

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

1. Influence of matric suction

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Summary. This paper reports 2 experiments that examine the influence of matric suction on radicle elongation in *Pinus caribaea* var. *hondurensis*. Experiment 1 where mechanical impedance of root development was negligible and aeration was not limiting, and experiment 2 in low strength soils where both air-filled porosity and moisture were allowed to vary.

In experiment 1, radicles were grown between sheets of Whatman No. 42 filter paper. The known wetting characteristic of this paper was used to prepare known pretial suctions and define postharvest suctions. The midpoint of the pretial–postharvest suction range was defined as nominal matric suction. Relationships between radicle elongation and nominal matric suction were developed for 6 *P. caribaea* var. *hondurensis* families. As matric suction increased from 0.0065 to 3.13 MPa, radicle elongation after 48 h of growth decreased monotonically to zero. Over the range of

matric suctions, there was no critical level, below which radicle elongation was unaffected by increasing suction. It was concluded that radicles were able to sense, and respond to, increasing suction. Significant family × matric suction interactions were observed.

In experiment 2, radicles were grown in 2 low-strength repacked soils. An optimal level of matric suction for radicle elongation was observed in both soils. At suctions below and above the optima, inadequate air-filled porosity and moisture stress respectively adversely impacted upon elongation.

The 2 experiments demonstrated that matric suction affects radicle elongation both directly and indirectly through interaction with other physical soil properties. Although increasing suction reduces radicle elongation, there may be a ‘non-limiting’ range of suctions in soil media over which radical elongation is relatively unaffected due to a concomitant improvement in aeration.

Additional keywords: radicle elongation, aeration.

Introduction

The incidence of management-induced compaction in commercial *Pinus* plantations in Queensland (Costantini 1995) has prompted research into the impacts of soil strength on crop root growth. In experiments designed for this purpose, both void ratio and/or matric suction are often allowed to vary in order to test a range of strength conditions (Voorhees *et al.* 1975). However, both of these can directly and indirectly affect root growth (Greacen and Sands 1980; Lety 1985; Taylor and Brar 1991), thus confounding interpretation of treatment responses (Barley and Greacen 1967; Hatchell 1970; Eavis 1972a; Greacen and Sands 1980; Cornish *et al.* 1984; Reisinger *et al.* 1988; Yapa *et al.* 1988).

Where the existence of a critical air entry limit has been assumed in root growth studies (see, for example,

Grable and Siemer 1968), the effect of aeration has been ignored providing the limit was exceeded (see, for example, Sands and Bowen 1978). In a study which examined how the strength of a repacked clay loam affected *Pinus radiata* taproot growth, Theodorou *et al.* (1991) compared 2 treatments (12.8% moisture content and 1.0 MPa strength; 14.5% moisture content and 1.84 MPa strength), and attributed superior growth in the 12.8% moisture content treatment to the greater importance of soil strength relative to soil moisture. Their conclusion assumed that aeration differences between the 2 treatments (22 and 8% respectively) were unimportant. Evidence from a number of studies, however, suggests that root elongation is sensitive to a wide range of air-filled pore spaces (Eavis 1972a, 1972b; Voorhees *et al.* 1975; Simmons and Pope 1987), particularly in warm soils (Cannell 1977).

Matric suction is perhaps the most important parameter whose effects on root growth is confounded with soil strength (Yapa *et al.* 1988). Techniques which have been used to separate soil strength and suction effects in root growth studies are not always conclusive. For example, Masle and Passioura (1987) examined the impact of soil strength on the growth of wheat seedlings in a repacked, ventilated silty loam. They observed that: (i) increases in soil strength achieved by increasing bulk density at constant soil moisture content or by decreasing soil moisture at constant bulk density, had similar impacts; and (ii) plots of residuals against soil moisture and bulk density showed no trends. They therefore concluded that growth was affected more by soil strength than soil moisture. However, both increasing bulk density at constant soil moisture and decreasing soil moisture at constant bulk density can increase matric suction (Box and Taylor 1962). Furthermore, if soil strength is highly correlated with soil moisture and bulk density, then the distribution of residuals for regressions of growth on soil strength might not suggest relationships with either.

Plant root elongation has been widely observed to decrease progressively as matric suction increases over the range of agronomic interest (0.01–1.5 MPa: Hillel 1979; Kramer 1983).

The aim of the 2 experiments reported here was to define the impact of matric suction on *P. caribaea* Morelet. var. *hondurensis* Barr. *et* Golf. radicle growth in order to improve interpretation of soil strength–root growth studies.

Materials and methods

Experiment 1. Pregerminated seeds in filter paper

The known wetting characteristic of 7 cm diameter, Whatman No. 42 filter paper (Fawcett and Collis-George 1967) was used to produce a range of matric suctions in

which pregerminated seed of 6 *P. caribaea* var. *hondurensis* families were grown. By growing radicles between filter paper sheets, mechanical resistance to elongation was minimal and aeration was non-limiting.

Four replicates of 11 matric suction levels were prepared. Each replicate comprised sets of 20 filter papers wet to the desired matric suction (Fawcett and Collis-George 1967). Low suction treatments were prepared by: (i) filling 10 pipettes each with one-tenth of the required distilled water; (ii) placing filter papers, 2 at a time, into a 7.05 cm diameter by 7.7 mm deep petri dish; and (iii) dripping and spreading water onto each filter paper pair (while pressing down). High suction treatments were prepared by adding distilled water in 0.025 mL aliquots using steps (ii) and (iii) above. About 90 s after beginning of wetting, petri dishes were sealed, and allowed to equilibrate at 25°C for 2 days. After equilibration, one petri dish of each matric suction treatment was opened, and sheets 9–11 were weighed to the nearest milligram to determine pretorial matric suction (after Fawcett and Collis-George 1967).

Two days before preparing the filter papers, seeds of 6 full-sib *P. caribaea* var. *hondurensis* families were sown onto germination paper overlaying a bed of moist vermiculite, and allowed to develop for 4 days in a growth cabinet, without light, at 25°C, until radicles averaged 2.5 mm in length. One pregerminated seed of each family was randomly selected, measured for radicle length and placed between the tenth and eleventh filter papers in a prepared petri dish. Each seed was allocated to one-sixth of the filter paper, 1 cm from its edge, with the radicle facing the centre of the paper. Petri dishes were sealed and returned to the growth cabinet. Placement was restricted to 60 s to limit evaporation.

Three additional petri dishes were prepared with pregerminated seed placed on germination paper overlaying a bed of moist vermiculite. The intention was

Table 1. Experiment 1. Matric suction range (MPa) associated with the nominal suctions used to model *Pinus caribaea* var. *hondurensis* radicle elongation

Nominal matric suction	Matric suction calculated from filter paper moisture content		Matric suction with s.e. adjustment	
	Pretrial	Postharvest	Pretrial – s.e.	Postharvest + s.e.
0.0065	0.006	0.007	0.005	0.008
0.0115	0.01	0.013	0.008	0.016
0.0185	0.016	0.021	0.013	0.026
0.031	0.029	0.033	0.023	0.042
0.0515	0.045	0.058	0.034	0.076
0.140	0.10	0.179	0.072	0.25
0.26	0.20	0.32	0.138	0.46
0.63	0.30	1.32	0.191	2.46
1.68	0.85	2.51	0.54	3.98
3.13	1.59	4.68	1.10	6.76

to produce a treatment without the overburden of filter paper and with optimal moisture supply for comparison with the low matric suction treatment.

Seeds were grown for 48 h in a growth cabinet, without light, at 25°C. Radicles elongated between, and not through, the filter papers. At harvest, seeds were removed, and filter papers weighed immediately to determine postharvest matric suction (after Fawcett and Collis-George 1967). Radicle lengths were then measured.

A pretrial and postharvest matric suction range was defined for each treatment (Table 1). A 'nominal' matric suction (Table 1) was defined as the midpoint of this range. The 95% standard errors of the suction estimates were calculated according to Fawcett and Collis-George (1967). These were deducted from, and added to, the pretrial and postharvest suction estimates respectively, to calculate 95% confidence limits (Table 1).

Initial plots of radicle elongation versus the natural log of nominal suctions suggested sigmoidal negative relationships that were asymptotic to zero for all families. Non-linear regression (Genstat 5 Committee 1987) was used to define relationships. Family 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.

A 1-way analysis of variance using the model described in Steel and Torrie (1981) for a completely random design was used to compare radicle elongation in the non-moisture limiting vermiculite dishes with the 0.0065 MPa nominal suction treatment.

Experiment 2. Pregerminated seeds in repacked soils

In the second experiment, pregerminated seed of the 6 *P. caribaea* var. *hondurensis* families used in experiment 1 were grown in 2 repacked soil media with a range of matric suctions and air-filled porosities.

Soil was collected from 5–15 cm depth in the structured clay loam A1 horizon of a red dermosol and the massive sandy loam A1 horizon of a brown sodosol [Table 2, nomenclature follows Isbell (1993)], transported to the laboratory, air-dried on plastic sheets and sieved to remove particles >2 mm. Soil moisture characteristic curves were determined. One kilogram lots of sieved soil were placed in heavy duty plastic bags, wet to the desired moisture content by adding an appropriate quantity of distilled water as an atomised

spray, physically agitated, sealed and allowed to equilibrate for 3 days with inversion twice daily. Soils were hand packed with gentle tapping into 6.0 cm long x 7.25 cm diameter brass cylinders, and a 0.5 cm long x 7.25 cm diameter brass ring was taped to the top of the filled cylinder. Three replicates with the top ring, and one without, were prepared for each soil moisture and soil type. All cylinders were sealed and stored for 24 h then a Geotester penetrometer was used to ensure that penetration resistance of soils in cylinders without the top rings was less than 0.2 MPa.

One pregerminated seed of each *P. caribaea* var. *hondurensis* family was randomly selected, and after radicle length was measured, transferred to a prepared cylinder. Each seed was allocated to one-sixth of the soil surface, placed into a 3–4 mm diameter x 2 mm deep spatula hole which was located 1 cm from the cylinder edge, and covered with about 4 mm of the same loose soil. The rings were then set on a glass tray, sealed inside a 500 mm plastic beaker, and transferred to a growth cabinet with a 12 h day/night environment at 25/20°C. Radicle lengths were assessed after 4 days. At the same time, penetration resistance was assessed at the base of each sample ring.

Results were analysed in the same manner as for experiment 1.

Results

Experiment 1. Pregerminated seeds in filter paper

No fungal or bacterial growth was observed during experimentation. All families showed a continuous decrease in elongation with increasing matric suction. The response of radicle elongation (*y*) to changes in nominal suction (ϕ) was best modelled by the Gompertz equation modified to be asymptotic to zero by deleting the constant (Fig. 1):

$$y = c \times \exp(-\exp[-b(\ln \phi - m)])$$

where *c*, *b* and *m* are coefficients (Genstat 5 Committee 1987). Differences between family regression equations were highly significant ($P < 0.001$). At suctions less than about 0.15 MPa, radicle elongation was greatest in families 1 and 4 (Fig. 1). For example, predicted average radicle elongation in families 3 and 4 for the 0.0065 MPa treatment were 2.6 and 3.7 cm respectively. At matric suctions greater than about 0.15 MPa, there was little difference in root elongation responses for families 2–6. Family 1 showed superior elongation capacity at these suctions. Radicle elongation was zero at 1.68 MPa nominal suction for all families.

Analysis of variance revealed no significant differences ($P > 0.05$) between radicle elongation in the non-moisture limiting vermiculite petri dishes (3.36 cm average for all families) and in the 0.0065 MPa nominal matric suction treatment (3.33 cm average for all families).

Table 2. Experiment 2. Particle size characteristics (mean \pm s.d.) of study soils at 10 cm depth

Soil type	Sand (%)	Silt (%)	Clay (%)
Red dermosol	44 \pm 7.4	34 \pm 6.3	22 \pm 7.1
Brown sodosol	73 \pm 3.3	17 \pm 3.4	10 \pm 2.0

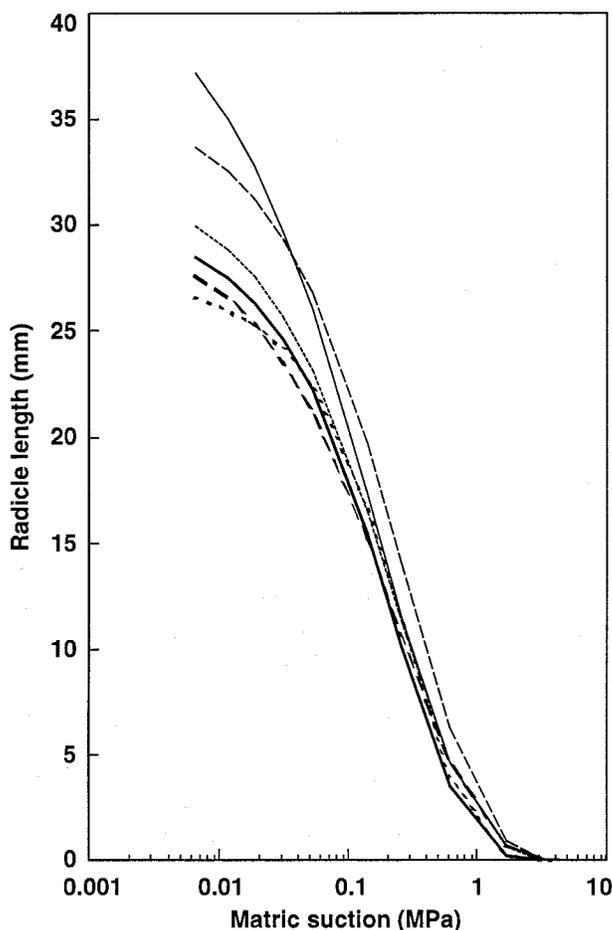


Figure 1. Experiment 1. The predicted impact of matric suction on 48 h radicle elongation for six families of *Pinus caribaea* var. *hondurensis*. --- Family 1, $R = 0.98$; — family 2, $R = 0.96$; ··· family 3, $R = 0.97$; —·— family 4, $R = 0.97$; - - - family 5, $R = 0.91$; ··· family 6, $R = 0.93$.

Experiment 2. Pregerminated seeds in repacked soils

Calculated matric suctions (from the moisture characteristic curves) and air-filled porosities for each treatment are presented in Table 3.

The response of radicle elongation (y) to the nominal suction (ϕ) for each family in each soil type was best modelled by the critical exponential equation (Fig. 2):

$$y = a + [b + c \times (\ln \phi)] \times r^{\ln \phi}$$

where a , b , c and r are coefficients (GENSTAT 5 Committee 1987).

Radicle elongation was optimal at 0.05 and 0.04 MPa suction for the red dermosol and brown sodosol respectively. For both soils, there was a narrow range of suctions (0.03–0.08 MPa and 0.03–0.06 MPa for the red dermosol and brown sodosol respectively), throughout

which matric suction had only a slight impact on radicle elongation (Fig. 2). These suctions equated to moisture contents of 24–18% and 12–8% respectively. Radicle elongation of all families decreased with matric suctions both above and below these optima.

In both soils, radicle elongation was severely suppressed by matric suctions in excess of 1.0 MPa. The relationship between matric suction and radicle elongation differed significantly ($P < 0.001$) between the red dermosol and brown sodosol growing media. Growth in the brown sodosol was more sensitive to suction changes, both above and below, the optimum.

Family differences in the regression relationships between radicle elongation and matric suction were highly significant ($P < 0.001$). Maximum radicle elongation at optimal matric suction was greatest in families 1 and 4. These families also performed better over much of the matric suction range 0.02–1.0 MPa for both growing media.

Discussion

Since plant and seed growth involves water uptake, it is difficult to provide experimental growing media with constant and uniform matric suction (Hillel 1980). The filter paper methodology developed for experiment 1 did not produce discrete matric suctions for each treatment. Rather, each treatment represented a suction range (Table 1), as a consequence of evapotranspiration. However, as all families were subjected to the same growing environment, the methodology enabled a comparison of family differences.

The filter paper method is simple, cost effective and quick to use. It should be possible to refine the technique to further limit moisture loss during experimentation, for example, by growing seeds for shorter periods, and operating in near-saturated atmospheres. The technique could also be used to investigate the impact of water-soluble nutrients or salts on radicle elongation, and to investigate matric suction \times temperature interactions.

Radicle elongation in the 0.0065 MPa nominal suction treatment was similar to that in the non-moisture limiting vermiculite dishes, suggesting: (i) that the overburden pressure of filter paper had not restricted elongation; and (ii) that moisture availability in both treatments was not limiting. If the 0.0065 MPa treatment, which had the wettest and therefore heaviest overburden filter paper did not impede root elongation, then negligible mechanical impedance can be assumed for the other treatments.

Radicle elongation decreased monotonically with increasing matric suction, ceasing at 1.68 MPa. Elongation was sensitive to suction throughout the range tested. Indeed, over the suction range 0.0065–0.031 MPa, where water availability might not be expected to be limiting (Hillel 1980; Kramer 1983), radicle elongation of

Table 3. Experiment 2. Moisture contents (%), matric suctions (MPa), bulk densities (g/cm³) and calculated air-filled porosities (%) for each treatment

Moisture content	Red dermosol			Moisture content	Brown sodosol		
	Matric suction	Bulk density	Air-filled porosity		Matric suction	Bulk density	Air-filled porosity
10	2.5	1.04	50	2.5	2.0	1.16	53
12	1.0	1.01	49	4	0.45	1.16	52
15	0.35	0.91	52	6	0.09	1.15	50
18	0.08	1.03	43	8	0.065	1.12	49
21	0.05	1.15	32	10	0.045	1.09	48
24	0.03	1.19	27	12	0.033	1.21	40
27	0.015	1.20	22	14	0.024	1.39	28
30	0.011	1.22	17	16	0.015	1.49	20
33	0.008	1.21	14	18	0.011	1.56	14
36	0.0055	1.22	10	20	0.0085	1.59	8
39	0.004	1.23	6				

all families declined by 14% from an average 3.33 cm to an average 2.88 cm. There was a rapid decline in radicle elongation at nominal matric suction greater than 0.031 MPa.

Passioura and Gardner (1990) observed that the relative leaf expansion rate of wheat grown in a silty loam with bulk density 1.30 g/cm³, decreased linearly in response to increasing matric suction (about 0.05–0.10 MPa). They postulated that wheat roots were capable of sensing small changes in both soil suction and strength, and that inhibitory signals emanating from the roots restricted leaf biomass development. Tardieu (1994) examined the growth and functioning of roots in compacted soils, and postulated that roots produce growth-inhibiting signals as a consequence of: (i) mechanical impedance, and (ii) water stress caused by restricted root system development in high mechanical impedance soils. In the filter paper experiment reported here, pretrial radicle lengths were similar for all treatments. The negative relationship between radicle elongation and increasing matric suction therefore suggests that radicles are able to sense small changes in water stress.

The relationships in Figure 1 between radicle elongation and matric suction may assist interpretation of studies designed to examine the impact of soil strength on root growth. If different strength treatments are achieved by allowing suction to vary, then both suction and strength will impact upon root growth. The relative contribution of the two may be difficult to separate, and indeed, may be additive (Mirreh and Ketcheson 1973; Veen and Boone 1990).

In experiment 1, matric suction was varied in an environment where aeration and mechanical impedance were not limiting. By contrast, in experiment 2, matric suction and air-filled porosity were varied in an

environment where penetration resistance did not exceed 0.2 MPa. The different responses in radicle elongation to increasing suction in the 2 experiments (Figs 1 and 2) can be attributed to an interaction between air-filled porosity and matric suction.

For treatments with less than 0.03 MPa suction in experiment 2, air-filled porosities clearly limited radicle elongation (Fig. 2). This suction equates to air-filled porosities of about 25 and 35% for the red dermosol and brown sodosol respectively (Table 3). Such levels are not normally considered limiting to growth (Sands and Bowen 1978; Theodorou *et al.* 1991); though Eavis (1972a) has reported aeration impacts on root growth with air-filled porosities of 30, 22 and 11% in low, medium and high bulk densities respectively. Three possible explanations for the observed sensitivity to air-filled porosity can be advanced: (i) there is no critical level of aeration, above which radicle elongation will be unaffected by air-filled porosity; (ii) the repacked soil has a relatively uniform pore size distribution, which at low matric suctions, limits the continuity of air-filled pores; and/or (iii) matric water held at suctions less than 0.03 MPa is redistributed downwards in the growth cylinders, resulting in lower air-filled porosities at depth. The latter 2 explanations imply that the optimum matric suction for radicle elongation in repacked soils will depend upon bulk density (see also Eavis 1972a).

The relationships between radicle elongation and matric suction over the range 0.1–1.0 MPa in experiments 1 and 2 are similar (Figs 1 and 2). A suction of 0.1 MPa equates to air-filled porosities of about 45 and 50% for the red dermosol and brown sodosol respectively (Table 3). This result implies that the adverse effects on radicle elongation of increasing suction above 0.1 MPa have dominated any positive effects of increasing air-filled porosities.

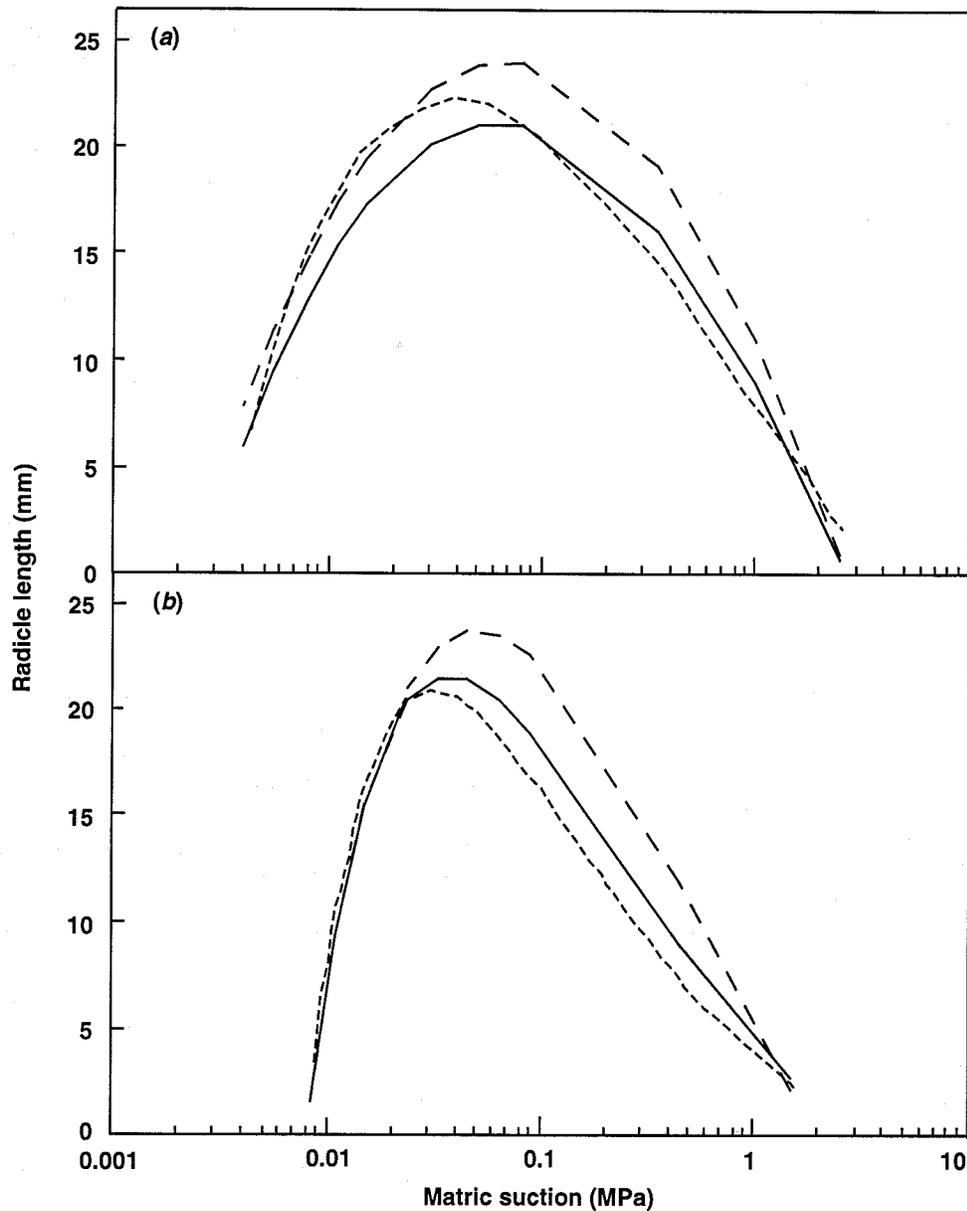


Figure 2. Experiment 2. The predicted effect of matric suction on radicle elongation in two soil media for three of the six *Pinus caribaea* var. *hondurensis* families tested. (a) Red dermosol: — family 1, $R = 0.87$; — family 2, $R = 0.92$; - - - family 5, $R = 0.83$. (b) Brown sodosol: — family 1, $R = 0.82$; — family 2, $R = 0.87$; - - - family 5, $R = 0.84$.

Elongation of *P. caribaea* var. *hondurensis* radicles in the repacked soil media is sensitive to both matric suction and air-filled porosity. In high strength growing media, it is likely that radicle elongation will be inhibited by increasing mechanical impedance (see Costantini *et al.* 1996), increasing matric suction and decreasing air-filled porosity. Letey (1985) proposed a useful model for conceptualising the effect of water content on plant growth

in soil media. He defined a 'non-limiting water range' over which water content had no impact on plant growth. At decreasing water contents, mechanical impedance limited growth, and at higher water contents aeration limited growth. Letey (1985) observed that the non-limiting water range was dependent upon bulk density and structure, decreasing with higher bulk densities and poorer structure (see also Voorhees *et al.* 1975).

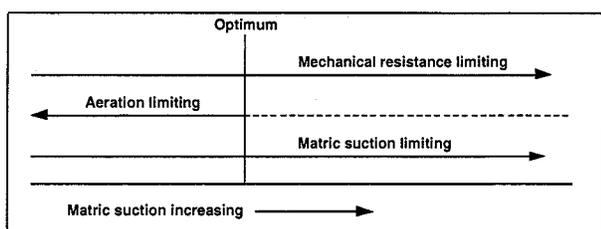


Figure 3. Generalised relationship between water content and dependent physical parameters which limit *Pinus caribaea* var. *hondurensis* radicle elongation (after Letey 1985).

In order to describe the matric suction–aeration–mechanical resistance interactions that affect *P. caribaea* var. *hondurensis* radicle elongation, the model of Letey (1985) must be modified by including a matric suction effect, and refining the concept of a non-limiting water range (Fig. 3). Results from experiment 1 have demonstrated a monotonic decrease in radicle elongation as suction increased: strictly, there is no ‘non-limiting water (matric suction) range’ over which water content has no impact on radicle elongation. Because of the interaction between matric suction and air-filled porosity in soil media, however, a matric suction range can be defined, over which radicle elongation is little affected. This range was less in the more compact brown sodosol than the red dermosol.

The dashed line in Figure 3 implies that there may be an aeration effect at matric suctions greater than the optimum which are over-shadowed by mechanical resistance and matric suction effects (see also Froehlich and McNabb 1984). Bulk density (Eavis 1972a), temperature (Letey 1985), structure (Letey 1985) and pore size distribution would all influence the location of the optimum in Figure 3. The model in Figure 3 implies that increasing matric suction will act to decrease *P. caribaea* var. *hondurensis* radicle elongation, but that there may be a matric suction range over which elongation is relatively unaffected because of the interaction between aeration, mechanical resistance and matric suction effects.

The ‘family x matric suction’ interactions observed in both experiments may be of interest to breeding programs, and warrant further investigation. If radicle development can be correlated with desirable productivity parameters, it may be possible to use the methods presented in this paper to select families at an early age for suitability to dry soils.

Conclusions

Over a matric suction range 0.0065–3.13 MPa, the relationship between radicle elongation in an environment where neither matric suction nor aeration were limiting, and the natural logarithm of suction was

best defined by a Gompertz equation constrained to be asymptotic to zero. There was no critical suction below which elongation was unaffected; rather, elongation was sensitive to suction throughout the range tested. Radicles appeared to be able to sense, and respond to, increasing suction. Elongation ceased at a nominal matric suction of 1.68 MPa.

In low strength, repacked soil growing media where both air-filled porosity and matric suction were varied, an optimum matric suction range for radicle elongation was observed. At lower suctions, air-filled porosities less than 25 and 35% in a clay loam red dermosol and sandy loam brown sodosol respectively, reduced elongation. At higher suctions, radicle elongation decreased with increasing moisture stress. In soil growing media, both air-filled porosity and matric suction interact to affect radicle elongation. Whilst increasing matric suction will act to decrease *P. caribaea* var. *hondurensis* radicle elongation, there may be a suction range in soil media, over which elongation is relatively unaffected because of an interaction with aeration.

The findings reported here highlight the need to separate matric suction and aeration effects from soil strength effects when investigating root growth in soil media with different strengths.

A method for using the wetting characteristics of Whatman No. 42 filter paper to investigate the impact of matric suction on radicle elongation was presented. The technique made it possible to define the relationship between radicle elongation and matric suction, and to define differences in root growth between families.

Significant differences in the responses of families to matric suction were observed. If these differences could be correlated with performance in the field, then they might serve as a useful early indicator of suitability to dry soils.

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