

# Early *Pinus caribaea* var. *hondurensis* root development

## 2. Influence of soil strength

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**Summary.** The influence of penetration resistance (PR), an easily measured indicator of soil strength, on the growth of *Pinus caribaea* var. *hondurensis* radicles and seedlings was investigated. Negative exponential relationships between PR and both radicle and primary root elongation were observed. All root elongation ceased at PR levels of 3.25 MPa. Tip diameters of radicles and primary roots were positively correlated with PR values up to 2.4 MPa, whilst numbers of primary roots, total root lengths and lengths of longest roots were all negatively correlated with PR.

Hypocotyl elongation was also reduced by increasing

PR, although the reductions occurred at higher PRs than those which inhibited root development. In contrast, primary shoot development was unaffected by PR levels which were sufficient to stop root elongation, but was reduced in soil with a PR of 4.8 MPa.

There were significant family x soil type and family x PR interactions for radicle, hypocotyl, primary root and primary shoot development. If these interactions are correlated with performance in the field, then they may serve as useful indicators of family suitability to both soil type and high strength soils.

**Additional keywords:** radicle elongation, root growth, penetration resistance.

### Introduction

Constantini *et al.* (1996) presented a qualitative model, adapted from Letey (1985), which depicted the effect of soil strength, matric suction and aeration on early *Pinus caribaea* Morelet. var. *hondurensis* Barr. *et* Golf. root growth. Conclusions drawn: (i) highlighted the need to separate matric suction and aeration effects from soil strength effects when investigating root growth in soil media with different strengths; and (ii) quantified the effects of matric suction and aeration on early root growth. The experiments reported in this paper were designed to investigate the impact of soil strength on radicle elongation and seedling growth in *P. caribaea* var. *hondurensis*.

Roots elongate due to division and elongation of cells in the 'zone of elongation' of growing tips (Barley and Greacen 1967; Dexter 1987). An individual elongating root cell will be at equilibrium when the water potentials both inside and outside are equal:

$$\psi_s + \pi_s = \psi_c + \pi_c \quad (1)$$

where,  $\psi_s$  is soil matric potential,  $\pi_s$  is soil osmotic potential,  $\psi_c$  is cell turgor pressure and  $\pi_c$  is cell osmotic pressure. For the cell to elongate,  $\psi_c$  must exceed the resistance of the cell wall ( $W$ ) and the mechanical

resistance (strength) of the soil ( $\sigma$ ) such that, at equilibrium:

$$\psi_c = W + \sigma \quad (2)$$

Rewriting equations 1 and 2:

$$\psi_s + \pi_s = W + \sigma + \pi_c \quad (3)$$

Greacen and Oh (1972) observed that the cell can adjust  $\pi_c$ , and hence  $\psi_c$ , through osmoregulation (equation 1). On this basis, Greacen (1986) postulated that the relationship between elongation rate and  $\sigma$  should be linear. However, as mechanical resistance also affects cell shape and cell production, Greacen (1986) concluded that the relationship between elongation rate and mechanical resistance would actually be curvilinear. Veen and Boone (1990) and Tardieu (1994) suggest that the Greacen and Oh (1972) model may not completely describe the response of root elongation rate to soil strength. They noted that cell wall characteristics influencing the equation 3 equilibrium may be sensitive to small changes in pressure, impedance or osmotic forces. Indeed, Hsiao and Bradford (1983) described cell elongation in the following terms: (i) the cell wall relaxes, thereby decreasing  $W$ , and resulting in the left hand side of equation 3 exceeding the right hand side;

(ii) water moves into the cell as a result of the non-equilibrium, providing the force for elongation, and diluting the cell solutes, reducing  $\pi_c$ ; and (iii) translocation of solutes into the cells re-establishes the equilibrium.

In order to elongate, roots must either extend through pores larger than themselves, or physically displace soil (Cannell 1977). It is clear from equation 3 that an increase in soil mechanical resistance will make it harder for roots to displace soil, and hence, to elongate (Barley *et al.* 1965; Taylor *et al.* 1966).

Barley and Greacen (1967) demonstrated that, even though penetration of soils by roots and penetrometer cones differed markedly, mechanical root impedance was typically well correlated with penetration resistance (PR) (see also Bengough 1991). As a result, relationships between PR, an easily measured indicator of soil strength, and the early growth of *P. caribaea* var. *hondurensis* radicles and roots were investigated.

## Materials and methods

### Experiment 1. Pregerminated seeds in repacked soils

Soil was collected from 5–15 cm depth in the clay loam A1 horizon of a red dermosol and the sandy loam A1 horizon of a brown sodosol, and treated using the techniques described for experiment 2 in Costantini *et al.* (1996). Moisture contents achieved were 11.9, 15.5, 18.5 and 23.5% for the red dermosol, and 6.0, 7.9, 9.6 and 11.7% for the brown sodosol. Equivalent matric suctions calculated from moisture characteristic curves were 1.2, 0.3, 0.075 and 0.03 MPa for the red dermosol, and 0.1, 0.075, 0.05 and 0.025 for the brown sodosol, respectively.

Soils were packed to achieve a range of PR values between 0.01 and 4.0 MPa. The technique involved placing prepared soil into three 6.0 cm long by 7.25 cm diameter brass cylinders, which were then enclosed inside a brass sleeve, and placed inside a uniaxial compression chamber capable of applying compaction equally at both ends. At moisture contents >23 and 9.6% for the red dermosol and brown sodosol respectively, it was not possible to achieve PR values greater than 1 MPa. Four replicates were prepared for each soil type  $\times$  each soil moisture content  $\times$  loading (bulk density). Cylinders of repacked soil were sealed and stored for 24 h. One replicate was then selected for PR assessment using a Geotester penetrometer with a 6.5 mm diameter blunt tip (3 evenly spaced measures were made at the top and bottom of the selected soil cylinder).

A 0.5 cm long by 7.25 cm diameter cylinder was taped to the top of each remaining soil cylinder. One pregerminated seed of each of the 6 *P. caribaea* var. *hondurensis* families studied in Costantini *et al.* (1996) was randomly selected and transferred to each soil cylinder. Each seed was allocated to one-sixth of the soil surface; placed into a 3–4 mm diameter by 2 mm deep

spatula hole, located 1 cm in from the cylinder edge; and covered with about 4 mm of loose soil. Cylinders were then set on a glass tray, sealed inside a 500 mL plastic beaker, and transferred to a growth cabinet (12 h day/night at 25/20°C). Radicle lengths were measured at the beginning of the study and at harvest on day 4. Hypocotyl growth, which was zero at the beginning of the study, was also assessed at harvest.

### Experiment 2. Pregerminated seeds in field soils

Experiment 2 differed from experiment 1 in that field soils instead of repacked soils were used. Soils were collected from the 2 soil types using the sample cylinders as core samplers. The cutting edges of the cylinders were sharpened as described by McIntyre and Loveday (1974), in order to minimise compaction of the core. Samples were collected by carefully removing the surface 1.5 cm and driving the sampler vertically into the soil profile. Eight samples, across a range of field bulk densities, were collected from both soil types.

Samples were transferred to a moisture plate with water at the surface, and allowed to wet for 2 days. They were then removed and placed on a free-draining vermiculite bed for 2 days before experimentation. Growth trials used the same families and techniques as described in experiment 1. At the time of harvest, PR was assessed for each sample using the Geotester penetrometer.

### Experiment 3. Cuttings in repacked soils

The soil types tested and soil collection procedures used in this experiment were identical to those described for experiment 1. Soils were air-dried and compacted into cylindrical pots 15 cm in diameter by 33 cm deep. Pots were constructed from 1 mm gauge galvanised iron, spot welded on the sides and base to permit drainage, and lined with a perforated polyethylene bag. Pots were filled to a depth of 30 cm in 1 cm intervals. The weight of soil required to fill a single pot (at a specific bulk density) was divided into 30 equal portions, and individually packed using a piston plate mounted on a 60 t industrial press. Soils were compacted to bulk densities of 1.00, 1.40, 1.60 and 1.70 g/cm<sup>3</sup> for the red dermosol, and 1.15, 1.25, 1.35, 1.45, 1.55, 1.65, 1.75 and 1.85 g/cm<sup>3</sup> for the brown sodosol. There were 4 replicates of each bulk density and soil type. Once compacted, the red dermosol and brown sodosol soils were wet up to 17 and 9% respectively by adding a solution of distilled water and nitrogen, phosphorus and potassium fertiliser.

The soils were covered and left to equilibrate for 2 days. Penetration resistance was measured at 6 sites over the surface of each pot using the Geotester penetrometer. A 4 cm external diameter by 15 cm deep core was removed from the centre of each pot using a

1 mm thick copper corer. The cutting edge of the corer had been sharpened on the outside to prevent the cut walls from being compacted. After removal of the core, the hole wall was gently rubbed with a fine wire brush to roughen the surface and remove any glazing. Two cores from each soil type were retained for analysis of soil moisture distribution. The cores were divided into 3 equal lengths and soil moisture was measured gravimetrically for each.

Cuttings of 2 *P. caribaea* var. *hondurensis* families (mean height  $\pm$  s.d.:  $27.6 \pm 2.6$  and  $31.6 \pm 4.6$  cm for families 1 and 2 respectively; mean basal diameter  $\pm$  s.d.:

$5.8 \pm 0.94$  and  $6.0 \pm 1.06$  mm for families 1 and 2 respectively), raised according to Haines and Walker (1993), were then transplanted into the pots to give 2 replicates of each family  $\times$  soil type  $\times$  bulk density. Both families were genetically superior stock produced by the Queensland Department of Primary Industries Forestry Tree Propagation Research Program, although the second had been deleted from operational propagation because of its unsatisfactory rooting in the nursery. The cuttings were removed from their containers, which were the same diameter as the holes prepared in each pot, and planted into pots by firmly pushing them into the

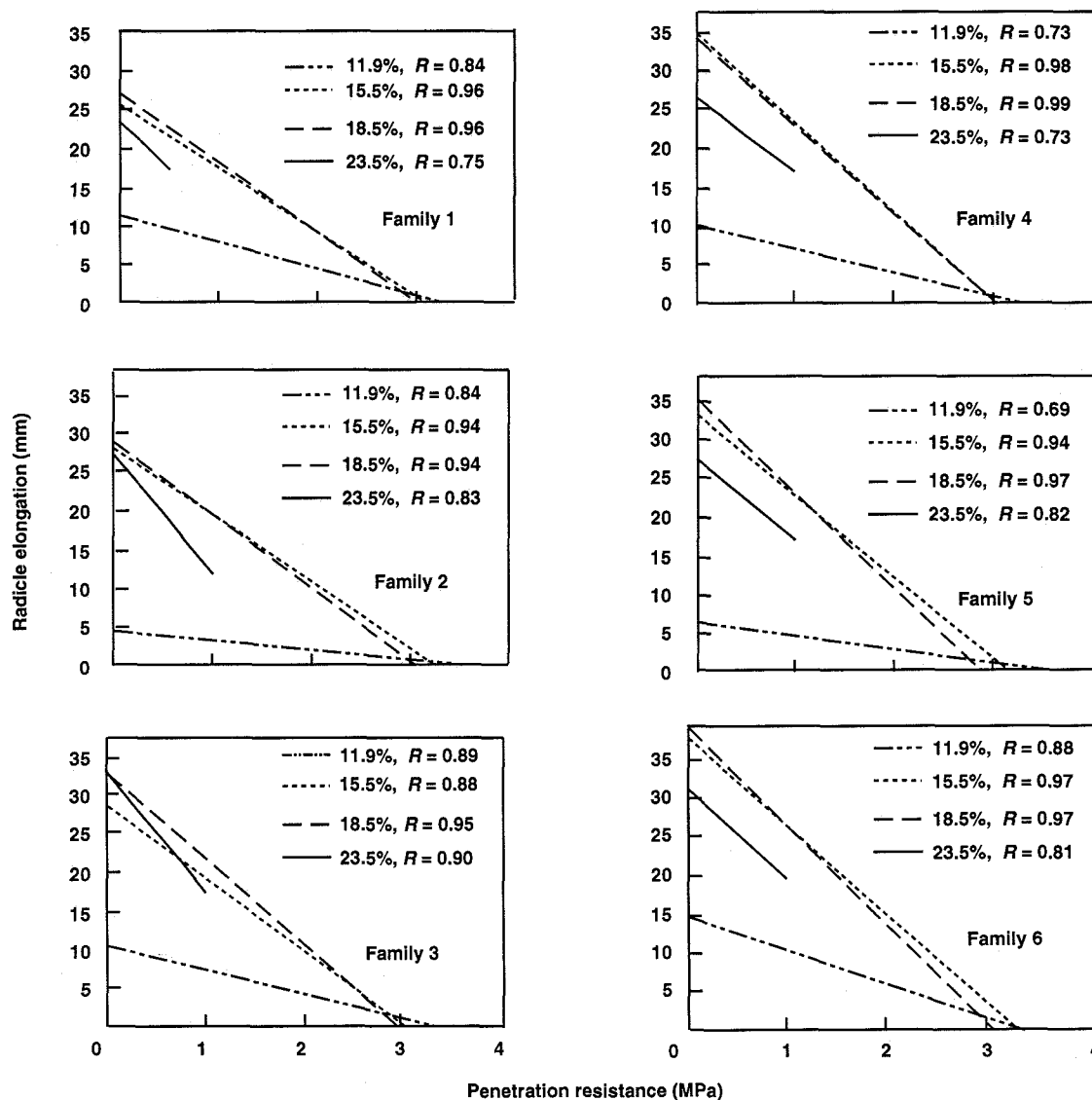


Figure 1. Experiment 1. Predicted relationships between penetration resistance and radicle elongation after 3.5 days for six *Pinus caribaea* var. *hondurensis* families in a repacked red dermosol at a range of moisture contents.

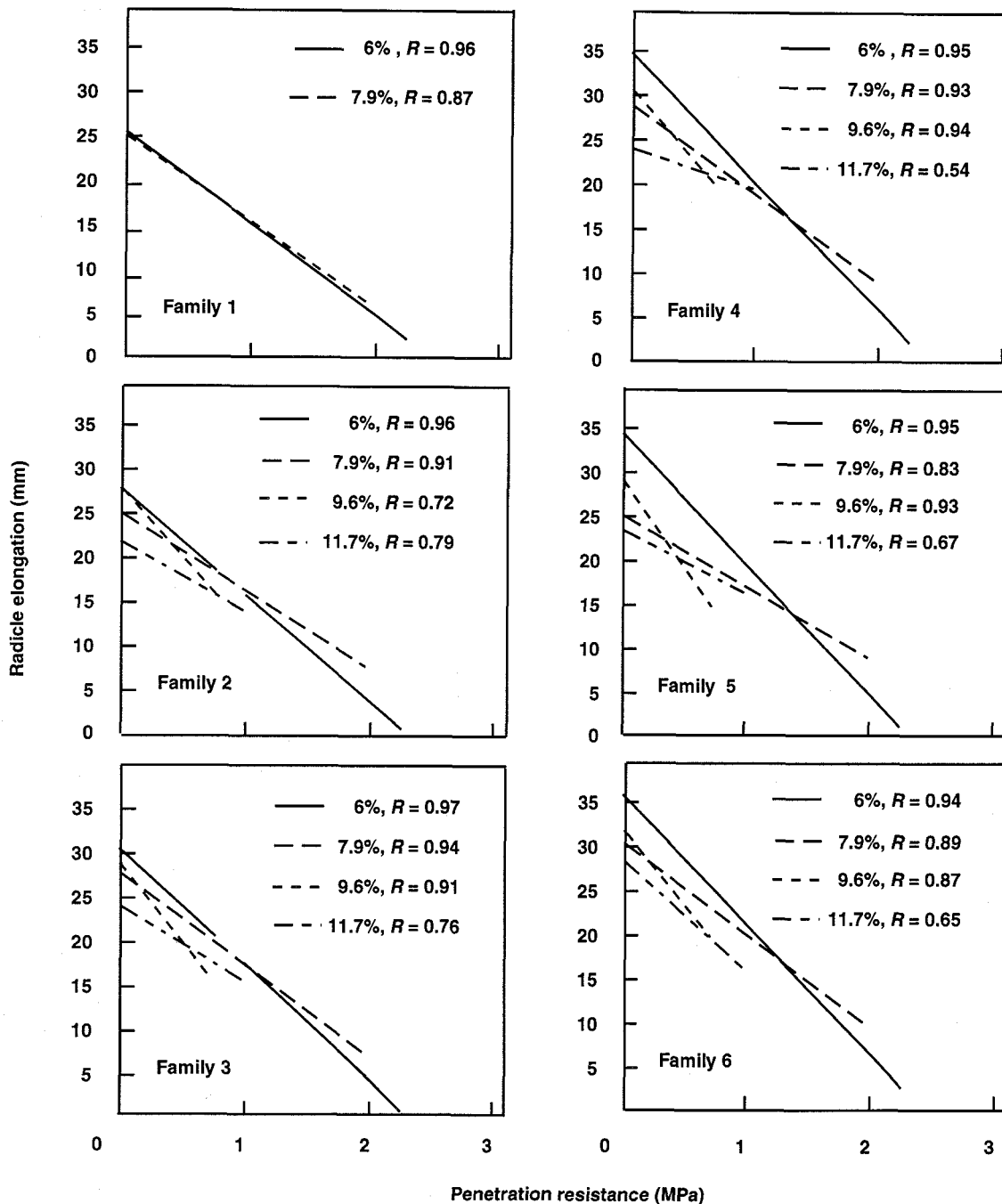


Figure 2. Experiment 1. Predicted relationships between penetration resistance and radicle elongation after 3.5 days for six *Pinus caribaea* var. *hondurensis* families in a repacked brown sodosol at a range of moisture contents.

prepared holes. Vermiculite (20 g) was placed on the surface of each pot to reduce evaporation and dissipate the potential energy of applied water.

Cuttings were grown in a glasshouse fitted with mist irrigation, which was applied for 1.5 s every 15 min

between 0600 and 1800 hours, in order to maintain high humidities but not saturate the vermiculite. Pots were weighed every second day and maintained at the desired moisture content by adding the appropriate volume of distilled water. A thermohygrograph recorded daily

temperature ranges of  $18.9 \pm 3.7$  ( $\pm$  s.d. 0600 hours) to  $29.1 \pm 2.6^\circ\text{C}$  ( $\pm$  s.d. 1430 hours) and daily humidity ranges of  $71 \pm 7.5$  ( $\pm$  s.d. 1430 hours) to 100% at night.

Cuttings were transplanted into pots on 1 November 1989 and harvested on 4 December 1989. Measurements made at harvest included shoot height, shoot basal diameter, shoot oven-dried weight, number and length of surface lateral roots, number and length of roots leaving the base of the transplanted core, length of longest root, total root length and average diameter of the 3 thickest root tips 1 cm back from the apex.

#### Statistical analyses

A preliminary investigation of relationships was conducted by plotting measured growth parameters against PR. Appropriate linear and non-linear curve fitting techniques of GENSTAT 5 Committee (1987) were used to define these relationships. The square root of the coefficient of determination is reported as a measure of fit. Where relationships were linear, family and soil type differences were tested using a Bartlett test to check for homogeneity of variance (Brownlee 1965) and the *F*-test to check for differences in regression coefficients and constants. For non-linear relationships, differences were detected by examining changes in residual sums of squares from fitting a combined model and fitting separate models for each data set, and comparing with the *F*-test.

## Results

### Experiment 1. Pregerminated seeds in repacked soils

Radicle elongation and PR for all families were negatively correlated (Figs 1 and 2). For all families combined, the Bartlett test revealed significant differences ( $0.001 < P < 0.01$ ) between the variances of radicle elongation in the 2 soil types.

In both soils, radicle elongation increased as moisture content increased until an optimum was reached, and thereafter decreased (Figs 1 and 2). In the red dermosol, there were significant differences in the relationships between PR and radicle elongation for all moisture contents except 15.5 and 18.5%, and for all families. With a PR of 0.01 MPa, for example, radicle elongation increased on average 3-fold as moisture content increased from 11.9 to 15.5%, and decreased on average by 20% as moisture content increased from 18.5 to 23.5%. For the brown sodosol, the relationships between PR and radicle elongation differed significantly for all moisture contents, except 6 and 7.9% in families 1 and 2. For the remaining families, only the constant term differed between the 6 and 7.9% moisture contents.

At moisture contents of 11.9, 15.5 and 18.5% in the red dermosol, radicle elongation ceased for all families at PR values of 2.9–3.5 MPa. Interestingly, for each of the families in Figure 1, the PR value at the point where the abscissa is intersected is greatest for the 11.9% moisture content and least for the 18.5% moisture content.

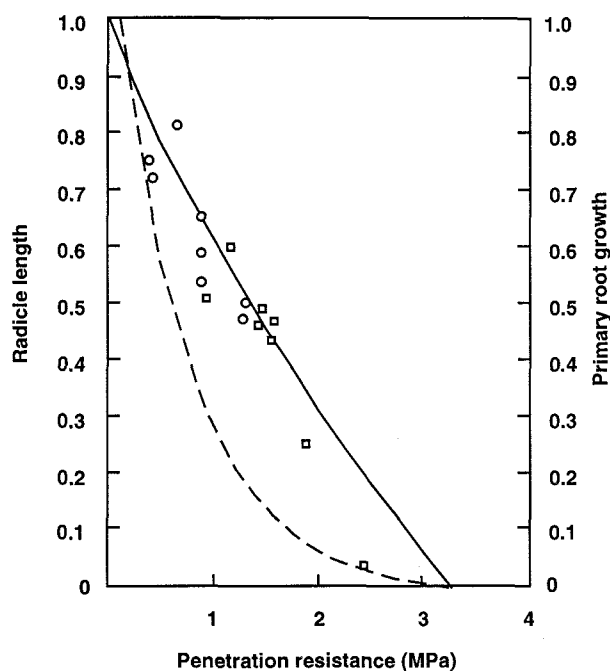


Figure 3. Effect of 0.01 MPa penetration resistance on potential radicle elongation, and 0.1 MPa penetration resistance on potential primary root development for all families and both sites. Data points for the undisturbed field soils are averaged for six families. —, Predicted radicle elongation in repacked soil; □, actual radicle elongation in undisturbed red dermosol; ○, actual radicle elongation in undisturbed brown sodosol; - - -, predicted primary root development in remoulded soil.

There were no statistical differences in radicle elongation between the 15.5 and 18.5% moisture contents in the red dermosol and between the 6 and 7.9% moisture contents in the brown sodosol. For each soil, radicle elongation was at a maximum at these moisture contents, and the relative reduction in radicle elongation as PR increased beyond 0.01 MPa was well described by an exponential model:

$$RE = a + b \times r^{PR} \quad (4)$$

where RE is radicle elongation relative to elongation at 0.01 MPa, and *a*, *b* and *r* are constants (Fig. 3, solid line:  $R^2 = 64.9$ ; square root residual mean square = 0.20).

Radicle width, 0.5 cm from the apex, was strongly correlated with PR, and the relationships differed between the 2 soil types. For the red dermosol, the relationship was best described by a simple power model (Fig. 4a):

$$RW = a + b \times PR^2 \quad (5)$$

whereas, for the brown sodosol the relationship was best described by a logistic model (Fig. 4b):

$$RW = a + c/[1 + \exp(-b(PR - m))] \quad (6)$$

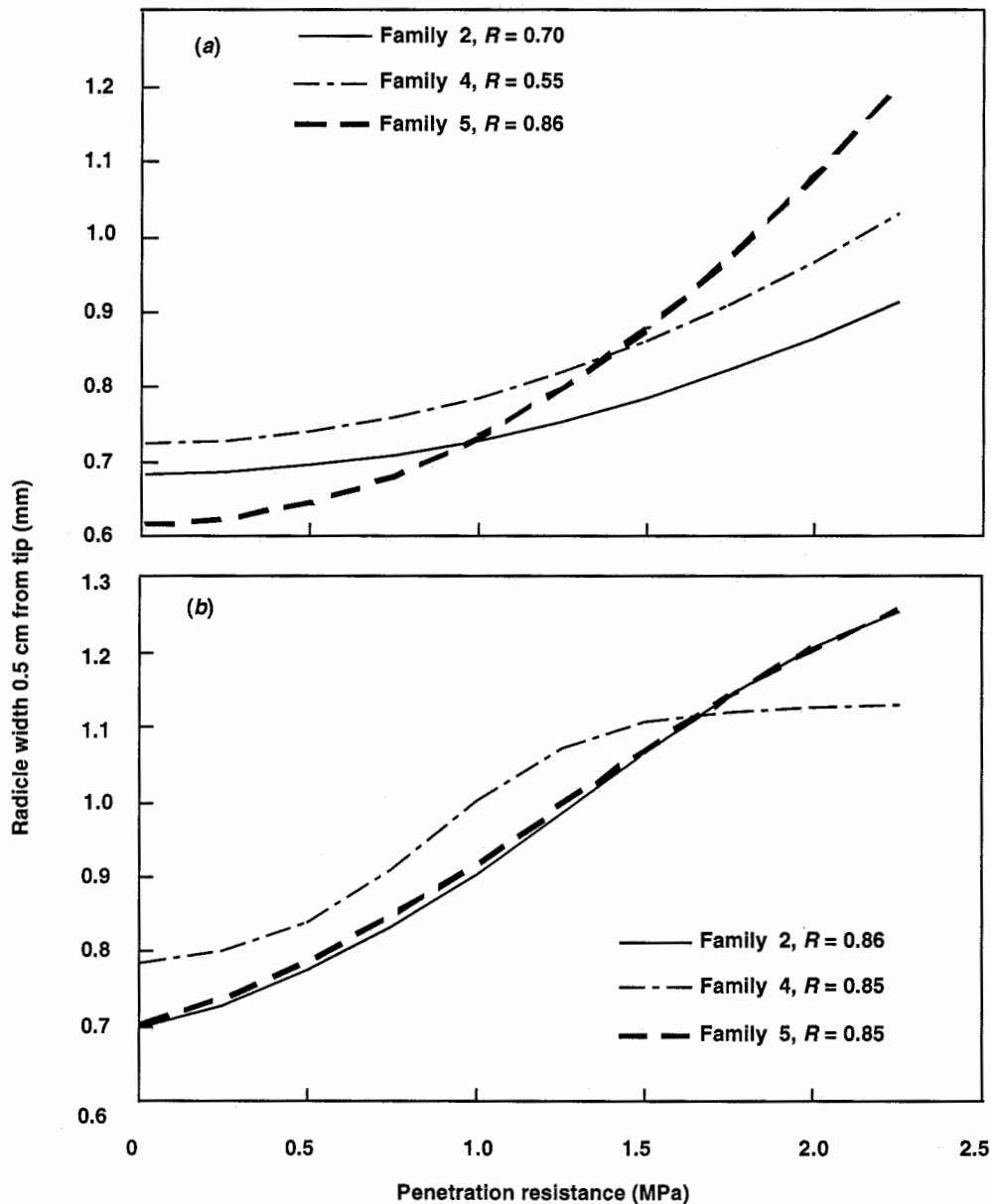


Figure 4. The predicted effect of penetration resistance on radicle width for three *Pinus caribaea var. hondurensis* families in two growth media. (a) Red dermosol, (b) brown sodosol.

where RW is radicle width, and  $a$ ,  $b$ ,  $c$  and  $m$  are constants.

For the red dermosol, there was no hypocotyl development in any 11.9% moisture content treatments. There were no differences in hypocotyl development between the 15.5 and 18.5% moisture contents in the red dermosol or between the 6 and 7.9% moisture contents in the brown sodosol. Data from these treatments were combined in order to analyse the impact of PR on hypocotyl

growth for each soil type. The remaining moisture content treatments were excluded because they sampled a narrow range of PR. For both soil types the relationship between PR and hypocotyl growth was best described by an exponential model (see equation 4 and Fig. 5).

Soil type and family differences in the relationship between hypocotyl growth and PR were highly significant ( $P < 0.001$ ). For the brown sodosol, hypocotyl growth was relatively insensitive to PR levels less than 1.5 MPa

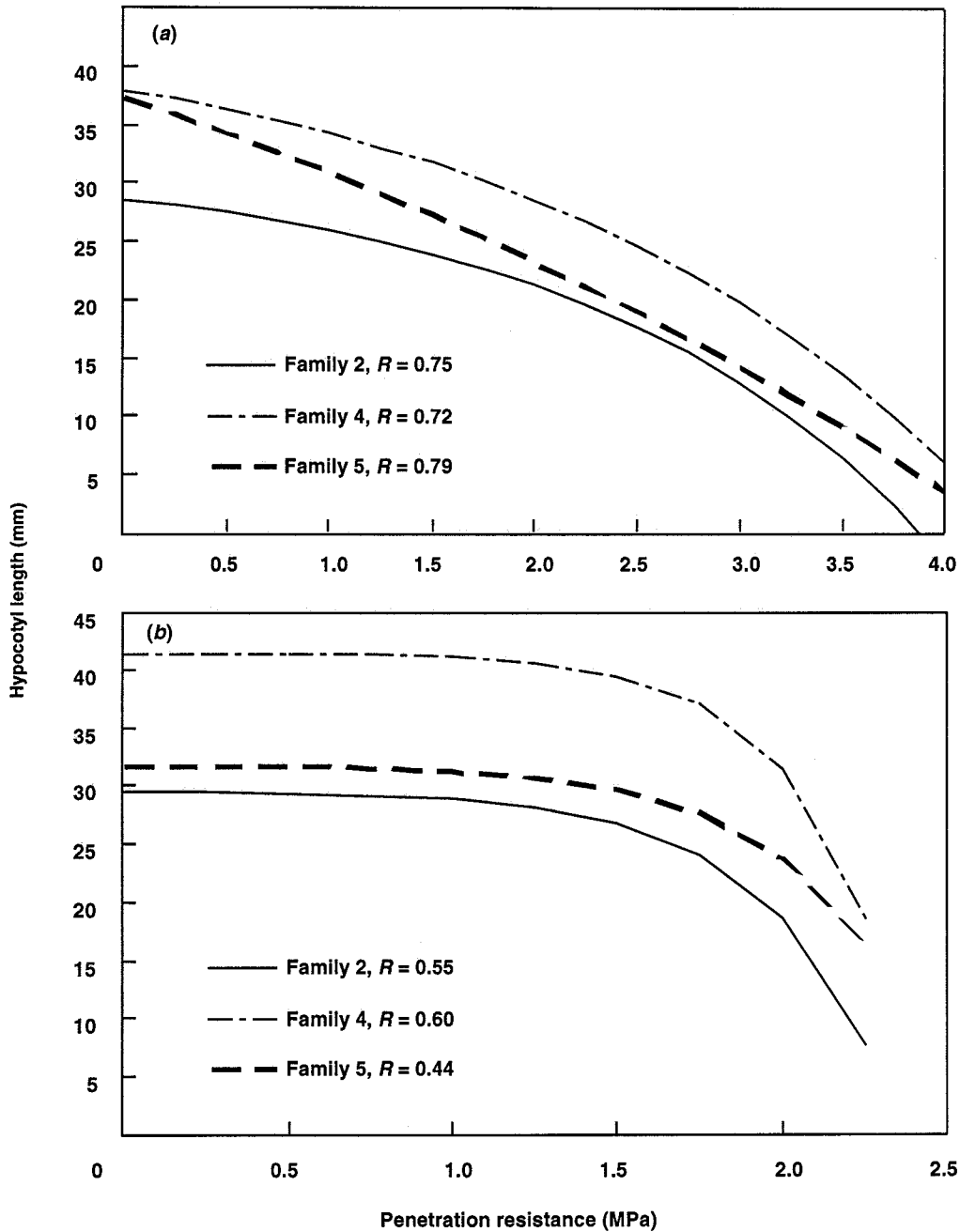


Figure 5. The predicted effect of penetration resistance on hypocotyl growth for three *Pinus caribaea* var. *hondurensis* families in two growth media. (a) Red dermosol, (b) brown sodosol.

(Fig. 5b), whereas in the red dermosol, there was no evidence of a threshold PR, below which hypocotyl growth was unaffected by PR (Fig. 5a). In both soil types, family 4 showed superior hypocotyl development. With PR values of 0.5 MPa for example, family 4 hypocotyl height was 34 and 45% greater than that of family 2

in the red dermosol and brown sodosol respectively.

#### Experiment 2. Pregerminated seeds in field soils

As there was effectively only one replicate of each family for each PR and soil type in experiment 2, data for all families were combined. Actual radicle elongation relative

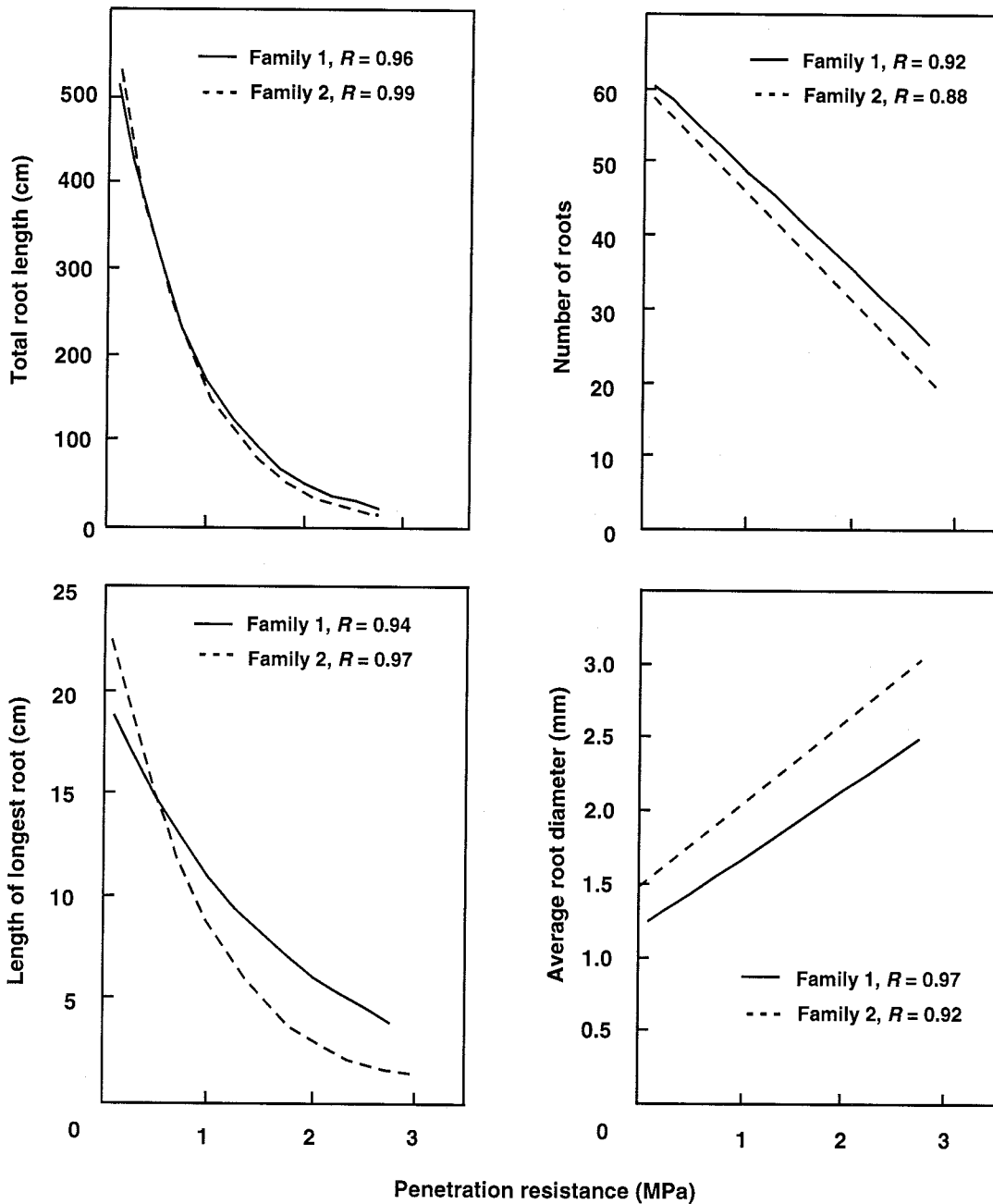


Figure 6. Experiment 3. The predicted effect of penetration resistance on the development of the primary root system of two *Pinus caribaea* var. *hondurensis* families grown in repacked red dermosol soil.

to growth in the 0.01 MPa treatment of the repacked soils in experiment 1 is shown in Figure 3 for both soil types.

#### Experiment 3. Cuttings in repacked soils

Moisture contents of the subsamples from individual cores differed by less than 2% moisture content, and no consistent systematic gradients along the cores were observed.

Both lateral and surface root development was poor for all treatments and both soils (poor early development of lateral roots was in fact a characteristic of cutting stock produced by the Queensland Department of Primary Industries Forestry Propagation Program at the time of the study). The limited development which did



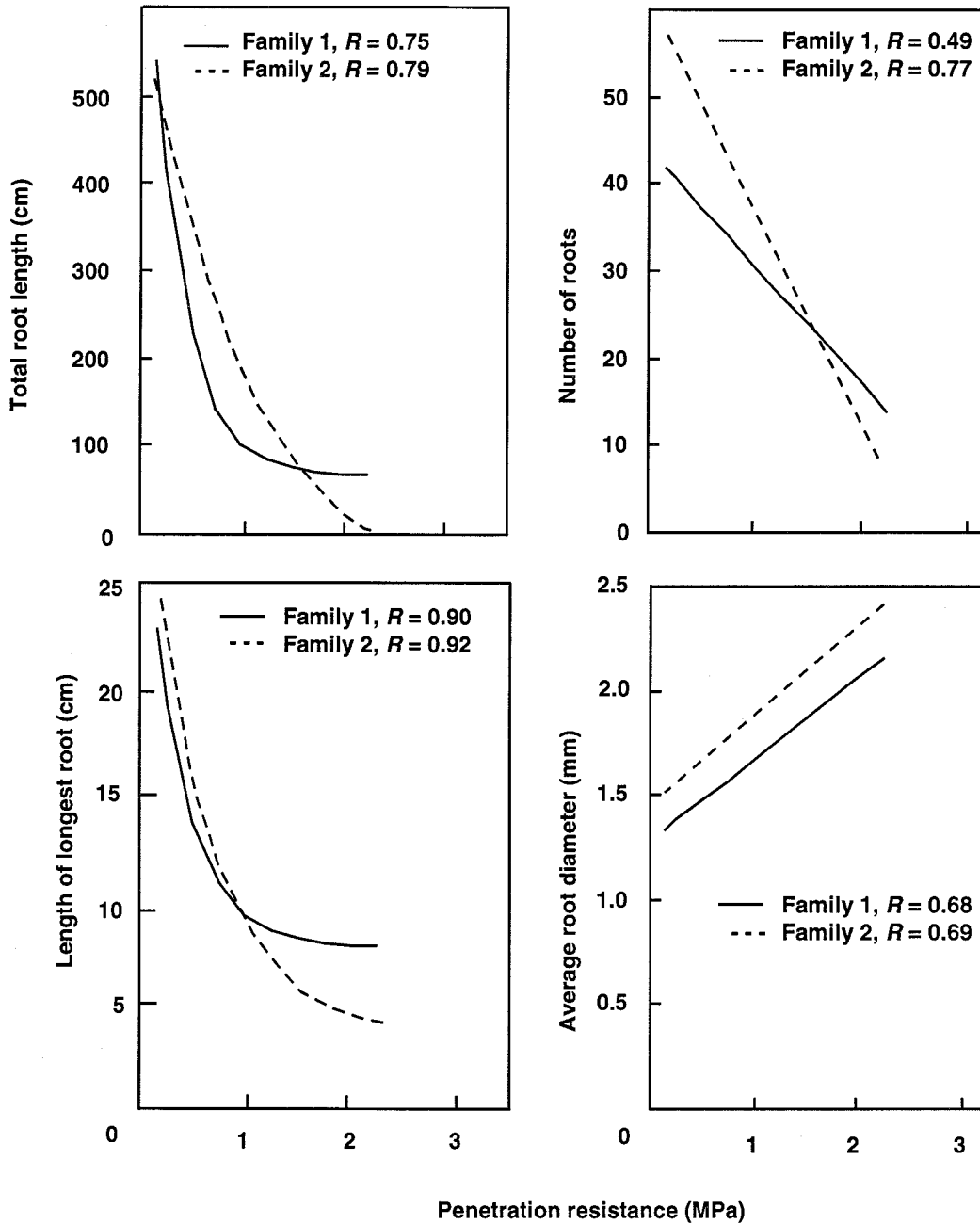
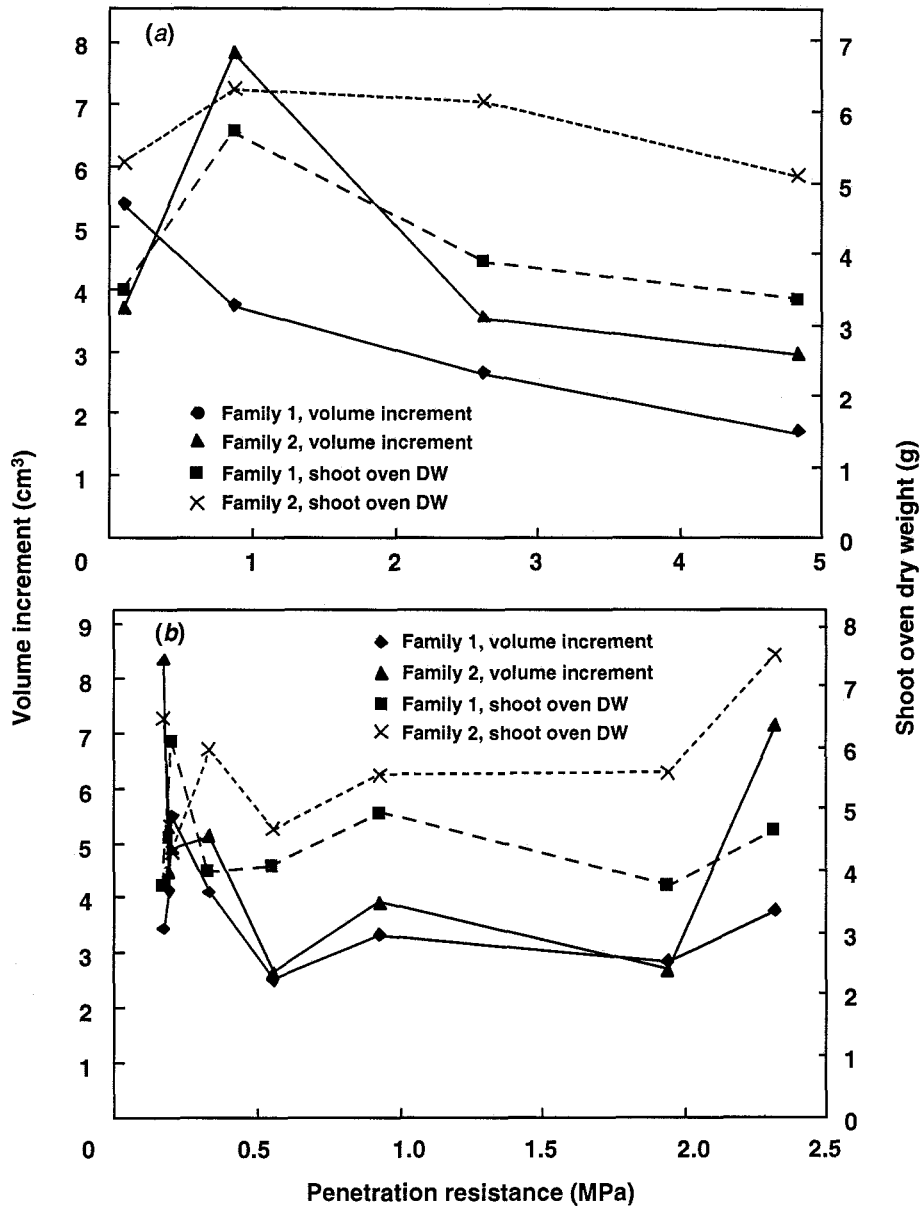


Figure 7. Experiment 3. The predicted effect of penetration resistance on the development of the primary root system of two *Pinus caribaea* var. *hondurensis* families grown in repacked brown sodosol soil.

occur appeared unrelated to PR. Vertical root growth was, by contrast, strongly correlated with PR. For both soil types, the relationships between PR and total root length and length of the longest root were best described by equation 4 exponential models. The number of roots penetrating the pots, and the average diameter of the

3 thickest roots 1 cm behind the apex were linearly related to PR (Figs 6 and 7). With the exception of total root length development in the red dermosol, there were significant family and soil type differences for all measured vertical root growth parameters.

For both families and all treatments combined, the



**Figure 8.** Experiment 3. The effect of penetration resistance on early shoot development for two *Pinus caribaea* var. *hondurensis* families. Each data point is a mean of two replicates. (a) Red dermosol, (b) brown sodosol.

relative reduction in total primary root length by increases in PR beyond 0.1 MPa was well described by an equation 4 exponential model (Fig. 3, dashed line:  $R^2 = 69.9$ ; square root residual mean square = 0.23).

Over the PR range 0.01–3 MPa, there was no consistent relationship between PR and shoot development (Fig. 8). At 4.8 MPa PR in the red dermosol, however, all shoot development indicators were less than those observed for lower levels of PR (Fig. 8a).

#### Discussion

*Pinus caribaea* var. *hondurensis* radicle and primary root elongation decreased to zero as PR increased to a value of 3.25 MPa (Fig. 3). Greacen *et al.* (1968) reported similar negative correlations between root elongation and PR for a number of species, and noted that root elongation ceased at PR levels ranging from 0.8 to 5.0 MPa, depending upon species, soil type and penetrometer design. Sands *et al.* (1979) observed that

*P. radiata* roots preferentially penetrated soil zones of low PR, and that root penetration was severely restricted where PR exceeded 3.0 MPa. Results from the present studies suggest that tolerance of both *P. caribaea* var. *hondurensis* and *P. radiata* roots to high strength soils are similar.

Notwithstanding its inability to penetrate high strength soils with PR exceeding 3.0 MPa, Greacen and Sands (1980) noted limited *P. radiata* root colonisation of field soils with PR values as high as 7.0 MPa. They concluded that high strength field soils were heterogenous, containing low PR zones and structurally weak areas such as fissures and ped interfaces, which could be colonised by roots. It is also probable that roots penetrate high strength soils when soil moisture is high and PR reduced. Growth of *P. caribaea* var. *hondurensis* roots in field soils was not investigated in the studies reported here. However, whilst colonisation of low strength zones in predominantly high strength field soils can be expected, the results reported here suggest that root development in high strength soils will be severely restricted. Soil compaction which results in increased PR can therefore be expected to restrict root growth.

In Costantini *et al.* (1996), it was demonstrated that aeration, matric suction and PR interact to influence *P. caribaea* var. *hondurensis* radicle elongation. Notwithstanding a monotonic negative relationship between radicle elongation and increasing matric suction, repacked soils typically exhibit a 'non-limiting water range' over which water content has little impact on radicle elongation. At lower and higher moisture contents, matric suction and aeration respectively limited growth. A similar 'non-limiting water range' is observed in Figures 1 and 2. In the red dermosol, for example, radicle elongation increased as moisture content increased from 11.9 to 15.5%, but decreased at moisture contents above 18.5%, due to limited aeration. At the 15.5 and 18.5% moisture contents, the interactions of aeration, matric suction and PR seem to have a similar impact upon growth. Whilst only a narrow range of PR and matric suction were tested in the brown sodosol (Fig. 2), aeration was clearly limiting at 11.7% moisture content, and likely to have been limiting at 9.6% moisture content. For PR values less than 1.0 MPa, radicle elongation in the brown sodosol was maximised by 6% moisture content, whereas if PR exceeds 1.2 MPa, elongation was maximised by 7.9% moisture content.

The observation that the predicted radicle elongation-PR relationships for the red dermosol in experiment 1 intersected the abscissa at increasingly lower values for the 11.9, 15.5 and 18.5% treatments (Fig. 1) is difficult to explain. PR levels that would prevent radicle elongation were not tested in the brown sodosol, so it was not possible to determine if a similar trend applied in that soil. At all PR levels below

2.75–3.0 MPa in the red dermosol, root elongation was significantly greater at 15.5 and 18.5% moisture contents than at 11.9% moisture content (Fig. 1). Yet, for all 6 families tested, radicle elongation in high strength dry soils was greater than that observed in high strength moist soils. There are 2 possible physiological explanations for this result: (i) the germinants have increased relative radicle elongation in the drier soils by reallocating resources, possibly solutes, from hypocotyl development (hypocotyl growth was zero in the 11.9% treatments); and (ii) aeration was limiting elongation in the high strength, moist soils (high PR values for a particular moisture content in experiment 1 were achieved by increasing bulk density).

Penetration resistance is strongly influenced by soil water content (Koolen and Kuipers 1983; Campbell and O'Sullivan 1991). When plants in pots are watered from the surface, as occurred in experiment 3, there will be transient vertical water gradients, and hence PR gradients. Superimposed on these gradients will be gradients away from active roots. The result will be a growing medium with variable PR (Boone and Veen 1982), which may account for some of the differences between the impact of increased PR on radicle elongation and primary root elongation (Fig. 3). However, the 2 relationships in Figure 3 converge by definition at low PR, but interestingly also converge at high PR, suggesting that the 2 root types do respond differently to PR increases, with the primary roots being more sensitive.

Greacen and Sands (1980) report that the relationship between root elongation and PR are typically negative exponential. This was the case for primary root development in *P. caribaea* var. *hondurensis* (Figs 6 and 7). In experiment 1, the relationships between PR and radicle elongation for individual families at constant moisture contents were negative linear (Figs 1 and 2). Interestingly, when the data for all families were combined, the relationship was negative non-linear (Fig. 3).

The diameter of both *P. caribaea* var. *hondurensis* radicles and primary roots increase as PR increases (Fig. 4). A similar positive relationship between growing root tip diameters and PR has been widely reported (Barley 1962; Taylor and Ratcliff 1969; Eavis 1972). Abdalla *et al.* (1969) postulated that radial swelling tends to reduce soil strength ahead of the growing tip, thereby improving penetration of compacted soils.

Observed root development for family 2 in experiment 3 was inconsistent with the poor rooting performance that originally led to its deletion from the propagation program. Indeed, there was a significant family x root development x soil type interaction. In the red dermosol, the total length of root development in both families were similar, though the length of the

longest root and total root numbers were slightly greater for family 1 (Fig. 6). In the brown sodosol, total root development was greater for family 2 at PR values less than 1.5 MPa (Fig. 7), and greater for family 1 at higher PR. Family 2 shoot development was generally superior in both soil types. The results suggest that family 2, and other families which have been deleted from the propagation research program, may be able to be included in breeding programs if the nursery growing medium is changed.

Increasing PR in the experiment 3 pot trial resulted in decreasing growth in the weight, volume and length of roots and in the length of shoots. Sands and Bowen (1978) reported similar findings for *P. radiata* seedling development. A comparison of the data from experiment 3 with that reported by Sands and Bowen (1978), however, suggested that shoot development was less sensitive to increasing PR in *P. caribaea* var. *hondurensis* cuttings than in *P. radiata* seedlings.

The relative decrease in *P. caribaea* var. *hondurensis* hypocotyl growth with increasing PR was less than that observed for radicle and primary root growth (Figs 1, 2, and 5). Thus, radicle elongation in the red dermosol was inhibited by PR values in the range 2.9–3.5 MPa, yet hypocotyl elongation averaged 17 mm at 3.0 MPa and 7 mm at 4 MPa (Figs 1 and 5). Similarly, *P. caribaea* var. *hondurensis* shoot growth was less sensitive to increasing PR than hypocotyl growth. For the red dermosol, there was only a slight reduction in shoot growth at PR values of 4.8 MPa (Fig. 8a). It can be concluded that pretransplant root systems of the cuttings used in experiment 3 were better able to support shoot development in poor environments for root growth, than the 1–2 mm long radicles of the pregerminated seeds used in experiment 1. This result is consistent with observations made by Goss and Drew (1972) that the growth of unimpeded crop shoots is not necessarily restricted by poor root development, if water, oxygen, nutrients and anchorage are not limiting. In the field situation, however, these elements may be all limiting at various times. Restricted root system development, as a consequence of compaction, for example, can therefore be expected to reduce above-ground biomass production (Nambiar 1983).

Significant family x soil type and family x PR interactions were observed in all studies. Eavis *et al.* (1969) and Greacen (1986) have observed similar intra-specific differences in the maximum pressures that roots can exert. Gerard *et al.* (1982) observe that the critical PR above which root elongation ceases, is soil-type dependent. Whilst no large family differences in the ability of roots to penetrate high strength soils were observed, significant differences in performance in low strength soils were observed. There were, however, large family differences in both hypocotyl and seedling shoot development for plants grown in high strength media.

## Conclusions

The effects of PR, an easily measured indicator of soil strength, on the early development of *P. caribaea* var. *hondurensis* germinants and seedlings were investigated. Strong negative exponential relationships between PR and both radicle and primary root elongation were observed. The critical level of PR beyond which elongation ceased was about 3.25 MPa for both root types. Root tip diameters were positively correlated with PR, whilst numbers of primary roots, total root lengths and lengths of longest roots were negatively correlated.

Hypocotyl development was negatively correlated with increasing PR, though the relationships were less sensitive than those observed for root development. By contrast, primary shoot development was unaffected by PR values that prevented root elongation. At PR levels of 4.8 MPa, slight reductions in shoot development were observed. It was concluded that compaction of forest soils had the potential to: (i) reduce *P. caribaea* var. *hondurensis* root system development; and (ii) reduce above-ground biomass development as a result of reduced water, oxygen and nutrient uptake capacity and less effective anchorage.

Significant family x soil-type interactions were observed in the reported studies. One genetically superior family, which was deleted from operational planting programs because its cuttings rooted poorly in nursery growing media, was observed to grow well in 2 soil media. It was suggested that the nursery rooting performance of some families might be improved by changing growing media. Significant family x PR interactions were observed for radical, hypocotyl, primary root and primary shoot development. If these differences could be correlated with performance in the field, then they might serve as a useful early indicator of suitability to high strength soils.

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