RESISTANCE TO WATER UPTAKE BY

CONIFER SEEDLINGS

by

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ABSTRACT

Water availability for uptake by tree seedlings is
determined both by the soil water potential in relation to seedling
needle water potential and by the resistance to flow of water
through the soil, root and stem, to the needles. This study was
designed to focus principally on water uptake resistances. The
effects of soil texture and tree species on this water uptake
resistance were quantified through the use of an Ohm's Law model
suited to water flow through the soil-plant system.

The study was conducted on one-year-old potted seedlings in
a controlled environment growth chamber.

Needle water potential (ψ_N) of Douglas-fir is not much
affected by soil water potential (ψ_S) down to about -2.5 MPa, where
the calculated water uptake rate becomes very small. However, soil
texture does significantly affect the resistance to flow into the
seedling and thus affects the water uptake rate by the seedling. The
total resistance to water uptake increases as the soil dries. Coarser
textured soils show consistently higher water uptake resistances over
the soil water potential range -0.5 to -2.5 MPa. It is inferred that
differences in resistance are associated with unsaturated hydraulic
conductivity characteristics of the soil and soil-root contact.

Unlike Douglas-fir, both western and mountain hemlock show
a large decrease in needle water potential as the soil dries down to

a ψ_s of about -3.0 MPa. The water potential difference $(\psi_s - \psi_N)$ for

hemlocks is less where ψ_s is higher than -1.8 MPa, and greater where

ψ_s is less than -1.8 MPa, than $(\psi_s - \psi_N)$ for Douglas-fir in these

experiments. Despite these differences, the resistance to water uptake

for both hemlock species is much greater over the soil water potential

range -0.5 to -2.5 MPa, and thus the water uptake rates are much

less than for Douglas-fir with the same soil, even though root

densities and root surface areas are much larger for the hemlocks.

This behavior is most pronounced with mountain hemlock. These differences

are thought to be related to higher tissue and (perhaps) soil-root

contact resistances in the hemlock species. The soil resistance

appears to be small, at least down to ψ_s of about -2.0 MPa, in these

experiments. However, root densities are probably much greater than

one might expect in the field.

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CHAPTER 1: INTRODUCTION

Unlike factors affecting water loss from leaves, some factors affecting water uptake by plants are not well understood, especially with regard to tree species. Water stress in tree seedlings, which results from an imbalance between loss and uptake, is recognized as a major contributor to forest regeneration failures in western North America, where the growing season coincides with hot, dry summers (Isaac, 1935; Kummel, *et al.*, 1944; Utzig and Herring, 1974).

In western Oregon and Washington and southern coastal British Columbia, Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) is by far the most widely used reforestation species. However, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is being used increasingly in wetter areas, and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) at higher elevations (Waring, 1970; Van Eerden, 1974; Dimock *et al.*, 1976; Stein, 1976). Considerable information exists on the water relations of Douglas-fir under low water stress conditions, but little is available concerning its behavior under high stress conditions. In addition, very little information at all is available concerning water stress relationships of either hemlock species. Clearly, knowledge of water uptake characteristics of these species over a wide range of moisture conditions would be very useful for describing water stress relationships

in order to facilitate assessment and prevention of regeneration failures with these species.

A characteristic of the mountainous terrain of this region is the wide variety of surface soil materials in which seedlings must extract water if they are to survive and grow. The water flow properties of these materials might be very important to water uptake by seedlings. The objective of this study was to quantify water uptake by these three species and to assess some factors influencing this uptake from different soil materials.

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CHAPTER 2: LITERATURE REVIEW AND THEORY

Often the only soil factor evaluated in relation to water stress is the soil water potential, a measure of the energy required to remove water from the soil. However, the resistance to water flow between soil and plant may also be significant (Gardner, 1960; Cowan, 1965). This resistance might vary from soil to soil, at the same water potential, because of hydraulic conductivity differences. Even in the same soil, the resistance might vary from seedling to seedling because of differences in root distribution or tissue conductivity. This study was designed to focus principally on this matter of water flow resistances.

Water taken up by the seedling flows through the soil to the root surfaces whence it passes radially across the root to the xylem, in which it moves upward toward the transpiring leaf surfaces. Water moves in response to water potential energy differences, from regions of high water potential energy, e.g. in the soil, toward regions of lower water potential energy, e.g. in the leaves. The rate of flow through all or any portion of the pathway is proportional to the magnitude of the water potential difference across that portion of the pathway and inversely proportional to the resistance to water flow along that pathway. Symbolically stated,

$$U = \frac{\psi_1 - \psi_2}{R} \qquad (1)$$

where U is the water uptake rate, ψ_1 and ψ_2 are the water potentials at either end of the pathway, and R is the resistance to water flow. This equation is analogous to Ohm's Law describing electrical current flow and can be used as a simple model to describe water flow through the soil-plant system (van den Honert, 1948; Cowan, 1965; Hillel, 1971).

At steady state, where the uptake rate is the same through all parts of the system, the total resistance (R) can be described by the sum of all series-linked resistances in the pathway. Any change in resistance in one segment will change the total resistance and hence change the flow rate and/or the water potentials as the system moves toward a new steady state condition. Thus, the total water uptake system can be considered as a continuum of dynamically interdependent segments (Philip, 1966).

Water uptake by the plant appears to be in passive response to water potential differences except, perhaps, at very low water uptake rates, where active uptake, if it does occur, may become relatively large (Kramer, 1969; Cowan, 1965). Over most of the water uptake range, the water uptake resistance (R) through any segment of the pathway is dependent upon the path length of that segment, the cross-sectional area of that flow pathway, and the hydraulic conductivities of the pathway media.

In the soil, water moves dominantly in the liquid phase, but vapor diffusion becomes increasingly important as the soil becomes drier (Philip, 1966). In the plant, flow is in the liquid phase by

diffusion across membranes or as viscous flow through conducting

tissues. Thus, there are several different mechanisms of water

transport through the soil-plant system, and the contributions of these

mechanisms vary in magnitude. Accordingly, resistance may vary with

environmental conditions and the total resistance of the pathway

might be dominated by different component resistances under different

conditions.

Rearranging equation (1) to get

$$R = \frac{\psi_1 - \psi_2}{U} \qquad (2)$$

allows us to quantitatively evaluate the total resistance to water

uptake by equating ψ_1 and ψ_2 to soil and needle water potential,

respectively, and U to the water uptake rate.

Recent studies have shown that for some plants rooted in

soil, the total resistance to water uptake from the soil to leaves

increases as the soil dries (Taylor and Klepper, 1975; among others).

Thus, the decrease in water uptake rate that is normally observed as

the soil dries is greater than can be simply explained by a change

in the water potentials in soil and leaves. However, there is

considerable debate over which segments of the pathway offer the

greatest resistance and under what conditions they might do so.

Studies on a few herbaceous and woody species, with roots

in solution, indicate the presence of a very large resistance to water

flow in the roots (Jensen *et al.*, 1961; Tinklin and Weatherley, 1966;

Boyer, 1969; Stoker and Weatherley, 1971). In many plants, most of
this resistance probably occurs radially across the root to the
xylem (Lang and Gardner, 1970; Boyer, 1971). In a variety of plants,
resistance to flow through the stem appears to be relatively small
(Jensen *et al.*, 1961; Tinklin and Weatherley, 1966; Boyer, 1971;
Herkelrath *et al.*, 1977a). Indications are that resistances through
roots and through the stem vary and increase as the flow rate decreases
(Tinklin and Weatherley, 1966; Kozlowski, 1966; Andrews and Newman,
1969), although the mechanism is uncertain.

For plants rooted in soil, the resistance to water flow
through the soil to the root may be significant. Gardner (1960)
pointed out that water flows less easily through soil as the soil dries,
since the unsaturated hydraulic conductivity decreases rapidly as
the water content, and, hence, the soil water potential decreases.
His calculations indicate that the resistance through soil may become
significantly large as the soil water potential falls below -0.5 MPa,
but that the magnitude of this resistance is highly dependent upon
the amount of absorbing root surface area and its distribution
through the soil volume, as these affect both the absorbing pathway's
cross-sectional area and the average distance water must flow through
the soil to the roots (Gardner, 1960; 1964).

It is generally agreed that for plants rooted in very wet
soil, the resistance to water flow through the plant is much larger
than that through the soil, but that soil resistance becomes

increasingly important as the soil dries. However, there is

considerable debate about the condition under which soil resistance

becomes significant and dominant in relation to the total resistance.

Boyer (1969) reported plant resistance to be thirty times as great

as that in moist soil for sunflower. Others have claimed that soil

resistance remains smaller than plant resistance even down to -1.5 MPa

and beyond (Andrews and Newman, 1969; Newman, 1969a). But Tinklin

and Weatherley (1968) inferred, from their data, significant resistance

in the soil adjacent to roots in sand, even though the soil water

potential of the bulk soil was only -0.0025 MPa. However, after

reviewing the evidence, Newman (1969b) claimed that there is still

no definitive evidence that the soil resistance is limiting at soil

water potentials above -0.7 MPa, under normal rooting conditions.

More recently, studies by Herkelrath *et al.* (1977a, 1977b)

have indicated the presence of significant resistance in the region

of the roots which cannot be explained by the addition of soil and

plant resistances alone. They suggest that this resistance is located

at the soil-root boundary, and increases as the soil dries, as a

result of decreasing contact between water films around soil particles

and the root surface. This has the effect of decreasing the

effective area of liquid soil water contact with root surfaces. This

resistance may be compounded by root shrinkage, which has been found

to occur with increasing plant water stress (Huck *et al.*, 1970).

Nnyamah *et al.* (1978) found that soil-root contact resistance could

account for as much as one-half of the total resistance between bulk

soil and root xylem in 20 year-old Douglas-fir trees.

Resistance to water flow through the soil, to and into the

root may be modified by mycorrhizal fungi. In very wet soil, Safir

et al. (1971) found lower resistances to water uptake by endomycorrhizal

soybean plants than those without mycorrhizae. They suggested several

possible mechanisms for this observed behavior, including an increase

in the effective absorbing surface area provided by fungal hyphae,

and perhaps, penetration of the root cortex by fungal hyphae providing

a lower resistance pathway for water movement radially across the

root to the xylem. In view of Herkelrath's soil-root contact

resistance hypothesis, the physical presence of a fungal mantle around

absorbing roots might also provide an increasingly important bridge

for liquid flow across any developing vapor gap as the soil dries.

Clearly, both soil and plant factors influence the resistance

to water uptake, and these factors are variable, but their summed

effect is to increase the total resistance as the soil dries, at

least for plants reported in the literature. Resistance in the region

of the roots appears to dominate, whether it lies in the soil, roots

or both. The relative magnitudes of these component resistances

vary with species and soil and plant conditions.

Through equation (2), the total water uptake resistance

can be quantified for tree species. Although the resistance for

components of the pathway cannot be quantified without intermediate

water potential measurement between soil and needles, comparison of total resistances in response to treatment can be informative.

Evaluating the total resistance (R) for seedlings of the same species and similar size, but rooted in soils of differing hydraulic conductivity characteristics, will allow us to quantify the effect of soil water conductivity on water uptake rates and water stress.

Evaluation of total resistance for seedlings of different species rooted on the same soil will allow comparison of the combined effects of root distribution and soil-root contact as well as tissue resistance differences. These comparisons can be made over a wide range of soil water potentials as the soil dries.

CHAPTER 3: METHODS AND MATERIALS

3.1. Experimental Treatments

Considerable physiological information is available for Douglas-fir which can facilitate analysis of experimental data in this study. For this reason, Douglas-fir seedlings from a medium-elevation (500 meters) provenance were chosen as the yardstick by which soil and species treatments can be compared. Western and mountain hemlock seedlings were obtained from coastal provenances of similar medium elevation (1100 meters). All seedlings were obtained from British Columbia Forest Service nurseries. (For provenance descriptions, see Appendix 2.)

Since, in theory, pore size distribution and arrangement greatly influence the relationship between soil water potential and unsaturated hydraulic conductivity of the soil, and since they are known to be influenced by particle size distribution, three soils of widely differing texture were chosen to test the effect of soil water flow characteristics on water uptake. The soils, silty clay, silt loam and loamy sand, were obtained from Ap horizons at the University of British Columbia Research Forest and represent the range of surface materials commonly found in this region. These soils were expected to yield a wide range of unsaturated hydraulic conductivity characteristics. (For soil properties, see Appendices 3, 4, and 5.)

3.2 *Strategy*

Ideally, concurrent knowledge of fluxes and water potential differences would require simultaneous measurement of these parameters on the same seedling. However, the lack of simple non-destructive plant water potential measurement techniques forced the study to be developed around separate studies of water uptake and water potential difference, on large sample populations under similar environmental conditions. Because of the complexity of the environmental variables concerned, experiments were conducted on one-year-old potted seedlings in growth chambers. Under growth chamber conditions, soil water potential can be used as the independent variable to which uptake rate and water potential difference can be related. All measurements were treated as steady state values and were taken at times when this condition was closely approximated.

The average needle water potential (ψ_N) was measured using sample chambers with dew-point hygrometers on excised needles. Concurrently, dew-point hygrometer probes were used in the soil to measure the soil water potential (ψ_s), which was assumed to represent the average soil water potential at a point approximately halfway between roots. In calculating water potential difference ($\psi_s - \psi_N$), the gravitational potential difference was ignored, as it is of the order of only 10 kPa, a magnitude too small to have a significant effect in interpreting the results. Evapotranspiration was evaluated in terms of weight loss rate over four-hour periods when steady state was approximated. Evaporation rate was estimated as the asymptotic value

of weight loss rate plotted over soil water potential since, under

very dry soil conditions, the transpiration rate becomes very nearly

zero, and since evaporation rate was restricted to a near constant

rate over the full soil water potential range used in these experiments.

Constant evaporation rates were approximately achieved by enclosing

the soil in plastic bags which restricted the vapor pressure gradient

and the vapor diffusion resistance to nearly constant magnitudes.

At approximately steady state, transpiration rate is very nearly equal

to water uptake rate and thus was used as a reasonable approximation

of water uptake rate in these experiments. Using equation 2 from the

previous chapter, resistance to water uptake was calculated for each

treatment over the range where significant water uptake occurred, or

approximately -0.5 to -2.5 MPa soil water potential.

3.3 *Experimental Preparation*

3.3.1 *Seedling Preparation*

In order to be able to attribute experimental differences

to experimental treatments, all samples were handled similarly

before and during experimental periods. In order to reduce

variation within treatments, environmental extremes were avoided

before experimentation and all seedlings were prepared in a manner

such that, within treatments, they would exhibit similar size

and form without seriously altering the characteristic behavior

of the treatment. The preparations included (1) potting conditions

and techniques, (2) pruning, (3) greenhouse environment including watering and fertilization schedules, and (4) selection and preparation for experimentation.

Five hundred seedlings each, of six-month-old styroblock western and mountain hemlock, and one thousand six-month-old plug Douglas-fir were obtained from British Columbia Forest Service nursery cold storage warehouses in Surrey and Duncan, respectively, in March, 1976. The seedlings were stored in a refrigeration unit on the U.B.C. campus for three weeks until potting. At that time, seedlings showing mold, breakage and obvious crown or root deficiencies or excesses were discarded.

The three soils were sieved while moist, through a 5-mm mesh. Since very little gravel was present, further sieving was not considered necessary.

All hemlock seedlings were potted in the medium texture (silt loam) soil and equal numbers of Douglas-fir were potted in all three soils in early April, 1976.

At the time of potting, the roots were gently washed to remove the nursery soil mix, and transplanted into 150-cm^3 (5.7-cm wide) plastic pots, using pre-weighed amounts of soil packed to equal volumes. This allowed close control and calculation of soil bulk density for all treatments. The bulk density of the silty clay was about 500 $\text{kg}\cdot\text{m}^{-3}$, silt loam 750 $\text{kg}\cdot\text{m}^{-3}$ and loamy sand 1120 $\text{kg}\cdot\text{m}^{-3}$.

All seedlings flushed within three weeks after potting. Within one month, obvious variation in crown size was observed. To reduce this variation, the seedlings were lightly pruned to similar needle surface areas. Approximately 15% of each treatment population was discarded due to deficient or excessive crown sizes. It was hoped that pruning would also indirectly control root growth of larger seedlings.

The attempt to equalize needle surface areas was hindered by the indeterminate behavior of the hemlocks. However, a second flush by the Douglas-fir in early summer did reduce differences between species.

The seedlings were kept in the greenhouse until experimentation. The ventilation system maintained daytime temperatures between 20 and 25°C, with a relative humidity of about 80%. Irradiance during the daytime was probably 20 to 25% of full sunlight.

The seedlings were watered to field capacity daily on sunny days, and every other day on cool or cloudy days. This frequency was necessary in order to maintain soil water potentials above -0.5 MPa. It was soon noticed that the hemlock pots dried much more slowly than those of Douglas-fir, so the frequency of watering of hemlock seedlings was reduced to avoid overwatering. It was hoped that pruning to similar crown sizes would help reduce this kind of variation within treatments.

All seedlings were fertilized regularly with 5.0 ml of full strength modified Hoagland's solution (see Appendix 1) during the period of rapid growth in spring, and then periodically thereafter. Fertilization was intended to prevent deficiency symptoms which might affect water uptake behavior and normal growth, and possibly discourage infection of root systems by mycorrhizal fungi which might complicate experimental results.

The seedlings were kept in the greenhouse from March until the end of experiments in November.

Prior to the beginning of experiments, Douglas-fir seedlings which exhibited extremely large crowns as a result of the second flush were discarded. In addition, all pots with much greater or much less than average soil volumes were discarded to reduce soil variation. Average soil volume for this purpose was determined visually.

For the experiments, sample seedlings were selected randomly from the remaining treatment populations.

Because of the wide range of soil water potential expected in these experiments, soil dew-point hygrometers (PT-51, Wescor Inc.) were used in conjunction with a dew-point microvoltmeter (HT-33, Wescor Inc.) to measure this variable. All hygrometer measurements were made in dew-point mode because of lower sensitivity change with temperature and good agreement with psychrometric mode on plant tissue and soil samples (Nnyamah and Black, 1977).

One to two days before an experiment, all sample
seedlings were watered to field capacity. A 0.3-cm hole was
made vertically into the soil, about 1 cm from the root
collar, with a nail. A wetted ceramic bulb sensor was then
forced into the hole to a point near the middle of each pot
and anchored by tape to prevent movement of the sensor during
measurements. The pots were then watered again to insure good
contact between the sensor bulb and the soil.

Drainage holes in the bottom of each pot were taped
closed and the soil volumes were measured and recorded.

Each seedling pot was placed in a plastic bag to
restrict evaporation from the soil to a reduced and near constant
rate throughout the experiment. All bags were closed around the
stem in a similar manner so that vapor pressures would be held
within a very narrow, nearly saturated range by the soil water
potential and high diffusive resistance of the bag. During
experimental periods, but after a day's measurements, the bags
were opened every other day for ten mintues to allow for exchange
of soil atmosphere. This was considered sufficient time since
the plastic bag, when closed, contained a large volume of air
around the pot and acted as an oxygen reservoir for respiring
roots. The plastic bags and the air volume surrounding the pot
within the bags acted as a thermal insulator to prevent excessive
thermal gradients through the soil, thus reducing soil water

potential measurement error. Excessive soil water potential

errors have been demonstrated under large thermal gradients

across dew-point hygrometer sensors (Wiebe *et al.*, 1977).

3.3.2 *Experimental Environment*

In the growth chambers, light periods of 15 hours per

day were used with a photon flux density within the visible spectrum

of about 450 to 550 $\mu E \cdot m^{-2} \cdot s^{-1}$ at midcrown level as provided by

a bank of incandescent and fluorescent lamps (see Appendix 6).

This flux density corresponds to about 1/4 of sunlight at full

solar noon in midsummer. Systematic variation of about 20%

occurred over the bench. 300 $\mu E \cdot m^{-2} \cdot s^{-1}$ has been determined in the

field as the intensity at which light becomes the limiting factor

to stomatal opening in 40-year-old Douglas-fir (Tan *et al.*, 1977).

No comparable data are available for either hemlock species.

Light period temperatures were controlled to 20 ± 1°C.

However, the soil temperatures were measured to be about 24°C.

These soil temperatures are not high in relation to soil surface

horizon temperatures in the field (Isaac, 1938; Herman, 1963;

Ballard *et al.*, 1977) even at higher elevations (Brook *et al.*,

1970). Presumably these elevated soil temperatures were the

result of a greenhouse effect caused by the plastic bags. Nighttime

temperatures were reduced to 15 ± 1°C.

The relative humidity was controlled by humidifiers

to 65 ± 5% during light periods and 80 ± 5% during dark periods.

Humidity and temperature were recorded continuously by calibrated

hygrothermograph and checked regularly throughout all

experiments.

The growth chamber was ventilated at a rate of about

$0.35 \ m \cdot s^{-1}$ in order to minimize changes in CO_2 concentration,

reduce boundary layer resistance, and to reduce variation in

temperature and humidity across the growth chamber bench.

Seedlings were systematically arranged, by treatment,

to avoid treatment bias due to radiation and ventilation variation.

3.4 *Experimental and Analytical Procedures*

3.4.1 *Water Potential*

In this study, the needles were considered to be the

endpoint of the water uptake flow. Calculation of the water uptake

resistance required concurrent measurement of soil and needle

water potential. Water potential of the soil was measured by

dew-point hygrometer probes and needle water potential by

dew-point hygrometers on excised needles in sample chambers.

Voltage output from the hygrometer microvoltmeter is

linearly proportional to the water potential. All hygrometers

were individually calibrated and used in dew-point mode. Fifty

PT-51 soil hygrometers were calibrated by immersion into

solutions of 0.05, 0.2, 0.3, and 0.5 mol NaCl/kg water representing

osmotic potentials of -0.23, -0.9, -1.34, and -2.24 MPa,

respectively, at 20°C. All solutions were held to 20°C $\pm$ 0.02°C by immersion of solution containers in a constant temperature water bath. Using each sensor, one measurement was made in each solution to check linearity of calibration. Then, four or five measurements were made using these sensors and an additional 50 sensors in the 0.5 molal solution. The average microvolt output readings were calculated to determine the calibration slope for each sensor.

Only those sensors which had slopes between 6 and 8 μV$\cdot$MPa^{-1} and with less than $\pm$ 0.7 μV variation in output for the four to five measurements in the 0.5 molal solution were used in experiments. This variation represents about $\pm$ 0.1 MPa at a water potential of 2.2 MPa (for summary, see Appendix 10).

Calibration intercepts were determined at the end of experimentation by immersion in distilled water. This provided both an intercept value, which was very close to zero (see Appendix 10), and a check against possible sensor error.

Soil hygrometer data were recorded in microvolts and later converted to megapascals.

In order to quantify the variability in soil water potential measurements to be expected within a single pot, several seedlings were set up, as described previously, except with two hygrometer sensors placed 2 cm apart on opposite sides of the stem. The seedlings were placed in the growth chamber and concurrent soil water potentials were measured twice a day

until the soil dried to about -4 MPa. These data indicated that

as much as ± 0.3 MPa variation can be expected within a single

pot over the range of about -0.5 to -4.0 MPa soil water potential.

This variation may be due to (1) inherent sensor equipment

and reading error, (2) proximity of sensors to absorbing roots,

(3) imperfect integrating power of roots, (4) variable contact

between sensor bulb and soil, and (5) thermal gradients within

the pot. Because of the relative constancy of measured variation

as the soil dried, sources (1) and (5) may be dominating.

Occasional differences of up to 1 MPa measured within one pot

might indicate the possibility of occasional large error due to

(5).

Two thermocouple hygrometer sample chambers were used in

these experiments (C-51 and C-52, Wescor Inc.). Each sample

chamber was calibrated against known water potentials, using

solutions of 0.0, .05, 0.2, 0.3, 0.5, and 0.9 mol NaCl/l ow water,

in a constant temperature room. The data showed excellent linearity

between -0.23 and -4.16 MPa for both sample chambers, and

accuracy to within ± 0.025 MPa for estimating water potential of

the vapor-equilibrated chamber. However, careful technique was

necessary to ensure reasonable vapor equilibration with needle

tissue which accurately represents water potential conditions in

intact needles immediately before sampling.

Vapor equilibration times were prohibitively slow (up

to several hours) on excised, untreated needles. During such

long times, significant changes in average needle water potential

might occur. Two techniques were tested for effectiveness in

reducing vapor equilibration times and producing reliable

estimates of needle water potential: (1) cutting the excised

needles into thirds, crosswise, and (2) wiping the needle

surfaces lightly with a xylene-moistened Kimwipe and cutting into

thirds. Cutting the needles with a razor blade was done to

expose some water surfaces to the chamber atmosphere to promote

evaporation without rupturing a large number of cells. The xylene

treatment, used for its cuticle solvent ability and rapid drying,

was performed to increase epidermal evaporation without causing

serious damage to tissues, which might change the water potential

(Neumann and Thurtell, 1972). The sample chamber holders were

coated with melted and resolidified paraffin wax, as suggested by

Boyer (1967), to reduce water adsorption to the holder surfaces.

Tests showed that equilibration with cut needles took

about 2 to 3 hours. However, when treated with xylene, equilibration

varied from 8 to 40 minutes, but always within 0.2 MPa of the

equilibrium value at 20 minutes. The final equilibrated reading

was the same for both treatments, indicating that xylene treatment

had no measurable effect on the average water potential of the

sampled needles. For subsequent experiments, a 30-minute

equilibration time was used.

Sample preparation for all needle water potential measurements consisted of pulling off 20 to 30 young needles from the midpoint of a lateral twig, brushing the needles lightly with a xylene-moistened brush and quickly wiping the surfaces with a Kimwipe. Within a few seconds, the needle surfaces were dry. The needles were cut into thirds, and the sample holder was filled with tissue and sealed in the chamber. This process took about 90 seconds to complete. Speed was critical in order to prevent significant evaporation from the tissue before sealing inside the chamber, which would cause lower water potentials to be measured.

To avoid error caused by contaminants on the hygrometer junction and sample holder, the units were cleaned every other day with acetone or soap and rinsed thoroughly with distilled water. The calibrations were rechecked periodically.

Four experimental runs (16 seedlings from each treatment per run) were conducted between September and November, 1976. All seedlings were prepared as described previously and placed in the growth chamber two days before the experiment, to allow diurnal fluctuations to be reduced.

Needle water potential and soil water potential were measured concurrently on two seedlings from each treatment daily. Only one measurement was taken for each seedling, since the destruction of needles might have had some effect on the seedling's

water balance, influencing subsequent measurement. Times of measurement and the sample chamber used were alternated systematically to remove sampling and measurement bias. All measurements were taken between 7 1/2 and 10 hours after the beginning of the light period so that the average time for each treatment was about 8 3/4 hours. Full measurement on each pot was about 40 minutes.

Each experimental run lasted about eight days. Bags were left open on some seedling pots to facilitate evaporation and thus reduction of soil water potentials, but were closed again at least two full days before measurements on those seedlings, in order to allow the soil to approach conditions of steady state transpiration and smaller vertical gradients of soil water potential.

From the data obtained by the methods outlined above, the relationship between needle water potential and soil water potential was described for each treatment. Since, in theory, water uptake ceases when the measured needle water potential equals the soil water potential, only those data points within the soil water potential range where $\psi_N < \psi_s$ were included in a regression to define a relationship in the range where significant water uptake occurred. A simple covariance analysis was performed to test for differences between treatments (Osborn *et al.*, 1972).

Using the above regression equations the relationships
between water potential difference (between soil and needles) and
soil water potential for each treatment were calculated and
compared over the soil water potential range where signficant
water uptake occurred.

3.4.2 *Water Uptake Rate*

Average water uptake rates for each treatment were
calculated from weight loss data measured concurrently with soil
water potential. Two runs of 7 or 8 seedlings from each
treatment were conducted between July and September, 1976. The
seedlings were prepared as described in a previous section, and
placed in the growth chamber two days before measurements began.
Weight loss rates were determined during subsequent light periods
by weighing each pot three times daily, (beginning four hours
after the start of the light period) at 9:30, 1:30 and 5:30, on
a 0.05·g-division top-loading balance. This permitted calculation
of the average weight loss rate for each seedling over two four-hour
periods each day. Soil water potential measurements, taken
concurrently with weighings, were averaged to produce the
corresponding average soil water potential over each period.

The measurements were continued daily, on each seedling,
until the soil water potential was consistently measured at less
than -4.0 MPa for Douglas-fir and -3.5 MPa for the hemlocks. This
period varied between 10 and 20 days, depending upon the treatment
and seedling.

Water uptake rates are directly affected by the influence of seedling size on the dimensions of the water flow pathway. Since the limiting resistances to uptake and loss generally appear to occur in the regions of the roots and the leaves of plants, information concerning pathway dimensions in these regions was considered to be useful for analysis of water uptake data among seedlings and treatments. Therefore, for each seedling used in the weight loss rate experiments, estimations were made of (1) needle surface area, (2) root surface area and length, and (3) extent of mycorrhizal infection and root hair development.

Needle surface areas (one-sided) of each seedling were calculated by measuring the oven-dry mass of all needles (16 hours at 80°C) and multiplying by the ratio of needle surface area to oven-dry mass, determined for each species. These ratios were determined by excising all needles from four seedlings of each species, and carefully laying the needles as closely together as possible, without overlap, on slightly adhesive graph paper with a 1-mm grid. The areas for each seedling were recorded and the needles carefully removed and oven-dried. The average ratio for each species was calculated from these data (see Appendix 7 for values).

These cross-sectional areas of segments of the water uptake pathway in the region of the roots outside the xylem are

proportional to the root surface area (Gardner, 1960). The
path length of water flow is dependent upon root distribution
as determined by the distance between absorbing roots. This
distance tends to be inversely proportional to the total length
of roots within the soil volume.

In order to calculate root surface area and root
length for each seedling, the roots were assumed to be approximately
cylindrical within narrow ranges of diameter, and evenly
distributed throughout the soil volume. All roots were assumed
to be equally permeable to water. Fresh root surface area (A)
can be calculated by

$$A = 2\pi r l \tag{3}$$

where r is the average fresh root radius and l is the average
length of fresh roots. Likewise, fresh root volume (V)

$$V = \pi r^2 l \tag{4}$$

and since fresh root density (ρ) is

$$\rho = \frac{m}{V} \tag{5}$$

where m is the fresh root mass, then

$$A = \frac{2m}{\rho r} \tag{6}$$

Three root radius classes were distinguished: 0.5 mm to stem base radius, 0.25 to 0.5 mm, and 0 mm to 0.25 mm. The average radius (r) of each size class was calculated from these range values. Fresh root tissue densities were obtained for each species and size class by flotation in fluids of different density (see Appendix 7). All root densities ranged between 950 and 1080 $kg \cdot m^{-3}$.

Fresh root mass was determined after the final weight loss measurements were taken for each seedling (at ψ_s of about -3.5 to -4.0 MPa). The soil around the roots was lightly crumbled free of the roots and then lightly sieved to remove broken roots. All roots were carefully washed in water and blotted dry. Using a dial caliper and small scissors, the roots were cut into the three size classes. By the time this was done (30 minutes), the root surfaces were dry, presumably to a moisture condition similar to the undisturbed plant roots, and so represent an average degree of hydration in the roots like those of the undisturbed seedling during the weight loss experiment. The roots were then weighed to arrive at the mass of the fresh roots (m).

Root surface areas were calculated for each size class and summed to produce the total root surface area for the seedling. In all cases, more than 80% of the total seedling root surface area was provided by the smallest radius class.

The root length was calculated by

$$1 = \frac{m}{\rho \pi r^2} \qquad (7)$$

for each size class, and summed to produce the total root

length for the seedling.

From the above data, additional calculations were made

to further describe the water uptake pathway near the roots.

By weighting the average radii of the size classes by

the length of roots in each size class relative to the total,

and then summing, the average root radius for the seedling (r_i)

was obtained.

$$r_i = (\frac{1_1}{1_{total}})r_1 + (\frac{1_2}{1_{total}})r_2 + (\frac{1_3}{1_{total}})r_3 \qquad (8)$$

Assuming that the roots were equally distributed

throughout the total measured soil volume, the equation

$$n = (\frac{V_s}{1_t})^{\frac{1}{2}} \qquad (9)$$

is obtained, where 1_t is the total root length for the seedling,

V_s is the volume of soil, and n becomes the closest distance

between root centers. The point farthest from an adjacent

root center is located $2^{\frac{1}{2}}(n/2)$ from the root center. It is

assumed, for purposes of calculation, that ψ_s is measured at

a point halfway between that furthest point and the adjacent

root center, i.e. at a distance

$$s = 2^{\frac{1}{2}}(n/4) = (V_s/81_t)^{\frac{1}{2}} \qquad (10)$$

from the root center.

Theoretically, s approximately represents the average

direct distance water must travel from the point where ψ_s is

measured to the point where it enters the xylem. By subtracting

the average radius (r_i) of the root system from the value s,

$$z = s - r_i \qquad (11)$$

one obtains an estimate of the pathlength (z) through the

soil to the seedling root surface, from the point where ψ_s is

measured. Calculated values of z for various treatments have no

absolute meaning, because of underlying assumptions. However, they

enable some comparison of relative pathlengths of water movement

through the soil (see Appendix 8 for summary of calculated values).

All parts of the seedling were oven-dried to calculate

root:shoot dry mass ratios.

The relative abundance of root hairs and abundance of

mycorrhizal hyphae were noted for each treatment, as they might

influence water flow resistance at the root surface.

From weight loss rate data for each seedling, a non-linear least squares curve fit, by stepwise Gauss-Newton iterations, was produced for each seedling to yield an equation for weight loss rate (W) in relation to soil water potential.

The equation

$$W = d + ab^{(\psi s - c)} \qquad (12)$$

was found to fit all seedlings reasonably well.

The asymptotic d value was assumed to approximate the evaporation rate from the bag and was subtracted to yield the water uptake rate (U) for each seedling. Water uptake rates were expressed on the unit root surface area basis: In an attempt to reduce variation for seedlings within treatments,

$$U = \frac{W - d}{A_r} = \frac{ab^{(\psi s - c)}}{A_r} \qquad (13)$$

Using equation 13 equal numbers of equally distributed points were calculated for each seedling over the soil water potential range of -0.4 to -4.0 MPa. These generated data points for all seedlings within a treatment were then fitted by equation 14 to produce the treatment average water uptake rate per root area, in relation to soil water potential:

$$U = ef^{(\psi s - g)} \qquad (14)$$

The above procedure was performed to reduce bias toward seedlings of particular water uptake behavior. Seedlings which

were slow to reach -4.0 MPa soil water potential had more data

points collected and this slower rate might have been due to

seedling size differences. These seedlings also tended to have

disproportionately more data points in the wet end of the soil

water potential range.

Several seedlings, especially those with very fast

water uptake rates, had no data in the very wet end. Therefore,

it was felt that the treatment water uptake rate in relation to

soil water potential, and hence, the resistance to water uptake

can be accurately described only to an upper limit of about -0.5 MPa

soil water potential.

The above calculation procedure presented a prohibitively

complex statistical problem. Therefore, to simplify, analyses

of variance of generated data points at -0.6 and -2.0 MPa were

performed as a rough test for differences between treatments

(for summary see Appendix 9). The close fit of individual seedling

data to equation (12) and low variation among these data lend

additional support to this kind of analysis. However, considerable

variation among seedlings within treatments was expected and

observed.

Having calculated the water uptake rate per unit root

surface area in relation to soil water potential for each

treatment, multiplication by the treatment average seedling root surface

area produced the treatment average water uptake rate per seedling

in relation to soil water potential.

3.4.3 *Resistance*

By equation 2 (Chapter 2), the average resistance to water uptake was calculated over the soil water potential range of -0.5 MPa to about -2.5 to -3.2 MPa, depending upon the value of soil water potential where the water potential difference is about zero. This measure of resistance afforded a useful comparison of treatments if the pathway dimensions were similar. However, when this condition was not met, the resistance was calculated on a root surface area basis to provide a more realistic basis of comparison.

CHAPTER 4: RESULTS AND DISCUSSION: SOILS

4.1 Water Potential

Needle water potential for Douglas-fir seedlings does not change much with decreasing soil water potential over the range where significant water uptake occurs, down to ψ_s of about -2.5 MPa. Needle water potentials for all three soils remain at about -2.5 MPa to -2.7 MPa over this range (Figures 1a, b, and c). Beyond this range, continual water loss from the plant, without compensating water uptake, causes needle water potential to decline.

A comparison of soils in Figure 2 shows that in silt loam, and more so in loamy sand, there is a slight decline in needle water potential with decreasing soil water potential, a result which would be consistent with the lower unsaturated hydraulic conductivities and consequently higher uptake resistances that one might expect at low soil water potentials in coarse-textured soils. However, despite apparent differences between these lines, there were no statistically significant differences.

Since the relationships between needle water potential and soil water potential have slopes very near zero, the water potential difference between soil and needle is a virtually linear function of soil water potential above about -2.7 MPa in these experiments (Figure 3).

4.2 Water Uptake Rate

In order to reduce variation, water uptake rates were expressed on a per unit root area, per needle area, as well as

per seedling basis. In Figures 4a, b, and c each series of data

points represents an individual seedling. Although expression on a

root area basis reduced variation somewhat, considerable variation

remains at the wet end of the graph. Expression on a needle area

basis was no better. Since no consistent relationships were found

between individual seedling dimensions and their corresponding

water uptake rates, it is inferred that much of this variation in

water uptake per unit root area may be due to differences in

irradiance and ventilation across the growth chamber bench as well as

physiological variation within this provenance.

Water uptake rate per unit root area decreased rapidly in

all soils as the soil dried from about -0.5 MPa to about -2.5 MPa,

and did not approach zero until about -3.0 MPa. The major reason

that the uptake rate did not approach zero until well below equilibrium

conditions (that is, when needle water potential equalled soil water

potential) appears to be a result of the relative inaccuracy of

equation 12 to describe the water uptake data below about -2.2 MPa

soil water potential. Observations of the graphic data and curve

output for each seedling show a smoothing tendency by the curve

produced by equation 12 which does not precisely describe the more

abrupt levelling off behavior of the uptake rate data below about

-2.2 MPa. There appears to be a consistent slight overestimation of

water uptake rate per unit root area, by the curve, between -2.2 and

-2.8 MPa, and a consistent underestimation below about -2.8 MPa.

Thus, the asymptotic values (d) of the curves are almost certainly

underestimates of the evaporation rate from the bag, and water

uptake rates per unit root area between -2.2 MPa and -2.8 MPa are

slightly overestimated. However, this error is not so serious that

it changes the resistance results materially over other parts of the

soil water potential range.

Despite the observed variation in Figures 4a, b, and c,

silty clay was significantly different (p = .01) from loamy sand at

the wet end of the curve (Figure 5). Silt loam behaved intermediately

to silty clay and loamy sand, which was expected from soil unsaturated

hydraulic conductivity characteristics. However, silt loam was not

significantly different from the other textures. There were no

significant differences between curves at -2.0 MPa.

The curves of average seedling water uptake rate (Figure 6)

are very similar to those of average seedling water uptake rate per unit

root surface area, due to very similar average root surface areas between

treatments. The uptake rate for silty clay is about 15% higher than

for silt loam and about 40% higher than for loamy sand. The proportions

remain similar over much of the soil water potential range.

4.3 *Resistance*

For all three soil textures, the average seedling resistance

to water uptake changed very little with decreasing soil water potential

between -0.5 and -1.0 MPa (Figure 7). This agrees well with Nnyamah's

observations on 20-year-old Douglas-fir in the field (Nnyamah *et al.*,

1978).

With declining soil water potential from -1.0 to -2.2 MPa, resistance increased about 2-fold. Loamy sand, with slightly higher water potential differences and much lower uptake rates, consistently yielded the highest resistance, and silty clay, with lower water potential difference and much higher uptake rates, yielded the lowest resistance at all soil water potentials. Silt loam was consistently intermediate. The resistance in loamy sand is almost twice that of silty clay at -0.5 MPa and increases more rapidly, as the soil dries, than for silty clay.

Below about -2.2 MPa, in all three soils, the calculated resistance decreases rapidly. This decrease is probably an artifact resulting from the overestimate of water uptake at the very dry end. This overestimate becomes relatively very large as the soil dries below -2.2 MPa. Calculations based upon water uptake falling to zero when water potential difference equals zero, show a consistent increase in resistance in this range, which probably represents a more accurate description.

4.4 *Discussion*

Douglas-fir seedling water stress, as indicated by the needle water potential, is not much affected by soil drying down to about -2.7 MPa, so long as water can flow into the plant. Thus, these seedlings appear well able to regulate their water balance, to maintain almost constant needle water potential, so long as there is a significant rate of water flow into the seedlings.

However, the resistance to this flow increases greatly as the soil dries below about -1.0 MPa. Because root surface areas, root lengths, and soil volumes are similar for all three soil textures, it is inferred that unsaturated hydraulic conductivity of the soil and, perhaps, the soil-root contact, are major contributing factors to differences in resistance among the three soils. The ranking of textures in terms of resistance is predictable from their ranking in terms of unsaturated hydraulic conductivity. Texture apparently does influence water flow resistance and hence influences the rate of water uptake by the seedling. The differences in resistance and uptake rate may be very large in moderately dry soils of different texture.

However, the resistance in the plant component of the flow pathway is extremely important in the total resistance. As soil unsaturated hydraulic conductivity is known to change considerably between -0.5 and -1.0 MPa (Gardner, 1960), the lack of change in resistance, found in this study, over this range suggests that at higher soil water potentials (up to -0.5 MPa) the plant resistance, and perhaps the soil-root contact resistance, dominate the total resistance. Calculations based upon Gardner's (1960) water flow model through soil to absorbing roots and using his values for unsaturated hydraulic conductivity for a loam soil (but substituting values determined in this study for seedling average total root length (l_t), root radius (r_i) and distance from hygrometer sensor to the root center (s), indicate that soil resistance is about an order of magnitude

less than total resistance in this range. These results appear to
agree with Newman's (1969b) argument that soil resistance remains
small until the soil becomes quite dry. This might indicate important
root-soil contact resistance differences between soils which account,
to a large degree, for differences in total resistance to water uptake
in this soil water potential range. Because mycorrhizal mantles
surrounding roots of these seedlings were observed to be only slight
on silty clay and very slight on silt loam and loamy sand, and because
contact resistance perhaps may affect water movement to hyphae,
mycorrhizae are not considered to affect these results materially.
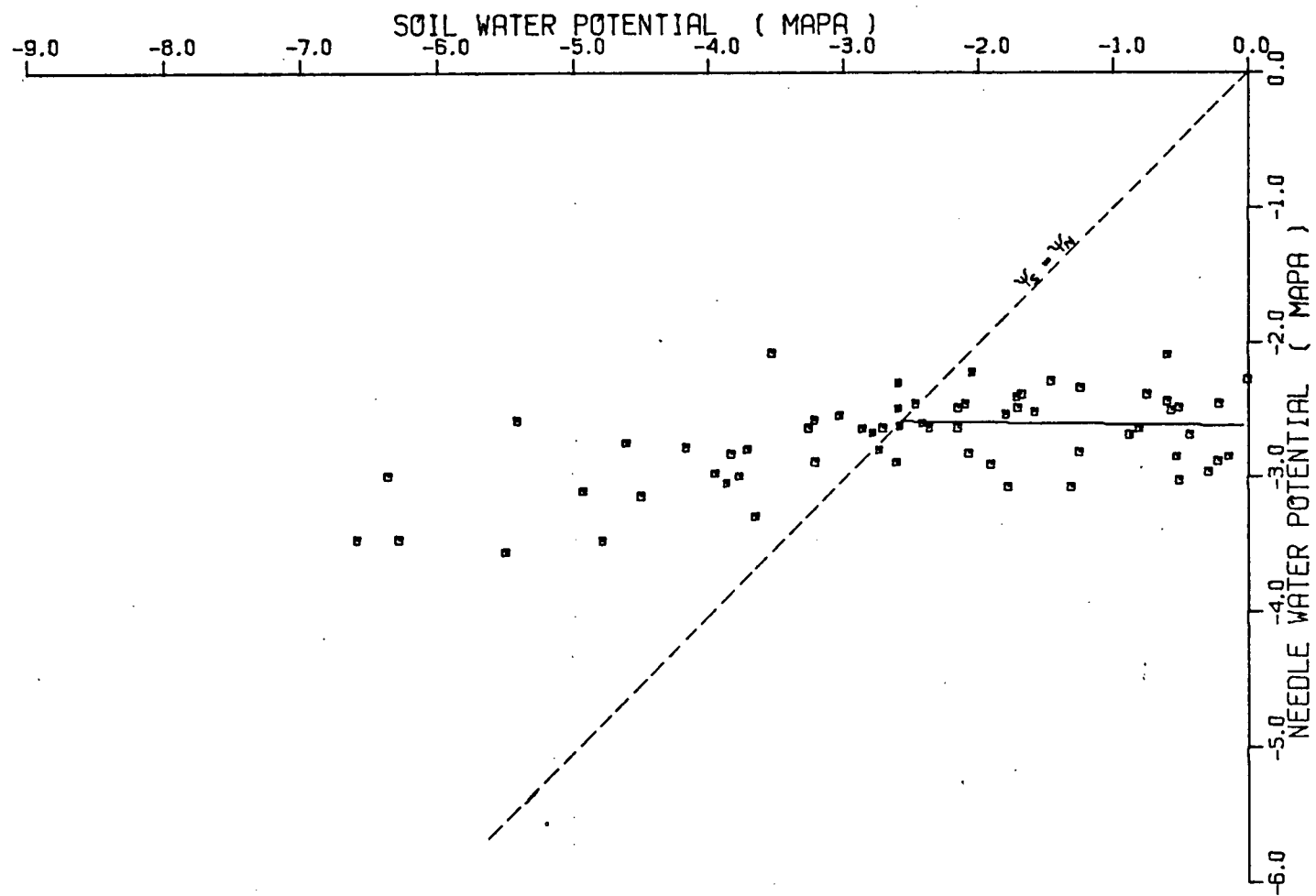
FIGURE 1a: Needle water potential in relation to soil water potential for
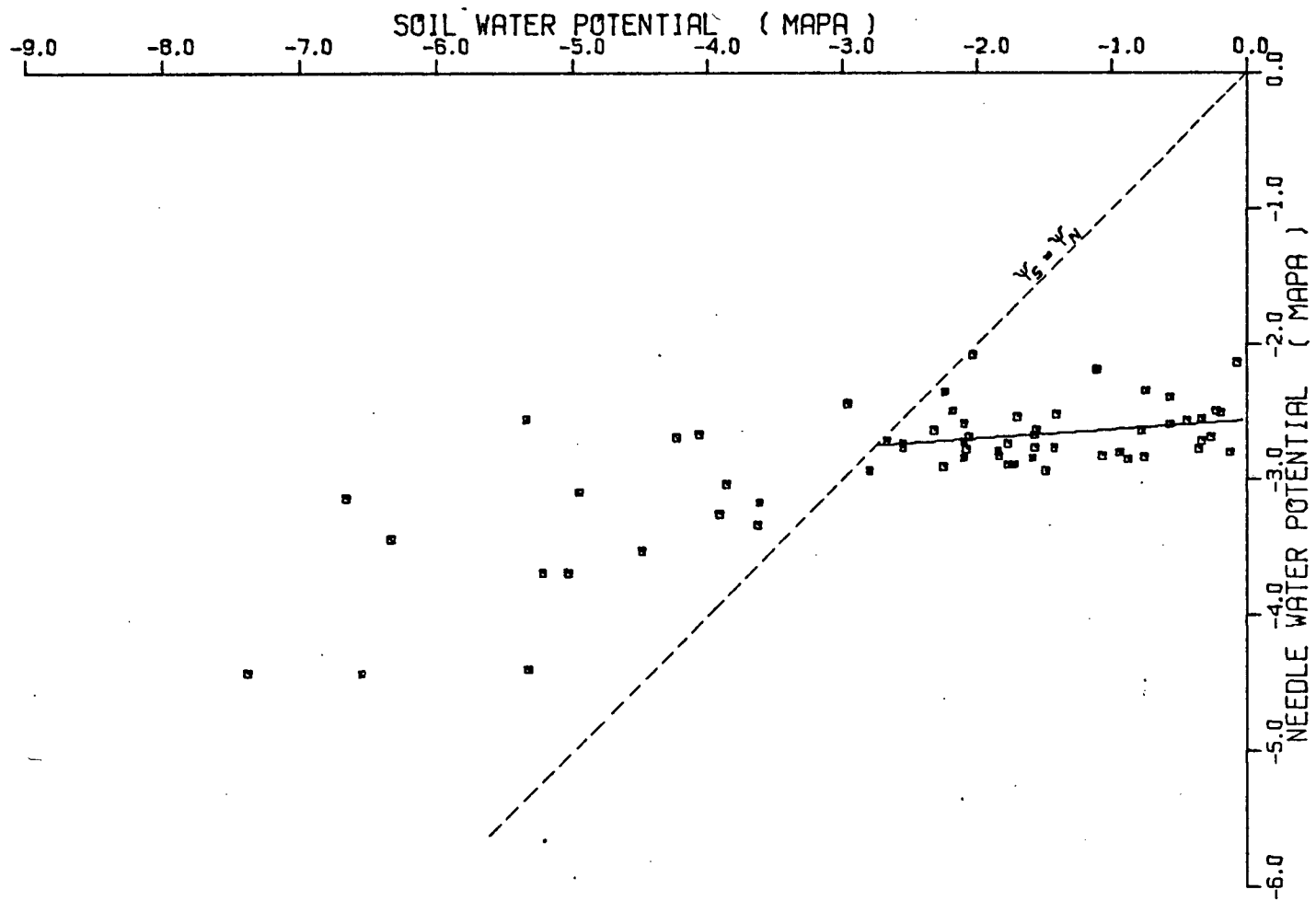   Douglas-fir on silty clay soil.

FIGURE 1b: Needle water potential in relation to soil water potential for
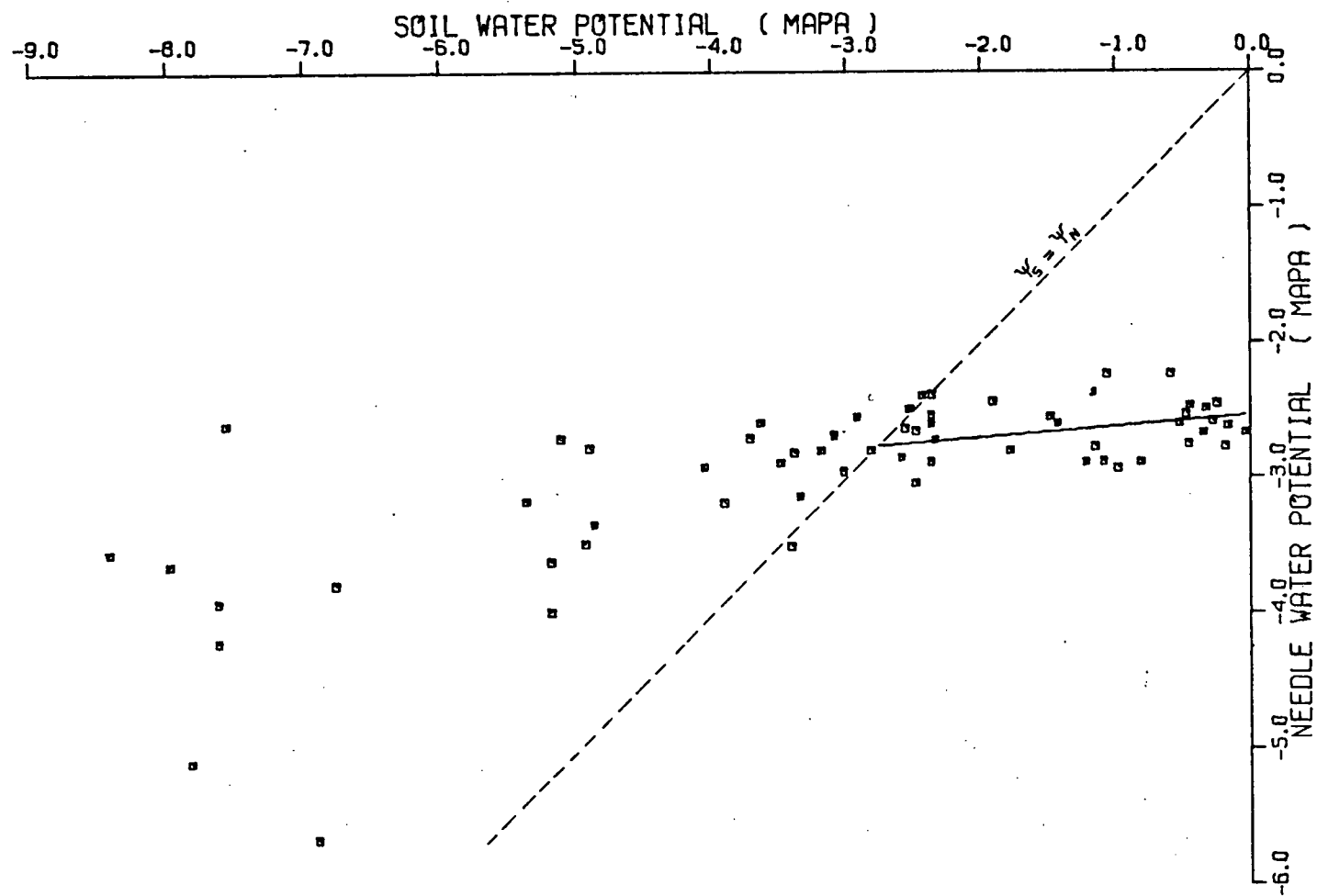   Douglas-fir on silt loam soil.

FIGURE 1c: Needle water potential in relation to soil water potential for
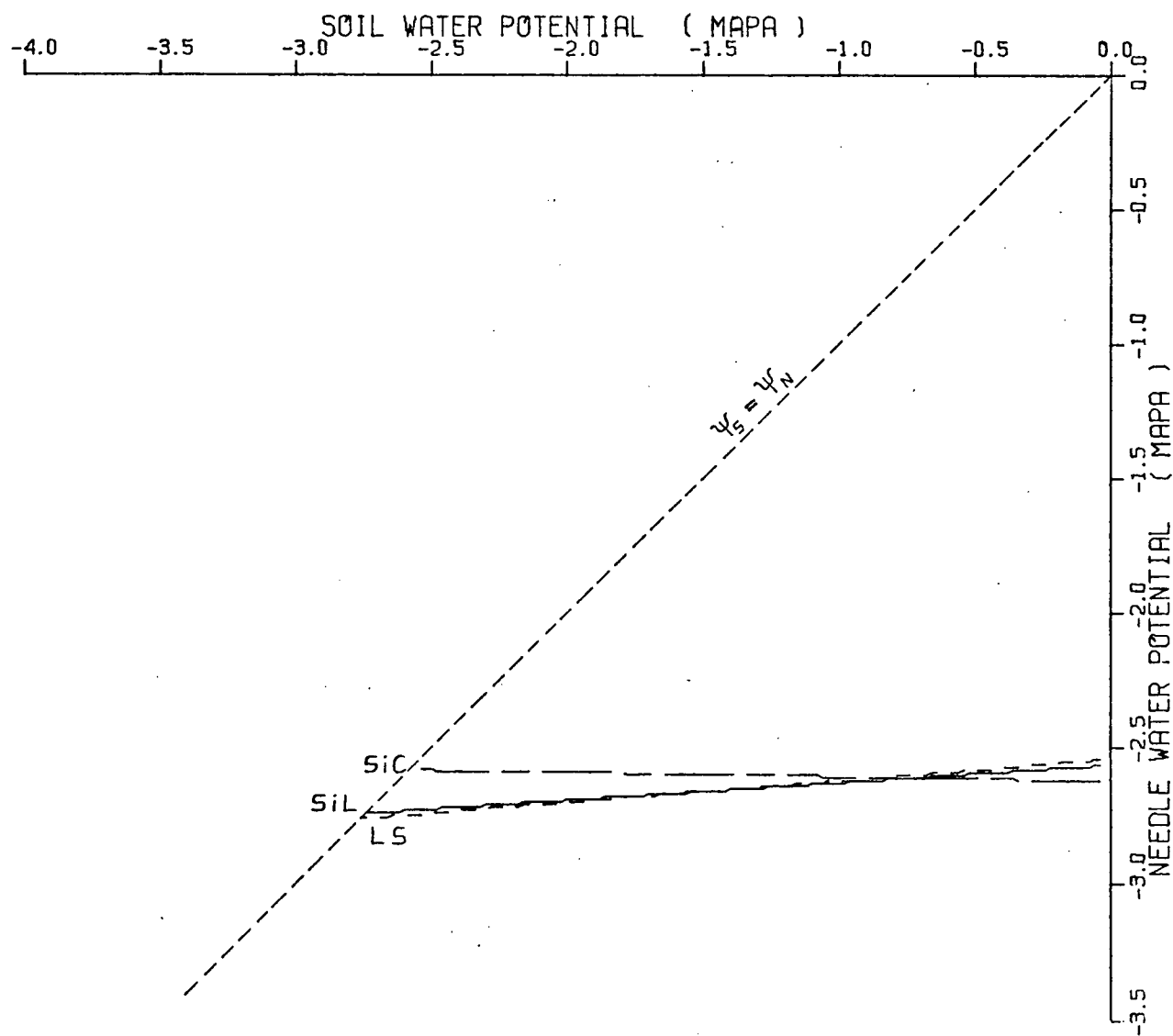Douglas-fir on loamy sand soil.

FIGURE 2: Needle water potential in relation to soil water potential
for Douglas-fir: A comparison of soils; silty clay (SiC),
silt loam (SiL) and loamy sand (LS).

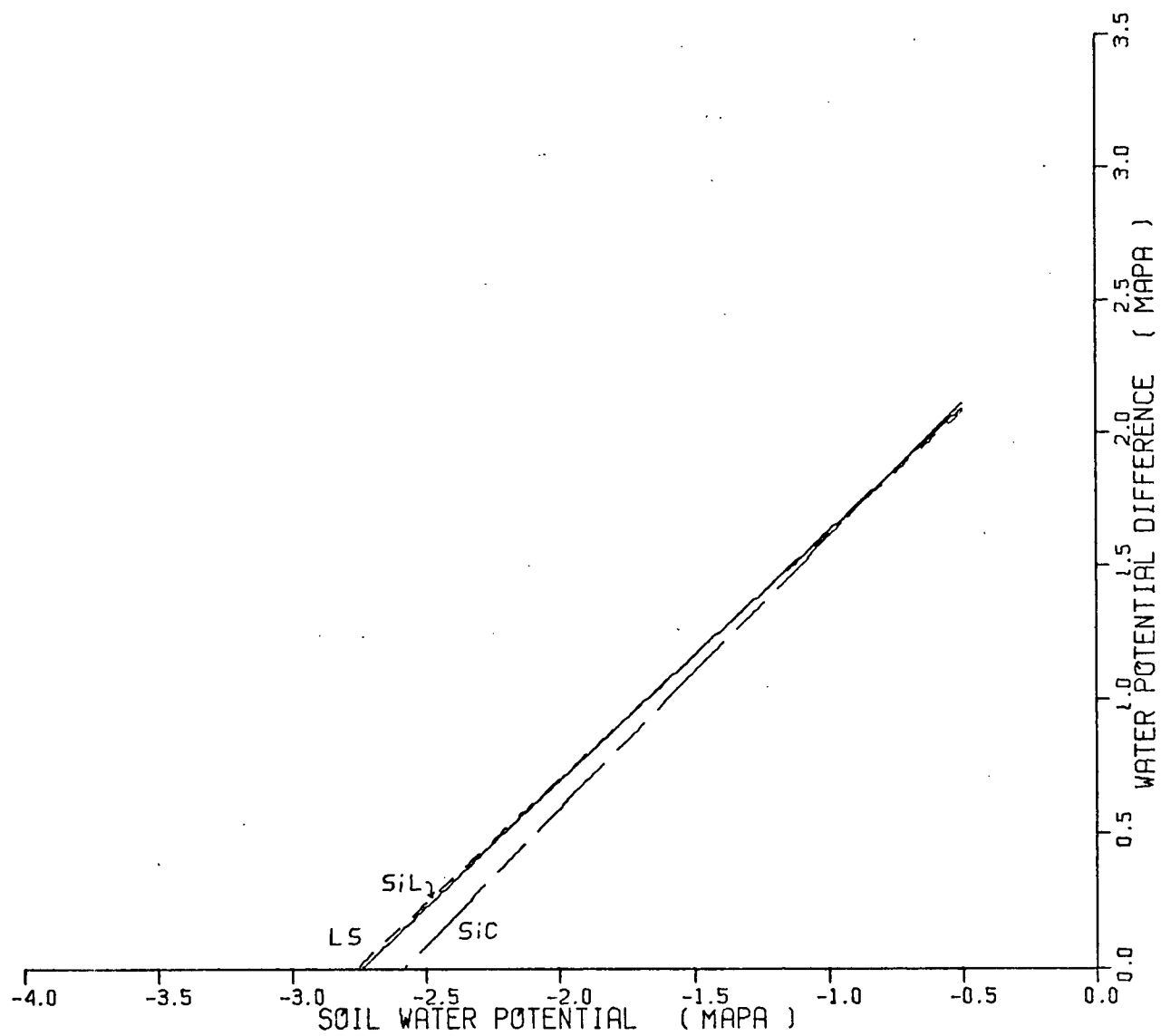FIGURE 3: Water potential difference in relation to soil water
potential for Douglas-fir: A comparison of soils;
silty clay (SiC), silt loam (SiL) and loamy sand (LS).

FIGURE 4a. Average seedling water uptake rate per unit root surface
            area in relation to soil water potential for Douglas-fir
            on silty clay soil. This relationship was arrived at
            through equation 14.

FIGURE 4b: Average seedling water uptake rate per unit root surface
            area in relation to soil water potential for Douglas-fir
            on silt loam soil. This relationship was arrived at
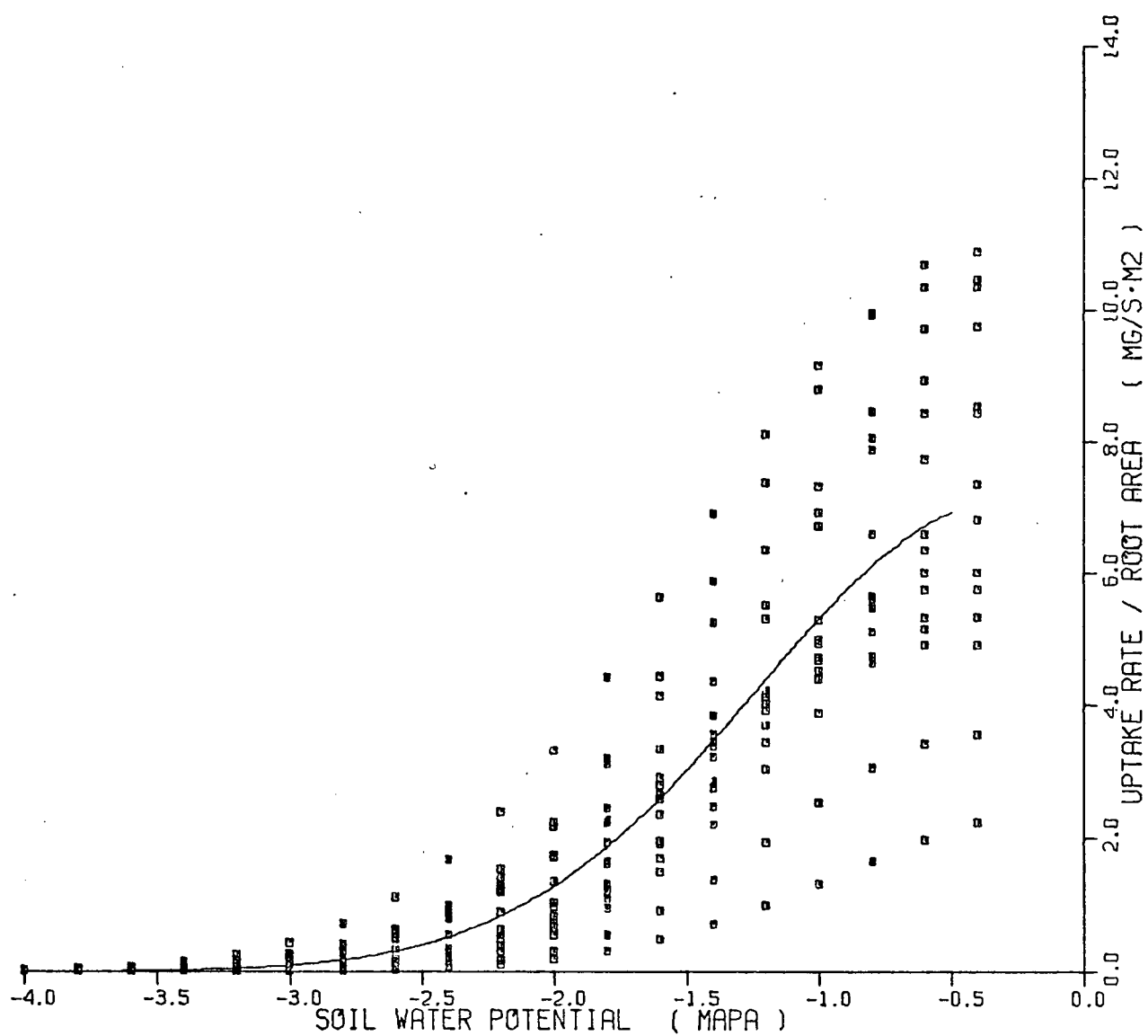   through equation 14.

FIGURE 4c: Average seedling water uptake rate per unit root surface
area in relation to soil water potential for Douglas-fir
on loamy sand soil. This relationship was arrived at
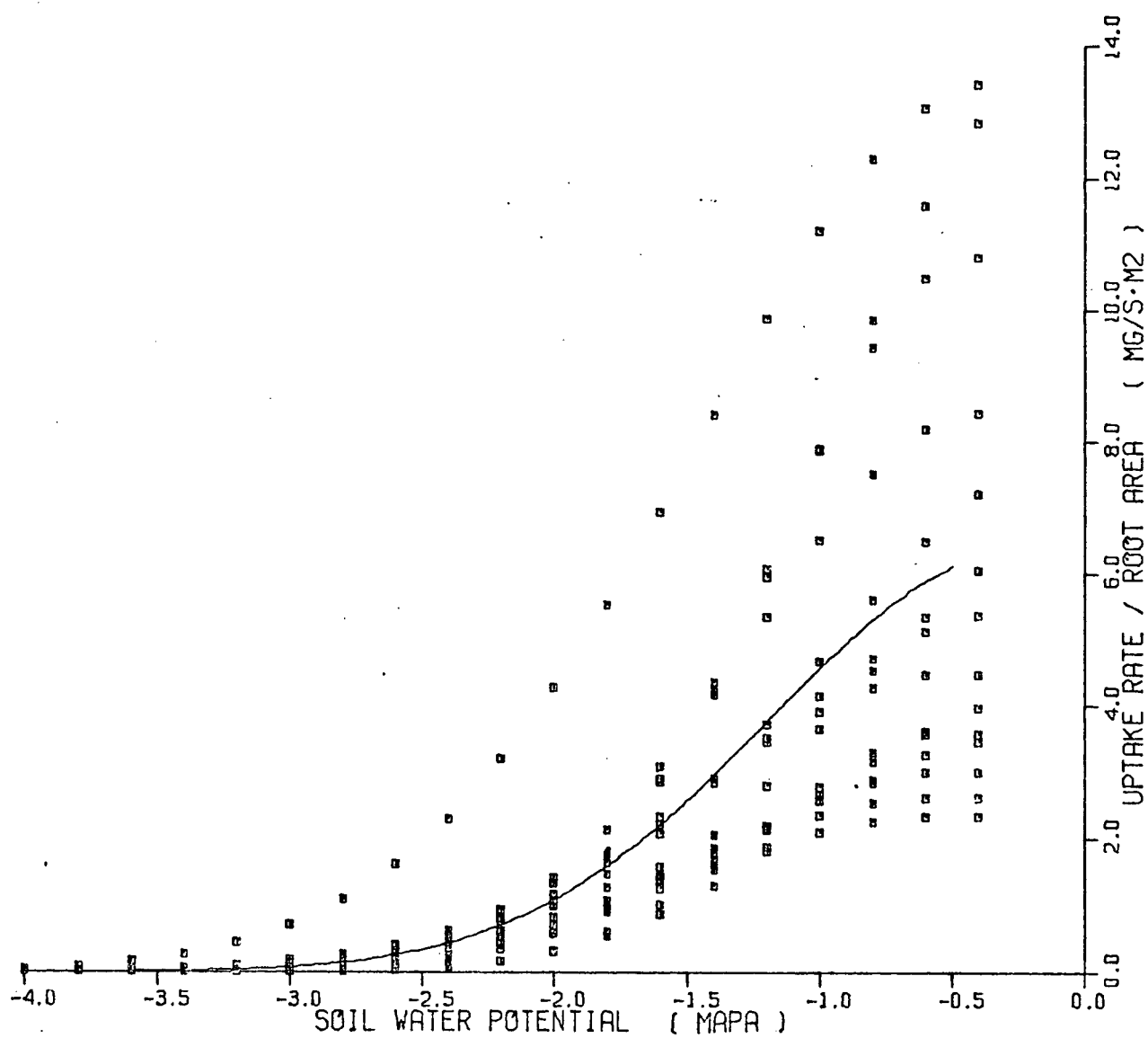through equation 14.
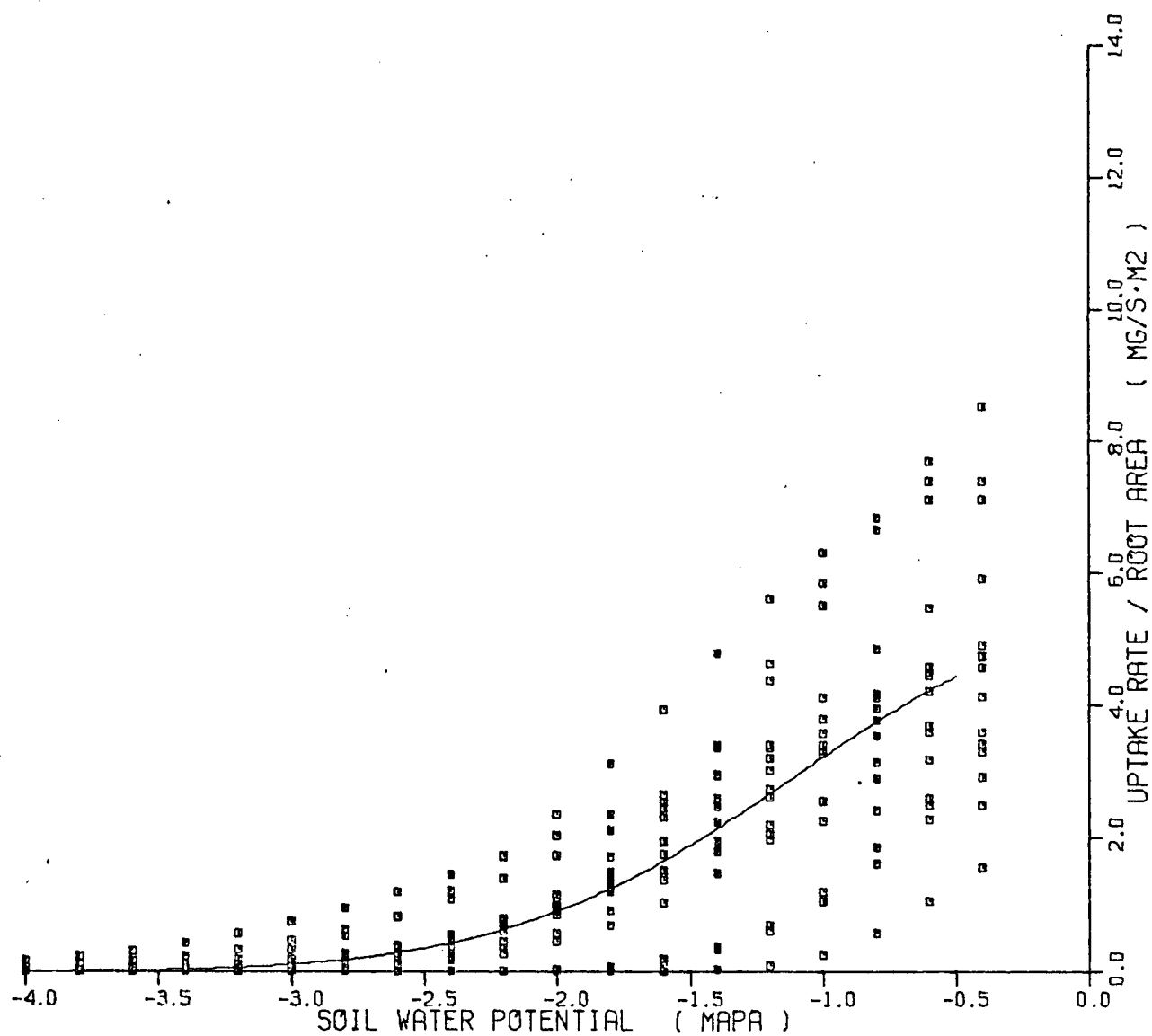
FIGURE 5: Average seedling water uptake rate per unit root surface
area in relation to soil water potential for Douglas-fir:
A comparison of soils; silty clay (SiC), silt loam (SiL)
and loamy sand (LS).

FIGURE 6: Average seedling water uptake rate in relation to soil
water potential for Douglas-fir: A comparison of soils;
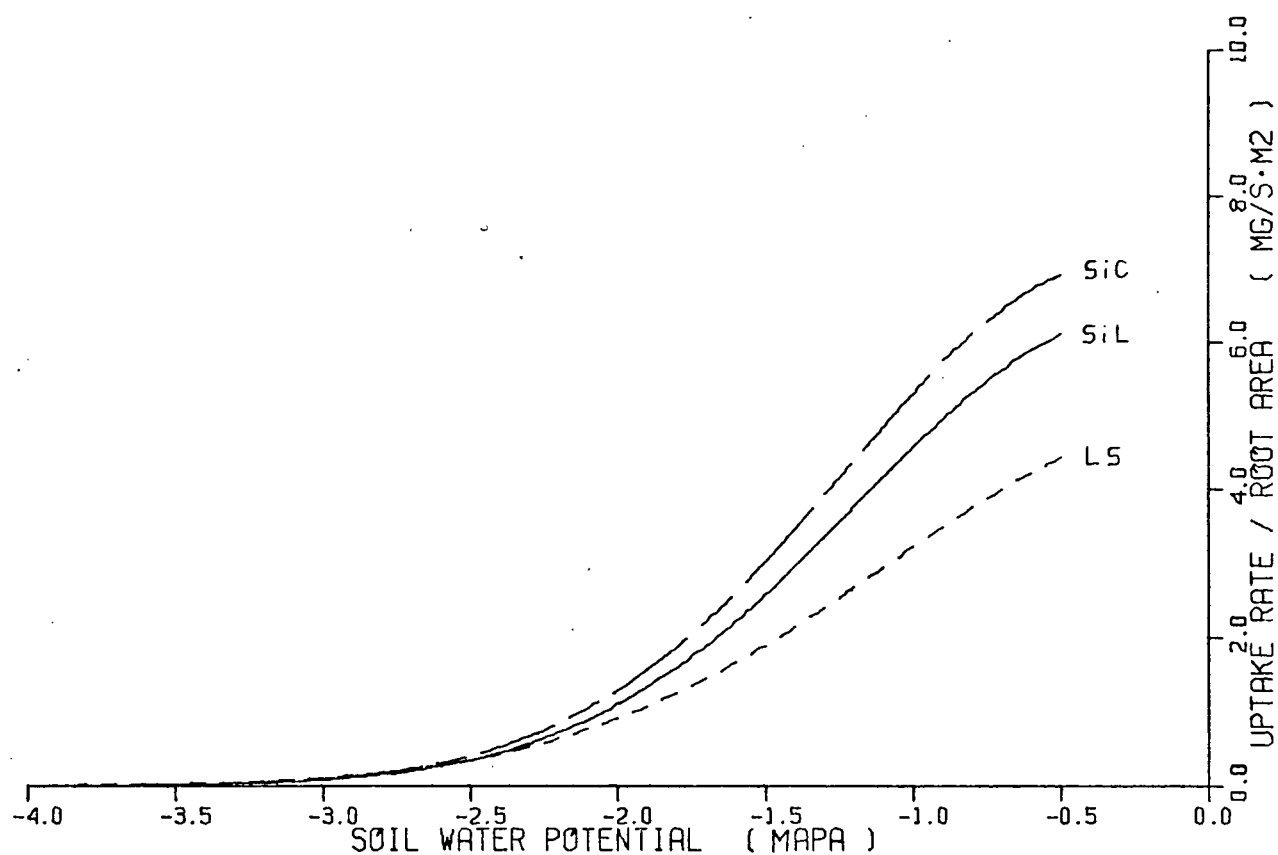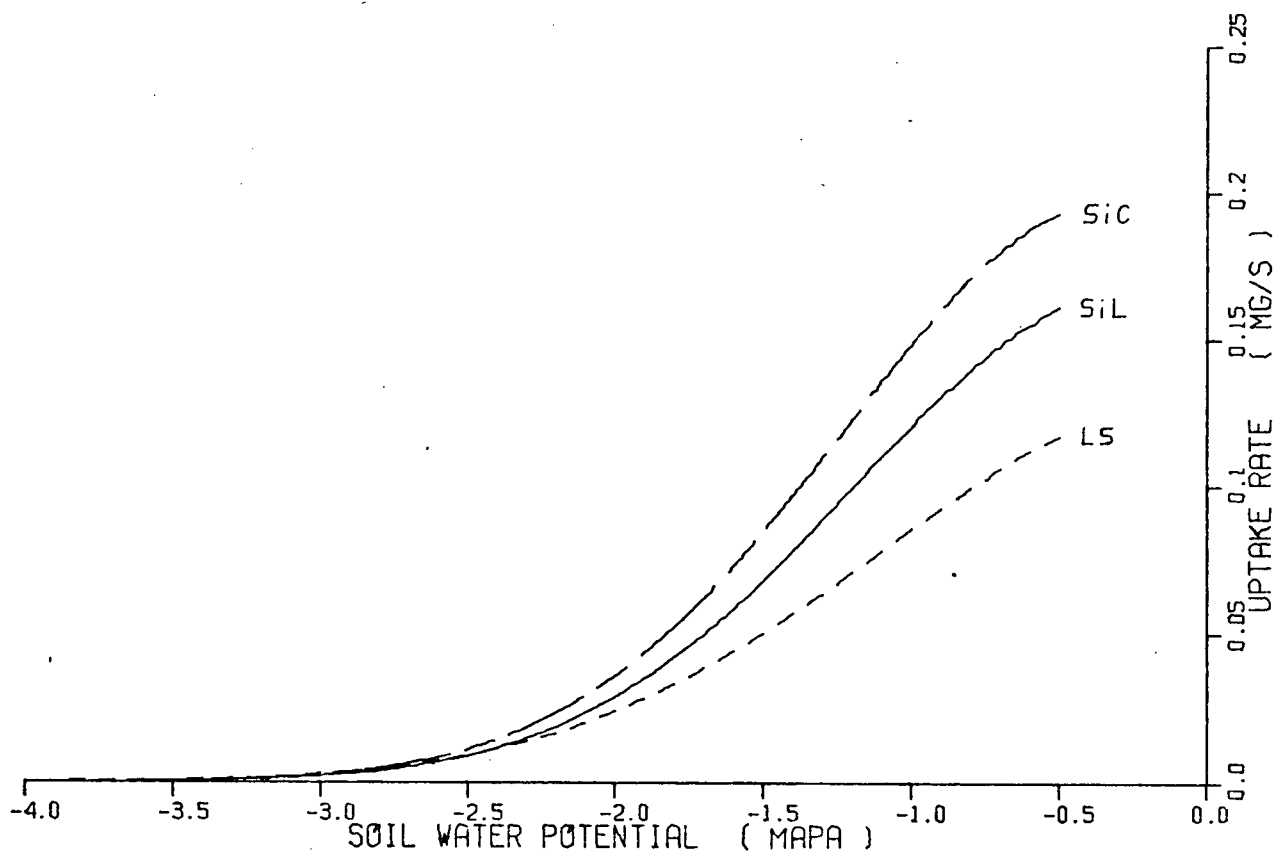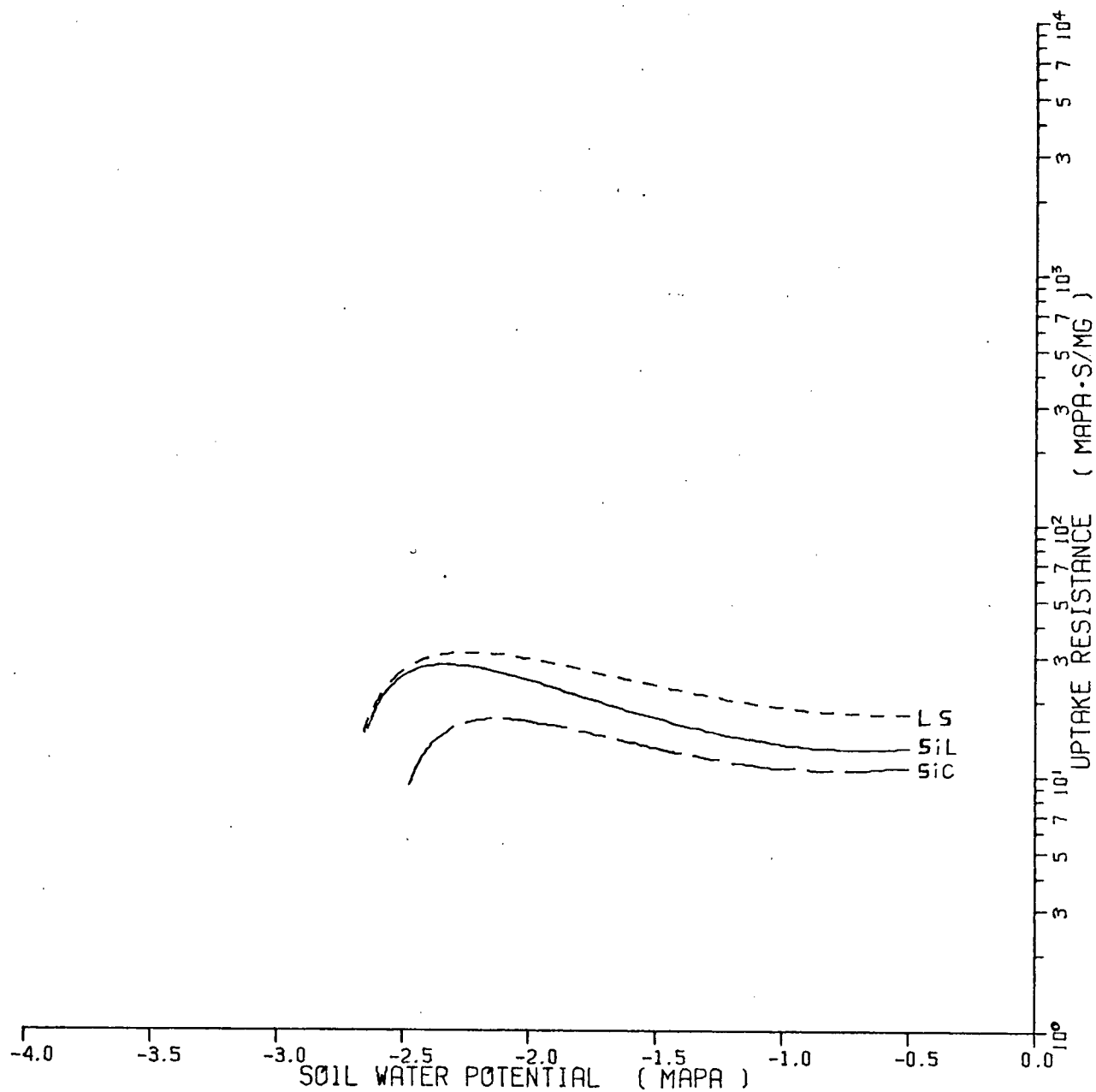silty clay (SiC), silt loam (SiL) and loamy sand (LS).

FIGURE 7: Average seedling water uptake resistance in relation to
soil water potential for Douglas-fir: A comparison of
soils; silty clay (SiC), silt loam (SiL) and loamy sand
(LS). The decrease in resistance below about -2.2
megapascals is probably an artifact of the calculation
process.

CHAPTER 5: RESULTS AND DISCUSSION: SPECIES

5.1 Water Potential Difference

Unlike Douglas-fir, both western and mountain hemlock show a relatively large decrease in needle water potential as the soil dries from near zero to about -3.0 MPa (Figures 8a, b, and c). Western hemlock shows slightly less tendency to change than mountain hemlock. As with Douglas-fir, this relationship appears to be a linear function of soil water potential over this range.

A comparison of species (Figure 9) shows that both hemlocks appear less able to maintain near-constant needle water potentials than Douglas-fir as the soil dries to about -3.0 MPa. Douglas-fir is significantly different (p = .01) from both hemlock species, and the two hemlock species also differ significantly (p = .05).

Since the relationship between soil water potential and needle water potential is approximately linear with slopes less than 1, the water potential differences decrease as the soil dries down to about -2.7 to -3.3 MPa in these experiments (Figure 10). However, mountain hemlock shows consistently the lowest water potential difference and Douglas-fir the highest, down to about -1.8 MPa, where the curves cross. Western hemlock is intermediate at all soil water potentials.

5.2 Water Uptake Rate

Average seedling water uptake rates per unit root surface area for both hemlock species were much lower than for Douglas-fir at

all soil water potentials and decreased as the soil dried, approaching

zero at -2.5 MPa soil water potential (Figures 11a, b, and c).

Mountain hemlock consistently showed the lowest uptake rate over

this range (Figure 12). All lines were significantly different

(p = .01) from each other at ψ_s = -0.6 MPa. At ψ_s = -2.0 MPa,

Douglas-fir was significantly different (p = .01) from either hemlock

species, but there is no significant difference between hemlock

species.

Comparison of average seedling water uptake rate per unit

root surface area (Figure 12) and average seedling water uptake rate

(Figure 13) show similar trends. However, there is a lesser difference

between species on a seedling basis because the hemlock species have

much more root surface area per seedling. At -0.5 MPa, the Douglas-fir

average seedling water uptake rate is 44% higher than for western

hemlock and 53% higher than for mountain hemlock. These proportions

remain fairly similar over the full soil water potential range.

It is very interesting to note that although mountain hemlock

has the highest root surface area (on the average, almost twice that of

Douglas-fir), it shows only half the water uptake rate. Similarly,

western hemlock has about 1.5 times the root area of Douglas-fir,

and shows only 44% of the water uptake rate in wetter soil. In addition,

both hemlock species have 20% greater needle surface area than for

Douglas-fir. Apparently the resistance to water uptake by both

hemlock species is sufficiently larger to offset their larger absorbing

and transpiring surfaces relative to Douglas-fir.

5.3 *Resistance*

For all three species, the average seedling water uptake
resistance changes slowly between -0.5 and -1.0 MPa, but increases
at an increasing rate as the soil dries below -1.0 MPa (Figure 14).
In Douglas-fir, the increase is about 2-fold between -0.5 and -2.5 MPa.
However, the increase in resistance is about 10- and 20-fold for
western and mountain hemlock, respectively.

At ψ_s above -1.8 MPa, the lower water potential differences
and much lower water uptake rates in the hemlocks reflect uptake
resistances that are 2 to 3 times that for Douglas-fir. Below this
range, extremely small water uptake in response to higher water
potential differences in hemlocks than Douglas-fir, reflects resistance
differences of up to a full order of magnitude. Western hemlock
is intermediate between mountain hemlock (with the highest resistance)
and Douglas-fir (with the lowest resistance) at all soil water
potentials.

Since all three species show markedly different root surface
areas, the uptake resistance is calculated on a root surface area
basis, to offer clearer comparison (Figure 15). Because the root
surface area of Douglas-fir is lowest and that of mountain hemlock
is highest, the resistance to water uptake on a root area basis shows
much larger differences between species than when expressed on a
seedling basis. Evidently, there is dramatically higher resistance
to water uptake, through comparable areas of roots, for hemlocks
than for Douglas-fir.

As previously noted, decrease in resistance in the very
dry end is considered to be an artifact of the calculation processes
and is much smaller for the hemlocks than for Douglas-fir.

5.4 *Discussion*

Unlike Douglas-fir, both western and mountain hemlock appear
less able to control needle water potential as the soil dries. Needle
water potential for both hemlocks decreases about 1.0 MPa from soil
water potential of near zero down to about -3.0 MPa where needle water
potential becomes equal to soil water potential, whereas Douglas-fir
maintains almost constant needle water potential down to about -2.7 MPa.
In theory, these values represent the lower limit of soil dryness
for water uptake by these species (at least, under these experimental
conditions). However, the resistance to water uptake increases as
the soil dries, and hence, the water uptake flux decreases more
rapidly than can be accounted for simply by a decrease in water potential
differences. The data suggest that the resistance in hemlocks becomes
so large, as the soil water potential decreases, that the uptake rate
decreases to near zero in soil almost 1.0 MPa wetter than -3.0 MPa
(the ψ_s value where $\psi_s - \psi_N$ becomes equal to zero). The resistance is
much smaller in Douglas-fir, which shows a significant water uptake
rate over the full range of soil water potential where water potential
differences exist. Because root surface areas and root lengths are
much larger for both hemlocks than for Douglas-fir, and soil volumes
are similar, it is inferred that the plant tissue, and perhaps

soil-root contact, are major factors contributing to differences in resistance between species.

Because both hemlock species have higher root surface areas and root lengths than Douglas-fir, the resistance to water flow through the soil to the root is less than for Douglas-fir. In view of the low soil resistance, as mentioned in the previous chapter, calculated by Gardner's model, the plant tissue and perhaps the soil-root contact resistances are dominating the total resistance, at least in the wet end.

The soil-root contact, which, in the same soil, is affected by the morphology of the root surfaces, might play an important role in causing differences in total resistance between species. It was noted that Douglas-fir develops a large number of lateral root hairs, about 0.5 to 1.0 mm long, over all roots smaller than 1.0 mm in diameter. It is possible that this morphological characteristic may be advantageous to the seedling, for keeping in close contact with soil water films as the soil dries, as well as decreasing the effective distance water must travel to the root surface and increasing the total absorbing root surface area. The slight mycorrhizal infection on some Douglas-fir roots might also have similar effect. Although ectomycorrhizal mantles, common to conifer species, appear to suppress or cover root hairs in regions where mantles form (Harley, 1969), the physical presence of the thick mantle and hyphae may help to maintain close contact with soil water films in a similar manner as root hairs on

nonmycorrhizal roots. However, both hemlock species were observed

to have neither significant root hair development nor perceptible

mycorrhizae association. This condition might explain, to a large

degree, the hemlock's larger and more rapidly increasing resistance

differences relative to Douglas-fir as the soil dries.

Since western hemlock uptake resistance is less than that for

mountain hemlock, even though there is less absorbing surface area and

larger average distance between roots, it is inferred that the

resistance to water uptake through the plant tissues of western hemlock

is lower than for mountain hemlock at a given soil water potential.

For hemlocks, the proliferation of roots through the soils,

as found in these experiments, might be of considerable ecological

importance if much of the water uptake resistance occurs in the

region of the roots. In the absence of root hairs, proliferation of fine

roots may reduce water uptake resistance through soil and across the

root in a similar manner as root hairs. Although this cannot be

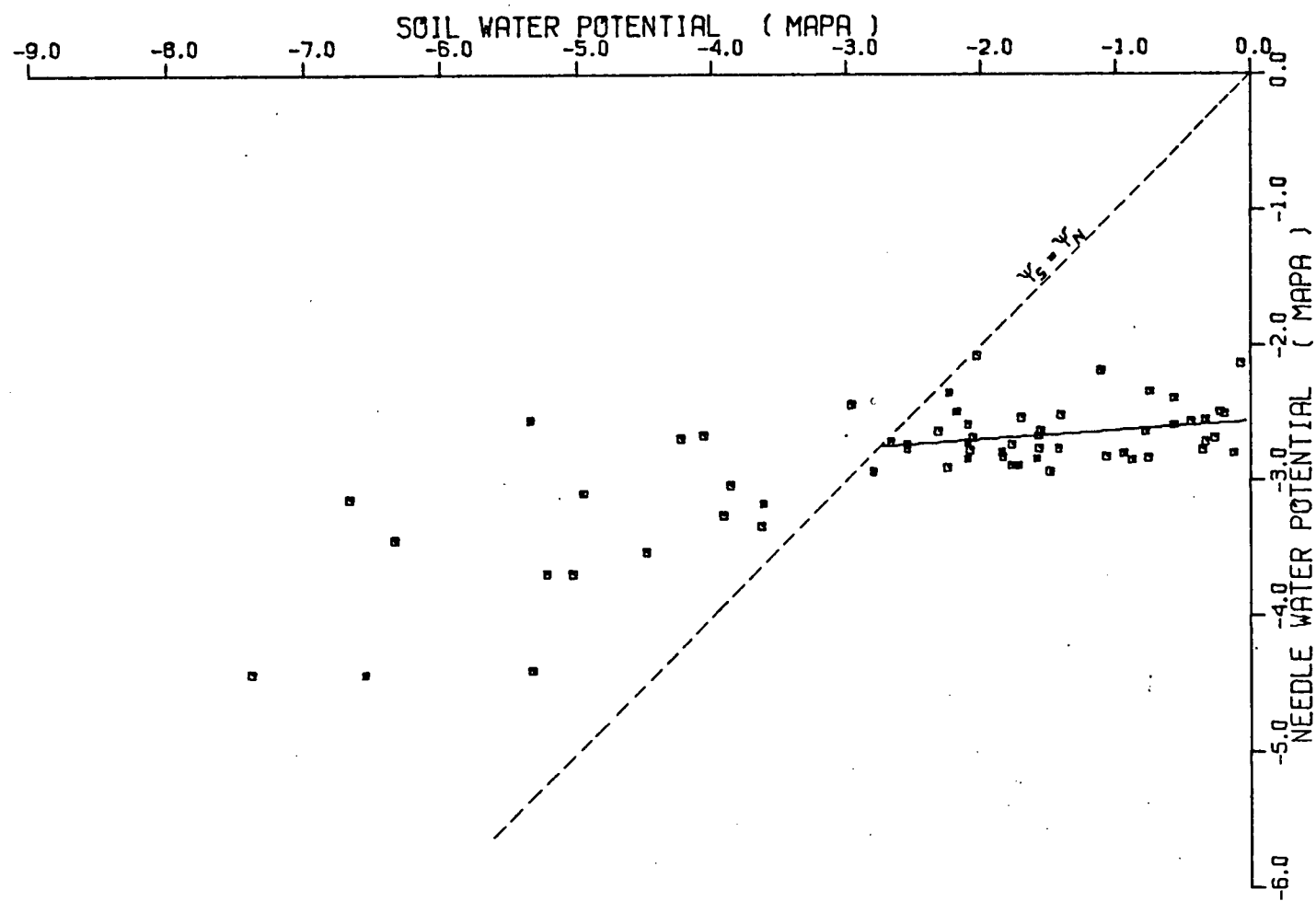concluded in this study, it does indicate an interesting trend.

FIGURE 8a. Needle water potential in relation to soil water potential for
Douglas-fir on silt loam soil. (same as Figure 1b)
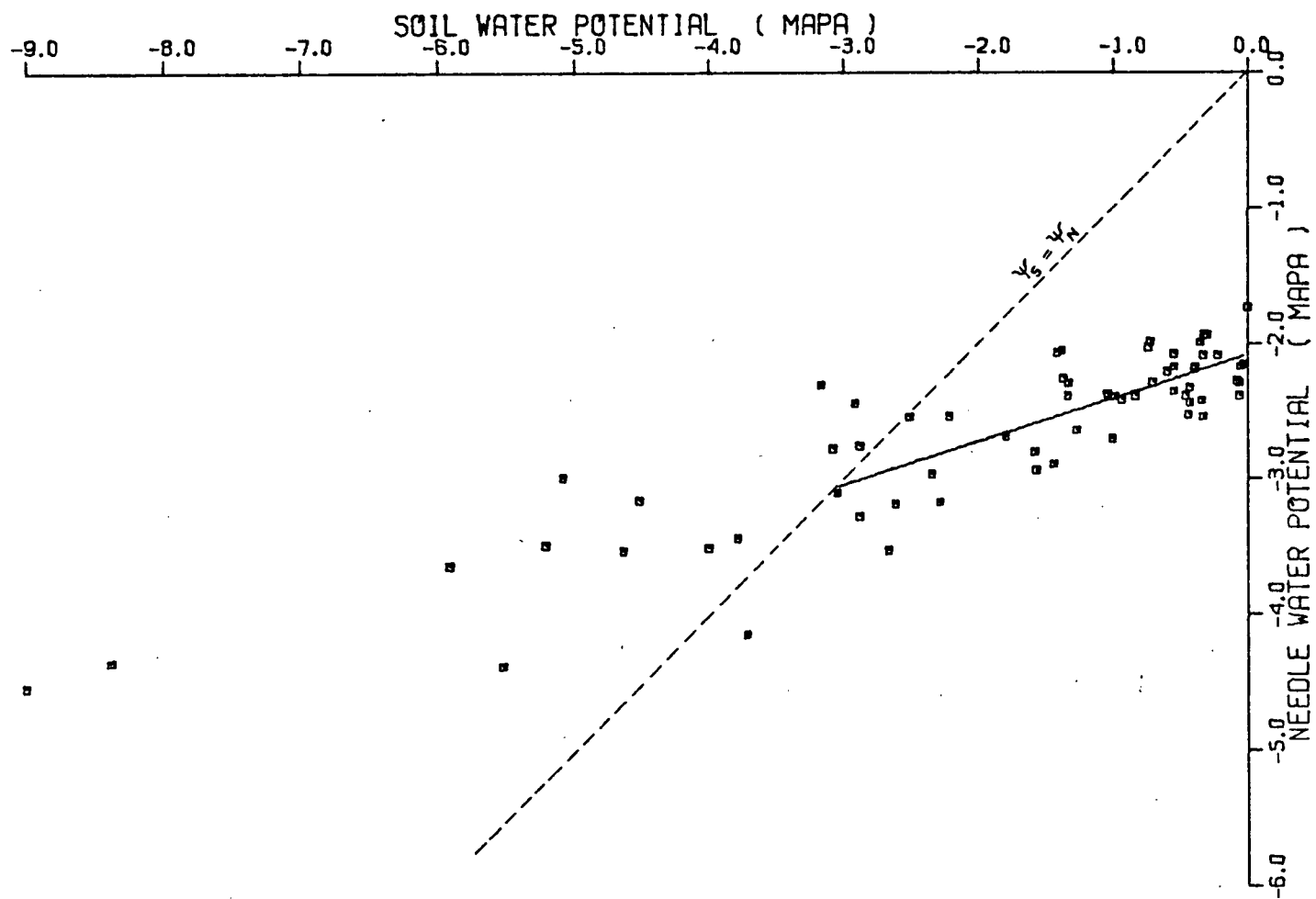
FIGURE 8b: Needle water potential in relation to soil water potential for western
hemlock on silt loam soil.
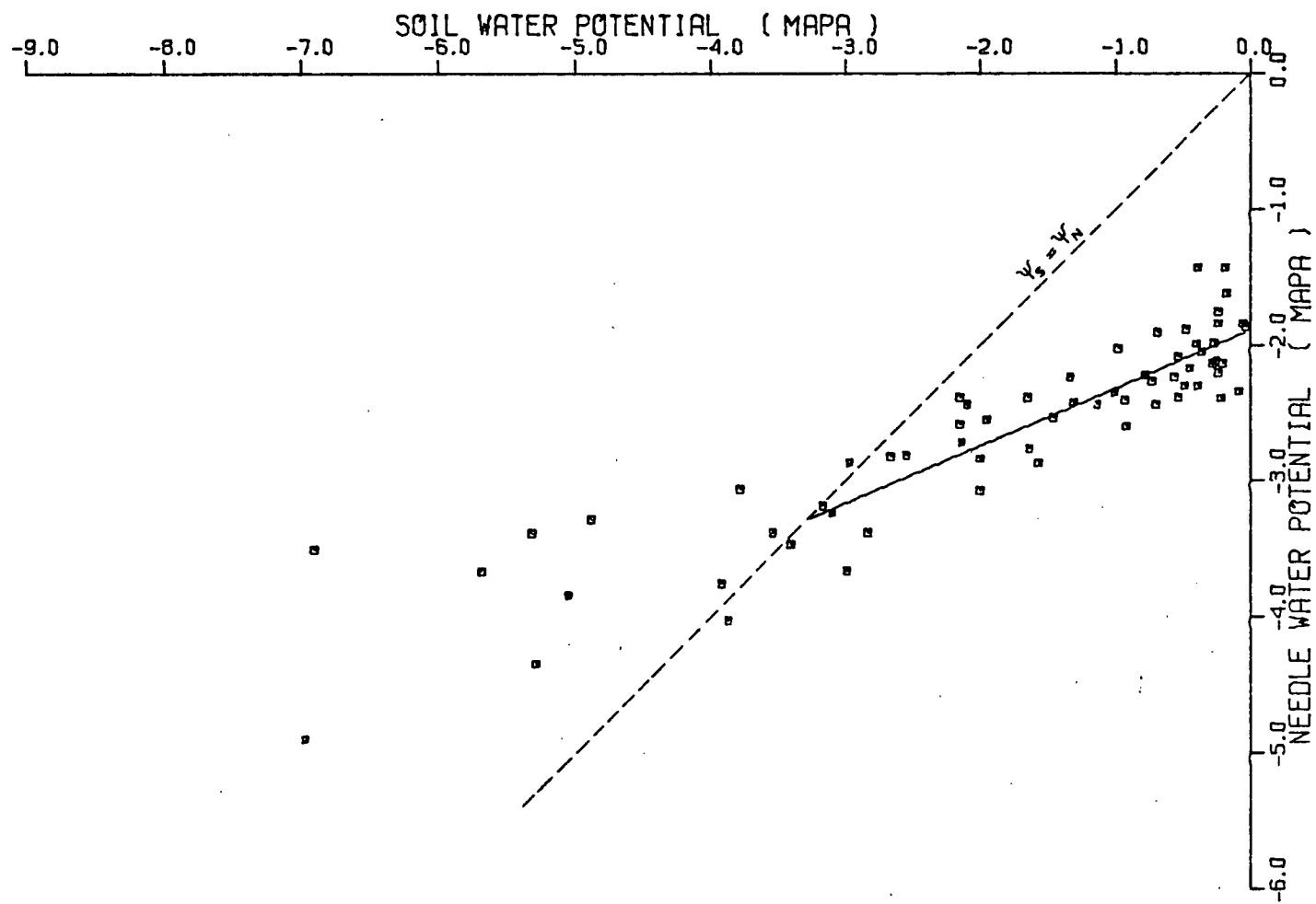
FIGURE 8c: Needle water potential in relation to soil water potential for mountain hemlock on silt loam soil.

FIGURE 9: Needle water potential in relation to soil water potential for seedlings on silt loam soil: A comparison of species; Douglas-fir (DF), western hemlock (WH) and mountain hemlock (MH).

FIGURE 10: Water potential difference in relation to soil water
potential for seedlings on silt loam soil: A comparison
of species; Douglas-fir (DF), western hemlock (WH) and
mountain hemlock (MH).
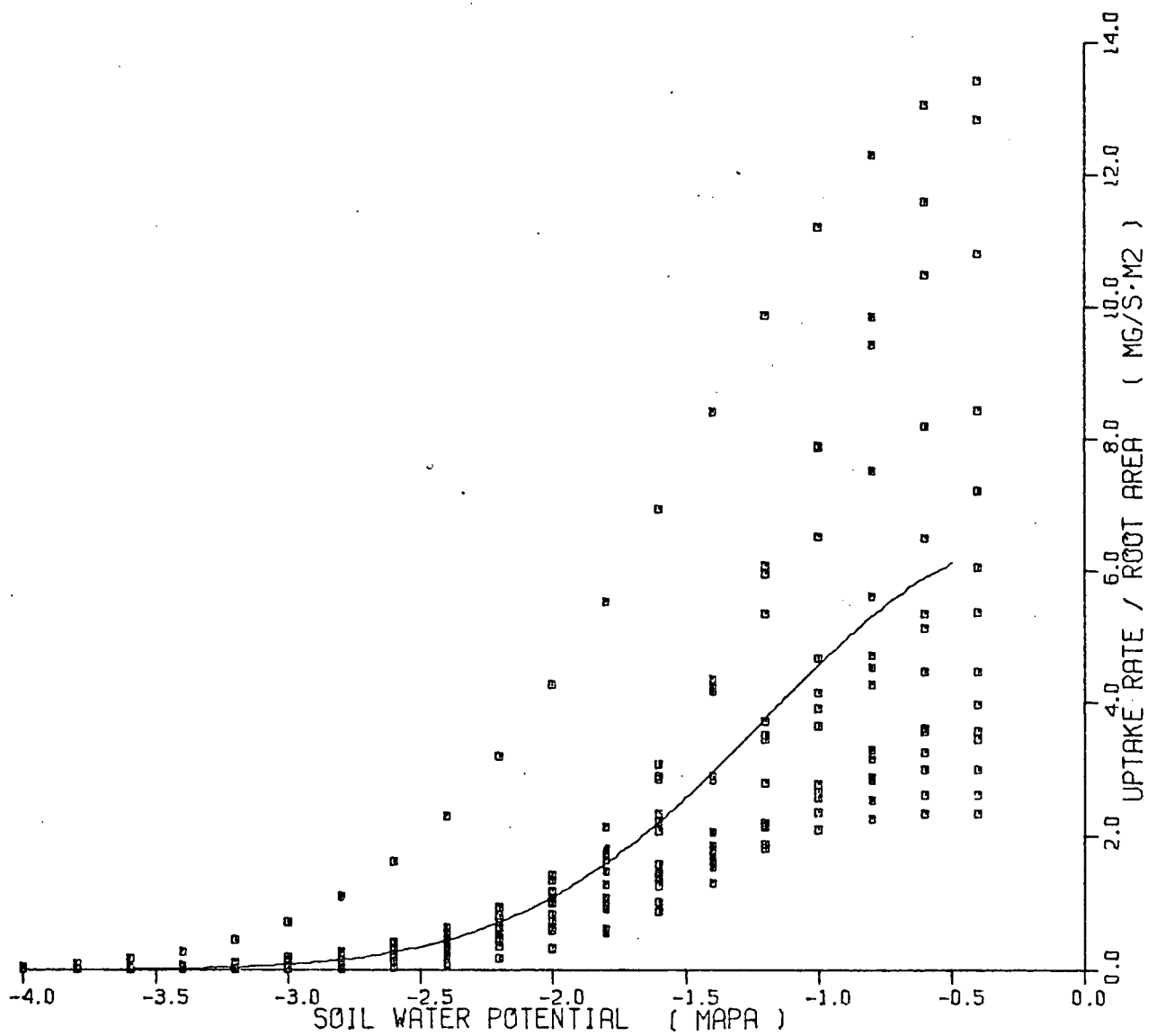
FIGURE 11a: Average seedling water uptake rate per unit root surface
area in relation to soil water potential for Douglas-fir
on silt loam soil. This relationship was arrived at
through equation 14 .
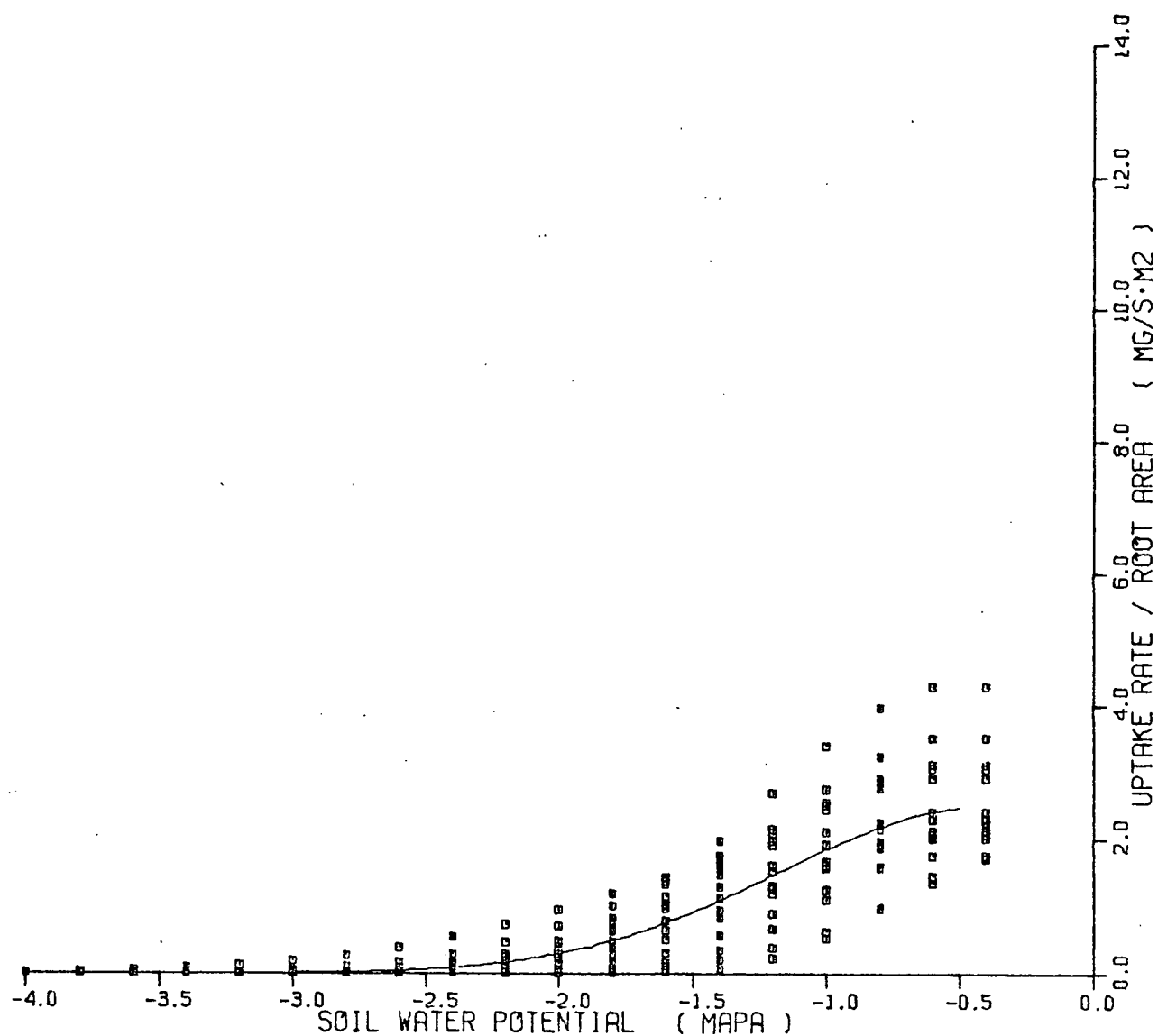
FIGURE 11b: Average seedling water uptake rate per unit root surface area in relation to soil water potential for western hemlock on silt loam soil. This relationship was arrived at through equation 14.
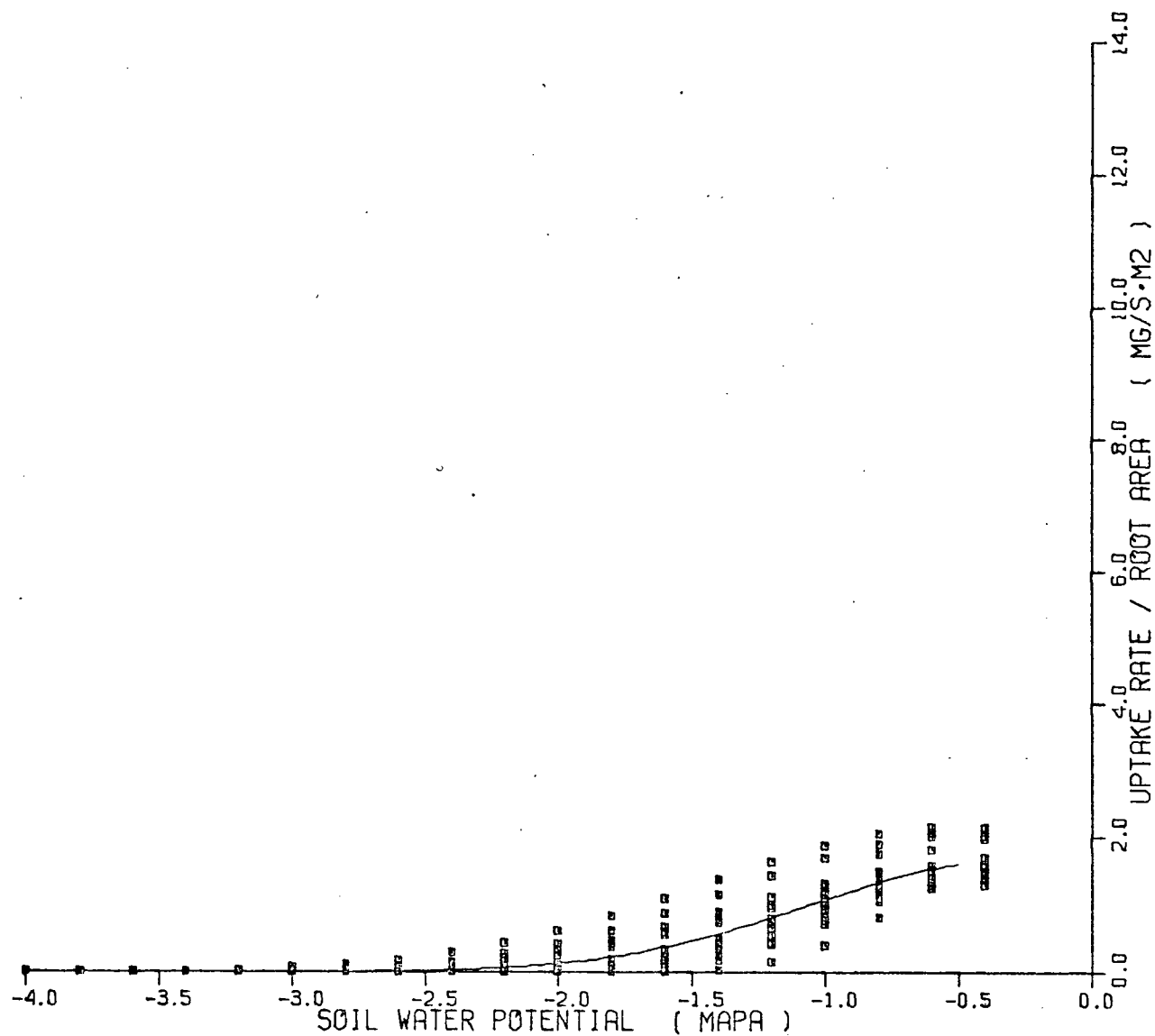
FIGURE 11c: Average seedling water uptake rate per unit root surface area in relation to soil water potential for mountain hemlock on silt loam soil. This relationship was arrived at through equation 14.

FIGURE 12: Average seedling water uptake rate per unit root surface
area in relation to soil water potential for seedlings
on silt loam soil: A comparison of species; Douglas-fir
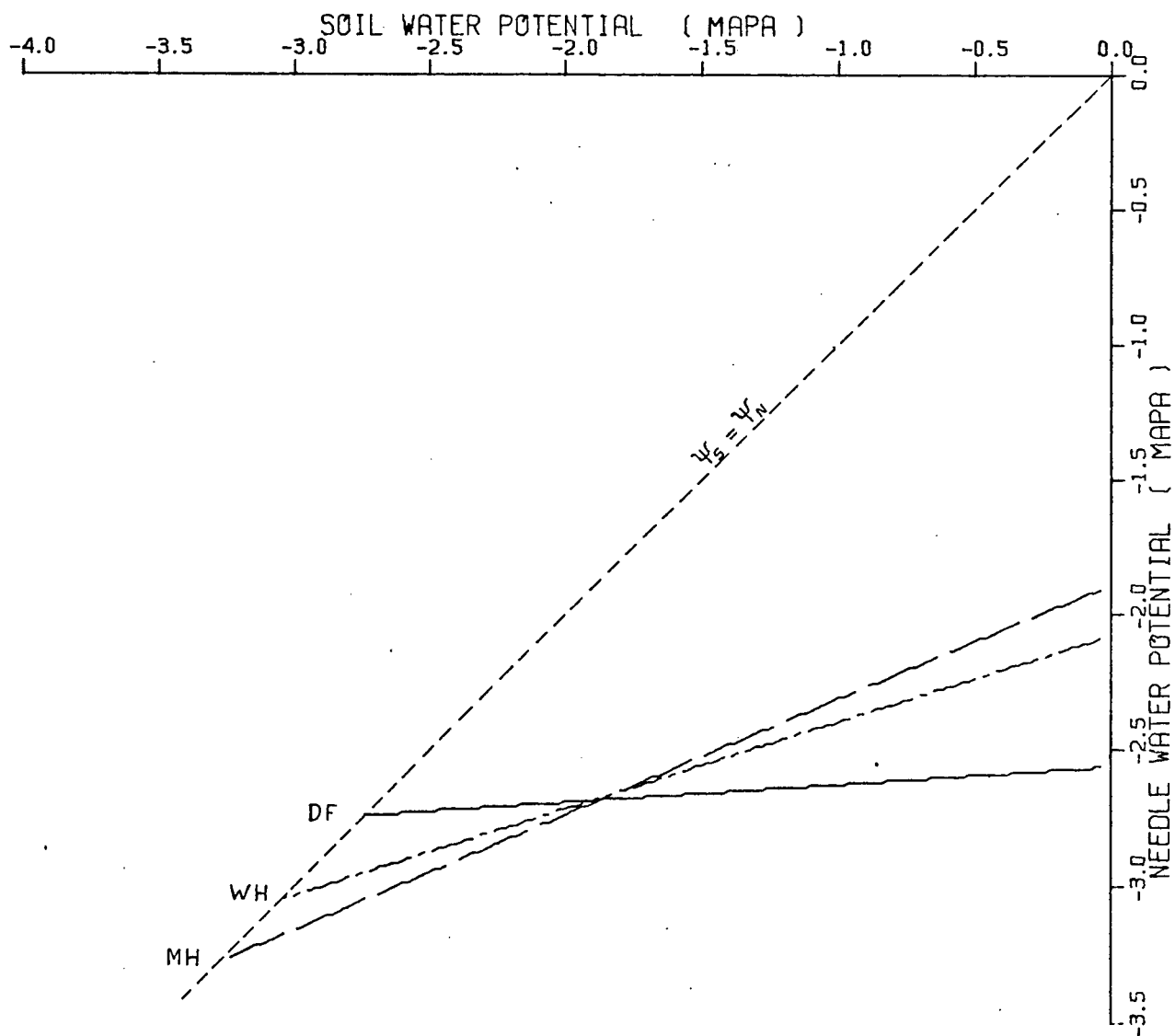(DF), western hemlock (WH) and mountain hemlock (MH).

FIGURE 13: Average seedling water uptake rate in relation to soil
water potential for seedlings on silt loam soil: A
comparison of species; Douglas-fir (DF), western hemlock
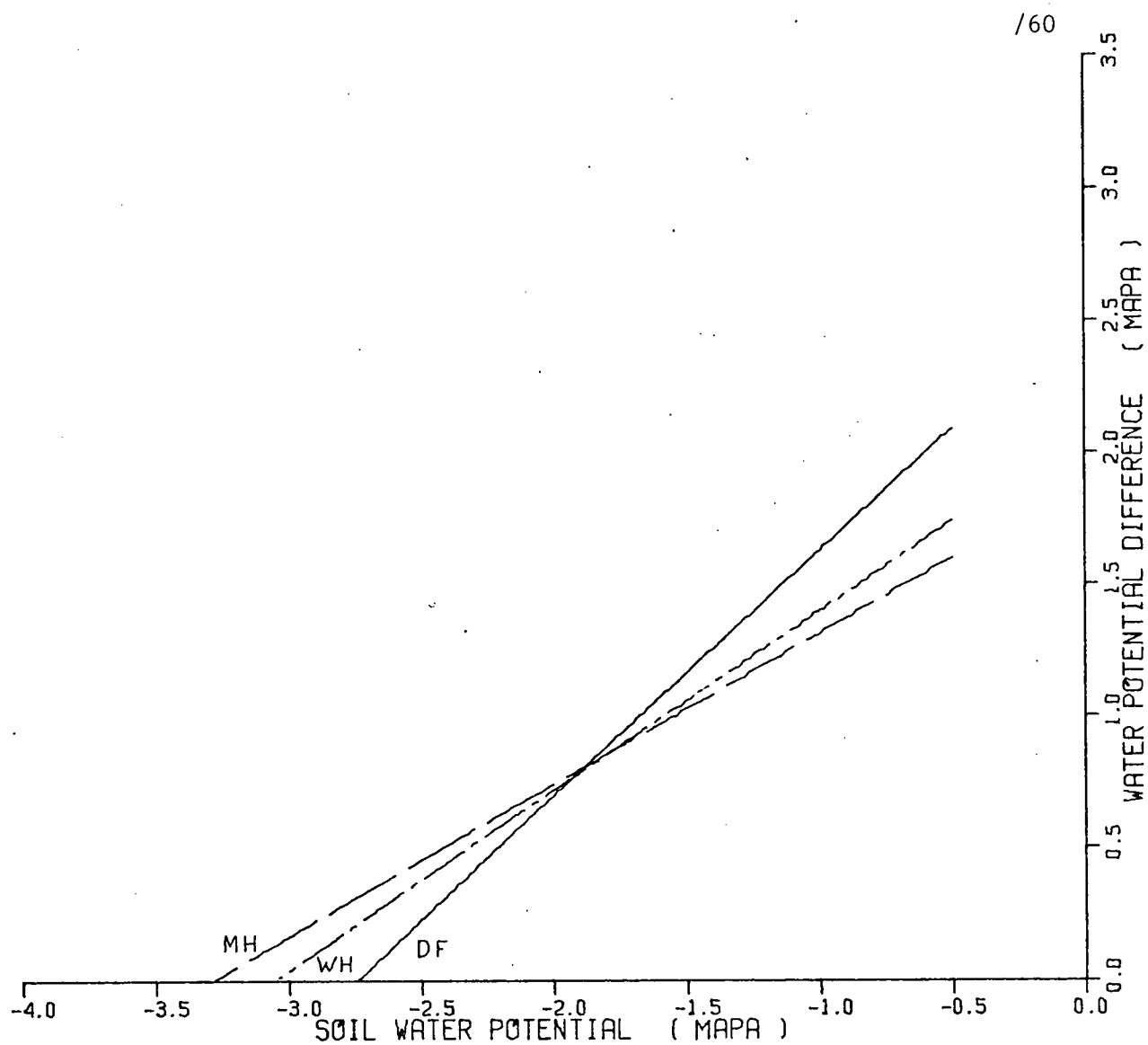(WH) and mountain hemlock (MH).

FIGURE 14: Average seedling water uptake resistance in relation to soil water potential for seedlings on silt loam soil: A comparison of species; Douglas-fir (DF), western hemlock (WH) and mountain hemlock (MH). The decrease in resistance in the very dry end is probably an artifact of the calculation process.
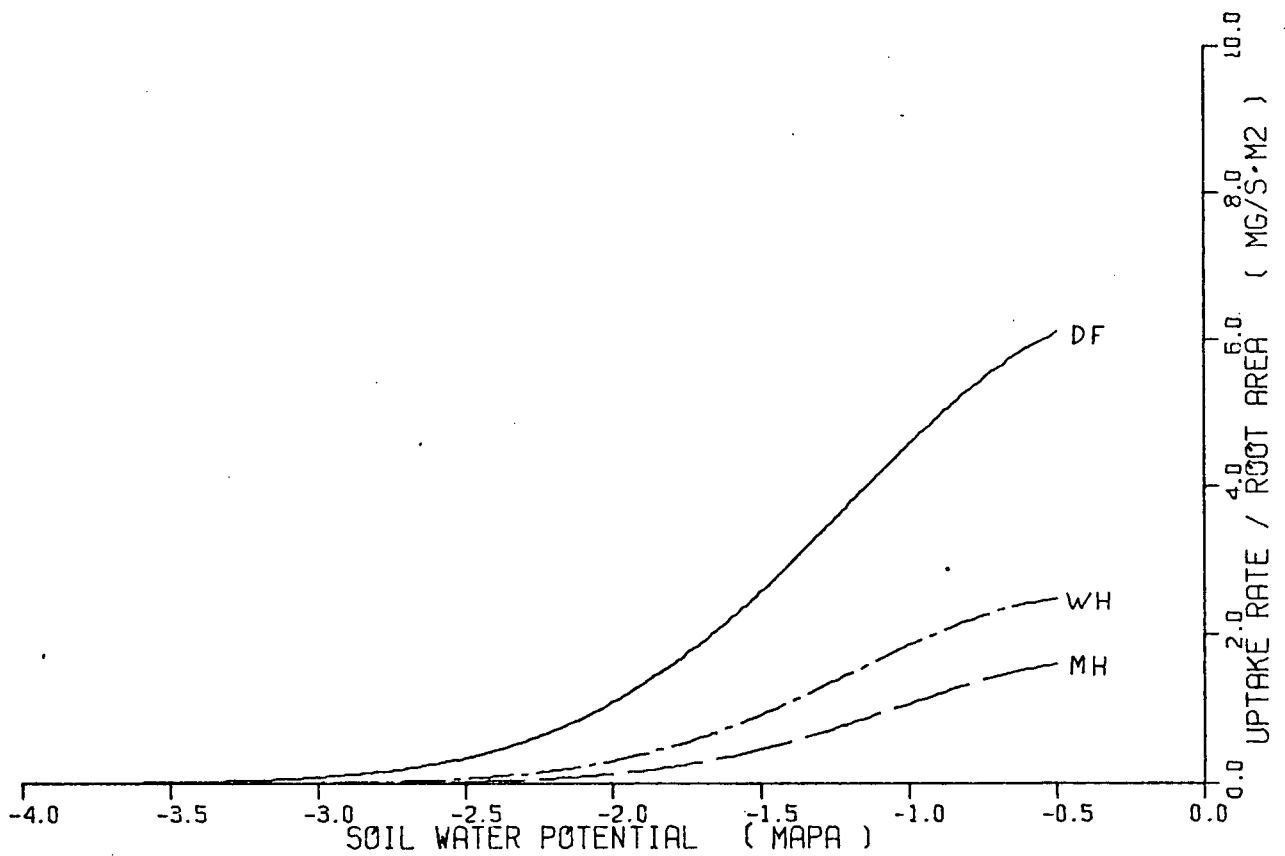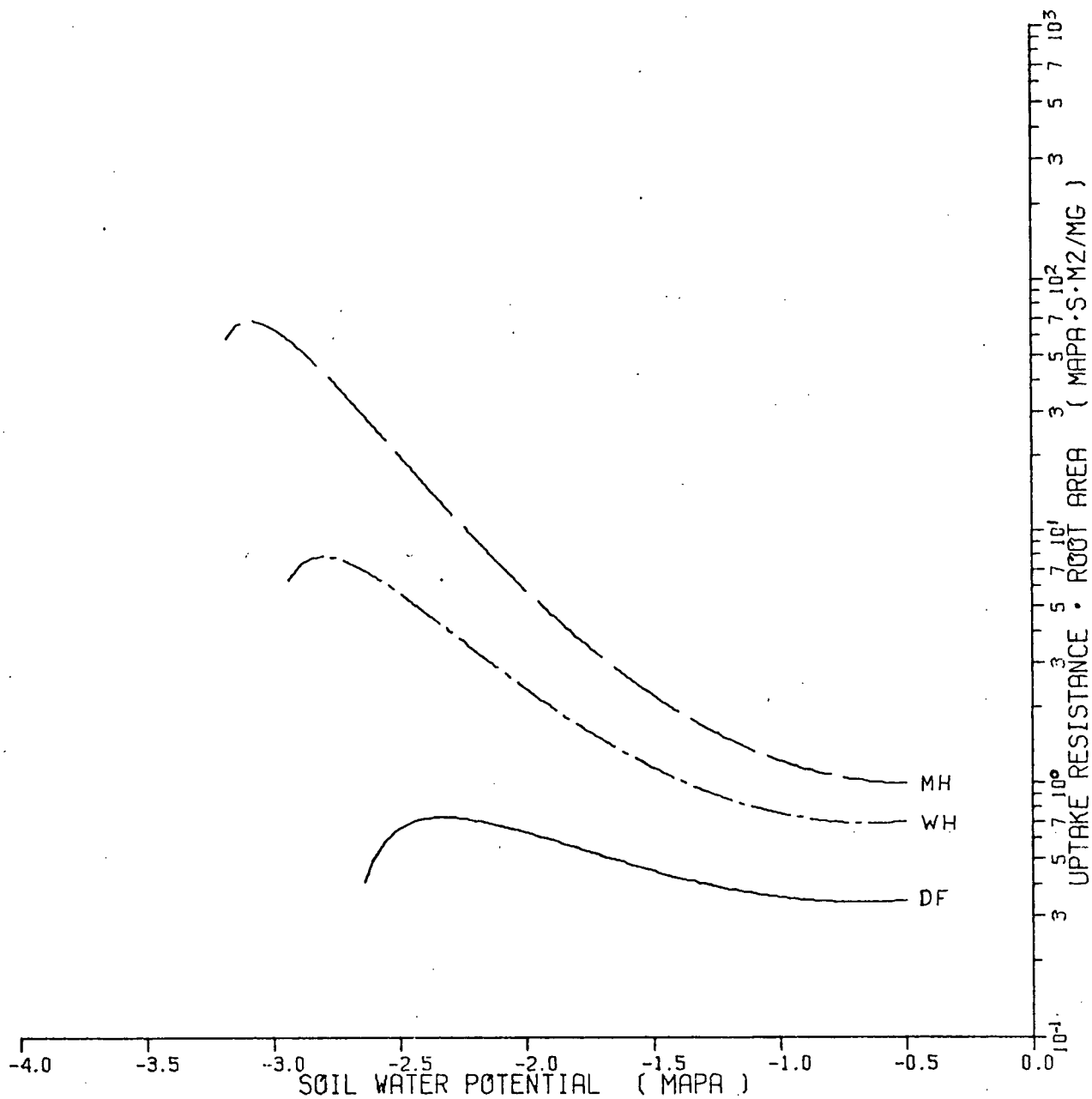
FIGURE 15: Average seedling water uptake resistance on a unit root
surface area basis in relation to soil water potential
for seedlings on silt loam soil: A comparison of species;
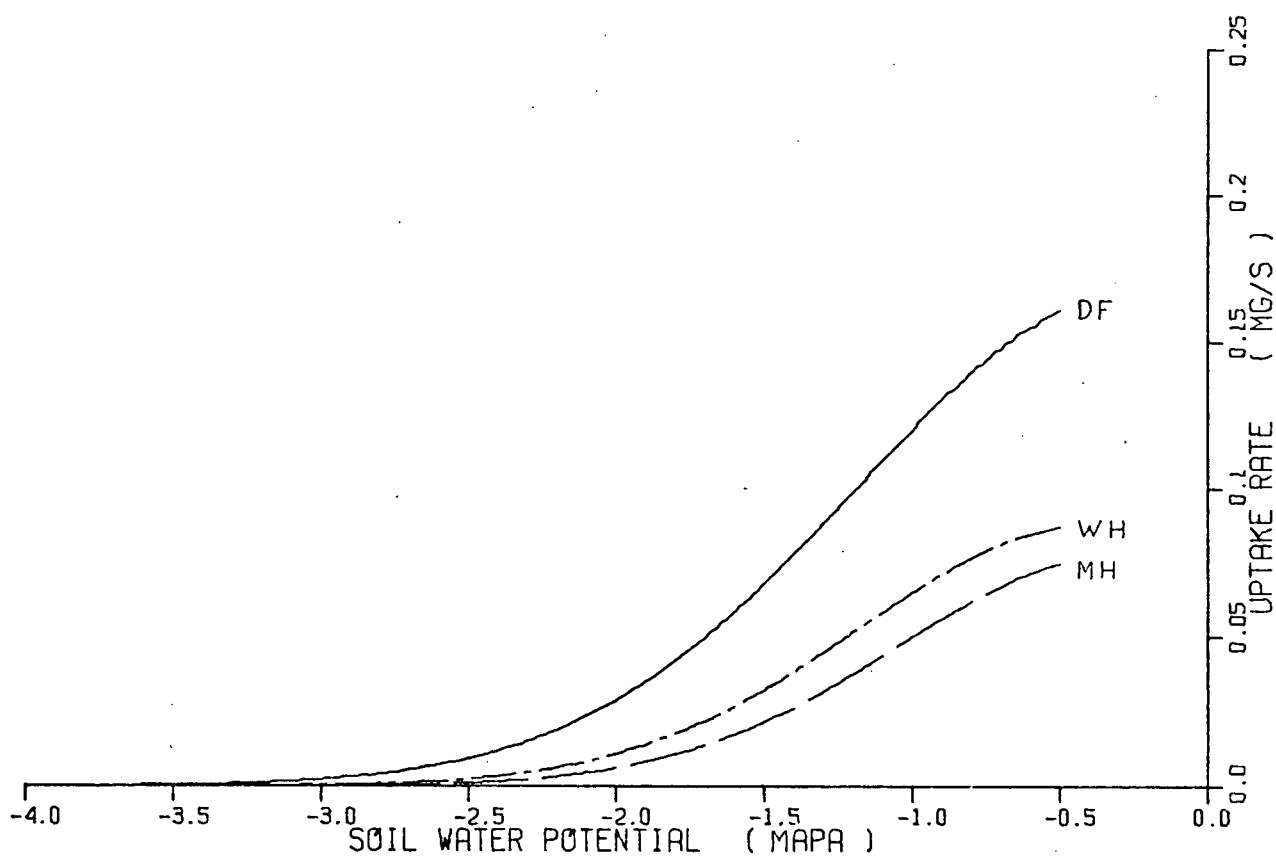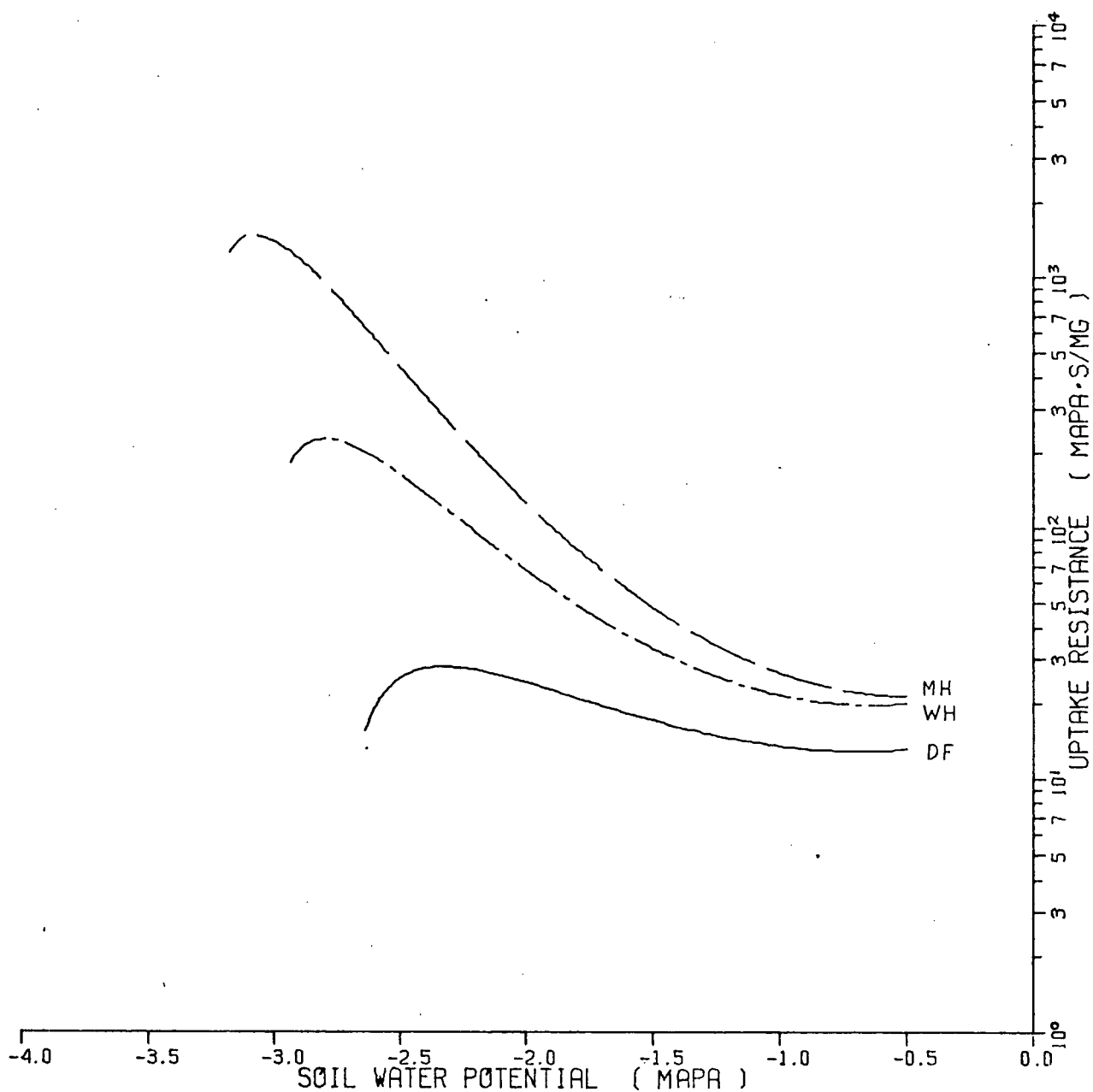Douglas-fir (DF), western hemlock (WH) and mountain
hemlock (MH). The decrease in resistance in the very dry
end is probably an artifact of the calculation process.

CHAPTER 6: SUMMARY AND CONCLUSIONS

In this study, the resistance to water uptake from the soil to the needles, for all three species and on all three soils, increases as the soil dries. That is, water uptake rates decrease faster than can be explained simply by the reduction of water potential difference between soil and needles. This is in agreement with the literature for a variety of herbaceous species and some woody plants.

The total resistance to water uptake by Douglas-fir is higher and increases more rapidly with soil drying for seedlings rooted in coarser textured soil than in finer textured soil. While, for Douglas-fir, the higher resistance in coarse soils does not significantly influence the seedling water potential in relation to soil water potential, it does result in substantially lower water uptake rates over the soil water potential range of -0.5 to -2.5 MPa. The effect of texture on resistance appears to result from lower unsaturated hydraulic conductivity of soil and poorer soil-root contact in coarser soil at a given soil water potential. Thus, texture does influence the total resistance to water uptake, and hence, influences the rate of water uptake by the seedling.

Rough calculations suggest that the resistance in the soil portion of the pathway is probably not large, relative to the total, until the soil dries to below -2.0 MPa, in this study where root densities are high.

In the same soil, Douglas-fir seedlings have a much lower resistance to water uptake than both western hemlock and mountain hemlock. The resistance in hemlocks becomes so high, as the soil dries, that water uptake is reduced to near zero by -2.0 MPa, almost 1.0 MPa above the point where soil water potential becomes equal to needle water potential. Higher plant tissue and, perhaps, soil-root contact resistances in western and mountain hemlock than in Douglas-fir may account for these obvious differences in total resistance. Thus, in this study, there are large differences between Douglas-fir seedlings and western and mountain hemlock seedlings in their water stress and water uptake characteristics. These characteristics are controlled both by the ability to control water potential difference through needle water potential and by the resistance to water flow to the absorbing root surface, into the root and through the xylem to the needles. Thus soil water potential alone may be an insufficient indicator of water availability to tree seedlings.

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APPENDICES

APPENDIX 1: Hoagland's Nutrient Solution, Modified

Salt	Mass Dissolved in 1 Liter H_2O (g)	ml Solution/Liter Full Strength
$NH_4H_2PO_4$	115	1
KNO_3	202	3
$Ca(NO_3)_2 \cdot 4H_2O$	315	4
$MgSO_4 \cdot 7H_2O$	164	3
H_3BO_3	2.86	1
$MnCl_2 \cdot 4H_2O$	1.81	1
$ZnSO_4 \cdot 7H_2O$	.22	1
$CuSO_4 \cdot 5H_2O$	.08	1
$(NH_4)_6Mo_7O_{24} \cdot H_2O$	.02	1

APPENDIX 2:   SEEDLING PROVENANCES

Douglas-fir   Latitude: 48° 50'

                     Longitude: 123° 48'

                     B.C.F.S. Seed Lot Ident.   92B13/B2/315/1.5
                       No.

Western hemlock   Latitude 49° 40'

                     Longitude 123° 50'

                     B.C.F.S. Seed Lot Ident.   92H11/B3/2476/112B
                       No.

Mountain hemlock   Latitude 49° 40'

                     Longitude 121° 20'

                     B.C.F.S. Seed Lot Ident.   92G5/B3/2368/1097
                       No.

APPENDIX 3: SOIL PROPERTIES

Soil	% Sand[a]	% Silt[a]	% Clay[a]	% OM[b]	pH[c]	K
Silty Clay	12	42	46	13.3	4.5	6.3[d]
Silt Loam	39	52	9	9.8	4.9	15.3[e]
Loamy Sand	84	12	4	2.4	5.0	130.4[e]

[a]Percentages based upon 2 mm and smaller fraction by hydrometer method.

[b]by Walkley-Black method.

[c]1:5 Soil:Water

[d]Unsaturated hydraulic conductivity at 12 cm tension by tensiometer-outflow method (cm day^{-1}).

[e]Unsaturated hydraulic conductivity at 22 cm tension by tensiometer-outflow method (cm day^{-1}).

APPENDIX 5: Water Retention Curves for Silty Clay (SiC),
Silt Loam (SiL) and Loamy Sand (LS).
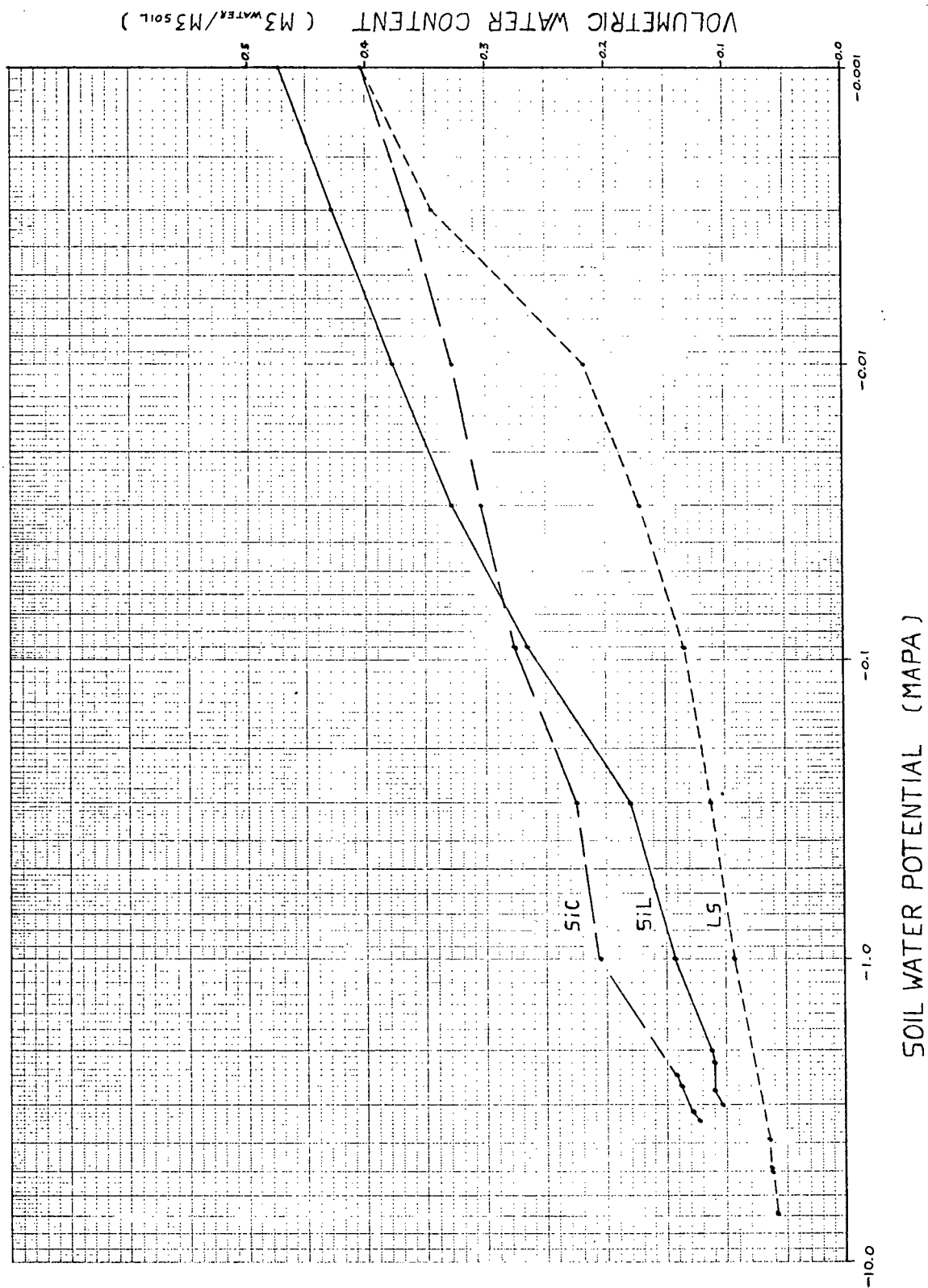
APPENDIX 6:   Photon Flux Densities Across the
Growth Chamber Bench[f]

Growth Chamber 1

450	480	460
510	550	510
470	480	460

91 cm

←——— 130 cm ———→

Growth Chamber 2

450	480	460
510	530	510
460	470	460
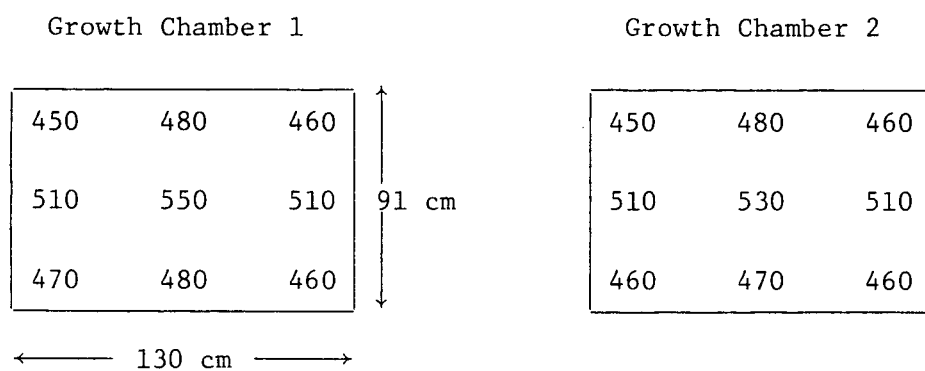
[f]Measured by Quantum Radiometer in .4 – .7 µm spectrum in $\mu E \cdot m^{-2} \cdot s^{-1}$ at midcrown level.

APPENDIX 7: Fresh Root Tissue Densities[g] and Needle Area:
             Oven-dry Weight Ratios

	Root Diameter Class			Needle Area:
	.5 mm −	.5-1.0 mm	1.0 mm +	Dry wt. (cm^2/g)
Douglas-fir	1.04	.95	1.03	140
Western hemlock	1.08	1.08	1.00	117
Mountain hemlock	1.03	1.08	1.07	112

[g] by flotation in Water (.998 g cm^{-3}), Glucose solutions (1.05 and 1.097), Olive Oil (.918), and Boiled Linseed Oil (.942).

APPENDIX 8:   Seedling and Water Flow Pathway Dimensions (Treatment Averages)

	Soil BD $(kg \cdot m^{-3})$	V_s (cm^3)	l_t (cm)	z (cm)	r_i (cm)	A needles (cm^2)	A roots (cm^2)	$\dfrac{\text{A needles}}{\text{A roots}}$	root:shoot ratio
Douglas-fir/silty clay	550	138	3075	.060	.0146	108	279	.40	.88
Douglas-fir/silt loam	750	139	2885	.063	.0143	128	263	.49	.85
Douglas-fir/loamy sand	1120	144	2894	.064	.0146	126	265	.48	.88
Western hemlock/ silt loam	760	138	3952	.052	.0141	142	350	.43	.83
Mountain hemlock/ silt loam	760	138	5467	.043	.0136	142	465	.31	1.00

APPENDIX 9:   Summary of Analysis of Variance of Water Uptake Rate per Unit Root Surface Area

Soil Water Potential	-.6 MPA					-2.0 MPa			
	Source	d.f.	S.S.	M.S.		Source	d.f.	S.S.	M.S.
Silty Clay	Treat.	1	.00032	.00032					
X	Error	28	.0188	.00067					
Silt Loam	Total	29	.0192						
	F = 0.48								
Silty Clay	Treat.	1	.003415	.003415		Treat.	1	.000118	.000118
X	Error	28	.00869	.000308		Error	28	.001327	.000474
Loamy Sand	Total	29	.0121			Total	29	.001445	
	F = 11.06					F = 2.49			
Silt Loam	Treat.	1	.0016	.0016					
X	Error	28	.0161	.000575					
Loamy Sand	Total	29	.0177						
	F = 2.78								
Douglas-fir	Treat.	1	.00684	.00684		Treat.	1	.00035	.00035
X	Error	28	.01284	.000459		Error	28	.00097	.000035
Western hemlock	Total	29	.01968			Total	29	.00132	
	F = 14.9					F = 10.1			
Douglas-fir	Treat.	1	.040451	.040451		Treat.	1	.000716	.000716
X	Error	28	.012271	.000438		Error	28	.00093	.0000332
Mountain hemlock	Total	29	.052722			Total	29	.001646	
	F = 92.3					F = 21.6			
Western hemlock	Treat.	1	.00044	.00044		Treat.	1	.0001	.0001
X	Error	28	.00076	.000027		Error	28	.00011	.000004
Mountain hemlock	Total	29	.0012			Total	29	.00012	
	F = 16.2					F = 2.55			

APPENDIX 10: Sample Chamber and Soil Hygrometer
Calibration Information

Sample Chambers (using dew-point mode)

C-51   slope = 7.99 µV MPa^{-1} (from -.234 to -4.158 MPa)
interpolated intercept = 2.1 µV at 0 MPa
measured intercept = 1.7 µV at 0 MPa (using distilled water)
max. measured variation ≈ ± .4 µV (at water potentials
-.234 to -4.158 MPa)

C-52   slope = 7.22 µV MPa^{-1} (from -.234 to -4.158 MPa)
interpolated intercept = 0.2 µV at 0 MPa
measured intercept = 0.7 µV at 0 MPa (using distilled water)
max. measured variation ≈ ± .3 µV (at water potentials
-.234 to -4.158 MPa)

The maximum measured variation did not change significantly for
either unit over the water potential range -.234 to -4.158 MPa.

Soil Hygrometers

100 PT51-5 and PT51-10 soil hygrometers were purchased in 1974 and
1976. Of these 100 sensors, 20 were considered unusable by calibrating
at greater than 8.0 µV MPa^{-1}, calibrating at less than 6.0 µV MPa^{-1},
demonstrating excessive measurement drift, no readable output or
measuring a variation of greater than ± .7 µV in calibration osmotic
potential solution of -2.241 MPa. Output of .7 µV corresponds
to about .1 MPa water potential.

All hygrometer sensors were calibrated in osmotic solutions of -2.241
MPa at 20°C and later in distilled water using dew-point mode on a
Wescor HR-33T dew-point microvoltmeter and a constant temperature
(± .02°C) water bath. The following is a summary of the calibration
data for the 80 remaining sensors.

slope   range = 6 to 8 µV MPa^{-1}
                        mean = 7 µV MPa^{-1}

measured intercept   range = 0 to .4 µV (using distilled water)
                        mean = .2 µV

measurement variation   range = ± .05 to ± .7 µV at -2.241 MPa
                        mean = ± .4 µV

The measurement variation mean for soil hygrometers might be
applicable to a wide range of water potentials since *sample chamber*
variation in dew-point mode did not change over the water potential
range of -.234 MPa to -4.158 MPa.

Hygrometer Sensor Calibrations for the 80 Remaining Sensors

#	Average μV output .5m NaCl	h variation (±)μV	μV output distilled H_2O	μV bar^{-1}	#	Average μV output .5m NaCl	Variation (±)μV	μV output distilled H_2O	μV bar^{-1}
1	15.00	.4	.1	.665	56	17.96	.35	.2	.793
4	15.35	.35	.1	.680	58	17.80	.4	.1	.790
7	15.70	.1	.3	.687	60	17.28	.4	.3	.758
8	16.15	.3	.2	.712	61	15.78	.15	.2	.695
9	16.58	.4	.1	.735	62	15.45	.35	.1	.685
11	15.75	.35	.1	.698	63	13.66	.55	.1	.605
12	16.13	.55	.0	.720	64	16.70	.25	.3	.732
13	15.18	.2	.4	.660	65	14.48	.35	.2	.637
14	15.65	.2	.1	.694	66	15.78	.3	.0	.704
15	16.46	.6	.1	.730	67	14.99	.4	.1	.664
16	15.75	.5	.1	.698	68	14.04	.65	.3	.613
18	15.65	.4	.0	.698	69	16.73	.35	.2	.738
19	14.85	.3	.0	.663	70	15.90	.35	.2	.701
21	15.32	.45	.1	.679	71	16.78	.4	.1	.744
22	15.78	.35	.1	.700	72	15.48	.35	.3	.677
24	15.20	.15	.0	.678	73	17.20	.35	.4	.750
26	14.70	.4	.3	.656	74	16.15	.45	.1	.716
27	15.80	.35	.1	.701	76	15.24	.2	.1	.676
28	17.18	.35	.2	.758	77	15.16	.25	.2	.668
29	15.55	.35	.3	.680	78	15.93	.5	.1	.706
30	13.82	.45	.1	.612	79	14.83	.25	.1	.657
31	15.45	.15	.1	.685	80	15.50	.6	.2	.683
32	15.53	.55	.1	.689	81	15.52	.45	.0	.693
33	14.90	.2	.0	.665	83	15.06	.4	.0	.672
34	15.74	.1	.0	.702	84	15.28	.45	.1	.677
35	14.18	.35	.3	.619	85	15.86	.2	.0	.708
37	16.53	.15	.3	.724	86	14.64	.05	.2	.644
38	15.44	.4	.1	.685	87	16.35	.2	.1	.726
40	14.46	.55	.1	.641	88	15.54	.2	.1	.690
41	17.76	.5	.3	.779	90	14.84	.2	.1	.658

(continued)...

#	Average μV output .5m NaCl	h variation (±)μV	μV output distilled H_2O	μV bar^{-1}	#	Average μV output .5m NaCl	Variation (±)μV	μV output distilled H_2O	μV bar^{-1}
43	16.23	.6	.1	.720	91	14.94	.4	.0	.667
44	14.18	.2	.2	.624	92	15.50	.5	.2	.683
45	14.52	.65	.2	.639	93	16.06	.55	.0	.717
47	15.08	.15	.2	.664	94	14.66	.7	.0	.654
48	17.45	.25	.3	.765	95	14.06	.55	.0	.627
50	16.85	.45	.3	.739	96	16.24	.45	.1	.720
51	16.95	.05	.0	.756	97	15.32	.6	.0	.684
52	16.83	.15	.2	.742	98	16.54	.6	.1	.734
53	16.03	.3	.3	.702	99	14.56	.5	.0	.650
54	15.75	.35	.2	.694	100	15.52	.35	.2	.684

h: $\dfrac{\text{(maximum measured value } - \text{ lowest measured value)}}{2}$ = variation