one or a combination of the following: a) physical reinforcement of aggregates by the high root length density of this species, b) organic binding of the aggregates by materials released from roots and the associated fungal hyphae, and c) increasing soil stability by compaction by effective water stresses generated as the soil dried due to water absorption by the roots.

6.5 Concluding Remarks

The results of the study show that structural properties of soil in the field were influenced by the growth of roots in this soil. However, structural properties of soil in the field could also be influenced by factors like climate and microbial activity which can not easily be controlled. Experiments were therefore conducted in the glasshouse to examine in more detail the factors contributing to structural development by plant roots. These studies are reported in Sections 7 and 8.

SECTION 7

Formation of Aggregates by Plant Roots in Homogenised Soils

7.1 Introduction

The results reported in Sections 5 and 6 have shown that plant species differ in their ability to penetrate strong soil. This may suggest that plant species differ in their ability to change the structure of soils. While the roles of plant roots in creating soil aggregates are well known (Harris *et al.*, 1966; Martin *et al.*, 1955), the mechanisms involved have not been precisely defined or quantified. Tempstra 1989, 199

An aggregate is defined here as a naturally occurring cluster or group of soil particles in which the forces holding the particles together are much stronger than the forces between adjacent clusters (Martin *et al.*, 1955). There is still need for more and better understanding of the processes and mechanisms underlying the dynamics of soil aggregation by plant roots. A better understanding of these processes will not only contribute to knowledge, but may provide a means of improving soil structure for plant growth.

The work reported in this section was aimed at studying the abilities of roots of different plant species to form aggregates from initially homogenised soils and to compare quantitatively the properties of the resulting aggregates. The influence of wetting and drying by plant roots on aggregation was also investigated.

7.2 Materials and methods

7.2.1 Soils

Two agricultural soils in South Australia, Urrbrae loam which is a member of the red-brown earths and a hydromorphic black earth of the Claremont group were used. The soils are classified under the Northcote system as Dr 2.23 and Ug 5.16 (Northcote, 1979). Equivalent classifications are Calcic luvisol and Pellic vertisol for the red-brown earth and black earth respectively (FAO, 1974). Some properties of the soils are given in Table 7.1. Bulk samples from the surface layer (0.0-0.1 m) were collected and air-dried before being homogenised (to destroy the existing macro structure) by grinding and sieving through a 0.5 mm screen. The distributions of particle sizes after homogenisation of the two soils were determined by the hydometer method (Day, 1965) and are presented in Fig. 7.1.

Table 7.1 Some properties of the red-brown earth and black earth (0.0-0.1 m depth).

Property	Red-brown earth	Black earth
Particle size distribution:		
% sand (> 53 μm)	30.5	17.4
% silt (2 - 53 μm)	51.0	15.8
% clay (< 2 μm)	18.5	66.8
Texture	fine sandy loam	heavy clay
Surface area ($m^2 g^{-1}$)[a]	11	64
Dominant clay minerals[a]	illite & kaolinite	illite & smectite
Atterberg limits:		
plastic limit (kg kg^{-1})	0.196	0.302
liquid limit (kg kg^{-1})	0.242	0.496
Organic carbon (%)	1.23	2.40
pH (in 1:5 soil :water suspension)	5.6	7.7
$EC_{1:5}$ (mS cm^{-1})	0.073	0.11
Cation exchange capacity (cmol kg^{-1})[a]	117	498

[a] Values obtained from Grant (1989).

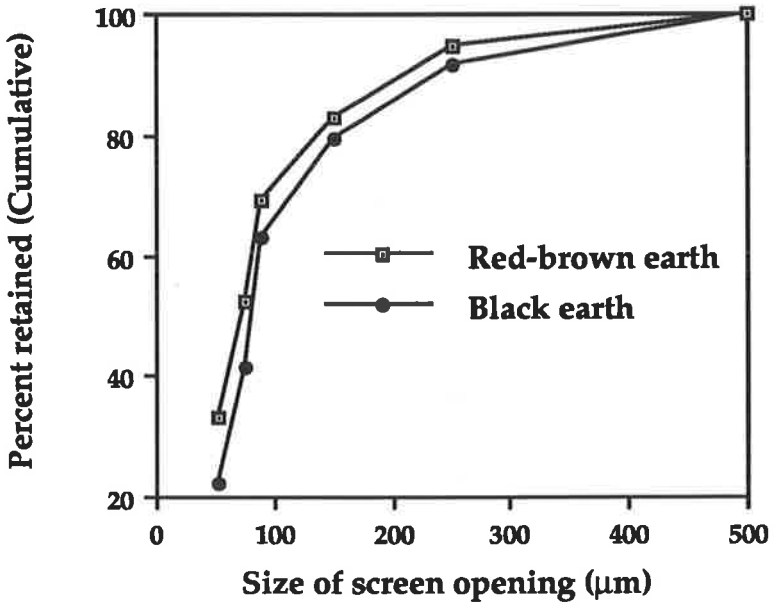


Fig. 7.1 Distribution of particle sizes in the red-brown earth and black earth after homogenisation.

7.2.2 Soil shrinkage

The soils were moulded at their lower plastic limits and pressed into cylindrical brass moulds. They were slowly dried at 20°C for 2 days and then oven-dried at 105°C for 24 h. Volume shrinkage was used as a measure of the shrinkage potential of the soils and was 26% and 4% for the black earth and red-brown earth respectively.

7.2.3 Minirhizotrons -construction and packing

Forty-eight root observation chambers with internal measurements of 100 mm by 50 mm and a depth of 300 mm were constructed from rectangular PVC tube (Fig. 7.2). These chambers will be referred to as minirhizotrons in this thesis. Glass was used at the front of the minirhizotrons to allow observation of root growth and cracking in the soil. The glass was covered with aluminium foil between observations to shield the roots from light. A 12 mm diameter PVC pipe perforated along its length was placed in the centre of each minirhizotron and used for watering the plants. A 10 mm layer of black plastic beads and a steel wire mesh were placed at the base to permit drainage.

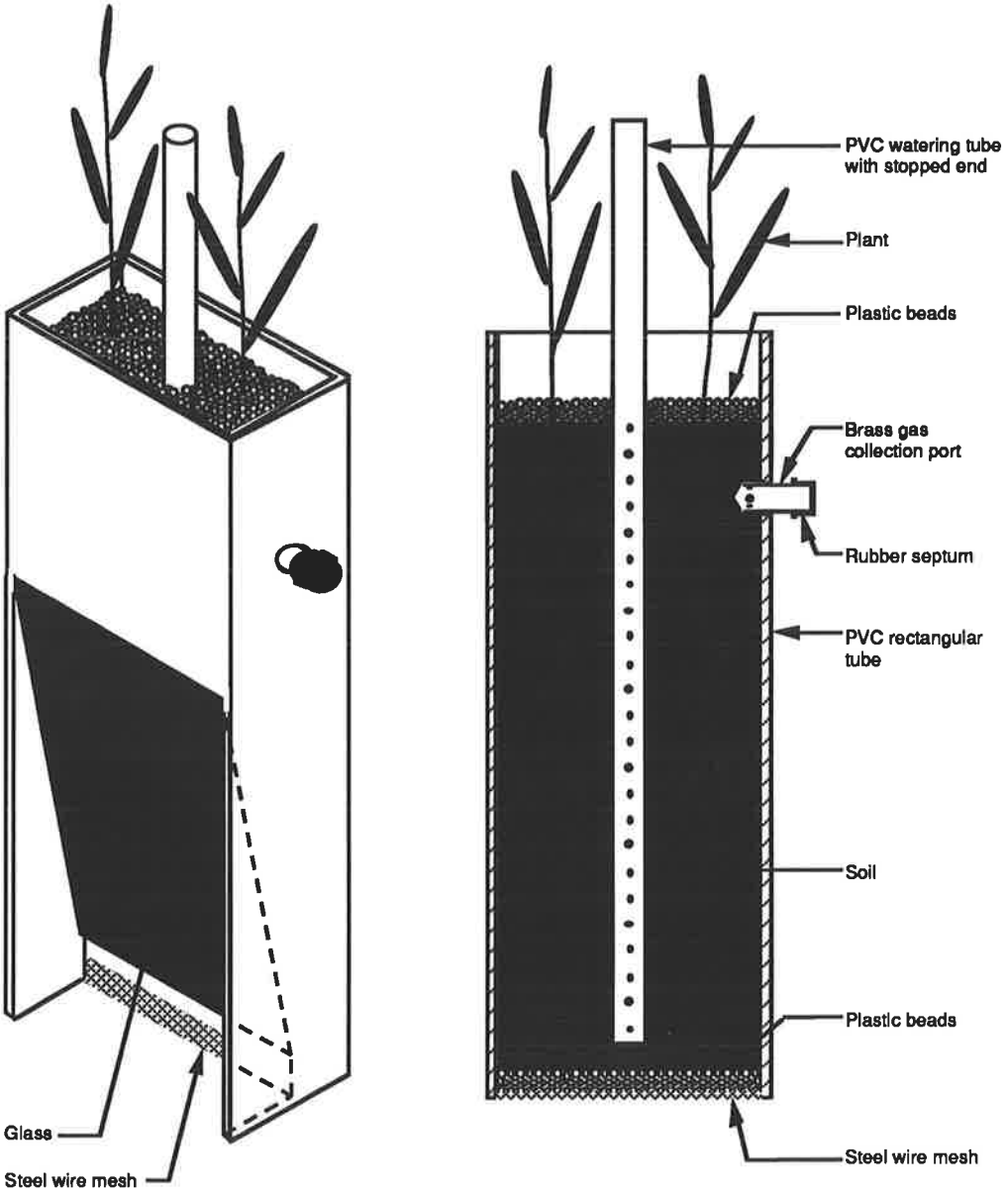


Fig. 7.2 Three dimensional and cross-sectional views of a minirhizotron.

Except for the control treatments, loss of water by evaporation from the minirhizotrons was reduced by covering the top with a layer (30 g) of black plastic beads. For each soil, twenty-four minirhizotrons were each filled with 1.5 kg of the homogenised soil. Before packing, soil for each minirhizotron was thoroughly mixed with NH_4NO_3 fertiliser at a rate of 5 g N kg^{-1}. The packing densities were 1.06 and 1.12 Mg m^{-3} for the red-brown earth and black earth respectively.

7.2.4 *Plant Species*

Pea (*Pisum sativum* cv Greenfeast), wheat (*Triticum aestivum* cv Kite) and ryegrass (*Lolium rigidum* cv Wimmera) were used. These species were chosen because they have different rooting systems (see Section 2.3.3) and so would offer a good comparison in this study. Seeds were sown at a depth of 2.5 cm below the surface of the soil. Thinning after germination left 3, 2 and 5 plants of pea, wheat and ryegrass respectively. Choice of these numbers was based on the sowing rates of these species used in the field. Fig. 7.3 shows plants growing in a minirhizotron.

7.2.5 *Water regimes*

All the minirhizotrons were watered from the bottom the first time. Later waterings took place from the top down the PVC watering pipe. To study the influence of wetting and drying cycles on aggregation, the minirhizotrons were allocated to two groups after the initial wetting with two water regimes as follows.

1. Continously wet (c/w): the soil with these treatments was never allowed to dry below a matric potential of -100 kPa.

2. Wetting and drying (w/d): the soil with these treatments was left to dry to a water potential of -1.5 MPa. When this potential was reached, or when the plants started to wilt, the soil was watered back to field capacity.

The water content of the soil was obtained by weighing the minirhizotrons. The relationships between water content and water potential of the soils were determined by pressure plate apparatus and are presented in Fig. 7.4.

7.2.6 *Experimental design*

A 2 * 4 * 2 factorial experiment was used in a completely randomised design with three replications. The factors were soil type (2 levels), plant species (4 levels including the non-planted control) and water regime (2 levels).

7.2.7 *Growth conditions*

Plants were grown in June 1990 through fifteen w/d cycles in a glasshouse, which took to 4 and 5 months for the red-brown earth and black earth soils respectively. The control treatments took 6 and 7 months to complete the w/d cycles. The soils in the control treatments dried much more slowly because there were no transpiration losses. The mean minimum and maximum air

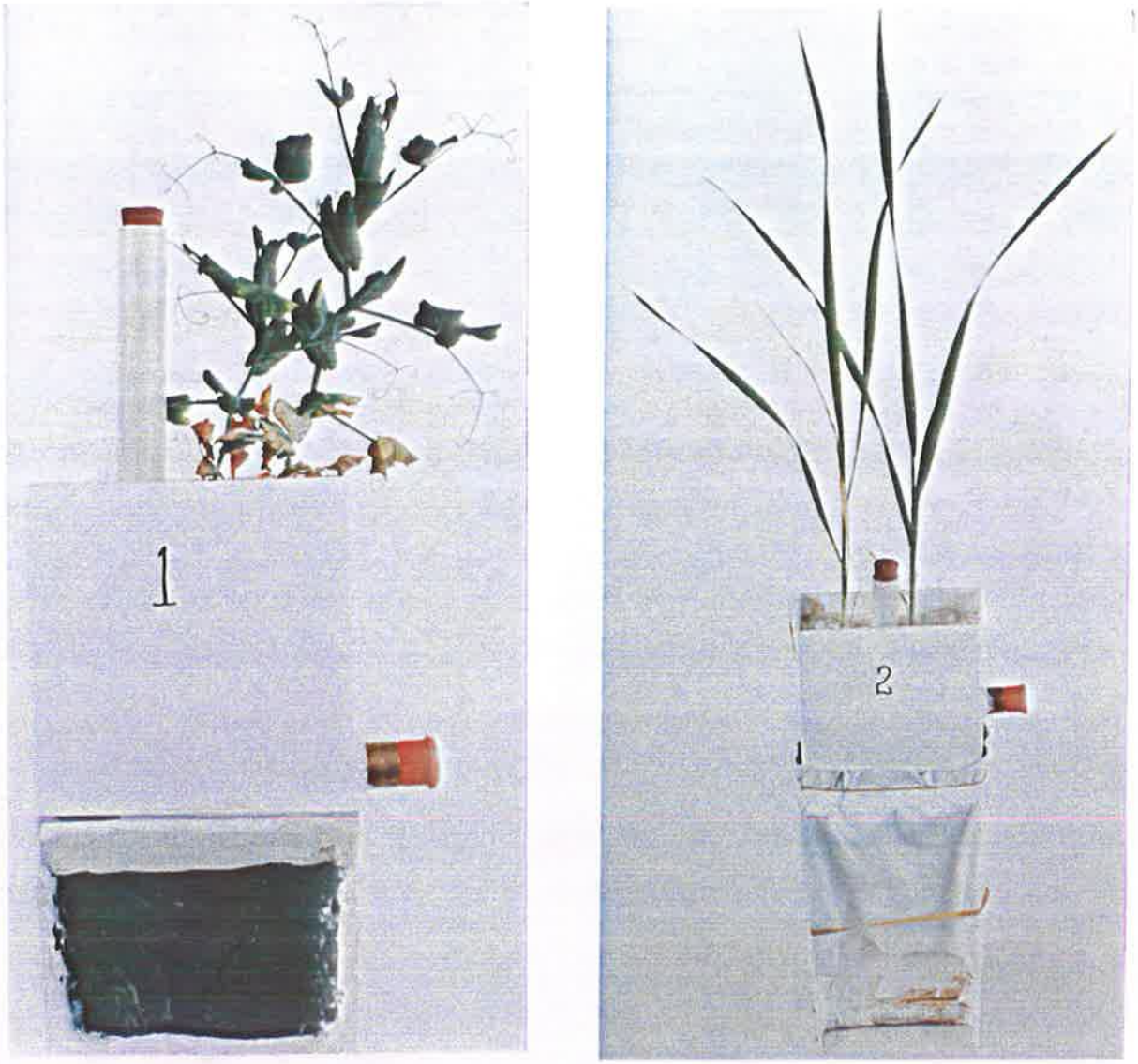


Fig. 7.3 Pea (1) and wheat (2) plants growing in minirhizotrons.

temperatures were 16° and 24°C respectively. Relative humidity ranged between 30% and 70%. After the required wetting and drying cycles in each soil, plants were cut off at the surface of the soil and the minirhizotrons opened. At the same time, plants from the c/w treatments were also harvested. The soil from the minirhizotrons was air-dried before being sieved for aggregate size distribution.

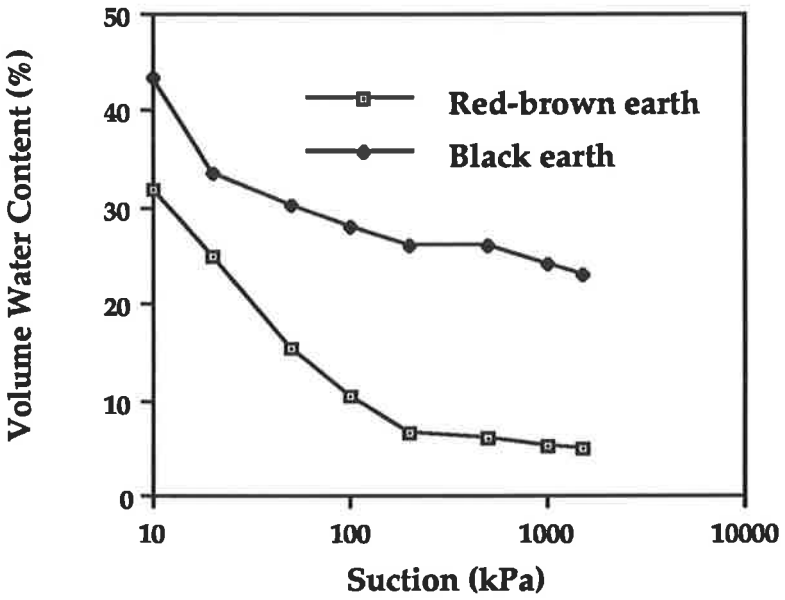


Fig. 7.4 Water retention characteristic of the red-brown earth and black earth after homogenisation.

7.2.8 Aggregate size distribution (ASD)

ASD was determined by the method described in Section 6.2.2. Aggregates of the 2-4 mm fraction were used for the measurement of all subsequent properties reported in this section. This size was chosen because it had the largest amount of aggregates from all the treatments and so offered the best opportunity for comparison.

7.2.9 Aggregate stability (AS)

The stability of aggregates in water was determined with air-dry aggregates in the wet-sieving technique described in Section 6.2.3. Aggregate stability was expressed as the > 0.25 mm fraction stable to the wet sieving treatment.

7.2.10 Aggregate tensile strength (ATS)

Tensile strength of aggregates was measured by an indirect tension (crushing) test described in Section 6.2.3. Forty aggregates from each treatment were crushed.

7.2.11 Root length density (RLD)

For efficient separation of roots from soil, the air-dry soil from each minirhizotron was ground by milling for 20-30 seconds in a Christie and Norris mill. This process cuts the roots into small sections to aid soil-root mixing. This mixture was spread on a tray, stirred, and three subsamples of 30 g each were taken for each treatment and used for measuring root length. Roots were separated from the soil using the procedure outlined by Hignett (1976). Root length, L, (cm g^{-1}) was measured by a microcomputer image analysis system developed at the CSIRO Division of Soils in Adelaide, South Australia. The system was calibrated by the manual line-intersection method (Newman, 1966a). Average root length density in the minirhizotron, L_v, (cm cm^{-3}) was calculated by the relationship

$$L_v = (L)r_b \qquad [7.1]$$

where r_b (g cm^{-3}) is the bulk density of the soil (Hignett, 1976)

7.2.12 Aggregate bulk density (ABD)

The bulk density of air-dry aggregates was determined using the method of McIntyre and Stirk (1954). Each aggregate was weighed and then dipped into molten paraffin wax at 100-110°C. At such temperature paraffin very quickly penetrated the aggregate pores and sealed them. The thickness of the paraffin coat on the aggregates was very small and the volume change of the total aggregate was considered not significant. The volume of the aggregates was determined from their displacement in water. Aggregate densities were corrected for water contents which were gravimetrically determined on separate sub-samples from the same batch. Thirty aggregates were measured for each treatment.

7.2.13 Organic carbon in soil (OC)

Total carbon was determined using a dry combustion on a LECO carbon determinator (Tiessen *et al.*, 1981). Total carbon was taken to be organic carbon because carbonates were absent from the surface horizons of the two soils. Samples were prepared by grinding 5 g of air-dry aggregates containing the roots

with a pestle and mortar and passing it through the machine. Each value reported is the mean of three sub-samples.

7.2.14 Analyses of data

Data were analysed with the Genstat 5 software package (Genstat 5 Committee, 1987) on a VAX computer. The LSD test was used to indicate the significance of differences between means.

7.3 Results

A statistical summary of analyses of variance (Table 7.2) shows that all the factors (plant species, soil type and water regime) had significant influence on the properties of aggregates. OC and RLD however were not influenced by water regime (*i.e.* w/d cycles). The only significant interaction is for ASD where plant species interacted with water regime in both soils.

Table 7.2 A statistical summary of analyses of variance for the soil properties.

Source of variation	Soil Property[a]					
	RLD	OC	ASD	AS	ATS	ABD
Main effects:						
Plant species	***	**	***	***	***	**
Soils	*	***	***	***	***	**
Water regime	ns	ns	***	**	**	*
Interactions:						
Plant species with Soils	ns	ns	*	ns	ns	ns
Plant species with Water regime	ns	ns	*	ns	ns	ns
Soils with Water regime	ns	ns	ns	ns	ns	ns
Plant species with Soils with Water regime	ns	ns	*	ns	ns	ns

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; ns = not significant

[a]abbreviations: RLD=root length density; OC=organic carbon; ASD=aggregate size distribution; AS=aggregate stability; ATS=aggregate tensile strength; ABD=aggregate bulk denstity

Figure 7.5 shows the ASD of the two soils after dry-sieving. The red-brown earth had a higher percentage of coarse aggregates (> 9.5 mm) over all plant species and water regimes than the black earth. The w/d cycles reduced the percentage of coarse aggregates and increased the proportion of smaller aggregates compared with c/w in both soils. Planted soils had a smaller proportion of coarse aggregates than the controls. For example, ryegrass reduced

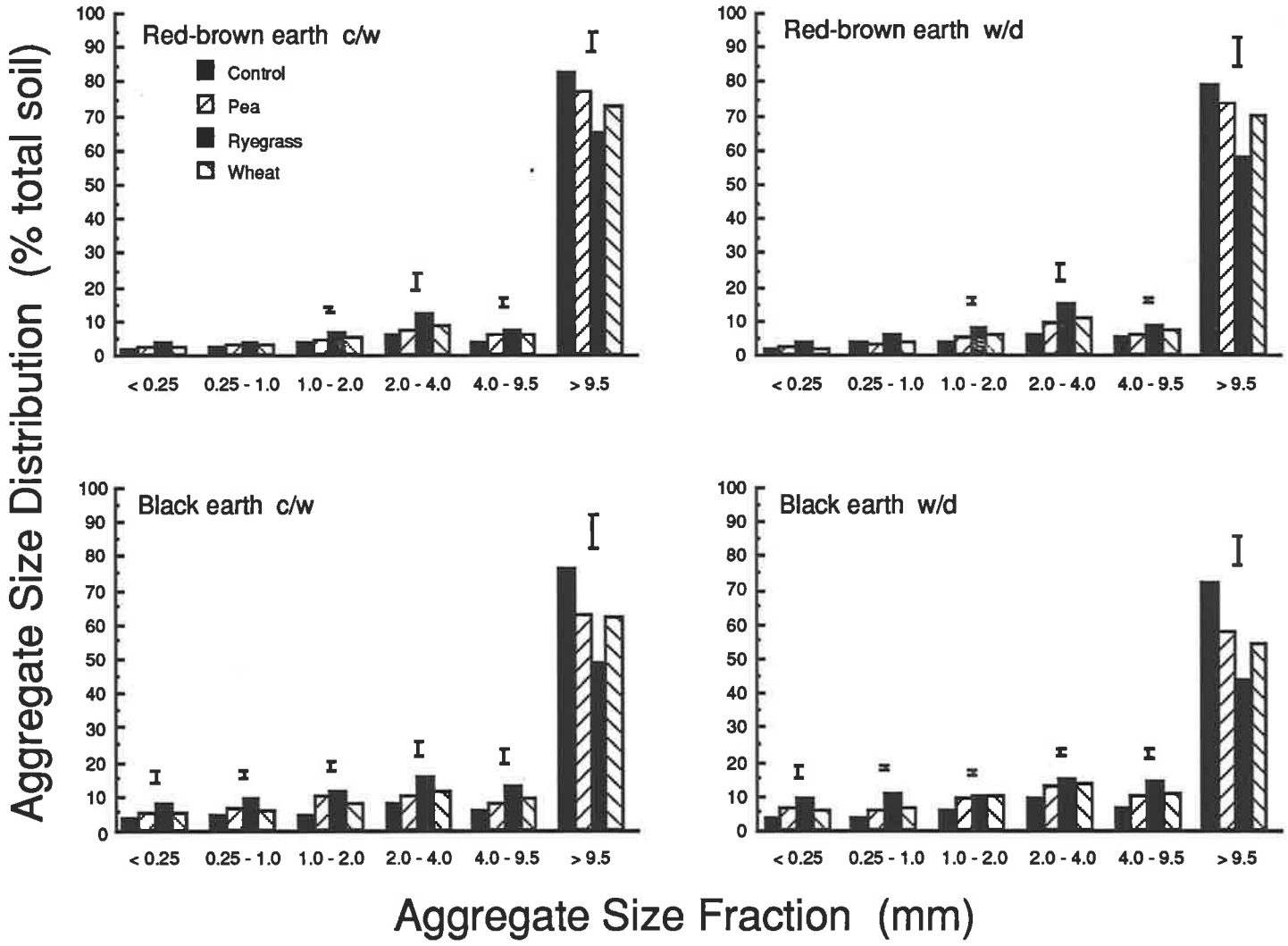


Fig 7.5 Influence of continuous wetting (c/w), wetting and drying (w/d) and plant species on aggregate size distribution for the red-brown earth and black earth. Vertical bars represent LSD ($p \leq 0.05$).

the proportion of > 9.5 mm aggregates in the black earth to about 40 percent. There was also a large difference between plant species in their influence on ASD. The proportion of coarse aggregates decreased in the order pea > wheat > ryegrass.

Table 7.3 shows significant differences in the RLD of the three plant species. Ryegrass had the highest RLD in both soils. It is interesting to note that c/w treatments produced slightly higher RLD than w/d treatments. This could be due to reduced growth of roots in the w/d treatments due to water stress when the the soils were being dried.

Table 7.3 Root length densities (cm cm^{-3}) of the plant species.

Plant species	Red-brown earth c/w	w/d	*mean*	Black earth c/w	w/d	*mean*
Pea	4.2[a]	3.9	4.0	6.0	5.9	5.9
	(0.6)	(0.5)		(0.4)	(0.9)	
Ryegrass	83.2	81.6	82.4	90.1	87.6	88.8
	(7.6)	(4.3)		(4.1)	(5.5)	
Wheat	30.3	27.8	27.8	40.0	37.5	38.8
	(1.2)	(2.9)		(2.8)	(1.8)	
mean	39.2	37.8		45.4	43.7	
LSD, $p \leq 0.05$						
Plant species	7.6			13.4		

[a]numbers in parenthesis are the standard errors of the mean of three replicates

Total carbon (OC) contents of the soils with the different treatments are presented in Table 7.4. The black earth had higher inherent OC than the red-brown earth. Plant growth had increased the OC of the soils compared with the controls. The increase in OC was in the order ryegrass > wheat > pea. This could be related to the RLD of the species because the root mass contributed organic material to the soils.

Table 7.5 shows that the tensile strength of the black earth aggregates was significantly higher than those of the red-brown earth. This could be because of differences in the clay content (and also type of clay) of the two soils. The black earth had a higher clay content which would give high interparticle attraction during drying. However, w/d cycles made aggregates in both soils stronger than c/w. The aggregates formed in the presence of plants were stronger than those from the controls in both soils. There were also significant differences among the plant species. The strength of aggregates in the planted soils was in the order

ryegrass > wheat > pea. A similar trend of results is observed when the stability of aggregates is considered (Table 7.6).

Table 7.4 Total organic carbon (%) in soil from the aggregates in the minirhizotrons.

Plant species	Red-brown earth c/w	w/d	*mean*	Black earth c/w	w/d	*mean*
Control	1.20	1.25	1.23	2.37	2.41	2.39
Pea	1.52	1.51	1.52	3.00	2.98	2.99
Ryegrass	1.76	1.73	1.75	3.31	3.25	3.28
Wheat	1.57	1.54	1.56	3.02	2.99	3.00
mean	1.51	1.51		2.93	2.91	
LSD, $p \leq 0.05$						
Plant species	0.12			0.23		

Table 7.5 Influence of plant species and water regime on tensile strength (kPa) of oven-dried aggregates.

Plant species	Red-brown earth c/w	w/d	*mean*	Black earth c/w	w/d	*mean*
Control	33.1	43.0	38.1	126.3	234.3	180.3
Pea	37.7	53.1	45.7	197.4	238.9	218.2
Ryegrass	54.5	82.0	62.3	344.4	514.7	429.6
Wheat	45.9	57.4	51.6	247.2	321.8	284.5
mean	42.8	59.1		228.8	327.4	
LSD, $p \leq 0.05$						
Water regime	7.8			74.0		
Plant species	5.5			52.3		

The bulk densities of air-dry aggregates (ABD) of the black earth were generally higher than those of the red-brown earth for all plant species and water regimes (Table 7.7). Aggregates from planted soil had significantly higher ABD

than the controls. Differences between plant species were evident. Aggregates from soils planted with ryegrass had the highest bulk density while those of wheat were higher than pea.

Table 7.6 Influence of plant species and water regime on the stability (% > 0.25 mm) of aggregates.

Plant species	Red-brown earth c/w	w/d	*mean*	Black earth c/w	w/d	*mean*
Control	24.5	31.4	28.0	56.1	67.4	61.7
Pea	41.7	49.5	45.6	73.2	87.6	80.4
Ryegrass	59.7	64.4	62.0	82.9	90.9	86.9
Wheat	46.8	55.6	51.2	79.3	85.3	82.3
mean	43.2	50.2		72.9	82.2	
LSD, $p \leq 0.05$						
Water regime	1.3			2.05		
Plant species	0.9			1.05		

Table 7.7 Influence of plant species and water regime on bulk density (Mg m^{-3}) of aggregates.

Plant species	Red-brown earth c/w	w/d	*mean*	Black earth c/w	w/d	*mean*
Control	1.08	1.06	1.07	1.19	1.26	1.23
Pea	1.23	1.27	1.25	1.32	1.41	1.37
Ryegrass	1.41	1.44	1.43	1.47	1.60	1.54
Wheat	1.28	1.33	1.31	1.34	1.37	1.36
mean	1.25	1.28		1.33	1.41	
LSD, $p \leq 0.05$						
Water regime	0.04			0.04		
Plant species	0.02			0.03		

7.4 Discussion

The results indicate that plant species and water regime significantly influenced aggregation. This discussion will consider the mechanisms likely to be involved by these factors.

7.4.1 Water regime

The process of homogenising the soils involved the breakage of bonds between the individual particles. However, after the soils were wet and left over time, the soils regained some of their strength. This observation is consistent with 'age-hardening' (Kemper and Rosenau, 1984; Utomo and Dexter, 1981a) in which several mechanisms are involved. According to Dexter *et al.* (1988), if the soil is kept at constant water content, the two mechanisms involved are: (1) soil particle reorientation into positions of minimum free energy and/or; (2) chemical cementation at the points of contact or near-contact of mineral particles. However, if the water content changes, as was the case with w/d treatments, other mechanisms become important.

7.4.2 Effects of drying

Formation of cracks

As the soil dries, the soil colloids shrink. One of the factors implicated in the shrinkage characteristics of cohesive materials in soils is determined by the amount of clay. Shrinkage in the black earth was higher (26%) than in the red-brown earth (4%). Shrinkage of soil material leads to the development of internal tensile stresses. Tensile stresses are generated when the drying of a soil is not uniform *e.g.* in rapid drying from a surface or by water extraction from soil by plant roots. Consequently, unequal stresses and strains arise throughout the soil mass (Towner, 1987a). When the tensile stress exceeds the tensile strength of the soil, cracks are initiated in the soil (Towner, 1987ab). The cracks constitute the boundaries and initial faces of micro-aggregates in an initially non-aggregated soil (Dexter, 1991; Grant and Dexter, 1986; White, 1966) and also form pathways for rapid water infiltration, aeration and root penetration. Extensive cracking was observed in the black earth when the soil was left to dry and this could explain the higher proportion of smaller aggreates in this soil compared with the non-shrinking red-brown earth, and also with w/d cycles compared with c/w.

Effective stress

Drying of soil by uptake of water by plant roots causes local changes in pore water pressure within the soil mass and generates effective stresses. It has long been recognised (Haines, 1926) that a significant temporary cohesive strength exists in wet soils as a result of the surface tension and capillary forces associated with the interparticle water films throughout the soil matrix. The effective

(intergranular) stress, σ', is the stress controlling changes in volume or strength of the soil and is given for saturated soil by the equation of Terzaghi (quoted by Skempton, 1961) as

$$\sigma' = \sigma - u_w \qquad [7.2]$$

where σ is the total stress and u_w is the water pressure in the pore space. However, both the surface tension and capillary forces require the presence of gas/liquid/solid interfaces, which do not exist in saturated soils. In unsaturated soils equation (7.2) becomes

$$\sigma' = (\sigma - u_a) + \chi(u_a - u_w) \qquad [7.3]$$

where u_a is the pore air pressure and χ is a factor which depends on the degree of saturation of the soil. The factor χ represents the proportion of the matric pressure that contributes to the effective stress (Aitchison, 1961; Groenevelt and Kay, 1981; Hettiaratchi and O'Callaghan, 1980). The adhesive forces between soil particles and water ensures that the soil particles are pulled together to form aggregates (Towner, 1961). This causes the mineral particles to rearrange into greater units thereby creating a greater number of contact points and hence giving greater cohesive forces to the aggregates (Barley, 1968; Towner and Childs, 1972; Williams and Shaykewich, 1970).

According to Horn and Dexter (1989) and Semmel *et al.* (1990) the increase of aggregate and soil strength with time after homogenisation can be caused either by an increase of the number of contact points between mineral particles or by higher effective stresses per contact point. This can been illustrated by a model proposed by Horn and Dexter (1989) and presented in Fig. 7.6. According to this model, during the primary shrinkage of the homogenised wet soil (A) the single particles will be pulled together by water menisci forces (pore water pressure in the effective stress equation) forming stronger aggregates with intra- and inter-aggregate pores (B). In this way, the increase in soil density is greater the drier the soil has become as shown by (C).

During wetting, aggregates not only become weaker, but a further heterogenisation of the pore and grain size distribition takes place resulting in the formation remnants of soil aggregates and a more homogenous soil mass. The more intensively the aggregates have been dried previously, the more pronounced is the irreversibility of the pore size alteration during the swelling process (D). Semmel *et al.* (1990) have also explained strength increase in aggregates which have been wetted and dried as being due to cementation of the particles at contact points during drying. Salts, humic acids and soil colloids

which are transferred in water films to the points of contact because of hydraulic gradients formed due to soil drying cause the particles to be cemented together more strongly.

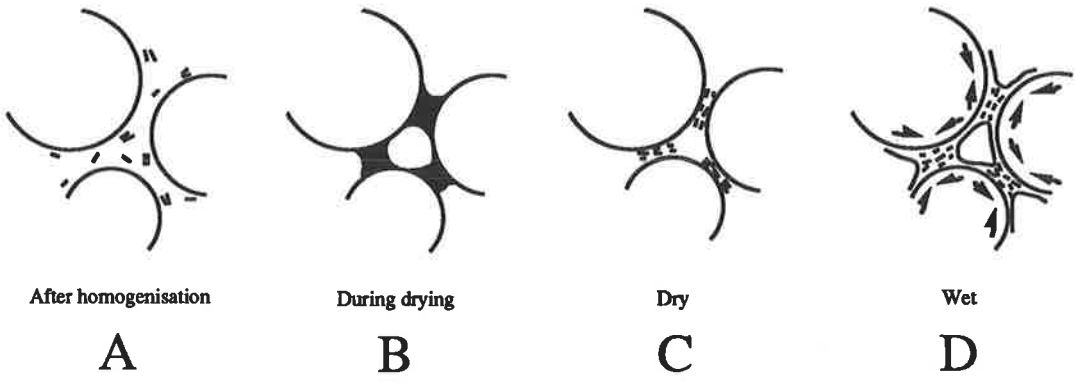


Fig. 7.6 A proposed mechanism for aggregation in a homogenised soil (re-drawn from Horn and Dexter, 1989).

The above explanations are consistent with the observations made in this study that the aggregates subjected to wetting and drying cycles had higher tensile strength and bulk density than those kept continuously wet. It is suggested that the more intensive drying in soils with wetting and drying cycles caused higher cohesion between particles due to stronger effective stresses and hence ATS and ABD are higher in wetted and dried than continuously wet soils.

7.4.3 Effects of wetting

Tensile strength

When dry soil is wetted, the combined effects of differential swelling and pressure build up in entrapped air generates tensile stress which can exceed the tensile strength of the soil. This causes arrays of micro-cracks to form throughout the soil mass (Dexter *et al.*, 1984; Grant and Dexter, 1990). These micro-cracks which were very prominent in the black earth subjected to the w/d treatments, make the soil weaker and more friable. This process has been referred to as 'soil mellowing' by Utomo and Dexter (1981b). The effects of rapid wetting on the generation of soil structure through the production of micro-cracks have been shown quantitatively by fracture surface analysis (Dexter and Håkannson, 1989). It is suggested that the reduction in the proportion of coarse aggregates in the black earth which had been wetted and dried might be a result of the micro-cracks formation due to tensile stresses formed during the wetting (watering) of the soils.

7.4.4 Plant species

The influence of plant roots on aggregation is evident from the significant positive correlations ($p \leq 0.05$) between RLD and most of the properties of the soil that were measured (r=0.72*, 0.69*, 0.57, 0.54, and -0.66* for RLD and OC, AS, ATS, ABD and ASD respectively). Thus the differences in soil properties observed among plant species might be a result of the differences in the rooting densities. The mechanisms underlying the influence of roots on aggregation will now be considered.

It is logical to assume that root growth can result in a slight compaction of soil caused by volume expansion of the roots (Dexter, 1987a). As the root grows into the soil, it occupies space that was previously occupied by soil pore space and soil particles. Since root diameters are usually larger than soil pores, soil particles are pushed aside and the bulk density of the soil near the root may increase. Greacen *et al.* (1968) showed increases in bulk density of the soil next to the root to 1.6 and 1.7 g cm^{-3} from an initial level of 1.5 g cm^{-3}. Similar results were also presented by Guidi *et al.* (1985). However, the net effect of volume expansion of roots on the bulk density of aggregates is considered to be negligible in causing the increases in ABD observed in this study *i.e.* 16 and 25% for black earth and red-brown earth respectively. The average root volumes in the two soils were 1.5%, 3.2% and 2.1% for pea, ryegrass and wheat respectively calculated from root diameters of 0.75 mm, 0.22 mm and 0.26 mm and the average root length densities given in Table 7.3. These root volumes could account for only about one tenth of the observed changes in density of aggregates. This suggests that the effects of compression by effective stress were greater than compression by roots *i.e.* the density increased due to increase in effective stress as $\chi(u_a - u_w)$ (Equation 7.3) increased on drying.

Plant roots can also produce aggregates within a soil mass by another mechanism which does not involve water extraction. This is through generation of tensile stresses at the soil-root interface which can crack the soil. Misra *et al.* (1986b) estimated the radial and tangential stresses adjacent to the soil-root interface and predicted that the tensile stress could result in plastic failure of finite sized aggregates during root penetration. This can provide locations of crack initiation in the soil.

A more obvious role of roots is their ability to stabilise soil aggregates. Plant roots support a large population of micro-organisms such as fungi and bacteria which may mechanically and or chemically stabilise aggregates, and the roots themselves produce mucilage to which soil particles adhere (Molope, 1987). According to Tisdall and Oades (1982), larger aggregates (> 250 μm) derive much of their water stability from being enmeshed in living or partially decomposed

plant roots and fungal hyphae associated with the rhizosphere. The mechanisms of bonding of the organic materials to the inorganic particles have been extensively studied (*e.g.* Chaney and Swift, 1986; Oades, 1984). The high organic carbon contents of the aggregates from planted soil could be attributed to the contribution of organic materials by the root mass of the different species. The root mass could also increase substrate for biological activity which in turn could contribute to the increased stability of the aggregates. Although it is felt that the effect of compression by effective stress due to changes in water content is likely to be the most important mechanism of stabilisation in this study, it should be emphasised that the higher stability of aggregates from the planted soil is a result of chemical, physical and biological processes.

7.5 Concluding remarks

The experiment has shown the important influences of soil type, wetting and drying cycles and growth of plant roots on the formation and properties of aggregates. It is concluded that cracking of soil, which led to the production of smaller aggregates was caused by the heterogeneity of water extraction giving rise to tensile stress patterns within the grid of roots. Compression of the aggregates by effective stresses generated as a result of water extraction from soil by plant roots is considered to be the main mechanism responsible for the higher bulk density and tensile strength of aggregates in both the red-brown earth and black earth soils.

Soil homogenisation, as used in this study is one extreme of structural degradation which offer conditions for studying the processes involved in regenerating structure of soil by plant roots. Another extreme condition of soil structure is when soil has abundance of coarse aggregates. The processes responsible for generating structure under this condition may be different from those studied here. The next section reports a study in which the ability of roots to generate structure in beds of coarse aggregates was examined.

Section 8

Modification of Soil Aggregation by Roots Growing Through Beds of Coarse Aggregates

8.1 Introduction

Beds of sieved aggregates with a narrow distributions of sizes are often used in experiments because they represent a reproducible and well-defined structure (Braunack and Dexter, 1989). They also provide a means by which the results of experiments conducted in different places and times can be compared quantitatively.

Plant roots are known to grow preferentially in weak aggregates or in voids between aggregates (Dexter, 1986a; Ehlers *et al.*, 1983; McSweeney and Jansen, 1984; Whiteley and Dexter, 1983, 1984a). When a plant root makes contact with the surface of an individual aggregate in a bed of aggregates larger than the diameter of the root, it may penetrate or displace or be deflected by the aggregate (Misra *et al.*, 1986b; Whiteley and Dexter, 1984). Penetration is determined by the strength of the aggregates and by the angle of incidence at which the root tip contacts the aggregate (Dexter and Hewitt, 1978). The size of aggregates has also been reported to influence the penetration of roots into aggregates (Logsdon *et al.*, 1987). An understanding of the above processes has led to the development of models that predict the effects of aggregate size and strength on rate of root growth, distribution and their implications for nutrient uptake (*e.g.* Dexter, 1978; Hewitt and Dexter, 1979; Misra *et al.*, 1988c).

Most of the previous studies on root growth in large aggregates have centred primarily on the influence of aggregate size on seedling emergence, shoot growth and root growth (Alexander and Miller, 1991; Donald *et al.*, 1987; Logsdon *et al.*, 1987; Taylor, 1974a). Relatively little attention seems to have been given to how the growth of the roots may change the properties of aggregates. The results of work reported in Section 7 have shown that growth of roots had significant influence on aggregation of homogenised soils. The effect of root growth in soils with large aggregates could however be different as the mechanisms involved in aggregation could also be different.

The purpose of this study was to compare the influence of growth of roots of three plant species through beds of coarse aggregates on aggregation and properties of the resulting aggregates.

8.2 Materials and methods

8.2.1 Soil

The soil used in this study was collected from the surface layer (0.0-0.1 m) of Urrbrae loam at the Waite Agricultural Research Institute, South Australia. This is the red-brown earth which was used in the experiment described in Section 7.0. Its characteristics have already been presented in Table 7.1.

8.2.2 Preparation of aggregates

Aggregates collected from the field were found to be unsuitable for this study because of the large variations in density, strength and shape. Artificial aggregates were therefore prepared in the laboratory from sieved (< 2 mm) air dry soil.

A thin layer of soil was spread evenly on an aluminum tray and a mixture of de-ionised water and 1% laboratory reagent grade poly (vinyl alcohol), PVA, molecular weight = 22,000 was sprayed onto the soil using a spray atomiser. When soil became about 1.2 times wetter than the plastic limit, a knife was used to mix the water with soil and cause the soil particles to aggregate. The aggregates were wetted by a light spray of water and dry soil was added while the tray was being shaken. In this way, as the soil was rolled, the aggregates increased in size. Mixing at saturation was avoided to minimize smearing of aggregates. The aggregates were air dried before being packed into beds.

8.2.3 Properties of aggregates

Aggregates of between 18 and 21 mm diameter (mean 19.8 mm) were selected by sieving. The aggregates were almost spherical in shape and looked similar to aggregates collected from the field. The aggregates had irregular surfaces which would result in a high probability of roots encountering a surface at an angle of incidence favourable for penetration (Dexter and Hewitt, 1978). The bulk density of the air-dried aggregates was 1.34 ± 0.16 g cm^{-3} (n=100). The PVA was distributed through the aggregates and strengthened them internally against collapsing in the aggregate bed. It did not prevent roots penetrating the aggregates. Penetrometer resistance and tensile strength of the aggregates at the two soil water contents used in this study are presented in Table 8.1. The methods used to determine these properties are discussed in Section 8.2.8.

8.2.4 Packing of aggregate beds

The experiment was performed by growing plant roots through beds of soil aggregates in PVC pots. The pots had internal dimensions of 90 mm diameter and 300 cm high. Holes (3 mm diameter) were drilled at the base to allow

drainage of excess water. In all the pots, the beds of aggregates were packed by pouring aggregates (200 g at a time) from a beaker. This was done in several layers until 1.0 kg of aggregates filled each pot. The mean bulk density of beds of aggregates prepared in this way was about 1.02 Mg m^{-3} as determined in a 5 L measuring cylinder.

Table 8.1 Penetrometer resistance (Q_P) and tensile strength (ATS) of aggregates at two water contents used in the study.

Matric potential (kPa)	Water content (kg kg^{-1})	Q_P (MPa)	ATS (kPa)
-10	0.224	0.32±.02	40.4±2
-1500	0.102	1.83±.36	236.0±19

Numbers are means ± standard error (n=100)

8.2.5 Experimental treatments and design

A 4 * 2 factorial design with four replicates was used. The factors were: three plant species, *viz* pea (*Pisum sativum* cv Greenfeast), ryegrass (*Lolium rigidum* cv Wimmera), wheat (*Triticum aestivum* cv Kite) and a non-planted control; and two soil watering regimes *viz* continuously wet (c/w) and wetting and drying (w/d). The soil in c/w treatments was dried out to field capacity (water content of about 0.22 kg kg^{-1}, corresponding to about -10 kPa water potential) mainly by transpiration of the plants, and then watered. The soil in the w/d treatment was left to dry to a water content of 0.102 kg kg^{-1} or until wilting occurred (corresponding to water potential of -1.5 MPa) and then it was watered to field capacity. The pots were arranged on benches in the glasshouse in randomised blocks (Fig. 8.1).

8.2.6 Growing of plants

To ensure sufficient soil/root contact at the start of growth of plants, moist fine sand (< 250 μm) was spread on the surface of each aggregate bed (pot) to about 1 cm depth. Six germinated seeds of each plant species were placed evenly on the sand and covered with a thin layer of sand. The sand was wetted every morning with a fine spray of No. 1 Hoagland's nutrient solution (Hoagland and Arnon, 1950) using a spray atomiser. The nutritive composition of the nutrient solution has been given in Section 3.2.8.

Replicate 1 Replicate 2 Replicate 3

Fig. 8.1 Pots showing the placement of replicates on a bench in the glasshouse.

When the seedlings were about 10 cm high, plants were thinned to leave three plants in each pot for all treatments except the w/d controls, the surface of the sand was covered with a layer (1 cm thick) of black plastic beads to prevent slaking of the aggregates during watering and to cut down evaporation. Plants were grown through 15 wetting and drying cycles (corresponding to 3 and 4.5 months for the planted and unplanted treatments respectively). The experiment was conducted between May and September 1992 in a glasshouse, where the mean minimum and maximum air temperatures were 16°C and 20°C respectively. Relative humidity was not controlled and ranged between 30% and 70%.

8.2.7 Sampling aggregates after plant growth

At harvest, the shoots of the plants were clipped at the surface of the soil. One-half of the replicates (2 pots for each treatment) was used for destructive measurements of root length, and the other half was used for measuring properties of the aggregates. The pots were opened and the aggregates were air dried before dry sieving to obtain the distribution of aggregate sizes. To investigate the physical influence of roots on tensile strength, half of the aggregates from each treatment were incubated at 0.25 kg kg^{-1} water content in aluminium foil trays at 30°C for 6 weeks. Incubation allowed some of the roots to decompose. Measurements of tensile strength made on incubated aggregates were compared with measurements made on aggregates which had not been incubated.

8.2.8 Measurements on aggregates

Selected physical properties of aggregates were determined. The properties were: penetrometer resistance, bulk density, aggregate size distribution, tensile strength, organic carbon and the stability of aggregates in water. The methods used for making these measurements were as follows.

Penetrometer resistance of aggregates

Penetrometer resistance of aggregates was measured with a motor-driven (3 mm min^{-1}) steel probe, having a cone diameter of 1.0 mm and a total included tip angle of 30°. The shaft was relieved for 7 mm behind the tip. Each aggregate to be probed was placed on the pan of a top-loading electronic balance (Mettler type PC-4400) and the maximum force (kg) exerted by the probe was recorded (when the penetrometer tip passed the centre of the aggregate or cracked it). Penetrometer resistance, Q_p, was calculated from the penetration forces as

$$Q_p = F_{max}/\pi r^2, \text{ kPa} \qquad [8.1]$$

where F_{max} = Ma (in N), M is electronic balance reading (kg) and a is the gravitational acceleration constant (9.806 m s^{-2}), and r is the probe radius (m). Fifty aggregates were probed for each treatment.

Aggregate bulk density (ABD)

The bulk density of aggregates was determined on 15-20 aggregates with the paraffin coat method (McIntyre and Stern, 1954). Each air-dried aggregate was weighed and then dipped into molten paraffin wax to seal the aggregate surface. The thickness of the paraffin coat was too small to cause any significant change to the volume of the aggregates. The volume was determined by displacement of water.

Aggregate size distribution (ASD)

The distribution aggregate sizes was determined by a method similar to that described by Kemper and Rosenau (1986). An air-dried sample of aggregates, about 1 L by volume from each treatment, was passed through a set of sieves of sizes 12.7, 16.0, 18 and 21 mm by gently shaking the sieves with hands. The fractions of aggregates in each size range (12.7-16, 16-18 and 18-21 mm) were weighed and the proportions in the whole sample of aggregates were calculated.

Tensile strength of aggregates (ATS)

Aggregate tensile strength of oven dried aggregates was measured by an indirect tension (crushing) test (Dexter, 1988b; Dexter and Kroesbergen, 1985). Details of the method and calculations used have been described in Section 6.2.3. Aggregates of 18-21 mm diameter were used for this measurement. At least 50 aggregates were measured for each treatment.

Organic carbon of soil (OC)

Total carbon was determined using a dry combustion on a LECO carbon determinator (Tiessen *et al.*, 1981) as described in Section 7.2.13. This was taken to be organic carbon as carbonates were not present in the soil.

Aggregate stability (AS)

Aggregate stability was measured using a modification of a Yoder (1936) method. The modification consisted of using one sieve with openings of 18 mm instead of a nest of sieves. The equivalent of 30 g of oven-dried aggregates (> 18

mm diameter) were wet by rapid immersion and sieved for 10 minutes in an apparatus with a stroke of 35 mm operating at 40 strokes per minute. Results are presented as the percent of the soil remaining on the sieve after sieving. Four replicates were sieved for each treatment.

Root measurements

Total length of roots for each species was determined for two replicates of each treatment immediately after the plant tops were harvested. The contents of the pot were soaked in water for two days to soften the soil. The soil was washed over a sieve of 70 μm mesh to get roots onto the sieve. Total length of roots was estimated using the line intersection method of Newman (1966a). Root dry weight was determined gravimetrically after drying for 48 h at 65°C.

To estimate root length density, twenty five aggregates from each treatment were individually weighed and their root length determined as described above. Root length for each aggregate was divided by the weight of the aggregate to obtain rooting density (cm g^{-1}). Root length density (cm cm^{-3}) was calculated by multiplying the average bulk density of aggregates (1.34 g cm^{-3}) by the root density.

8.2.9 Statistical analysis

Analysis of variance was performed on data sets with the Genstat 5 software package (Genstat Committee, 1987) on a VAX computer. Tukey's test was used to separate means when significance was indicated.

8.3 Results

A summary of the analyses of variance of the properties of the soil is presented in Table 8.2. Soil watering regime had a significant ($p \leq 0.05$) influence on ASD and ATS of aggregates while plant species had significant influences on all the soil properties except ABD. The only significant ($p \leq 0.05$) interaction was that for ASD.

The influence of watering regime on ASD and ATS is shown in Table 8.3. Soils which were kept continuously wet had higher percentage of small (*i.e.* < 18 mm) aggregates compared with those which had been wetted and dried. A visual examination of the aggregates revealed a higher number of roots penetrated individual aggregates in the c/w regime than w/d. In the latter case, roots were observed to curve around aggregates. The aggregates which had w/d were stronger than those which were c/w. Both the proportion of small aggregates and tensile strength were higher in aggregates with plants than in the control, where no plants were grown.

Table 8.2 Summary of analyses of variance for the different properties of the soil.

Source of variation	df	Soil Property[a]				
		ASD	ATS	OC	AS	RLD
Species	2	**	*	*	*	*
Watering regime	1	*	*	ns	*	*
Species x watering regime	2	ns	ns	ns	ns	ns

[a]ASD=aggregate size distribution; ATS= aggregate tensile strength; OC= organic carbon; AS= aggregate stability; RLD=root length density. Significance is given as ** ($p \leq 0.01$); * ($p \leq 0.05$); ns= not significant.

The effect of plant species on the distribution of aggregate size classes is shown in Fig 8.2. The proportion of coarse aggregates was reduced by the presence of roots of all species under both watering regimes. Ryegrass had a higher proportion of small aggregates, then wheat, which in turn had more small aggregates than pea. The proportion of coarse aggregates (18-21 mm) with the c/w treatments was reduced from 100% to about 50, 70 and 80% by ryegrass, wheat and pea respectively, while that with w/d was 70, 90 and 95% respectively.

The total lengths of roots, root length density (RLD) and total dry weight of roots for the different species are presented in Table 8.4. The w/d regime produced significantly ($p \leq 0.05$) lower total root length and RLD in all the species compared to c/w. This is likely to be a direct effect of reduced root growth in the w/d aggregates as a result of high soil strength and water stress. There were distinct differences between species in the total length and RLD in both watering regimes. Total root length and RLD decreased in the order ryegrass > wheat > pea.

Table 8.5 shows the influence of plant species and incubation on the tensile strength of the aggregates. The non-incubated samples were about 30% stronger than the incubated samples, suggesting that the presence of roots, or some other factor degraded by incubation, indeed strengthenedthe aggregates.

Table 8.3 Influence of soil watering regime on size distribution (ASD) and tensile strength (ATS) of aggregates from soil with and without plants.

Watering regime[a]	With plants			Without plants		
	(a) ASD, percent (mean, n=6)					
	Aggregate size (mm)			Aggregate size (mm)		
	12.7-16	16-18	18-21	12.7-16	16-18	18-21
c/w	12.1a	19.8a	68.2	0	0	100
w/d	5.0b	13.7b	81.3	0	0	100
	(b) ATS, kPa (mean ± s.e.)					
c/w	346±23a			181±37a		
w/d	380±41b			314±31b		

[a] c/w=continuously wet; w/d=wetting and drying
Means within a column with the same letter are not significantly different ($p \leq 0.05$) by the Tukey's test; s.e = standard error

Organic carbon and stability of aggregates are presented in Table 8.6. The OC of aggregates from soil which had been planted was higher than that of thecontrol. There were significant differences among the plant species in their influence on OC of the aggregates. The OC of the aggregates containing ryegrass was significantly higher than that of the other species. The higher OC is likely to be a direct result of the higher RLD and root biomass of ryegrass compared with the other species. Aggregates from soil which had been planted were more stable than those from soil which had no plants.

A correlation matrix of the properties of aggregates is presented in Table 8.7. There are significant ($p < 0.05$) correlations among RLD, ASD, ATS, OC and AS. The role of the roots could be a direct physical effect on aggregate properties or an indirect contribution to these properties of aggregates possibly through release of organic materials from the roots to the aggregates.

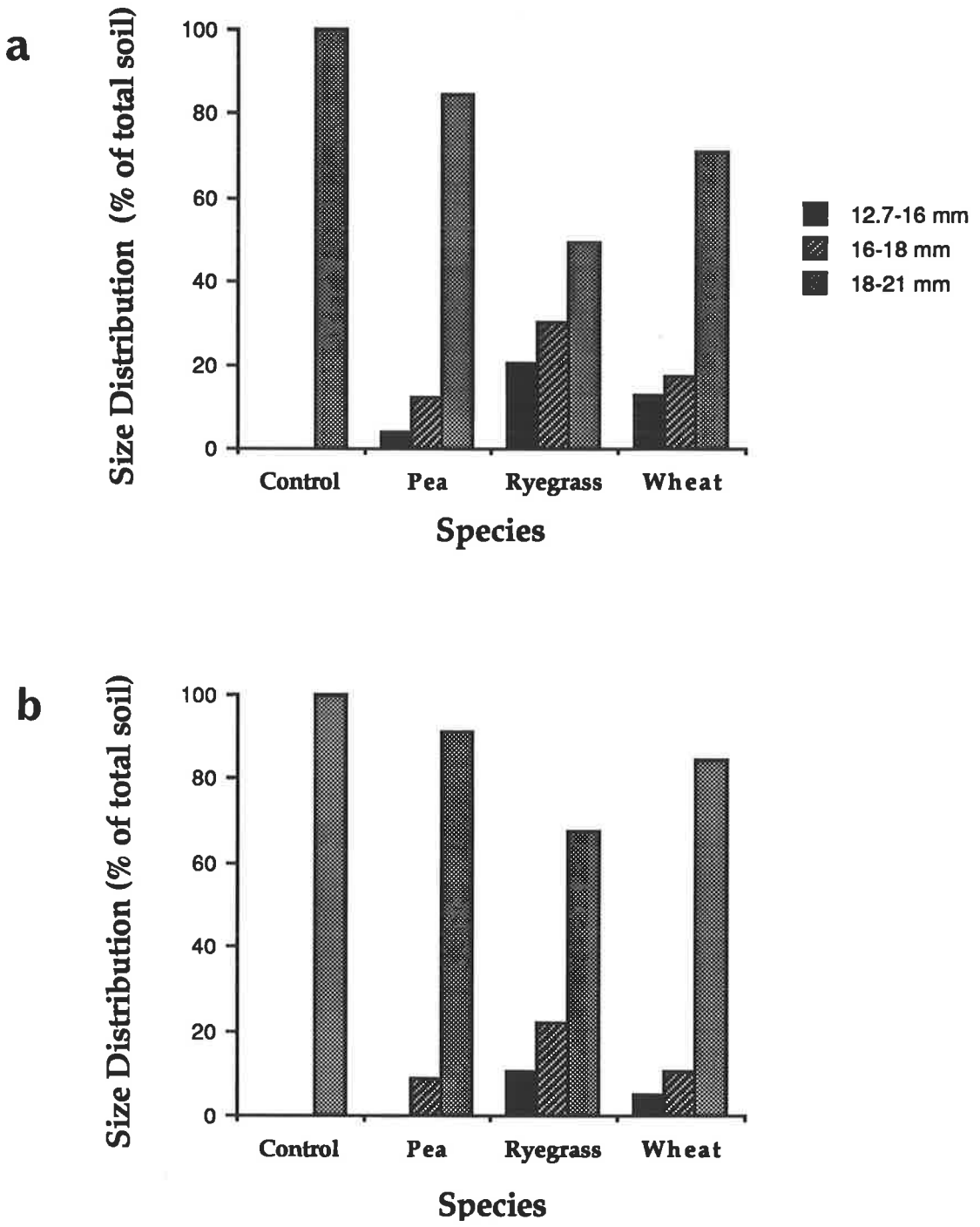


Fig. 8.2 Distribution of aggregate sizes after growing plants in soils which had (a) been kept continuously wet (c/w) and (b) wetted and dried (w/d).

Table 8.4 Total root length, root length density (RLD) and root dry weight for the plant species at two soil watering regimes.

Plant species	Soil watering regime		Soil watering regime	
	c/w	w/d	c/w	w/d
	(a) Total root length (m pot^{-1})		(b) RLD (cm cm^{-3})	
Pea	4.03±0.4a	3.51±0.2a	7.9a	2.5a
Ryegrass	10.19±1.5b	7.63±0.9b	33.6b	22.9b
Wheat	6.26±0.7c	4.31±0.5a	16.8c	9.9c
	(c) Root dry weight (g pot^{-1})			
Pea	1.68a	0.97a		
Ryegrass	3.04b	2.15b		
Wheat	1.12a	1.03a		

Means within a column with the same letter are not significantly different ($p \leq 0.05$) by the Tukey's test.

Table 8.5 Effect of plant species and incubation on tensile strength (mean ± s.e., kPa) of aggregates.

Plant species	Incubated			Not incubated		
	c/w	w/d		c/w	w/d	
			Mean			*Mean*
Control	241±14a	259±13a	***247***	323±23a	374±20a	***349***
Pea	279±17b	311±20b	***295***	370±25b	436±34b	***403***
Ryegrass	339±26c	365±23c	***352***	393±20b	403±33b	***398***
Wheat	313±19b	331±19b	***320***	382±15b	439±21b	***411***
Mean	293	316		367	413	

Numbers in italics are means for plant species at the two watering regimes.
Means within a column with the same letter are not significantly different ($p \leq 0.05$) by the Tukey's test.

Table 8.6 The influence of plant species and soil watering regime on organic carbon (OC) and stability (AS) of aggregates.

Plant Species	OC (%)			AS (% > 18 mm)		
	c/w	w/d	*mean*	c/w	w/d	*mean*
Control	1.24a	1.20a	1.22	27	34	30.5
Pea	1.66b	1.59b	1.63	43	51	47.0
Ryegrass	2.33c	2.11c	2.22	71	77	74.1
Wheat	1.76b	1.63b	1.70	58	63	60.5
Mean	1.75	1.63		49.8	56.3	

Means within a column with the same letter are not significantly different ($p \leq 0.05$) by the Tukey's test.

Table 8.7 Correlation matrix showing correlation coefficients (r) between the soil properties[a].

	RLD	ASD	OC	AS	ATS
RLD	-	-0.85**	0.79**	0.54*	0.62*
ASD	-	-	0.51	0.41	-0.43
OC	-	-	-	0.69*	0.85**
AS	-	-	-	-	0.89**
ATS	-	-	-	-	-

[a]RLD=root length density; ASD=aggregate size distribution; OC=organic carbon; AS=aggregate stability; ATS=aggregate tensile strength. *, ** = significant at ($p \leq 0.05$) and ($p \leq 0.01$) respectively.

8.4 Discussion

The major difference among the treatments was the rooting density which differed considerably among plant species. An examination of correlations revealed that RLD was significantly related to the properties of aggregates (ASD, ATS, AS, and OC) in both c/w and w/d soils. Ryegrass which had the highest RLD had higher ATS, AS and OC and also had the higher proportion of

It is unlikely that aeration within the beds of aggregates would have limited the growth of roots. The packing and size of aggregates created spaces for sufficient oxygen circulation within the beds. There were no visible signs of lack of adequate aeration in the plants.

small sized aggregates (< 21 mm) compared with wheat and pea. The high correlation between RLD and aggregation implies that roots may have been involved directly or indirectly in the processes which modify aggregation and the properties of the aggregates.

The higher proportion of small aggregates in the planted soil compared with the unplanted controls could have resulted from break down of the larger aggregates as roots penetrated through them. The high proportion of small aggregates in soil planted with ryegrass could thus be due to the high RLD and more subsequent penetration of the aggregates by roots,thereby increasing the chances of the aggregates to break. The effect of RLD on ASD was found to be associated with the watering regime of the soil. Plant roots were not able to penetrate the aggregates in the w/d as easily due to high mechanical strength. Also, roots could have lower turgor due to water stress so that root growth pressures may have been lower. The reduced penetration of roots into aggregates resulted in less breakage of the large aggregates.

OC was higher in soils which had plants in them probably as a result of additions of organic materials to the soil from roots and root exudates. Although there is no information on the proportion of carbon contributed to the soil by roots and by exudates, it is likely that the high OC in soil planted with ryegrass was due to its high RLD and root mass. This finding is consistent with the claim of Tisdall and Oades (1979) who reported that the amount of organic material released by the root is related to the length of the root. They also noted that roots of most plants secrete mucilage at the tip and near the root hairs, so that the plant which produce the most root hairs or root tips would be the ones which produce more organic material for stabilising aggregates. Similar views have been held by other authors (*e.g.* Chaney and Swift, 1986; Goss and Reid, 1979; Reid and Goss, 1980). However, it is also possible that the differences in the ability of the roots of species to stabilise aggregates could be related to the amount of mucilage produced by the species.

The increased stability and strength of aggregates from the soil which had been planted can be a result of a combined effect of the mechanical action of roots and the contribution from their organic materials and the associated fungal hyphae. Fine roots and root hairs grow into the large aggregates leading to enmeshment and improved anchorage of the aggregate (Waldron and Dakessian, 1982). Similarly, Willatt and Sulistyaningsih (1990) have shown that the roots of rice can increase the strength and stabilise soil by increasing the shearing resistance of the soil.

Plant roots would also have contributed some organic materials which could act as cementing agents for the soil particles in the aggregates and thus

increase the both strength and stability of the aggregates. Ryegrass has been shown to produce polysaccharide material which are more effective in stabilising aggregates (Tisdall and Oades, 1979). The increase in strength of aggregates which had not been incubated compared with those which had been incubated suggest that the physical reinforcement of roots on aggregates would have made a major contribution to the strength of the aggregates in this study.

The influence of soil watering regime on AS and ATS was evident. Aggregates from soil which had been wetted and dried were stronger and more stable in water than those which were kept continuously wet. The increase in strength of aggregates which had been wetted and dried could be due the following reason. Wetting and drying cycles could contribute to the increase in ATS of the aggregates by a mechanism of 'age-hardening'. Disturbance of soil (*e.g.* by remoulding) decreases the strength and water stability of the soil. It has been shown that if a disturbed soil is left at constant water content and density, then its water stability and strength are gradually regained with time (Mitchell, 1960). The regain of strength is caused by reorganisation of the soil particles to new positions of lower free energy and partly by the re-formation of cementing bonds between the soil particles (Utomo and Dexter, 1981a; Molope *et al.*, 1985). The importance of the age hardening process in increasing the stability and strength of both field and artificial aggregates in the absence of biological activity has been shown by Blake and Gillman (1970).

8.5 Concluding remarks

Although the controlled environmental conditions under which the experiment was conducted and the restricted volume of the pots would be expected to magnify the effects of different plants on aggregation, the results of this study indicate that growth and activities of roots may be an important factor in controlling changes in aggregation and therefore soil structure in beds of large aggregates. Both RLD of the species and soil watering regimes were associated with the changes in ASD and properties of the aggregate. The practical significance of this result is that may be possible to use plant roots to alter the tilth of a seedbed for both seed germination and control of erosion.

Section 9

General Discussion and Conclusions

9.1 Introduction

This final section of the thesis considers and discusses the findings of the whole research project. It attempts to integrate the conclusions drawn from each experiment and identifies future research needs. Finally, some general conclusions are drawn from the work. The discussion will be presented in two main sections, *viz* that related to the ability of roots to penetrate strong soil and that dealing with formation and/or modification of aggregates by plant roots.

9.2 Penetration of roots in strong soil

The work of Sections 3 and 4 was aimed at providing a link between basic plant physiological properties on the one hand and the response of roots to practical soil management programmes on the other. Evidence from the results of experiments from the study support the claim that the process of biological ploughing does occur and that plant species differ in their ability to creat biopores in strong soil.

The main finding from the study was that the elongation of roots in strong soil was related to the diameter of the root. A summary of the relationships between root diameter and elongation under osmotic and mechanical stress conditions in the laboratory studies are presented in Fig. 9.1. A similar relationship was found for the penetration of roots into a compacted subsoil in a field experiment (Section 6). The relationship between the relative root diameter (RRD) and the percent of roots penetrating into the compacted subsoil (P_p) for all the species was found to be

$$P_p = -15.52 + 40.54\ RRD \qquad (R^2 = 0.94) \qquad [9.1]$$

The exact mechanism(s) responsible for the difference in the ability of roots of different species to penetrate strong soil cannot be clearly identified from this work. However, the results from both laboratory (Sections 3 and 4) and field (Section 5 and 6) suggest that root diameter may have strong influence on the penetration of roots into strong soil. This has been related to the maximum root growth pressure exerted by the roots and its effects on the mode of soil deformation. Radial enlargement of roots may also facilitate

root penetration by a mechanism of tensile failure ahead of the root (Barley, 1963). Large diameter roots may require less pressure to penetrate soil surfaces of a given strength than small diameter roots. However, Greacen (1986) has hypothesized that maximum growth pressures of roots are temperature dependent. It would be appropriate to test how root growth pressure is influenced by temperature.

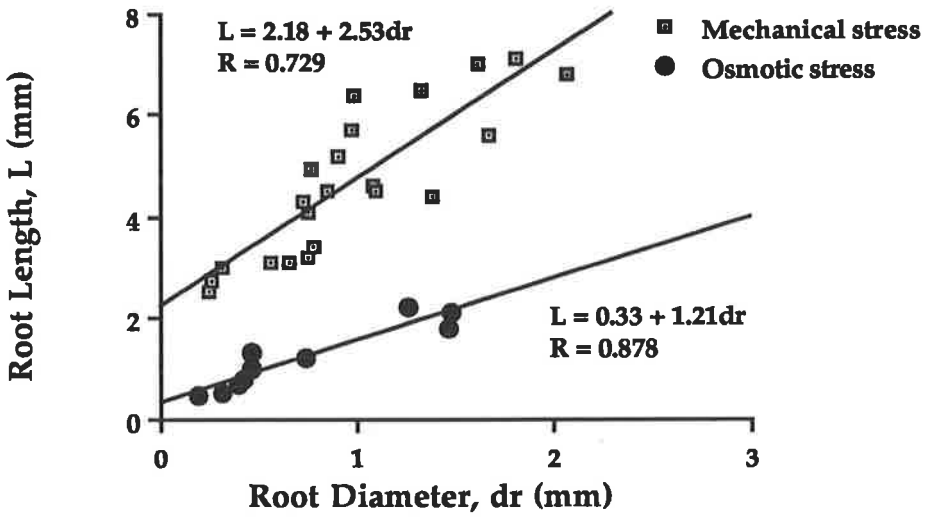


Fig. 9.1 Relationships between diameter and length for the roots of the plant species grown under mechanical (1.14 MPa) and osmotic (1.0 MPa) external stresses.

The above finding is significant in that it emphasises the importance of the morphological characteristics of roots in the process of biological ploughing. It suggests that the penetration of thin roots in compacted soils may be limited while that of thicker roots could still proceed slowly. This means that there is a possibility of selecting plants for the ability of their roots to penetrate strong soil. The methods developed in this study can be important tools in the selection of species whose roots have the greatest potential to penetrate strong soil.

Although the main discussion on the differences in the penetration of roots by the species has centred on root morphology *i.e.* physical interpretation of the influence of root expansion on soil deformation, there are also physiological characteristics of roots (*e.g.* rheological properties of the cell wall and efficiency of roots to osmoregurate against stress) which

could account for the differences in the ability of roots of species to penetrate strong soil. These will now be discussed.

The rheological (plastic and elastic) properties of the walls of root cells influence the extensibility (m in Equations 2.3 and 2.4) of the cell, and have been shown to play a major role in controlling the growth of roots (*e.g.* Pritchard *et al.*, 1987; Cleland, 1971). Cell extensibility has been shown by Lockhart (1965) to be a function of cell wall thickness and cell radius. This is consistent with the finding of Elkins *et al.* (1977) who reported that roots of bahiagrass have a fibrous sheath beneath the epidermis and claimed that this enabled them to penetrate strong soil, probably because they were more resistant to buckling. Rigidity of root tips was not investigated in the species used in this study and so cannot be claimed to be the main reason for the differences. It is recommended that future studies on root penetration in strong soil should include measurements of elastic properties of the roots. Methods of assessing the elastic properties of roots are available (*e.g.* Whiteley and Dexter, 1981a; Whiteley *et al.*, 1982).

Another reason for the differences in penetration by different species could be related the efficiency of the root cells to osmoregulate against stress. Osmoregulation is an adaptive characteristic of the cell which allows the root to counteract a decrease in its water potential. It involves passive accumulation of electrolytes in the cells leading to maintenance of turgor and hence continued growth of the root (Morgan, 1984). Substantial differences in osmotic adjustment may exist between species. Efficiency of osmoregulation has been related to the type of solutes accumulated in the cells (Atwell, 1988; Morgan, 1984). It would be interesting to study the nature of solutes accumulated for osmotic adjustment under the conditions of mechanical and osmotic stress used in this study and relate them to the efficiency of osmoregulation and root penetration.

The results reported in Section 6 show that biopores formed by roots improved the drainage of water through a compacted subsoil. This means that the structure of degraded subsoils could be regenerated by careful management of root action. Management of root systems for this purpose could include the isolation of genes (if any are responsible), which enable some plant roots to penetrate strong soil, and incorporate these through breeding and/or genetic engineering into some useful cultivars. This could produce species with superior ability to penetrate strong soil. The species could then be incorporated into existing cropping systems for creating biopores in soils with compacted layers.

It has been postulated that having many biopores made by roots with large diameters in the compacted subsoil might benefit subsequent crops by providing better access for roots to water and nutrients in the subsoil. However, the specific beneficial effects from such biological ploughing on the subsequent crops have not been established in this study. In most studies where improved growth of crops has been attributed to biological ploughing (*e.g.* Angus *et al.*, 1991; Elkins *et al.*, 1977; Henderson, 1989; Hulugalle and Lal, 1986), improved porosity of the subsoil was only partly responsible for the improvement in crop growth. It is difficult to separate the specific effects of pre-existing biopores from other beneficial effects of crop rotation such as disease control, nitrogen fixation and other changes in the soil. There is need for future work to quantify the specific effects of biopores from bilogical tillage on root growth, water use and yields of suceeding crops.

Benefits of biological tillage will obviously depend on the soil type and climatic conditions. Jakobsen and Dexter (1988), for example, showed from a computer model that a large number of pores were needed to ensure timely root penetration to depth in a short growing season. By contrast, in dry conditions, improved root penetration might possibly decrease wheat grain yield due to increased early water use resulting in less soil water being available at grain filling. Their calculations further showed that the effects of biopores on transpiration vary from year to year depending on rainfall and its distribution in time, and on the amount of soil water stored at time of sowing. This suggests that the benefits of biological tillage are seasonally dependent and so we need to consider the specific weather conditions under which such an approach would be effective. Little is also known about the number or diameter of biopores needed to ensure adequate root growth in the subsoil by the succeeding crop under specific climatic and soil conditions. Further work is needed to quantify the size, number and distribution of biopores required by different crops.

Another area that needs to be understood in biological ploughing is the question of whether the growth of roots into these existing biopores does not affect their functional efficiency in the subsoil. Kirkegaard J 1991 (Personal communication) has suggested the possibility that when roots grow in subsoil through pre-existing channels, their functional efficiency might be reduced (relative to roots growing through weak soil) because of some or a combination of the following reasons.

(a) Roots clustered into biopores act effectively as a single root in a large volume of soil. The major resistance to water uptake thus shifts from the root itself to the rapidly drying soil sorrounding roots (Passioura, 1988;

Tardieu *et al.*, 1992). The uptake of water and immobile nutrients such as phosphorus would be particularly compromised by clumped root distribution (Baldwin *et al.*, 1972) although the subsoil would not be expected to contain much phosphorus in a form available to plants.

(b) Depending on the size of the pores, roots growing in pores larger than their own size may suffer a further impediment to taking up water because the intimate contact between root and soil is missing when a root grows in an existing pore. This may reduce the efficiency of water and nutrient uptake by the root. Herkelrath *et al.* (1977) have shown that when roots are clumped together in macropores, the clumps may be so widely spaced in the soil that nominally available water is poorly accessible. The result may be that roots fail to extract water, especially from deep in the subsoil, even though a substantial length of root is present at this depth.

(c) A seminal/nodal root which encounters a biopore is likely to continue to grow there until the biopore ends, even if it is not vertical, because the root tip will strike the pore walls at low angle of incidence and be deflected. Lateral roots arising from this root will strike the pore walls more or less perpendicularly, which gives the greatest chance of penetration (Dexter, 1986a). If penetration of the pore wall is successful, then problems of poor root distribution and poor root to soil contact can be overcome. However, the lateral roots face two problems when striking the wall of a biopore which are not experienced by the seminal/nodal roots.

Firstly, the soil at the walls of biopores made by roots would have been compressed as the root moved forward, and by secondary thickening of the root. Dexter (1987a) has shown in a model that the density of soil decreases exponentially with distance from the root surface with an exponent which is a constant multiple of the root diameter. Secondly, the roots striking the wall of a biopore are unconfined laterally, and thus the maximum pressure a root can exert may be limited by buckling stress of the root (Whiteley *et al.*, 1982). The greater the air gap which a lateral root must traverse before striking the wall, the lower will be the axial pressure which will cause buckling. Buckling of roots lowers the angle of incidence between the root tip and the pore wall, causing the root to be deflected so that it grows along the biopore (this assumes that the biopores are vertical).

(d) Living and dead roots provide substrate for microorganisms so that the microbial activity in the rhizosphere can be very different from the bulk soil. Roots clustered in biopores could be subjected to a strong dose of either symbiotic or pathological organisms, which have not been diluted by effects of tillage (Evans and Miller, 1988; Chan *et al.*, 1989). Similarly, Kimber (1973)

has shown that decomposition of certain crop residues can have potent allelopathic effects on subsequent crops.

Although above explanations highlight some problems which could be faced by roots growing through biopores in a compacted layer compared to roots growing in weak soil, it should be emphasized that in very strong and non cracking soil, clumped roots may be preferable to having no roots at all. It is clear however that more information on the benefits arising from biological ploughing on growth of succeeding crop is needed. If benefits from biological ploughing can be clearly demonstrated and documented, there are several options to manipulate cultural practices to utilise the process. It is unlikely under dryland conditions that deep rooted species which do not have a commercial return in their own right could be justfied economically and grown solely for beneficial effects on soil structure. However, crop rotations could be adjusted so that deep rooted species such as safflower and lupins preceed crops with low penetration ability such as ryegrass. Opportunities may also exist under irrigation or in horticultural enterprises to grow short season cover crops for improvement of soil structure between main crops.

It is also possible that increased rooting due to increased number of large biopores might have some secondary benefits on structure, especially of cracking clay subsoils. The increased rooting depth with subsequent greater drying of the subsoil might produce shrinkage cracks that improve subsoil structure. When the profile wets up, the shrinkage cracks will close but the biopores may remain open and continue to provide paths for root penetration (Dexter, 1991).

Masle and Passioura (1987) suggested that roots may be able to "sense" the strength of the soil environment and send signals to the leaves which reduces the rate of expansion of the leaf and stomatal conductance of the leaves. Passioura and Gardner (1990) have suggested that these inhibitory chemical signals are induced by both the strength of the soil as it dries and by the fall in water potential of the soil. It looks as if roots can affect changes in the soil as well as the shoot at the same time. Measurements of shoot characteristics were not made in plants used in this study. It is recommended that characteristics of the shoot *e.g.* leaf expansion rate, leaf-water potential and stomatal resistance should be examined in future investigations and interpreted together with the root information.

9.3 Formation and/or modification of aggregates by plant roots

The experiments reported in Sections 7 and 8 examined and compared the ability of roots of different plant species to form aggregates in soil. It presents the options and mechanisms likely to occur in the process of aggregate formation by plant roots. The results showed that plant roots influence the size and properties of aggregates differently in different soils. The aggregation process occurred more intensively when there was a high amplitude and frequency of wetting and drying cycles in the soil. The significance of this finding is that since the amounts of roots in the soil can easily be modified by management (*i.e.* choice of species, planting density and pattern of planting), it is possible that the process of aggregation in a soil can be controlled by management of the root system. Such management options could include the manipulation of root system distribution in the profile to optimize the RLD (root length density) which in turn would control the drying of the soil.

The large variations in RLD between species made it difficult to isolate the specific effects of root morphology on aggregation (*e.g.* pea produces a tap root whereas wheat and ryegrass produce a fibrous root system). To isolate the effects of root morphology on aggregation would require designing an experiment where all the species had the same RLD so the only difference between the roots was their morphology. It is not known whether such an experiment would lead to conclusions similar to those in this study.

One soil property which was significantly influenced by the growth of plant roots (Sections 6, 7 and 8) was the size and distribution of aggregates. Aggregate size distribution is an important issue when considering soil erosion and optimum seedbed tilth for germination. Small aggregates are more vulnerable to erosion by wind and water than large aggregates. However an optimum seedbed for germination requires a combination of both large and small aggregates. The significance of the findings is that plant species could be selected or combined so that their roots produce the distribution of aggregate sizes which offers optimum conditions for crop growth. The results of this work also confirm the well known effects of roots in maintenance of water-stable aggregates. Stable aggregates have the benefit of reducing surface crusting and erosion of soil.

The results of this study have shown that root characteristics responsible for penetration in strong soil are different from those responsible for enhancing the formation of aggregates. It should be emphasized that penetration of roots and aggregation are interrelated. Both

are aspects of generating soil structure as soil structure involves both pores and aggregates. They are also dependent on each other *e.g.* the size and distribution of aggregates does influence the porosity of the soil and vice versa. This means that both the ability of roots to penetrate strong soil and the ability of roots to stabilise aggregates are important and should be considered when selecting species for soil amelioration. It may require that plant species be matched so that a species that can penetrate a compacted layer is followed by one which encourages reaggregation and stabilisation of aggregates.

9.4 General Conclusions

1. The exposure of roots to external mechanical and osmotic stress under controlled conditions in the laboratory has shown that root growth is sensitive to stress. Both stresses caused significant reduction in the elongation and increase in the diameter of roots of all the twenty-two plant species investigated.

2. Plant species differ in their responses to stress. Species whose roots thickened most tended to elongate more under stress than those which did not. There was strong correlation between root diameter of stressed plants and penetration in stressed plants.

3. High soil strength in the subsoil of a red-brown earth significantly reduced the elongation of roots of all species and caused the diameters of the roots to increase. Differences in the penetration ability of the roots were found to be related to the size of the root. Species with bigger diameters (mostly dicotyledonous) penetrated to greater depth than monocotyledons (with smaller diameters). The superior penetration of thick roots was interpreted to mean that thick roots were more efficient at deforming the soil during penetration than thin roots.

4. A comparison of the accuracy of the two laboratory methods to predict the ability of roots to penetrate strong soil in the field showed that the method involving mechanical stressing of roots is better than that involving osmotic stress. In both methods however, the ability of the root to thicken when under stress was found to be a better indicator of root penetration than the ability of the root to elongate.

5. Biopores created by the roots during penetration had significant influences on the flow of water through the compacted soil. The higher sorptivities in soils planted with dicotyledonous species compared to those with monocotyledons was attributed to possibility of larger biopores being created by the roots of the dicotyledons.

6. Growth of plants in homogenised soil and in beds of coarse aggregates resulted in significant changes in the extent of aggregation and in properties of the aggregates. The main properties of aggregates which were affected by the growth of roots were the size distribution, tensile strength and stability of the aggregates. Plant species differ in their influence on these properties. The differences were attributed to differences in the root length density of the species. Aggregation of soil by plant roots was strongly influenced by the shrink/swell properties of soil and the degree to which the soil had been wetted and dried. The following processes may be involved.

(a) Compression of aggregates by effective stresses generated as a result of water extraction from soil by plant roots was considered an important mechanism responsible for the high bulk density and tensile strength of aggregates formed by plant roots from homogenised soils. Wetting and drying of soil lead to the formation of smaller but stronger aggreates in soil with high clay content.

(b) In soils with high clay content, cracking of soil leads to production of smaller aggregates due to tensile stresses generated within the root zone. Plant roots play an important role in the formation of aggregates by drying the soil.

SECTION 10

References

Abdalla A M, Hettiaratchi D R P and Reece A R 1969 The mechanics of root growth in granular media. *J. Agric. Engng. Res.* **14**, 236-248.

Abe K and Iwamato M 1986 An evaluation of tree-root effect on slope stability by tree-root strength. *J. Jpn. For. Soc.* **68**, 505-511.

Aggarwal G C and Prihar S S 1975 A simple technique to determine axial root growth force. *Plant Soil* **42**, 485-489.

Aitchison G D 1961 Relationships of moisture stress and effective stress functions in unsaturated soils. *In* Pore Pressure and Suction in Soils. pp 47-52. Butterworths, London.

Alexander K G, and Miller M H 1991 The effect of soil aggregate size on early growth and shoot-root ratio of maize (*Zea mays* L.). *Plant Soil* **138**, 189-194.

Allison F E 1968 Soil aggregation - some facts and fallacies as seen by a microbiologist. *Soil Sci.* **106**, 136-143.

Anderson G, Pidgeon J D, Spencer H B and Parks R 1980 A new hand-held recording penetrometer for soil studies. *J. Soil Sci.* **31**, 279-296.

Angus J F, van Herwaarden A F and Howe G N 1991 Productivity and break crop effects of winter-growing oilseeds. *Aust. J. Exper. Agric.* **31**, 669-677.

Atwell B J 1988 Physiological responses of lupin roots to soil compaction. *Plant Soil* **111**, 277-281.

Atwell B J and Newsome J C 1990 Turgor pressure in mechanically impeded lupin roots. *Aust. J. Plant Physiol.* **17**, 49-56.

Aubertin G M and Kardos L T 1965 Root growth through porous media under controlled conditions: I. Effect of pore size and rigidity. *Soil Sci. Soc. Am. Proc.* **29**, 290-293.

Baldwin J P, Tinker P B and Nye P H 1972 Uptake of solutes by multiple root systems from soil. II. The theoretical effects of rooting density and pattern on uptake of nutrients from soil. *Plant Soil* **36**, 693-708.

Barber D A and Martin J K 1976 The release of organic substances by cereal roots into soil. *New Phytol.* **76**, 69-80.

Barley K P 1954 Effects of root growth and decay on the permeability of a synthetic sandy loam. *Soil Sci.* **78**, 205-210.

Barley K P 1962 The effects of mechanical stress on the growth of roots. *J. Expt. Bot.* **13**, 95-110.

Barley K P 1963 Influence of soil strength on growth of roots. *Soil Sci.* **96**, 175-180.

Barley K P 1968 Deformation of the soil by the growth of plants. Trans. 9th Int. Congr. Soil Sci. Soc. Vol. 1, pp 759-768. The International Society of Soil Science and Angus and Robertson, Sydney.

Barley K P 1976 Mechanical resistance of the soil in relation to the growth of roots and emerging shoots. *Agrochimica* **20**, 173-182.

Barley K P and Greacen E L 1967 Mechanical resistance as a soil factor influencing the growth of roots and underground shoots. *Adv. Agron.* **19**, 1-43.

Barley K P, Farrell D A and Greacen E L 1965 The influence of soil strength on the penetration of a loam by plant roots. *Aust. J. Soil Res.* **3**, 69-79.

Barnes K K, Carleton W M, Taylor H M, Throckmorton R I and vanden Berg G E 1971 Compaction of Agricultural Soils. Am. Soc. Agric. Engrs. Monograph. St. Joseph. Michigan.

Bekendam J and Grob R 1979 Handbook for Seedling Evaluation. 2nd edition. The International Seed Testing Association. Zurich, Switzerland.

Bengough A G 1991 The penetrometer in relation to mechanical resistance to root growth. *In* Soil Analysis: Physical Methods. Eds. K A Smith and C E Mullins. pp 431-445. Marcel Dekker Inc., New York.

Bengough A G 1988 The Use of Penetrometers in Estimating Mechanical Impedance to Root Growth. Ph. D. Thesis, University of Aberdeen, Scotland.

Bengough A G and Mullins C E 1990a The resistance experienced by roots growing in a pressurised cell : a reappraisal. *Plant Soil* **123**, 73-82.

Bengough A G and Mullins C E 1990b Mechanical impedance to root growth: a review of experimental techniques and root growth responses. *J. Soil Sci.* **41**, 341-358.

Bengough A G and Mullins C E 1991 Penetrometer resistance, root penetration resistance and root elongation rate in two sandy loam soils. *Plant Soil* **131**, 59-66.

Bennie A T P 1991 Growth and mechanical impedance. *In* Plant Roots: The Hidden Half. Eds. Y Waisel, A Eshel and U Kafkafi. pp 393-414. Marcel Dekker Inc., New York.

Bennie A T P and Botha F J P 1986 Effect of deep tillage and controlled traffic on root growth, water-use efficiency and yield of irrigated maize and wheat. *Soil Tillage Res.* **7**, 85-95.

Bennie A T P and Burger R Du T 1981 Root characteristics of different crops as affected by mechanical resistance in fine sandy soils. Proceedings 10th National Congr. Soil Sci. Soc. Southern Africa, East London: 29-32.

Bennie A T P and Krynauw G N 1985 Causes, adverse effects and control of soil compaction. *S. Afr. J. Plant Soil* **2**, 109-114.

Bennie A T P, Taylor H M and Georgen P G 1987 An assessment of the core-break method for estimating rooting density of different crops in the field. *Soil Tillage Res.* **9**, 347-353.

Beven K and German P 1982 Macropores and water flow in soils. *Water Resour. Res.* **18**, 1311-1325.

Blackwell P S, Green T W and Mason W K 1990 Responses of biopore channels from roots to compression by vertical stresses. *Soil Sci. Soc. Am. J.* **54**, 1088-1091.

Blake G R and Gillman R D 1970 Thixotropic changes with aging of synthetic soil aggregates. *Soil Sci. Soc. Am. Proc.* **34**, 561-564.

Blake G R and Hartge K H 1986 Bulk density. *In* Methods of Soil Analysis. Part 1-Physical and Mineralogical Methods. Agronomy Monograph no 9, 2nd edition. Ed. A Klute. pp. 363-375. Am. Soc. Agron. Madison, Wisconsin.

Blake G R, Nelson W W and Allmaras R R 1976 Persistence of subsoil compaction in a mollisol. *Soil Sci. Soc. Am. J.* **40**, 943-948.

Boels D, Davies D B and Johnston A E (Eds.) 1982 Soil Degradation. Proceedings of the land use seminar on soil degradation. A A Balkema, Wageningen, Netherlands.

Böhm W 1979 Methods of Studying Root Systems. Springer-Verlag, Berlin.

Boone F R and Veen B W 1982 The influence of mechanical resistance and phosphate supply on morphology and function of maize roots. *Neth. J. Agric. Sci.* **30**, 179-192.

Bradford J M 1980 The penetration resistance in a soil with well-defined structural units. *Soil Sci. Soc. Am. J.* **44**, 601-606.

Braunack M V 1978 Properties af Aggregated Seedbeds. Ph. D. Thesis. University of Adelaide, South Australia.

Braunack M V and Dexter A R 1989 Soil aggregation in the seedbed: a review. II. Effect of aggregate sizes on plant growth. *Soil Tillage Res.* **14**, 281-298.

Brewer R and Sleeman J R 1960 Soil structure and fabric: their definition and description. *J. Soil Sci.* **11**, 172-185.

Brewer R and Sleeman J R 1988 Soil Structure and Fabric. CSIRO Division of Soils, Adelaide, Australia.

British Standards Association 1967 Methods of Testing Soils for Civil Engineering Purposes, **BS 1377**. British Standards Institution, London.

Cahn M D, Zobel R W and Bouldin D R 1989 Relationship between root elongation rate and diameter and duration of growth of lateral roots of maize. *Plant Soil* **119**, 271-279.

Campbell D J 1975 Liquid limit determination of arable topsoils using a drop-cone penetrometer. *J. Soil Sci.* **26**, 234-240.

Chan K Y, Mead J A, Roberts W P and Wong P T W 1989 The effect of soil compaction and fumigation on poor early growth of wheat under direct drilling. *Aust. J. Agric. Res.* **42**, 221-228.

Chaney K and Swift R S 1986 Studies on aggregate stability. II. The effect of humic substances on the stability of re-formed soil aggregates. *J. Soil Sci.* **37**, 337-343.

Ciamporova M and Luxova M 1976 The effect of polyethylene glycol-induced water stress on the maize root apex. *Biol. Plant.* **18**, 173-178.

Cleland R E 1971 Cell wall extension. *Annu. Rev. Plant Physiol.* **22**, 197-222.

Cockroft B, Barley K P and Greacen E L 1969 The penetration of clays by fine probes and root tips. *Aust. J. Soil Res.* **7**, 333-348.

Coutts M P 1982 Growth of sitka spruce seedlings with roots divided between soils of unequal matric potential. *New Phytol.* **92**, 49-61.

CSIRO 1988 The CSIRO Disc Permeameter-Instruction Manual. CSIRO Centre for Environmental Mechanics, Canberra.

Day P R 1965 Particle fractionation and particle-size analysis. *In* Methods of Soil Analysis. Part 1-Physical and Mineralogical Methods. Agronomy Monograph no 9, 1st edition. Eds. C A Black *et al.* pp 545-567. Am. Soc. Agron. Madison, Wisconsin.

Dettmann M G 1958 Water uptake by pure clays and soil crumbs. *J. Soil Sci.* **9,** 306-315.

Dexter A R 1978 A stochastic model for the growth of roots in tilled soil. *J. Soil Sci.* **29,** 102-116.

Dexter A R 1986a Model experiments on the behaviour of roots at the interface between a tilled seed-bed and a compacted sub-soil. I. Effects of seed-bed aggregate size and sub-soil strength on wheat roots. *Plant Soil* **95,** 123-133.

Dexter A R 1986b Model experiments on the behaviour of roots at the interface between a tilled seed-bed and a compacted sub-soil. II. Entry of pea and wheat roots into sub-soil cracks. *Plant Soil* **95,** 135-147.

Dexter A R 1986c Model experiments on the behaviour of roots at the interface between a tilled seed-bed and a compacted sub-soil. III. Entry of pea and wheat roots into cylindrical biopores. *Plant Soil* **95,** 149-161.

Dexter A R 1987a Compression of soil around roots. *Plant Soil* **97,** 401-406.

Dexter A R 1987b Mechanics of root growth. *Plant Soil* **98,** 303-312.

Dexter A R 1988a Advances in characterization of soil structure. *Soil Tillage Res.* **11,** 199-238

Dexter A R 1988b Strength of soil aggregates and of aggregate beds. *In* Impact of Water and External Forces on Soil Structure. Eds. J Drescher, R Horn and M de Boodt. *Catena Supplement* **11,** 35-52.

Dexter A R 1989 Soil structural decline and restoration on fragile soils: the research task. *In* The Theory and Practice of Soil Management for Sustainable Agriculture. A workshop of the wheat research council, 2-3 February 1989. Australian Government Publications Service, Canberra.

Dexter A R 1991 Amelioration of soil by natural processes. *Soil Tillage Res.* **20,** 87-100.

Dexter A R and Hewitt J S 1978 The deflection of plant roots. *J. Agric. Engng. Res.* **23,** 17-22.

Dexter A R and Håkansson I 1989 Internal micro-structure of soil clods measured by fracture surface analysis. *Swedish J. Agric. Res.* **19**, 77-83.

Dexter A R and Kroesbergen B 1985 Methodology for determination of tensile strength of soil aggregates. *J. Agric. Engng. Res.* **31**, 139-147.

Dexter A R and Tanner D W 1973 The force on spheres penetrating soil. *J. Terramechanics* **9**, 31-39.

Dexter A R, Horn R and Kemper W D 1988 Two mechanisms for age-hardening of soil. *J. Soil Sci.* **39**, 163-175.

Dexter A R, Kroesbergen B and Kuipers H 1984 Some mechanical properties of aggregates of top soils from the IJsselmeer polders. II. Remoulded soil aggregates and the effects of wetting and drying cycles. *Neth. J. Agric. Sci.* **32**, 215-227.

Donald R G, Kay B D and Miller M H 1987 The effect of soil aggregate size on early shoot and root growth of maize (*Zea mays* L.). *Plant Soil* **103**, 251-259.

Drew M C and Nye P H 1969 The supply of nutrient ions by diffusion to plant roots in soil. II. The effect of root hairs on the uptake of potassium by roots of ryegrass (*Lolium multiflorum*). *Plant Soil* **31**, 407-424.

Drew M C and Saker L R 1980 Assessment of a rapid method, using soil cores, for estimating the amount and distribution of crop roots in the field. *Plant Soil* **55**, 297-305.

Eavis B W 1967 Mechanical impedance and root growth. Institute Agricultural Engineering Symposium, Silsoe. Paper no 3/F/39. pp 1-11.

Eavis B W, Ratliff L F and Taylor H M 1969 Use of a dead-load technique to determine axial root growth pressure. *Agron. J.* **61**, 640-643.

Ehlers W, Kopke U, Hesse F and Böhm W 1983 Penetration resistance and root growth of oats in tilled and untilled Loess soil. *Soil Tillage Res.* **3**, 261-275.

Elkins C B 1985 Plant roots as tillage tools. *In* Proc. Int. Conf. on Soil Dynamics. Vol. 3: Tillage Machiney Systems as Related to Cropping Systems. Auburn, Alabama. pp 519-523.

Elkins C B, Haaland R L and Hoveland C S 1977 Grass roots as a tool for penetrating soil hardpans and increasing crop yields. *In* Proc. 34th Southern Pasture and Forage Crop Improvement Conf. Auburn Alabama. pp 21-26.

Ellis T W 1990 Controlled traffic cropping at Roseworthy-The first year. *In* Proc. Conf. Agric. Engng. 1990. Institute of Engineering Australia. Publ. No. 90/13, Toowoomba, Queensland. pp 25-29.

Emerson W W 1977 Physical properties and structure. *In* Soil Factors in Crop Production in a Semi-Arid Environment. Eds. J S Russell and E L Greacen. pp 78-104. University of Queensland Press, Brisbane.

Evans D G and Miller M H 1988 Vesicular-arbuscular mycorrhizas and the soil-disturbance-induced reduction of nutrient absorption in maize. I. Causal relations. *New Phytol.* **110**, 67-74.

FAO (Food and Agriculture Organisation) 1974 FAO-UNESCO Soil Map of the World. Vol. 1: Legend. UNESCO, Paris.

Farrell D A and Greacen E L 1966 Resistance to penetration of fine probes in compressible soil. *Aust. J. Soil Res.* **4**, 1-17.

Gardner H R and Danielson R E 1964 Penetration of wax layers by cotton roots as affected by some soil physical conditions. *Soil Sci. Soc. Am. Proc.* **28**, 457-460.

Gaultney L, Krutz G W, Steinhardt G W and Liljedahl J B 1982 Effect of subsoil compaction on corn yield. *Trans. Am. Soc. Agric. Engrs.* **25**, 563-569.

Genstat 5 Committee 1987 Reference Manual for Genstat 5. Clarendon Press, Oxford.

Gibbons J D 1974 Non Parametric Statistical Inference. McGraw-Hill Book Co., London.

Gill W R and Bolt G H 1955 Pfeffer's studies of the root growth pressures exerted by plants. *Agron. J.* **47**, 166-168.

Gish T J and Jury W A 1983 Effect of plant roots and root channels on solute transport. *Trans. Am. Soc. Agric. Engrs.* **26**, 440-444.

Gliński J and Lipiec J 1990 Soil Physical Conditions and Plant Roots. CRC Press, Boca Raton, Florida.

Gooderham P T 1973 Soil Physical Properties and Plant Growth. Ph. D. Thesis. University of Reading, England.

Goss M J 1977 Effects of mechanical impedance on root growth in barley (*Hordeum vulgare* L.) I. Effects on the elongation and branching of seminal root axes. *J. Expt. Bot.* **28**, 96-111.

Goss M J 1987 The specific effects of roots on the regeneration of soil structure. *In* Soil Compaction and Regeneration. Eds. G Monnier and M J Goss. pp 145-155. A A Balkema, Boston.

Goss M J and Drew M C 1972 Effect of mechanical impedance on root growth of seedlings. Agric. Res. Council, Letcombe Laboratory Annual Report. pp 35-42.

Goss M J and Reid J B 1979 Influence of perennial ryegrass roots on aggregate stability. Agric. Res. Council, Letcombe Laboratory Annual Report. pp 24-25.

Goss M J and Reid J B 1981 Interaction between crop roots and soil structure. *In* Aspects of Crop Growth. Eds. J Davies and F E Shotton. Proceedings of a conference organised by the Agricultural Development and Advisory Service at Bournemouth 20-21 January 1981. pp 34-48. Albeit Gait Ltd, London.

Goss M J and Russell R S 1980 Effects of mechanical impedance on root growth in barley (*Hordeum vulgare* L.). III. Observations on the mechanism of response. *J. Expt. Bot.* **31**, 577-588.

Graf G L and Cooke J R 1980 Soil stresses around a growing root tip. *Proc. Am. Soc. Agric. Engrs*: 80-1024.

Grant C D 1989 Soil Structure and Tensile Strength in Relation to the Microtopography of Soil Fracture Surfaces. Ph. D. Thesis. University of Adelaide, South Australia. pp 138.

Grant C D and Dexter A R 1986 Soil structure generation by wetting and drying cycles. Trans. 13th Int. Congr. Soil Sci. Soc., Vol. 2, pp 60-62.

Grant C D and Dexter A R 1989 Generation of microcracks in moulded soils by rapid wetting. *Aust. J. Soil Res.* **27**, 169-182.

Grant C D and Dexter A R 1990 Air entrapment and differential swelling as factors in the mellowing of moulded soil during rapid wetting. *Aust. J. Soil Res.* **28**, 361-369.

Greacen E L 1986 Root response to soil mechanical properties. Trans. 13th Int. Congr. Soc. Soil Sci., Vol. 5, pp 20-47.

Greacen E L and Oh J S 1972 Physics of root growth. *Nature New Biology* **235**, 24-25.

Greacen E L, Barley K P and Farrell D A 1969 The mechanics of root growth in soils with particular reference to the implications for root distribution. *In* Root Growth. Ed. W J Whittington. Proceedings of the 15th Easter School in Agricultural Science. pp 256-269. Butterworths, London

Greacen E L, Farrell D A and Cockroft B 1968 Soil resistance to metal probes and plant roots. Trans. 9th Int. Congr. Soil Sci. Soc. Vol. 1, pp 769-779.

Greacen E L, Farrell D A and Forrest J A 1967 Measurement of density patterns in soil. *J. Agric. Engng. Res.* **12**, 311-313.

Green P B, Erickson R O and Buggy J 1971 Metabolic and physical control of cell elongation rate. *Plant Physiol.* **47**, 423-430.

Groenevelt P H and Kay B D 1981 On pressure distribution and effective stress in unsaturated soils. *Can. J. Soil Sci.* **61**, 431-443.

Guidi G, Poggio G and Petruzzelli G 1985 The porosity of soil aggregates from bulk soil and from soil adhering to roots. *Plant Soil* **87**, 311-314.

Habib L, Morel J L, Guckert A, Plantureux S and Chenu C 1990 Influence of root exudates on soil aggregation. *Symbiosis* **9**, 87-91.

Hadas A 1987 Long-term tillage practice effects on soil aggregation modes and strength. *Soil Sci. Soc. Am. J.* **51**, 191-197.

Haines W B 1926 Studies in the physical properties of soils. II. A note on the cohesion developed by capillary forces in an ideal soil. *J. Agric. Sci.* **15**, 529-535.

Håkansson I 1982 Long-term effects of vehicles with high axle load on subsoil compaction and crop response. *In* Proc. 9th Int. Soil Tillage Research Organisation Conference. Osijek, Yugoslavia. pp 213-218.

Håkansson I, Voorhees W B, Elonen P, Raghavan G S V, Lowery B, van Wijk A L M, Rasmussen K and Riley H 1987 Effect of high axle-load traffic on subsoil compaction and crop yield in humid regions with annual freezing. *Soil Tillage Res.* **10**, 259-268.

Hamblin A P 1985 The influence of soil structure on water movement, crop root growth and water uptake. *Adv. Agron.* **38**, 95-158.

Harris R F, Chesters G and Allen O N 1966 Dynamics of soil aggregation. *Adv. Agron.* **18**, 107-169.

Heinonen R 1986 Alleviation of soil compaction by natural forces and cultural practices. *In* Land Clearing and Development in the Tropics. Eds. R Lal, P A Sanchez and R W Cummings. pp 285-297. A A Balkema, Boston.

Henderson C W L 1989 Lupin as a biological plough: evidence for, and effects on wheat growth and yield. *Aust. J. Expt. Agric.* **29**, 99-102.

Herkelrath W N, Miller E E and Gardner W R 1977 Water uptake by plants. II. The root contact model. *Soil Sci. Soc. Am. J.* **41**, 1039-1043.

Hettiaratchi D R P 1990 Soil compaction and plant root growth. *Phil. Trans. R. Soc. Lond.* **B 329,** 343-355.

Hettiaratchi D R P and Ferguson C A 1973 Stress-deformation behaviour of soil in root growth mechanics. *J. Agric. Engng. Res.* **18,** 309-320.

Hettiaratchi D R P and O'Callaghan J R 1974 A membrane model of plant cell extension. *J. Theor. Biol.* **45,** 459-465.

Hettiaratchi D R P and O'Callaghan J R 1980 Mechanical behaviour of agricultural soils. *J. Agric. Engng. Res.* **25,** 239-259.

Hewitt J S and Dexter A R 1979 An improved model of root growth in structured soil. *Plant Soil* **52,** 325-343.

Hewitt J S and Dexter A R 1984 The behaviour of roots encountering cracks in soil. II. Development of a predictive model. *Plant Soil* **79,** 11-28.

Heyn A N J 1940 The physiology of cell elongation. *The Bot. Rev.* **6,** 515-574.

Hignett C T 1976 A method for sampling and measuring cereal roots. *J. Aust. Inst. Agric. Sci.* **42,** 127-129.

Hillel D 1980 Fundamentals of Soil Physics. Academic Press. New York.

Hoagland D R and Arnon D I 1950 The water culture method for growing plants without soil. *Calif. Agric. Exp. Sta. Cir.* **347.**

Horn R and Dexter A R 1989 Dynamics of soil aggregation in an irrigated desert loess. *Soil Tillage Res.* **13,** 253-266.

Hulugalle N R and Lal R 1986 Root growth of maize in a compacted gravelly tropical alfisol as affected by rotation with a woody perennial. *Field Crops Res.* **13,** 33-44.

Itoh S and Barber S A 1983 Phosphorus uptake by six plant species as related to root hairs. *Agron. J.* **75,** 457-461.

Jackson W T 1962 Use of carbowaxes (polyethylene glycols) as osmotic agents. *Plant Physiol.* **37,** 513-519.

Jakobsen B F and Dexter A R 1988 Influence of biopores on root growth, water uptake and grain yield of wheat (*Triticum aestivum*) based on predictions from a computer model. *Biol. Fertil. Soils* **6**, 315-321.

Janes B E 1961 Use of polyethylene glycols as solute to increase the osmotic pressure of nutrient solutions in studies of the physiology of water in plants. *Plant Physiol.* **36**, 24.

Johnson C M, Stout P R, Broyer T C and Carlton A B 1957 Comparative chlorine requirements of different plant species. *Plant Soil* **8**, 337-353.

Johnson J F, Voorhees W B, Nelson W W and Randall G W 1990 Soybean growth and yield as affected by surface and subsoil compaction. *Agron J.* **82**, 973-979.

Johnson W C 1962 Controlled soil cracking as a possible means of moisture conservation on wheatlands of the Southwestern Great Plains. *Agron. J.* **54**, 323-325.

Kaufmann M R 1968 Water relations of pine seedlings in relation to root and shoot growth. *Plant Physiol.* **43**, 281-288.

Kawasaki T, Akiba T and Moritsugu M 1983 Effects of high concentrations of sodium chloride and polyethylene glycol on the growth and ion absorption in plants. I. Water culture experiments in a greenhouse. *Plant Soil* **75**, 75-85.

Kays S J, Nicklow C W and Simons D H 1974 Ethylene in relation to the response of roots to mechanical impedance. *Plant Soil* **40**, 565-571.

Kemper W D and Rosenau R C 1984 Soil cohesion as affected by time and water content. *Soil Sci. Soc. Am. J.* **48**, 1001-1006.

Kemper W D and Rosenau R C 1986 Aggregate stability and size distribution. *In* Methods of Soil Analysis. Part 1-Physical and Mineralogical Methods. Agronomy Monograph no 9, 2nd edition. Ed. A Klute. pp 425-442. Am. Soc. Agron. Madison, Wisconsin.

Kimber R W L 1973 Phytotoxicity from plant residues. II. The effect of time of rotting of straw from some grasses and legumes on the growth of wheat seedlings. *Plant Soil* **38**, 347-361.

Kirby J M 1989 Measurements of the yield surfaces and critical state of some unsaturated agricultural soils. *J. Soil Sci.* **40,** 167-182.

Kirkegaard J A, So H B and Troedson R J 1992 The effect of soil strength on the growth of pigeonpea radicles and seedlings. *Plant Soil* **140,** 65-74.

Klepper B 1987 Origin, branching and distribution of root systems. *In* Root Development and Function. Eds. P J Gregory, J V Lake and D A Rose. Society for Experimental Biology Seminar Series 30, pp 103-124. Cambridge University Press, London.

Klepper B 1992 Development and growth of crop root systems. *In* Advances in Soil Science, Vol. 19: Limitations to Plant Root Growth. Eds. J L Hatfield and B A Stewart. pp 1-25. Springer-Verlag, New York.

Kolodny L and Neal O R 1941 The use of micro-aggregation or dispersion measurements for following changes in soil structure. *Soil Sci. Soc. Am. Proc.* **6,** 91-95.

Kramer P J 1983 Water Relations of Plants. Academic Press. Orlando, Florida.

Lagerwerff J V, Ogata G and Eagle H E 1961 Control of osmotic pressure of culture solutions with polyethylene glycol. *Science* **133,** 1486-1487.

Lal R and Stewart B A (Eds.) 1990 Soil Degradation. Advances in Soil Science Vol. 11. Springer-Verlag, New York.

Larionov A K 1982 Methods of Studying Soil Structure. Amerind Publishing Co., New Delhi.

Lawlor D W 1969 Plant growth in polyethylene glycol solutions in relation to the osmotic potential of the root medium and the leaf water balance. *J. Expt. Bot.* **20,** 895-911.

Lawlor D W 1973 Growth and water absorption of wheat with parts of the roots at different water potentials. *New Phytol.* **72,** 297-305.

Letey J 1991 The study of soil structure: science or art. *Aust. J. Soil Res.* **29,** 699-707.

Lockhart J A 1965 An analysis of irreversible plant cell elongation. *J. Theor. Biol.* **8**, 264-275.

Logsdon S D, Allmaras R R, Nelson W W and Voorhees W B 1992 Persistence of subsoil compaction from heavy axle loads. *Soil Tillage Res.* **23**, 95-110.

Logsdon S D, Parker J C and Reneau R B 1987 Root growth as influenced by aggregate size. *Plant Soil* **99**, 267-275.

Low A J 1955 Improvements in the structural state of soils under leys. J. *Soil Sci.* **6**, 179-199.

Lungley D R 1973 The growth of root systems - a numerical computer simulation model. *Plant Soil* **38**, 145-159.

Marshall T J 1962 The nature, development and significance of soil structure. Trans. Joint Meeting Comm. IV and V, Int. Soil Sci. Soc. Parmerston, New Zealand. pp 243-257.

Martin J P, Martin W P, Page J B, Raney W A and De Ment J D 1955 Soil aggregation. *Adv. Agron.* **7**, 1-37.

Masle J and Passioura J B 1987 The effect of soil strength on the growth of young wheat plants. *Aust. J. Plant Physiol.* **14**, 643-656.

McIntyre D S and Stirk G B 1954 A method for determination of apparent density of soil aggregates. *Aust. J. Agric. Res.* **5**, 291-296.

McKenzie B M and Dexter A R 1985 Mellowing and anisotropy induced by wetting of moulded soil samples. *Aust. J. Soil Res.* **23**, 37-47.

McSweeney K and Jansen I J 1984 Soil structure and associated rooting behaviour in minesoils. *Soil Sci. Soc. Am. J.* **48**, 607-612.

Meek B D, Rechel E R, Carter L M, DeTar W R and Urie A L 1992 Infiltration rate of a sandy loam soil: effects of traffic, tillage and plant roots. *Soil Sci. Soc. Am. J.* **56**, 908-913.

Meyerhof C G 1961 The ultimate bearing capacity of wedge-shaped foundations. Proc. 5th Int. Conf. Soil Mech. Vo. II, pp 105-109.

Michel B E and ElSharkawi H M 1970 Investigation of plant water relations with divided root systems of soybean. *Plant Physiol.* **46,** 728-731.

Miller R M and Jastrow J D 1990 Hierarchy of root and mycorrhizal fungal interactions with soil aggregation. *Soil Biol. Biochem.* **22,** 579-584.

Mirreh H F and Ketcheson J W 1973 Influence of soil water matric potential and resistance to penetration on corn root elongation. *Can. J. Soil Sci.* **53,** 383-388.

Misra R K, Alston A M and Dexter A R 1988a Role of root hairs in phosphorus depletion from macrostructured soil. *Plant Soil* **107,** 11-18.

Misra R K, Dexter A R and Alston A M 1988b Root growth and phosphorus uptake in relation to the size and strength of soil aggregates. II. Prediction by a stochastic model. *Soil Tillage Res.* **11,** 117-132.

Misra R K, Alston A M and Dexter A R 1988c Root growth and phosphorus uptake in relation to the size and strength of soil aggregates. I. Experimental studies. *Soil Tillage Res.* **11,** 103-116.

Misra R K, Dexter A R and Alston A M 1986a Maximum axial and radial growth pressures of plant roots. *Plant Soil* **95,** 315-326.

Misra R K, Dexter A R and Alston A M 1986b Penetration of soil aggregates of finite size. II. Plant roots. *Plant Soil* **94,** 59-85.

Mitchell J K 1960 Fundamental aspects of thixotropy in soils. *J. Soil Mech. Fndn. Div., Am. Soc. Civil Eng.* **86** (SM3), 19-52.

Molope M B 1987 Soil aggregate stability: the contribution of biological and physical processes. *S. Afr. J. Plant Soil* **4,** 121-126.

Molope M B, Grieve I C and Page E R 1985 Thixotropic changes in the stability of molded soil aggregates. *Soil Sci. Soc. Am. J.* **49,** 979-983.

Monroe C D and Kladivko E J 1987 Aggregate stability of a silt loam as affected by roots of corn, soybeans and wheat. *Commun. Soil Sci. Plant Anal.* **18,** 1077-1087.

Morgan J M 1984 Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.* **35**, 299-319.

Nelson W W and Allmaras R R 1969 An improved monolith method for excavating and describing roots. *Agron. J.* **61**, 751-754.

Newman E I 1966a A method of estimating the total length of root in a sample. *J. Appl. Ecol.* **3**, 139-145.

Newman E I 1966b Relationship between root growth of flax (*Linum usitatissimum*) and soil water potential. *New Phytol.* **65**, 273-283.

Nishida Y 1961 Determination of stress around a compaction pile. Proc. 5th Int. Conf. Soil Mech. Vol. II, pp 123-128.

Northcote K H 1979 A Factual Key for the Recognition of Australian Soils. 4th edition. Rellim Technical Publications. Adelaide, South Australia.

Oades J M 1984 Soil organic matter and structural stability: mechanisms and implications for management. *Plant Soil* **76**, 319-337.

Oades J M and Waters A G 1991 Aggregate hierarchy in soils. *Aust. J. Soil Res.* **29**, 815-828.

Oussible M, Crookston R K and Larson W E 1992 Subsurface compaction reduces the root and shoot growth and grain yield of wheat. *Agron. J.* **84**, 34 -38.

Passioura J B 1988 Water transport in and to roots. *Annu. Rev. Plant Physiol.* **39**, 245-265.

Passioura J B and Gardner P A 1990 Control of leaf expansion in wheat seedlings growing in drying soil. *Aust. J. Plant Physiol.* **17**, 149-157.

Perroux K M and White I 1988 Designs for disc permeameters. *Soil Sci. Soc. Am. J.* **52**, 1205-1215.

Prihar S S, Singh P and Gajri P R 1975 Effect of simulated plow-sole on water uptake and yield of dryland wheat. *Agron J.* **67**, 369-373.

Pritchard J, Tomos A D and Jones R G W 1987 Control of wheat root elongation growth. I. Effects of ions on growth rate, wall rheology and cell water relations. *J. Expt. Bot.* **38**, 948-959.

Reid J B and Goss M J 1980 Changes in aggregate stability of a sandy loam effected by growing roots of perennial ryegrass (*Lolium perenne*). *J. Sci. Food Agric.* **31**, 325-328.

Richards B G and Greacen E L 1986 Mechanical stresses on an expanding cylindrical root analogue in granular media. *Aust. J. Soil Res.* **24**, 393-404.

Rosenberg N J and Willets N A 1962 Yield and physiological response of barley and beans grown in artificially compacted soils. *Soil Sci. Soc. Am. J.* **26**, 78-82.

Rovira A D, Foster R C and Martin J K 1970 Note on terminology: origin, nature and nomenclature of the organic materials in the rhizosphere. *In* The Soil-Root Interphase. Eds. J L Harley and R S Russel. pp 1-4. Academic Press, London.

Russell E W 1971 Soil structure: its maintenance and improvement. *J. Soil Sci.* **22**, 137-151.

Russell R S 1977 Plant Root Systems: Their Function and Interaction with the Soil. McGraw-Hill Book Co., London.

Russell R S and Goss M J 1974 Physical aspects of soil fertility - the response of roots to mechanical impedance. *Neth. J. Agric. Sci.* **22**, 305-318.

Schuurman J J 1965 Influence of soil density on root development and growth of oats. *Plant Soil* **22**, 352-374.

Schuurman J J and Goedewaagen M A J 1971 Methods for the Examination of Root Systems and Roots. 2nd ed. Pudoc, Wageningen.

Semmel H, Horn R, Hell U, Dexter A R and Schulze E D 1990 The dynamics of soil aggregate formation and the effect on soil physical properties. *Soil Technology* **3**, 113-129.

Scholefield D and Hall D M 1985 Constricted growth of grass roots through rigid pores. *Plant Soil* **85**, 153-162.

Skempton A W 1961 Effective stress in soils, concrete and rocks. *In* Pore Pressure and Suction in Soils. pp 4-16. Butterworths, London.

Soil Survey Staff 1975 Soil Taxonomy: A Basic System of Soil Classification for making and interpreting Soil Surveys. Agricultural Handbook No. 436. USDA Soil Conservation Service, Washington, DC.

Stolzy L H and Barley K P 1968 Mechanical resistance encountered by roots entering compact soils. *Soil Sci.* **105**, 297-301.

Tardieu F, Bruckler L and Lafolie F 1992 Root clumping may affect the root water potential and the resistance to soil-root water transport. *Plant Soil* **140**, 291-301.

Taylor H M 1971 Effects of soil strength on seedling emergence, root growth and crop yields. *In* Compaction of Agricultural Soils. Eds. Barnes K K, Carleton W M, Taylor H M, Throckmorton R I and vanden Berg G E, pp 292-304. Am. Soc. Agric. Engrs., St. Joseph, Michigan.

Taylor M S 1974a The effect of soil aggregate size on seedling emergence and early growth. *E. A. Agric. For. J.* **40**, 204-213.

Taylor H M 1974b Root behaviour as affected by soil structure and strength. *In* The Plant Root and its Environment. Ed. E W Carson. pp 271-291. The University Press of Virginia, Charlottsville.

Taylor H M 1980 Mechanical impedance to root growth. *In* Priorities for Alleviating Soil-Related Constraints to Food Production in the Tropics. IRRI, Los Baños, Phillipines. pp 389-404.

Taylor H M and Brar G S 1991 Effect of soil compaction on root development. *Soil Tillage Res.* **19**, 111-119.

Taylor H M and Burnett E 1964 Influence of soil strength on the root-growth habits of plants. *Soil Sci.* **98**, 174-180.

Taylor H M and Gardner H R 1960 Relative penetrating ability of different plant roots. *Agron. J.* **52**, 579-581.

Taylor H M and Ratliff L F 1969 Root growth pressures of cotton, peas, and peanuts. *Agron. J.* **61**, 398-402.

Taylor H M, Huck M G and Klepper B 1972 Root development in relation to soil physical conditions. *In* Optimising the Soil Physical Environment Toward Greater Crop Yields. Ed. D Hillel. pp 75-77. Academic Press, New York.

Terpstra R 1989 Formation of new aggregates under laboratory-simulated field conditions. *Soil Tillage Res.* **13**, 13-21.

Terpstra R 1990 Formation of new aggregates and weed seed behaviour in a coarse-and in a fine-textured loam soil. A laboratory experiment. *Soil Tillage Res.* **15**, 285-296.

Tiessen H, Bettany J R and Stewart J W B 1981 An improved method for the determination of carbon in soils and soil extracts by dry combustion. *Commun. Soil Sci. Plant. Anal.* **12**, 211-218.

Tisdall J M and Oades J M 1979 Stabilization of soil aggregates by the root systems of ryegrass. *Aust. J. Soil Res.* **17**, 429-441.

Tisdall J M and Oades J M 1982 Organic matter and water-stable aggregates in soils. *J. Soil Sci.* **33**, 141-163.

Towner G D 1961 Influence of soil-water suction on some mechanical properties of soils. *J. Soil Sci.* **12**, 180-187.

Towner G D 1987a The tensile stress generated in clay through drying. *J. Agric. Engng. Res.* **37**, 279-289.

Towner G D 1987b The mechanics of cracking of drying clay. *J. Agric. Engng. Res.* **36**, 115-124.

Towner G D and Childs E C 1972 The mechanical strength of unsaturated porous granular material. *J. Soil Sci.* **23**, 481-498.

Trizek D T 1985 Methods of inducing water stress in plants. *HortScience* **20**, 1028-1038.

Uhland R E 1949 Physical properties of soils as modified by crops and management. *Soil Sci. Soc. Am. Proc.* **14**, 361-366.

Utomo W H and Dexter A R 1981a Age hardening of agricultural top soils. *J. Soil Sci.* **32**, 335-350.

Utomo W H and Dexter A R 1981b Tilth mellowing. *J. Soil Sci.* **32**, 187-201.

Utomo W H and Dexter A R 1981c Soil friability. *J. Soil Sci.* **32**, 203-213.

van Noordwijk M, Floris J and de Jager A 1985 Sampling schemes for estimating root density distribution in cropped fields. *Neth. J. Agric. Sci.* **33**, 241-262.

Veen B W 1982 The influence of mechanical impedance on the growth of maize roots. *Plant Soil* **66**, 101-109.

Vesic A S 1972 Expansion of cavities in infinite soil mass. J. Soil Mechanics and Foundations Division, *American Society of civil Engineers* **98** (SM 3), 265-290.

Voorhees W B 1983 Relative effectiveness of tillage and natural forces in alleviating wheel-induced soil compaction. *Soil Sci. Soc. Am. J.* **47**, 129-133.

Voorhees W B 1992 Wheel-induced soil physical limitations to root growth. *In* Advances in Soil Science, Vol. 19: Limitations to Plant Root Growth. Eds. J L Hatfield and B A Stewart. pp 73-95. Springer-Verlag, New York.

Voorhees W B, Nelson W W and Randall G W 1986 Extent and persistence of subsoil compaction caused by heavy axle loads. *Soil Sci. Soc. Am. J.* **50**, 428-433.

Waldron L J 1977 The shear resistance of root-permeated homogeneous and stratified soil. *Soil Sci. Soc. Am. J.* **41**, 843-849.

Waldron L J and Dakessian S 1982 Effect of grass, legume, and tree roots on soil shearing resistance. *Soil Sci. Soc. Am. J.* **46**, 894-899.

Walker J and Chong S K 1986 Characterisation of compacted soil using sorptivity measurements. *Soil Sci. Soc. Am. J.* **50**, 288-291.

Wang J, Hesketh J D and Woolley J T 1986 Preexisting channels and soybean rooting patterns. *Soil Sci.* **141**, 432-437.

White E M 1966 Subsoil structure genesis: theoretical consideration. *Soil Sci.* **101,** 135-141.

White I and Perroux K M 1987 Use of sorptivity to determine field soil hydraulic properties. *Soil Sci. Soc. Am. J.* **51,** 1093-1101.

White I and Sully M J 1987 Macroscopic and microscopic capillary length and time scales from field infiltration. *Water Resour. Res.* **23,** 1514-1522.

Whiteley G M and Dexter A R 1981a Elastic response of the roots of field crops. *Physiol. Plant.* **51,** 407-417.

Whiteley G M and Dexter A R 1981b The dependence of soil penetrometer pressure on penetrometer size. *J. Agric. Engng. Res.* **26,** 467-476.

Whiteley G M and Dexter A R 1983 Behaviour of roots in cracks between soil peds. *Plant Soil* **74,** 153-162.

Whiteley G M and Dexter A R 1984a The behaviour of roots encountering cracks in soil. I. Experimental methods and results. *Plant Soil* **77,** 141-149.

Whiteley G M and Dexter A R 1984b Displacement of soil aggregates by elongating roots and emerging shoots of crop plants. *Plant Soil* **77,** 131-140.

Whiteley G M, Hewitt J S and Dexter A R 1982 The buckling of plant roots. *Physiol. Plant.* **54,** 333-342.

Whiteley G M, Utomo W H and Dexter A R 1981 A comparison of penetrometer pressures and the pressures exerted by roots. *Plant Soil* **61,** 351-364.

Wiersum L K 1957 The relationship of the size and structural rigidity of pores to their penetration by roots. *Plant Soil* **9,** 75-85.

Wiersum L K 1967 Potential subsoil utilisation by roots. *Plant Soil* **27,** 383-399.

Willatt S T and Sulistyaningsih N 1990 Effect of plant roots on soil strength. *Soil Tillage Res.* **16,** 329-336.

Williams B G, Greenland D J, Lindstrom G R and Quirk J P 1966 Techniques for the determination of the stability of soil aggregates. *Soil Sci.* **101,** 157-163.

Williams J and Shaykewich C F 1969 An evaluation of polyethylene glycol (P.E.G.) 6000 and P.E.G. 20,000 in the osmotic control of soil water matric potential. *Can. J. Soil Sci.* **49,** 397-401.

Williams J and Shaykewich C F 1970 The influence of soil water matric potential on the strength properties of unsaturated soil. *Soil Sci. Soc. Am. Proc.* **34,** 835-840.

Yoder R E 1936 A direct method of aggregate analysis of soils and a study of the physical nature of erosion losses. *J. Am. Soc. Agron.* **28,** 337-351.

Zekri M and Parsons L R 1990 Comparative effects of NaCl and polyethylene glycol on root distribution, growth, and stomatal conductance of sour orange seedlings. *Plant Soil* **129,** 137-143.

Publications from the thesis

1. Materechera S A, Dexter A R and Alston A M 1991 Penetration of very strong soil by seedling roots of different plant species. *Plant and Soil* **135**, 21-31.

2. Materechera S A , Dexter A R and Alston A M 1992 Formation of aggregates by plant roots in homogenised soils. *Plant and Soil* **142**, 21-31.

3. Materechera S A, Dexter A R, Alston A M and Kirby J M 1992 Growth of seedling roots in response to external osmotic stress by polyethylene glycol 20,000. *Plant and Soil* **143**, 85-91.

4. Materechera S A, Alston A M, Kirby J M and Dexter A R 1992 Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil* **144**, 297-30.

5. Materechera S A, Alston A M, Kirby J M and Dexter A R 1993 Field evaluation of laboratory techniques for predicting the ability of roots to penetrate strong soil and of the influence of roots on water sorptivity. *Plant and Soil* **149**, 149-158.

Materechera, S. A., Dexter, A. R. & Alston, A. M. (1991). Penetration of very strong soils by seedling roots of different plant species. *Plant and Soil, 135*(1), 31-41.

Materechera, S. A., Dexter, A. R. & Alston, A. M. (1992). Formation of aggregates by plant roots in homogenised soils. *Plant and Soil, 142*(1), 69-79.

Materechera, S. A., Dexter, A. R., Alston, A. M. & Kirby, J. M. (1992). Growth of seedling roots in response to external osmotic stress by polyethylene glycol 20,000. *Plant and Soil, 143*(1), 85-91.

Materechera, S. A., Alston, A. M., Kirby, J. M. & Dexter, J. M. (1992). Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil, 144*(2), 297-303.

Materechera, S. A., Alston, A. M., Kirby, J. M. & Dexter, A. R. (1993). Field evaluation of laboratory techniques for predicting the ability of roots to penetrate strong soil and of the influence of roots on water sorptivity. *Plant and Soil, 149*(2), 149-158.

THE UNIVERSITY OF ADELAIDE

Roseworthy Campus

FACULTY OF AGRICULTURAL AND NATURAL RESOURCE SCIENCES

10th February, 1993

Mr. S. A. Materechera
Department of Soil Science
Waite Campus
The University of Adelaide

Dear Simeon,

I have pleasure in formally advising you that you have been awarded the 1992 K.P. Barley Prize for research performance in a postgraduate degree.

The citation from the Department of Soil Science recognised the outstanding quality of your work on the generation of soil structure by plant roots and the techniques you have developed which allow rapid screening of plants for the ability of their roots to penetrate strong soil.

I congratulate you on your achievement.

Sincerely

Harold Woolhouse
Dean

Roseworthy, South Australia 5371
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