

LABORATORY STUDIES OF THE EFFECT OF SOIL
IMPEDANCE AND SOIL MOISTURE ON ROOT ELONGATION
OF SEEDLINGS OF PINUS RADIATA D. DON.

by

*Gordon
Richard*

G.R. Davis B. For. Sc. (Hons.) (Melb)

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This thesis contains no material which has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge, contains no copy or paraphrase of material previously published or written by any other persons except where due reference is made in the text of the thesis.

A handwritten signature in dark ink, appearing to read 'G.R. Davis', with a stylized, cursive script.

G.R. Davis

Forestry Commission

Burnie

Tasmania

Australia

October, 1987.

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ABSTRACT

In a drying soil root elongation rate often declines. Whether the reduction in elongation is due to reduced soil moisture or increased soil strength is disputed.

The objectives of this study were to develop an empirical model of radiata pine root elongation and to determine the relative importance of soil strength and soil moisture content on root elongation, and further, to quantify the parameters of a net-pressure mechanistic model of root elongation for pine and to compare the values with those observed for a more commonly studied crop (peas).

The empirical model showed seedling root elongation to be three times more sensitive to increased soil strength than to decreased soil moisture content. The observed pattern of root behavior could be logically explained by a concept of total external stress, where total external stress was a summation of soil moisture potential and an index of penetrometer resistance.

Measurement of pine root segment osmotic potential gave values for cell threshold pressure (below which no elongation takes place) and cell wall elasticity consistent with values reported in the literature for other crops.

The response of pine and pea seedlings to moisture stress in the absence of soil restraint was recorded. Although root elongation of both species declined as moisture potential decreased, pine seedlings showed no

osmotic adjustment to moisture potential and consequently cell turgor decreased as root elongation declined. However, for peas, turgor was maintained but the correlation between turgor and elongation was poor, suggesting that the decline in elongation was due to increased threshold pressure or decreased cell wall elasticity.

Measurement of pea root potential, after seedling growth in pots packed with soil of known penetrometer resistance and moisture potential, showed 11% osmotic adjustment to soil restraint and 41% adjustment to moisture potential. The data was consistent with the empirical data for radiata pine root elongation.

Root behavior, on growing into a more compact soil layer, was consistent with a net-pressure model of root elongation when studied in situ using a neutron radiography technique. The technique was refined to allow a greater number of exposures for a given reactor run.

Soil strength can be considered a general influence on radiata pine root growth except where extremes of soil moisture exist. Any increase in soil strength may reduce the ability of the root to tolerate moisture stress. The general influence of soil impedance on root growth and the slow recovery of some soils after compaction, suggests a better understanding of the likely effects of forest operations on soil strength is needed if productivity losses following harvesting are to be minimized.

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SYMBOLS AND ABBREVIATIONS

Re - root elongation
P - total potential of soil or root
Po - osmotic potential of root
Pt - root turgor pressure
Pp - penetrometer resistance
Ps - external soil restraint on root
Y - threshold wall pressure
m - cell wall elasticity
pb - soil bulk density
g - gram
kPa - kiloPascal
cm - centimeter
d - day
hr - hour

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L. LITERATURE REVIEW

L1. Introduction

The relative influence of soil strength and soil moisture on Pinus radiata D. Don. root elongation, and an examination of whether root growth declines in a drying soil due to increasing soil impedance or decreasing soil moisture potential have been studied. Pressure-balance or net pressure models of root elongation have been advanced to provide a mechanistic explanation of root elongation in soil (Barley and Greacen, 1967). Whether a pressure-balance concept offered a satisfactory model of root elongation or not was tested for pine and pea seedlings.

Mechanised forest operations are increasingly favoured for reasons of cost efficiency and demands from wood-using industries for a uniform raw material. Site productivity may decline following harvesting operations (Greacen and Sands, 1980). Root growth may be reduced as a result of forest harvesting because of adverse soil conditions such as compaction, mixing of horizons, or soil removal through erosion (Froehlich, 1973). Growth of trees in damaged soils can sometimes be improved by the addition of fertilizer to the site. However the reason for poor tree growth may be inadequate root development rather than nutrient deficiency

within the soil (Sands, 1981). Thus, it is important to understand the principles of soil physics and root behavior if informed decisions on site productivity are to be made.

The objectives of this study were:

I. Development of an empirical model relating penetrometer resistance and soil moisture potential to seedling root elongation for radiata pine.

II. Measure the parameters of a pressure-balance model of root growth and test whether the model can logically explain root elongation in terms of soil moisture potential and penetrometer resistance.

III. Use neutron radiography to non-destructively observe root growth and development in soil filled pots.

The literature reviewed here relates to soil physical properties and forest growth, measurements of soil impedance, factors affecting root growth, and mechanistic models of root elongation. The literature on forest tree root growth largely consists of in situ root distribution studies. To understand the process of root elongation at a mechanistic level, material describing root elongation of non-forest crops is included in the review.

L2. Soil Physical Properties and Forest Growth

Sutton (1968) states that the development and activity of root systems strongly influences the growth of trees, and the systems are very sensitive to factors in the soil environment such as temperature, availability of water and nutrients, aeration, mechanical impedance, pathogens and predators.

Machines used in forest operations apply heavy loads to the surface soil and for reasons of cost, tend to be kept in operation throughout the year. Many factors including topography, type, depth and moisture content of the soil, amount of litter and slash, amount, size and type of timber removed, harvesting machines, pattern of extraction tracks and frequency of entry determine the degree and extent of any resultant soil degradation (Froehlich, 1973). Any soil compaction, deformation, soil mixing, wheel rutting or root damage may cause a growth reduction or predispose the site to soil removal through erosion. The variability and heterogeneity of soil disturbance in forests make it difficult to predict the magnitude of any damage following a particular operation.

Machines impose on the soil both a static downward loading and a shear stress resulting from movement across the surface. The ability to resist deformation and transmit forces is best measured by assessing soil strength (Greacen and Sands, 1980). If soil strength is inadequate to

counteract the applied loads then wheel rutting, compaction and mixing of soil horizons may result.

Ground contact pressures for a range of forest machines are quoted and presented by Greacen and Sands (1980).

TABLE L2.1.

Ground contact pressures of various forest harvesting machines. Data from Kerruish and presented in Greacen and Sands, (1980).

Machine type	Ground contact pressure (kPa)	
cable, skyline logger	0	
flexible track skidder	30-40	(may also be additional loading of up to 100kPa from the log)
crawler tractor	50-60	
rubber tyred skidder	55-85	
forwarder with rear bogie	85-100	
forwarder with single rear bogie	120+	

Greacen and Sands (op cit.) consider the shear forces generated by pushing and pulling of loads may be of a similar magnitude. If conditions of wheel slip exist, total force may be five times greater (Cohron, 1971). Total pressures in wheel tracks could then approach 500kPa.

The ground pressure and number of passes for various forest operations are also given by Greacen and Sands (1980) from the unpublished data of Kerruish.

TABLE L2.2.

Relationship between the number of passes of harvesting machines and ground pressure (kPa). Unpublished data from Kerruish.

Forest type	Operation	Number passes	Ground pressure (kPa)
Plantation	clearing	1-4	55
	ploughing	1	55
	planting	1	55
	thinning	6-300	0-125
	clearfelling	2-300	0-125
Native forest	selective logging	2-5	50-80
	clearfelling	2-300	0-80

The data indicate that clearfelling and thinning are the operations most likely to cause soil degradation. Clearfelling is generally closely followed by replanting of seedlings or sowing of seed. The seedlings are therefore establishing in soil before any substantial amelioration of conditions is possible, unless cultivation is carried out. A knowledge of the factors influencing seedling root growth and development is necessary if estimations of the effects of soil degrade on forest productivity are to be made.

Greacen and Sands (1980) reviewed 142 studies of the effect of compaction on crop yield, and reported that 117 showed yield reduction, 12 an increase in yield, 8 both yield increase and decrease and 5 no effect on yield. A reduction in yield was reported for commercially important species such as Pinus radiata, P. elliotii Englm., P. taeda

L., and P. ponderosa Laws.

Froehlich (1979) measured a 14% decrease in Douglas fir growth increment after mechanical forest thinning compared with controls. Moehring and Rawls (1970) found that when a crawler tractor passed a tree six times, basal area increment was reduced by up to 43% over five years if the soil was wet. There was no effect on basal area increment if the soil was dry when the tractor passed the tree. This emphasises that the susceptibility of a soil to degradation depends strongly on its moisture content. Soil strength generally increases as moisture content decreases. Wingate-Hill and Jakobsen (1983) reported that a 3% reduction in gravimetric moisture content may double soil strength. Season of operation can then become significant in determining the degree and extent of any degradation following logging. Steinbrenner (1955) observed logging operations in Washington State during summer and winter, and concluded that one passage of a tractor in winter caused similar effects on the soil to four passages in summer. Hatchell et al. (1970) measured a greater decrease in air porosity and water infiltration rate following winter logging when compared with summer operations.

Variable patterns of disturbance and the interactions between soil factors, water availability, aeration and nutrients make predictions of the likely effects of mechanised operations difficult. Davis et al. (1983) when studying Pinus radiata root distribution in five Tasmanian

forest soils, reported that on some sites up to 62% of the total root length occurred in the top 10cm of the soil. Any operation which increased soil strength and was widely distributed over such forests, for instance mechanised thinning, could affect subsequent productivity. Roots preferentially penetrate areas of reduced soil strength (Sands et al., 1979) so increases in mean strength may not necessarily lead to reduced growth if there are sufficient zones of weakness throughout the site.

Soil physical properties are sometimes not recognized as affecting forest productivity, because tree growth can often be improved by the application of mineral fertilizer (Sands, 1981). Total nutrient uptake can be increased by a greater root length in the soil or greater uptake of nutrient per root.

The rate of recovery of soils after harvesting degradation depends on soil type and the degree of compaction. Clay soils can often recover with successive wetting and drying cycles if they swell and shrink but sands may not recover for more than 50 years after logging (Sands et al., 1979). Thorud and Frissell (1976) artificially compacted soils of various field textures under mature oak trees. Recovery of the 0 to 8cm layer was comparatively rapid (5 to 9 years), but the more compacted 15 to 25cm layer showed no recovery after nine years. Other studies have quoted 19 years (Hatchell et al., 1970), 12 years

(Dickerson, 1976) and 18 years (Miles, 1978) as being necessary for the moderation of the soil physical effects after logging. Data from the southern forests of Tasmania indicate that after eight years the average bulk density of a xanthozem soil formed on dolerite was 1.2gcm^{-3} for the top 10cm when measured on snig tracks. This was not significantly different (t-test, $P = 0.95$) from the bulk density of 1.0gcm^{-3} measured in adjacent undisturbed forest (Davis unpubl. data). Eighteen months after tractor logging in Eucalyptus diversicolour forest in Western Australia, Wronski (1984) measured root density down to 200cm depth. In soil compacted to 1.6gcm^{-3} root density was 16% of the root density in uncompacted soil (bulk density 1.4gcm^{-3}).

Many studies have been made of forest tree root growth but few have examined the interaction between soil moisture and soil strength on root growth (Sutton, 1968). Studies, such as those of Heilman (1981) and Squire et al. (1978), where bulk density is used as a measure of soil strength, cannot be interpreted in terms of theories of root elongation involving a concept of resistance to root penetration of the soil as bulk density is a poor indicator of soil strength when comparing different soils. It is, however, useful to compare the levels of bulk density reported to restrict root development of forest trees with those reported for other crops.

Foil and Ralston (1967) found that root length and root weight of loblolly pine (Pinus taeda L.) decreased

linearly with an increase in bulk density above $\approx 0.9\text{gcm}^{-3}$. An upper limit of bulk density of 1.25gcm^{-3} for Douglas fir (Pseudotsuga menziesii (Mirb.)Franco) and 1.8gcm^{-3} for western red cedar (Thuja plicata D.Don ex Lamb) root expansion were determined by Forristall and Gessel (1953) for trees growing on a compacted glacial till. In a pot study using a sandy loam, Minore et al. (1969) reported that a bulk density between 1.45gcm^{-3} and 1.59gcm^{-3} severely restricted root growth, and Heilman (1981) reported that values of about 1.8gcm^{-3} restricted tree root growth in three soils from Washington State. Squire et al. (1978) reported that for 8 year old stands of Pinus radiata, soil bulk density and root growth were inversely related at some depths sampled in North-Eastern Victoria.

Sands and Bowen (1978) grew radiata pine seedlings in compacted Mt. Burr sand and measured an 87% decrease in the dry weight of roots when bulk density increased from 1.35gcm^{-3} to 1.60gcm^{-3} . They also recorded a decrease in total root length, fresh and dry weights of seedling tops, root volume and top height. Davis et al. (1983) found that the correlation coefficient for root length and bulk density varied between -0.97 and 0.28 in five Tasmanian soils of varying field texture and pedality. This indicated that bulk density was an imperfect index of soil strength if comparisons of critical values were to be made between sites.

Roberts (1976) attempted to relate initiation of new root tips of sitka spruce (Picea sitchensis) to certain soil properties (soil temperature, soil water content and soil pH) and concluded, after sampling by cores, monoliths and trenches, that the initiation of new root tips was not readily related to the soil environment. He further concluded that it was not reasonable to correlate soil properties with root growth, when root growth could be reflecting growth conditions of the tree shoot rather than the root, and that the main factors measured were probably inter-related.

The variability of data and interpretations reported in the literature suggests that field studies are unlikely to be useful in precisely determining the factors influencing root elongation in forest soils. Laboratory studies, where greater control over variables is possible, are required to develop an understanding of the mechanism of root elongation.

L3. Measurements of Soil Strength

The soil resistance to penetration by a metal probe (penetrometer resistance) can be used as an indication of soil strength, which can be related to root elongation (Barley et al., 1965; Eavis, 1967; Taylor and Ratliff, 1969a). Soil strength, when measured as penetrometer resistance, depends on bulk density, soil moisture properties and penetrometer characteristics (Barley and Greacen, 1967). Properties of the penetrometer including rate of advance, method of advance, depth of measurement, and point geometry can effect the readings obtained (Bradford, 1980; Cockroft et al., 1969).

Probe diameter is not considered to be important unless the radial constraint of the system is less than 20 times the diameter of the probe (Voorhees et al., 1975; Bradford et al., 1971). Probe geometry is more important in sandy soils than soils of finer texture (Voorhees et al., 1975). Penetrometer measurements taken at a depth greater than 3 to 4 probe diameters should provide satisfactory readings (Whiteley et al., 1981). Rates of penetration over the range of 0.1 to several 10's of mm hr⁻¹ have not been found to greatly influence penetrometer readings in sandy soils (Eavis, 1967; Whiteley et al., 1981; Bradford, 1980; Blanchar et al., 1978), but Cockroft et al. (1969) found that point resistance was inversely related to rate of penetration for a clay soil.

In shinking or cracking clay soils, penetrometer readings are more variable and less precise. A clear understanding of the purpose of the measurement is needed, as readings taken while the probe moves through voids will only represent skin friction on the shaft of the instrument (Bradford, 1980). If the soil strength measurement is being made to determine soil impedance to root elongation, perhaps the pattern of cracks and voids is more relevant than a measure of penetrometer resistance.

Typically root elongation decreases exponentially as soil strength increases (Taylor and Gardiner, 1963). Greacen et al. (1969) tabulated values of penetrometer resistance at which root elongation ceased for a number of species, penetrometer techniques, and soil conditions. Critical values of penetrometer resistance ranged from 800kPa to 5000kPa with a mean of 2500kPa. Resistance to penetration is about 10 times applied soil load (Farrell and Greacen, 1966) so a soil loading greater than 250kPa could reduce root exploitation if applied uniformly to the soil. Machines used in forest operations commonly apply loads to the soil of this order, but in practice it is difficult to predict the magnitude of any increase in soil penetrometer resistance which results from the use of a machine with a particular ground contact pressure. This is because of the relationship between soil strength and soil moisture and the variability of forest soils.

Penetrometer resistance is a function primarily of soil

bulk density and soil moisture content (Eavis, 1967; Bradford, 1980; Farrell and Greacen, 1966). Mirreh and Ketcheson (1972) measured penetrometer resistance of a clay loam soil (40% sand, 28% clay) with soil bulk densities ranging from 1.0gcm^{-3} to 1.5gcm^{-3} , and moisture potentials from -100kPa to -800kPa . They developed a model to predict penetrometer resistance:

$$P_p = f(X_1 + X_2 + X_1^2 + X_2^2 + X_1X_2), R^2 = 0.95$$

where X_1 is soil matric potential, and X_2 is bulk density. All regression terms were significant with the two second order terms accounting for 90.7% of the variability of penetrometer readings. This indicates a strong interaction between soil moisture potential and bulk density in determining penetrometer resistance. Maximum penetrometer resistance was measured at -400kPa to -600kPa moisture potential. They interpreted the decline in penetrometer resistance for the lower potentials as evidence that inter-particle water bonds that are initially formed as the soil dried, were breaking as the soil moisture content declined, thereby reducing soil strength.

Gerard et al. (1982) proposed that penetrometer resistance could be related to measurable soil factors by:

$$P_p = f(X_1 + X_2 + X_3)$$

where X_1 is volumetric moisture content, X_2 is soil voids ratio, and X_3 is clay %. They tested the model by comparing

predicted and actual penetrometer resistance for different depths within one soil and reported a correlation of $r^2 = 0.86$ between predicted and measured penetrometer resistance. When the model was used to predict penetrometer resistance for soils of differing clay contents, the correlation between predicted and actual penetrometer reading was still quite close ($r^2 = 0.75$).

Consideration of the soil organic matter content can improve the prediction of penetrometer resistance. Sands et al. (1979) correlated penetrometer resistance and root growth under radiata pine forests in the Mt. Gambier region of South Australia. They found that at constant bulk density, soil strength decreased with increasing organic matter content, and that penetrometer resistance was largely independent of soil moisture content.

In summary, the relationship between penetrometer resistance, bulk density and soil moisture content can be well defined for a particular soil but universal models designed to predict penetrometer resistance for a range of soils are generally less robust.

L4. Root Growth, Soil Strength, and Soil Moisture

Root elongation rate generally declines with increasing soil strength, and as soil moisture levels decrease there is often an increase in soil strength (Greacen and Sands, 1980). Whether the observed decrease in root elongation is attributable to the increase in soil strength, the decreased soil moisture or a combination of both is not clear. Some studies have shown no effect of soil moisture on root elongation, and have attributed reduced growth to increasing soil strength (Greacen and Oh, 1972; Taylor and Ratliff, 1969a; Barley et al., 1965). Others consider that the reduced elongation is due to greater moisture stress (Bar-Yosef and Lambert, 1981; Mirreh and Ketcheson, 1973), or a combination of other factors (Gerard et al., 1982). It is necessary to determine the relative influence of soil moisture and soil strength on root elongation if an understanding of the effects of increased soil strength on forest tree growth is to be developed.

Gerard et al. (1982) produced models to predict cotton root growth in two southern USA soils. Growth was enhanced by soil moisture and soil voids, and retarded by increases in strength, bulk density, clay % and depth.

For a model of the form:

$$Re = f(X_1 + X_2 + X_3 + X_4)$$

where X_1 is penetrometer resistance, X_2 volumetric moisture %, X_3 soil voids % and X_4 clay %, the correlation between

actual and predicted root elongation was $r^2 = 0.76$. The level of soil strength which stopped root elongation was related to clay % by the formula:

$$P_p = 185.7X^{-0.49}, \quad R^2 = 0.95$$

with critical values of penetrometer resistance of 5500kPa for the 0-15cm layer of a sandy loam (76% sand, 11% clay), and 3600kPa for the same horizon in a clay loam (45% sand, 29% clay). The results indicate that soil moisture and soil voids decrease soil strength while bulk density and soil depth increase penetrometer resistance. Experiments by Taylor and Ratliff (1969a) showed that elongation of cotton roots growing in sandy loam still proceeded, but at 50% of the maximum rate, when the measured penetrometer resistance was greater than 720kPa. For peanuts they recorded that root elongation was reduced to 50% of the maximum recorded when penetrometer resistance was greater than 190kPa. Mirreh and Ketcheson (1973) grew corn seedlings in a clay loam soil, and when the soil had a moisture potential of -800kPa, root elongation began declining when penetrometer resistance was greater than 10kPa. However, when the soil moisture potential was -1200kPa root elongation declined for all increments in penetrometer resistance.

For Pinus radiata growing on Mt Burr sand, Sands et al. (1979) found that root distribution was closely related to penetrometer resistance, with little root elongation at penetrometer resistances over 3000kPa. Boone and Veen (1982)

growing maize seedlings in sandy loam soil found that by increasing the penetrometer resistance from 900kPa to 3000kPa root growth was reduced by 50%. Taylor and Gardner (1963) reported a strong correlation ($R^2 = 0.96$) between taproot penetration and soil strength. Other authors with similar results include Hemsath and Mazurak (1974), Gerard et al., (1972); Barley et al., (1965); Blanchar et al., (1978) and Vine et al., (1981).

Increased penetrometer resistance is generally associated with reduced root elongation. The value of penetrometer resistance at which root elongation is reduced significantly is fairly constant over the range of soils and plant species reviewed. This suggests that there is a similar relationship between soil strength and root elongation for many crops.

Whether moisture levels per se have an effect on root elongation is disputed. Bar-Yosef and Lambert (1981) grew corn seedlings in a sandy loam soil, and by using a pot system where the root system could be split between treatments of varying soil strength and moisture potential, fitted an equation to the measured corn root elongation of the form:

$$dL/dt = C.L$$

where L is current length of roots capable of longitudinal growth, t is time and C is the specific root elongation

rate. They concluded that C was a function of moisture potential for any level of impedance and that there was an effect of moisture per se. The relationship between soil bulk density and penetrometer resistance was determined using a 5mm diameter blunt-tipped penetrometer. The results may not therefore be comparable with the more usual angled probes, as tip geometry may affect penetrometer readings in sandy soils (Bradford, 1980). After studying the root growth of sitka spruce seedlings with roots split between wet and dry soil treatments, Coutts (1982) reported that in dry loam (-60kPa moisture potential) and dry peat (-30kPa), root growth was less than that in the wetter soils of -6kPa and -5kPa respectively. Unfortunately, no soil strength measurements were made. If the root system was split between wet and dry treatments, growth was not increased in the dry soil when compared with a dry/dry treatments. It was suggested that effects observed at such comparatively small potentials may have been due to a lower water potential at the root surface compared with the bulk soil. However, without direct measurement of soil strength and hydraulic conductivity, it is difficult to determine if there was an effect of moisture per se.

Greacen and Oh (1972) grew peas in a loam with moisture potentials as low as -830kPa and found no effect of moisture on elongation at the levels of moisture potential tested. In contrast, Eavis (1967) reported that pea seedling root growth was reduced when the moisture potential of a

sandy loam was less than -350kPa .

Most authors have conducted experiments in loam or sandy loam soils where the dependence of soil strength on soil moisture levels may be weak. Unless soil strength is specifically measured for each soil moisture treatment, it is difficult to conclude whether there was an effect of moisture per se on root elongation.

Gill and Bolt (1955) defined root growth pressure as the force available to a root to accomplish work against an external constraint. The maximum longitudinal force which a pea root can exert varies between 300kPa and 900kPa (Taylor, 1974; Russell, 1977; Eavis et al., 1969; Eavis, 1967; Eavis and Payne, 1969). Taylor and Ratliff (1969b) measured the maximum axial pressure developed by cotton, pea, and peanut roots under conditions of zero moisture stress and found it varied between 900kPa and 1200kPa .

Greacen et al. (1969), listed possible reasons for the lesser root growth pressures when compared to the penetrometer resistance of the soil they deform. Cylindrical expansion of the root behind the growing tip was considered to relieve the longitudinal stress opposing elongation (Abdalla et al., 1969; Barley, 1962). Rotation of the root tip in the soil, and the transfer of materials to and from the root tip and the soil may reduce the friction between the root and the soil, and small scale variations in the mechanical impedance of the soil may not be detected by

penetrometer measurement. This may facilitate preferential root elongation in areas of lower soil strength.

It is likely that all these factors have some effect in facilitating the advancement of the root through the soil. Whiteley et al. (1981) reported a strong correlation ($R^2 = 0.94$) between penetrometer resistance and root pressure of peas grown in remoulded soil cores. Stolzy and Barley (1968) measured a close relationship between root cell osmotic potential and growth pressure, indicating a physiological mechanism in the process of developing root growth pressures to deform the soil.

Under the influence of mechanical impedance root diameter increases (Barley, 1965; Taylor and Ratliff, 1969b; Eavis, 1967). An increase in root diameter may be important as a mechanism to reduce the resistance to root elongation through the soil (Greacen et al., 1969; Richards and Greacen, 1986), as the increase in cylindrical size behind the root tip effectively reduces the soil strength directly in front of the root cap. Changes in cell wall structure and cell development were noted by Wilson and Robards (1977). In a glass bead system a constraining force of 20kPa resulted in a thicker cortex which largely accounted for an increased root diameter. The thicker cortex was composed of a greater number of cells, some larger, some smaller, than the cells measured in unimpeded controls.

Non-soil media have been used in root elongation

studies to separate the effects of physical constraint on elongation from other factors affecting root growth. The most common non-soil medium used to study the relationship between impedance and growth has been glass beads enclosed within membranes to which a known pressure can be applied (Goss, 1977; Barley, 1962; Aubertin and Kardos, 1965a; Aubertin and Kardos, 1965b; Gill and Miller, 1956). Calculation of pore sizes is possible as the diameter of the beads is known. Goss (1977) argues that in glass bead systems with circulating aerated nutrient solutions it is possible to accurately measure the force the root has to overcome to penetrate the material. The effects of possible confounding factors in soil, such as water potential and gas exchange, are limited. Growing maize seedlings in 1mm glass beads (pore size 1.6×10^{-2} cm) with a constant flow of aerated nutrients, Veen (1982) found a 75% decrease in root elongation and a 50% increase in root diameter when compared to unimpeded controls when a pressure of 40kPa was applied to the system. An external pressure of 20kPa was sufficient to reduce barley (Hordeum vulgare L.) root elongation to 50% of controls (Goss, 1977). Other studies have shown similar effects on root elongation for applied pressures less than 100kPa (Abdalla et al., 1969; Barley, 1962).

Castillo et al. (1982) filled a triaxial cell with a loam soil to a bulk density of 1.2gcm^{-3} and applied pressure to soybean seedling roots. Root elongation with no external pressure was 424mm. With an applied pressure of 58kPa, root

elongation reduced to 269mm, a reduction of 36%.

The reductions in root elongation reported for media studies occur at applied pressures c. 5% of critical soil strength levels reported from penetrometer experiments (Greacen et al., 1968). Boone and Veen (1982), when considering the glass bead experimental system, compared the smaller critical applied pressures compared with soil systems and suggested they may be due to the disproportionate decrease in big pores with small compaction pressures of the glass bead system. There would be disproportionate increases in strength which would be compounded by limited oxygen transport to the root due to roots filling the total pore space.

The appropriateness of a metal penetrometer as a root analogue was questioned by Russell and Goss (1974), who stated that a rigid metal probe could not be representative of a more flexible root. Systems where external pressure could be applied would more accurately reflect soil conditions. However, more recently Richards and Greacen (1986) have successfully modelled the relationship between externally applied pressure and the constraining force on the root, both in soil and a glass bead medium. They demonstrated that the constraining force on the root is c. 10 times the externally applied pressure. Re-analysis of studies where external pressure was applied using the factor developed by Richards and Greacen (1986) suggests that constraining forces where root elongation is reduced to 50% of

unimpeded controls, are in the range 200kPa to 800kPa. These results are comparable with penetrometer studies, if the ratio of penetrometer resistance to constraining force is considered to be c. 5:1 (Whiteley et al., 1981).

L5. Mechanistic Models of Root Elongation

The process of cell elongation and the physical basis for that elongation have been reviewed in the literature (Lockhart, 1965; Lockhart, 1967; Cleland, 1971; Ray et al., 1972).

Lockhart (1965) proposed that plant cell elongation could be described in physical terms and developed a model for plant growth. This model related the rate of cell enlargement to the net turgor pressure inside the cell and the elasticity of the cell wall:

$$R = mW$$

where R is rate of cell elongation, m the cell wall extensibility (elasticity) and W the net pressure acting on the inside of the cell wall. The model is usually accepted for plant tissue where there are no restraining external forces to cell expansion. For plant roots, other than when grown in solution culture, there is generally some external soil physical constraint on elongation and a more sophisticated model is needed.

The model of Lockhart (1965) was developed further by Barley and Greacen (1967) by the inclusion of a soil pressure term to accomodate the restraining force of the soil on the root. Their model for root growth into soils was:

$$\begin{aligned} Re &= (P - P_o - Y - P_s)m \quad \text{for } P_o < (P + Y + P_s) \\ &= (P_t - Y - P_s)m \quad \text{for } P_t > (Y + P_s) \end{aligned}$$

where Re is rate of root elongation, P_t is the turgor pressure of the elongating root cells, P_s is pressure applied externally by the soil, Y is the threshold turgor below which elongation ceases, m is extensibility, and P and P_o are the total and osmotic potentials of the elongating cells respectively. The model compares the net pressure in the cell with the external restraint, and is therefore commonly known as a pressure-balance model, or net pressure model of root growth.

Pressure balance models consider that the rate of root elongation is directly related to the net wall pressure ($P_t - Y$) in the cell. If the external constraining forces are less than the wall pressure the plant cell can expand and the root elongate. Conversely, if the external forces are greater than net wall pressure, there will be no elongation. When wall pressure is greater than restraining force, elongation rate will be proportional to the magnitude of net wall pressure.

Cell turgor is the difference between total cell pressure (P) and cell osmotic potential (P_o). If, for a small root in close contact with the soil, it is assumed that total cell potential must approach total soil water potential, then indirect estimates of root turgor can be made if soil potential and root osmotic potential are

measured.

To maintain growth as the soil dries and soil strength increases, root elongation rate must be buffered against increasing applied pressure (P_s) and decreasing total potential (P) by increasing turgor (P_t) or decreasing threshold turgor (Y) (Sands, 1981). Increases in turgor occur by osmotic adjustment (osmoregulation). It has been widely reported that many plant stems and leaves lower osmotic potential to maintain turgor in response to moisture stress (Zimmermann, 1978; Meyer and Boyer, 1972; Boyer, 1970; Munns and Wier, 1981). Often there is full osmotic adjustment by roots to moisture stress (Greacen and Oh, 1972; Michelana and Boyer, 1982), but other authors report less complete adjustment (Mirreh and Ketcheson, 1973). Meyer and Boyer (1972) withheld water from soybean hypocotyls and reported they maintained turgor at c. 450kPa as the medium dried by reducing osmotic potential from -1000kPa to -1400kPa until eventually threshold potential increased and elongation ceased.

The relation between applied pressure and osmotic adjustment is not as clear. If there is no osmotic adjustment when pressure is applied to the root or the root meets a soil of greater strength, then the pressure balance model predicts that root elongation would be severely restricted as net turgor would effectively be reduced by the greater external pressure. If osmotic adjustment is less complete than that for moisture, then root growth would be

more sensitive to increases in soil strength than to decreases in soil moisture.

Greacen and Oh (1972) working with pea seedlings growing in 'Parafield' loam compacted to different densities, found that for a 100kPa increase in soil resistance there was a 70kPa decrease in osmotic potential, or 70% osmotic adjustment. But osmotic adjustment to declining moisture potential was calculated to be 100%. They concluded that root elongation was therefore more sensitive to changes in soil strength than to soil moisture. Meyer and Boyer (1972) sealed soybean hypocotyls in a Scholander bomb and when pressure was applied there was no osmotic adjustment. Turgor declined immediately and the sensitivity of cell elongation to low moisture potentials increased. Kibreab and Danielson (1977) found that radish roots osmotic potential decreased from -750kPa to -1200kPa when the pressure on two rubber membranes between which the roots grew increased from 400kPa to 850kPa. They concluded that the root had the capacity to react to an external constraint by the lowering of osmotic potential and therefore maintaining its rate of expansion. It could be questioned, however, whether radish expansion is a satisfactory analogue of root elongation as the radish is expanding radially while root elongation is a longitudinal extension.

Any decrease in osmotic potential in root cells is achieved by an accumulation of solutes. The type of solute

appears to vary with proline (Prasad et al., 1982), proteins (Pilet and Senn, 1980), sugars (Munns and Weir, 1981; Stevenson and Cleland, 1981), and salts (Stevenson and Cleland, 1981) being reported. It is not, however, within the scope of the study to examine the mechanism of solute accumulation.

L6. Hormone-Mediated Models of Root Growth

Hormone-mediated models of root elongation suggest that the mechanism of response to applied pressure is essentially independent of physical processes. Root caps meet a constraint or barrier and hormone-induced changes in cell physiology follow. Goss and Russell (1980) considered that root elongation in an environment where there was external constraint could not be adequately explained by the pressure balance model. They proposed a hormone-mediated model for root elongation into compacted media based on the results of experiments where roots were grown in glass bead systems to which known pressures were applied (Goss, 1977). The conclusion of Goss and Russell (op cit) that a pressure-balance model was not adequate to explain root elongation was based on observations summarized by Lachno et al. (1982) as:

"cell volume was not necessarily reduced when pressure was applied to elongating roots." (Goss and Russell felt it was demanded by the pressure hypothesis as the model implies that elongation of individual cells will decline).

"recovery of root after restriction is removed is not immediate. The delay in resuming the previous growth rate and also the time taken for the maximum growth pressure to build up is indicative of a hormonal mechanism."

"the presence of the root cap affects the response. If the root cap was removed before pressure was applied the

roots maintained their previous rate of elongation." (Goss and Russell considered that the root cap initiated the root response to soil impedance)

A reduction in the threshold pressure (Y) the cell must generate before elongation can begin is a possible mechanism by which a hormone-mediated mechanism could control the rate of root elongation (Goss and Russell, 1980). Lowering of threshold turgor by additions of auxin have been reported by Evans (1976) and Cleland (1971). Changes in threshold turgor were the major mechanism reported by Green et al. (1971) to maintain cell expansion in the case of the giant algal cell, Nitella sp. Threshold turgor has been directly measured for leaves using microprobes (Boyer, 1970; Cosgrove and Steudle, 1981; Van Volkenburgh and Cleland, 1981) and derived for roots (Greacen and Oh, 1972) with values between 340kPa and 900kPa being reported.

Sands (1981) suggested that with a high threshold turgor value, a small increase in restraining force could restrict elongation significantly. A pressure balance model will still be valid and therefore reductions in root elongation for small external pressure increases did not per se invalidate a pressure-balance concept of root elongation.

In any comparison of the possible mechanisms of root elongation, it is relevant that the pressure-balance model of root elongation models root cell elongation, but because of the difficulty of measuring cell turgor directly

experimental data are calculated for bulk tissue. It may not be useful, therefore, to cite individual cell behavior (Goss and Russell, 1980) as evidence that the model is not an appropriate analogue for the mechanism of root elongation in soil, as ultimately elongation against a physical restraint must be related to a physical process.

L7. Conclusion

The root environment is complex, with interactions between moisture, mechanical impedance, nutrients, pathogens, temperature, aeration, and predators. Resultant root growth is also a function of plant age, shoot vigour, and season (Sutton, 1968). The complexity of the system makes determination of critical factors and levels in the field extremely difficult except in the case of gross disturbances such as inundation or loss of soil volume through erosion. Studies of tree roots in the forest are limited because of the difficulty in collecting accurate reproducible data. The depth of the root system makes in situ observation expensive. Observation is always accompanied by a degree of disturbance, while the roots of understorey species and neighbouring trees need to be identified and accounted for in any determination (Davis et al., 1983). The areal extent of roots within the forest is poorly understood, so reliable sampling becomes difficult and root grafting within and between species can make the determination of the order of any root within the system inaccurate. Variability of soil conditions within the root sphere means that extrapolation of results from a particular sample to the whole tree may not be valid. The strong influence of season on root activity in most situations necessarily make most studies long term. These factors combine in practise to limit root studies in the field to empirical determinations of rooting depth, root

distribution, seasonal growth and development, and other site influences on root growth (Bohm, 1980).

It is therefore necessary to determine principles and mechanisms of root elongation and growth in simplified systems such as pots, artificial media, or liquid culture. Studies of root behaviour in the laboratory have produced empirical relationships relating soil strength and soil moisture content to root elongation (Eavis, 1967). General responses such as a reduction in root elongation with increasing soil bulk density and declining moisture have been demonstrated (Foil and Ralston, 1967). But the relationship between the measured factor such as bulk density, moisture potential or penetrometer resistance, and the conditions at the root tip or surface to which the root actually responds, are vague and variable. This reflects the complexity of the interactions which govern root activity.

There is little published data on the effect of soil physical factors on the root elongation of radiata pine or other forest species at a single root level. The variability of results from experiments designed to determine critical levels of soil moisture or soil strength for root elongation suggests that factors of technique, soil used and stage of plant growth are significant. The data obtained is useful for the development of empirical models, but to gain a greater understanding of the process of root elongation, a mechanistic approach is needed. An understanding of the relative importance of the different soil physical factors

affecting root growth is required to understand the amelioration of soil conditions in the field (Greacen and Sands, 1980). If soil strength is the major influence on root elongation, then cultivation or ripping may have beneficial effects for root exploitation of the soil. If soil moisture deficits are limiting root expansion, then options to ameliorate the site are fewer.

To satisfactorily develop an understanding of the mechanism of the empirical responses observed, a model for the root elongation process is needed. The pressure-balance model seeks to explain root behavior in purely physical terms. The hormone-mediated model suggests that the elongation process is more complex and under the control of plant growth substances. In considering such a complex system it would be naive to suggest that a simple pressure-balance model would explain all aspects of root elongation in the forest. It is probable that for the individual root, immediate responses to changed soil conditions can be satisfactorily explained in physical terms alone.

The pressure-balance model of root growth is a logical extension of empirical studies. It attempts to model the influence of soil physical factors on root elongation by relating the external and internal forces. Experimental validation of the model for Pinus radiata would demonstrate a mechanism by which soil physical factors may affect root elongation. This would permit a better understanding of the

relative influence of soil strength and soil moisture on
root elongation in the field.

E. MODELS

E1. Introduction.

Figure E1 and Figure E2 have been prepared to provide a framework for experimentation and highlight the interactions between soil physical factors and root growth of interest in the study. Soil and plant factors which may affect the interpretation of root elongation data but are not central to the study are discussed here, and the experimental treatment of those factors outlined.

Figure E1 is a diagrammatic representation of the relationship between the major soil factors affecting root elongation. Figure E2 is a similar diagram which relates the components of a pressure balance model to root elongation.

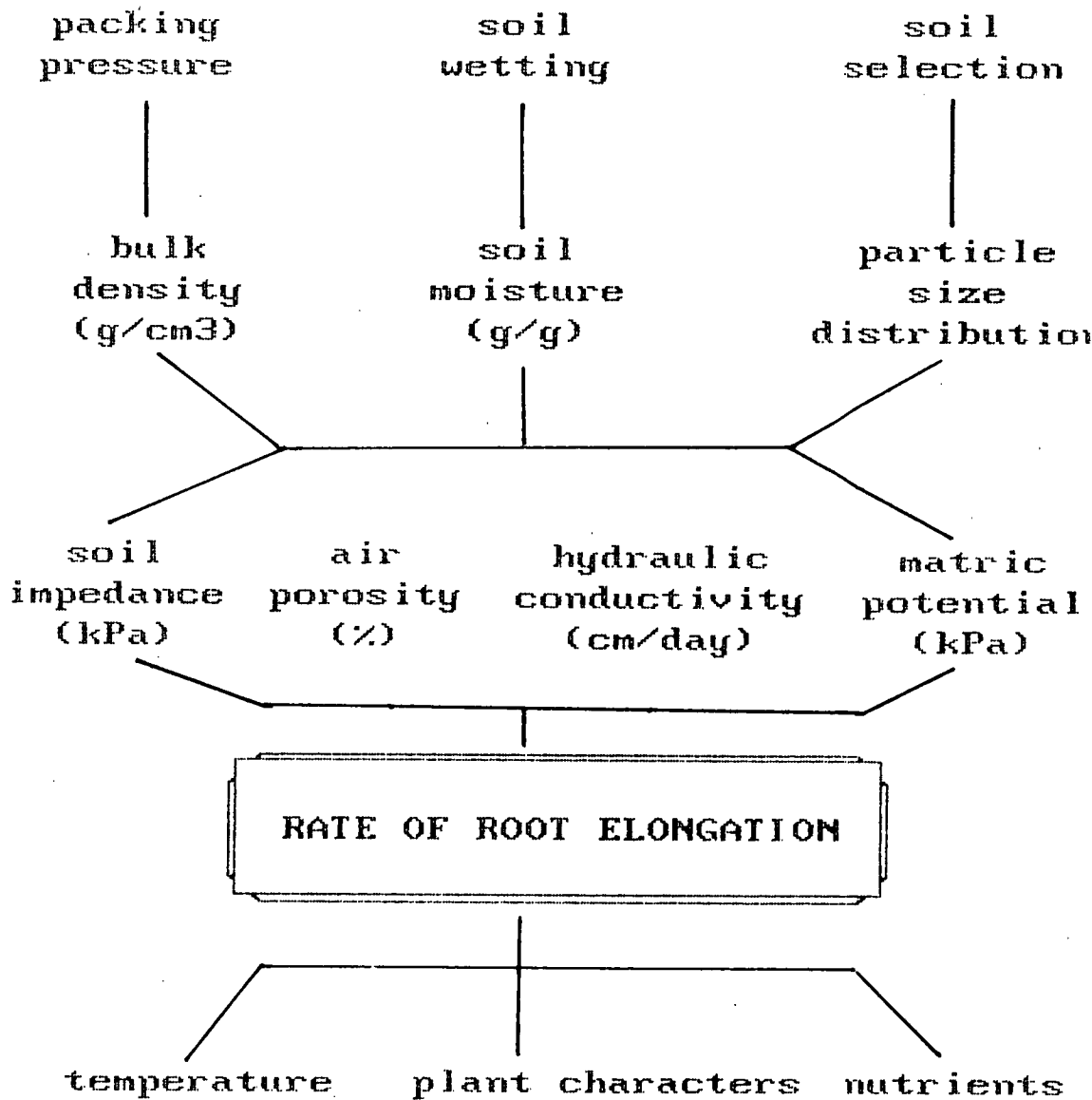
E2. Soil Factors Affecting Root Growth.

Figure E1 illustrates that the soil physical factors directly affecting root elongation rate are soil impedance and soil moisture potential. The magnitude of the restraining force of the soil on the elongating root can be estimated by measurement of soil impedance. Penetrometer resistance is commonly used as an index of soil impedance (Section L3). For soil moisture contents below saturation and when gaseous exchange is unrestricted, total soil moisture potential is the sum of the gravitational, matric and osmotic potentials. In pot experiments gravitational potential is insignificant, as the difference in height between the top and bottom of the pot is generally less than 150mm. Soil osmotic potential was estimated by Bar - Josef and Lambert (1981) at -60kPa after KH_2PO_4 and K_2SO_4 had been added to a sandy loam soil (79% sand, 5% clay) at the rates of 200mg kg^{-1} and 100mg kg^{-1} of soil respectively. Passioura (unpublished data) measured soil osmotic potential at c. -15kPa for a fertile loam soil, also after the addition of nutrients, while Mirreh and Ketcheson (1973) reported that for a clay loam soil, osmotic potential could be reckoned at zero. Soil matric potentials established in pot experiments commonly range from -10kPa to -1500kPa. Unless nutrients are added to the soil, or the soil has a high concentration of solutes (such as saline soils), matric potential can be considered to equate to total soil water potential.

Poor aeration, nutrient deficiencies and limitations on

FIGURE E1

A diagrammatic relationship
between the soil physical factors
affecting root elongation



the rate of moisture movement through the soil may significantly reduce the ability of the root to respond to increases in soil impedance, or decreasing soil moisture potential. Many authors (Bradford, 1980; Eavis, 1967; Mirreh and Ketcheson, 1973; Gill and Miller, 1956) have reported effects of poor aeration when studying root growth in the laboratory and in the field. Minimum levels of air porosity for root growth are a function of plant age, plant species, soil properties and degree of compaction. About 10% air filled porosity is often considered minimal (Greenwood, 1975), although the situation can be more complex (Smith, 1977). As mechanical impedance increases, the sensitivity of root growth to aeration may decrease. Eavis (1967) growing pea seedlings found that inadequate aeration limited root elongation in soils with a bulk density of 1.7gcm^{-3} at 11% air filled pores, while at a bulk density of 1.1gcm^{-3} less than 22% of air filled pore space limited elongation. After growing Douglas-fir in a range of forest soils, Heilman (1981) reported that total pore space less than 27% and 30% limited root growth. Root growth pressure was reduced from 1100kPa to 500kPa when the atmosphere surrounding cotton roots was reduced from 21% to 3% oxygen (Stolzy and Barley, 1968). This indicated a direct effect of aeration on the ability of the root to elongate against soil restraint.

Laboratory experiments are commonly carried out with soils of coarser texture where high moisture potentials can be established at moderate gravimetric soil moisture

contents of less than 20g g^{-1} (Section R1.3.). If air filled porosity is greater than 25% inadequate aeration should not limit root elongation under such conditions.

Tree roots will preferentially grow in localised areas of higher nutrient status (Coutts and Phillipson, 1977; Squire et al., 1978; Phillipson and Coutts, 1977). Soil compaction may increase the uptake of less mobile ions, because of an increase of the apparent diffusion coefficient of the ions which results from closer packing of soil particles and consequently greater concentrations of ions (Kemper et al., 1971). However, soil compaction will also reduce root length. Whether or not compaction will result in a net increase or decrease in uptake cannot be predicted. Castillo et al. (1982) studied the growth of soybean seedling roots in a system where external constraint could be applied and reported that uptake of nutrients (Ca, Mg, K, Mn) was reduced when the soil was compacted to a density of 1.28g cm^{-3} compared with plants growing in soil with a bulk density of 1.16g cm^{-3} . Whiteley et al. (1982) showed that nitrate content of the soil did not affect the buckling pressure of pea and wheat seedlings in growth media, and concluded that nitrate was not significant in affecting the ability of the root to grow through soil with greater impedance. Boone and Veen (1982) studied the interaction between phosphorus nutrition and root growth. They found that the reduction in root growth following an increase in soil impedance was greater in conditions of adequate

nutrition than the reduction of growth observed in conditions of inadequate nutrition.

Burstrom (1981) reported that pea hypocotyl growth was reduced by 75% if the seed was excised, with the reduction in growth being attributed to a lack of organic nutrients which suggests that nutrition was primarily provided from the seed during early growth.

In the experiments which follow here, growth periods were generally less than 7 days and all root growth took place prior to the appearance of seedling cotyledons. It is reasonable to assume that soil nutrient status would not influence root elongation in the experiments.

Limited moisture flux from the growing media to the root may affect the interpretation of results from experiments which test the effect of soil moisture on root growth (Newman, 1969). If the hydraulic conductivity of the soil is relatively low, the rate of moisture movement through the soil to the root maybe inadequate to support root elongation. Root growth may thus decline, although soil moisture potential may be quite moderate and not expected to reduce growth per se.

Gardner (1960) developed a relationship between unsaturated hydraulic conductivity and the moisture potential difference between the root and soil required to drive the moisture flux necessary for root elongation. He

calculated for soils with little moisture holding capacity and high transpirational demand, that large gradients in potential would exist between the root and the surrounding soil. Cowan (1965) reached a similar conclusion. Newman (1969) considered the available experimental evidence and concluded that large gradients were unlikely to exist in many soils, and that the potential drop required to drive the moisture flow had been overestimated.

Williams (1974) using Pinus carribea, found that the difference between the potential of the root and that of the soil was less than predicted by Gardner (1960) and Cowan (1965). Reicosky and Ritchie (1976) calculated that root resistance to water flow would be far higher than that in the soil, until the soil hydraulic conductivity was about $10^{-6} \text{ cm d}^{-1}$. The more recent studies suggest that the importance of the rate of moisture transport to the root surface has been over estimated for soils of finer texture in the past.

Warnaars and Eavis (1972) found no effects of water availability when they grew pea seedlings in five sands of varying grain size. Bar-Yosef and Lambert (1981) observed a decrease in root elongation when moisture content decreased and soil strength remained constant. They suggested it may have been due to a decrease in hydraulic conductivity with increasing bulk density as reported by Kemper et al. (1971). Mirreh and Ketcheson (1973), suggested the difference in root elongation rate when seedlings were grown in soils of

different texture but penetrometer resistance and moisture potential were similar, reported by Taylor et al. (1967), may be attributable to differences in hydraulic conductivity.

Precise measurement of unsaturated hydraulic conductivity is difficult and it is often not measured in laboratory experiments relating root growth to soil impedance and moisture content. Anomalous results can sometimes be interpreted by assuming inadequate hydraulic conductivity. However, critical levels of conductivity are usually calculated from theoretical models of moisture flow from the soil to the root, and not from experimental results. Hydraulic conductivity of the Wynyard sandy loam used for experimentation was measured (Section R1.4.) and considered in assessing the root elongation data to ensure that any significant influence of soil hydraulic conductivity on root elongation was detected.

Seedling age may have an effect on the ability of the root to resist applied stress. Castillo et al. (1982) reported that root elongation for soybean seedlings 10 days old was 100% greater than for seedlings 5 days old, when an identical stress was applied to the roots growing in a triaxial load cell. All seedlings used in this study were of uniform age to eliminate any differential effects of seedling age between treatments.

E3. Mechanistic Model of Root Elongation.

Root elongation can be considered a turgor pressure mediated response (Figure E2). A simple model (Barley and Greacen, 1967) for root elongation with mechanical constraint from the soil can be written as:

$$Re = (P - Po - Y - Ps) m$$

where Re is root elongation, P is root water potential, Po is root osmotic potential, Y is the threshold turgor pressure below which root elongation ceases, Ps is the external restraining pressure, and m is a measure of cell wall elasticity (Section L5).

As:

$$Pt = (P - Po)$$

where Pt is root turgor pressure, we have

$$Re = (Pt - Y - Ps)m$$

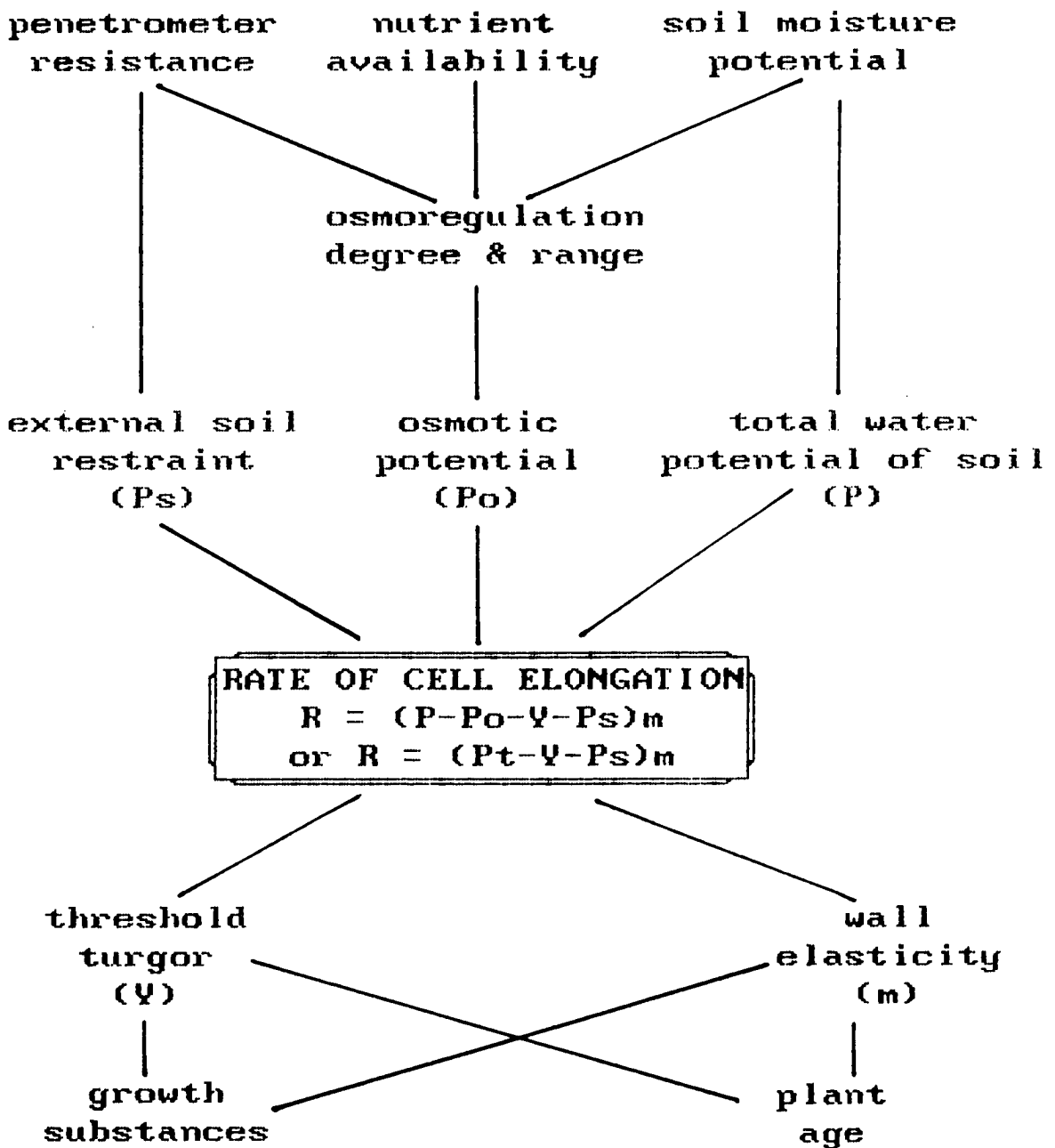
as a mechanistic model of root elongation for roots growing in soil with an external restraining force.

Root elongation rate may therefore be affected directly by changes of the external constraint (Ps), turgor (Pt), threshold pressure (Y) or cell wall elasticity (m). A number of influences may alter the magnitude of these factors and therefore need consideration in experimentation.

The external constraint on root elongation (Ps) is

FIGURE E2

A diagrammatic relationship of the factors in a pressure-balance model of root elongation



difficult to measure in soils. Farrell and Greacen (1966), and Greacen et al. (1968) related penetrometer resistance to the force normal to the cylindrical expansion of the probe. It was used as a measure of the force opposing elongation of the root and can be represented as follows:

$$P_s = P_p(1 + \tan b \cot a)$$

where P_s is force normal to the probe, P_p is soil strength measured as penetrometer reading, a is the probe semi-angle, and b is the angle of soil metal friction which varies with soil particle size distribution, bulk density and soil moisture content (Greacen and Sands, 1980).

Bradford (1980) measured angles of soil metal friction for a silt loam soil (5% sand, 62% silt) with weak fine sub-angular blocky structure. Using a strain controlled direct shear machine b varied from 20° at -10kPa soil moisture potential to 23° at -100kPa . The formula of Farrell and Greacen (op cit.) predicts that the ratio of penetrometer resistance to root growth pressure will be between 2 for a soil with a small angle of internal friction and 5 when b is about 40 degrees.

Much of the evidence relating P_s and P_p is indirect evidence based on comparisons between the known maximum pressure which a root can exert, and the much higher value of penetrometer pressure at which root elongation either ceases or can continue at a reduced rate. Eavis (1967) and

Eavis and Payne (1969) compared the axial pressures exerted by pea roots entering soil cores, with the pressures on a metal probe of similar shape and diameter. The penetrometer probe required a pressure between 4 and 8 times greater than for the roots. Greacen et al. (1968) summarized all the available literature on the value of probe measurements at which root elongation ceased. They varied between 800kPa and 4000kPa, or between 1 and 4 times the maximum pressures which roots can exert (Section L4.1.3.). Whiteley et al. (1981) directly measured the relationship between external soil restraint and penetrometer resistance using remoulded cores of Urrbrae fine sandy loam (26% sand, 17% clay, organic matter content 1.7%). The growth pressure necessary for pea seedling roots to penetrate cores of known penetrometer resistance was measured at a soil moisture potential of c. -100kPa. The ratio between penetrometer resistance and growth pressure for remoulded cores was determined as 3.83:1.

To calculate root turgor values for use in a pressure balance model of growth, root osmotic potential (P_o) and total root potential (P) need to be measured (Figure E2.). Osmotic potential of expressed root sap was measured psychrometrically in this study (Section M232). Total root potential was not measured directly, but assumed to be equal to the moisture potential of the soil or solution in which the root was growing. In fact there must be a finite potential difference between the soil and root for moisture

to flow to the root. This is usually small compared to applied moisture treatments (Newman, 1969). Greacen and Oh (1972) grew pea seedlings in 'Parafield' loam, and calculated that for the maximum growth rate they recorded of 24mm d^{-1} , an inward flow of moisture to the elongating root of $0.013\text{ cm}^3\text{ cm}^{-1}\text{ hr}^{-1}$ would be needed to increase the volume of the root. As the seedlings they used had not developed cotyledons, transpirational demand was nil. A potential drop of -10kPa was determined to be adequate to produce the flow required in the soil. This is quite small when compared with soil moisture potentials commonly established in experimental treatments. It is therefore reasonable experimentally to assume that in the absence of transpirational demand for moisture soil matric potential is equal to total root potential except possibly in dry sands where the rate of moisture flow to the root is limited.

Changes in threshold pressure below which no elongation occurs (Y), or the extensibility of the cell wall (m), will alter root elongation rate. Growth substances, particularly auxins, may alter the threshold pressure or the fluidity of the cell wall. Authors undertaking empirical studies on the influence of growth substances on the ability of roots to penetrate compacted soils report variable results. Studying the interaction between mechanical impedance and ethylene production by bean (Vicia faba L.) seedlings, Kays et al. (1974) found that ethylene evolution increased by as much as six times when compared with unimpeded controls.

Applications of exogenous ethylene also increased root diameter, indicating that ethylene may act as a growth regulator where mechanical resistance is high. Examining the cell wall structure of maize seedlings, Veen (1982) observed a similar orientation of cell wall fibrils when seedlings were grown in a constrained system compared with the effect of ethylene application. He suggested that ethylene may act as an intermediate factor, and be produced by the root cap and then transported back to the zone of cell elongation where the physiological response to impedance is observed.

Lachno et al. (1982) grew maize seedlings in sand/loam mixtures at 1.2gcm^{-3} and 1.6gcm^{-3} bulk density. There were no measureable differences in levels of abscisic acid (ABA) but indole-acetic acid (IAA) levels were 3 times higher in the roots grown in the more compacted soil. These authors suggested that an investigation as to whether IAA was affecting root growth directly, or whether it was promoting the production of ethylene, would be worthwhile. Wilkins et al. (1978) found variable results when assessing the ability of pea roots to penetrate compact soil after the addition of dibromo-hydrobenzoic acid (DBHB) or dichloro-hydrobenzoic acid (DCHB) to the soil. Saini (1979) found that gibberellic acid (GA3) aided root penetration of compacted subsoils by alfalfa.

The influence of growth substances in the response of roots to mechanical impedance is unclear. Very few studies have been conducted in soil systems because of the

difficulties in controlling application rates and accurately measuring effects. Growth substances may have a greater role in linking the physical constraint on the root to the observed response, rather than having an effect per se.

If the equation of a pressure balance model of root elongation is as follows:

$$Re = (Pt - Y - Ps) m$$

and it is quantified experimentally, then it would be expected that the relationship between the various factors would be consistent and logical for the model to be valid. Root elongation should be related to turgor if soil restraint is constant, and should decline if turgor is maintained and soil restraint increases. Estimates of threshold pressure and wall elasticity should be reasonably constant for particular conditions. A decline in root turgor as distance from the root tip increases may be expected unless Y and m also vary with distance from the root tip. The degree and range of osmotic adjustment to declining soil moisture can be tested by observing the relationship between osmotic potential (P_o) and total potential (P). Likewise the degree and range of osmotic adjustment to increasing soil strength can be determined by measurement of osmotic potential and soil restraint (P_s).

The pressure balance model of root elongation implies a concept of total stress which the root can oppose. The

minimum osmotic potential the root can generate will determine whether turgor, and hence elongation, can be maintained in varying conditions of soil strength and soil moisture. For the limiting condition ($Re = 0$), the minimum osmotic potential the root can develop is -2000 kPa, then, in conditions of zero external physical constraint ($Ps = 0$), assuming threshold turgor (Y) to be c. 400 kPa, the root will elongate as follows:

$$Re = (P - Po - Y - Ps)m$$

$$0 = (P - (-2000) - 400 - 0)m$$

and as m must be greater than 0 :

$$0 = P - (-2000) - 400 - 0$$

$$P = -1600 \text{ kPa}$$

This implies the root will elongate until the medium has a potential of less than -1600 kPa. In contrast, if the external soil constraint to elongation is 1000 kPa, then this would be equivalent to a penetrometer resistance of c. 4000 kPa and as before:

$$Re = (P - Po - Y - Ps)m$$

$$0 = (P - (-2000) - 400 - 1000)m$$

$$P = -600 \text{ kPa}$$

Here root elongation will be reduced if the moisture potential of the medium is less than -600 kPa. The behavior of the root between extremes will be determined by the degree and range of any osmotic adjustment to soil strength and soil moisture.

MATERIALS AND METHODS

M1. Experimental Plan

Experiments were planned to satisfy the objectives detailed in Section L1. The sequence of experimentation was:

1. Selection and testing of standard methods and techniques for experimentation with soil and seedlings.

2. Experiments to achieve a laboratory quantification of values for an empirical model of root growth in terms of soil strength and soil moisture for radiata pine.

3. Experiments to separate and quantify the components of total root potential and to test a mechanistic pressure-balance model of root elongation for pine and pea seedlings.

4. The use of neutron radiography to observe the pattern of root development in soil-filled pots.

M2. Standard Methods.

To facilitate experimentation, standard methods of soil and seedling treatment were adopted. The collection, preparation and storage of the soil used for pot experiments is described. Soil physical properties and soil moisture characteristics were measured. The soil wetting and pot packing process is detailed along with seedling germination and growth procedures. For the experiments requiring the measurement of plant osmotic potentials, techniques for sample preparation and storage, psychrometer calibration and recording, and the pot system used are described.

M2.1. Soil collection and characteristics

All soil used in experimentation came from the same site. The site, collection and basic physical properties of particle size, moisture characteristic and hydraulic conductivity are described here.

M2.1.1. Site description and soil collection.

The soil was collected from beneath a radiata pine forest in North West Tasmania, 4km south of Wynyard in Compartment 55 of Oldina State Forest (Grid reference, 901580, Inglis Sheet (8015) 1:100,000 Land Tenure Index Series, Lands Department, Hobart, 1983). The standing radiata pine crop was planted in 1953 at a spacing of 2.4m by 2.4m (1700 stems per hectare) and was subsequently

thinned to around 350 stems per ha. The mean annual rainfall was 1100mm (Wynyard Airport), the elevation of the site was 50m above sea level, and the aspect was to the north west with a 5° slope.

Geological survey (Burnie Sheet (SK 55-3) 1:250,000, Lands Department, Hobart, 1983) indicated Permian mudstone or sandstone parent material. The soil formed was a reddish yellow (7.5 YR 6/8) duplex soil with a sandy loam surface with average depth of around 2 metres. Classification (Northcote, 1974) using the Factual Key is Dy4.61.

The soil for experimentation was collected from 10cm to 30cm depth below the surface, primarily to avoid high concentrations of needle duff and other organic matter in the surface layers (0-10cm). The soil was placed in 50 litre plastic bins and transported to the laboratory where all the bins were emptied onto a clean concrete floor. After air-drying for one week at about 20°C, the soil was mixed with a shovel prior to sieving through a 2mm aperture sieve. The less than 2mm soil material was stored in 50 litre plastic bins until required.

M2.1.2. Particle size analysis

A 100g sample of air-dried soil was taken from each of six 50 litre plastic bins. These samples were bulked, mixed, and a 200g sub-sample taken for particle size analysis. The hydrometer and sedimentation cylinder technique of Bouyoucos, (1927) was used. The results are presented in

Section R1.1.

M2.1.3. Organic matter content

Organic matter content was estimated from the loss of weight on ignition of the sample in an electric furnace. Soil samples were selected from a bulked sub-sample representative of all less than 2mm soil in the storage bins. The air-dried soil was passed through a 1mm round-hole sieve. After oven drying (105°C for 24 hours) to remove moisture, 10 duplicate samples of about 50g were weighed to obtain oven dry weight, placed in crucibles and fired in an electric furnace at 550°C for four hours. After cooling to around 200°C the samples were removed and placed in a desiccator to prevent moisture absorption while cooling to room temperature. Final fired weight was determined using a laboratory balance. Loss on ignition was calculated as the difference between oven dry weight and fired weight divided by the initial oven dry weight and expressed as a percentage. The results are presented in Section R1.2.

M2.1.4. Soil moisture characteristic

A moisture release curve was established for the collected soil. A ceramic suction plate with a hanging water column was used to determine the relationship between gravimetric soil moisture content and water potential for the 0kPa to -100kPa range of soil water potential. A pressure membrane device (Richards, 1947) was used following

the technique of Loveday (1974) for the range -100kPa to -1500kPa.

The ceramic suction plate was connected by a plastic tube on the outflow side to a dish of water which provided a free water surface. The ceramic plate could be raised or lowered relative to the free water surface creating a hanging water column of variable length. Unconsolidated soil cores 75mm in diameter were placed on the ceramic plate. The ceramic plate was lowered until level with the free water surface. Water was added until the sample was saturated. The ceramic plate was then raised above the free water surface to create the desired potential. Equilibrium was assessed by recording the outflow from the plate. When outflow stopped, triplicate 20g samples of soil were taken for determination of gravimetric moisture content by oven drying at 105°C for 24 hours. The plate was then raised to create the next lowest potential and the procedure repeated.

For determination of the moisture characteristic at lower potentials, air-dried soil was placed on the celluloid sheet of a pressure membrane device. The samples were unconsolidated and rubber rings were used to separate samples on the sheet. Each soil sample had a mass of about 30g. Soils were wetted by flooding the celluloid sheet until moisture was visible on the upper surface of the sample. When soil samples were saturated, the chamber was sealed and air pressure applied. Outflow was collected

and weighed to determine equilibrium. When outflow ceased at a particular pressure, the chamber was opened and three samples were removed and oven dried (105°C, 24 hours) to determine gravimetric moisture content. The next greater pressure was then established in the pressure membrane device and the process repeated. The moisture characteristic is plotted in Figure R1.3 and numerical data in Table R1.3.

M2.1.5. Hydraulic conductivity

Hydraulic conductivity was calculated to allow later consideration as to whether root growth was likely to be constrained in dry soils by the rate of water flow to the root.

Measurements of the bulk density of unconsolidated soil were made and a moisture release curve was prepared from the moisture characteristic. The relationship of volumetric moisture content and soil water potential is shown in Figure R4.1. Hydraulic conductivity was calculated using the modification of Marshall's (1958) method given by Green and Corey (1971) where hydraulic conductivity is calculated from the water retention characteristics of the soil. The procedure consisted of dividing the moisture release curve into equal water content intervals and estimating average soil moisture potential values of each of the intervals. The shape of the hydraulic conductivity function was then estimated using the model and matched to an experimentally measured saturated hydraulic conductivity determined at

known water content.

Saturated hydraulic conductivity was determined using soil cores and a constant suction device. Saturated cores 75mm in diameter and 70mm deep and were placed on a column of sand, the base of which was sitting in a bowl of water to provide an effective suction of 15cm. A water column with a fine air entry hole to provide a constant suction of 7.5cm was bedded onto the top of the core. The resultant difference in suction between the top and base of the core was 7.5cm. The volume of water flow through the core was measured and saturated hydraulic conductivity for the cores calculated. The model was fitted to the data using a computer program developed by C.S.I.R.O. Division of Soils. The moisture release curve and hydraulic conductivity function are presented in Section R1.4.

M.2.2. Soil and seedling preparation

Elements of the soil and seedling preparation process such as wetting of soil and soil packing techniques were standardized throughout the experiments. The standard techniques are described here. Actual levels of factors used in particular experiments are described in Section M4.

M2.2.1. Soil wetting and packing of pots

The amount of soil needed was taken from storage bins and placed in 5 litre cylindrical plastic containers. An

oven-dry (105°C, 24 hours) moisture content was determined on a sub-sample from each container. To wet the soil to the treatment moisture content, water was sprayed onto the soil using a hand sprayer while the soil was tumbled on a laboratory roller. After the addition of water, the 5 litre containers were sealed and rolled for one hour. The containers were then stored for a minimum of two days in the laboratory before gravimetric moisture content was determined by oven-drying triplicate sub-samples. Adjustments to moisture content were then made by addition of more water if necessary. Soils were considered ready for use if the range in gravimetric moisture content determinations was less than 0.05% over three samples. To prepare pots for sowing of seedlings, soil of the desired moisture content was packed into the pots to a known bulk density using a hydraulic press.

Aluminium pots were used for all experiments. Rectangular pots (25mm by 25mm by 40mm deep) were used in early experiments while in later experiments cylindrical pots (50mm diameter and 100mm length) were used. Larger rectangular aluminium pots (25mm by 100mm by 150mm deep) were used for some experiments where neutron radiography (Section M3.2) was used to assess root growth. The aluminium pots were strong enough to resist deformation when soil was hydraulically packed, and, having no base or top, facilitated pressing of soil from both ends of the pot.

Pots were filled with a known mass of soil of known moisture content and packed to a measured depth and the bulk density calculated.

A hydraulic press with a depth stop was used to drive a close fitting steel piston into the pot to about 75% of the final depth. The piston was withdrawn and the pot inverted. The piston was then driven down until the required depth was indicated.

Soil was weighed to 0.5g. For the smallest pots used (25mm x 25mm x 40mm deep) and a nominal bulk density of 1.5gcm^{-3} , a 0.5g variation in soil mass will alter bulk density by 1.3% or $\pm 0.02\text{gcm}^{-3}$. Similarly for the larger cylindrical pots (50mm diameter, 100mm deep) bulk density could vary by 0.33% or $\pm 0.005\text{gcm}^{-3}$.

The pots were sealed to minimize moisture and soil loss prior to and during experimentation. Pots were sealed with either paraffin wax applied to both ends with a fine brush and wrapped in plastic film, or by close fitting aluminium lids. Pots in which soil of very low moisture content was packed to low bulk densities needed careful handling to prevent soil loss from the bottom of the pot, as the soil was not very cohesive at low bulk densities.

M2.2.2. Seed germination, seedling growth and assessment of root elongation

Radiata pine seedlings were all grown from seedlot Castra 1187, graded large. Pea seedlings (Pisum sativum L.) used in later experiments were variety Greenfeast. Radiata pine seed was soaked overnight, drained, then stored at 4°C for 28 days prior to sowing. This resulted in concentrated germination over a shorter time period. Pea seeds were not pre-treated. Seeds were germinated on moist filter paper at 25°C in an incubator.

Pine seedlings were sown directly into the aluminium pots when the seedling root was about 10mm long. Seedling roots were c. 3 days old at the time of sowing. An Indian ink dye dot was placed on the root with a fine hypodermic needle 10mm back from the tip immediately before sowing. Pea seedling roots were about 15mm long at sowing with the dye dot being placed 10mm from the tip. The dye dot was well behind the zone of root elongation (Section M2.3.3). Seedlings were sown into small holes pressed into the top of the packed pots. One seedling was sown per pot. Soil at the treatment moisture content was firmed around the seed and the pots sealed. The pots were placed in a constant temperature growth chamber at 25°C. The exact growth period depended on the purpose of the experiment and rate of growth of the seedling roots. After the growth period the plug of soil was pushed from the pot and the root recovered. Root elongation was assessed by measuring the distance from the

dye dot to the root tip. The initial distance was subtracted to give a measure of root elongation.

M2.3 Experiments measuring the components of potential.

The osmotic potential of sap expressed from seedling root segments was measured using a dewpoint psychrometer. A pressure bomb (Scholander et al., 1965) was found to be unsatisfactory because of the small size and soft tissue of the seedling root material. The rubber sealing rings crushed the root if the sealing ring was tightened sufficiently to prevent the root being ejected from the bomb when pressure was applied to the chamber.

Seedlings were germinated and grown in soil-filled pots (Section M2.2.2.) or grown in clear plastic boxes 100mm X 200mm X 70mm deep filled with vermiculite saturated with polyethylene glycol (PEG). The average molecular weight of the batch of PEG used was stated to be 4000. In each box 55 seedlings were placed in holes drilled through the top (5 X 11 rows). The system was designed to allow measurement of root elongation in conditions of minimal physical constraint to elongation but known moisture potential.

M2.3.1. Sample preparation and storage

Methods for root segment sampling and storage, sap extraction, and psychrometry were standardised to simplify subsequent experiments.

For vermiculite medium experiments, PEG was mixed with distilled water to create solutions of varying water potential. Measurement of solution water potentials were made the following day using the method described in Section M2.3.2. Sufficient PEG solution was added to washed vermiculite in the rectangular plastic growth box to cover the vermiculite. The boxes were sealed with plastic film and left over-night. The next day the boxes were inverted and excess PEG allowed to drain from the vermiculite prior to insertion of the seedling roots. Measurements were made of the porosity and bulk density of a typical vermiculite treatment (Table M2.3.1.).

Root samples for measurement of osmotic potential were prepared after the growth period following remeasurement of the dye dot to determine elongation. The surface of the root was washed with distilled water and then dried between folds of tissue. The root tip of approximately 1mm was removed with a scalpel blade and then the root sectioned into 5 segments each 3mm in length. Normally five roots from the treatment were sampled. All segments of the same distance from the root tip were wrapped in a foil envelope and frozen in liquid nitrogen to ensure semi-permeable cellular

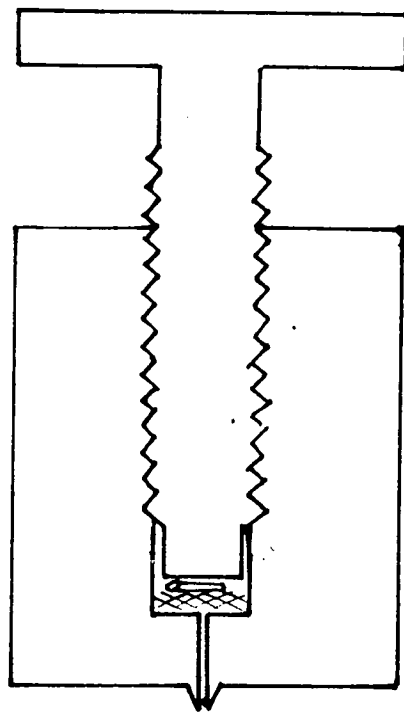
membranes were ruptured (Muchow, 1980). Bulking of root segments was necessary to ensure a sufficient volume of expressed sap was collected for psychrometric determination of cell osmotic potential. The sample preparation was rapidly carried out in a humid environment to minimize moisture loss. Storage of the foil envelopes was at -18°C .

M2.3.2. Psychrometer method and calibration

The basic method of Muchow (1980) was followed for the psychrometric determinations of root cell osmotic potential using a Wescor microvoltmeter (HR 33-T) and C-52 sample chamber. Frozen root segments were thawed in the foil envelope for 30 minutes at 20°C on the laboratory bench. The foil envelope was opened and the root segments placed on a No. 30 stainless steel gauze disc in a hand operated screw micro press. The details of the press are shown in Figure M2.3.2. The press was screwed down until hand tight and a bead of expressed sap appeared at the outlet. The sap was collected in a disposable micropipette. A sample of sap of $\approx 2 \times 10^{-3} \text{ cm}^3$ was expressed from the micropipette on to a filter paper (No. 42) disc sitting in the C-52 sample chamber. The filter paper discs were approximately 4mm in diameter, filling the recess in the insert of the sample chamber. The sample chamber was sealed and the psychrometer reading taken after a 3 minute equilibration. A 10 second cooling time was used for all readings. (Turner, 1979)

FIGURE M2.3.2.

Sketch of the micro-press
used to express sap from root
segments for measurement of
root osmotic potential by
psychrometry



handle

fine pitch
thread

sample

No. 30 stainless
steel mesh

sap collection
point

The psychrometer was calibrated twice daily from standard NaCl solutions (Lang, 1967). The standard solutions were pipetted onto filter paper discs placed in the chamber and a reading taken after 3 minutes equilibration. Standard solutions giving a range of water potentials from -230kPa to -4550kPa were used in each calibration. The molality of the standard NaCl solution and corresponding water potential at 20°C are given in Table M2.3.2.1. A curve relating millivolt psychrometer reading to solution potential was prepared for each calibration. Sample regressions for calibration curves are shown in Table M2.3.2.2. After the reading was taken, the chamber was opened and the metal insert washed, dried and left to equilibrate to 20°C on the laboratory bench.

M2.3.3. Zone of root elongation of pine and peas

The pressure balance model of root growth implies turgor pressure of root cells in the zone of elongation must be greater than further back along the root (Section E). The experiment was designed to identify the root segment where the majority of root elongation occurred. Indian ink dots were placed at 2mm intervals on seedling roots of pine and peas using a fine hypodermic needle. After a period of growth in vermiculite and distilled water, the distance between the dots was remeasured and elongation per sector calculated. The results are presented in Tables R3.1.1. for pine seedlings, Table R3.1.2. for pea seedlings and in

Figure R3.2. where the zone of elongation of both species is shown.

M2.4. Statistical analysis of results

Results were analysed using standard statistical techniques. Analysis of Variance, mean separation using Duncans Multiple Range test, and regression analysis followed the procedures of Little and Hills (1978). Tests for significance were done at a probability level of $P = 0.05$ (95% confidence level) and $P = 0.01$ (99% confidence level). The number of replications for each treatment is shown beneath the Tables detailing the results. The number of replications varied between experiments depending on the total number of pots available and the number of treatments selected.

M3. Methods and Techniques Developed

Methods were developed where published methods were unsuitable. This work was necessary to establish that the particular conditions required could be created and maintained for experiments in the study.

M3.1. Soil experiments

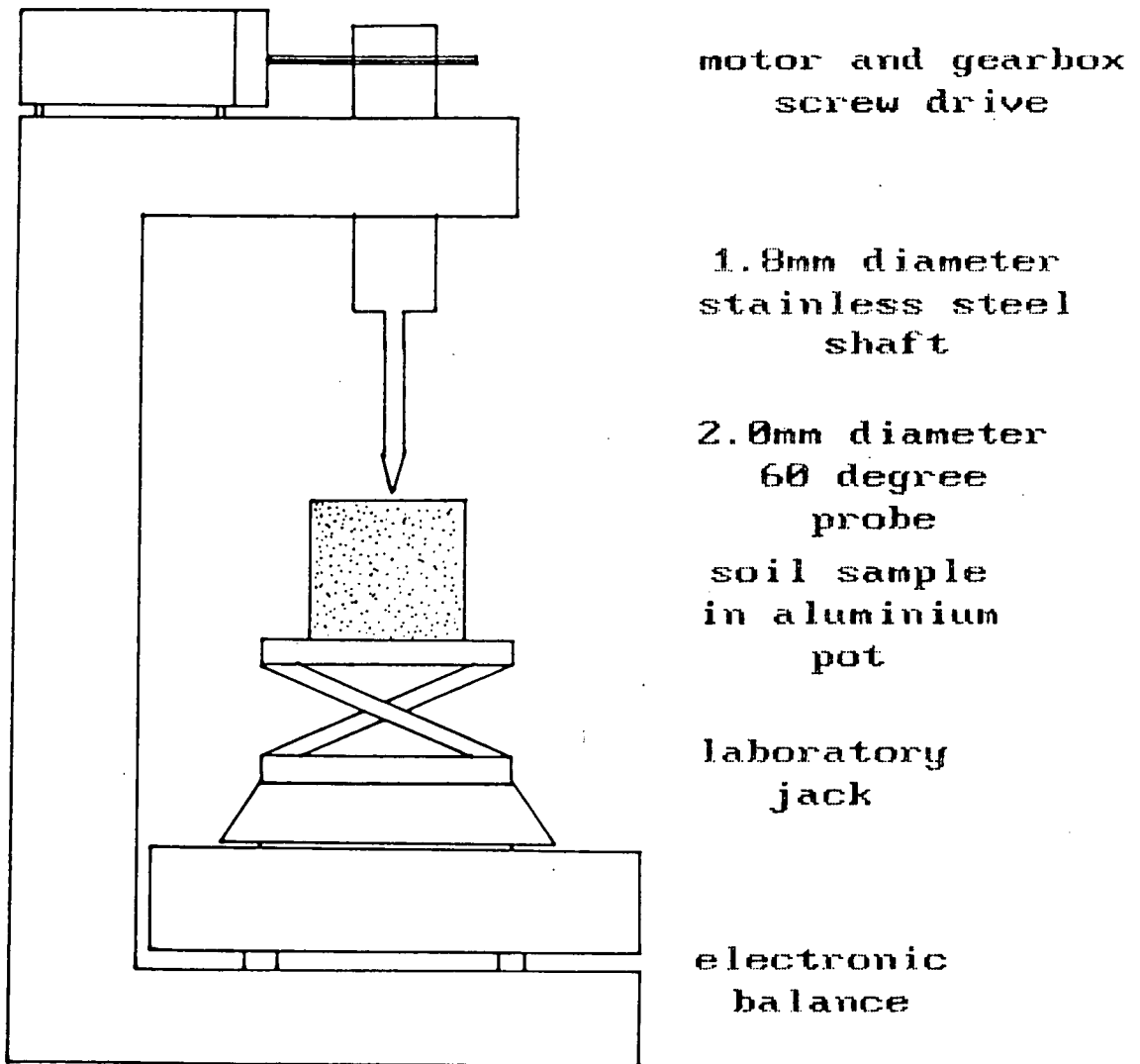
M3.1.1. Penetrometer technique

A penetrometer was designed and constructed to measure probe resistance in pots packed with soil. The basic technique was a modification of the method of Eavis (1972) where a balance was used to measure resistance to the travel of a metal probe through soil packed into a pot. The soil filled pot was placed on the top of a laboratory jack which was in turn placed on an electronic balance (Figure M3.3.1.). The jack was raised until the probe was near to the soil surface and the balance tared. A 2mm diameter stainless steel probe with a 60° apical angle was driven into the soil by a vertical screw driven by an electric motor and reduction gearbox to provide a feed speed for the probe of 1.52mm min⁻¹. The motor was run at this speed x10 in reverse to clear the probe from the soil after measurement was completed. The probe was machined to 1.8mm behind the head to relieve soil to metal friction as the probe progressed into the soil.

The probe was driven into the soil for 5 minutes before

FIGURE M3.1.1.

General arrangement of the
penetrometer apparatus
described in Section M3.1.1.



readings commenced. The reading on the electronic balance was then recorded every 15 seconds for the next 5 minutes. The average of the recordings was taken as the balance reading for the particular pot. The balance reading was converted to standard units (kPa) by adjustment for the probe diameter.

M3.1.2. Verification of methods

Techniques for soil packing, penetrometer measurement and seedling root growth were verified. A series of pots were packed and penetrometer resistance tested at the School of Agriculture, Latrobe University.

Cylindrical pots of 50mm diameter were packed with soil wetted to 6.4% gravimetric moisture content. Four packing pressures were selected and bulk density was calculated from the mass of wet soil and the height of soil in the tube. The La Trobe penetrometer had a probe of 2mm diameter with a 60° angle and a 1.5mm diameter shaft. An electrically driven moving table of adjustable speed raised the pot onto the penetrometer. A pressure transducer connected to a chart recorder provided a continuous plot of penetrometer resistance as the probe moved into the soil. In Table M3.1.2. bulk density and measured penetrometer resistance are recorded. The data are graphed in Figure M3.1.2. (Section M5)

M3.2. Neutron radiography

Serial observations of root elongation are not possible on the same root when destructive sampling techniques are used. Glass sided root observation boxes allow serial observation, but growing conditions on the glass surface may not be identical to the bulk soil. As a result root concentrations at the interface can differ from the bulk soil (Taylor and Bohm, 1976).

Neutron radiography has been used to show detail of root systems growing in bulk soil and for the collection of serial data on individual root growth (Willatt et al., 1978). The methods described here made use of the neutron radiography facility at the Australian Atomic Energy Commission Establishment at Lucas Heights. The techniques developed were used to establish the possible resolution of roots using radiography and the efficacy of the method for serial observation of root elongation and growth. The techniques developed in this study and prints of radiographs illustrating the main features of the method are presented and discussed in Section M5.

M3.2.1. Basic method.

A root represents a local concentration of water when growing in a soil mass. Volumetric water contents of roots range from 70% to 93% (Kramer, 1969) while sandy soil at field capacity may have volumetric moisture contents between

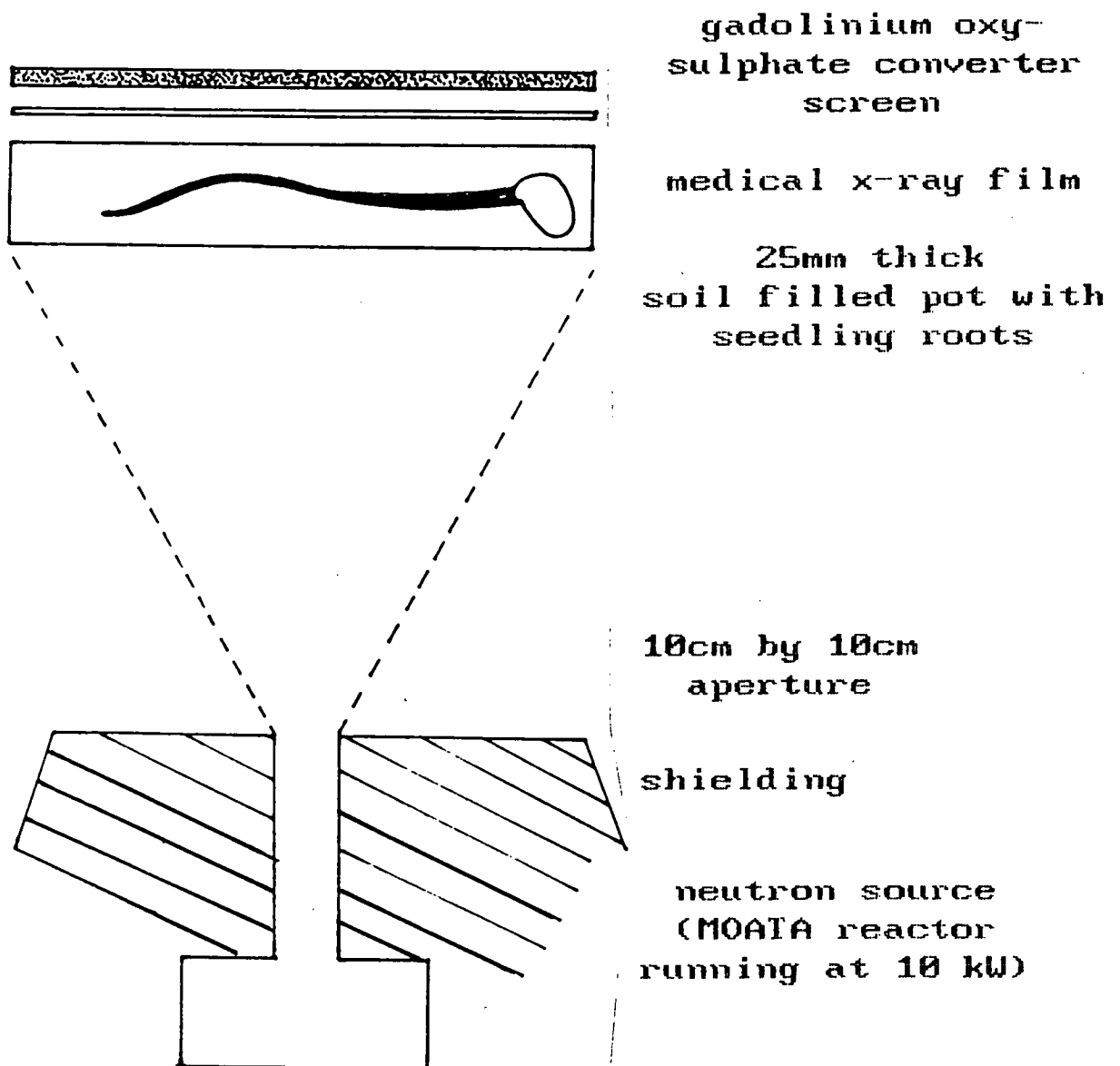
5% and 30%. If a beam of neutrons passes through a mass of soil in which roots are growing, the roots will attenuate more neutrons by scattering and absorption than does the moist soil. The greater attenuation by roots effectively removes neutrons from the beam (Willatt et al., 1978) which will produce a radioactive image on a metal or metal oxide converter screen, which can be transferred to X-ray film. The image of the root can then be seen in contrast to the soil on the processed film. The MOATA reactor and neutron source at Lucas Heights have been described by Willatt and Wall (1978). A schematic view of the neutron source, sample, converter screen and X-ray film cartridge are shown in Figure M3.2.1.

Aluminium pots 100mm x 25mm x 150mm deep or 25mm x 25mm x 40mm deep were used to give a soil thickness of 25mm. Soils were wetted and packed using the methods described in Section M2.2.1., and seedlings prepared as described in Section M2.2.2.

The suitability of converter screens coated with gadolinium foil and gadolinium oxy-sulphate was assessed for radiography. With gadolinium foil and a 20 minute exposure to the neutron beam, resolution of roots was similar to that obtained using a gadolinium oxy-sulphate converter and a 10 minute exposure time. Gadolinium oxy-sulphate converter screens were used for all subsequent experiments because of the greater number of exposures possible for a given reactor

FIGURE M3.2.1.

General arrangement of
neutron source and plant-soil
samples for neutron
radiography



run. Single emulsion medical X-ray film (Kodak Lanex) was used for all experiments. The film was developed using Kodak D76 developer and an 8 minute developing time. Contact prints were made directly from the negatives, therefore figures are actual size.

A series of radiographs was taken to determine the moisture differential between the root and the soil necessary to obtain satisfactory contrast. Aluminium pots 100mm wide by 25mm thick by 150mm deep were each filled with three soils of different field textures packed in layers approximately 40mm deep. The soils used were the Wynyard sandy loam soil (Section M2.1.1), a clay loam formed on Permian sediment, and a krasnozem formed on Tertiary basalt. The soils were equilibrated to a moisture potential of -100kPa on a pressure membrane device (Section M2.1.4) prior to filling of the pots. Gravimetric moisture contents of the soils after equilibria was reached were 6.5% for the sandy loam, 17.3% for the clay loam, and 30% for the clay soil. Each layer of soil was packed to a bulk density of 1.30gcm^{-3} . Pine seedlings were planted into the pots and grown for 14 days. Radiographs were taken at the end of the growth period. A sample print of a radiograph is seen in Figure M3.2.2. (Section M5).

Sequential radiographs of pine roots were taken to determine if the resolution of these radiographs was sufficient to accurately measure root elongation rates and observe general root development. Sandy loam soil (Section

M2.1.1.) with a moisture content of 6.5% (-100kPa) was packed into 100mm x 25mm x 150mm deep aluminium pots to a bulk density of 1.4gcm^{-3} . A radiograph was taken after 18 days growth with a second exposure at 24 days growth. Figure M3.2.3. is a print of a radiograph of radiata pine roots taken at 24 days.

Radiographs of developing pea roots were taken to show the general rooting pattern and to determine the limits of resolution of fine roots. Figure M3.2.4. is a print of a radiograph of a pea seedling taken after 5 days growth in a sandy loam soil with 6.5% moisture content and a bulk density of 1.4gcm^{-3} .

M3.2.2. Effects of radiographs on seedling root growth

The sensitivity of the roots to the neutron radiation flux of the radiography procedure was tested. A previous study observed no effect of radiography on root elongation of maize and corn seedlings with an average age of 27 days (Willatt et al., 1978). As the root radicals being used for the neutron radiography studies were on average 7 days old, sensitivity to the irradiation may have been greater than for the older plants. A factorial arrangement of treatments was established with two levels of neutron exposure (nil and 10 minutes), and two levels of gravimetric soil moisture content (6% and 9%). There were seven replications of each

treatment. Aluminium pots 25mm x 25mm x 40mm deep were sown with radiata pine seedlings after the pots were packed to a bulk density of 1.54gcm^{-3} . Initial root lengths were recorded prior to sowing of seedlings. Neutron treatment pots were exposed to the neutron source for 10 minutes prior to a 96 hour growth period at 20°C on a laboratory bench. After the growth period, all pots were radiographed to determine root elongation. The results are presented in Section R5.1.

M3.2.3. Root growth into compact soil layers

An experiment was undertaken to monitor root behaviour on meeting a compacted layer of soil. The experiment demonstrated to best advantage the ability of the neutron radiograph technique to monitor root behavior without disturbing the soil.

Aluminium pots 100mm x 25mm x 150mm deep were packed with sandy loam soil wetted to 7.2% gravimetric moisture content. The lower 50mm of the pots were packed to a bulk density of 1.63gcm^{-3} and the remainder to a bulk density of 1.54gcm^{-3} . Corresponding levels of penetrometer resistance were 1000kPa and 3000kPa respectively (Section M3.1.2.). Two radiata pine seedlings were sown in each of ten pots. One pea seedling was sown separately in each of ten pots. Radiographs were taken 21 days after sowing for pine treatments and 7 days after sowing for pea treatments. Root elongation rate, whether the root had penetrated the

compacted layer, and the pattern of buckling upon meeting the compacted layer, were recorded. The data are presented in Section R5.2.

M4. Individual Experimental Methods

Standard methods and techniques have been described in Section M2. The treatment combinations, levels of factors and number of replications for the experiments are detailed in the tabulated data in Section R7.

M5. Discussion of Materials and Methods.

The soil bulk density and moisture content of experimental pots must be accurately and precisely established to reduce variability between treatment replications and for soil conditions to be comparable with other experiments. The measurement of penetrometer resistance and soil moisture potential in turn need to be accurate and precise to allow for comparison of results. To achieve the uniformity of soil conditions necessary for experimentation, the techniques of soil wetting and packing must be consistent. There was no evidence of any variation between batches of soil used for different experiments. If soil lots were not uniform, variation in the moisture characteristics due to differing organic matter contents, or variation in the relationship between bulk density and penetrometer resistance may have been observed. Wetting the soil by misting while rolling and then storing the moist soil for a minimum of 2 days ensured a uniform moisture content within each batch while the technique of packing soil limited variations in bulk density in the pots to no more than $\pm 0.02 \text{gcm}^{-3}$ (Section M2.2.1).

To ensure uniformity of bulk density within the pots, the soil was pressed to about 75% of the final soil depth, the piston retracted and the pot inverted before pressing to the final depth. A similar technique is described by Heilman (1981) and Mirreh and Ketcheson (1972) who reported that there were no gradients in penetrometer resistance

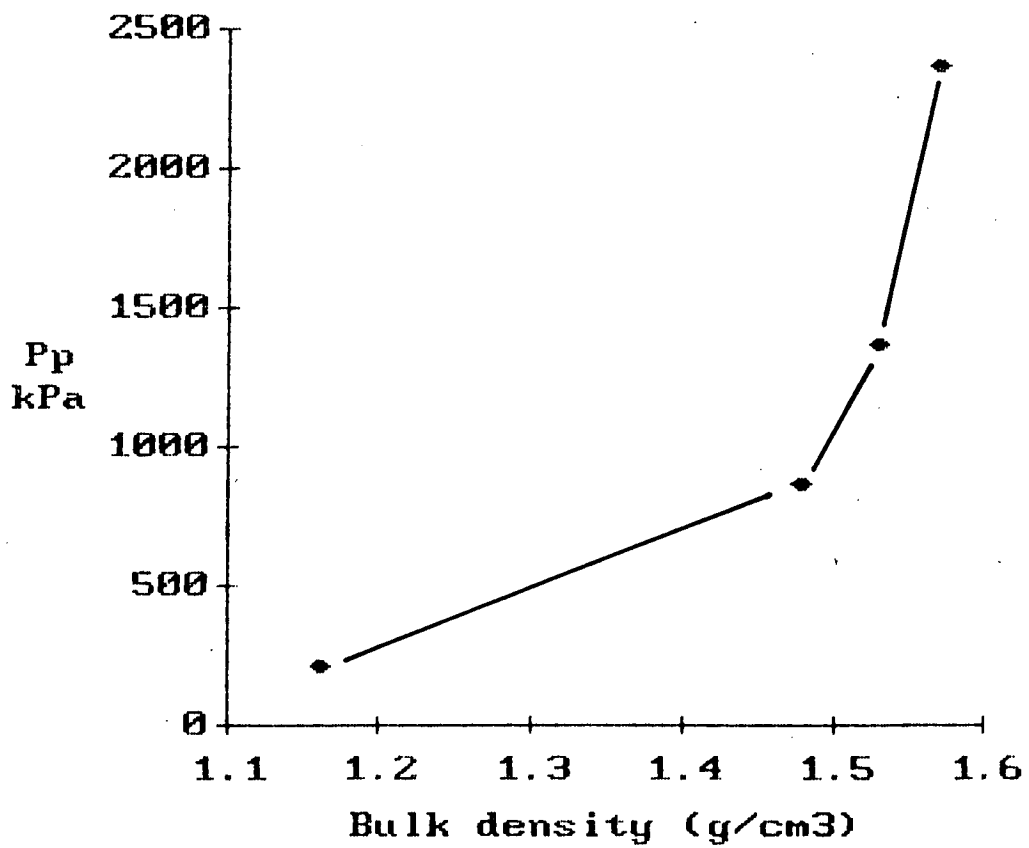
through experimental pots, other than an initial build-up of probe resistance for a depth equivalent to c. 2 probe diameters. Although not explicitly tested, there was no evidence from penetrometer readings that the soil consolidation process had created non-uniform densities. The penetrometer (Section M3.1.1.) recorded increasing probe resistance for the initial few millimetres of soil insertion, then no further increment. Bradford (1980), using a probe of 2.0mm diameter, disregarded readings for the first 6mm when taking penetrometer measurements on a silt loam soil, while Eavis (1967) using a sandy loam soil found penetrometer resistance reached an equilibrium value after the probe had entered between 0.5mm and 1.0mm into the soil. Taylor and Ratliff (1969a) measuring penetrometer resistance in a loamy sand soil, disregarded readings from the initial 10mm of soil. The rate of advance of the penetrometer described in Section M3.1.1. was 1.52mm min^{-1} so, by disregarding the first 5 minutes of readings the probe had advanced c. 7.5mm (or 3.5 probe diameters), into the soil before recordings of penetrometer resistance commenced. Relief of skin friction by a reduction in probe diameter behind the point (Bradford, 1980) was effective, as no gradual build-up in readings was observed as the probe advanced into the soil. If skin friction was not effectively being relieved, then the readings would have increased as the length of penetrometer shaft in contact with the soil increased.

The aluminium pots used for this study were 25mm square or 50mm diameter. The 25mm square pots were radially constrained the soil at c. 10 times probe diameter. This is less than the 20 times probe diameter quoted by Voorhees et al. (1975) as being necessary to obtain accurate penetrometer readings free from influence of the pot wall. The radial constraint on the larger 50mm diameter pots used in this study was 25 times probe diameter. Penetrometer readings for the larger pots were comparable with the smaller pots. It is concluded that for the particular soil and bulk density range established here that radial constraint did not affect penetrometer readings. Penetrometer readings obtained using another instrument (Table M3.1.2. and Figure M3.1.2.) were comparable with those reported in later experiments (Section R2.2.) and also obtained on the apparatus described in Section M3.1.1. It is further concluded the machine type and method were measuring penetrometer resistance accurately and precisely.

PEG was used to produce various solution potentials in vermiculite medium (Section M2.3.1.). Potentials were directly measured from PEG solutions expressed from the PEG-vermiculite medium to negate any effects of variation between batches of PEG due to variation in molecular weight (Thill et al., 1979). Solution potentials were measured before and after the seedling growth period without significant variation. There was no evidence of PEG solution potentials varying over time as reported by Berkat and

FIGURE M3.1.2.

Penetrometer resistance (Pp)
versus bulk density for sandy
loam soil



Briske (1982).

From Table M2.3.1. it can be seen that the vermiculite medium had a low bulk density (0.16gcm^{-3}). Although penetrometer resistance was not measured, soil impedance would have effectively been zero due to the low bulk density. Air filled porosity of the PEG-vermiculite medium was 60% therefore root growth would not have been affected by oxygen availability in the medium.

Root segment osmotic potential was measured using a dewpoint psychrometer (Section M2.3.2.). Pressure-volume determinations with a Scholander bomb are preferred by Turner (1981), as a method to accurately measure tissue turgor. Wilson et al. (1977) reported that data from the use of the Scholander bomb technique were less variable than determinations using psychrometry. However, the need to determine turgor gradients in the root, and the size and soft tissue of the roots prevented the use of a Scholander bomb in these experiments, as there was no effective technique for sealing small soft tissue in the neck of the bomb.

Individual root segments of 3mm in length and c. 1mm diameter have a total volume of c. $2.5 \times 10^{-3}\text{cm}^3$. The micro-press (Section M2.3.1.) was only likely to express around 50% of the total sap volume contained by the root tissue (Greacen and Oh, 1972). Several segments of root tissue were needed to reliably obtain a sample volume of $2.5 \times 10^{-3}\text{cm}^3$

of sap for psychrometric measurement (Turner, 1981). Five segments of pea roots and 11 segments of pine roots were needed to provide sufficient sample volume. The number of replications of osmotic potential measurement decreased as the number of root segments per sample increased because the number of seedling roots available for segmentation was constant.

When grown in soil, roots of both species were of smaller diameter when compared with those grown in vermiculite medium. Volumes of expressed sap were inadequate in some instances to provide for the planned number of determinations of osmotic potential. This is reflected in the standard error of the mean for some treatments in Section R4. Other workers report the need to bulk root segments when measuring osmotic potential. Meyer and Boyer (1972) when studying osmotic adjustment of soybean hypocotyls bulked 6-8 root segments to obtain the necessary volume for psychrometric measurement, and Greacen and Oh (1972) used the expressed sap from 15 segments for each measure of osmotic potential.

Total root potential is the sum of turgor and osmotic potential ($P = P_t + P_o$). When measuring osmotic potential of expressed sap, turgor is reduced to zero by freezing the tissue and thereby rupturing the semi-permeable cell membranes. The psychrometer effectively measures the relative vapour pressure of the expressed sap, which is a

function of the solutes present in the sap (Muchow, 1980).

In the freezing-thawing-sap expression process it is possible that the cell vacuole contents (symplastic water) may be diluted by water previously held in the cell wall (apoplastic water). This will effectively raise the recorded osmotic potential as apoplastic water commonly has an osmotic potential in the range -20kPa to -100kPa , while the osmotic potential of symplastic water is generally in the range -1000kPa to -3000kPa (Tyree, 1976). When apoplastic water and symplastic water mix there is a dilution of the symplastic water by the apoplastic water. Tyree (1976) estimated dilution error in the measurement of osmotic potential could be as high as 18%, and considered that the most likely cause of negative turgor values for plant tissue reported in the literature is due to not accounting for this dilution effect. When comparing the Scholander bomb method of determining turgor, which does not involve a dilution error, with a psychrometric method Wenkert (1980) reported a dilution error of 11-16%. Turner et al. (1978) measured a dilution error in the determination of osmotic potential of 7% for sorghum and 15% for soybean leaves irrespective of the degree of moisture stress. They concluded that dilution errors could be ignored in a relative sense, but must be considered if absolute comparisons were to be made between species.

Not all authors report dilution effects when measuring osmotic potential using expressed sap. Wilson et al.

(1977) compared turgor measured using pressure-volume curves and turgor calculated from measurement of the osmotic potential of expressed sap, and found no evidence of dilution. Greacen and Oh (1972) considered dilution errors were insignificant in the measurement of osmotic potential of pea root segments as they only expressed 50% of the possible sap volume, with no freezing prior to expression. In these circumstances it is presumed that little apoplastic water would be expressed as the symplastic water is not mechanically bound to the cell wall material. Symplastic water would be expressed before apoplastic water which is held within the cell material by a matric potential. Cavalieri and Boyer (1982) made no correction for dilution when measuring the osmotic potential of soybean segments after freezing and thawing. They calculated the cell wall was only 3% of cell volume and therefore the dilution of symplastic water by apoplastic water would be negligible.

There is, therefore, no clear consensus of the importance of this dilution error in the measurement of tissue osmotic pressure. But any determination of negative turgor could indicate a dilution error. Zimmermann (1978) stated that in the absence of direct measurement, a lot of assumptions are needed to develop estimates of turgor in bulk tissue. Munns (1980) considered the problems of instrument error, dilution effects, and technical skill of experimenters, and concluded that the measurement of turgor will only be reliable to $\pm 100\text{kPa}$ at least.

The contrast between the soil and the root when radiographs are printed is dependent on the moisture content and texture of the soil. In Figure M3.2.2. the upper layer of soil was a sandy loam with a moisture content of c. 9%. The root is clearly contrasted against the surrounding soil. In the clay loam layer (moisture content, 17%), the root is less clear while in the clay soil which had a moisture content of c. 30%, the root is difficult to detect. Coarse textured soils are preferred for neutron radiography studies because adequate contrast can be obtained even when soil moisture potentials are relatively high.

Figure M3.2.3. is a print of a radiograph of pine seedling roots taken after 24 days of growth. The roots are clearly visible in the print. Pine roots are generally about 1mm diameter (Section R2.4.) so it would appear that potential resolution is better than 1mm. No lateral roots had formed, contrasting with the root development of a 5 day old pea seedling seen in Figure M3.2.4. The pea root exhibits a great degree of branching and lateral root formation. Fine roots can be resolved to c. 0.5mm. The dark patch deep in the pot was part of a fertilizer tablet which had absorbed more water than the surrounding soil. The darker flecks seen through the soil were probably local concentrations of organic matter which again had a greater moisture content than the surrounding soil. Willatt et al. (1978) used loamy sand and silt loam soils with moisture

FIGURE M3.2.2.

Neutron radiograph of pine
roots growing in a pot packed
with layers of soil of
different field texture and a
moisture potential of -100
kPa

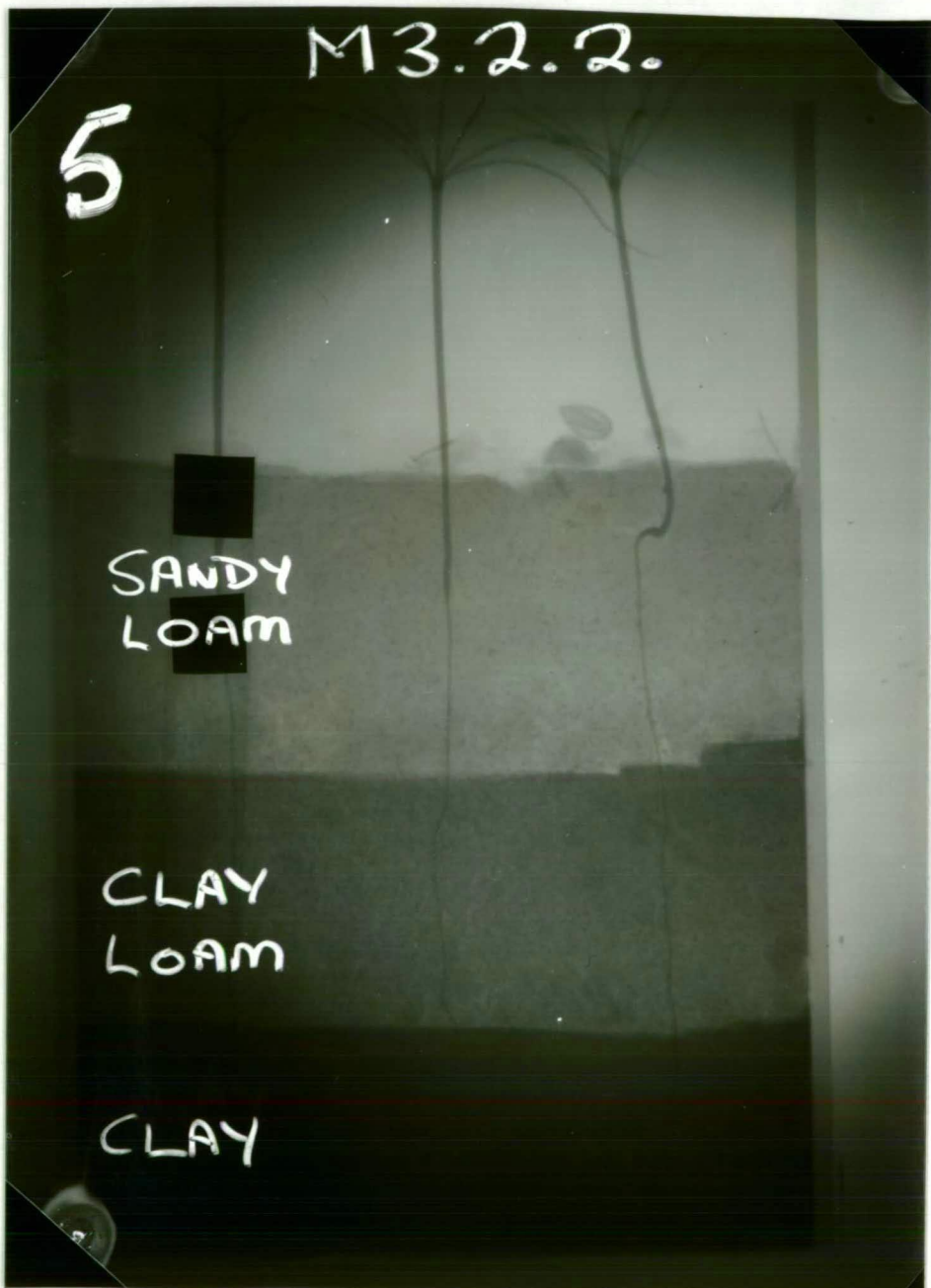


FIGURE M3.2.3.

Neutron radiograph of pine roots after 24 days growth in a sandy loam showing pattern of root development and root behavior on meeting the base of the pot

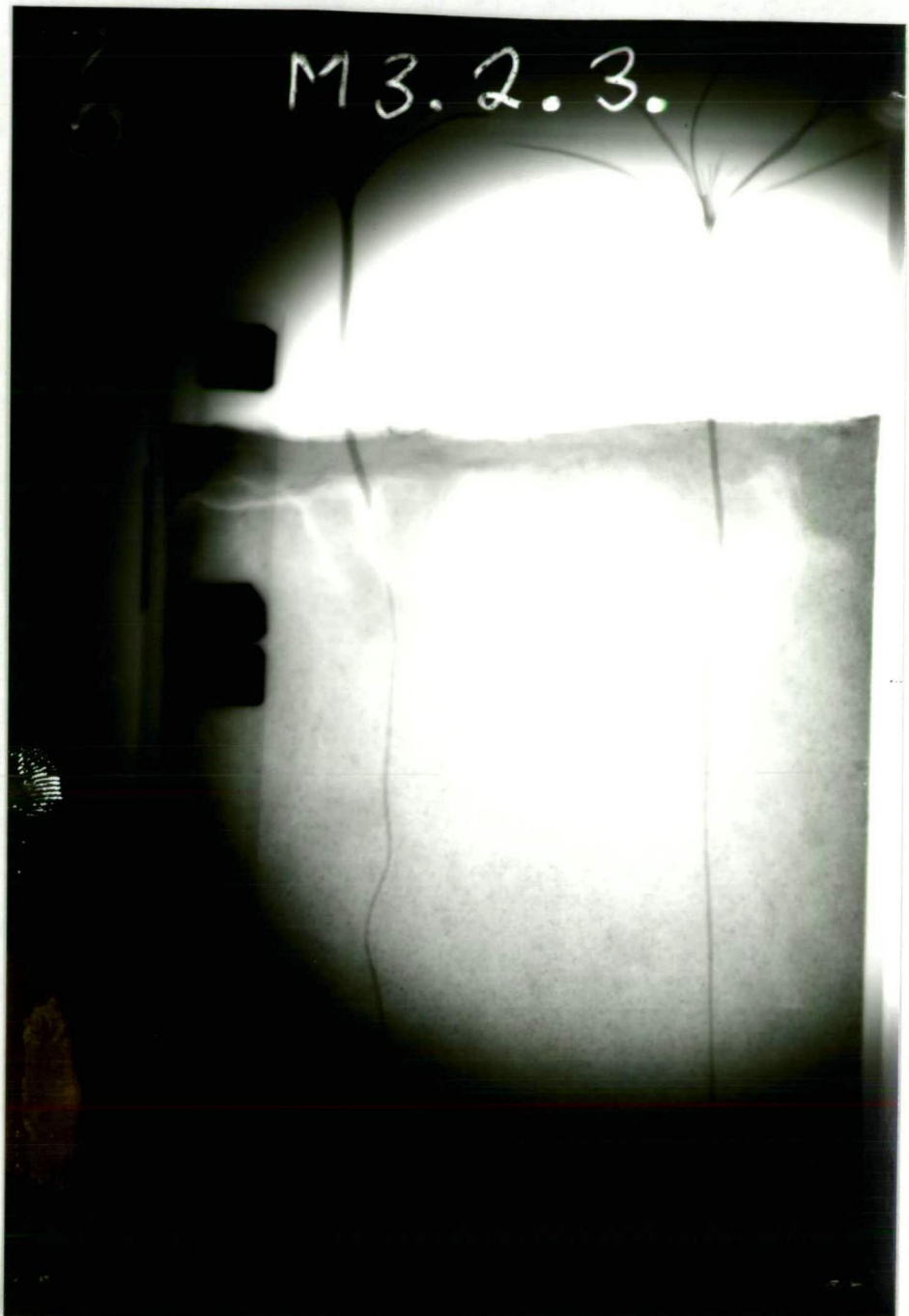
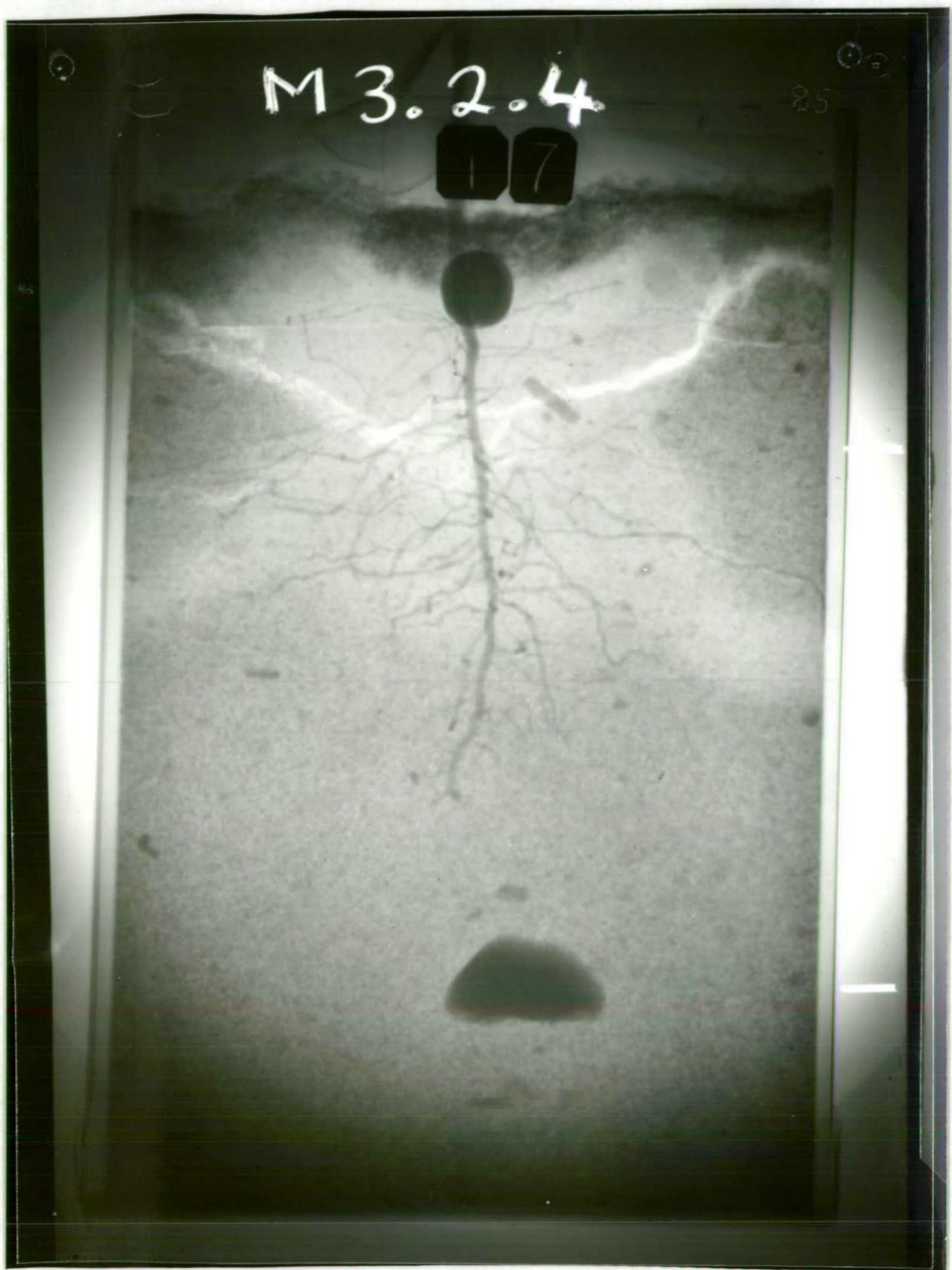


FIGURE M3.2.4.

Neutron radiograph of pea
roots after 5 days growth in
a sandy loam showing the
pattern of root development
and resolution of fine roots



contents of 9% (c. -30kPa) when determining the possible resolution of soybean roots possible. They inserted a cadmium strip bored with fine holes of varying diameters into the soil and observed that resolution of a hole of 0.33mm diameter was possible.

In conclusion, neutron radiography can resolve to c. 0.5mm in coarser textured soils and sequential radiographs allow accurate measurement of root elongation. Neutron radiography is particularly suited to non-destructive studies of root development, such as the behavior of roots on meeting a layer of greater soil strength.

M6. Tables

TABLE M2.3.1.

Air porosity and bulk density of vermiculite and PEG solution.

	air porosity ($\text{cm}^3\text{cm}^{-3} \times 100$)	bulk density (gcm^{-3})
mean	60	0.16
standard error	0.7	0.01
samples	7	7

TABLE M2.3.2.1.

Molality and water potential of standard NaCl solutions used for psychrometer calibration.

Molality (M)	Water Potential (kPa)
0.05	-230
0.1	-454
0.2	-900
0.5	-2241
0.8	-3612
1.0	-4550

(data of Lang, 1967)

TABLE M2.3.2.2.

Representative calibration data for the Wescor psychrometer and sample chamber shown as the linear regression of millivolt reading versus solution potential ($P = a + b(\text{mV})$). The coefficient of correlation (R^2) for each calibration regression is also listed.

determination	a	b	R^2
1	1.54	0.56	0.99
2	1.33	0.59	0.99
3	1.17	0.61	0.98
4	0.87	0.67	0.99
5	0.74	0.77	0.99
6	0.46	0.80	0.99
7	1.87	0.61	0.96

TABLE M3.1.2.

Relationship between bulk density and penetrometer resistance for sandy loam soil determined using a moving table penetrometer and continuous recording load cell. Penetrometer and bulk density data are the mean of ten determinations.

pot bulk density (gcm^{-3})	1.16	1.48	1.53	1.57
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penetrometer resistance (kPa)	200	850	1350	2350
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standard error of mean value	25	59	124	172
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RESULTS AND DISCUSSION

R1. Characteristics of the Soil used for Experimentation

R1.1. Particle size analysis

The method used to determine particle size analysis was described in Section M2.1.2. The results showed the soil to be a sandy loam soil with 75% sand, 10% silt and 15% clay. Other authors studying root growth in the laboratory who have used sandy loam soils of similar particle size distribution include Whiteley et al. (1981) with 26% sand, 17% clay, Taylor and Ratliff (1969a) with 75% sand, 18% clay, Eavis (1967) with 63% sand, 11% clay, Bar-Yosef and Lambert (1981) with 79% sand, 5% clay, and Hainsworth and Aylemore (1986) with 85% sand, 15% clay. The choice of such relatively coarse textured soils for laboratory experimentation is because of the aeration status of the soils. High moisture potentials can be maintained at moderate gravimetric moisture contents (Section R1.3.). Air porosity at relatively high bulk densities is generally adequate for plant growth. If finer textured soil with a greater clay content were used, shrinking and swelling of the soil with wetting and drying would make determination of pot bulk density and soil strength difficult.

R1.2. Organic matter content

Soil organic matter content was measured by loss of mass on ignition of a soil sample. The method followed is detailed in Section M2.1.3. Mean loss on ignition of the 10 samples was 5.2%. In comparison, Sands et al. (1979) reported that Mt Burr sand collected under mature pine forest had organic matter contents measured by loss on ignition of 2.46% for surface soil to 0.012% for subsoil. Whiteley et al. (1981) measured organic matter content in a sandy loam soil as 1.7% while Bradford (1980) reported an organic matter content of 2% for a silt loam soil (7% sand, 17% clay).

Davis et al. (1983) collected data on the organic matter content of five Tasmanian soils of contrasting field texture. All sites were supporting 10 year old radiata pine forest. Soil organic matter content declined as soil depth increased on all sites. For a Strahan sand, organic matter content for the 0-10cm horizon was 13.5% declining to 0.2% for the 70-80cm horizon. For the 10-20cm depth, organic matter content was 5.1%. Organic matter contents for the 10-20cm depth of soils of other field textures were 6% for a krasnozem formed on Tertiary basalt, 2.6% for a podzolic soil on Permian sediments, and 2.5% for a podzolic soil on granitic outwash material.

The organic matter content of 5.2% measured for the Wynyard sandy loam soil was higher than organic matter

contents generally recorded for cropping soils (Bradford, 1980) however, it is comparable with other determinations of soil organic matter content under pine forest. It is likely that the higher organic matter contents recorded for forest soils reflect the greater amount of litter on the forest floor when compared with agricultural soils.

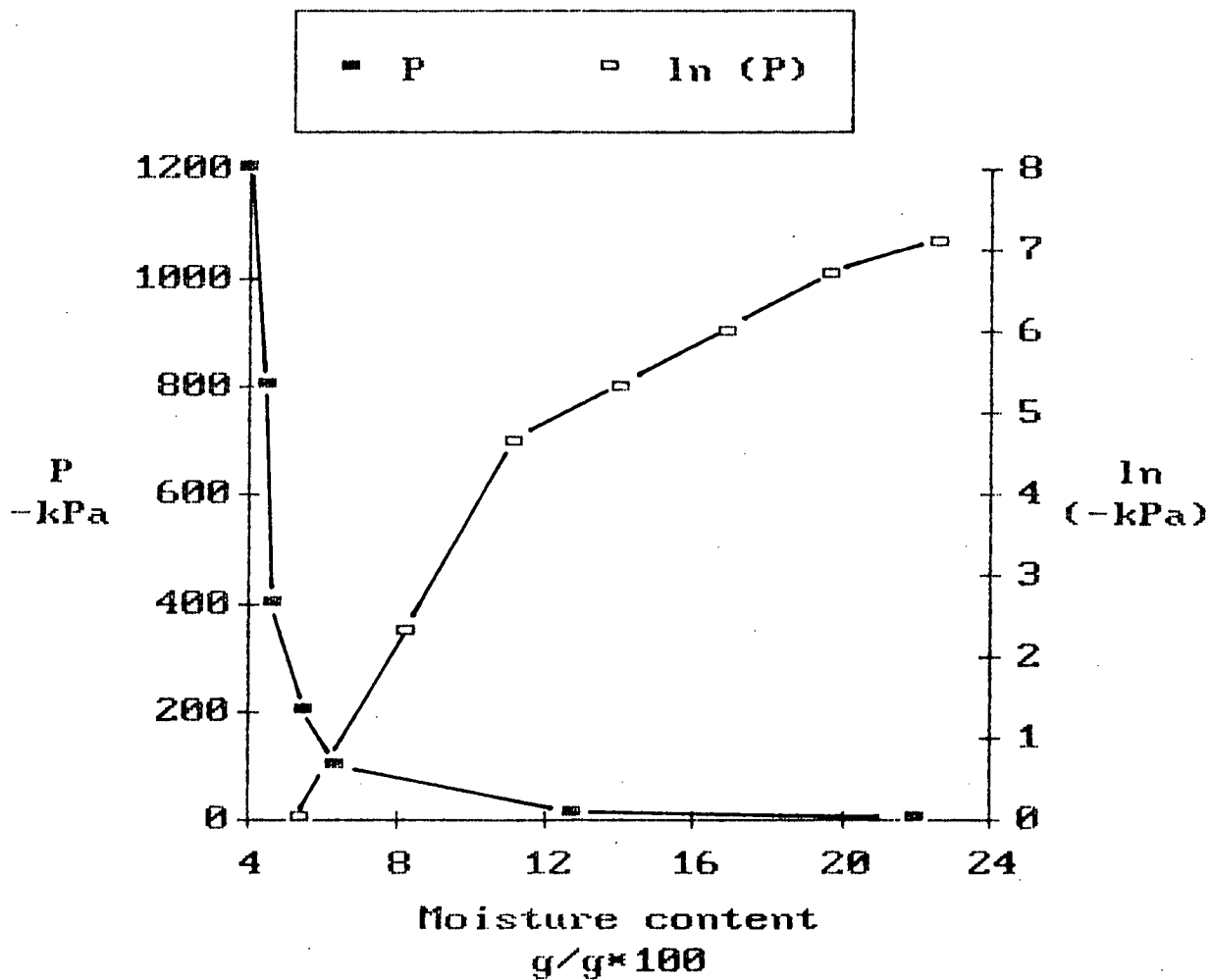
R1.3. Moisture characteristic

The moisture characteristic was prepared after determination of gravimetric moisture content at known moisture potentials. The technique is described in Section M2.1.4. The results are tabulated in Table R1.3. In Figure R1.3. moisture potential versus gravimetric moisture content and natural logarithm of moisture potential versus gravimetric moisture content are plotted.

In Figure R1.3. it can be seen that moisture potential rapidly declines when gravimetric moisture content falls below 6%. The large change in moisture potential for a small change in gravimetric moisture content is best demonstrated by the natural logarithm plot. There is a 900% decrease (-100kPa to -1000kPa) in moisture potential for a 2% decrease (6.4% to 4.4%) in gravimetric moisture content. The pattern of rapid initial outflow at high soil moisture potentials in response to small differences in soil moisture potentials is characteristic of sandy soils. Bar-Yosef and Lambert (1981) reported that for a sandy loam soil, gravimetric moisture content was 30% when moisture

FIGURE R1.3.

Moisture potential (P) and
natural logarithm of moisture
potential versus gravimetric
moisture content for sandy
loam soil



potential was -5kPa , but gravimetric moisture content had dropped to 7.5% when moisture potential was -100kPa . Sands et al. (1979) recorded that for a moisture potential of -10kPa , gravimetric moisture content was 9.18% when measured in a sand (95% sand) with an organic matter content of 2.46%. In contrast for a finer textured soil (7% sand, 17% clay), Bradford (1980) measured a gravimetric soil moisture content of 31% at a moisture potential of -10kPa and 9.2% at a moisture potential of -1500kPa .

It is concluded that the moisture characteristic was typical for a soil of this particle size distribution. To accurately determine moisture potential in experimental pots, precise measurement of gravimetric soil moisture content was needed (Section M2.2.1.). A small error in measurement of soil moisture content would have given a large error in the estimation of soil moisture potential, particularly for soil moisture contents below 6% where moisture potential is extremely sensitive to gravimetric moisture content.

R1.4. Hydraulic conductivity

The unsaturated hydraulic conductivity of the experimental soil was measured using the method described in Section M2.1.5. The volumetric moisture content, water potential, and hydraulic conductivity for the soil are listed in Table R1.4. The moisture release curve (Section

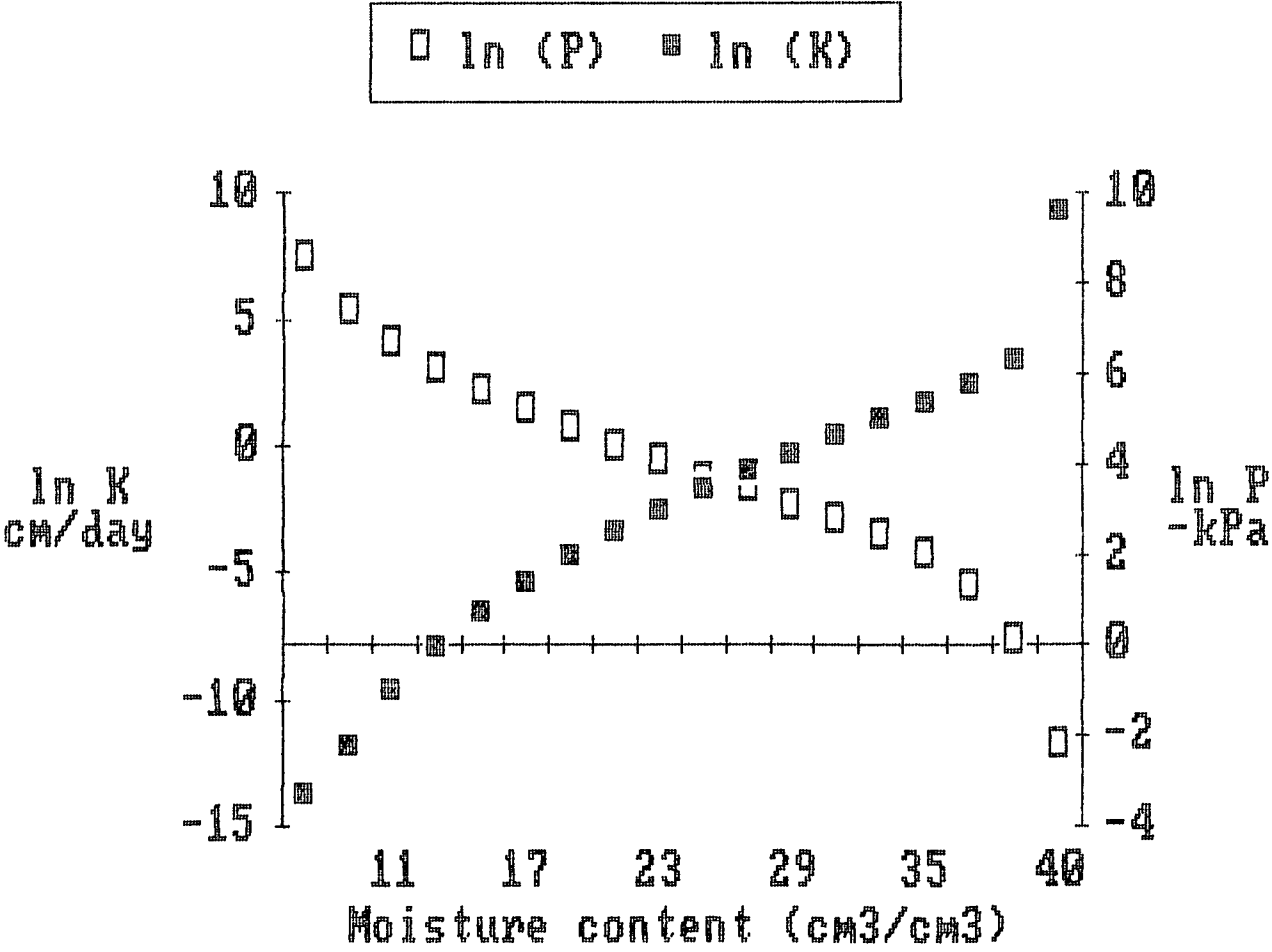
M2.1.5.) and the relationship between hydraulic conductivity and volumetric moisture content are plotted in Figure R1.4.

There was a rapid decline in hydraulic conductivity with decreasing soil volumetric moisture content. From saturation (40% volumetric moisture content) to a soil moisture potential of -1000kPa, hydraulic conductivity declined by a factor of 10^6 . The moisture release curve mirrored hydraulic conductivity, with a rapid initial outflow for small potential steps at high volumetric moisture contents, followed by significantly less moisture outflow when volumetric moisture content fell below 20%.

Sands et al. (1979) reported that the hydraulic conductivity of Mt. Burr sand was $1.9 \times 10^{-6} \text{ cm d}^{-1}$ at -1500kPa soil moisture potential and 0.23 cm d^{-1} at -10kPa. Comparable values of hydraulic conductivity for the Wynyard sandy loam were $5.9 \times 10^{-6} \text{ cm d}^{-1}$ and 2.33 cm d^{-1} , which was ten times greater conductivity for the Wynyard soil at -10kPa and four times greater conductivity at -1500kPa. The difference in conductivity for these sandy soils may have been due to the levels of soil organic matter. Sands et al. (1979) reported a soil organic matter content of 2.32% for the surface soil of Mt. Burr sand whereas for the Wynyard sandy loam soil, organic matter content was 5.2% (Section R1.2.). The greater organic matter content of would be expected to improve hydraulic conductivity (Sands et al., 1979).

FIGURE R1.4.

Natural logarithm of soil moisture potential (P) and natural logarithm of hydraulic conductivity (K) versus volumetric moisture content for sandy loam soil



Hydraulic conductivity may be reduced by compacting soil. Baligar et al. (1981) reported hydraulic conductivity declined from 0.17 cm hr^{-1} at a bulk density of 1.55 g cm^{-3} to $4.17 \times 10^{-3} \text{ cm hr}^{-1}$ at a bulk density of 1.85 g cm^{-3} . Hullugalle and Willatt (1983) used root density data to calculate that hydraulic conductivities c. $10^{-6} \text{ cm d}^{-1}$ could limit growth. For the Wynyard sandy loam, hydraulic conductivities of that order were measured for moisture potentials of c. -1500 kPa . In interpreting the data of experiments in this study, the possibility of inadequate moisture flux to the root affecting the results was considered.

R2. Effects of Soil Moisture Levels and Soil Strength on Radiata Pine Seedling Root Growth

The experiments were planned to allow separation of the effects of soil strength and soil moisture on the root elongation of radiata pine. Preliminary experiments were carried out to determine if soil moisture potential was influenced by bulk density at constant gravimetric moisture content and whether penetrometer resistance was a function of soil moisture content at a given bulk density.

R2.1. Soil moisture relationship

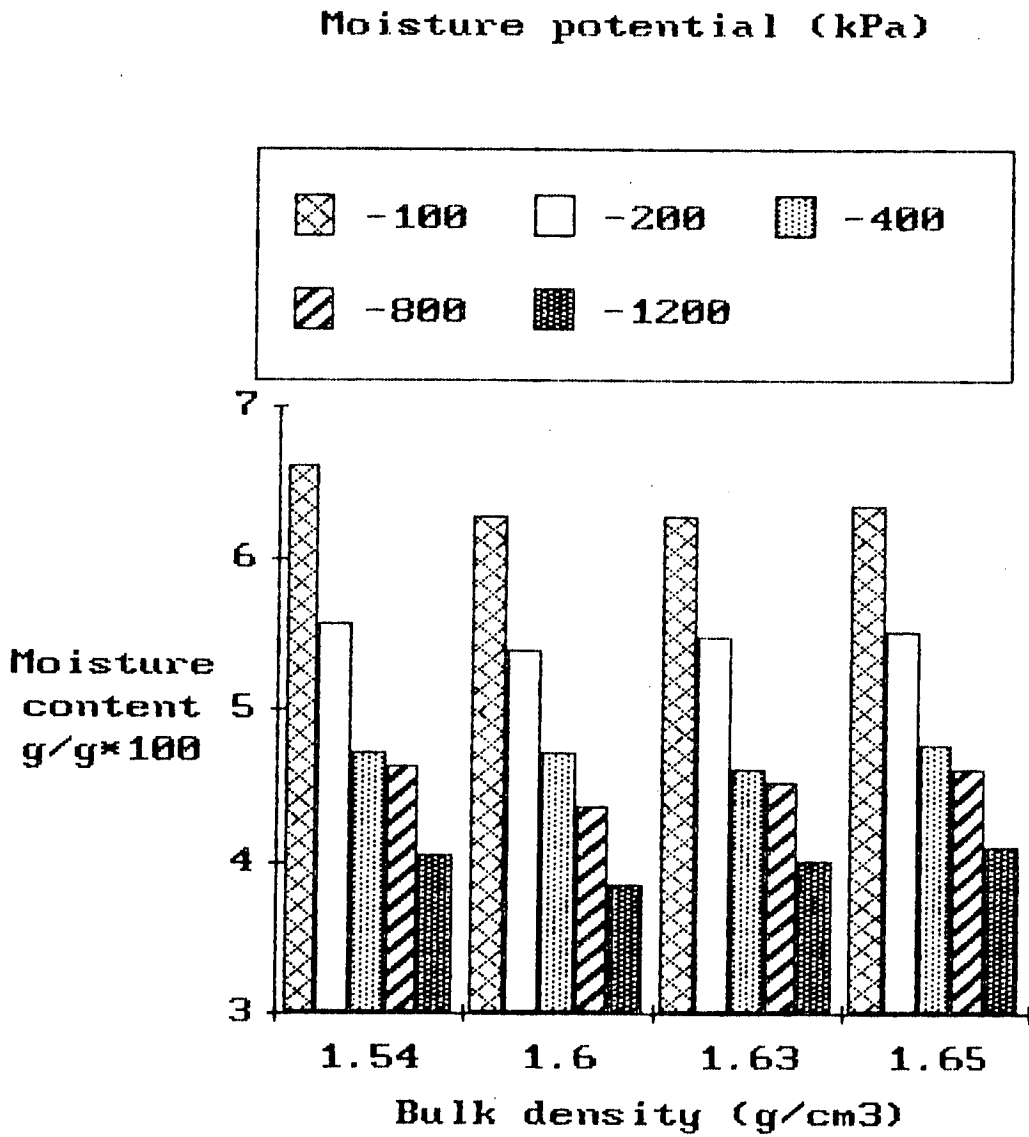
The relationship between bulk density, gravimetric moisture content and soil moisture potential was determined to test whether gravimetric moisture content was independent of bulk density at a particular soil moisture potential.

A pressure membrane device was used following the technique described in Section M2.1.4. and the results are presented in Table R2.1. and Figure R2.1.

Analysis of variance of the data in Table R2.1. showed moisture potential to be a significant treatment ($P = 0.01$) but bulk density to be non-significant. It is illustrated in Figure R2.1. where gravimetric moisture content is independent of bulk density for any soil moisture potential. Bar-Yosef and Lambert (1981) reported no change in gravimetric moisture content or moisture potential when bulk density of a sandy loam was increased from 1.1gcm^{-3} to

FIGURE R2.1.

Gravimetric moisture content of
sandy loam soil for four levels of
bulk density and five soil moisture
potentials



1.7gcm⁻³. Greacen and Oh (1972) reported similar independence of moisture potential and bulk density for a 'Parafield' loam.

The soil moisture potential-gravimetric moisture content relationship measured here was comparable with that recorded in Section R1.3. where unconsolidated soil was used. At a soil moisture potential of -100kPa, gravimetric moisture contents was 6.38% here and 6.41% in Section R1.3. For the lowest moisture potential tested in both experiments (-1200kPa), comparative moisture contents were 4.06% and 4.01%.

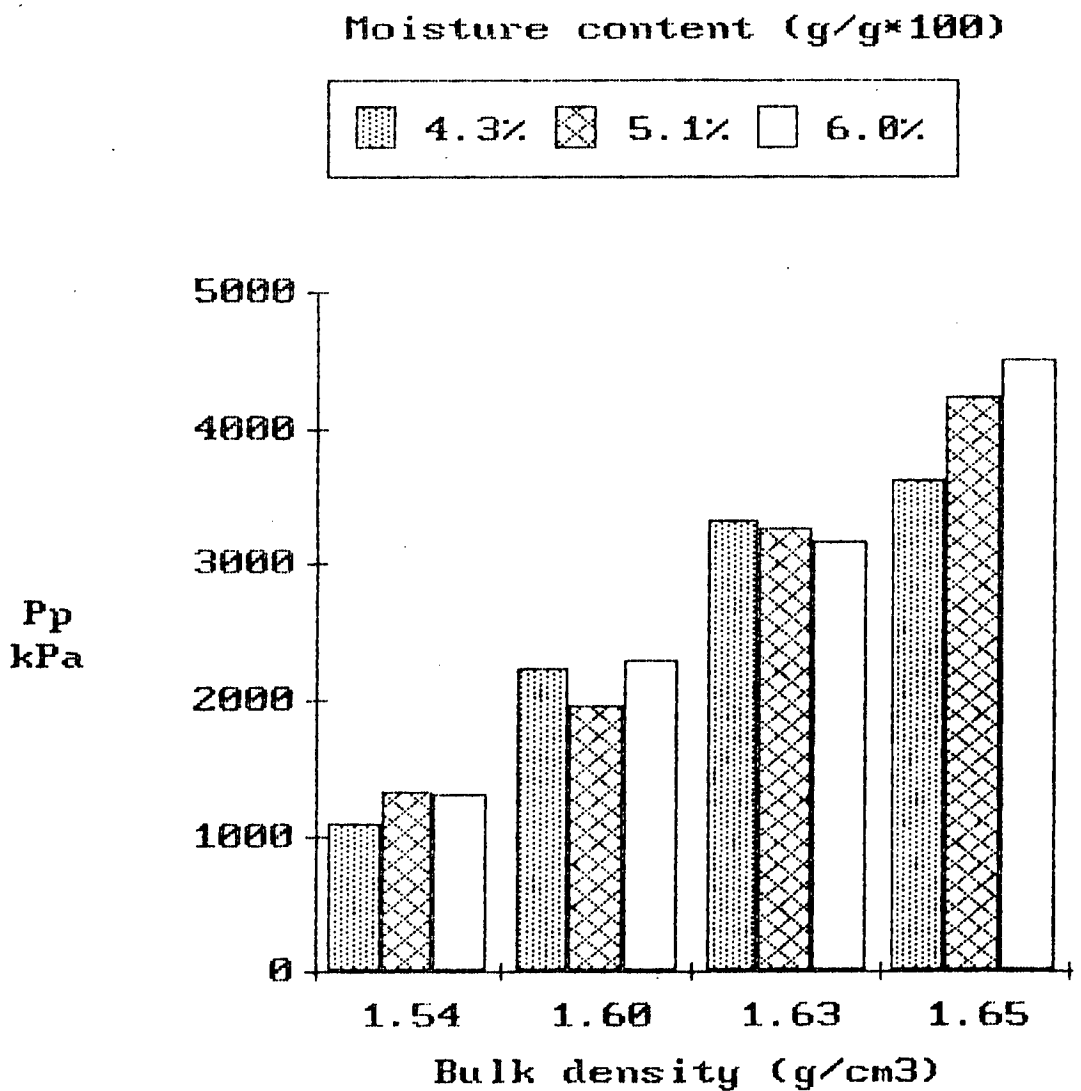
It is concluded that there is no effect of bulk density on moisture potential of the Wynyard sandy loam soil over the range of bulk densities tested. Moisture potential was directly determined from the moisture characteristic (Section R1.3) for the experiments which follow.

R2.2. Soil strength relationship

The relationship between penetrometer resistance, bulk density, and gravimetric soil moisture content was determined to test whether penetrometer resistance was independent of gravimetric soil moisture content for a particular bulk density. Table R2.2. and Figure R2.2. document the relationship between penetrometer resistance, bulk density and soil moisture content.

FIGURE R2.2.

Penetrometer resistance (Pp)
of sandy loam soil at
different levels of bulk
density and soil moisture
content



Penetrometer resistance increased as bulk density increased, however, there was no significant effect of soil moisture content on penetrometer resistance for any level of bulk density (Figure R2.2.). Penetrometer resistance increased from c. 1000kPa to c. 4000kPa as bulk density increased from 1.5gcm^{-3} to 1.65gcm^{-3} , an increment in bulk density of only 0.11gcm^{-3} indicating the sensitivity of penetrometer resistance (P_p) to small changes in bulk density (p_b). A linear model fitted to the data:

$$P_p = -38115 + 25427P_b, R^2 = 0.91$$

gave further emphasis to the sensitivity of penetrometer resistance to bulk density by the magnitude of the slope of the line of best fit. An increment of 0.1gcm^{-3} in bulk density will result in an increase in penetrometer resistance of 2542kPa.

Most authors report an increase in penetrometer resistance as soil moisture content decreases for constant bulk density. Taylor and Ratliff (1969a) found that for a bulk density of 1.3gcm^{-3} , penetrometer resistance of a loamy sand increased from 250kPa to 400kPa as soil moisture content declined from 7.4% to 4%. At a bulk density of 1.5gcm^{-3} , for the same moisture content change, they reported penetrometer resistance increased from 900kPa to 1750kPa. Bar-Yosef and Lambert (1981) found that a decrease in soil volumetric moisture content from 30% to 10% increased penetrometer resistance by 100% in a sandy loam

soil. Bradford (1980) recorded a similar percentage increase in penetrometer resistance when the moisture potential of a silt loam soil was reduced from -10kPa to -100kPa.

Greacen and Oh (1972) found no consistent relationship between their measure of probe resistance and moisture content for constant bulk density. For a bulk density of 1.4gcm^{-3} , probe resistance was 30% greater at a soil moisture content of 8.5% than probe resistance at a moisture content of 5%. For a bulk density of 1.6gcm^{-3} probe resistance was 100% greater at 8.6% moisture compared with 12.1% moisture. Sands et al. (1979) reported however, that penetrometer resistance of a sand (95% sand) was independent of moisture when tested over the range of 2% to 12% soil moisture content and for bulk densities of 1.4gcm^{-3} and 1.5gcm^{-3} .

The range of bulk densities tested in this experiment (1.54gcm^{-3} to 1.65gcm^{-3}) is quite small and the independence of penetrometer resistance and moisture content may not hold over a greater range of densities. The levels of soil moistures tested, 4.3% to 6.0%, correspond to a range in moisture potentials of -150kPa to -1000kPa. In this study if experimental treatments were established with density or moisture levels outside the range tested here, penetrometer readings were taken of the treatments rather than extrapolating these results.

R2.3. Root elongation

Radiata pine seedlings were grown in soil filled pots with varying levels of soil moisture and bulk density to determine the relative influence of moisture and density on root growth.

The relationship between soil bulk density, gravimetric moisture content and radiata pine seedling root elongation is shown in Table R2.3.1. Volumetric moisture content (Table R2.3.2.) and air porosity (Table R2.3.3.) were calculated from bulk density and gravimetric moisture content for all treatment combinations.

Examination of Table R2.3.1. reveals that for the 1.54gcm^{-3} and 1.60gcm^{-3} bulk density treatments, there was a decline in root elongation with decreased soil moisture content. However, for the greater bulk densities (1.63gcm^{-3} and 1.65gcm^{-3}) there is no significant trend in root elongation over the range of soil moisture contents tested. Analysis of variance of the data confirms the observed trend with bulk density being a highly significant treatment ($P = 0.01$), but soil moisture content being a non-significant treatment.

Root elongation is predicted to be zero at a bulk density of about 1.70gcm^{-3} . Heilman (1981) grew Douglas fir seedlings in pots packed with a sandy loam soil and found root elongation was zero when bulk density was between 1.74gcm^{-3} and 1.83gcm^{-3} , while Maurya and Lal (1979) growing

soybean in a loamy sand, reported that root elongation was zero when bulk density was 1.9gcm^{-3} .

As discussed in Section L3, bulk density is an inferior measure of soil impedance to root elongation compared with penetrometer resistance. Analysis of the root elongation data in terms of a pressure-balance model of root growth is discussed in Section R2.5. where root elongation is related to soil moisture potential and penetrometer resistance.

Mean volumetric moisture contents for the treatment combinations in Table R2.3.1. are shown in Table R2.3.2. Volumetric moisture contents ($\text{cm}^3\text{cm}^{-3} \times 100$) range from 5.5% to 10%. From the data in Section R1.4. this range in volumetric moisture content corresponds to hydraulic conductivities of about 10^{-6}cm d^{-1} for 10% volumetric moisture content, and less than 10^{-7}cm d^{-1} for 5.5% volumetric moisture content. The conductivities are of the order of those suggested by Hullugalle and Willatt (1983) and Reicosky and Ritchie (1976) as critical when analysing whether rate of moisture flow to the root is adequate to support plant growth. In this experiment there was no transpirational demand for moisture as the seedlings had not developed cotyledons. The only moisture needed by the seedling was to service the increase in root volume during elongation, and the data of Table R2.3.1. shows that at the lowest moisture content of 3.6%, root elongation for the 1.54gcm^{-3} bulk density treatment was 114% greater than that

for the 1.65gcm^{-3} bulk density treatment. If the rate of moisture flux to the root had been limiting elongation rate, this differential in root elongation for the different density treatments would not have been observed. It is unlikely that the rate of moisture movement to the root has significantly affected root elongation rate, even for the driest treatments.

Mean air porosities ($\text{cm}^3\text{cm}^{-3} \times 100$) for the treatment combinations are shown in Table R2.3.3. The lowest air porosity was 26% for the 1.65gcm^{-3} , 6.45% treatment. The mean air porosity over all treatments was 31%. Critical levels of air porosity quoted for sandy loam soils packed to similar densities are 11% for peas (Eavis, 1972), 27% to 30% for Douglas fir by Heilman (1981) and 27% for radiata pine (Sands et al., 1979).

The data of Table R2.3.3. and Table R2.3.1. indicate that aeration was not limiting root elongation in the experiment. At the highest level of bulk density tested, root elongation declined as soil moisture content fell whereas if aeration was limiting, a significant decline in root elongation would be expected for the treatments with greater moisture contents and consequently less air porosity.

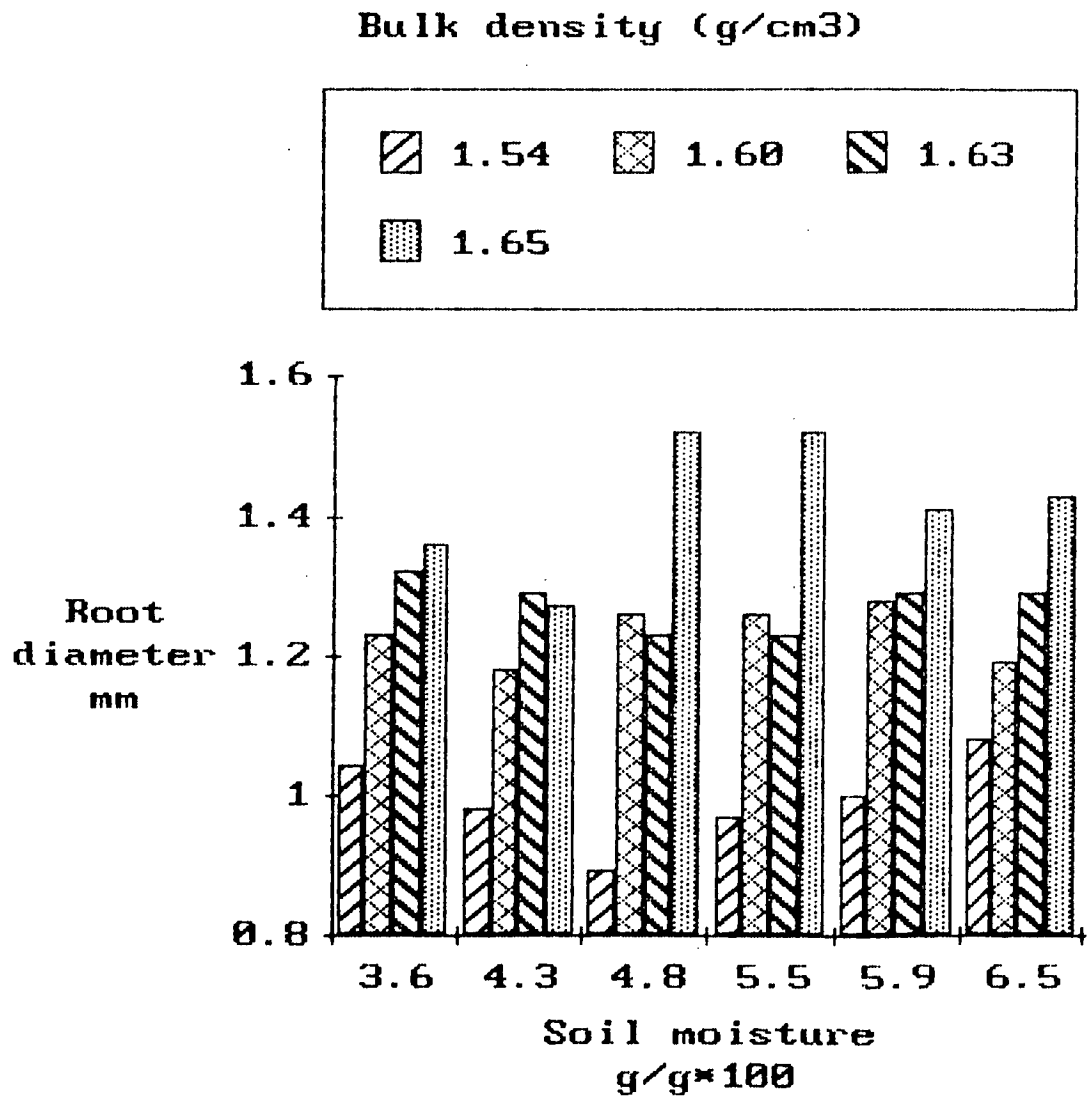
R2.4. Root diameter

It is commonly reported that root diameter increases as soil resistance becomes greater (Goss, 1977). Root diameters were measured (Table R2.4.) to determine if radiata pine seedling roots demonstrated any morphological changes with changing conditions of soil moisture and strength. An increase in root diameter with increased bulk density is seen in Figure R2.4. Analysis of variance showed that bulk density was a highly significant treatment ($P = 0.01$) but moisture a non-significant treatment. For all moisture treatments, root diameter increased on average by 30% as bulk density increased from 1.54gcm^{-3} to 1.65gcm^{-3} .

Baligar et al. (1981) sectioned soybean hypocotyls grown in a sandy loam soil with a bulk density of 1.85gcm^{-3} . They found the increased root diameter observed was due to a greater percentage of cell wall material and more radial cell expansion, when compared with sections of roots grown at lesser bulk density. Richards and Greacen (1986) described a mechanism where the greater root diameter which develops in more compact soils aided the advancement of the root into the soil. They concluded that the radial expansion of the root behind the root tip contributed to the failure of the soil surrounding the tip, and lowered the restraining force of the soil on the root. Abdalla et al. (1969) collected experimental evidence using a penetrometer and found that after expansion of the soil behind the tip of a probe, the probe advanced some distance into the soil if a

FIGURE R2.4

Seedling root diameter for six soil
moisture levels and four bulk
densities



constant force was applied to the probe. The increase in root diameter commonly reported when bulk density increases would appear to be an effective mechanism to maintain the rate of root elongation as soil strength increases.

R2.5. Soil strength, soil moisture, root elongation relationship

The relationship between radiata pine seedling root elongation, penetrometer resistance, and soil moisture potential is detailed in Table R2.5. and Figure R2.5.

Multiple linear regression of the data in Table R2.5. produced the model:

$$Re = 41.56 - 0.03P_p + 0.01P, R^2 = 0.89$$

The magnitude of the respective coefficients for moisture (P) and strength (P_p) show that root elongation was three times more sensitive to a 100kPa rise in soil strength than to a 100kPa decrease in soil moisture potential.

The actual force the root has to generate to elongate through a restraining soil has been estimated to be about 25% of the measured penetrometer resistance (Whiteley, et al., 1981). If the actual physical opposing force is reckoned at 25% of the penetrometer reading, then total external stress opposing root elongation (moisture potential (P) plus soil restraint (P_s)) can be calculated as:

$$-P + P_s = -P + 0.25P_p$$

In Figure R2.6., total external stress is plotted versus root elongation using the data from Table R2.5. The linear line of best fit:

$$R_e = 34.87 - 1.4 \times 10^{-2}(-P + P_s), R^2 = 0.53$$

predicts that total external stress when root elongation is zero will be 2490kPa. The extreme conditions would be nil soil restraint and a moisture potential of -2500kPa or nil moisture potential and soil restraint of 2500kPa which implies a penetrometer resistance of c. 10000kPa. In conditions of little soil moisture stress c. 3000kPa is often quoted as the critical penetrometer resistance for root growth (Greacen et al., 1968). As soil restraint is estimated as 25% of penetrometer resistance, soil restraint for a penetrometer resistance of 3000kPa would be c. 750kPa.

The difference in the estimates of critical strength suggest that at high values of soil strength, root elongation cannot be linearly related to penetrometer resistance and an exponential function would better model the response over a greater range of penetrometer resistances.

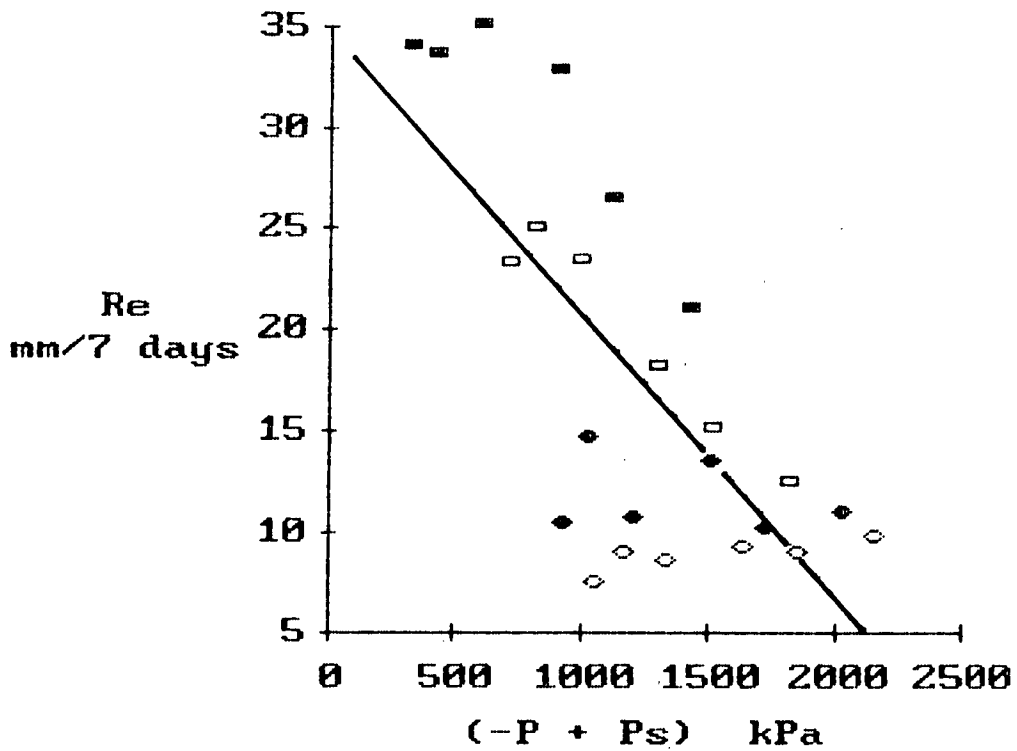
Figure R2.7. plots the root elongation data for corn seedlings reported by Mirreh and Ketcheson (1973) versus total external stress calculated from the soil moisture

FIGURE R2.6.

Sum of external soil
restraint (Ps) and soil
moisture potential (P) versus
root elongation for four
levels of soil strength.
Linear line of best fit shown

soil restraint (Ps)

◊ 998 ♦ 866 ◻ 667 ▪ 271



potential and penetrometer data they recorded. Although the results are more variable than those in Figure R2.6, the trend is similar and total stress when root elongation is nil, predicted to be c. 1100kPa. The data of Greacen and Oh (1972), for pea root elongation, has been similarly analysed and plotted in Figure R2.8. The estimate of total stress when $Re = 0$ from Figure R2.8. is c. 1200kPa which is 50% less than the estimate from Figure R2.6. A possible reason for the discrepancy may be the method of estimating soil restraint (P_s). Greacen and Oh (op cit.) provide an estimate of P_s based on the model of Farrell and Greacen (1966), but they record no penetrometer readings which would allow a comparison of the methods of estimating soil restraint.

In Section E it was argued that the only way a steady state Re may be maintained when external stress is increasing is by osmoregulation (decreasing P_o), decreasing threshold pressure (Y) or increasing wall elasticity (m). Values of Y and m were not determined here as the experiment was primarily concerned with the empirical effect of soil physical factors on root elongation rather than consideration of possible mechanisms, however, as discussed in Section L, changes in Y or m have been observed for some species when either external restraint or water potential alter.

The pattern of radiata pine root elongation observed demonstrated the relative sensitivity of Re to soil strength increases compared with soil moisture decreases. The

FIGURE R2.7

Data of Mirreh and Ketcheson (1973) where root elongation for corn seedlings grown in a clay loam is plotted versus the sum of the soil restraint and soil moisture potential ($P + P_s$)

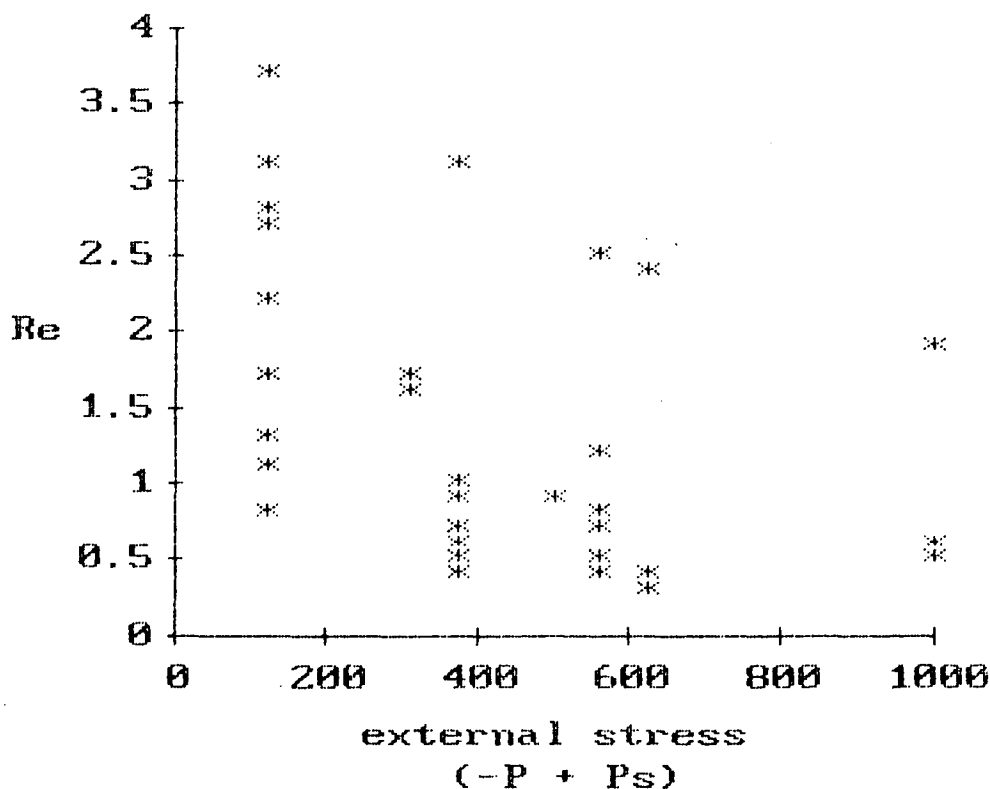
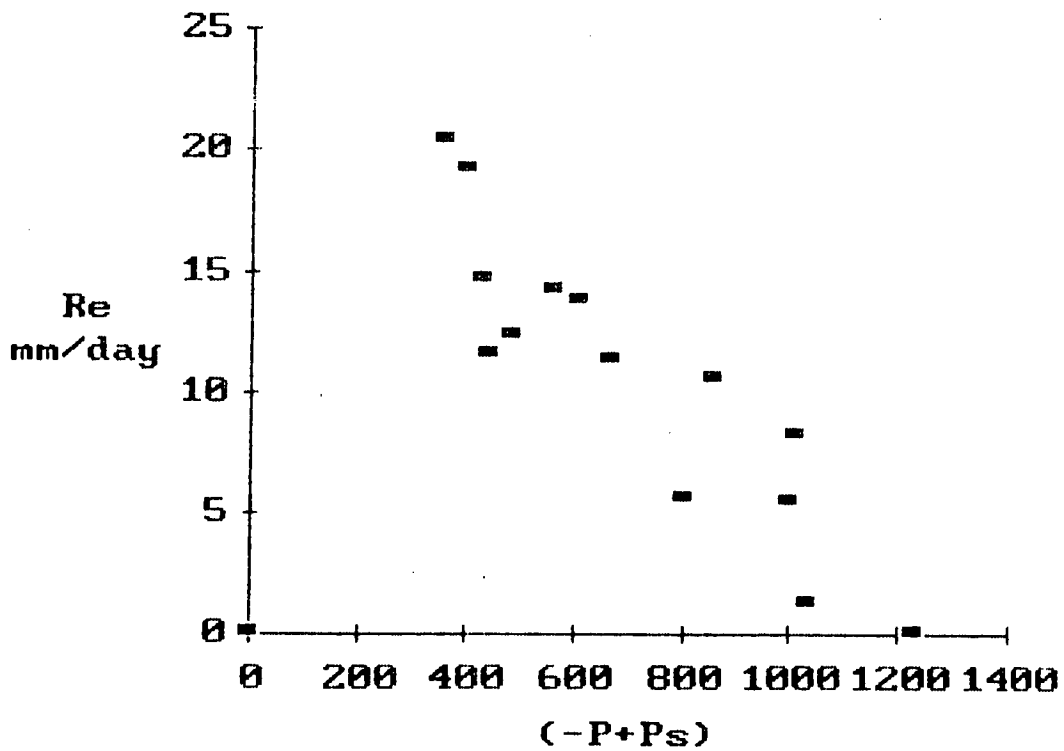


FIGURE R2.8.

Root elongation data of Greacen
and Oh (1972) plotted versus the
sum of soil restraint (P_s) and
soil moisture potential (P)



following experiment measured root osmotic potential values for radiata pine to quantify the individual elements of the model.

R3. Elongation and Osmotic Potential of Roots Growing in Vermiculite and PEG Solution.

A system of seedling growth in vermiculite filled plastic boxes, to allow measurement of root growth and root segment osmotic potential in conditions of near zero soil strength, has been described in Section M2.3.1. In this Section the relationship between solution potential and root osmotic potential was determined and any change in root osmotic potential further from the root tip was measured. It was assumed that total root potential would equate to solution potential so the difference between osmotic and solution potential could be interpreted as root turgor (Section E).

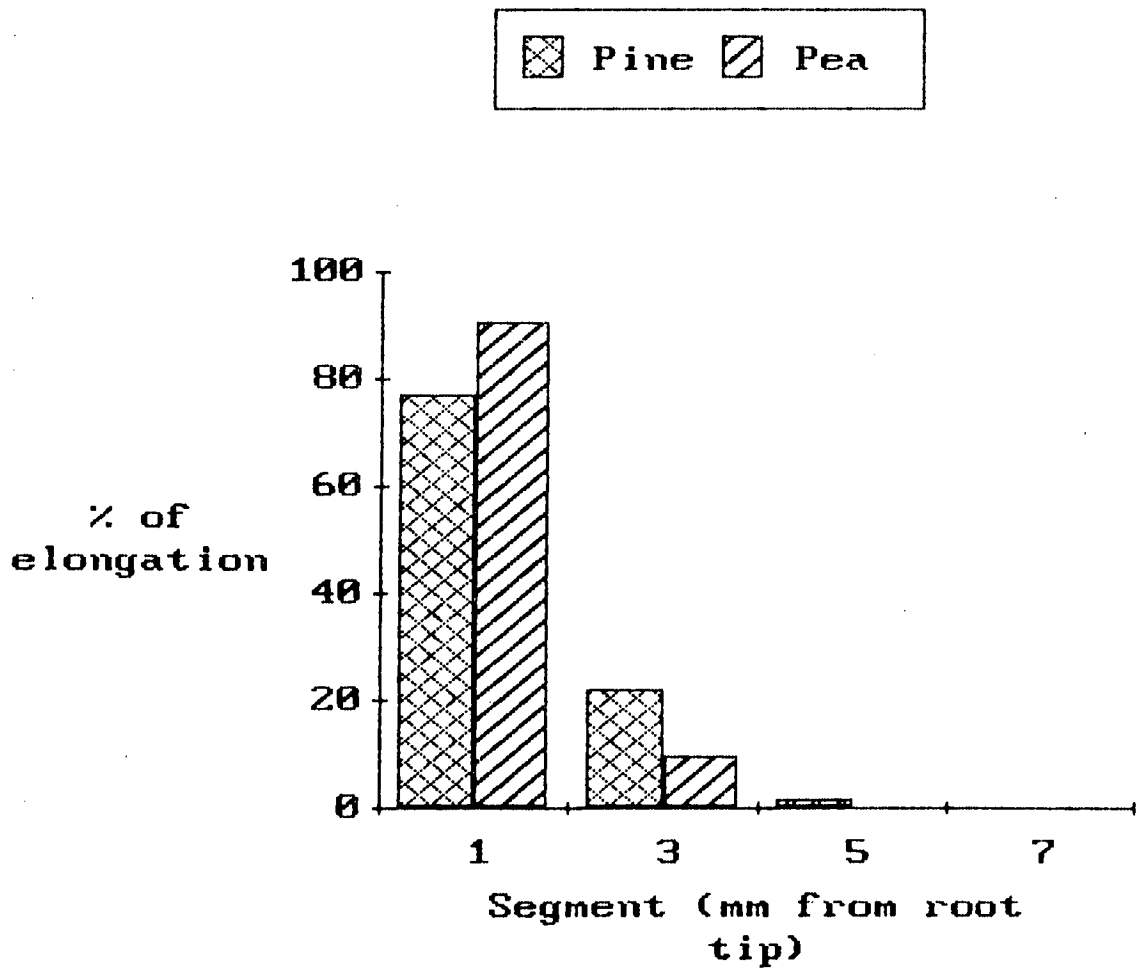
R3.1. Zone of root elongation of pine and pea seedlings

This experiment was designed to determine the precise zone of root elongation of pine and pea seedlings. Knowledge of the location of the zone of elongation was necessary to interpret root segment osmotic potential data after segmentation of seedling roots. The method has been described in Section M2.3.4. and the results are detailed in Table R3.1.1. (pine), Table R3.1.2. (pea) and illustrated for both species in Figure R3.1.

Examination of the data in Table R3.1.1. and Table R3.1.2. shows root elongation primarily takes place within 2mm of the root tip for both pea and pine seedlings. For

FIGURE R3.1.

Percentage of total root elongation versus distance from root tip for pine and pea seedlings



peas, 90% of elongation was recorded within the 0-2mm segment while for pines the 0-2mm segment recorded 77% of elongation. Further back from the root tip, little elongation was recorded for either species, with no pea root elongation further than 4mm from the root tip and only 1% of pine elongation in the 4-6mm zone. Eavis (1967) reported that there was no pea root elongation further than 5mm from the tip, with most elongation 2-3mm from the root tip. Pilet and Senn (1980) found a similar pattern with 57% of maize seedling root elongation in the first 2mm and 90% within 5mm of the root tip. They also reported that water content of the root in the elongating segment averaged 80%, while further from the tip water content approached 95%. The concentration of proteins and phenolics was 100% greater in the root segment where most elongation occurred. It could be inferred from their data that osmotic potential of the elongating segment would be less than the osmotic potential further from the tip, due to the greater concentration of solutes and the lower moisture content. As total root potential can be reasonably assumed to be constant over a short distance, any increase in osmotic potential would suggest that cell turgor was greater in the elongating root segment than for the expanded segments.

From the data in Table R3.1.1., the pattern of elongation observed for pine seedling roots is similar to that reported in the literature for other species and that demonstrated in Table R3.1.2. for pea seedlings. Any turgor

gradient in the root could therefore be expected to be observed by comparing turgor of the first 4mm of the root with turgor for segments further from the root tip.

R3.2. Pine root elongation and osmotic potential

Experiment R3.2. was designed to determine the response of pine seedling root elongation and root segment osmotic potential to moisture potential when soil strength was not limiting. Vermiculite and PEG solution was placed in growth boxes using the technique described in Section M2.3.1. Pine seedling root elongation (Re), root cell turgor (Pt) for the 1-7mm segment (average of 1-4mm and 4-7mm segments) and solution potential (P) are detailed in Table R3.2.1. and Figure R3.2.1.

Linear regression of the data in Table R3.2.1. produced the following lines of best fit:

$$Re = 7.23 - 4.46 \times 10^{-3}P, R^2 = 0.81 \quad - \quad (1)$$

$$Po = -2036 - 0.11P, R^2 = 0.04 \quad - \quad (2)$$

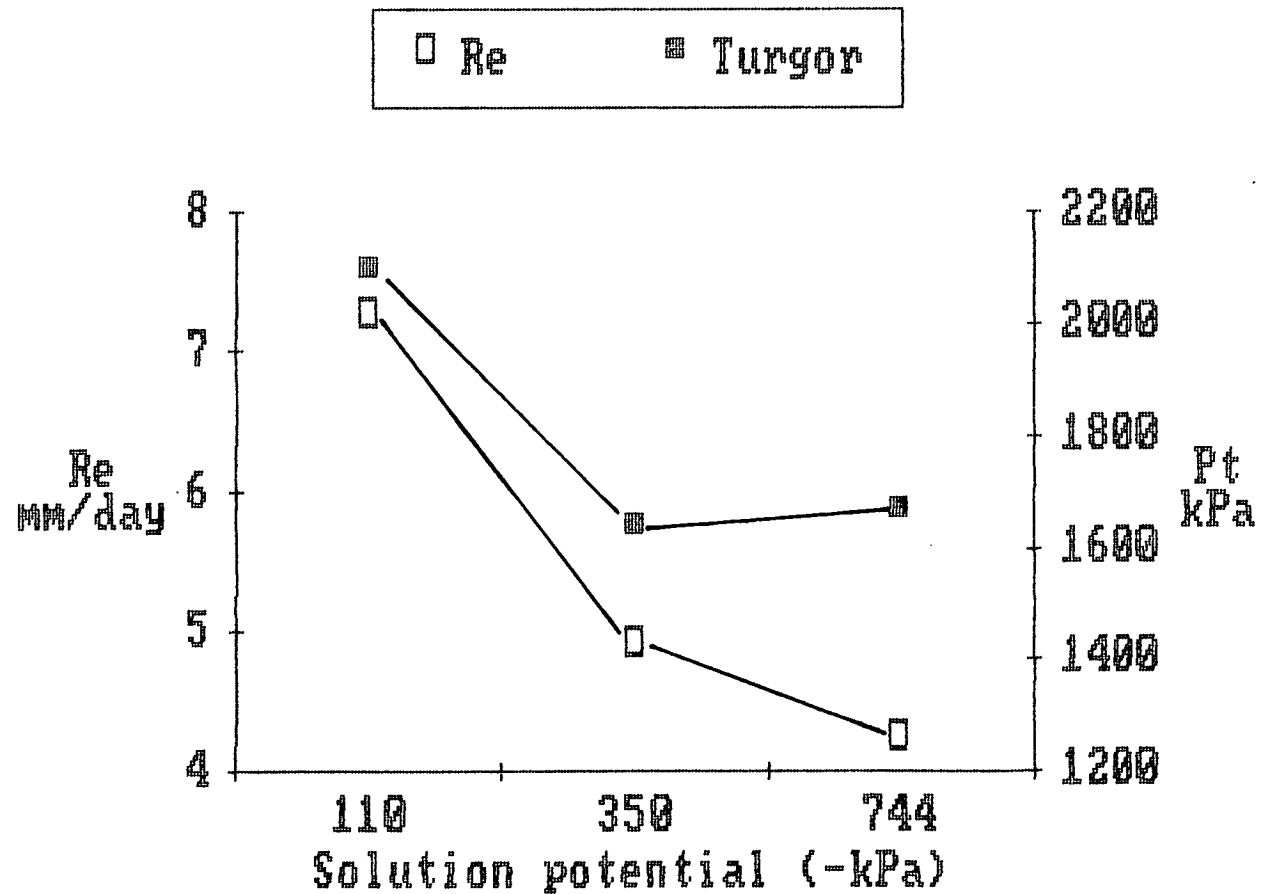
$$Pt = 2036 + 0.61P, R^2 = 0.57 \quad - \quad (3)$$

$$Re = -5.17 + 5.92 \times 10^{-3}Pt, R^2 = 0.93 \quad - \quad (4)$$

Figure R3.2.1. illustrates how root elongation declined with decreasing solution potential. When solution potential was -110kPa, root elongation was 7.28mm d⁻¹. However, at -744kPa solution potential, root elongation was nearly 50% less at 4.21mm d⁻¹.

FIGURE R3.2.1.

Root elongation (Re) and root cell turgor (Pt) of pine seedlings growing in vermiculite and PEG solutions of three moisture potentials



Regression (1) demonstrates the close relationship between solution potential and root elongation, indicating that moisture potential per se reduced elongation. The regression predicts that if root elongation was zero, solution potential would be -1621kPa .

Regression (2) quantifies the independence of root osmotic potential from solution potential. There was no uniform decline in osmotic potential as solution potential decreased and therefore no osmotic adjustment to solution potential. The absence of osmotic adjustment is reflected in Regression (3), where the decline in root turgor is correlated with the decline in solution potential.

Regression (4) indicates the mechanism for the reduction in root elongation with declining solution potential. Root elongation is seen to be closely correlated with root turgor, and Regression (4) predicts that when root elongation is zero, turgor would be 873kPa . Solution potential, when root turgor was 873kPa , would be -1906kPa . This is comparable with the data in Table R3.2.1. relating root elongation and PEG solution potential, which suggested root elongation would equal zero when solution potential equalled -1621kPa .

As there is no soil force constraining elongation in the vermiculite system, when root elongation is zero (873kPa), turgor can be interpreted as an estimate of threshold wall pressure (Y) below which no elongation will

occur.

From the general pressure-balance model of root growth for a system where external physical constraint is nil:

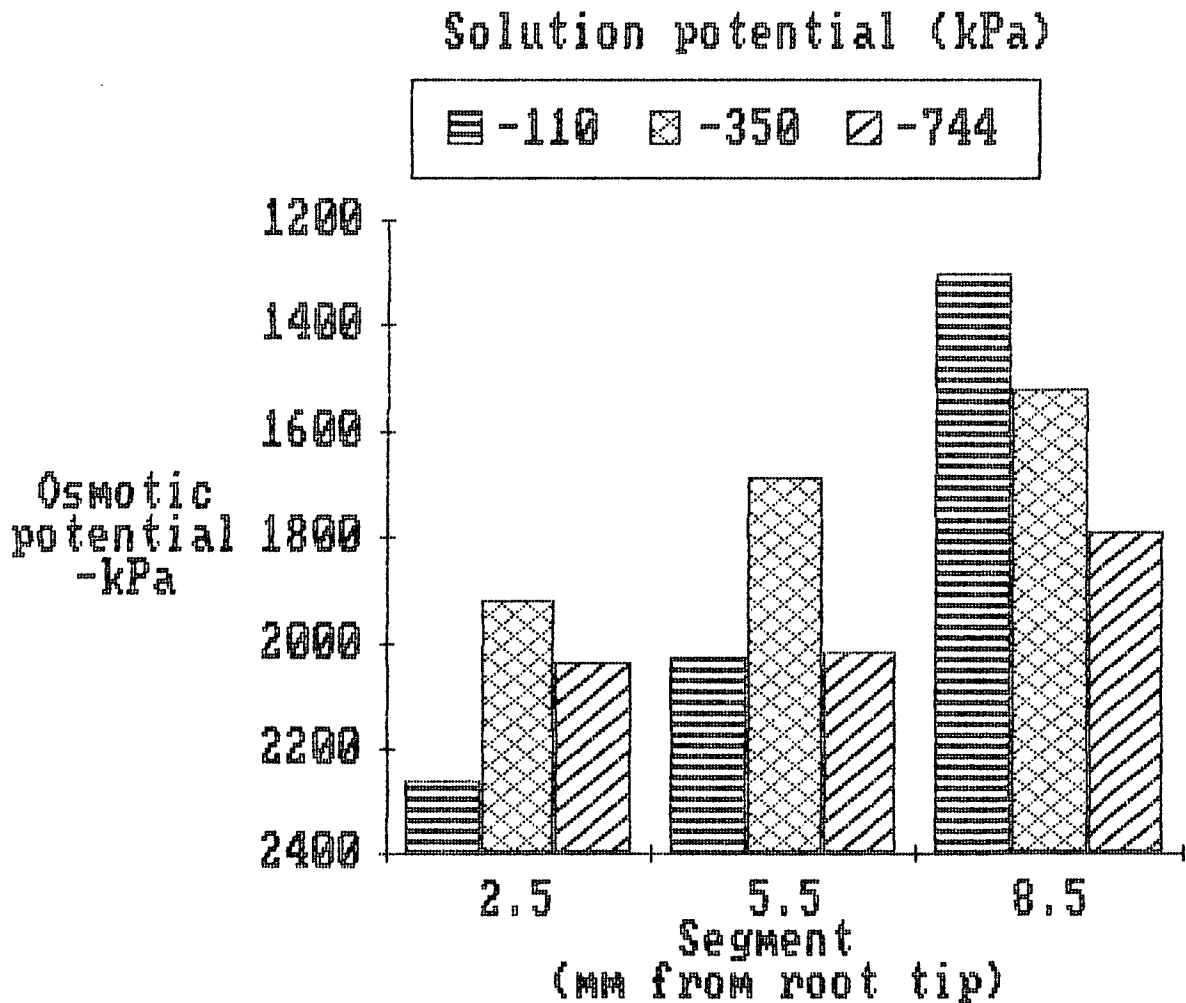
$$Re = (Pt - Y)m$$

cell wall elasticity (m) can be estimated from Regression (4) at $5.92 \times 10^{-3} \text{mm kPa}^{-1}$.

Table R3.2.2. records the osmotic potential of the root segments for each solution potential. Osmotic potential is plotted as a function of the distance of the segment from the root tip in Figure R3.2.2. Analysis of the data of Table R3.2.2. showed both solution potential and root segment to be non-significant in the determination of osmotic potential. However, Figure R3.2.2. indicates an increase in osmotic potential as distance from the root tip increased, but no consistent relationship between osmotic potential and solution potential. The increase in osmotic potential was most pronounced for the -110kPa solution potential treatment. Osmotic potential increased from -2260kPa for the 1-4mm segment to -1300kPa for the 7-10mm segment, or an increase of 42%. In contrast, for the -744kPa treatment, the increase in osmotic potential was 12% over the same range. Root elongation for the -110kPa treatment was 7.23mm d^{-1} compared with 4.21mm d^{-1} for the -744kPa treatment. A greater differential in osmotic potential between elongating root segments and segments further from the root tip would be expected for the more rapidly elongating root, as

FIGURE R3.2.2.

Osmotic potentials of pine root segments grown in vermiculite and PEG solutions of three moisture potentials



elongation was proportional to net cell pressure (Regression (4)). As solution potential is constant for any treatment over the segments measured, the trend in turgor ($P - P_o$) would parallel that for osmotic potential.

The osmotic potential determinations for pine root segments were quite variable and this is seen in the magnitude of treatment standard errors in Table R3.2.2. For two treatments the standard error could not be calculated, as there were insufficient replications due to inadequate volume of sap expressed from the root for psychrometric determination of osmotic potential. The total root segment volume for a pine root of 1mm diameter was c. $2.4 \times 10^{-2} \text{cm}^3$. It was estimated that to reliably express a $2 \times 10^{-3} \text{cm}^3$ sample, c. 10 segments of 3mm length would be needed. To replicate treatments in sufficient numbers to provide 10 segments per replication, would not have been practical as the number of pots needed for each treatment would have limited the number of treatments possible. For later experiments where measurement of root osmotic potentials was required, pea seedlings were grown. The average pea root diameter in vermiculite medium was c. 2mm and in soil c. 1.5mm which increases sample volume per segment between 250% and 400% when compared with pine segments.

R3.3. Pea root elongation and osmotic potential

Pea seedlings were grown in plastic growth boxes for 66 hours, at five levels of moisture potential established by using vermiculite and PEG (Section M2.3.1.). The interactions between the measurements recorded in Table R3.3.1. and Table R3.3.2. are best demonstrated by regressions relating root elongation (Re), solution potential (P), root osmotic potential (Po), and root turgor (Pt):

$$Re = 16.53 + 1.37 \times 10^{-2}P, R^2 = 0.99 \quad - \quad (1)$$

$$Po = -989 + 1.14P, R^2 = 0.95 \quad - \quad (2)$$

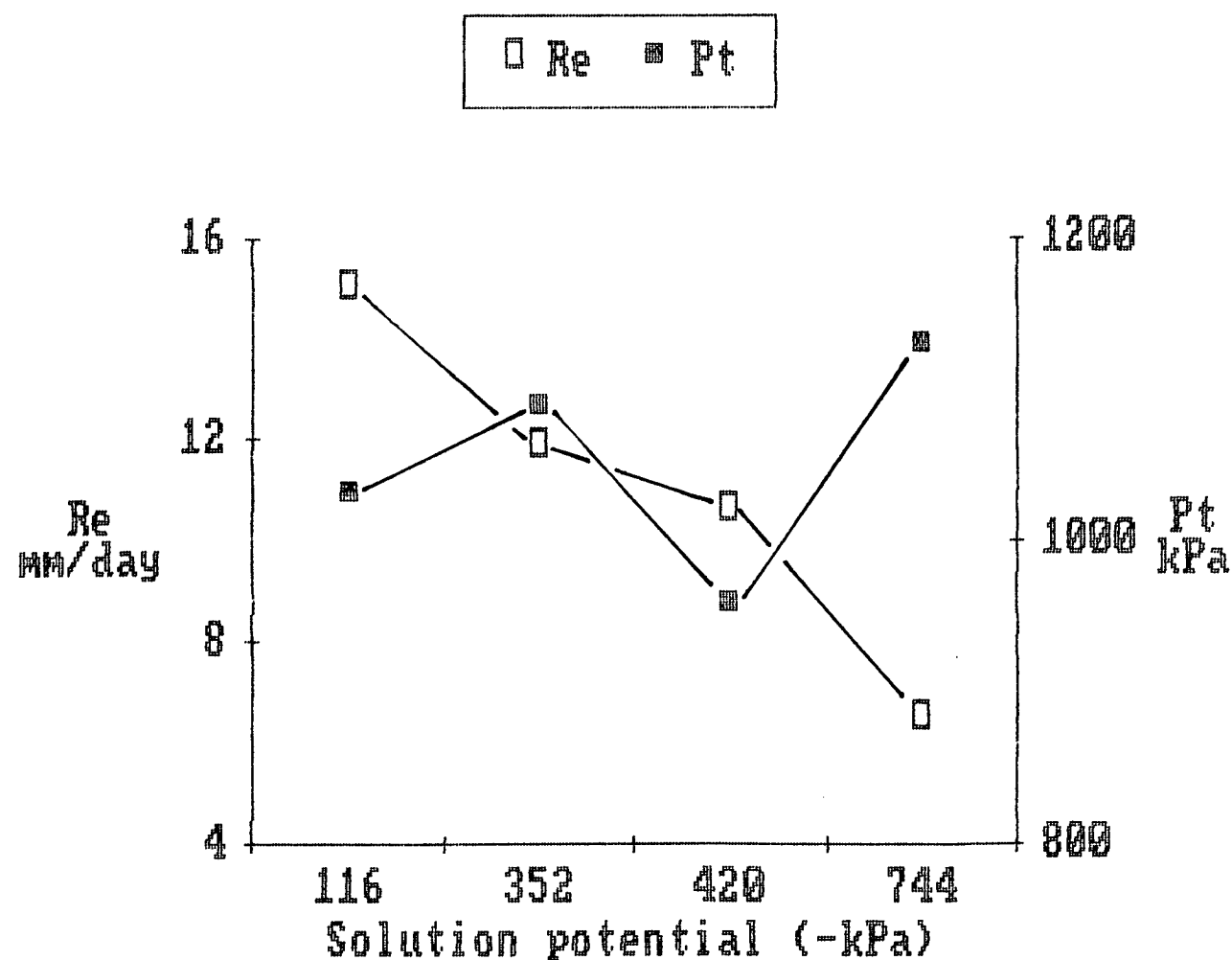
$$Pt = 989 + 0.14P, R^2 = 0.25 \quad - \quad (3)$$

$$Re = 34.11 - 0.02Pt, R^2 = 0.22 \quad - \quad (4)$$

Figure R3.3.1. illustrates the decline in root elongation as solution potential decreased. When solution potential was -116kPa , root elongation was 14.99mm d^{-1} . However, when solution potential was -744kPa , root elongation had declined to 6.42mm d^{-1} or a decline of 57%. Regression (1) shows the very close correlation between root elongation and solution potential, and predicts that when root elongation equals zero, solution potential would equal -1210kPa . The data indicated an effect of moisture potential per se on root elongation for the range of moisture potentials tested. Mirreh and Ketcheson (1973) recorded the elongation of corn seedling roots grown in aerated PEG solution. When the solution potential was reduced from -

FIGURE R3.3.1.

Root elongation (Re) and root cell turgor (Pt) of pea seedlings grown in vermiculite and PEG solutions of four moisture potentials



300kPa to -800kPa root elongation declined by 53%. For a similar reduction in solution potential (-352kPa to -744kPa) the data of Table R3.3.1. indicates a 46% reduction in root elongation.

Regression (2) quantifies the close correlation between solution potential and root osmotic potential. Osmotic potential will decline by 114kPa for a 100kPa decline in solution potential. This can be interpreted as 114% osmotic adjustment to moisture potential. Regression (3) and Figure R3.3.1. reflect the complete osmotic adjustment as root turgor was maintained as solution potential declined. Maximum recorded turgor was 1086kPa for a solution potential of -352kPa. Minimum turgor was 955kPa for a solution potential of -420kPa.

Root turgor was maintained yet elongation declined as solution potential decreased. Regression (4) shows the poor correlation between elongation and turgor. Interpretation of the results using a pressure-balance model suggests that the decreased root elongation for lower solution potentials could reflect increased wall threshold pressure (ψ) or decreased cell wall elasticity (m).

An Analysis of Variance of the data in Table R3.3.2. showed solution potential to be a highly significant treatment, and root segment to be non-significant in determining root osmotic potential. The close correlation between osmotic potential and solution potential is seen for

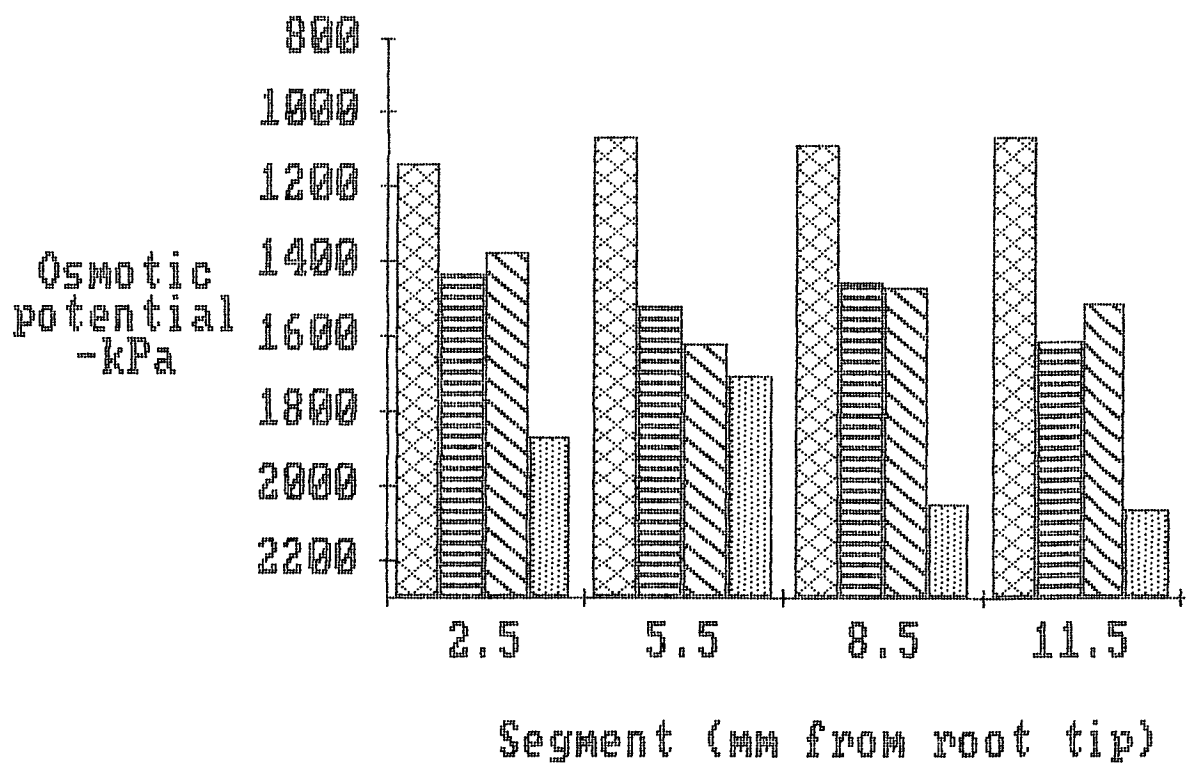
all root segments in Figure R3.3.2. The absence of an increase in osmotic potential as distance from the root tip increased implies that root turgor was constant for the segments sampled. As the root only elongates within the first 4mm of the tip, wall elasticity must have declined or threshold turgor increased further from the tip. It implies that the control of root elongation rate in this experiment was largely physiological, and is not readily modelled using a simple physical model. If threshold pressure (Y) is assumed to be constant, wall elasticity (m) can be calculated to vary between $1.5 \times 10^{-3} \text{mm kPa}^{-1}$ and $6 \times 10^{-3} \text{mm kPa}^{-1}$ while if wall elasticity is constant at $\underline{c.} \ 3 \times 10^{-3} \text{mm kPa}^{-1}$ threshold pressure would vary from 1127kPa to 3968kPa. For pea seedling roots, values of threshold pressure recorded are $\underline{c.} \ 500 \text{kPa}$ and wall elasticity $\underline{c.} \ 10^{-2} \text{mm kPa}^{-1}$ (Greacen and Oh, 1972). It is more likely that variations in wall elasticity are the mechanism for regulating elongation in conditions of little soil strength than variations in threshold turgor as the magnitude and range of threshold turgor necessary to regulate the observed elongation are beyond any reported in the literature. The variations in cell wall elasticity which would produce the variation in elongation are comparatively small and are within the range measured here and elsewhere (Greacen and Oh, 1972).

FIGURE R3.3.2.

Osmotic potential of pea root segments grown in vermiculite and PEG solutions of four moisture potentials

Solution potential (kPa)

■ -116 ▨ -352 ▩ -420 ▤ -744



R4. Root Elongation and Osmotic Potential of Pea Roots Grown in Soil Filled Pots Packed to Different Bulk Densities

Root elongation, segment osmotic potential and pot penetrometer resistance were measured to derive values for use in a pressure balance model of root growth including a soil strength term. Root cell turgor was determined as the difference between soil matric potential and root segment osmotic potential by assuming that total root potential was equal to total soil water potential. Total soil water potential was in turn assumed to be equal to matric potential (Section E).

R4.1. Pea roots grown at one level of soil moisture

Root elongation and root segment osmotic potential of pea seedlings grown in soil of known penetrometer resistance and at a soil moisture potential of -100kPa , were measured to quantify elements of a pressure balance model of root growth. Linear functions have been fitted to the data in Table R4.1.1. and Table R4.1.2. to show the relationship between root elongation (Re), root segment osmotic potential (Po), penetrometer resistance (Pp), soil restraint (Ps), and root turgor (Pt).

$$Re = 9.18 - 3.23 \times 10^{-3}Pp, \quad R^2=0.88 \quad - \quad (1)$$

$$Po = 996 - 1.01Ps, \quad R^2 = 0.79 \quad - \quad (2)$$

$$Re = 3.01 + 6.05 \times 10^{-3}(Pt-Ps), \quad R^2 = 0.85 \quad - \quad (3)$$

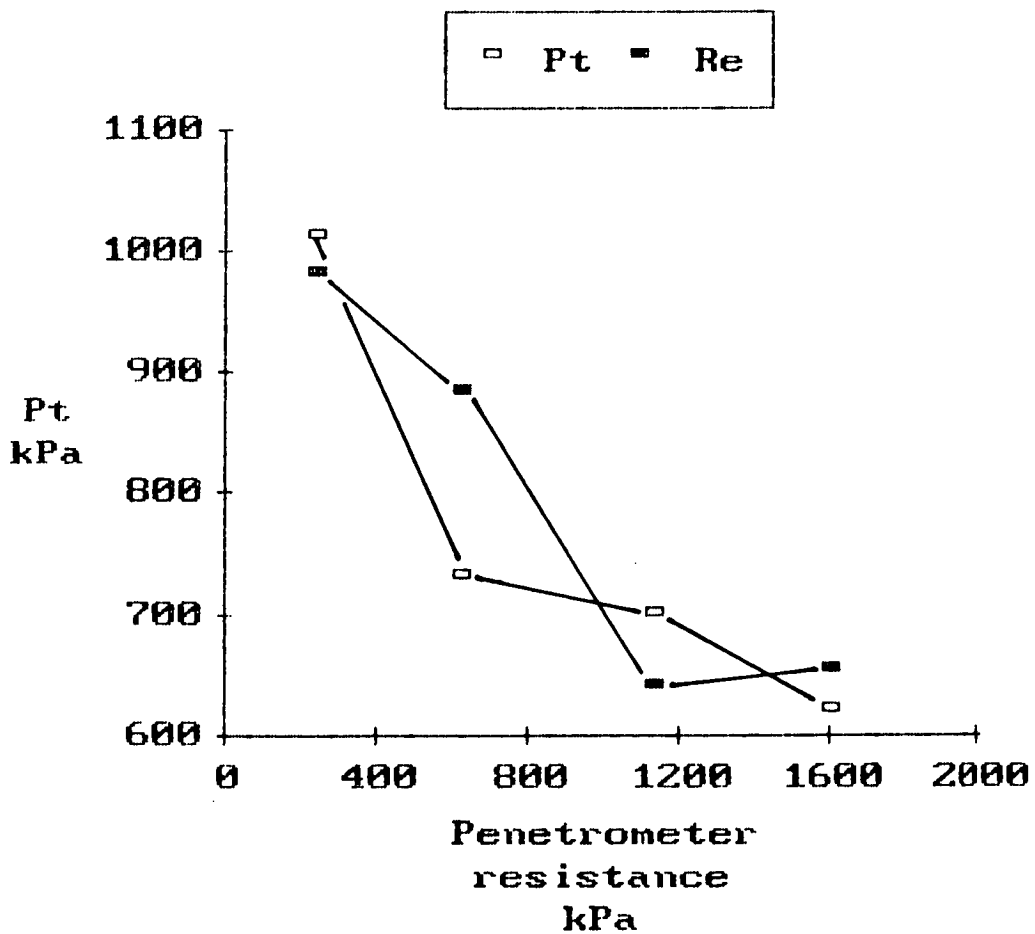
Table R4.1.1. and Figure R4.1.1. record a decline in root elongation with increasing penetrometer resistance. At a penetrometer resistance of 250kPa, root elongation was 8.5mm d^{-1} . For a penetrometer resistance of 1140kPa root elongation was 4.5mm d^{-1} . Regression (1) predicts that root elongation will be nil when penetrometer resistance is 2850kPa which is comparable with the values of penetrometer resistance which substantially reduce growth quoted by Greacen et al. (1968).

Figure R4.1.1. illustrates how root turgor declined with increasing penetrometer resistance. When penetrometer resistance was 250kPa, turgor was 1010kPa. When penetrometer resistance was 1600kPa, turgor had declined to 620kPa. If the actual soil physical force opposing root elongation (P_s) is reckoned at 25% of penetrometer resistance (Whiteley et al., 1981), then Regression (2) may be calculated. It shows that osmotic potential increased 101kPa for every 100kPa increase in soil restraint. Turgor would similarly have declined as total root potential was constant at -100kPa.

A close correlation between cell wall pressure ($P_t - P_s$), (Greacen and Oh, 1972) and root elongation is demonstrated in Regression (3). When root elongation is zero, net pressure is predicted to be 497kPa which is an estimate of wall threshold (Y). The regression implies a wall elasticity of $6.05 \times 10^{-3}\text{mm kPa}^{-1}$. In Section R3.2., for pine seedlings growing in vermiculite, a similar wall

FIGURE R4.1.1.

Root elongation (Re) and root cell turgor (Pt) versus penetrometer resistance for pea seedlings grown in pots packed with sandy loam soil having a moisture potential of -100kPa



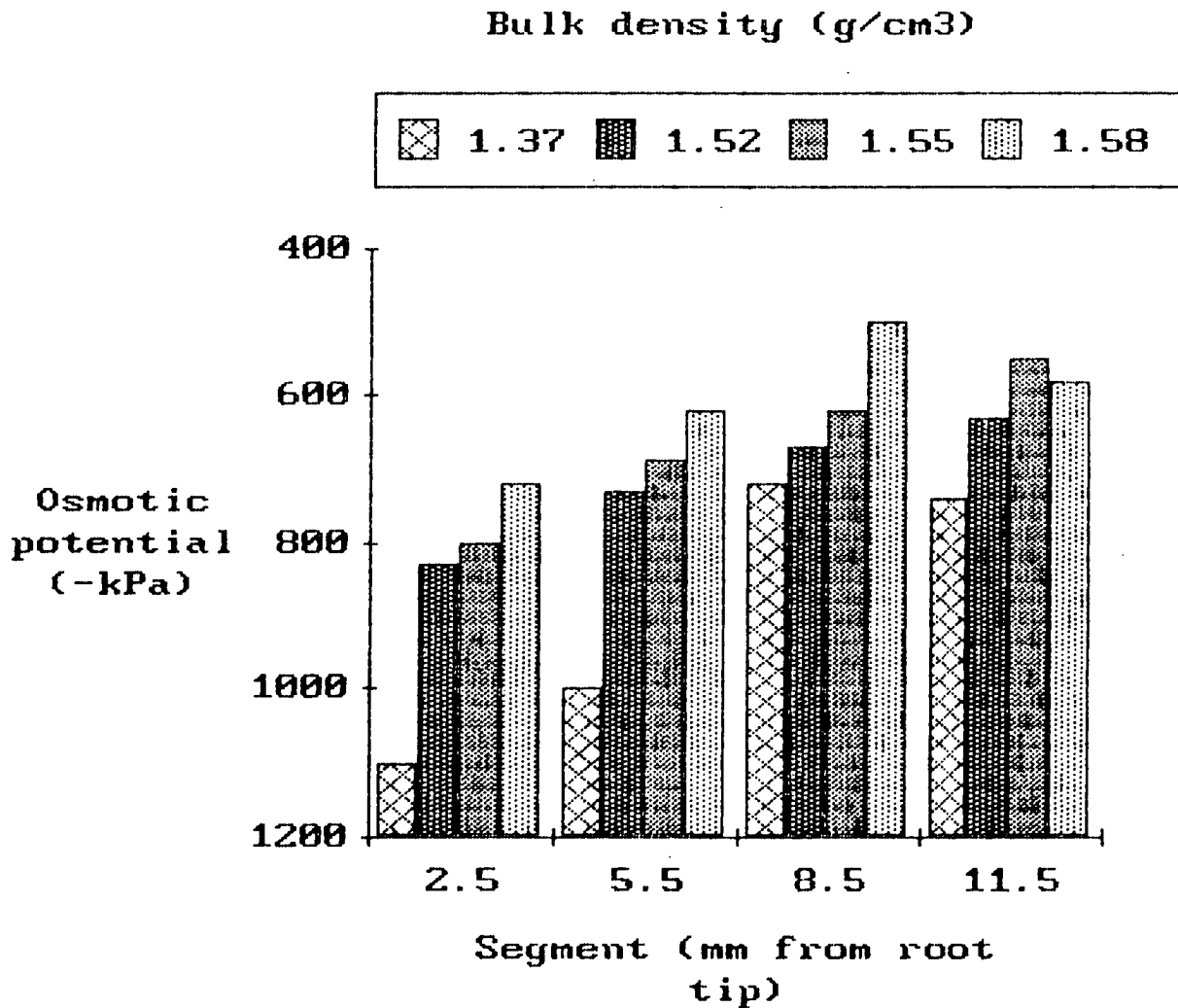
elasticity was calculated of $5.92 \times 10^{-3} \text{mm kPa}^{-1}$.

Greacen and Oh (1972) reported a minimum value of 220kPa and a maximum value of 600kPa for threshold pressure of pea seedlings and wall elasticities $c. 10^{-2} \text{mm kPa}^{-1}$.

Figure R4.1.2. shows an increase in root segment osmotic potential from 2.5mm to 8.5mm distance from the root tip. No difference in root segment osmotic potential was measured between 8.5mm and 11.5mm from the root tip. The pattern was consistent for the four bulk densities tested. An analysis of variance performed on the data showed both segment and bulk density to be significant at the $P = 0.01$ level. For a bulk density of 1.37gcm^{-3} , osmotic potential increased from -1110kPa to -740kPa, an increase of 35% between the 1-4mm and 10-13mm segments. As total root potential was assumed to be equal to soil matric potential and constant at -100kPa, the corresponding decline in turgor for the 1.37gcm^{-3} bulk density treatment was from 1010kPa for the 1-4mm segment to 640kPa for the 10-13 segment. The results of Section R3.1. showed that for pea roots there was no elongation further than 4mm from the root tip. Threshold wall pressures for pea seedlings in this experiment have been calculated at 497kPa. As there was no elongation despite a turgor of 640kPa, it can be assumed that cell wall elasticity has declined in the older and more differentiated root cell tissue. An increase in osmotic potential further from the root tip was observed for the

FIGURE R4.1.2.

Osmotic potential of pea root segments after growth in soils packed to four bulk densities and wetted to a soil moisture potential of -100kPa



other levels of soil bulk density. The magnitude of the differences in osmotic potential within the bulk density treatments declines with increasing distance from the root tip. For the 1-4mm segment, the range of potentials is from -1110kPa (1.37gcm^{-3}) to -720kPa (1.58gcm^{-3}) or 390kPa. For the 10-13mm segment the corresponding range of osmotic potential is only 160kPa. The close relationship between root elongation and turgor would imply the pattern observed as the turgor is greatest for the treatment with the lowest soil strength where the largest root elongation was recorded. Moving back from the root tip, the difference in osmotic potential between segments would be expected to diminish as elongation declines.

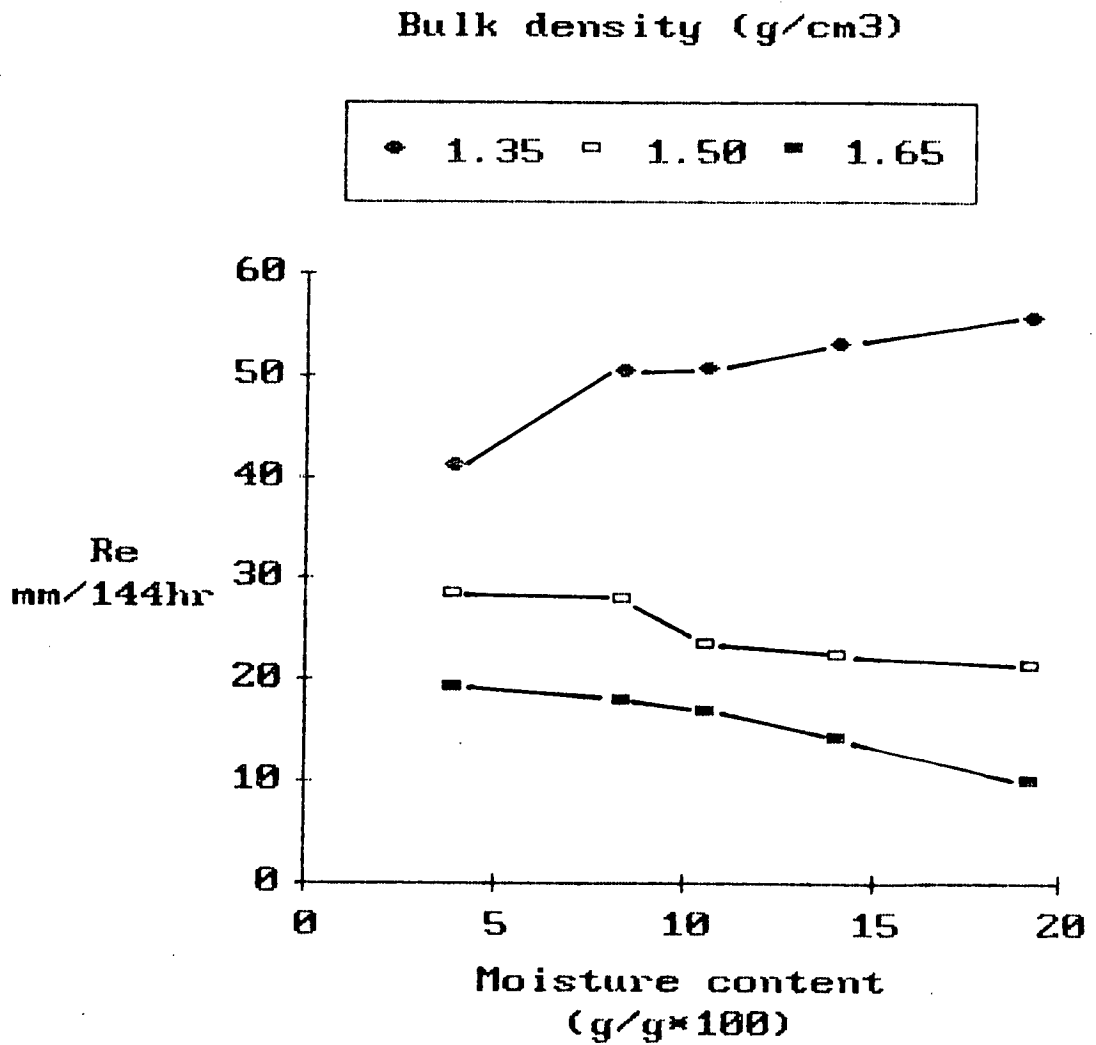
R4.2. Pea roots grown in soil with five soil moisture levels and three bulk densities

The experiment reported in Section Section R4.1. established that the osmotic potential of root segments grown in packed soil could be effectively measured. A subsequent experiment (Section R4.2.) was designed to increase the range of moisture treatments and to compare the ability of the root to adjust osmotically to soil strength and soil moisture.

Root elongations of pea seedlings grown in soils with five levels of soil moisture content and three bulk densities are recorded in Table R4.2.1. and plotted in Figure R4.2.1. Analysis of variance of the root elongation

FIGURE R4.2.1.

Root elongation (Re) for pea seedlings grown in pots packed with soil at three bulk densities and five moisture levels

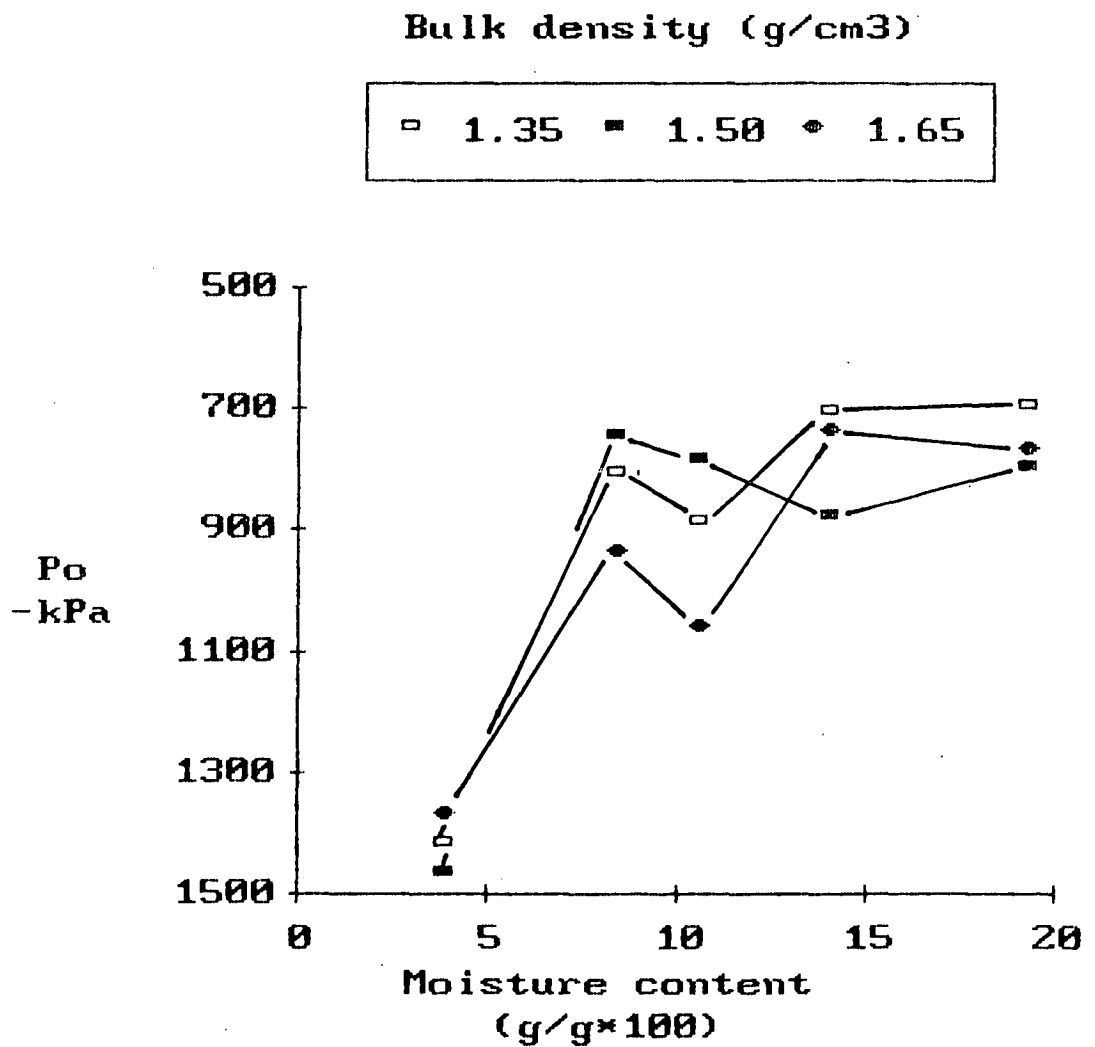


data in Table R4.2.1. showed soil moisture content to be a non-significant treatment but bulk density to be a significant ($P = 0.05$) treatment. There was an 80% decrease in mean root elongation from $50\text{mm } 144\text{hr}^{-1}$ to $10\text{mm } 144\text{hr}^{-1}$ when bulk density increased from 1.35gcm^{-3} to 1.65gcm^{-3} . The highest gravimetric moisture content (19.3%) corresponded to a soil moisture potential of -3kPa while the driest treatment (3.9%) was equivalent to a soil moisture potential of -1500kPa . There was no effect of moisture per se on root elongation for the range of soil moistures tested. A similar pattern of seemingly complete adjustment to soil moisture potential for low to moderate levels of soil strength was observed for radiata pine root elongation (Section R2.5).

Figure R4.2.2. illustrates the decrease in cell osmotic potential with decreasing soil moisture content. For all levels of bulk density, there was little decrease in osmotic potential until soil moisture content fell below 8.4%. The soil moisture potential corresponding to a gravimetric moisture content of 8.4% for Wynyard sandy loam soil was -50kPa , but the measurement of osmotic potential was not sufficiently precise to measure any osmotic adjustment over the range -3kPa (19.3%) to -50kPa . For the 19.3% moisture treatment, the average osmotic potential for all bulk densities was -756kPa , while for the 3.9% soil moisture treatment average osmotic potential was -1420kPa . Osmotic potential decreased by 664kPa while soil moisture potential

FIGURE R4.2.2.

Osmotic potential (P_o) of the 1-4mm
pea root segment after growth in
pots with three levels of bulk
density and five levels of
gravimetric soil moisture content



declined by 1497kPa, giving 44% osmotic adjustment to declining moisture potential.

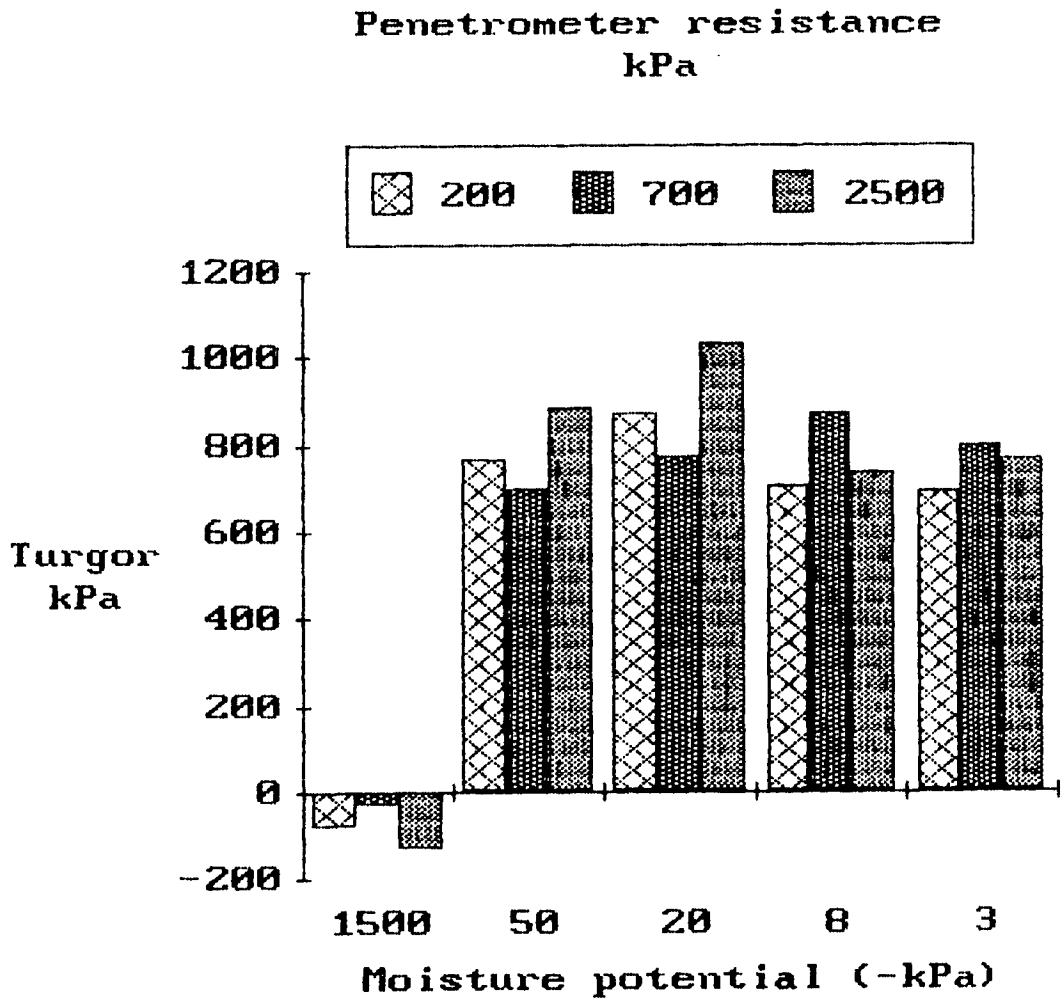
The lack of adjustment to bulk density is evidenced by the root elongation data and can be clearly seen in Figure R4.2.2. There is no meaningful difference in measured osmotic potential between bulk densities for any moisture level. Analysis of variance of the osmotic potential data confirmed that bulk density was a non-significant treatment, while soil moisture content was significant at the $P = 0.01$ level.

Root cell turgor derived from the soil moisture potential and osmotic potential is plotted in Figure R4.2.3. Turgor is independent of bulk density for any moisture potential, and only declines for the -1500kPa moisture potential treatment where turgor is near zero. The comparatively small negative turgors observed for the treatment are within the variability in the measurement of osmotic potential (Table R4.2.2.). They do however indicate a systematic error in the measurement of osmotic potential as root elongation was recorded for the -1500kPa treatment so that a minimum turgor at least equivalent to threshold pressure (c. 400kPa) would be expected. When net wall pressure ($P - P_o - P_s$) is calculated, the turgor for the -1500kPa moisture treatment became more negative.

The relationship between root elongation and net wall pressure for the range of soil moisture potentials and soil

FIGURE R4.2.3.

Root cell turgor of pea root segments (1-4mm from root tip) grown in soil with three levels of penetrometer resistance and five soil moisture potentials



strengths tested is shown in Figure R4.2.4., while in Figure R4.2.5. the data of Greacen and Oh (1972) have been analysed and are plotted for comparison.

A multiple linear regression relating root elongation (Re), soil restraint (Ps), and soil moisture potential (P) can be fitted to the data of Table R4.2.1.:

$$Re = 44.25 - 0.05Ps + 4.62 \times 10^{-4}P, R^2 = 0.66$$

The model predicts that if soil moisture potential is minimal, then root elongation will be zero when soil restraint (Ps) is 900kPa. Equivalent penetrometer resistance is c. 3600kPa, which is comparable with the critical levels reported by Greacen et al. (1968). The ratio of the coefficients of soil restraint and soil moisture potential is c. 10:1 reflecting the sensitivity of the root to increases in soil strength when compared with soil moisture deficits.

A linear model predicting osmotic potential:

$$Po = -779.85 - 0.11Ps + 0.41P, R^2 = 0.89$$

confirms the sensitivity of root elongation to soil strength. The coefficients indicated 11% osmotic adjustment to soil restraint and 41% osmotic adjustment to soil moisture. The data of Greacen and Oh (1972) seen in Figure R4.2.5. are less variable but exhibit the same trend. However there are no negative values for net wall pressure

FIGURE R4.2.4.

Root elongation of pea seedlings
versus cell wall pressure ($P-P_o-P_s$)
measured after growth in
soil with three levels of
penetrometer resistance and five
moisture potentials and where P_s
is estimated to be 25% of
penetrometer resistance

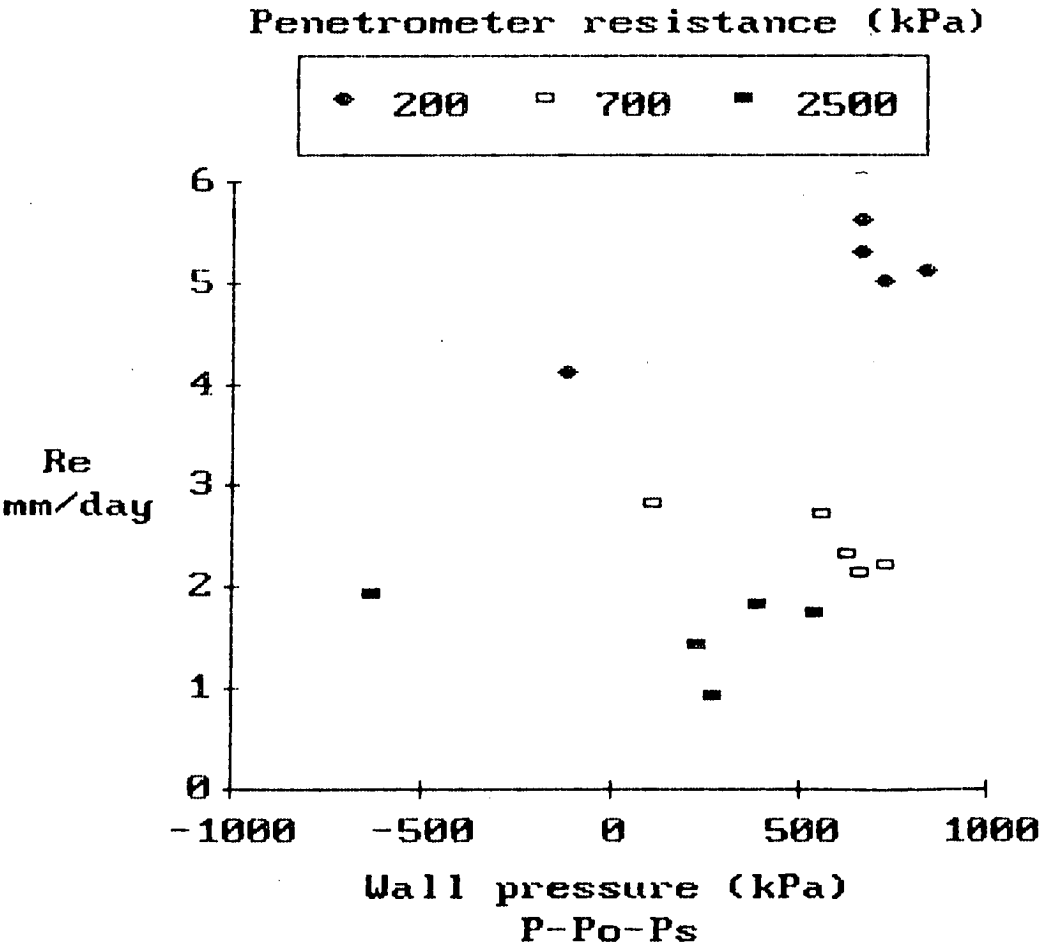
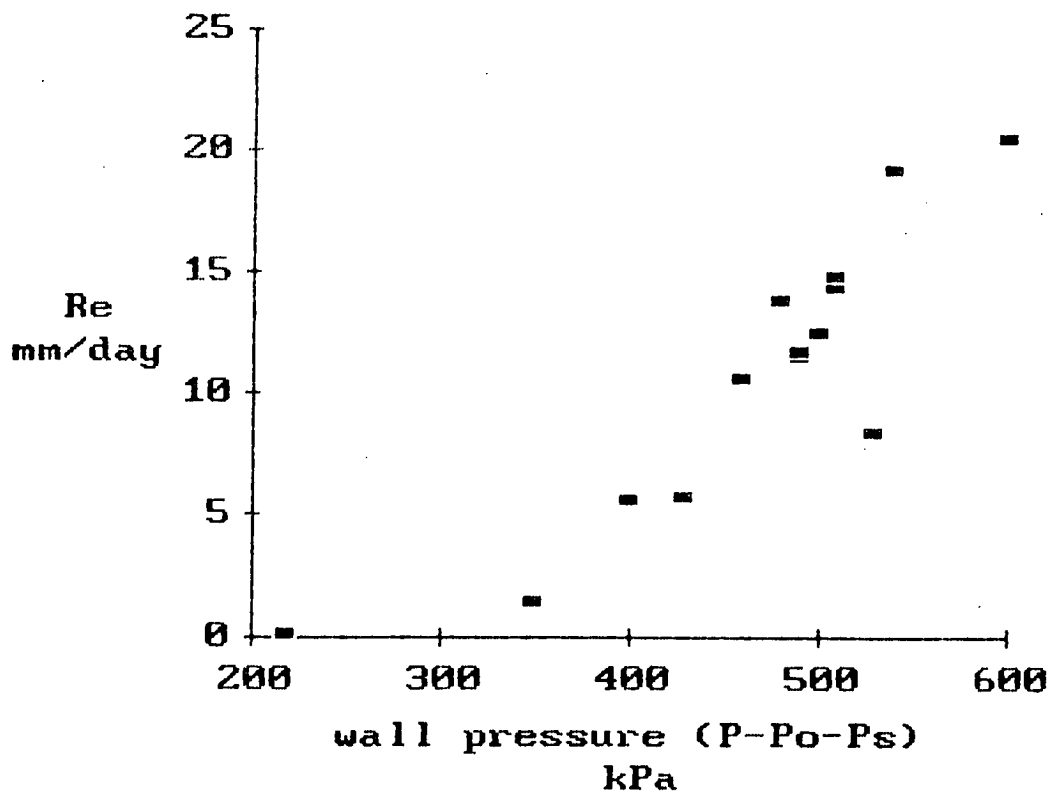


FIGURE R4.2.5

Full data set of Greacen and
Oh (1972) with root
elongation versus wall
pressure



as shown in Figure R4.2.4. The reason for the two negative wall pressures is not clear. The results of other experiments in Section R3 and Section R4 did not indicate any dilution error in the measurement of osmotic potential. If a dilution error of 15% was assumed for the measurement of osmotic potential, the calculated turgors for the -1500kPa treatment (Figure R4.2.3) would not be negative. Net cell pressure for the treatment where penetrometer resistance was 2500kPa and soil moisture potential was -1500kPa, would remain slightly negative but within the accuracy of determination of turgor.

In conclusion the data given in Section R4.1. and Section R4.2. demonstrate that a pressure-balance model of root elongation can provide a logical link to relate the observed empirical root behavior to a physiological mechanism and also provide a satisfactory explanation for the sensitivity of root elongation to increases in soil strength compared to decreases in soil moisture potential.

R5. Root Growth as Observed by Neutron Radiography

R5.1. Effects of radiographs on seedling root elongation

The sensitivity of the radiata pine seedling roots to the neutron radiation flux of the radiography procedure was tested using the technique described in Section M3.2.2. The results are detailed in Table R5.1. and plotted in Figure R5.1.1. A representative radiograph illustrating the pot system used and the pattern of root growth is shown in Figure R5.1.2.

Analysis of variance of the root elongation data showed moisture was a non-significant treatment, but neutrons were a significant ($P = 0.05$) factor in reducing root elongation. Figure R5.1.1. shows that for both levels of soil moisture, root elongation was slightly less for the pots exposed to the neutron flux. Willatt et al. (1978) observed no apparent effect of neutron radiography on the root development of 27 day old maize and corn seedlings. The effect recorded in Table R5.1. may be due to the younger age of the seedlings used or the statistical significance of the treatment may be an artifact of another experimental factor. From Figure R5.1.2. it can be seen that root elongation was quite variable between individual pots, and some seedlings exhibited little elongation. It was difficult to maintain constant temperature conditions for the duration of the experiments, although the average rate of root elongation

FIGURE R5.1.1.

Elongation of pine seedling roots
after exposure to a neutron beam
for 0 or 10 minutes and grown in
soil of 6% or 10% gravimetric
moisture content

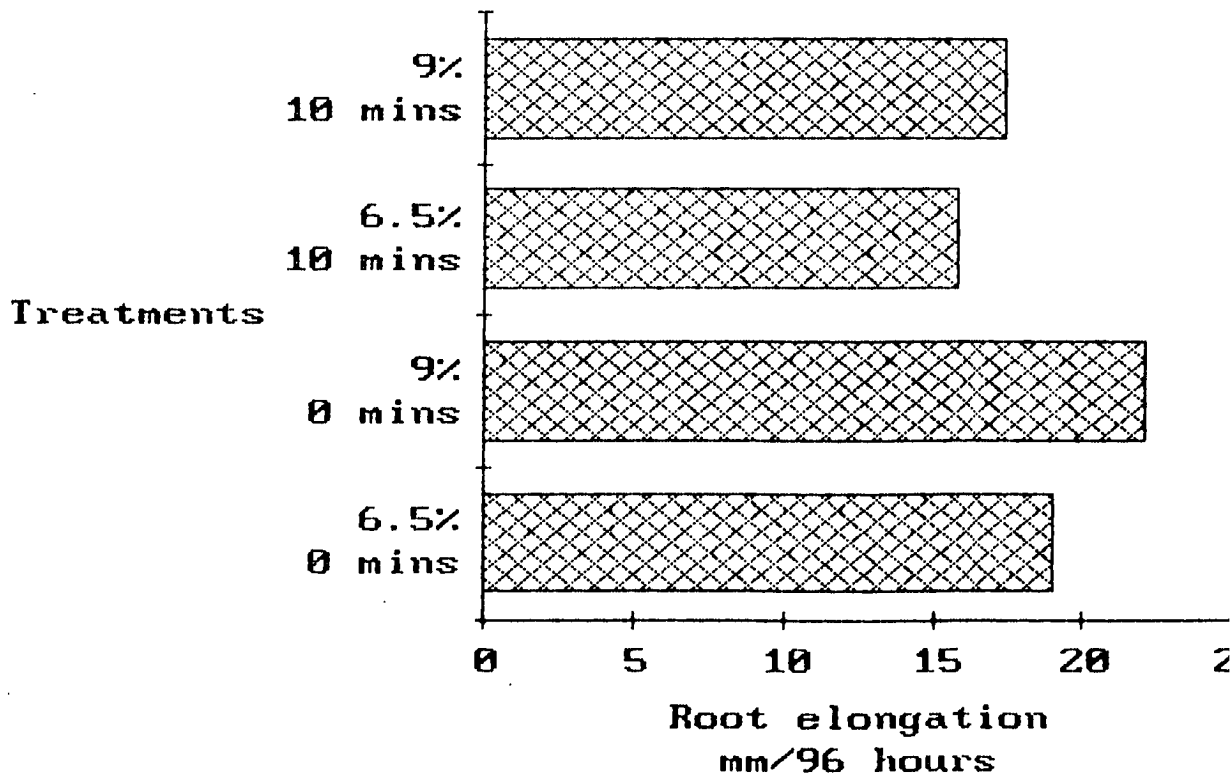
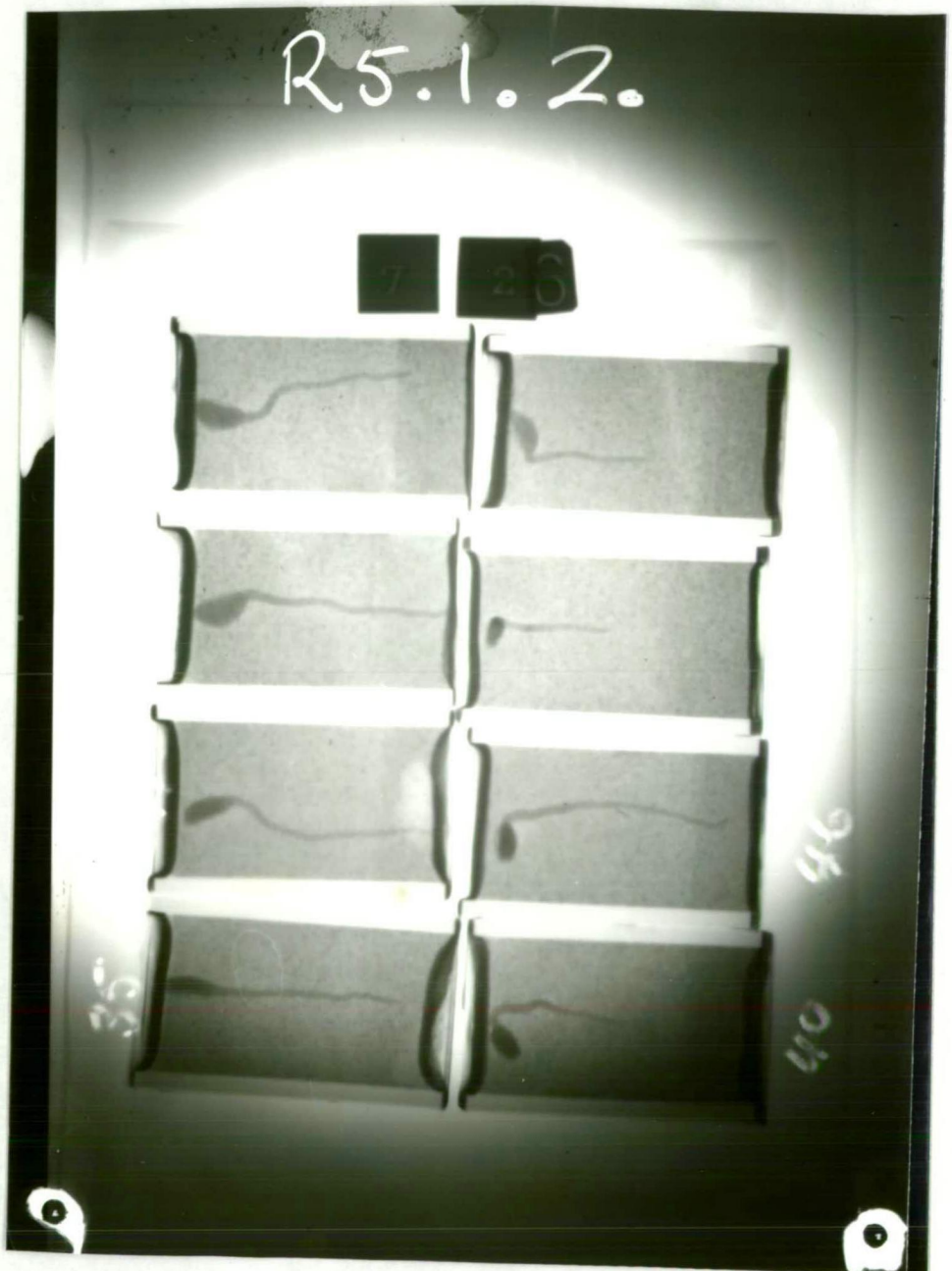


FIGURE R5.1.2.

Neutron radiograph of pine
seedling roots grown in
aluminium pots 25mm x 25mm
x40mm showing variability of
seedling root growth and
arrangement of pots for
radiography



recorded was comparable with that measured in Section R2.3., indicating that root elongation was not constrained by low soil temperatures overall. There may have been differential growth between treatments as pots to be exposed to radiography were stored separately to control pots as it was not practical to transport treatments to Lucas Heights unless radiography was planned.

As there was a possibility that radiography may affect the elongation rate of pine seedlings, in subsequent experiments all pots received the same exposure to the neutron source to eliminate any chance of differential root elongation due to exposure to radiography.

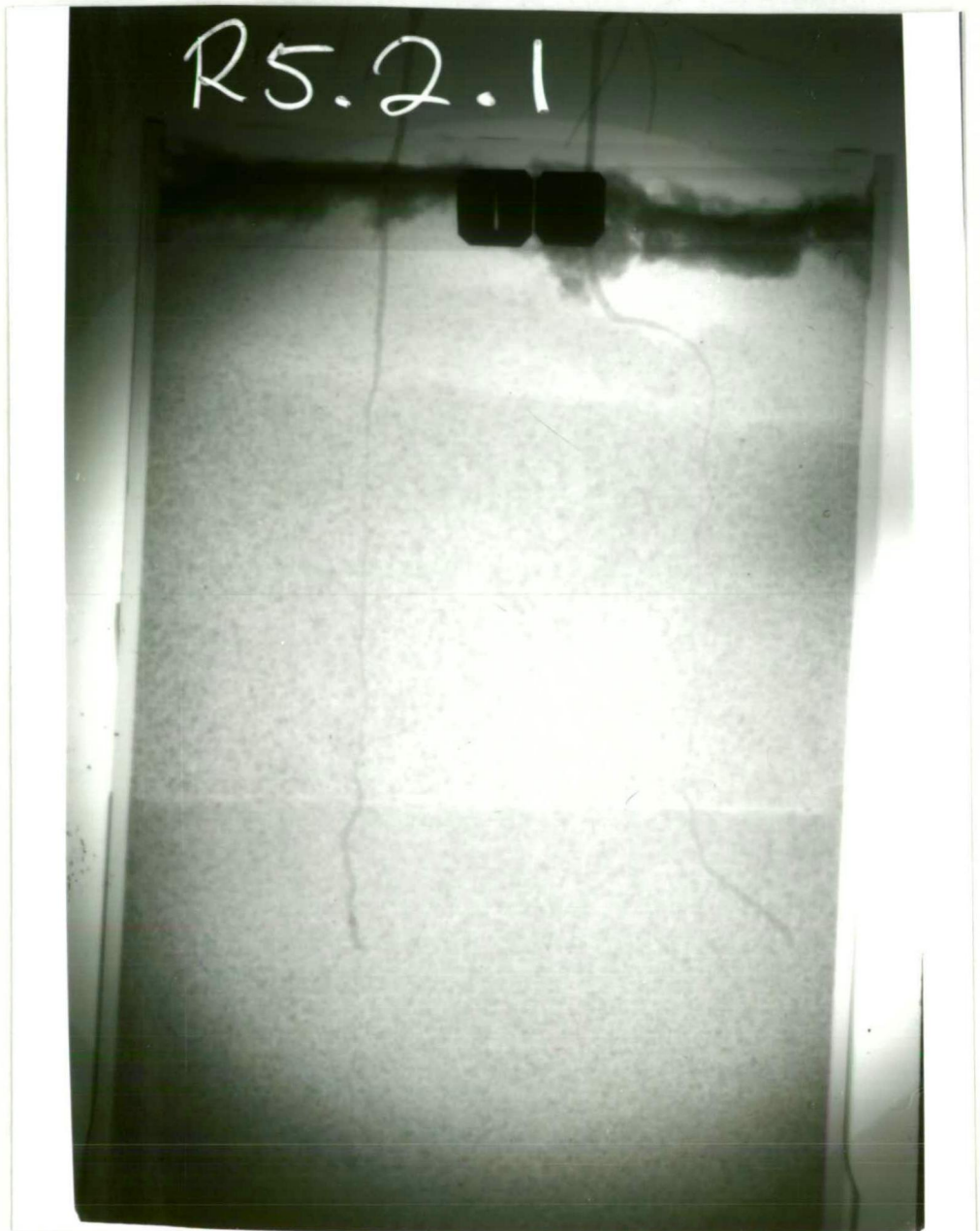
R5.2. Root growth into compacted layers

This experiment was undertaken to monitor root behaviour on meeting a compacted layer of soil. The method was described in Section M3.2.3. and Figure R5.2.1. is a print of a radiograph taken of a pine seedling root. Figure R5.2.2. is a typical print of a radiograph showing pea root development in soil.

In Figure R5.2.1. an increase in diameter of the seedling root can be clearly seen as the root grows into the more compact soil layer which had a bulk density of 1.65gcm^{-3} . Buckling of the root in the upper layer of soil of lower bulk density (1.54gcm^{-3}) is also observed. Examination of radiographs taken before the root began growing into the

FIGURE R5.2.1.

Neutron radiograph of pine seedling roots growing into a layer of greater soil bulk density and showing larger root diameter and buckling of roots in the less dense layer



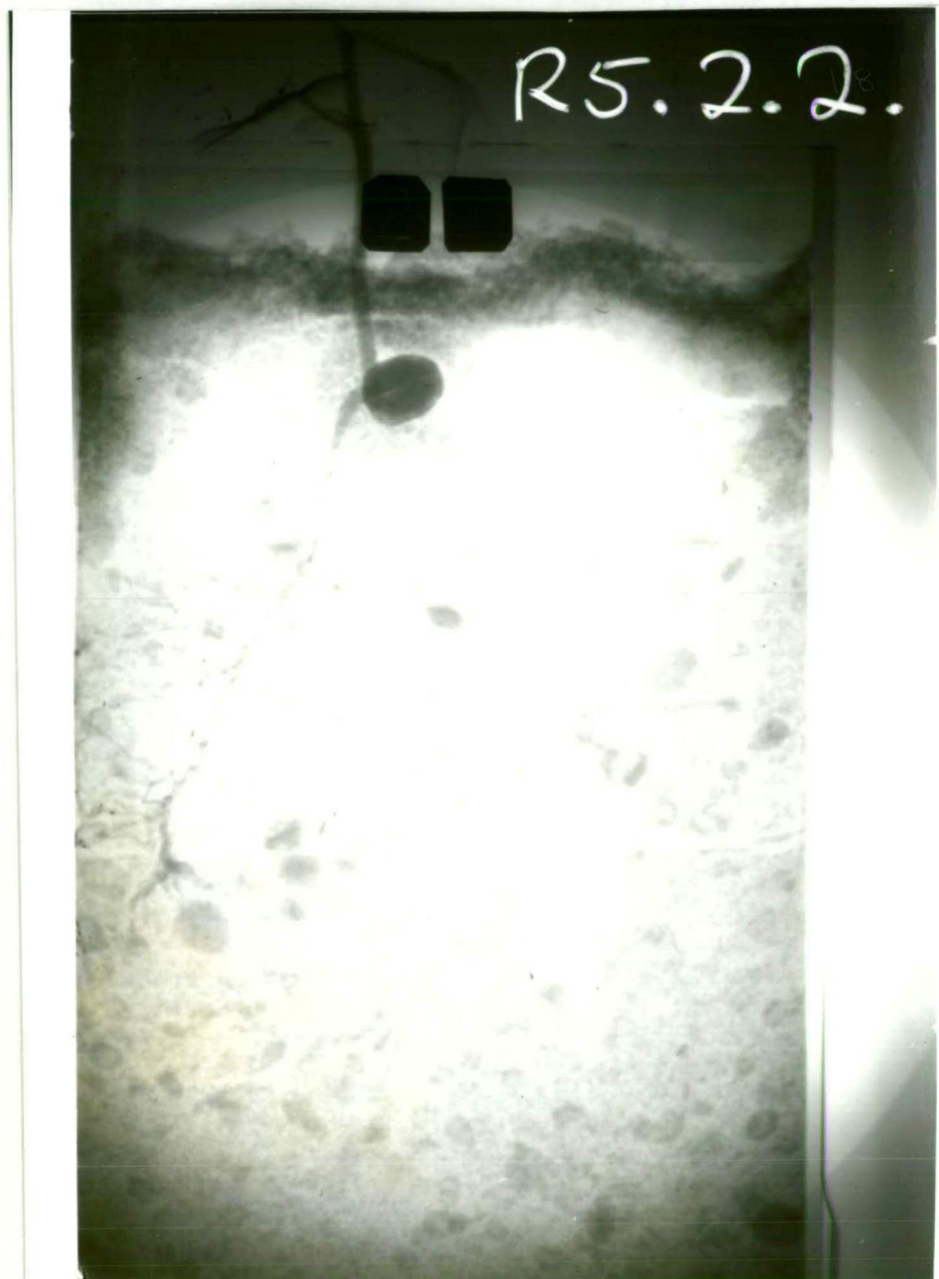
compact layer did not show any root buckling. Eavis (1967) reported that pea seedling roots moved backwards and buckled if reaction was insufficient to support the forward movement of the root tip. Whiteley et al. (1982) observed that the maximum pressure the root can develop may be limited by the degree of lateral constraint, as bending moments of roots are quite small.

The behavior of the pine root is consistent with a pressure-balance model of root elongation. Upon meeting the compact layer the rate of root elongation would decline as the external constraint increased, and the reaction force transmitted back up the root would also increase. As the soil constraining the root laterally was of insufficient strength to transmit the lateral forces without deformation, the root buckles until the forces are in equilibrium.

The presence of root hairs or lateral roots would assist the root in resisting buckling by better transmitting growth pressure to the soil. No buckling was observed for pea seedling roots (Figure R5.2.2.), but a similar increase in diameter is seen. The pea seedling roots show a proliferation of lateral roots in the less dense soil when compared with the more compact soil. Baligar et al. (1981) compared the development of soybean and sorghum roots above and in compact pans. Both species produced lateral roots above the pan at the expense of longitudinal growth into the pan, thereby maintaining total root length. The pea here seedlings exhibited a similar response to the compact soil

FIGURE R5.2.2.

Neutron radiograph of pea seedling roots growing into a layer of greater soil bulk density and showing larger root diameter and decreased branching in the more compact layer. Note also the proliferation of roots in the less dense layer



layer.

R6. Conclusions

The objectives of the study were stated in Section L1:

I. Development of an empirical model relating penetrometer resistance and soil moisture potential to seedling root elongation for radiata pine.

II. Measure the parameters of a pressure-balance model of root growth and test whether the model can logically explain root elongation in terms of soil moisture potential and penetrometer resistance.

III. Use neutron radiography to non-destructively observe root growth and development in soil filled pots.

Radiata pine seedling root elongation was described in terms of soil moisture potential and penetrometer resistance in Section R2.3. The recorded elongation could logically and consistently be related to a concept of total external stress. The effects of soil restraint and soil moisture were additive in their effect on root elongation. The level of penetrometer resistance and moisture potential which restricted root elongation was consistent with the levels reported in the literature for agricultural crops, indicating that the process of root elongation was similar for the forest tree seedlings. Objective I was satisfied.

The results of Section R3 and Section R4 were generally more variable and less definite when compared with the

results of Section R2, but were consistent with a pressure-balance model of root growth. Both pine and pea root elongation declined with decreasing moisture potential (Section R3) although the mechanism was different. The osmotic potential data suggested that the pine seedling root did not exhibit sufficient osmotic adjustment to maintain turgor as solution potential decreased and, as root elongation was closely correlated with turgor, root elongation declined. The osmotic potential data for pea seedlings in contrast showed that osmotic adjustment was complete and turgor was maintained as solution potential declined. There was, however, a poor relationship between turgor and root elongation and elongation decreased with declining solution potential.

The reduction in root elongation in response to moderate moisture potential observed in Section R3 is inconsistent with the results observed in Section R2 and Section R4, where root elongation was not sensitive to moderate moisture potential. Mirreh and Ketcheson (1973) compared root elongation of corn seedlings in PEG solutions and soil filled pots, and reported a greater root elongation rate for similar moisture potential in the PEG solutions and an effect of moisture per se in both media. Root elongation was greater in the PEG-vermiculite growth boxes (Section R3) than in the soil for both species (Section R2 - pines, Section R4 - peas), and there was no effect per se of moisture at moderate potentials in the soil system. The

results indicate a different root response to moisture potential in soil when compared with solution potential in vermiculite and PEG. Hydraulic conductivity (Hullugalle and Willatt, 1983), volumetric moisture content (Greacen and Sands, 1980), and moisture potential (Taylor and Ratliff, 1969b) have all been suggested as accurately reflecting the moisture status of the soil of relevance to the root. Further studies on the nature of the root-soil moisture relation will be needed to determine which indices of soil moisture status are of most relevance to root elongation.

Section R4 brought together an empirical relationship between root elongation, penetrometer resistance and soil moisture, and a mechanistic pressure-balance model of root elongation. The results quantified the greater sensitivity of root growth to soil restraint when compared to soil moisture potential. Regressions fitted to the data to predict root elongation and osmotic potential showed good correlation with measured values. The results confirmed that root elongation could be logically explained in soil using a pressure-balance model of growth. Objective II was satisfied.

The experiments where neutron radiography was used to observe root growth and development (Section R5) demonstrated the efficacy of the technique and highlighted suitable applications. The technique lends itself to more illustrative than quantitative studies due to the difficulty of accessing the neutron source. Topics where neutron

radiography would be a valuable technique include the study of root behavior near soil aggregates and soil additions such as fertilizer or points of drainage. The technique is superior to other methods of in situ study of roots, such as glass interface, when small pots are used. Objective III was satisfied.

In conclusion, soil strength can be considered a general influence on root growth except where extremes of soil moisture exist. Any increase in soil strength may reduce the ability of the root to tolerate moisture stress. If air, water and nutrients are plentiful, then less root length may be adequate and there may be no reduction in shoot growth following an increase in soil strength. Conversely if water, air or nutrients are limiting, then top growth may be reduced due to inadequate root length for sufficient uptake of water or nutrients in the soil. Seedling roots of Pinus radiata are more sensitive to increases in soil strength than to decreases in soil moisture potential and, are more sensitive to soil strength when subject to moisture stress. The general influence of soil strength on root growth and the slow recovery of some soils after compaction suggests a better understanding of the likely effects of forest operations on soil strength is needed if productivity losses following operations are to be minimized.

R7. Tables

TABLE R1.3.

Moisture characteristic for unconsolidated Wynyard sandy
loam soil

water potential -kPa	mean gravimetric moisture $\text{gg}^{-1} \times 100$	standard error of the mean value
1	22.00	1.61
10	12.74	0.95
100	6.41	0.18
200	5.52	0.04
400	4.71	0.08
800	4.59	0.05
1200	4.06	0.05
n=3		

TABLE R1.4.

Volumetric moisture content, water potential, and hydraulic conductivity of unconsolidated Wynyard sandy loam soil.

volumetric moisture content $\text{cm}^3\text{cm}^{-3}$	moisture potential -kPa	hydraulic conductivity cm d^{-1}
0.4	0.10	8510
0.39	1.09	23.1
0.37	3.31	9.09
0.35	7.08	4.51
0.33	10.96	2.33
0.31	15.48	1.20
0.29	21.37	0.62
0.27	30.19	0.31
0.25	39.81	0.15
0.23	54.95	6.52×10^{-2}
0.21	75.85	2.69×10^{-2}
0.19	109.64	1.03×10^{-2}
0.17	169.82	3.60×10^{-3}
0.15	263.02	1.11×10^{-3}
0.13	436.51	2.86×10^{-4}
0.11	758.57	5.30×10^{-5}
0.09	1479.10	5.91×10^{-6}
0.07	5011.87	8.46×10^{-7}

TABLE R2.1.

Gravimetric moisture content ($\text{gg}^{-1} \times 100$) of Wynyard sandy loam for four levels of bulk density and five soil moisture potentials. The standard error of the treatment mean is recorded beneath the mean.

soil moisture potential (kPa)	bulk density (gcm^{-3})			
	1.54	1.60	1.63	1.65
-100	6.62 0.33	6.28 0.03	6.28 0.03	6.34 0.01
-200	5.57 0.09	5.39 0.05	5.49 0.06	5.51 0.04
-400	4.73 0.07	4.72 0.14	4.62 0.07	4.77 0.08
-800	4.63 0.08	4.37 0.10	4.53 0.05	4.61 0.11
-1200	4.05 0.07	3.86 0.04	4.02 0.10	4.11 0.08
n=3				

Analysis of Variance - gravimetric moisture

source	df	ms	observed F	required 5%	F 1%	
moisture pot.	4	3.42	569**	3.26	5.41	
bulk density	3	0.04	0.7 ^{ns}	3.49	5.95	
error	12	0.06				
Duncans Multiple Range test -						
		apart	2	3	4	5
		LSD(D)	0.48	0.50	0.52	0.52

TABLE R2.2.

Penetrometer resistance (kPa) of Wynyard sandy loam for four levels of bulk density and three gravimetric soil moisture contents. The standard error of the treatment mean is shown beneath the mean.

soil moisture ($g g^{-1} \times 100$)	bulk density ($g cm^{-3}$)			
	1.54	1.60	1.63	1.65
4.3	1080 64	2240 35	3320 32	3630 215
5.1	1330 66	1960 94	3270 111	4230 143
6.0	1310 35	2300 182	3170 82	4510 202
n=3				

Analysis of Variance - penetrometer resistance

source	df	ms	observed F	required 5%	F 1%
moisture	2	65033	1.0ns	5.14	10.92
bulk density	3	4748031	72.9**	4.76	9.78
error	6	65055			
Duncans Multiple Range test - apart					
			LSD(D)	2 509	3 524
				4 534	

Linear Regression

$$P_p = -38115 + 25427 p_b, R^2 = 0.91$$

TABLE R2.3.1.

Radiata pine seedling root elongation (mm d^{-1} at 25°C) for six soil moisture levels and four bulk densities. The standard error of the treatment mean is shown beneath the mean.

soil moisture ($\text{g g}^{-1} \times 100$)	bulk density (g cm^{-3})			
	1.54	1.60	1.63	1.65
3.6	2.98 0.22	1.75 0.19	1.56 0.09	1.39 0.12
4.3	3.77 0.26	2.14 0.18	1.44 0.15	1.27 0.07
4.8	4.68 0.31	2.59 0.29	1.92 0.24	1.32 0.11
5.5	4.99 0.33	3.34 0.27	1.51 0.15	1.22 0.15
5.9	4.78 0.20	3.55 0.29	2.09 0.17	1.27 0.12
6.5	4.85 0.19	3.31 0.19	1.49 0.09	1.06 0.22

n=10

Analysis of Variance - root elongation

source	df	ms	observed F	required 5%	F 1%
moisture	5	0.60	2.75 ^{ns}	2.90	4.56
bulk density	3	11.42	52.24**	3.29	5.42
error	15	0.22			
Duncans Multiple Range test - apart			2	3	4
LSD(D)			0.58	0.61	0.63

TABLE R2.3.2.

Mean volumetric moisture contents ($\text{cm}^3\text{cm}^{-3}\times 100$)
for the treatments in Table R2.3.1.

gravimetric moisture content ($\text{g g}^{-1}\times 100$)	bulk density (g cm^{-3})			
	1.54	1.60	1.63	1.65
3.62	5.58	5.76	5.85	5.95
4.36	6.73	7.04	7.22	7.28
4.84	7.33	7.83	7.91	8.10
5.51	8.56	8.79	9.11	9.10
5.92	9.13	9.42	9.58	9.83
6.45	9.74	10.17	10.37	10.46

TABLE R2.3.3.

Mean air porosity ($\text{cm}^3\text{cm}^{-3}\times 100$) for the treatments
in Table R2.3.1.

gravimetric moisture content ($\text{g g}^{-1} \times 100$)	bulk density (g cm^{-3})			
	1.54	1.60	1.63	1.65
3.62	35.2	32.7	31.5	30.6
4.36	34.1	31.5	30.1	29.2
4.84	33.5	30.7	29.4	28.4
5.51	32.2	29.7	28.2	27.4
5.92	31.7	29.1	27.7	26.7
6.45	31.1	28.3	26.9	26.0

TABLE R2.4.

Radiata pine seedling root diameter (mm) for different soil moisture levels and bulk densities. The standard error of the treatment mean is shown beneath the mean.

soil moisture ($\text{g g}^{-1} \times 100$)	bulk density (g cm^{-3})			
	1.54	1.60	1.63	1.65
3.6	1.04 0.05	1.23 0.02	1.32 0.09	1.36 0.16
4.3	0.98 0.14	1.18 0.18	1.29 0.13	1.27 0.11
4.8	0.89 0.09	1.26 0.13	1.23 0.16	1.52 0.24
5.5	0.97 0.13	1.26 0.10	1.23 0.16	1.52 0.24
5.9	1.00 0.19	1.28 0.08	1.29 0.18	1.41 0.20
6.5	1.08 0.08	1.19 0.08	1.29 0.14	1.43 0.17

n=10

Analysis of Variance - root diameter

source	df	ms	observed F	required 5%	F 1%
moisture	5	0.002	0.5ns	2.90	4.56
bulk density	3	0.187	46.8**	3.29	5.42
error	15	0.004			

Duncans Multiple Range test - apart 2 3 4
LSD(D) 0.08 0.08 0.09

TABLE R2.5.

Radiata pine seedling root elongation ($\text{mm } 7\text{d}^{-1}$ at 25°C) at different soil moisture potentials and penetrometer resistances.

soil moisture potential	penetrometer resistance (kPa)			
	1043	2568	3331	3840
-60	34.0	23.2	10.4	7.4
-164	33.5	24.9	14.6	8.9
-338	35.0	23.4	10.6	8.5
-642	32.8	18.1	13.4	9.2
-860	26.4	15.0	10.1	8.9
-1164	20.9	12.3	10.9	9.7

TABLE R3.1.1.

Percentage of total elongation occurring as a function of distance from root tip for pine seedlings.

distance from root tip (mm)	percentage of elongation		
	mean	sample number	standard error
0 - 2	76.8	10	9.8
2 - 4	21.9	10	8.9
4 - 6	1.3	10	1.3
6 - 8	0	10	

TABLE R3.1.2.

Percentage of total elongation occurring as a function of distance from root tip for pea seedlings.

distance from root tip (mm)	percentage of elongation		
	mean	sample number	standard error
0 - 2	90.5	11	0.6
2 - 4	9.5	11	0.6
4 - 6	0	10	
6 - 8	0	10	

TABLE R3.2.1.

Elongation (mm d^{-1}) and turgor of pine seedling roots growing in vermiculite and PEG solutions of three moisture potentials.

PEG solution potential (kPa)	root elongation (mm d^{-1})		
	mean	standard error of mean	derived turgor (kPa)
-110	7.23	0.14	2090
-350	4.89	0.16	1630
-744	4.21	0.18	1658

n=5

TABLE R3.2.2.

Osmotic potentials (kPa) for pine root segments grown in vermiculite and PEG solutions of three moisture potentials. The standard error of the treatment mean is shown beneath the mean value.

PEG solution potential (kPa)	segment distance from root tip (mm)		
	1-4	4-7	7-10
-110	-2260	-2030 370	-1300 20
-350	-1920 120	-1690	-1520 20
-744	-2040 330	-2020 300	-1790 220
n=5			

Analysis of Variance - osmotic potential

source	df	ms	observed F	required 5%	F 1%
potential	2	44311	1.07 ^{ns}	6.94	18.00
segment	2	227744	5.48 ^{ns}	6.94	18.00
error	4	41544			

TABLE R3.3.1.

Elongation (mm d^{-1}) and turgor of pea seedling roots grown in vermiculite and PEG solutions of four moisture potentials.

PEG solution potential (kPa)	root elongation (mm d^{-1})		
	mean	standard error of mean	derived turgor (kPa)
-116	14.99	0.44	1028
-352	11.82	0.30	1086
-420	10.56	0.41	955
-744	6.42	0.42	1127
n=10			

TABLE R3.3.2.

Osmotic potential (kPa) of pea root segments grown in vermiculite and PEG solutions of four moisture potentials. The standard error of the treatment mean is shown beneath the mean.

PEG solution potential (kPa)	segment distance from root tip (mm)			
	1-4	4-7	7-10	10-13
-116	-1144 84	-1067 65	-1090 65	-1068 89
-352	-1438 31	-1518 52	-1455 34	-1614 148
-420	-1375 119	-1618 93	-1472 35	-1511 79
-744	-1871 368	-1709 236	-2051 92	-2066 88

n=5

Analysis of Variance - osmotic potential

source	df	ms	observed F	required 5%	F 1%
potential	3	461670	37.23**	3.26	5.41
segment	3	8992	0.73 ^{ns}	3.49	5.95
error	12	12400			

Duncans Multiple Range test - apart 2 3 4 5 6
LSD(D) 114 120 123 124 125

TABLE R4.1.1.

Root elongation of peas grown in soils of four bulk densities of known penetrometer resistance and with a moisture potential of -100kPa. The standard error of the treatment mean is shown beneath the mean value. Root turgor for the 1-4mm segment has been derived from soil moisture potential and root osmotic potential.

bulk density (gcm ⁻³)	root elongation (mm d ⁻¹)	penetrometer resistance (kPa)	root cell turgor (kPa)
1.37	8.57 0.55	249 10	1010
1.52	7.38 0.53	629 41	730
1.55	4.46 0.46	1141 79	700
1.58	4.63 0.46	1603 398	620
	n=18	n=3	n=3

TABLE R4.1.2.

Osmotic potential (kPa) of pea root segments after growth in soils packed to four bulk densities at -100kPa moisture potential. The standard error of the treatment mean is shown beneath the mean value.

bulk density (gcm ⁻³)	root segment (mm from root tip)			
	1-4	4-7	7-10	10-13
1.37	-1110 79	-1000 67	-720 38	-740 85
1.52	-830 52	-730 17	-670 17	-630 44
1.55	-800 27	-687 17	-620 23	-550 11
1.58	-720 57	-620 25	-500 44	-580 17
n=3				

Analysis of Variance - osmotic potential

source	df	ms	observed F	required 5%	F 1%
segment	3	53525	14.6**	3.86	6.99
bulk density	3	61482	16.7**	3.86	6.99
error	9	3672			
Duncans Multiple Range test - apart					
		LSD(D)	2	3	4
			112	116	120

TABLE R4.2.1.

Root elongation (mm) after 144 hours for pea seedlings grown in pots packed with soil to three bulk densities, and five gravimetric moisture levels. The standard error of the treatment mean is shown beneath the mean value.

moisture content ($g g^{-1} \times 100$)	bulk density ($g cm^{-3}$)		
	1.35	1.50	1.65
3.9	41.11 4.67	28.17 3.92	18.86 5.77
8.4	50.22 5.42	27.68 6.12	17.56 8.81
10.6	50.63 4.99	23.29 7.71	16.61 6.94
14.1	53.02 10.50	22.28 4.91	13.89 4.60
19.3	55.58 15.80	21.18 7.96	9.63 5.07
n=3			

Analysis of Variance - root elongation

source	df	ms	observed F	required 5%	F 1%
moisture	4	1.16	0.05ns	3.84	7.01
bulk density	2	1636	67.1**	4.46	8.65
error	8	24.4			
Duncans Multiple Range test - apart 2 3					
LSD(D) 9.3 9.7					

TABLE R4.2.2.

Osmotic potential (kPa) of pea root segments (1-4mm) after 144 hours of growth in pots packed with soil at three bulk densities and at five soil moisture levels. The standard error of the treatment mean is shown beneath the mean value.

moisture content (gg-1x100)	bulk density (gcm ⁻³)		
	1.35	1.50	1.65
3.9	-1420	-1470 276	-1370 203
8.4	-810 336	-750 128	-940 171
10.6	-890	-790 37	-1060 372
14.1	-710	-880 185	-740 181
19.3	-700	-800 120	-770 317
n=3			

Analysis of Variance - osmotic potential

source	df	ms	observed F	required 5%	F 1%
moisture	4	227083	25.7**	3.84	7.01
bulk density	2	6140	0.7ns	4.46	8.65
error	8	9573			
Duncans Multiple Range test					
	apart	2	3	4	5
	LSD(D)	184	191	195	198

TABLE R4.2.3.

Turgor (kPa) of 1-4mm pea root segments calculated from measurement of cell osmotic potential and an estimate of total root potential for three levels of soil strength and five levels of soil moisture potential.

moisture potential (kPa)	penetrometer resistance (kPa)		
	200	700	2500
-1500	-80	-30	-130
-50	760	700	890
-20	870	770	1040
-8	702	872	732
-3	697	797	767

TABLE R5.1.

Elongation of radiata pine roots at two moisture levels and after nil exposure or exposure for 10 minutes to the neutron beam with a growth period 96 hours.

moisture content (g/g x 100)	neutron exposure time (mins)	mean root elongation (mm.96hr ⁻¹)
6.5	0	19.14
6.5	10	15.86
9.0	0	22.14
9.0	10	17.57
n=7		

Analysis of Variance - neutron radiography

source	df	ms	observed F	required 5%	F 1%
moisture	1	38.9	2.20 ^{ns}	4.26	7.82
neutrons	1	108.0	6.03*	4.26	7.82
moist * neutr	1	2.9	0.16 ^{ns}	4.26	7.82
error	24	0.4			
Duncans Multiple Range test - apart					
(P = 0.05)			LSD(D)	2	3
				0.70	0.73
					0.76

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