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THE UNIVERSITY OF ALBERTA

EXPRESSION OF ROOT GROWTH POTENTIAL OF WHITE SPRUCE SEEDLINGS: SOIL TEMPERATURE AND MOISTURE EFFECTS

BY

LYN KONOWALYK

A THESIS

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in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

Root growth potential (RGP), the ability of tree seedlings to produce new roots under "optimum" conditions, is the most widely used test of seedling quality. To explain plantation success or failure it is necessary to understand both the physiological condition of seedlings, RGP, and the interaction of seedling quality with the environment (i.e., the "expression of RGP" or, in this study, actual root growth as a percentage of RGP). A series of controlled environment experiments was conducted to evaluate the effect and interaction of two primary environmental factors - soil temperature and moisture - on expression of RGP of cold-stored bareroot and containerized white spruce seedlings. Water relations of the containerized stock were also examined.

Number and total length of new roots were reduced when seedlings were grown under less than optimum levels of soil temperature (5, 10, 15°C) and moisture (-0.13, -0.03, -0.01 MPa matric potential) compared with seedlings grown under 'optimum' conditions (i.e., 20-25°C and -0.01 MPa). Total length of new roots was reduced more than was root number. Root growth of bareroot stock ranged from 3% at 10°C/-0.05 MPa to 50% at 15°C/-0.02 MPa (number) and 1% at 10°C/-0.05 MPa to 31% at 15°C/-0.02 MPa (total length). Root growth of containerized stock was higher, ranging from 32% at 5°C/-0.13 MPa to 100% at 15°C/-0.01 MPa (number) and 3% at

5°C/-0.13 MPa to 34% at 15°C/-0.01 MPa (total length).

Soil temperature had a greater effect on total length of new roots than soil moisture accounting for 26% (R^2) of variation in root length of containerized stock compared to 5% for moisture. Number of new roots was affected equally by soil temperature (R^2=13%) and moisture (R^2=12%).

Xylem pressure potential, stomatal conductance, and total water use of the containerized stock was reduced at the low levels of soil temperature/moisture. Subsequently, reduced photosynthesis at the lower levels likely limited root growth.

The magnitude of water uptake was not related to new root production (number or length). The volume of the planted root system was relatively more important for water uptake.

ACKNOWLEDGEMENTS

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1.0 INTRODUCTION

There has been a dramatic increase in tree planting in Canada in the last 10 years. The number of seedlings planted annually in Alberta increased from approximately 650,000 in 1976 to 1.5 million in 1980, to 4.4 million in 1983 and to 18.3 million in 1987 (Luchkow 1981; Smyth and Brownwright 1984). Additionally, there is an increased awareness of the importance of planting high-quality stock to ensure reforestation success (Duryea and Landis 1984; Navratil et al. 1986). High-quality stock was defined at the 1979 IUFRO workshop in New Zealand as "the degree to which planting stock realizes the objectives of management" (Navratil et al. 1986), which are seedling survival and growth.

Morphological characteristics of tree seedlings are inadequate indicators or predictors of survival and growth after outplanting. The physiological quality of seedlings should also be considered (Wakely 1948; Stone 1955). One physiological attribute considered indicative of seedling performance is root growth potential (RGP), the ability of tree seedlings to produce new roots after being planted into "optimum" environments. RGP is a condition induced by fixed genetic characteristics and environmental conditions during nursery growth and care (Krugman and Stone 1966; Stone and Jenkinson 1971). RGP represents a 'potential' to grow roots. As planting site conditions are rarely "optimum", rarely is RGP expressed fully. Following planting, the "expression of RGP", or actual root growth, is affected by soil temperature, soil moisture, and other factors (Ritchie 1985).

Stone and others (Stone 1955; Stone and Schubert 1959; Stone et al. 1963) developed procedures to measure RGP. These include potting a sample of seedlings and maintaining them for a given period of time in "ideal" environmental conditions for a particular species. After this period, traditionally 28 days, the seedlings are excavated and new root production is quantified (Stone and Jenkinson,1971; Ritchie, 1984). Root production is often quantified as total number or length of new roots.

The rationale of the test is based on two assumptions. Firstly, RGP determined under laboratory conditions provides an estimate of actual root growth in the field ("expression of RGP") and secondly, root growth is a major determinant of the ability of outplanted seedlings to avoid desiccation (Stone 1955). Therefore, it is Stone's contention that RGP is correlated with field performance because it is related to drought resistance (Stone 1955).

RGP is related to seedling survival or growth (Stone 1955; Stone et al. 1962; Burdett 1979; McMinn 1980; Sutton 1980, 1987; Burdett et al. 1983; Van den Driessche 1983; Feret and Kreh 1985; Feret et al. 1985; Larsen et al. 1986), but the correlations are not always strong; reported R^2

values range from -0.03 to 0.96. Brissette and Roberts (1984) found no relationship between RGP and field performance. When a relationship is weak or absent, confounding factors, such as site conditions, planting date or limited range of variation in RGP of the stock tested, are suspected (Sutton 1980, 1983; Burdett 1987). Whenever a poor relationship is found, questions arise about the validity of RGP as a test of seedling quality.

The assumptions underlying Stone's contention have been questioned. To date, no direct relationship has been found between RGP and its "expression" (i.e., actual root growth) in the field (Sutton 1980; 1983; Ritchie 1985). The recovery of normal water status in outplanted seedlings is usually accompanied by new root growth (Abod et al. 1979; Lopushinsky and Kaufmann 1984; Grossnickle and Blake 1985). However, changes in the permeability of older suberized roots (Grossnickle and Blake 1985) and changes in stomatal resistance (Blake 1983) can result in the recovery of water status independent of root growth. Therefore, other hypotheses are suggested. Ritchie (1985) proposed that RGP is correlated with field performance because it is related to cold hardiness and other types of stress resistance. Burdett (1987) suggested that RGP may be related to field performance because it is a good test of seedling viability. It is difficult to establish a clear cause-effect relationship between RGP and seedling survival after outplanting.

To explain planting success or failure it is necessary to understand the physiological condition of seedlings, RGP and the interaction of RGP with the environment (i.e., the "expression of RGP"). Soil temperature and moisture are primary site factors affecting root growth of outplanted seedlings (Ritchie and Dunlap 1980; Kaufmann 1977). Research has been conducted to determine the effects of soil temperature or soil moisture on root growth but studies including both factors are non-existent. Additionally, research has focused primarily on optimum levels, therefore little information exists on RGP expression under less favorable conditions.

Soil moisture levels near field capacity (Day and MacGillivray 1975; Larson and Whitmore 1970; Stone and Jenkinson 1970) and soil temperatures of 18 to 24°C (Ritchie and Dunlap 1980; Ruark et al. 1983) are optimum for root growth of many temperate zone species. Optimum levels of both soil moisture and temperature are rarely encountered in the field. Soil temperatures in Boreal forest cutovers during spring and autumn planting times are generally lower than optimum levels, usually ranging from 5 to 15°C (Day and Harvey 1984; Tear 1979; Silversides et al. 1985). The effect of low soil temperature can be mitigated by favorable supplies of water (Nielsen 1974). Thus it is of interest to study the interaction of the two factors. The objective of this study was to evaluate the effect and interaction of soil temperature and moisture on the "expression of RGP" of cold-stored bareroot and containerized white spruce (*Picea glauca* (Moench.) Voss) seedlings in a controlled environment. The study also examined stomatal conductance, xylem pressure potential, and total water use of containerized white spruce seedlings. The results are discussed in view of Stone's contention.

2.0 METHODS

Three trials were conducted. The first trial was two plantings of 90 bareroot seedlings, the second trial was one planting of 90 bareroot seedlings, and the third trial was two plantings of 90 containerized seedlings. Methodology was basically the same for each trial and thus will be presented collectively. The trials will be considered separately only where differences existed.

2.1 Plant Material

Trial 1. Fall-lifted (3+0) bareroot white spruce seedlings (seedlot DR 41-15-5-79) were obtained from Pine Ridge Forest Nursery. The seedlings were in frozen storage at -2°C for 8.5-10 months prior to planting in spring/summer of 1987.

Trial 2. Fall-lifted (3+0) bareroot seedlings from a different white spruce seedlot (DL 67-12-4-79) were obtained from the nursery in the winter of 1988. These seedlings were in frozen storage at -2°C for 10 weeks prior to planting in January, 1988.

Trial 3. Pine Ridge Forest Nursery also supplied containerized (1+0) white spruce seedlings (seedlot DW 60-20-5-83) grown in Spencer-Lemaire Root Trainers (container volume 40 cm^3). These seedlings were in frozen storage at -2°C for 6-7 months prior to planting in spring 1988.

2.2 Controlled Environment Conditions

In the first trial, the seedlings were placed in a growth chamber programmed to provide 'ideal' conditions (Day 1982) for root growth of white spruce seedlings. Such conditions included: 16-hour days at 25°C air temperature; 8-hour nights at 17.5°C; light intensities of 220 $umol.m^{-2}.s^{-1}$ and; a minumum relative humidity of 50%. Because seedling mortality was high in Trial 1, the chamber was re-programmed for the second and third trials to provide a constant air temperature of 20°C in an attempt to reduce transpirational stress of seedlings.

2.3 Soil Mixture

Sandy loam soil mixtures were prepared by combining fine sand, coarse sand, and loam (1:1:5, by volume). The components were thoroughly mixed and autoclaved at 120°C for 50 minutes. The soil mixture was then passed through a 2-mm screen.

A soil moisture desorption curve was established using a volumetric pressure plate apparatus (Richards, 1965). Because new shipments of loam and sand were available after the first trial, two soil moisture desorption curves were constructed. The curve for the first trial indicated -0.02, -0.05, and -0.32 MPa (1 MPa=10 bars) matric potentials at 18, 14, and 10% soil moisture contents (% dry weight) (Appendix I). Soil mixes at these moisture contents were prepared by mixing calculated quantities of moist soil (field capacity) with air dry soil and by equilibrating the mixtures in sealed drums (approximately 100 L) for several days (Stone and Jenkinson 1970).

Higher moisture contents were used for Trials 2 and 3. These were: 20, 16, and 12% (% dry weight) which exerted -0.01, -0.03, and -0.13 MPa soil water potential respectively, according to the second soil moisture desorption curve (Appendix I). For coarse-textured soils, -0.01 MPa represents 'field capacity' or the matric potential of soil after all free drainage water has been removed (Hillel 1971).

The soil mixes for Trial 2 were prepared in the same way as for Trial 1. The mixes for Trial 3 were prepared by repeatedly mixing a calculated amount of water with a small quantity (6 kg) of air dry soil until the appropriate amount of mixture was prepared. These mixtures were also left to equilibrate in sealed drums for several days.

One day prior to each planting, three samples were collected from each drum to determine the actual moisture contents (Appendix II). These moisture values were used to calculate the appropriate 'wet weight' of soil to be added to each container. In general, the actual moisture contents were lower than desired so the amount of water necessary to bring the moisture content to the desired level was also calculated.

2.4 Planting

Seedling size varied within each trial. Seedling fresh weight, stem height, and root collar diameter were measured at the time of planting (Table 1). Additionally, root volume of the bareroot stock was measured using a displacement technique (Burdett 1979). The bareroot stock (Trials 1 and 2) was larger than the containerized stock (Trial 3).

Each seedling was planted into a plastic container with a volume of approximately 1.2 L. A pre-determined 'wet weight' of the appropriate soil moisture mix was placed in each container to a pre-defined level (18 cm deep) to ensure equal soil volume (1190 cm^3) and bulk density (1.1 $Mg.m^{-3}$). The 'standard weight' of each container was determined by summing the container weight, seedling fresh weight, soil weight for the given moisture content, and amount of water,

Table 1. Means and (ranges) of seedling morphological characteristics.

Trial	Fresh weight (g)	Stem height (cm)	Root collar diameter (mm)	Root Volume (cm^3)
1	29.1 (13.2-65.5)	26.8 (18-37)	6.2 (4.0-9.7)	4.2 (0.5-13.9)
2	28.8 (7.8-45.7)	26.8 (17-39)	5.9 (3.8-8.0)	3.9 (1.1- 8.5)
3	25.3 (17.2-32.5)	10.6 (6.0-13.7)	2.1 (1.6-2.6)	n.d.[1]

[1] n.d. - not determined

when required. For Trial 3, in which containerized stock was used, seedling fresh weight included the weight of the moist peat plug.

2.5 Soil Moisture Treatment

After planting, each container held soil of approximately uniform moisture distribution. Thereafter, each container was weighed every 48 hours to determine the amount of water used. This amount was then replaced by watering the soil surface as uniformly as possible with a fine spray. Except during the brief watering period, the soil surface of each container was covered with styrofoam and aluminum foil to insulate the soil and minimize evaporative water loss.

The soil moisture distribution within the containers was examined at the end of each test period in conjunction with the harvest. As the seedlings were excavated, soil samples were collected from three relative positions (top, middle, bottom) of a subsample of the containers (i.e., two containers of each moisture/temperature combination). The lowest position sampled for Trial 3 was the area just beneath the plug; the plugs did not extend to the bottom of the containers.

The results of this monitoring demonstrated that the average moisture content per container was within |2%| of the target level for all trials (Appendix III). Differences in soil moisture existed within each container. Generally, the top layer of soil in each container was at the highest moisture content. At the various temperature/ moisture combinations, average absolute differences in % moisture content per container ranged from 2.2 to 6.1% 24 hours after watering and 0.5% to 6.8% 48 hours after watering in Trial 1 and 1.4 to 5.2% 48 hours after watering in Trial 2. For Trial 3 the range was 0.2 to 1.6% 24 hours and 0.6 to 2.6% 48 hours after watering.

2.6 Soil Temperature Treatment

Soil temperatures of 5, 10, and 15°C were maintained at +/-1.5°C by placing the potted seedlings into one of six insulated water baths. Each bath, 0.8x0.6x0.3 m in size, held a network of copper tubing. Cooled glycol was independently pumped through each network of copper tubing by thermostatically-controlled pumps. The water within each bath was continuously circulated to minimize temperature gradients. Two refrigeration units were available to cool the glycol so each unit cooled three water baths. The three water baths cooled by one refrigeration unit were set at the complete range of soil temperature (i.e., 5, 10, and 15°C). This resulted in the formation of two distinct blocks or replicates. Each bath was randomly assigned a temperature setting before each planting. Five containers of each moisture level were randomly placed within each bath for a total of 15 containers per bath.

2.7 Experimental Design

The water baths represented temperature as the whole unit factor and, with five seedlings at each soil moisture level within each bath, moisture was the sub-unit factor (Fig 1). Three water baths completed one experimental unit; the second three were a replicate. For some trials the experiment was also replicated in time. The experiment was repeated twice for Trials 1 and 3 and therefore, four replicates were obtained for each trial. Trial 2 was not repeated so only two replicates existed. The resulting design was a split plot (3x3 factorial); x number of repetitions or plantings of 2 blocks of 5 seedlings per soil moisture/temperature combination. This resulted in a total sample size of 180 seedlings for Trial 1, 90 seedlings for Trial 2, and 180 seedlings for Trial 3 (plantingsx2x5x3x3).

2.8 Standard RGP Test

In conjunction with each planting, 15 additional seedlings were potted. These seedlings were placed on the bench in the growth chamber. The soil surfaces of these containers were also covered with styrofoam and aluminum foil. Soil moisture of these containers was maintained at a high level (18 or 20%) by weighing each container every 48 hours and replacing the amount of water used. Soil

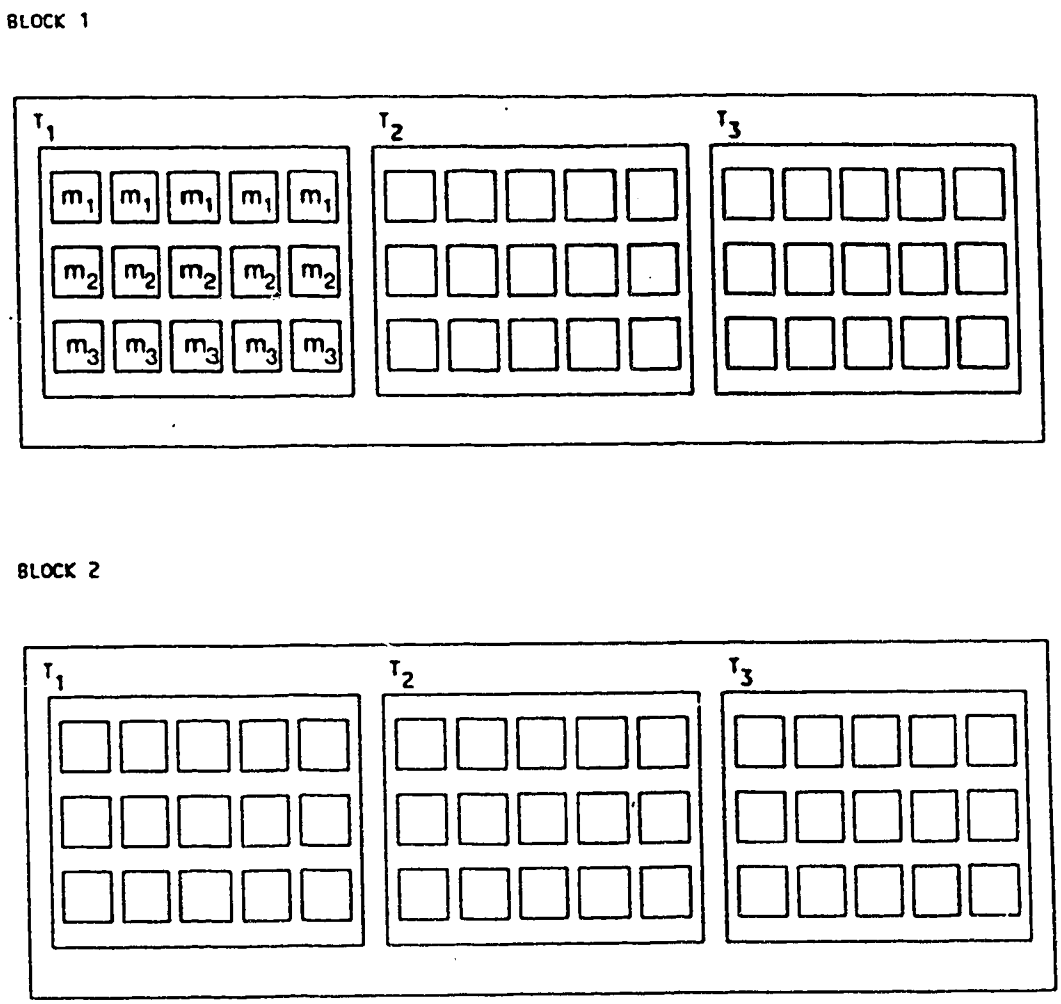


Figure 1. Schematic layout of experimental design. The largest boxes represent the blocks; the intermediate boxes represent the whole unit factor (temperature, T) and; the smallest boxes represent the sub-unit factor (moisture, m).

temperatures were allowed to equilibrate with air temperature of 25°/17.5°C (day/night) for Trial 1 and 20°C for Trials 2 and 3. This treatment was considered a 'standard RGP test'. The parameters of root growth obtained at the various experimental soil temperature and moisture levels were expressed as percentages of the mean standard RGP values.

2.9 Sampling Procedure

2.9.1 Root Measurement

Trials 1 and 2. At the end of the test period, the seedlings were carefully removed from the containers and the roots were washed. Each new root $\geq$ 1 mm in length was counted and measured. The test periods for these two trials were variable in length due to poor root growth. For the first planting of Trial 1, one block was harvested after 28 days, the other after 32 days. Both blocks in the second planting of Trial 1 were harvested after 28 days. In Trial 2 one block was harvested after 28 days; the other after 35 days.

Trial 3. The containerized seedlings were harvested after 21 days. The seedlings were removed from the containers and the plugs were gently washed to remove only the soil mixture adhering to the sides of the plug; the peat in the plug was left intact. Root growth was measured by counting the number and measuring the length of new roots extending at least 1 mm from the plug (i.e., root egress). Plugs were not washed completely to prevent breakage of new roots and to reduce measuring time. To be consistent with the rationale of RGP-testing, it was felt emphasis should be placed on new roots growing beyond the plug into the exterior.

2.9.2 Water Relations Components

A record was kept of the water added to each seedling over each test period. These values were corrected for evaporation/condensation and then used as estimates of water use per seedling. Estimates of evaporation/ condensation were obtained by conducting a small test at the end of the study. Soil of each moisture level was placed in 12 containers so that 36 containers were filled in a fashion similar to those of the trials. The soil surfaces of these containers were covered with styrofoam and aluminum foil as in each trial. Two containers of each moisture level were then placed in each water bath. The containers were weighed every 48 hours to determine the amount of water evaporated or condensed. When water was lost, the appropriate amount was replaced by watering the surface as uniformly as possible with a fine spray. The test was conducted for nine days.

The results of the test indicated that evaporation/condensation differed significantly with soil temperature but not with soil moisture (Appendix IV). Water use at 5°C was under-estimated because condensation occurred; water use at 10° and 15°C was over-estimated because there were evaporative losses. Thus water used per seedling every 48 hours was modified as follows: 5°C - 0.575 ml was added; 10°C - 0.1125 ml was subtracted and; 15°C - 1.0875 ml was subtracted.

For Trial 3, stomatal conductance (cm sec^{-1}) measurements were taken using a steady-state porometer (LI-1600, Li-Cor Ltd.) equipped with a cylindrical chamber. Two seedlings of each soil temperature/moisture combination per block were randomly selected for measurement. Current-year's needles of the terminal shoot tip were marked with fine string. Measurements were taken only once on day 21 at mid-morning (approximately two hours after 'lights on'). The terminal shoots were then clipped well below the needles used for the measurements, bagged, and kept in cold storage until needle lengths were measured. Needle length was related to leaf area by linear regression equations developed for the primary and secondary needles (Appendix V). Leaf area was determined using the glass bead technique (Thompson and Leyton 1971). Total needle surface area typically enclosed in the porometer cuvette was 60 cm^2.

Xylem pressure potential (MPa) measurements were taken immediately following the needle conductance measurements on day 21. The same terminal shoots used in the conductance measurements were measured using a pressure chamber and a hand-held lens.

2.10 Data Analysis

No statistical analyses were conducted on the results of Trials 1 and 2 because of missing data caused by seedling mortality. There was 42% and 52% mortality in Trials 1 and 2, respectively. Analysis of variance procedures (SAS statistical package, 1987) were used to test root growth and water relations data of Trial 3 for significant differences among the main effects (temperature and moisture) and the temperature/moisture interaction (Table 2). Due to the heterogeneous variances of the data, log-transformations were used. Rank transformations which provide a distribution-free test were employed (as recommended by Conover and Iman 1981) to verify the results. The results of the two tests were comparable in all cases. Significant effects were modelled using regression analysis so as to describe the relationships quantitatively.

Table 2. Analysis of variance model used to test root growth and water relations data of Trial 3.

Source	Degrees of freedom
Run (R)	1
Block/Run (B/R)	2
Temperature (T)	2
T.R + T.B/R	6
Moisture (M)	2
M.R + M.B/R	6
M.T	4
M.T.R + M.T.B/R	12
Seedlings/B/R.T.M	144
TOTAL	179

3.0 RESULTS

3.1 Trials 1 and 2 (Bareroot Stock)

3.1.1 Mortality

Mortality of bareroot seedlings was high (Figs 2 and 3). Seedlings which did not produce new roots by the end of the test period were considered dead. Seedling mortality increased with decreasing soil moisture. Overall mortality in Trial 1 was 72% at -0.32 MPa soil water potential, 43% at -0.05 MPa, and 17% at -0.02 MPa. At the higher soil moisture contents used in Trial 2, overall mortality was 83% at -0.13 MPa, 47% at -0.03 MPa, and 17% at -0.01 MPa. Seedling mortality was not greatly affected by soil temperature as indicated by the small differences in mortality between the temperature levels. Overall mortality for Trials 1 and 2 respectively, was 40% and 53% at 5^{o}C, 45% and 53% at 10^{o}C, and 47% and 40% at 15^{o}C.

3.1.2 Root Growth

Root growth obtained under the soil temperature and moisture treatments (the "expression of RGP") is presented as a percentage of the standard value (i.e., RGP) obtained for each planting (Table 3).

Generally, root growth was low at the lower levels of soil temperature and moisture. For Trial 1, the total length of new roots was less than 5% of the standard for all treatment levels except at 15^{o}C at the -0.05 and -0.02 MPa

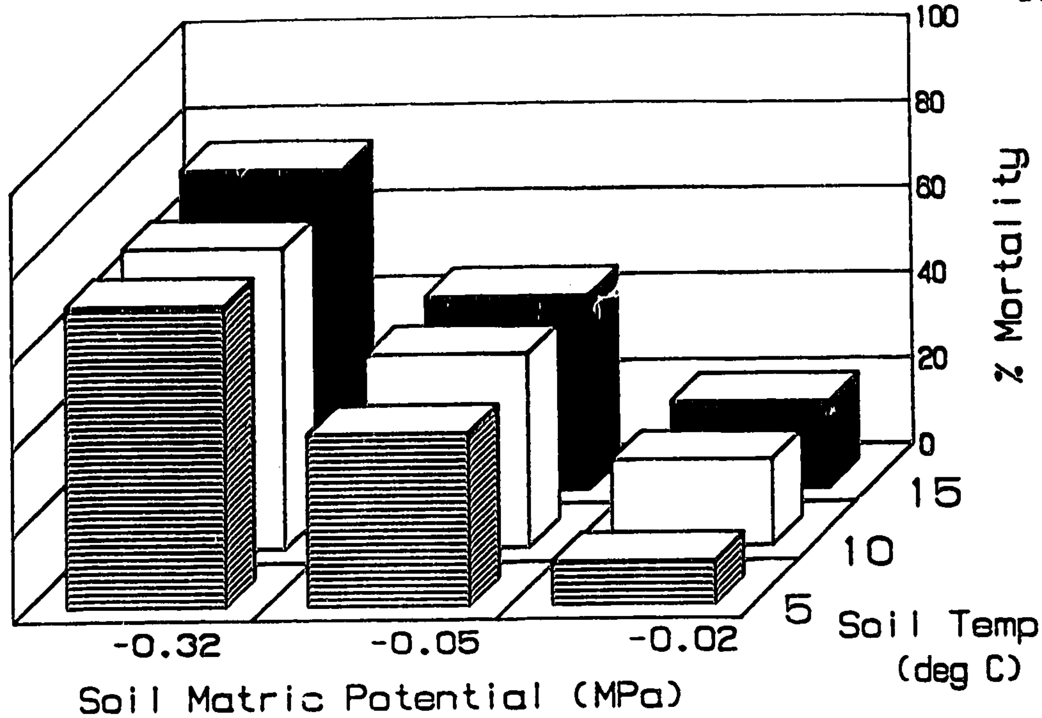


Figure 2. Trial 1: seedling mortality.

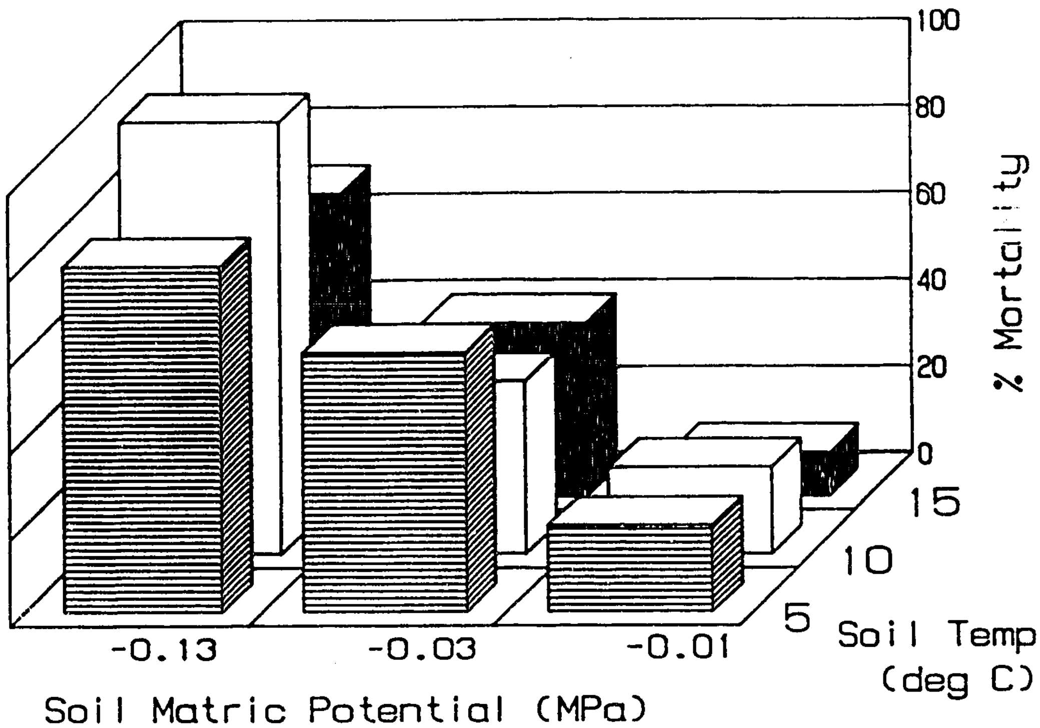


Figure 3. Trial 2: seedling mortality.

Table 3. Mortality (%) and standard RGP test results for Trials 1 and 2.

Trial	Run	Mortality (%)	Test Period (days)	n	New Roots Number		Length (cm)	
1	1	26.7	28	1	54.0	-	22.6	-
			32	10	79.2	(50.3)	54.1	(32.8)
	2	0.0	28	6	148.8	(67.2)	137.8	(74.3)
2	1	26.7	28	3	42.7	(7.9)	46.9	(42.5)
			35	6	46.6	(44.6)	56.6	(49.1)

Note: Values within parentheses are standard deviations; n=number of seedlings.

levels where length was 10 and 31% (Fig 4). Root number was 29% and 50% of the standard at 15°C at -0.05 and -0.02 MPa and 19% at 10°C and -0.02 MPa; at all other levels root number was less than 10% (Fig 5). For Trial 2, total root length was less than 5% of the standard with the exception of the highest temperature/moisture combination (15°C and -0.01 MPa) where length was 16% (Fig 6). Root number at the various temperature/moisture combinations was more variable (Fig 7). The greatest root number was 40% at 15°C and -0.01 MPa.

3.1.3 Water Relations

The volume of water used per seedling every 48 hours fluctuated slightly over time but generally remained at a constant level. Total water use per seedling over 28 days was greater at higher soil temperature/moisture levels (Fig 8 and 9). The trend in water use was similar to the trend in new root production but this is not necessarily a cause-effect relationship. Temperature and moisture treatments could affect water uptake capacity of the original roots as well. To identify the relationship between new root production and water uptake, correlations within each temperature/moisture level were analyzed.

Correlations (coefficients of determination, R^2) between total water use per seedling at each temperature/moisture level and the number and total length of new roots

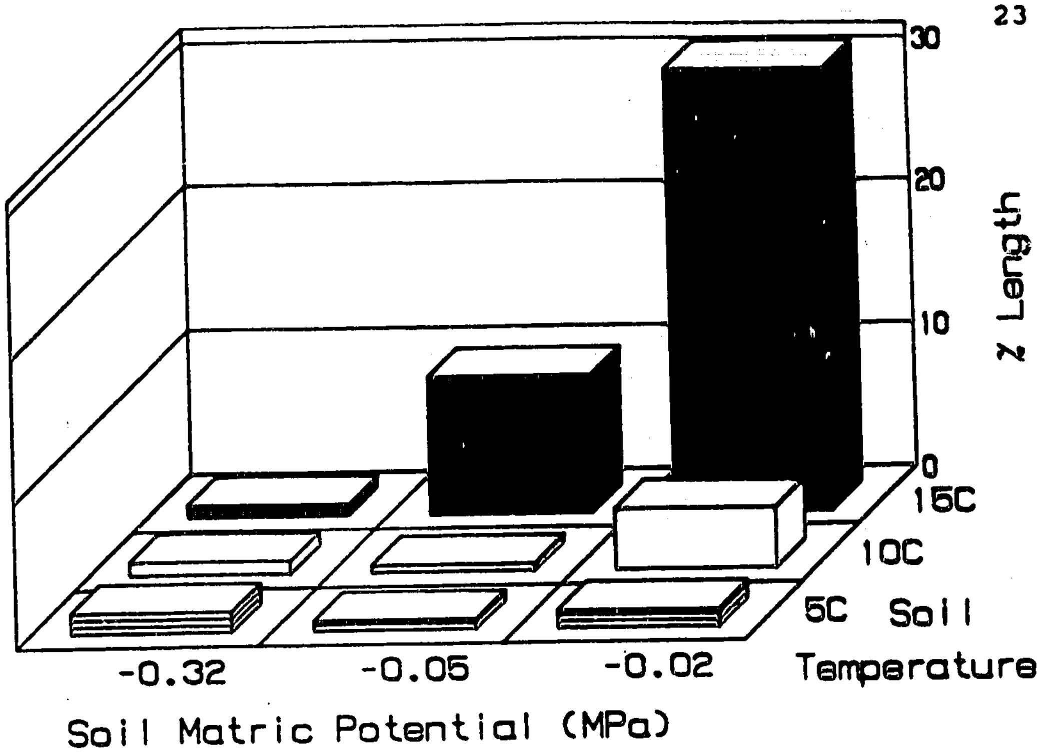


Figure 4. Trial 1: expression of total length of new roots.

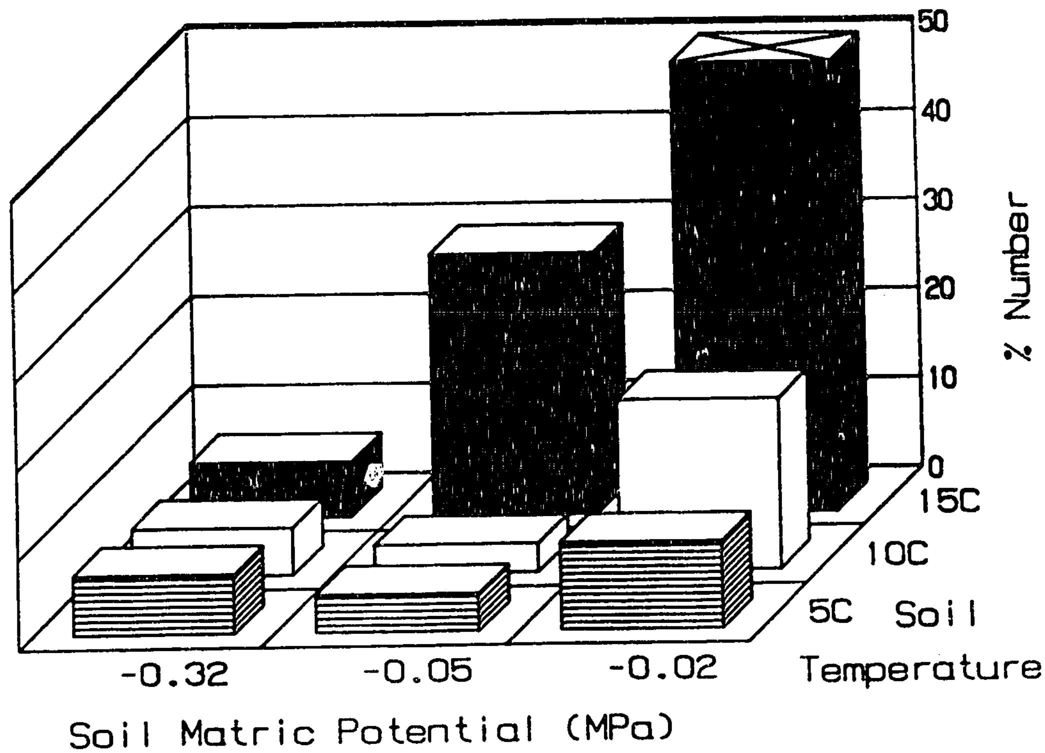


Figure 5. Trial 1: expression of number of new roots.

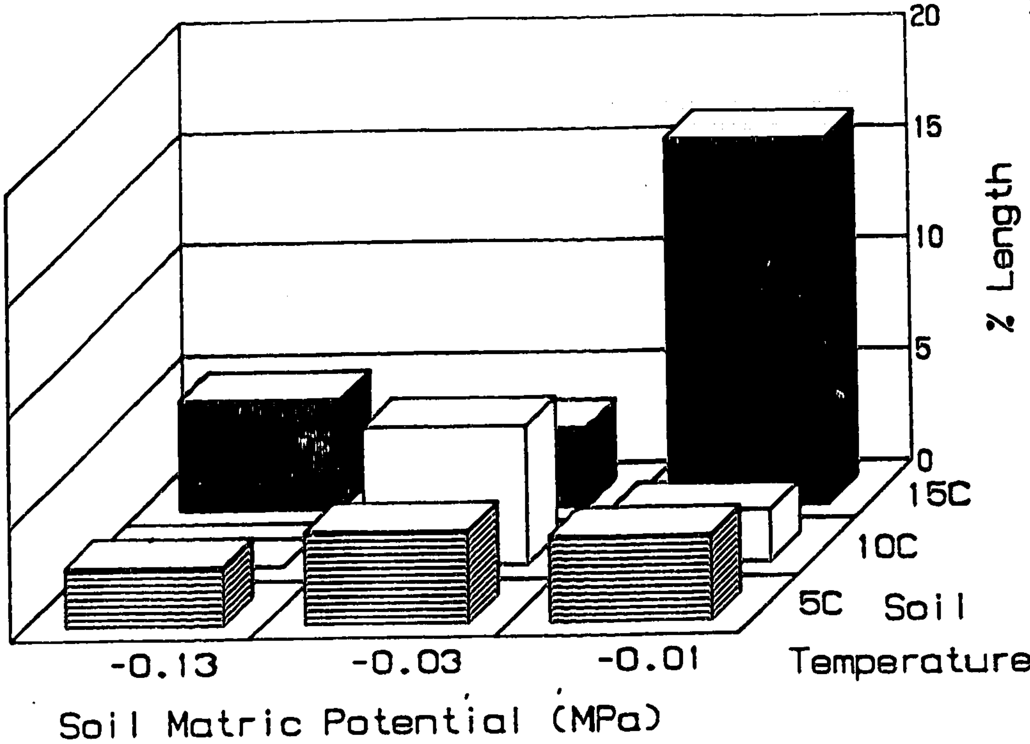


Figure 6. Trial 2: expression of total length of new roots.

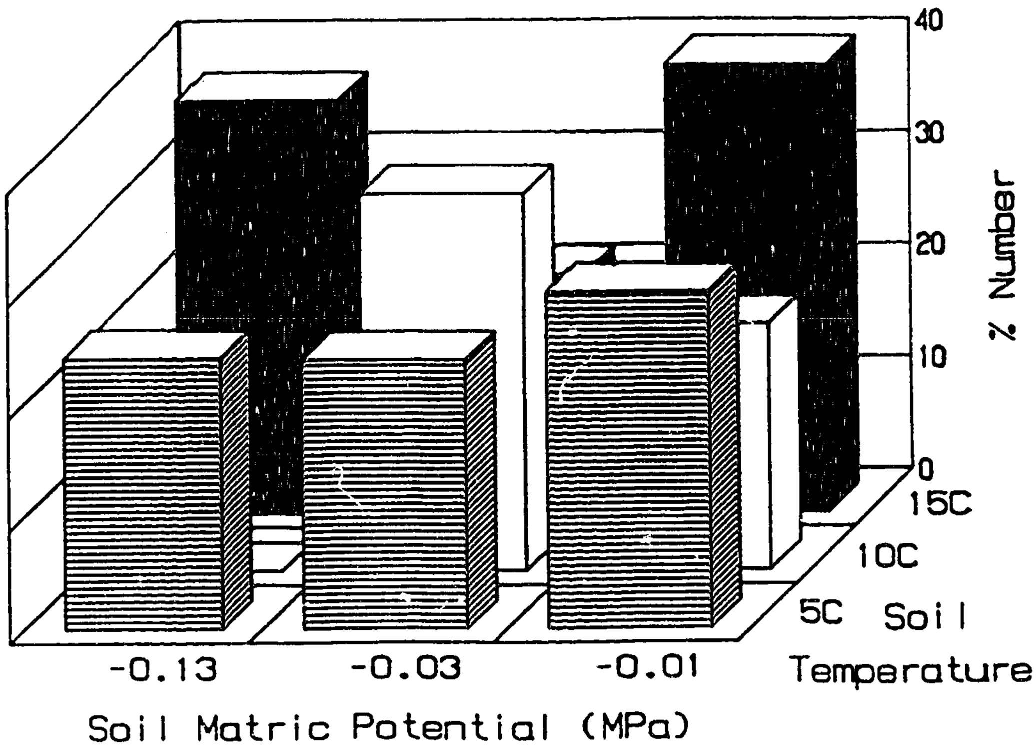


Figure 7. Trial 2: expression of number of new roots.

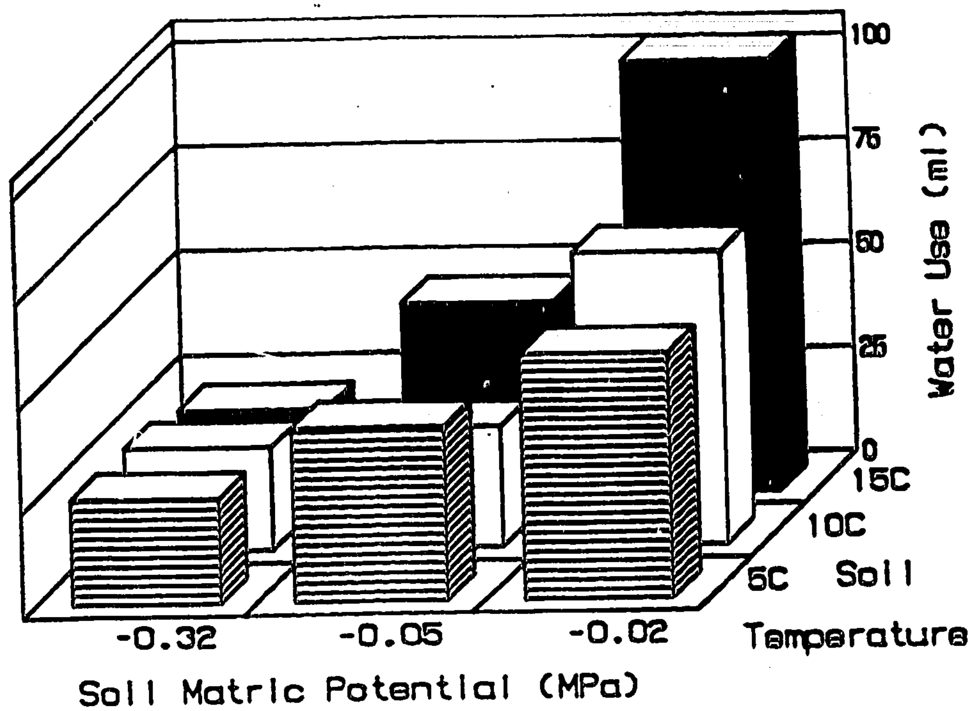


Figure 8. Trial 1: total water use corrected for evaporation/ condensation.

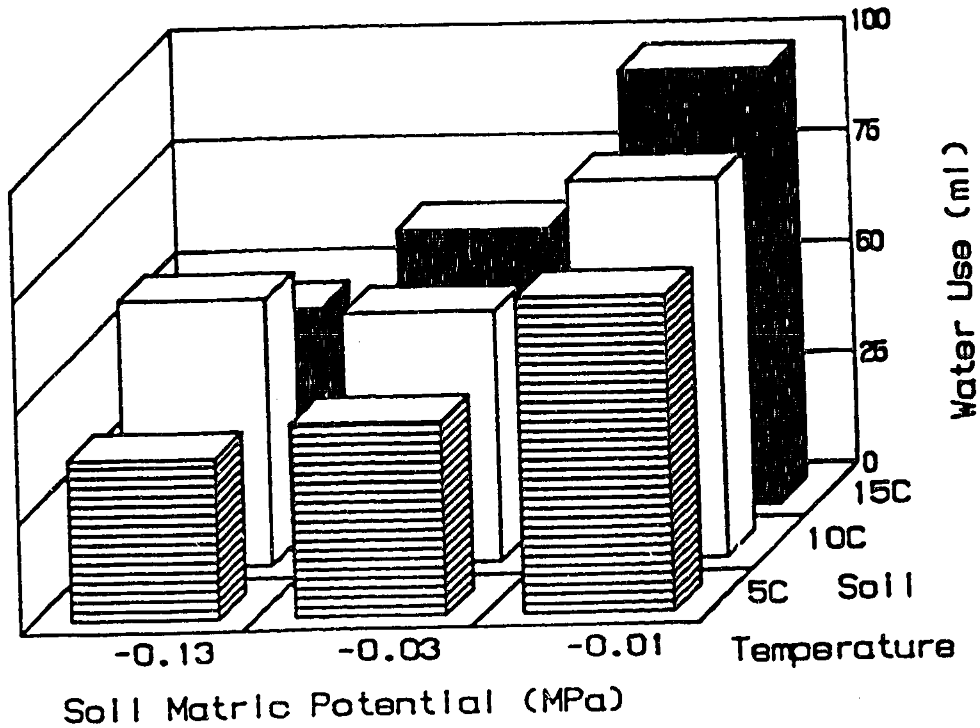


Figure 9. Trial 2: total water use corrected for evaporation/ condensation.

were poor, ranging from -0.44 to 0.87 for number and -0.99 to 0.67 for length. Only at two combinations of temperature/moisture (5°C/-0.05 MPa and 15°C/-0.01 MPa) were significant correlations obtained (Appendix VI). Better correlations existed between the original volume of the rooting system and total water use (Table 4). This demonstrated the relative importance of the planted root volume for water uptake.

3.2 Trial 3 (Containerized Stock)

3.2.1 Mortality

The containerized seedlings all survived.

3.2.2 Root Growth

Mean values for root growth of the 'standard' RGP test are presented in Table 5. Root growth was significantly affected by the soil temperature and moisture treatments (Table 6). The number and total length of new roots decreased with decreasing soil temperature and moisture (Fig 10 and 11). At 5, 10, and 15°C root number was 50%, 76%, and 91% and total root length was 5%, 12%, and 29% of the standard (Fig 12). At -0.13, -0.03, and -0.01 MPa soil matric potentials, root number was 52%, 77%, and 87% and length was 8%, 13%, and 16% (Fig 13).

Number and length of new roots represent separate physiological processes of initiation and elongation (Ritchie and Dunlap 1980), therefore it was not surprising

Table 4. Coefficients of determination (R^2) for significant ($p<0.05$) simple linear regression equations relating root volume at outplanting to total water use.
Model: $y= a + bx$ where y= total water use (ml) and
x= initial rooting volume (cm^3).

Treatment Temperature (°C)	Treatment Moisture (MPa)	n	R^2
5	-0.05	11	0.67
	-0.02	14	0.45
	-0.01	8	0.57
10	-0.02	14	0.38
	-0.01	8	0.82
15	-0.05	9	0.69
	-0.02	10	0.44
	-0.01	9	0.71

Note: n=number of seedlings.

Table 5. Standard RGP test results for Trial 3.

Run	n	New Roots Number		New Roots Length (cm)	
1	15	63.1	(19.2)	42.5	(32.7)
2	15	49.0	(18.2)	29.6	(21.5)

Note: Values within parentheses are standard deviations; n=number of seedlings.

Table 6a. Analysis of variance table for log and (rank) - transformation of number of new roots as a percentage of the standard value.

Source	df	MS	F
Run (R)	1	4.844 (15904.8)	
Block/Run (B/R)	2	0.168 (3472.3)	
Temperature (T)	2	1.086 (39143.4)	31.18* (31.72*)
T.R + T.B/R	6	0.035 (1233.9)	
Moisture (M)	2	0.836 (26697.5)	22.59* (27.07*)
M.R + M.B/R	6	0.037 (986.3)	
M.T	4	0.130 (3727.6)	1.58 (1.00)
M.T.R + M.T.B/R	12	0.082 (3724.0)	

*Significant at the 0.05 level.

Table 6b. Analysis of variance table for log and (rank) - transformation of length of new roots as a percentage of the standard value.

Source	df	MS	F
Run (R)	1	0.303 (10035.2)	
Block/Run (B/R)	2	0.307 (1832.7)	
Temperature (T)	2	8.234 (113697.5)	32.50* (36.84*)
T.R + T.B/R	6	0.253 (3086.1)	
Moisture (M)	2	1.426 (15319.6)	13.58* (12.36*)
M.R + M.B/R	6	0.105 (1239.2)	
M.T	4	0.129 (2256.9)	1.23 (1.44)
M.T.R + M.T.B/R	12	0.105 (1563.7)	

*Significant at the 0.05 level.

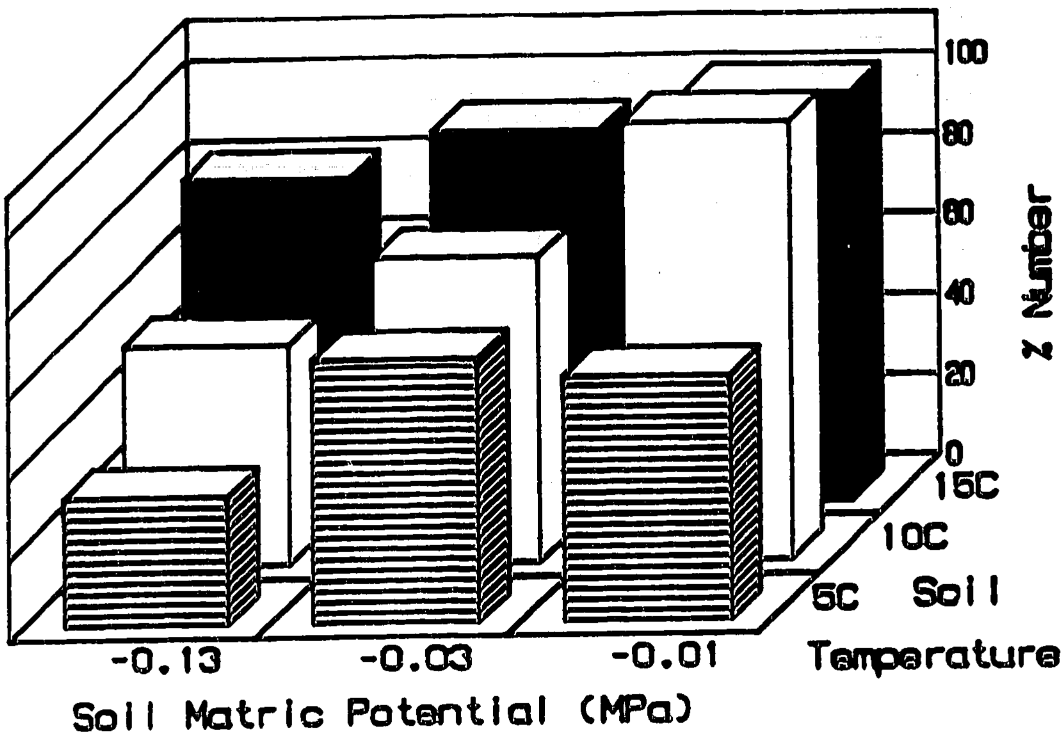


Figure 10. Trial 3: expression of number of new roots.

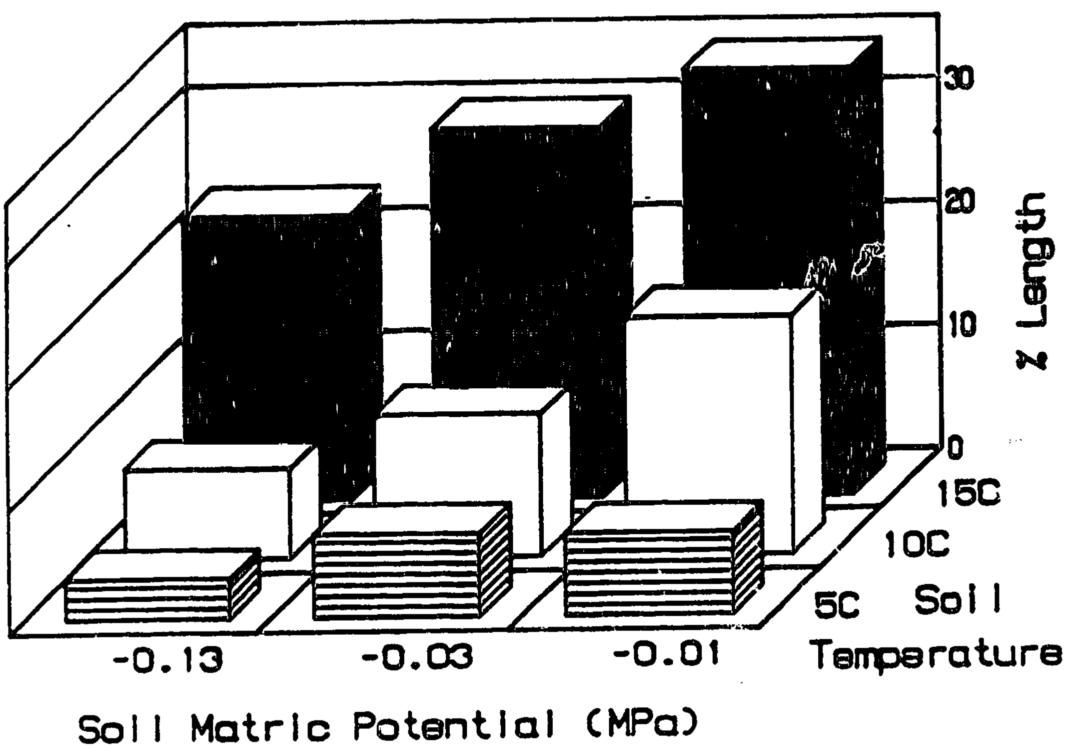


Figure 11. Trial 3: expression of total length of new roots.

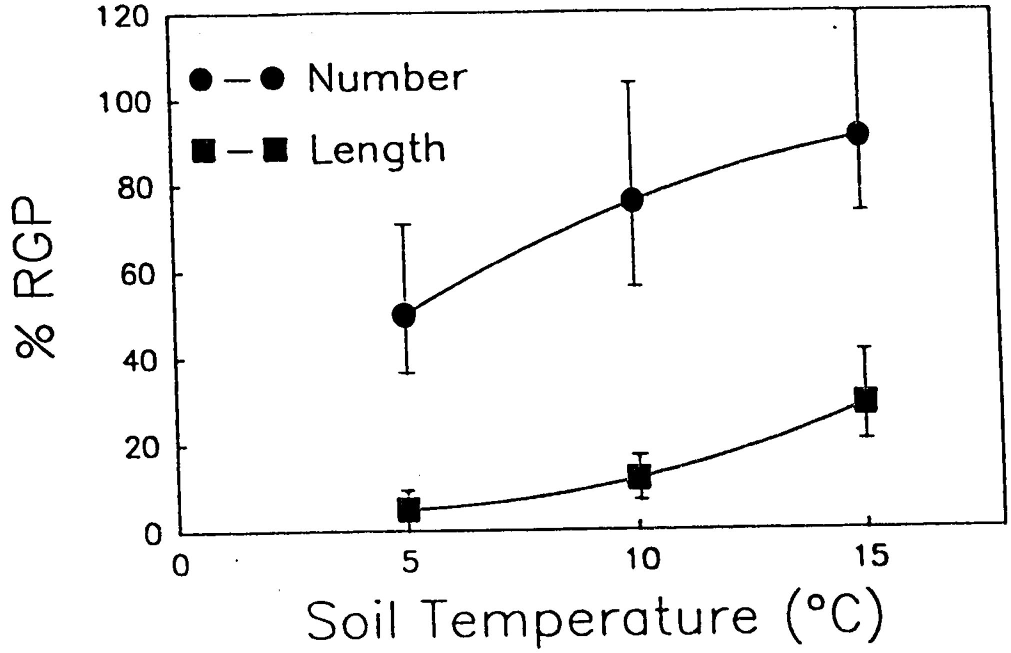


Figure 12. Main effect means of soil temperature on expression of RGP. Vertical bars= 95% confidence limits.

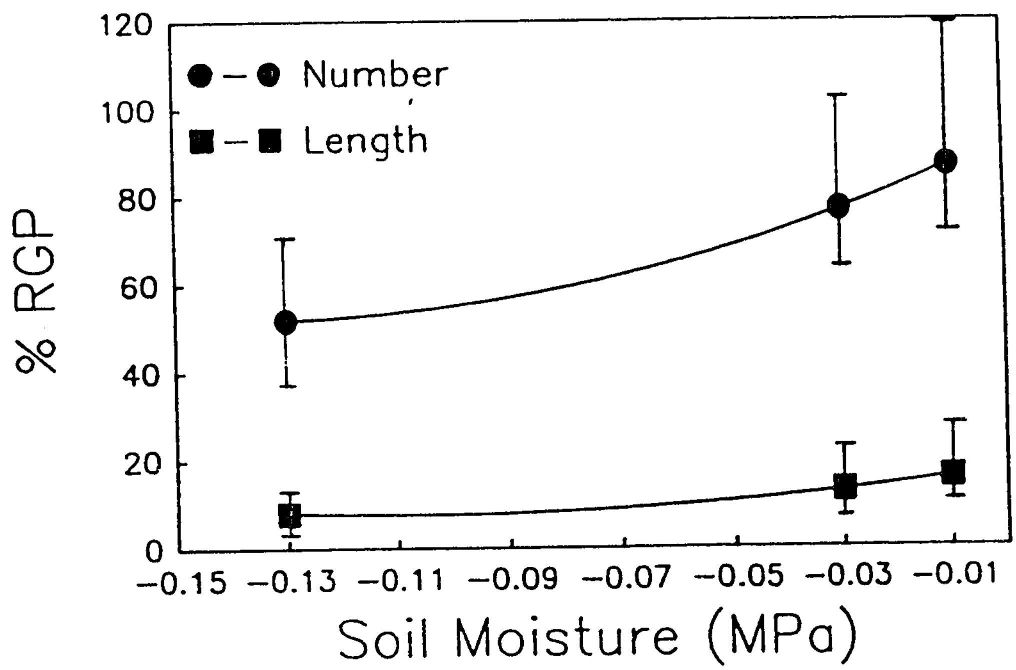


Figure 13. Main effect means of soil moisture on expression of RGP. Vertical bars= 95% confidence limits.

that the processes differed in response to the treatments. The low temperature and moisture levels resulted in a greater reduction of total length of new roots than of number of new roots. The greatest decrease in the number of new roots occurred between 10^{o} and $5^{o}C$ whereas the greatest decrease in the length of new roots occurred between 15^{o} and $10^{o}C$.

The interaction of soil temperature and moisture was not statistically significant, suggesting that soil temperature and moisture acted independently of each other. The simple effects of each factor were the same for all levels of the other factor. This was not expected because low soil temperature negatively affects water uptake by seedlings (Kaufmann 1975, 1977; Running and Reid 1980; Grossnickle and Blake 1985). It is likely that the interaction could not be detected due to the high variability in root growth. Coefficients of variation ranged from 50% to 132% for length and 37% to 60% for number (Appendix VII).

Upon comparing main effect means of soil moisture on total length of new roots (Fig 13) to the individual responses (Fig 11), some deviations from the main effects were evident. Main effect means suggested total length of new roots was not greatly affected by decreasing soil moisture. However, individual responses of root length to soil moisture levels increased at higher temperatures. At

15°C the difference in total length of new roots between -0.13 to -0.01 MPa soil moisture levels was 11.5%. At 5°C the difference was 3.4%.

The relationship between soil temperature, moisture, and actual root growth (percentages of RGP not used) was described by step-wise regression analysis as follows for number and total length of new roots:

number of new roots

number= -17.37 + 1.83 T + 2.19 M

R^2=0.25 n=180 standard error of estimate= 17.91

total length of new roots

length= 3.27 + 1.52 T + 0.78 M

R^2=0.31 n=180 standard error of estimate= 10.09cm

where T=temperature in °C and M=matric potential in MPa. The regression equations explained only 25% and 31% of the variation in root growth in terms of number and total length of new roots, respectively. Temperature and moisture singly accounted for similar magnitudes of the variation in number of new roots with R^2 values of 13% and 12%, respectively. Temperature was more important (26% R^2) in accounting for variation in total length of new roots; moisture only accounted for 5%.

3.2.3 Water Relations

Xylem pressure potential and stomatal conductance for seedlings from the standard RGP test are presented in

Table 7.

Xylem pressure potential of the containerized stock was significantly lower at low soil temperature and moisture levels (Table 8; Fig 14). Xylem pressure potential was lowest (-1.59 MPa) at $5^{o}C$/-0.13 MPa, higher (-1.20 MPa) at $15^{o}C$/-0.01 MPa, and highest (-0.80 MPa) for RGP seedlings ($20^{o}C$/-0.01MPa).

Stomatal conductance of current-year's needles was also lower at low soil temperature/moisture levels (Fig 15). ANOVA however, indicated no significant difference in stomatal conductance between the different temperature levels (Table 9). Conductance values were lowest (0.012 $cm.sec^{-1}$) at $5^{o}C$/-0.13 MPa and highest (0.057 $cm.sec^{-1}$) at $15^{o}C$/-0.01 MPa. In general conductance values were low. This was likely caused by including in the area calculations, the surface area of leaves which had not fully expanded. Little conductance occurs before leaves are fully expanded (Field 1987).

Total water use per seedling over the test period was significantly higher (Table 10) at the higher levels of temperature and moisture (Fig 16). The magnitude of water used per seedling changed over time. From day 8 or 9 onwards there was a steady increase in water use at the -0.01 and -0.03 MPa levels of soil water potential (Fig 17). The increase in water use likely occurred concurrently with new root production. However, at the -0.13 MPa level, water

Table 7. Xylem pressure potential and stomatal conductance values for seedlings of the standard RGP tests of Trial 3.

Run	Xylem pressure potential			Stomatal conductance		
	n	(MPa)		n	(cm/s)	
1	4	-0.96	(0.054)	4	0.0365	(0.0078)
2	3	-0.83	(0.024)	4	0.0532	(0.0086)

Note: Values within parentheses are standard deviations; n=number of seedlings.

Table 8. Analysis of variance table for log and (rank) - transformation of xylem pressure potential.

Source	df	MS		F	
Run (R)	1	0.028	(1860.5)		
Block/Run (B/R)	2	0.003	(379.7)		
Temperature (T)	2	0.005	(568.9)	7.81*	(9.33*)
T.R + T.B/R	6	0.0006	(61.0)		
Moisture (M)	2	0.859	(9263.6)	28.32*	(49.4^{3*})
M.R + M.B/R	6	0.003	(187.4)		
M.T	4	0.0002	(2.2)	0.10	(0.02)
M.T.R + M.T.B/R	12	0.002	(143.7)		

*Significant at the 0.05 level.

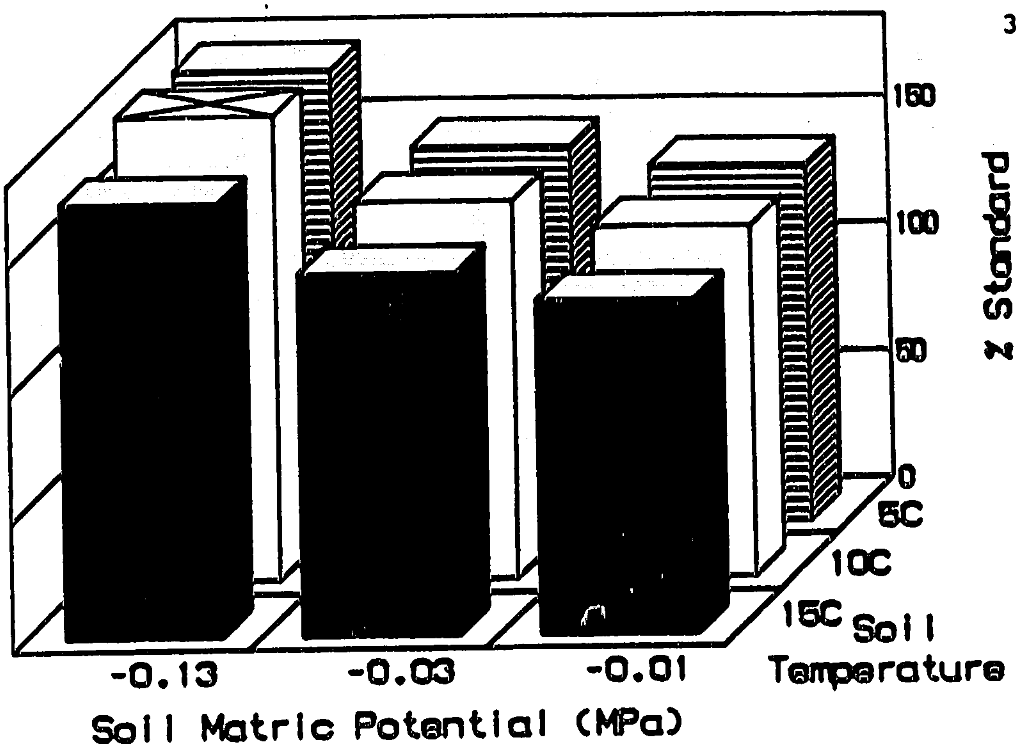


Figure 14. Xylem pressure potential (% of standard).

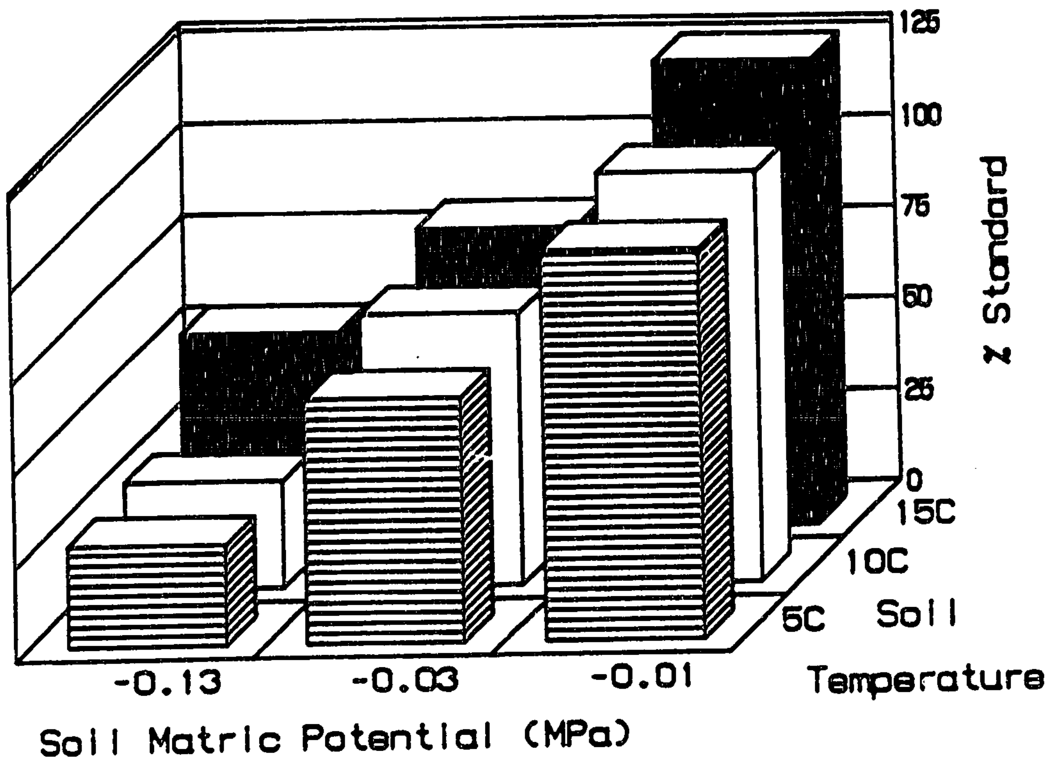


Figure 15. Stomatal conductance (% of standard) of current year's needles.

Table 9. Analysis of variance table for log and (rank) - transformation of stomatal conductance of current-year's needles.

Source	df	MS		F	
Run (R)	1	0.172	(1984.5)		
Block/Run (B/R)	2	0.032	(226.7)		
Temperature (T)	2	0.162	(574.9)	4.99	(4.93)
T.R + T.B/R	6	0.032	(116.7)		
Moisture (M)	2	1.639	(9775.3)	19.58*	(18.27*)
M.R + M.B/R	6	0.084	(534.9)		
M.T	4	0.042	(142.0)	4.29*	(3.37*)
M.T.R + M.T.B/R	12	0.010	(42.1)		

*Significant at the 0.05 level.

Table 10. Analysis of variance table for log and (rank) - transformation of water use corrected for evaporation/condensation.

Source	df	MS	F
Run (R)	1	0.190 (5600.1)	
Block/Run (B/R)	2	0.065 (222.5)	
Temperature (T)	2	0.468 (62116.3)	12.58* (33.3*)
T.R + T.B/R	6	0.037 (1865.7)	
Moisture (M)	2	3.632(115026.2)	24.28* (23.8*)
M.R + M.B/R	6	0.150 (4837.0)	
M.T	4	0.054 (2885.5)	1.60 (2.3)
M.T.R + M.T.B/R	12	0.034 (1263.6)	

*Significant at the 0.05 level.

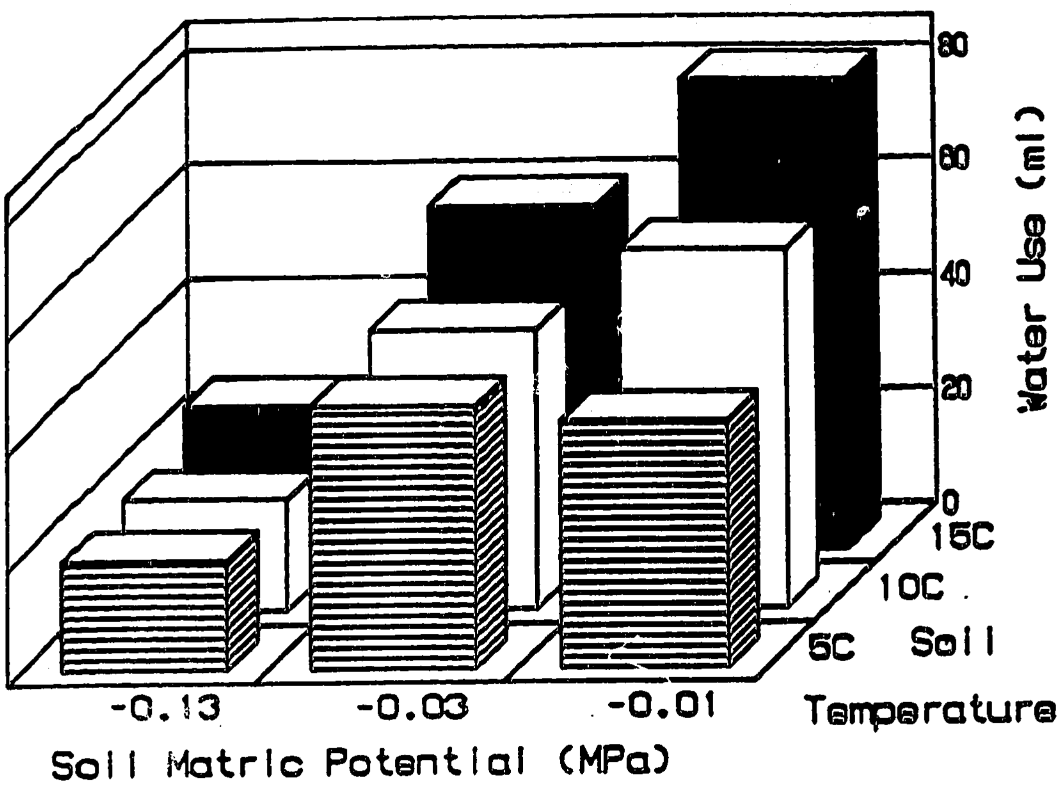


Figure 16. Total water use corrected for evaporation/condensation.

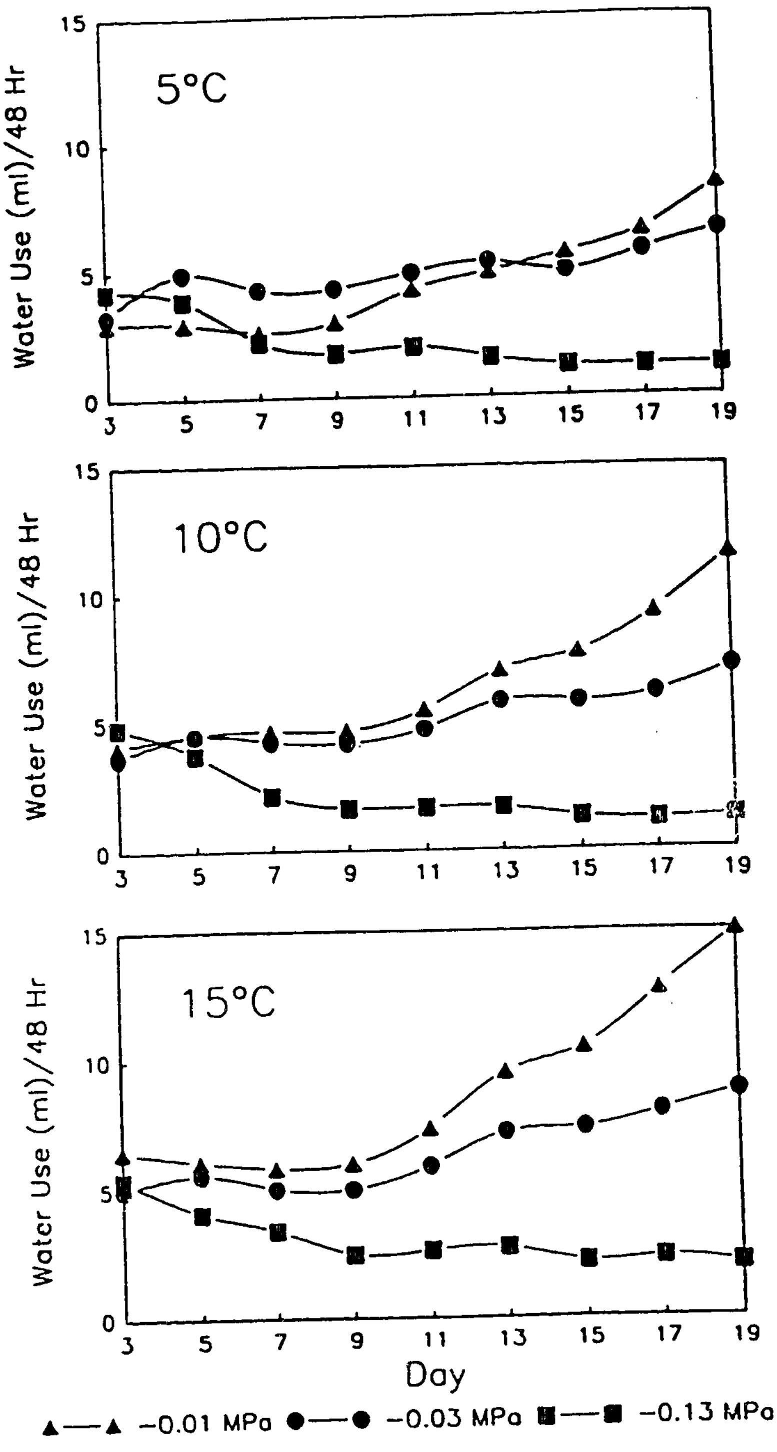


Figure 17. Average change in water use per seedling.

use per seedling declined until day 8 or 9 after which it remained relatively constant. New root production by seedlings grown at -0.13 MPa was less than seedlings grown at the higher moisture levels nevertheless, new roots were produced. Therefore, the increase in water use did not necessarily indicate the timing of initiation of new roots.

The increase in water use most likely was caused by an increase in transpiration. The change in transpiration might have been due to a change in stomatal conductance of year-old needles or to an increase in transpirational area.

The decrease in water use at the -0.13 MPa moisture level was most likely caused by a decrease in stomatal conductance. Stomatal conductance probably decreased in response to the relatively high levels of plant moisture stress. Xylem pressure potential at -0.13 MPa moisture level ranged from -1.6 MPa at 5°C to -1.5 MPa at 15°C. Daytime xylem pressure potentials of about -1.5 MPa can induce stomatal closure of _Picea engelmannii_ (Kaufmann 1976). These results suggested that a threshold level of water stress occurred between -0.13 and -0.03 MPa soil water potential for the white spruce seedlings. This is not surprising because -0.13 MPa soil matric potential occurs near the inflection point of the soil moisture desorption curve. Above this point soil moisture availability is low.

Correlations between total water use and new root production were usually low and inconsistent. Only at four combinations of soil temperature and moisture were regression equations significant, with R^2 values ranging from 0.15 to 0.50 ($p<0.05$) (Appendix VIII). Correlations between change in water use over time and new root production were also poor (Appendix VIII). Other regressions using transformations of the data were no more successful than regressions with untransformed data. This suggested that water uptake by the original rooting system was relatively high.

4.0 DISCUSSION

RGP of containerized and bareroot white spruce seedlings was weakly expressed under low levels of soil temperature and moisture. Low soil temperature and moisture, singly and in combination, can result in moisture stress and decreased stomatal conductance which, in turn can lead to reduced photosynthesis and growth (Lopushinsky and Kaufmann 1984). Root growth, xylem pressure potential and stomatal conductance of containerized white spruce stock were reduced at low temperature and moisture levels.

Low soil temperature also probably limited root growth by: reducing root metabolic activity; decreasing nutrient uptake; altering production and translocation of growth substances and; lowering the strength of the rooting system as a carbohydrate-sink (Nielsen 1974).

The number and total length of new roots differed in their responses to the treatments. The main effects of the containerized stock indicated low treatment levels reduced total length (i.e., index of initiation and elongation) more than number of new roots (index of initiation). This indicated that root elongation was affected more by low temperature and moisture than initiation. Similar findings are reported for Pinus resinosa (Anderson et al. 1986), Pinus taeda (Barney 1950), and Pinus radiata (Nambiar et al. 1980).

A difference in the relative impact of each factor on new root production was also noted. The number of new roots of containerized stock was equally affected by soil temperature and moisture. Soil temperature however, had a more pronounced effect on the length of new roots than did moisture. The range in RGP expression for the temperature treatments was 24% compared to 8% for the moisture treatments. Thus one might conclude soil temperature was the primary factor affecting root elongation.

However, comparing the main effect of temperature on the total length of new roots (Fig 12) to the individual responses (Fig 11), it was evident the simple effects at 5°C deviated from the main effects. There appeared to be a change in the magnitude of response of total length to moisture from one level of soil temperature to the next. At 15° the difference in the total length of new roots was 11.5%. At 5°C the difference was 3.4%. Even though these differences were not significant, they do suggest that both moisture and temperature were important at 10° and 15°C, while temperature was the dominant factor at 5°C. This would be in agreement with Day and MacGillivray (1970) who found a substantial decrease in root elongation of white spruce seedlings with decreasing soil moisture. In their experiment, soil temperature was allowed to equilibrate with an air temperature of 24:15.5°C (day:night).

Root growth of the bareroot stock responded similarly to the soil temperature and moisture treatments as the containerized stock. The number of new roots produced by the bareroot stock was expressed consistently to a greater extent than was the total length of new roots. Additionally, at 15°C the total length of new roots increased dramatically with increasing soil moisture but at 5° and 10°C there were only slight increases in new root length with increasing moisture.

Root growth of the bareroot stock also differed from that of the containerized stock. Expression of RGP of the bareroot stock abruptly increased at the highest temperature and moisture levels whereas the change in root growth of the containerized stock was less between treatment levels. Expression of RGP of the bareroot stock was less at all treatment levels than that of the containerized stock.

The greater expression of RGP of containerized seedlings might be attributed to their intact and undisturbed root systems which remain in close contact with the soil after outplanting. Planting moist plugs ensures containerized seedlings are planted with a short term supply of water. After lifting, bareroot seedlings have lost a portion of their fibrous roots and have lost all contact with soil. Immediate uptake of water by bareroot stock depends on soil water potential and hydraulic contact between roots and soil. Thus the risk of moisture stress is greater for bareroot stock.

The volume of seedling root systems must be adequate to support transpirational demands to prevent moisture stress immediately after outplanting. The magnitude of RGP expression after outplanting is limited by the amount of moisture stress seedlings undergo in the brief phase prior to root development (Carlson 1986). Additionally, according to the rationale behind RGP-testing, the RGP of seedlings must be high to ensure quickly expanding rooting systems and contact with the soil.

The second assumption of Stone is that new root production has an appreciable impact on water uptake capacity. No correlations between new root production of the containerized stock and the magnitude of total water use or change in water use over time were obtained in this study. This does not mean that new roots did not increase the absorptive capability of the rooting system. Unsuberized roots are more permeable than suberized roots but they constitute too small a percentage of the rooting system to account for water uptake requirements (Kramer 1949). By measuring hydraulic conductivity of roots (mg.min^{-1}) of *Pinus taeda* seedlings directly, Carlson (1986) found a relationship between hydraulic conductivity and root growth (measured by increment in root volume). The lack of a correlation in this study demonstrated the relative importance of the older suberized rooting system for significant water uptake.

5.0 SUMMARY

Soil temperature and moisture at levels less than "optimum" had a substantial effect on the expression of RGP of bareroot and containerized white spruce seedlings. In general, the total length of new roots was reduced more when compared to the values of the standard RGP seedlings than was new root number. Soil temperature had a greater effect on the total length of new roots than soil moisture; the effect of soil moisture became more apparent at higher soil temperature levels. The number of new roots was reduced to a similar degree by both low soil temperature and moisture levels.

RGP of containerized seedlings was expressed to a greater degree under lower soil temperature and moisture treatments than was that of bareroot seedlings.

Xylem pressure potential, stomatal conductance, and

water use of the containerized seedlings were reduced at the low levels of soil temperature and moisture. Subsequently, photosynthesis was likely reduced at the lower treatment levels and as a result root growth was likely limited.

Root growth of both stock types was related to soil temperature and moisture. The magnitude of water uptake was not related to new root production (number or length). The planted root system was relatively more important for water uptake.

6.0 PERSPECTIVES

RGP of tree seedlings often predicts relative field performance (Burdett 1987). The reason for the relationship is not known but several hypotheses exist. The contention underlying the development of RGP testing emphasized new root growth as the key to initial survival of outplanted seedlings. Even if new root growth <u>per se</u> is not solely responsible for the relationship, it is generally accepted that new root growth soon after outplanting is important for seedling establishment. New root growth increases soil-root contact and increases the volume of soil from which moisture can be obtained. From this perspective, the results of this study emphasize the importance of cultural practices used by nurserymen and silviculturalists; and question the use of RGP-testing to evaluate stock quality.

Nurserymen must employ practices to maximize both morphological and physiological quality of seedlings. As demonstrated in this study, the volume of root systems determines to a large degree the magnitude of water uptake at given levels of soil temperature and moisture. High root volumes can be obtained by managing the density of nurserybeds and other cultural practices such as undercutting and fertilization. Top growth of seedlings must also be managed so that transpirational demands will not exceed water uptake after outplanting. It may also be possible to condition seedlings to moisture stress (Rook 1973). If moisture stress immediately after outplanting can be reduced, the probability of greater root growth is higher. It follows also that management of irrigation, fertilization, root wrenching and pruning, lifting date, and storage (temperature and duration) is necessary to maximize RGP.

Silviculturalists faced with the challenge of site preparation can use techniques to increase soil temperature and moisture availability, and thereby increase expression of RGP of outplanted seedlings. Soil temperature can be increased by exposing mineral soil. Soil moisture can be increased by removing competing vegetation and can be re-distributed by altering the soil surface. Silviculturalists also can match stock types to sites. The results obtained in this study suggested containerized stock may be better than bareroot stock for sites where soil is cool and dry.

The question of minimum levels of RGP required to ensure successful seedling establishment remains unanswered.

A final question relates to the use of RGP to evaluate stock quality. RGP-testing provides nurserymen with a way to evaluate the effects of cultural practices. But both nurserymen and silviculturalists are faced with the problem of determining RGP levels at which seedlings should be culled because expected field performance is low.

To answer this question we must consider the interaction between outplanted seedlings and their environment (i.e., examine the expression of RGP). This study served as an initial step towards answering the question. The next step would be to conduct trials to model RGP expression under field conditions and to estimate field performance from RGP expression. There is a drawback to this approach however.

The drawback is the assumption that relative RGP of different stock will remain the same with changes in environmental conditions. Burdett (1979) reported root growth of lodgepole pine seedlings measured under a 30:25^{o}C day:night temperature regime was closely correlated with root growth of samples of the same stock measured at a constant temperature of 15^{o}C. However, Lavender (1988 pers. comm.) found that seedlings which had similar RGP at higher temperatures differed in their ability to produce new roots at 5^{o}C. Therefore, a large number of field trials would be required.

The predictive ability of the test could be improved by estimating field root growth directly rather than estimating 'potential' root growth. Field root growth was always less than the potential; it was as low as 5% of the potential. Seedlings should be tested under conditions more typical of field environments as these are likely more important than optimum levels.

7.0 LITERATURE CITED

Abod, S.A., K.R. Shepherd, and E.P. Bachelard. 1979. Effects of light intensity, air and soil temperatues on root regeneration potential of Pinus caribea var. Hondurensis and P. kesiya seedlings. Aust. For. Res. 9: 173-184.

Anderson, C.P., E.I. Sucoff, and R.K. Dixon. 1986. Effects of root zone temperature on root initiation and elongation in red pine seedlings. Can. J. For. Res. 16: 696-700.

Barney, C.W. 1951. Effects of soil temperature and light intensity on root growth of loblolly pine seedlings. Plant Physiol. 26: 146-163.

Blake, T.J. 1983. Transplanting shock in white spruce; effect of cold-storage and root pruning on water relations and stomatal conditioning. Physiol. Plant. 57: 210-216.

Brissette, J.C. and T.C. Roberts. 1984. Seedling size and lifting date effects on root growth potential of loblolly pine from two Arkansas nurseries. Tree Planters' Notes 35: 34-36.

Burdett, A.N. 1979. New methods for measuring root growth capacity: their value in assessing lodgepole pine stock quality. Can. J. For. Res. 9: 63-67.

Burdett, A.N. 1987. Understanding root growth capacity: theoretical considerations in assessing planting stock quality by means of root growth tests. Can. J. For. Res. 17: 768-775.

Burdett, A.N., D.G. Simpson, and C.R. Thompson. 1983. Root development and plantation establishment success. Plant and Soil 71: 103-110.

Carlson, W.C. 1986. Root system considerations in the quality of loblolly pine seedlings. Southern J. of Applied For. 10: 87-92.

Conover, W.J. and R.L. Iman. 1981. Rank transformation as a bridge between parametric and nonparametric statistics. The American Statistician 35: 124-129.

Day, R.J. and E.M. Harvey. 1984. Morphological and physiological stock quality in relation to field outplanting performance. Second report: 1982-83 results. Lakehead Univ. School of For., Thunder Bay, Ontario. 179pp.

Day, R.J. and G.R. MacGillivray. 1975. Root regeneration of fall-lifted white spruce nursery stock in relation to soil moisture content. For. Chronicle 51: 196-199.

Duryea, M.L. and T.D. Landis. 1984. Development of the Forestry Nursery Manual: a synthesis of current practices and research. In: Forestry nursery manual: production of bareroot seedlings. Edited by: M.L. Duryea and T.D. Landis. Martinus Nijhoff/Dr. W. Junk Publ. The Hague. pp. 3-5.

Feret, P. and R. Kreh. 1985. Seedling root growth potential as an indicator of loblolly pine field performance. For. Sci. 31: 1005-1011.

Feret, P., R.E. Kreh, and C. Mulligan. 1985. Effects of air drying on survival, height, and root growth potential of loblolly pine seedlings. Southern J. of Applied For. 9: 125-128.

Field, C.B. 1987. Leaf-age effects in stomatal conductance. In: Stomatal function. Edited by: E. Zeiger, G.D. Farquhar, and I.R. Cowan. Stanford Univ. Press, Stanford, California. pp. 367-384.

Hillel, D. 1982. Introduction to soil physics. Academic Press, Inc. Orlando 2^{nd} ed., 364pp.

Grossnickle, S.C. and T.J. Blake. 1985. Acclimation of cold-stored jack pine and white spruce seedlings: effect of soil temperature on water relation patterns. Can. J. For. Res. 15: 544-550.

Johnson-Flanagan, A.M. and J.N. Owens. 1985. Root growth and root growth capacity of white spruce (Picea glauca (Moench) Voss) seedlings. Can. J. For. Res. 15: 625-630.

Kaufmann, M.R. 1975. Leaf water stress in Engelmann spruce; influence of the root and shoot environments. Plant Physiol. 56: 841-844.

Kaufmann, M.R. 1976. Stomatal response of Engelmann spruce to humidity, light, and water stress. Plant Physiol. 57: 898-901.

Kaufmann, M.R. 1977. Soil temperature and drought effects on growth of Monterey pine. For. Sci. 23: 317-325.

Kramer, P.J. 1949. Plant and soil water relationships. McGraw-Hill Book Co., Inc. N.Y. 347pp.

Krugman, S.L. and E.C. Stone. 1966. The effect of cold nights on the root-regenerating potential of ponderosa pine seedlings. For. Sci. 12: 451-459.

Larson, H.S., D.B. South, and J.M. Boyer. 1986. Root growth potential, seedling morphology and bud dormancy correlate with survival of loblolly pine seedlings planted in December in Alabama. Tree Physiol. 1: 253-263.

Larson, M.M. and F.W. Whitmore. 1970. Moisture stress affects root regeneration and early groth of red oak seedlings. For. Sci. 16: 494-498.

Lopushinsky, W. and M.R. Kaufmann. 1984. Effects of cold soil on water relations and spring growth of Douglas-fir seedlings. For. Sci. 30: 628-634.

Luchkow, S.A. 1981. The status of container planting programs in Alberta. In: Proc. of the containerized tree seedling symp. Edited by: J.B. Scarratt, C. Glerum, and C.A. Plexman. Can. For. Serv. O-P-10. pp. 23-25.

McMinn, R.G. 1980. Root growth capacity and field performance of various types and sizes of white spruce stock following outplanting in the central interior of British Columbia. In: Proc., characterization of plant material. Edited by: H. Schmidt-Vogt. IUFRO meeting, Div. 1, Freiburg, Federal Republic of Germany. pp. 37-41.

Nambiar, E.K.S., G.D. Bowen, and R. Sands. 1979. Root regeneration and plant water status of *Pinus radiata* D. Don seedings transplanted to different soil temperatures. J. Exp. Bot. 30: 1119-1131.

Navratil, S., L.G. Brace, and I.K. Edwards. 1986. Planting stock quality monitoring. Can. For. Serv., North. For. Res. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-279. 21pp.

Nielsen, K.F. 1974. Roots and root temperatures. In: The plant root and its environment. Edited by: E.W. Carson. Univ. of Virginia. pp. 293-333.

Richards, L.A. 1965. Physical condition of water in soil. In: Methods of soil analysis. Edited by: C.A.

Black. Monograph 9. Amer. Soc. Agron., Madison, Wisconsin. pp. 128-152.

Ritchie, G.A. 1982. Carbohydrate reserves and root growth potential in Douglas-fir seedlings before and after cold storage. Can. J. For. Res. 12: 905-912.

Ritchie, G.A. 1984. Assessing seedling quality. In: Forest nursery manual: production of bareroot seedlings. Edited by: M.L. Duryea and T.D. Landis. Martinus Nijhoff/Dr. W. Junk Publ. The Hague. pp. 243-259.

Ritchie, G.A. 1985. Root growth potential: principles, procedures and predictive ability. In: Proceedings: evaluating seedling quality. Edited by: M.L. Duryea. Oregon State University, Corvallis. pp. 93-105.

Ritchie, G.A. and J.R. Dunlap. 1980. Root growth potential: its development and expression in forest tree seedlings. New Zealand J. For. Sci. 10: 218-248.

Rook, D.A. 1973. Conditioning radiata pine seedlings to transplanting by restricted watering. New Zealand J. For. Sci. 3: 54-69.

Ruark, G.A., D.L. Mader and T.A. Tattar. 1983. The influence of soil moisture and temperature on root growth and vigor of trees - a literature review. Part II. Arbor. J. 7: 39-51.

Running, S.W. and C.P. Reid. 1980. Soil temperature influences on root resistance of Pinus contorta seedlings. Plant Physiol. 65: 635-640.

Scarratt, J.B. 1981. Container stock specifications for Northern Ontario. In: Proc. of the Canadian containerized tree seedling symp. Edited by: J.B. Scarratt, C. Glerum, and C.A. Plexman. Can. For. Serv. O-P-10. pp. 343-354.

Silversides, R.H., S.W. Taylor and B.C. Hawkes. 1986. Influence of prescribed burning on seedling microclimate and its potential significance in northern interior British Columbia. Proceedings: Forest Climate. Orillia, Ontario. Nov. 17-21, 1986. Conference pre-print. 29pp.

Smyth, J.H. and A.J. Brownwright. 1984. Forest tree production centres in Canada - 1983. Can. For. Serv. Great Lakes For. Res. Cent., Sault Ste.

Marie, Ontario. Inf. Rep. O-X-357. 45pp.

Stone, E.C. 1955. Poor survival and the physiological condition of planting stock. For. Sci. 1: 90-94.

Stone, E.C. and G.H. Schubert. 1959. Root regeneration by ponderosa pine seedlings lifted at different times of the year. For. Sci. 5: 322-332.

Stone, E.C., J.L. Jenkinson, and S.L. Krugman. 1962. Root regenerating potential of Douglas-fir seedlngs lifted at different times of the year. For. Sci. 8: 288-297.

Stone, E.C., R.W. Benselor, F.J. Baron and S.L. Krugman. 1963. Variation in the root regenerating potential of ponderosa pine from four California nurseries. For. Sci. 9: 217-225.

Stone, E.C. and J.L. Jenkinson. 1970. Influence of soil water on root growth capacity of ponderosa pine transplants. For. Sci. 16: 230-239.

Stone, E.C. and J.L. Jenkinson. 1971. Physiological grading of ponderosa pine nursery stock. J. For. 69: 31-33.

Sutton, R.F. 1980. Planting stock quality, root growth capacity, and field performance of three boreal conifers. New Zealand J. For. Sci. 10: 54-71.

Sutton, R.F. 1983. Root growth capacity: relationship with field root growth and performance in outplanted jack pine and black spruce. Plant and Soil 71: 111-122.

Sutton, R.F. 1987. Root growth capacity and field performance of jack pine and black spruce in boreal stand establishment in Ontario. Can. J. For. Res. 17: 794-804.

Tear, E.C. 1979. Ecophysiology of white spruce regeneration. M.Sc. thesis. University of Alberta, Edmonton. 76pp.

Thompson, F.B. and L. Leyton. 1971. Method for measuring the leaf surface area of complex shoots. Nature (London), 229:572.

Van den Driessche, R. 1978. Seasonal changes in root growth capacity and carbohydrates in red pine and white spruce nursery seedlings. <u>In:</u> Proc. IUFRO Symp. on root physiol. and symbiosis. Edited by: A. Riedacker and J. Gagnaire-Michard. Nancy, France. pp. 6-19.

Van den Driessche, R. 1983. Growth, survival, and physiology of Douglas-fir seedlings following root wrenching and fertilization. Can. J. For. Res. 13: 270-278.

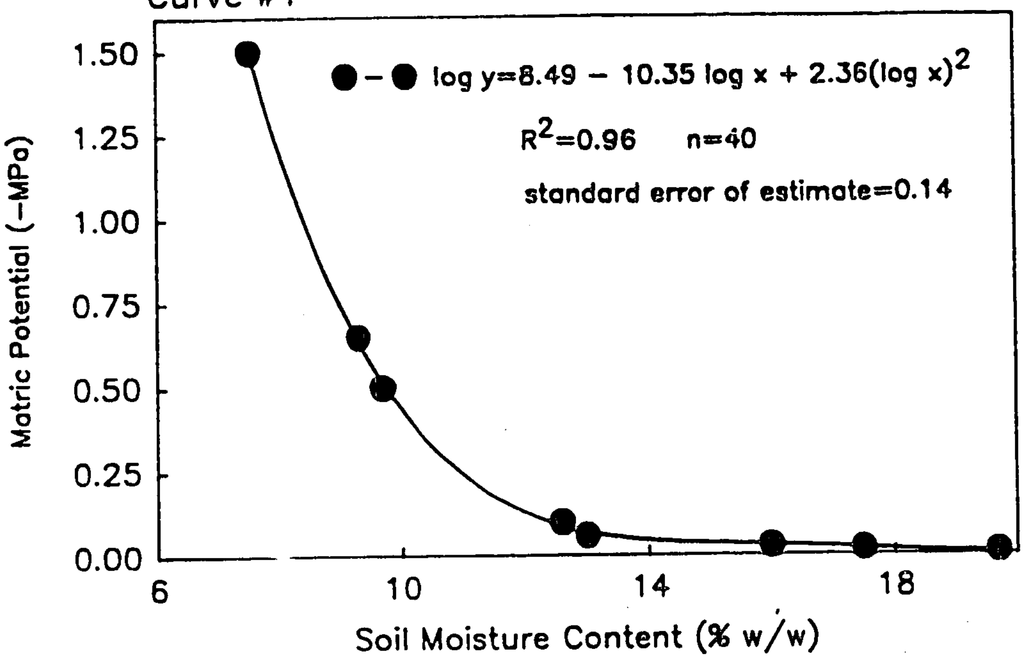
Van den Driessche, R. 1987. Importance of current photosynthate to new root growth in planted conifer seedlings. Can. J. For. Res. 17: 776-782.

Wakeley, P.C. 1948. Physiological grades of southern pine nursery stock. Proc. Soc. Am. For. Ann. Conv. 1948: 311-320.

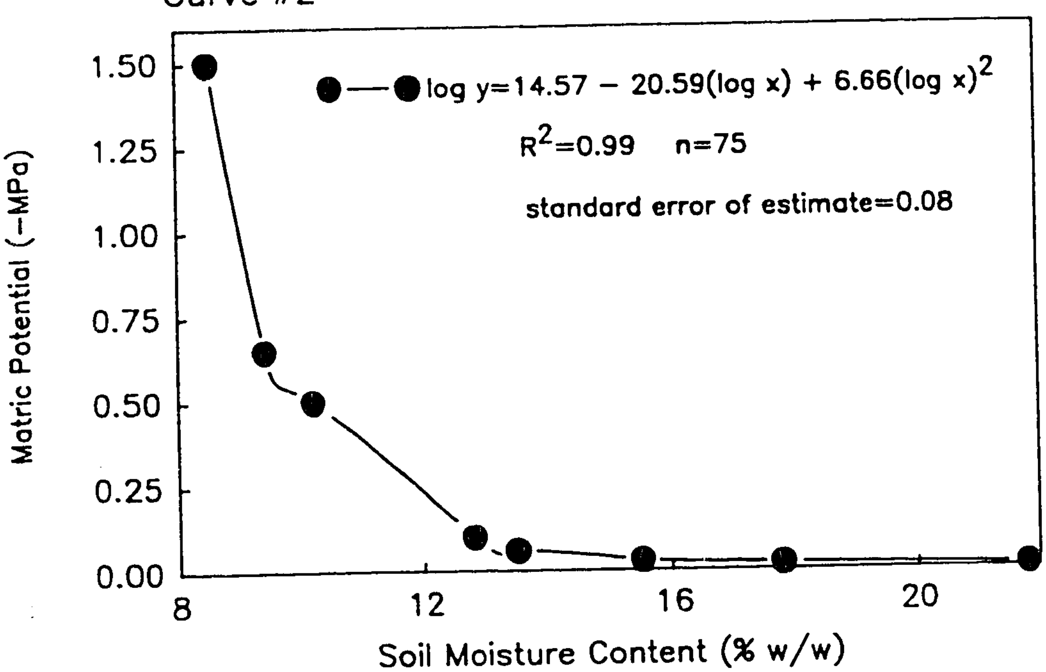
APPENDIX I

Soil moisture desorption curves[1].

Curve #1



Curve #2



[1]Logarithmic functions taken from Stone and Jenkinson (1970).

APPENDIX II

Moisture contents of soil within drums at planting.

Trial	1		2		3	
Run	1	2	1	-	1	2
Target Moisture Content (% w/w)						
10	9.8	10.3				
12			11.6	-	12.5	12.1
14	12.3	11.6				
16			17.1	-	16.8	15.3
18	17.4	20.0				
20			20.6	-	18.7	20.3

APPENDIX III

Trial 1 - Run 1. Average moisture content (% w/w) and average difference in moisture content per container approximately 24 hours after watering. (n=18)

Temperature Treatment (^{o}C)	MOISTURE CONTENT/ DIFFERENCE Moisture Treatment (% w/w) 10	14	18
5	10.98 / 3.23 (0.48) (1.97)	14.75 / 3.95 (0.62) (2.06)	18.73 / 3.13 (0.18) (0.38)
10	10.60 / 3.50 (0.41) (1.61)	14.70 / 6.10 (0.45) (2.07)	18.35 / 3.15 (0.72) (0.57)
15	10.93 / 2.93 (0.19) (2.93)	14.60 / 3.50 (0.54) (1.00)	18.25 / 2.18 (0.47) (0.96)

Note: Standard deviations are within parentheses and below the means.

Trial 1 - Run 2. Average moisture content (% w/w) and average difference in moisture content per container approximately 48 hours after watering. (n=18)

Temperature Treatment (^{o}C)	MOISTURE CONTENT/ DIFFERENCE Moisture Treatment (% w/w) 10	14	18
5	10.35 / 3.83 (0.42) (0.42)	14.63 / 7.20 (0.42) (1.67)	18.50 / 0.50 (0.37) (0.07)
10	10.70 / 4.80 (0.64) (1.72)	13.88 / 6.80 (0.16) (1.50)	17.65 / 1.28 (0.69) (0.95)
15	10.48 / 3.45 (0.38) (0.46)	13.30 / 4.88 (1.33) (1.36)	18.03 / 1.70 (0.34) (0.37)

Note: Standard deviations are within parentheses and below the means.

Trial 2 - Run 1. Average moisture content (% w/w) and average difference in moisture content per container approximately 48 hours after watering. (n=18)

Temperature Treatment (°C)	MOISTURE CONTENT/ DIFFERENCE Moisture Treatment (% w/w) 12	16	20
5	12.18 / 5.23 (0.18) (1.23)	15.55 / 2.05 (0.39) (1.15)	19.80 / 2.45 (0.31) (0.99)
10	12.18 / 3.43 (0.36) (1.61)	15.70 / 3.20 (0.38) (1.06)	19.60 / 1.80 (0.31) (0.76)
15	11.73 / 4.48 (0.38) (1.19)	15.43 / 2.90 (0.34) (1.60)	19.25 / 1.35 (0.36) (0.74)

Note: Standard deviations are within parentheses and below the means.

Trial 3 - Run 1. Average moisture content (% w/w) and average difference in moisture content per container approximately 24 hours after watering. (n=18)

	MOISTURE CONTENT/ DIFFERENCE Moisture Treatment (% w/w)		
Temperature Treatment (°C)	12	16	20
5	13.80 / 1.45 (0.19) (0.41)	16.13 / 1.60 (0.65) (0.77)	19.83 / 1.45 (0.15) (0.71)
10	13.30 / 1.05 (0.25) (0.15)	16.68 / 2.55 (0.38) (1.16)	19.45 / 1.15 (0.25) (0.56)
15	13.38 / 0.78 (0.48) (0.53)	16.18 / 2.70 (0.53) (0.46)	18.75 / 0.55 (0.05) (0.44)

Note: Standard deviations are within parentheses and below the appropriate mean.

Trial 3 - Run 2. Average moisture content (% w/w) and average difference in moisture content per container approximately 48 hours after watering. (n=18)

	MOISTURE CONTENT/ DIFFERENCE Moisture Treatment (% w/w)		
Temperature Treatment (°C)	12	16	20
5	13.23 / 1.50 (0.56) (0.46)	16.90 / 1.20 (0.80) (0.30)	19.53 / 0.35 (0.25) (0.11)
10	12.50 / 1.65 (0.39) (0.39)	16.50 / 1.23 (0.40) (0.48)	19.05 / 0.23 (0.21) (0.08)
15	12.45 / 0.90 (0.18) (0.59)	16.48 / 1.58 (0.37) (0.40)	18.75 / 0.28 (0.25) (0.15)

Note: Standard deviations are within parentheses and below the appropriate mean.

APPENDIX IV

Analysis of variance table for the evaporation/condensation test.

Source	df	MS	F
Block (B)	1	0.795	
Temperature (T)	2	8.374	164.5*
B.T	2	0.051	
Moisture (M)	2	0.043	6.1
B.M	2	0.007	
M.T	4	0.034	3.2
B.M.T	4	0.011	

*Significant at the 0.05 level.

APPENDIX V

Simple linear regression equation relating needle length in cm (x) to needle surface area (cm^2).

Surface area (cm^2) = 0.1622x - 0.0455

n=29
r^2=0.96
std error of estimate = 0.0186 cm^2

Note: Surface area was determined using a glass bead technique (Thompson and Leyton 1971); glass beads used were 18.15 $mg.cm^{-2}$.

APPENDIX VI

Bareroot runs: probabilities of greater F values (p>F) and coefficients of determination (R^2) for simple linear regression equations relating new root production to total water use (corrected for evaporation/condensation).
Model: y= a + bx where y= new root number or length (cm)
x= total water use (ml).

Treatment			Length		Number	
Temperature (°C)	Moisture (MPa)	n	p>F	R^2	p>F	R^2
5	-0.32	6	0.07	0.51	0.09	0.43
	-0.05	11	0.03*	0.41	0.04*	0.33
	-0.03	4	0.23	0.39	0.42	0.003
	-0.02	16	0.38	0.05	0.36	-0.01
	-0.01	8	0.21	0.12	0.31	0.03
10	-0.32	5	0.51	-0.12	0.51	-0.12
	-0.05	9	0.25	0.06	0.25	0.06
	-0.03	5	0.28	0.16	0.25	0.20
	-0.02	14	0.91	-0.08	0.88	-0.08
	-0.01	8	0.08	0.32	0.03*	0.50
15	-0.32	4	0.30	0.24	0.44	-0.02
	-0.13	3	0.95	-0.99	0.64	-0.44
	-0.05	9	0.09	0.26	0.14	0.18
	-0.03	5	0.76	-0.28	0.95	-0.33
	-0.02	10	0.99	-0.13	0.04	0.37
	-0.01	9	0.005	0.67*	0.001*	0.87

* significant at $p<0.05$; n=number of seedlings.

APPENDIX VII

Trial 3: coefficients of variation (%) for root growth.

Treatment: Temperature (^{o}C)	Treatment: Moisture (MPa)	New Roots: Total Length (cm)	New Roots: Number
5	-0.13	55	54
	-0.03	46	44
	-0.01	70	57
10	-0.13	88	47
	-0.03	115	47
	-0.01	91	48
15	-0.13	72	37
	-0.03	92	53
	-0.01	80	43

APPENDIX VIII

Coefficients of determination (R^2) for the significant ($p<0.05$) simple linear regression equations relating the number or length of new roots to total water use over the test period (sample size = 20).

Treatment		R^2	
Temperature (°C)	Moisture (MPa)	length (cm)	number
5	-0.03	0.22	0.15
5	-0.13	0.36	0.27
10	-0.13	0.36	0.19
15	-0.01	0.34	0.50

Coefficients of determination (R^2) for the significant ($p<0.05$) simple linear regression equations relating the number or length of new roots to the incremental change in water use from day 8 or 9 to the end of the test period (sample size = 20).

Treatment		R^2	
Temperature (°C)	Moisture (MPa)	length (cm)	number
5	-0.13	0.20	-
15	-0.01	0.26	0.40