

AN ABSTRACT OF THE THESIS OF

Jodie M. Sharpe for the degree of Master of Science in Botany and Plant Pathology presented on October 18, 2002.

Title: Variation of Drought Resistance and Root Regeneration Among Genotypes of Port-Orford-cedar (*Chamaecyparis lawsoniana*)

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Abstract approved \_\_\_\_\_

Donald B. Zobel

Drought resistance among genotypes of Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl., Cupressaceae) seedlings was evaluated both in the field and in the greenhouse. Field water potentials ( $\Psi$ ) of 5-year-old seedlings were measured at two high-elevation plantation sites where summer drought occurs. Measurements of  $\Psi$  were compared to survival two years prior at the same site. The north coastal breeding zone 1 had significantly lower mid-day  $\Psi$  and lower survival than the southern interior breeding zone 6. Percent survival at 3 years was significantly correlated with mid-day  $\Psi$ . A second assessment of drought resistance was performed in the greenhouse on 1-0 seedlings. Root growth potential (RGP) was measured in the winter under non-stress conditions and following a drought in the summer. Differences among breeding zones were opposite in pattern from outplanting measurements of survival and water potential; therefore, RGP may not be a good predictor of drought resistance or survival among different genotypes within a single species. Low-elevation, coastal families had greater root growth than inland, high elevation sources. Greater root growth occurred in seedlings with more shoot mass. Little regional specialization in RGP across the species' range was indicated as there was greater variation among families than among breeding

zones. In the summer RGP test following drought, only the two extremes of the range were evaluated; both north coastal and southern interior families showed decreased root growth compared to the winter RGP under non-stress conditions. Despite significantly higher predawn  $\Psi$  in inland, high elevation families, lower elevation coastal families had significantly more roots. Change in chlorophyll fluorescence yield measured on foliage of droughted plants was positively correlated with the absolute value of predawn  $\Psi$ ; however, it was not a sensitive predictor of predawn  $\Psi$  ( $R^2 = 0.06$ ) at the levels used in this study. Lower levels of  $\Psi$  may be necessary to produce severe stress to damage Port-Orford-cedar foliage.

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Variation of Drought Resistance and Root Regeneration Among Genotypes of Port-  
Orford-cedar (*Chamaecyparis lawsoniana*)

by  
Jodie M. Sharpe

A THESIS

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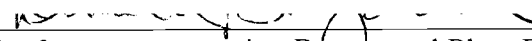
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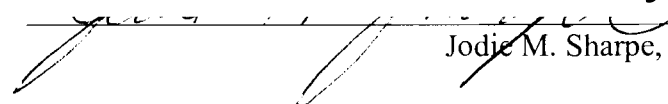
  
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## CONTRIBUTION OF AUTHORS

Dr. Don Zobel, Dr. Barbara Bond, and Dr. Everett Hansen provided editing expertise and research advice throughout this project.

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## DEDICATION

The author wishes to dedicate her thesis to God, her mother, Sheila Miller, who has supported her throughout her life, her husband, Hubert Melvin Morrison, and to her mentor, Thomas G. Huntington.

# VARIATION OF DROUGHT RESISTANCE AND ROOT REGENERATION AMONG GENOTYPES OF PORT-ORFORD-CEDAR (*CHAMAECYPARIS LAWSONIANA*)

## CHAPTER 1 – GENERAL INTRODUCTION

Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl., Cupressaceae), an evergreen conifer, typically grows in mesic habitats within a narrow range in southwestern Oregon and northern California. Although fossils related to Port-Orford-cedar occur as far east as Nebraska, a cooling and drying climate since the Tertiary period has restricted its distribution to near the Pacific coast (Edwards 1983). Late seed germination (in June) and continued growth during the dry season may restrict this species to sites where consistent summer moisture is available (Zobel 1990, Zobel et al. 2002). In addition to its restricted range within 2° latitude and longitude, populations of Port-Orford-cedar are further threatened by an exotic root rot, caused by *Phytophthora lateralis* Tucker and Milbrath (Zobel et al. 1985, Hansen et al. 2000). Introduced to the Pacific Northwest in the 1920's, this fungal-like oomycete thrives in the moist areas where this tree grows. The pathogen spreads via flowing water and mud moved by vehicles and animals, leaving dead Port-Orford-cedar along many creeks and roadsides.

Concern for the future of Port-Orford-cedar and the ecological consequences of losing local populations have led to federal and state cooperation. Since 1997, cuttings from potentially resistant trees across the range have been collected by the U.S. Bureau of Land Management and the U.S. Forest Service, and screened for resistance by Oregon State University (Bower et al. 2000). These efforts have produced ~1100 trees to be used

in a breeding program. Of the trees that tested resistant, < 1% display high resistance to the pathogen (Hansen et al. 2000, Sniezko and Hansen 2000, Sniezko et al. 2000). The U.S. Forest Service established an operational containerized seed orchard for the production of resistant Port-Orford-cedar seed; those trees with the highest level of resistance are from the north coastal breeding block 1 (USDA Forest Service 2002). Currently, the few trees displaying high resistance originate in low elevation areas, yet native populations of Port-Orford-cedar range from sea-level to 1950 m (6400 ft). The deployment of resistant trees throughout the range, therefore, may require planting genotypes outside their region of origin.

Within the horticultural industry, high genetic diversity in Port-Orford-cedar is suggested by the variety of shapes and colors and the development of > 200 cultivars. Given its small range, Port-Orford-cedar appears to have moderately high levels of allozyme variability among stands compared to other western conifer species. Expected heterozygosity was 15% for nine populations of *Ch. lawsoniana* and ranges from 0 in western redcedar to 33% in widespread Douglas-fir (Millar and Marshall 1991). Other Cupressaceae species like *Cupressus macrocarpa* (Monterey cypress) and *Calocedrus decurrens* (Incense-cedar) have slightly higher measures of allozyme diversity (18%) than that reported for Port-Orford-cedar.

Coastal and lower elevation populations of Port-Orford-cedar may be genetically more variable and differ more across soil types than inland and higher elevation populations (Millar and Marshall 1991, Millar et al. 1991). In 1992, a genetic variation study was conducted over the entire range of Port-Orford-cedar. Forty-six stands in California and 36 stands in Oregon were evaluated for allozyme diversity (Millar et al.

1992). Of those tested, two disjunct inland populations, the Sacramento and Trinity watersheds in California, had low allozyme variability. In both states, allozyme variation was strongly correlated to latitude, longitude, and elevation. Trends or clines of variability differed: Oregon showed the greatest differentiation along a north-south gradient while California had greater diversity along an elevational cline.

Similarly to Port-Orford-cedar, *Chamaecyparis nootkatensis* (D. Don) Spach (Alaska-cedar) grows along a narrow coastal strip within the Pacific Northwest but over an 18° larger latitudinal gradient than Port-Orford-cedar, occurring from northern California to south-central Alaska. A rangewide survey of isoenzyme variation in Alaska-cedar found an expected heterozygosity of 17.1% for 17 pooled populations (Ritland et al. 2001). Examination of morphological and physiological traits across its range suggests that both generalist and specialist modes of genetic adaptation have occurred. *Thuja plicata* Donn ex D. Don (western redcedar), on the other hand, shows little genetic differentiation among populations, exhibiting a generalist strategy of adaptation (Russell 1998). Unlike Alaska-cedar or Port-Orford-cedar, western redcedar is generally limited to lower elevation sites. Genetic diversity may be more adaptive in *Chamaecyparis* and *Thuja* species with specialized, high elevation populations. Port-Orford-cedar and Alaska-cedar both have disjunct stands that may be remnant populations from past bottlenecks or selection pressures from the more xeric, high elevation environments (Russell 1998). The absence of specialized, high-elevation populations may result from lower genetic variability in western redcedar.

Common garden studies of Port-Orford-cedar have been conducted in order to evaluate the adaptation of genotypes to field conditions. Two hundred ninety-eight



families from 52 stands representing 11 watersheds from across the range of Port-Orford-cedar were evaluated at an inland and a coastal outplanting site (Kitzmilller and Snieszko 2000). Significant differences in height were found among families of Port-Orford-cedar; southern, high elevation families grew less than those of northern, lower elevation seed sources. Among 54 families of Port-Orford-cedar (a subset selected from 266 families in a range-wide assessment), lower elevation, coastal families completed more of their height growth late in the growing season than higher elevation, inland families (Zobel et al. 2002). It is unclear what repercussions might follow on the survival of lower elevation resistant stock that is moved into interior, higher elevation areas, which are typically drier with earlier frosts than those of the coastal lowlands. Although coastal families of Port-Orford-cedar grow faster, survival and growth of coastal genotypes may be compromised when grown in drier, colder areas (Jenkinson 1996, Morgenstern 1996).

Comparisons between a coastal and an inland, high-elevation outplanting site show that overall, 3-year-old Port-Orford-cedar seedlings were 15% taller at the coastal site compared to the inland site (Jay Kitzmilller, U.S. Forest Service, Chico, CA, unpublished data). Coastal families appear to be more sensitive to movements involving a large increase in elevation compared to higher-elevation, inland families. At the inland site, northern coastal families from the Dunes watershed showed a 24% reduction in height growth compared to growth at the coastal site, while inland families from the Sacramento watershed were reduced in height by only 9% (significant at  $p < 0.05$ ).

This research focused on the variability of drought resistance among genotypes of Port-Orford-cedar, in order to determine the ecological ramifications of planting a

*Phytophthora*-resistant stock across the range of Port-Orford-cedar. Genetic differences in the response to water stress of Port-Orford-cedar genotypes were evaluated in both field plantings and greenhouse grown seedlings. Chapter 2 presents field measurements of water potential and survival, measured from two U.S. Forest Service outplanting sites. Field water potential should indicate the net drought response of seedlings to the environment due to water uptake or effective control of water loss (Larcher 1995). The purpose of this analysis is to determine whether or not genotypes of Port-Orford-cedar differ in their ability to maintain high water potential and the subsequent effects on their ability to survive at harsher sites outside their climate of origin.

Chapter 3 presents seedling root growth potential measurements taken in the winter when seedlings are normally outplanted into the field. A second assessment of root growth following a drought treatment during the summer will also be presented. Root growth potential may indicate more long-term adaptations that deal with a plant's ability to recover from or avoid drought (O'Toole and Chang 1979). Simultaneous measurements of water potential and chlorophyll fluorescence will help quantify the degree of stress imposed upon the seedlings. Chapter 4 discusses results from both studies and presents final conclusions.

Comparisons of the data were made on several levels because several geographic distinctions were used to identify sample trees. First, families are groups of Port-Orford-cedar seedlings that originate from seed from the same parent tree. Families of Port-Orford-cedar are located within watersheds, or areas of land within the same major river drainage. Several families of Port-Orford-cedar were usually sampled within each watershed. Breeding blocks combine watersheds that have apparently genetically similar

populations. Breeding blocks for Port-Orford-cedar were delineated based on topographical differences across the range and revealed patterns of variation in growth at the provenance outplanting sites (Kitzmilller et al. unpublished data).

## **ECONOMIC AND ECOLOGICAL VALUE OF PORT-ORFORD-CEDAR**

Port-Orford-cedar wood is highly valued due to its strength, straightness of grain, and resistance to shock (Zobel et al. 1985). The structural properties of Port-Orford-cedar wood reduce splintering; thus, it is easy to work with and has been used for many purposes, from interior trim to mine timbers. Historically, Port-Orford-cedar has brought high prices in the export market compared to other conifer species. Changing economies, however, have decreased the export market but stimulated the domestic market. Specialty products like arrow shafts and branches used in floral bouquets add more than \$1,000,000 to local and regional economies each year (Barnes et al. unpublished).

Although it is often a minor component of the forest, Port-Orford-cedar is ecologically important due to its unusual combination of fire- and shade-tolerance, being the only shade-tolerant conifer on low-elevation ultramafic soils. Port-Orford-cedar effectively absorbs Ca from ultramafic soils, which normally limit Ca uptake due to high Mg/Ca ratios (Zobel and Hawk 1980, Kiilsgaard et al. 1987). Thus, Port-Orford-cedar may enhance cycling of calcium within the ecosystem on ultramafic soils.

Port-Orford-cedar has a remarkably wide ecological amplitude despite its small geographic range, occurring in more than 93 plant associations in Oregon and California

(Zobel et al. 1985, Jimerson 1994). Port-Orford-cedar grows from sea-level in the coastal fog belt to subalpine forests at elevations up to 1950 m. It grows in all four vegetation zones recognized by ecologists in southwestern Oregon. Many forest communities with Port-Orford-cedar have among the richest plant species diversity in the region; many of these species are rare, threatened, or endangered. Scientists in the Six Rivers National Forest in north coastal California are investigating the relationship of rare plants to Port-Orford-cedar communities (Hoover unpublished). A concern is that loss of Port-Orford-cedar from riparian areas due to *Phytophthora* disease may decrease shade and produce conditions unsuitable for some rare and sensitive plants.

## **FIELD WATER POTENTIAL AND SURVIVAL**

In 1996, a long-term Port-Orford-cedar common garden study was initiated by the U.S. Forest Service on four forested sites (Jay Kitzmiller, U.S. Forest Service, Chico, CA, unpublished data). Average survival at the coastal Humboldt provenance site was high (~88%). Two drier, higher elevation sites were chosen for this study, in order to evaluate differences among genotypes at field sites prone to water stress. Average survival after 3 years was 80% at the Trinity Lake site in northern California and 50% at the Althouse site in southern Oregon.

Field survival and mid-summer water potential were evaluated in order to detect the overall response of seedlings to the environment and compare differences among genotypes of Port-Orford-cedar. Plant water potential integrates the net effect of plant

water relations' characteristics and their interaction with the environment. It shows the net result of resistance mechanisms and may indicate genotypes that are less resistant to drought. This study did not determine the physiological mechanisms behind changes in shoot water potential.

Plants adapt to water limitation by increasing water uptake, regulating water loss, or tolerating decreases in water potential. Different mechanisms contribute to drought resistance, often distinguished as avoidance and tolerance (Larcher 1995). Stomatal control or differences in leaf morphology are avoidance mechanisms that affect water potential by slowing water loss and helping to maintain cell turgidity. It has been shown that stomata in Alaska-cedar are extremely sensitive as water becomes limiting (Grossnickle and Russell 1991). In Port-Orford-cedar, characteristics that enable inland genotypes to survive in harsher, drier conditions may also limit photosynthetic activity and thus growth. For instance, waxy formations on leaf surfaces, fewer stomata, and sunken stomata may reduce transpiration but also limit CO<sub>2</sub> uptake (Grossnickle 1993, Miller et al. 1995). Zobel et al. (1978) found variation in stomatal frequency and size among the lateral leaves of three *Chamaecyparis* species grown in a common garden. A small comparison among Port-Orford-cedar seed from two contrasting sources, however, showed no consistent differences in leaf conductance between regions when grown in a common environment (Zobel and Liu 1980).

As water loss ensues, turgor losses in shoots can be compensated for by solute accumulation to alter osmotic potential, or by changes in tissue elasticity (Joly & Zaerr 1987, Kramer and Boyer 1995, Marshall & Dumbroff 1999, Zobel et al. 2001).

Mechanisms of tolerance like osmotic adjustment and elasticity allow cells to maintain

turgor during times of water shortage and have been studied in Port-Orford-cedar.

Osmotic potential at zero turgor in summer was high compared to many conifer species (-1.4 to -1.5 MPa) (Zobel et al. 2001), suggesting low tolerance to drought (Lambers et al. 1998). Compared with other conifers, however, Port-Orford-cedar has elastic tissue, indicating ability to maintain turgor during dehydration (Zobel et al. 2001). Weak and often insignificant correlations between water relations attributes and seed source location suggest little regional genetic variation for these characteristics within Port-Orford-cedar.

Grossnickle and Russell (1996) found that Alaska-cedar both increased elasticity and decreased osmotic potentials under mild drought stress, however, severe droughting showed increased osmotic adjustment with decreasing cell elasticity. Water potential at turgor loss ranged from -1.3 to -2.6 MPa, and was -1.28 MPa in summer, higher than for Port-Orford-cedar. First-year western redcedar seedlings planted in March at a coastal site in Canada showed similar levels of osmotic potential at turgor loss (-1.93 MPa) to Alaska-cedar just after planting in the field (Grossnickle 1993). Compared to western hemlock, turgor was maintained in western redcedar at lower relative water contents primarily by high cell wall elasticity.

## **ROOT GROWTH POTENTIAL**

Besides changes to shoot morphology or physiology, water stress may be alleviated through enhanced root growth. Root growth is an avoidance strategy about

which little is known for Port-Orford-cedar. Given the root disease, information on root growth among genotypes of Port-Orford-cedar would be useful.

Root growth potential (RGP), commonly defined as the number of roots (>1 cm) initiated in a given time period under favorable conditions, has been widely used to evaluate seedling quality at the time of planting (Stone 1955, Burdett 1979, Feret and Kreh 1985, McCreary and Duryea 1985, Palmer and Holen 1986, Binder et al. 1988). Rapid new root growth is important to establishment and drought resistance of newly planted conifer seedlings (Grossnickle & Reid 1984, Nambiar 1984, Sands 1984, Girard et al. 1997). The ability to grow roots may prevent or alleviate drought stress following planting or drought by re-establishing root/soil contact and increasing the area for water absorption, especially the number of root tips (Satoo 1956, Lauenroth et al. 1987, Sponchiado et al. 1989, Arnott et al. 1993, Kavanagh & Zaerr 1997, Tinus et al. 2000). Grossnickle (1993) speculates that 2.4 times as many average roots in the soil around western redcedar seedlings, compared to western hemlock, may explain its ability to inhabit drier sites.

Pathways of water movement, namely apoplastic and cell-to-cell, and root hydraulic conductivity will vary depending upon the forces driving water movement (Steudle 2000). As soil dries, root hydraulic conductance may decrease through suberization, thereby reducing water loss into the surrounding soil. Upon soil rehydration, however, rapid root growth may alleviate seedling stress and allow leaf growth to resume. Growth of roots is greater than that of the shoot under water stress and may help alleviate seedling water stress (Hsiao and Xu 2000). In this study, root growth potential will be evaluated under non-stress and drought-stress conditions and differences

among genotypes of Port-Orford-cedar will be related to field water potential and survival.

Most RGP tests have been done in the spring to assess survivability at the time of planting. Periods of high RGP correlate with the period in which species are most tolerant to desiccation (Hermann 1967, Ritchie and Dunlap 1980, Larson 1984, Ritchie and Tanaka 1990). However, one might wish to know RGP at varying times of the year under different physiological states (DeWald and Feret 1988). RGP varies with season and does not necessarily coincide with patterns of natural root growth. Douglas-fir, for instance, increases root growth in October and again in early spring; however, the *potential* for root growth (RGP) parallels the accumulation of chilling hours throughout the winter (Ritchie and Dunlap 1980).

Patterns of shoot phenology of *Pinus sylvestris* L. (Scots pine) across a latitudinal gradient were correlated to differences in carbohydrate concentrations in the roots, shoots, and twigs (Oleksyn et al. 2000). Overall, populations from warmer locations had up to 25% more starch in the needles and up to 10% higher soluble carbohydrate concentrations than trees from colder locations. Whether RGP follows the carbohydrate pool in roots, however, is not clear (Gilmore 1962, Winjum 1963, Lavender 1964, Krueger and Trappe 1967). Tinus et al. (2000) found that RGP levels paralleled the total carbohydrate concentration in the roots of *Pinus halepensis*, *Pinus radiata*, and *Pseudotsuga menziesii* var. *glauca* over a 24-week period during winter. Rose (1992) found no relationship between starch concentration in the roots of *Pinus taeda* (loblolly pine) and subsequent measurement of RGP; however, seedlings with higher whole-plant levels of starch did have greater RGP. Other studies with *Picea rubens* indicate wide



variation in root carbohydrate reserves, suggesting that either root carbohydrate concentrations are inherently variable or possibly soil factors or differences in methodology may lead to variable results (Schaberg et al. 2000).

Most studies indicate that new root growth occurs at the expense of recently synthesized photosynthate, unless photosynthesis is inhibited for a substantial time (Ritchie and Dunlap 1980, Van den Driessche 1987). Conifer genotypes capable of synthesizing more photosynthate or genotypes with a surplus of stored carbohydrates are likely to have higher RGP than genotypes with lower photosynthetic rates or with less stored carbohydrates (Van den Driessche 1987, Kozlowski 1992).

In my summer RGP test, water potential of coastal genotypes is likely to decline sooner than inland genotypes following the experimental drought (Chapter 2). Coastal genotypes may close their stomata sooner than inland genotypes to prevent water loss and thus they may experience less photosynthesis than normal. Mild levels of water stress may initially stimulate root growth in coastal genotypes (Huang and Fry 1998, Villar-Salvador et al. 1999). At severe levels of water stress, however, seedlings may exhibit little or no root growth (Girard et al. 1997, Tinus et al. 2000). I hypothesize that coastal genotypes may exhibit lower root growth compared to inland genotypes as a consequence of greater stress under droughting.

Natural root growth typically increases once shoot growth decreases, as the two processes rarely compete for photosynthate (Oleksyn et al. 2000). Higher elevation populations of Port-Orford-cedar do less shoot growth late in the growing season than lower elevation, coastal populations (Zobel et al. 2002). Root growth, therefore, may be innately higher in the higher elevation genotypes during late summer. Lower elevation

genotypes may be continuing their shoot growth, thus limiting resources available for root growth.

The interpretation of RGP in different genotypes of Port-Orford-cedar and its correlation to drought resistance could be confounded by differences in shoot size. Increased root growth, therefore, may not translate into greater drought resistance if shoot size and transpirational demand are also larger. Even so, evaluating root growth potential may provide insight into drought recovery, in particular, the physiological limitations of roots in resuming growth at times when root growth would benefit the plant, i.e., following dry conditions in the summer or after planting.

## **CHLOROPHYLL FLUORESCENCE**

During the summer drought test, measurements of chlorophyll fluorescence yield were used as a second assessment of seedling vigor (Lichtenthaler and Rinderle 1988, Mohammed et al. 1995, Eastman and Camm 1995). Some seedlings may display no root growth under a certain threshold of water stress (Hawkins and Binder 1990); therefore, fluorescence yield may be useful in quantifying stress levels in these seedlings.

Fluorescence is one of three pathways that dissipates excess absorbed light energy in leaves; therefore, it is generally inversely proportional to photosynthetic activity. About 3-5% of absorbed incident light energy is re-emitted as photons (i.e., fluorescence). Other pathways of de-excitation for light energy absorbed by chlorophyll molecules include heat dissipation. When measuring fluorescence, a pulse-modulated

light emitting diode (LED) excites chlorophyll fluorescence and a separate halogen light provides rapid pulses of actinic light (short  $\lambda$ ) to fully saturate and reduce photosynthetic electron carriers. In a dark-adapted leaf, fluorescence rises from a ground-level state ( $F_0$ ) to maximum fluorescence ( $F_m$ ) upon illumination when all electron carriers are reduced (Figure 1.1). Then, the maximum level of fluorescence decreases to steady-state ( $F_s$ ) as carbon assimilation begins in the Calvin Cycle. The drop from maximum to steady state fluorescence occurs due to several mechanisms. As the pH falls in the lumen of the chloroplast with increased activity in the light reactions, this gradient in pH signals photochemical quenching of fluorescence via heat dissipation. Also, reoxidation of Q, one of the primary electron acceptors in the electron transport chain, occurs as energy is passed from Photosystem II (PSII) to Photosystem I (PSI) (Vidaver et al. 1991). This reoxidation lowers fluorescence because other electron acceptors on the donor side of Q are able to accept electrons.

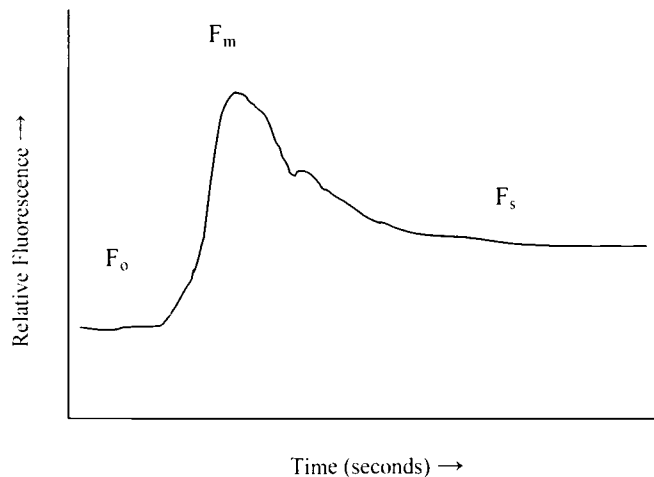


Figure 1.1. Generalized Graph of Chlorophyll Fluorescence Kinetics known as the “Kautsky Effect” (Kautsky and Hirsch 1931).

“Yield” is the ratio of maximum fluorescence ( $F_m$ ) minus steady-state fluorescence ( $F_s$ ) divided by maximum fluorescence ( $(F_m - F_s)/F_m$ ) (Lichtenthaler et al. 1986, Genty et al. 1989). This ratio represents the quantum efficiency of non-cyclic electron transport in photosynthesis. Unlike the fast phase of fluorescence (i.e., the initial rise to maximum fluorescence), which reflects primary processes of PSII, the slow phase from maximum to steady-state fluorescence represents biochemical processes in the stroma as well as photochemical processes in the thylakoid membrane (Bolhàr-Nordenkampf & Öquist 1993). Another advantage of measuring the decrease from maximum to steady-state fluorescence is that it does not require dark adaptation of the leaf (Lichtenthaler 1988). Measurements can be performed quickly in natural light.

Fluorescence yield can provide a quick assessment of the stress experienced by some plants. Havaux and Lannoye (1985) found that the slow transient kinetics of chlorophyll fluorescence were strongly reduced in drought sensitive cultivars of wheat. Similarly, a drought-sensitive species of *Populus* showed depressed electron transport rates following drought (calculated from measurements of chlorophyll fluorescence), compared to a more drought tolerant species (Li and Kakubari 2001).

With increasing stress, stomatal closure would limit  $\text{CO}_2$  uptake and thus slow the dark reactions of photosynthesis. Slower  $\text{CO}_2$  fixation would lead to increased fluorescence, to dissipate the absorbed light energy.  $F_m$  decreases and  $F_s$  rises, so fluorescence yield ( $(F_m - F_s)/F_s$ ) should decrease with increasing water stress (Lichtenthaler et al. 1986, Lichtenthaler 1988, Lichtenthaler and Rinderle 1988). Preliminary studies suggest that inland, southern genotypes (i.e. high elevation) of Port-Orford-cedar may maintain higher  $\Psi$  during the growing season than northern, lowland

genotypes when grown in the same environment (Chapter 2). Fewer stomata or a waxy coating on leaves of higher elevation genotypes may allow less water loss and thus greater drought resistance compared to lower elevation, coastal genotypes.

Differences in leaf chlorophyll concentrations among plant genotypes could result in innate differences in fluorescence yield (Lichtenthaler et al. 1986). Observing the change in chlorophyll fluorescence yield from non-stress to stressed conditions, rather than absolute values, should alleviate confounding effects of differences in chlorophyll content among genotypes. I hypothesize that the change in chlorophyll fluorescence yield from non-stress to droughted plants will be less in higher elevation genotypes than coastal, low-elevation genotypes.

**CHAPTER 2 – VARIATION OF FIELD WATER POTENTIAL AND  
SURVIVAL WITHIN PORT-ORFORD-CEDAR (*CHAMAECYPARIS  
LAWSONIANA*)**

**By Jodie M. Sharpe and Donald B. Zobel**

**ABSTRACT**

In order to estimate genetic variation in drought resistance across the range of Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl., Cupressaceae), plant water potential ( $\Psi$ ) was measured at two high elevation provenance plantations in southern Oregon and northern California, where 266 genotypes of Port-Orford-cedar were planted. Mid-day and predawn  $\Psi$  were measured on 5-year-old seedlings of 22 families representing the native range of Port-Orford-cedar during one week of the dry season and correlated to 3-year seedling survival. Predawn  $\Psi$  showed no significant differences among breeding blocks, watersheds, or families. Slight significant differences among watersheds and breeding blocks were found for mid-day  $\Psi$ . Percent survival at 3 years was strongly and positively correlated with mid-day  $\Psi$ . Overall, seedlings from the high elevation, interior breeding block had significantly greater control over mid-day  $\Psi$  and less mortality at the plantation sites compared to the north coastal breeding block.

## INTRODUCTION

Genetic differences in drought or frost tolerance exist across environments within many plant species (Campbell and Sorensen 1973, Lindgren and Nilsson 1992, Hawkins et al. 1994). Managing a variable species requires knowledge of the pattern of variation in order to determine how far genotypes can be moved successfully. The purpose of this study is to evaluate the variability in water potential of 5-year-old Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl., Cupressaceae) seedlings at two drought-prone provenance plantations and to correlate water potential with their 3-year survival. This research will provide information on the drought resistance among Port-Orford-cedar genotypes and their ability to survive at drier field sites.

Plant water potential and field survival reflect the net result of several plant mechanisms of drought resistance. Predawn water potential ( $\Psi_{pre}$ ) should be near equilibrium with the wettest portion of the rhizosphere (Ritchie and Hinckley 1975) and indicates the water status with which a plant begins a daylight period.  $\Psi_{pre}$  measured in the field from native Port-Orford-cedar saplings across its range averaged above  $-1$  MPa in late August in the *Tsuga heterophylla* and *Abies concolor* vegetation zones. Some sites in the mixed pine community had average predawns below  $-1$  MPa, for example,  $-1.7$  and  $-2.2$  MPa (Zobel and Hawk 1980). Average  $\Psi_{pre}$  of Alaska-cedar (*Ch. nootkatensis*) ( $-1$  MPa) at one rocky, upland site was comparable to that of Port-Orford-cedar (Antos and Zobel 1986). After a one-month dry period, predawn water potentials averaged  $-1.20$  MPa in western redcedar (*Thuja plicata*) seedlings at a reforested coastal site in Canada (Grossnickle 1993). Predawn water potential of *Ch. taiwanensis*, a

Taiwanese species with greater leaf resistance than Port-Orford-cedar, ranged from –1.4 to –2.2 MPa during the driest month of March (Zobel and Liu 1980).

Mid-day plant water potential ( $\Psi_{\text{mid}}$ ) represents the water status at the time of day when evaporative stress is typically greatest. Diurnal changes between mid-day and predawn water potential indicate a plant's ability to resist water loss and subsequently equilibrate with soil water potential, respectively. Predawn and mid-day usually represent the maximum and minimum water potentials within a day.

Port-Orford-cedar is an ecologically important, highly valued timber species in forests of southwestern Oregon and northern California (Zobel et al. 1985). Port-Orford-cedar is noted for its wide ecological amplitude, occurring in more than 93 plant associations in Oregon and California (Zobel et al. 1985, Jimerson 1994). Isolated, disjunct stands occur at higher elevations in the southeastern corner of its range, indicating possible refugia for a species whose range has become coastally restricted over geologic time (Edwards 1983). In addition to its restricted range within 2° latitude and longitude, populations of Port-Orford-cedar are further threatened by an exotic root pathogen, *Phytophthora lateralis* Tucker and Milbrath (Hansen et al. 2000). Late germination (in June) and continued growth into the dry season often restrict this species to wet sites where the pathogen thrives (Zobel 1990, Zobel et al. 2002), leaving dead Port-Orford-cedar along many creeks and roadsides (Zobel et al. 1985).

Concern for the future of Port-Orford-cedar and the ecological consequences of losing local populations have led to federal and state cooperation. Since 1997, cuttings from potentially resistant trees across the range have been collected by the U.S. Bureau of Land Management and the U.S. Forest Service, and screened for resistance by Oregon



State University (Bower et al. 2000). These efforts have produced ~1100 trees to be used in a breeding program. Of these collections, a few select trees display high resistance to the pathogen (Hansen et al. 2000, Sniezko and Hansen 2000). The majority of highly resistant trees originate in low elevation areas (E.M. Hansen, Oregon State University, personal communication); in contrast, native populations of Port-Orford-cedar range from sea-level to 1950 m (6400 ft).

Its wide ecological amplitude, and the 200+ cultivars that have been developed for horticultural use, indicate genetic diversity within Port-Orford-cedar. Allozyme studies indicate moderately high levels of variability among stands of Port-Orford-cedar; expected heterozygosity from nine populations was 15%, intermediate among values from 0 to 33% for other northwest conifer species (Millar and Marshall 1991). Lower elevation populations of Port-Orford-cedar may be genetically more variable and differ more across soil types than inland and higher elevation populations (Connie Millar, USDA Forest Service, Berkeley, CA, unpublished data).

Several common garden studies have been used to evaluate the variation in adaptation of Port-Orford-cedar genotypes from throughout its range (Table 2.1). Two hundred ninety-eight seedling “families” (groups that originate from seed from the same parent tree), representing 52 stands from 11 watersheds across the range of Port-Orford-cedar, were evaluated in raised beds at inland and coastal nurseries (Kitzmilller and Sniezko 2000). Significant differences in height occur among families; southern, high elevation families grew less than those of northern, lower elevation seed sources. Among 54 families of Port-Orford-cedar, lower elevation, coastal families produced a higher

proportion of growth in late season than higher elevation, inland families (Zobel et al. 2002) (Table 2.1).

Table 2.1. Locations and Descriptions of Range-wide Studies on Port-Orford-cedar

Study Type	Site/s	Lat °N	Long °W	Elev (m)	Data Source
Raised Bed	Dorena	43.78	122.96	245	Kitzmilller & Sniezko 2000, Zobel et al. 2001, 2002
	Humboldt	40.98	124.08	76	
Field	Humboldt	40.98	124.08	76	Jay Kitzmilller, US Forest Service, unpublished data
Outplanting	Althouse	42.05	123.52	916	unpublished data
	Trinity Lake	40.85	122.83	920	
	Chetco	42.23	124.13	496	
Greenhouse	Dorena	43.78	122.96	245	Sharpe et al. Chapter 3

Weak and often insignificant correlations between water relations' attributes and geographic seed source information, however, suggest little regional genetic variation for osmotic potential and tissue elasticity within Port-Orford-cedar (Zobel et al. 2001). In general, Port-Orford-cedar has high osmotic potential at zero turgor compared to other conifer species (-1.4 to -1.5 MPa) and high tissue elasticity, suggesting both low and high tolerance to dehydration, respectively (Lambers et al. 1998). Comparisons among families at a coastal nursery suggest that northern families may have greater ability to adjust osmotic potentials as the environment changes, compared to southern, interior populations (Zobel et al. 2001). Therefore, genotypes closer to the coast had slightly

higher relative water content at zero turgor ( $RWC_z$ ) than more inland genotypes, suggesting less resistance to desiccation in coastal sources.

Given its wide ecological range and genetic differences in height growth, the question arises about how widely low elevation, resistant stock can be planted across the range of Port-Orford-cedar. It is unclear what repercussions might follow on the survival of low elevation resistant stock that is moved into inland areas that are drier than those of the coastal lowlands where resistant genotypes originate. Although coastal families are able to grow faster than inland, high elevation sources, survival and growth of coastal genotypes may be compromised when grown in drier, colder areas (Jenkinson 1996, Morgenstern 1996). This study will evaluate the drought resistance among genotypes of Port-Orford-cedar by measuring water potential and field survival.

## **MATERIALS AND METHODS**

### **Site Information**

In 1996, a long-term Port-Orford-cedar common garden study was initiated by the U.S. Forest Service with field outplantings on four formerly forested sites (Jay Kitzmiller, U.S. Forest Service, Chico CA, unpublished data) (Table 2.1). Two hundred sixty-six families of Port-Orford-cedar were planted at each site in the spring. Test designs of each plantation are random, complete, interlocking blocks, with 3 sets of 8 contiguous blocks per set (i.e. reps within sets, and families randomized and replicated within blocks) (Jay Kitzmiller, U.S. Forest Service, Chico, CA, unpublished data 1995).

Two inland, high-elevation, provenance plantations were chosen for this study.

Survival was measured at these plantations in fall of 1998 by the U.S. Forest Service and was correlated to the water potential measurements made in 2000. Average survival after three growing seasons at the coastal Humboldt provenance site was higher (~88%) than that from the two drier, higher elevation sites chosen for this study. Average survival was 80% at the Trinity Lake site in northern California and 50% at the Althouse site in southern Oregon.

Direct comparison between families at the two plantation sites was not possible because the same families were not available to be sampled at both sites. High mortality at the Althouse site limited data collection and the number of observations from many families (Table 2.2).

Table 2.2. Families and Number of Replicates Sampled For Water Potential at Trinity Lake and Althouse Provenance Sites, August 2000.

<b>Breeding Block</b>	<b>Watershed</b>	<b>Trinity Lake Family Codes</b>	<b>Althouse Family Codes</b>
1	Coos Bay (COOS)	IF(4), IZ(4)	HZ(2), IF, IY
1	Dunes (DUN)	MF(4), MH(4)	LI, LW, LX, MF, MG(2)
1	Elk (ELK)	LN (4), LT(4)	LG(2), LJ, LN(2), LT(2),
1	Rogue (ROG)	DH(3), DJ(4)	DZ(2), EC(2)
3	Coquille (COQ)	CY(8)	CX, CY, IZ, KG(2), KU, LA, LB,
3	Umpqua (UMP)	CU(6), CV(4)	-
4	Applegate (APP)	ES (4), EX(4)	ER, EX , EZ, FF(3)
4	Illinois Valley (ILV)	FO (8)	FO(2), FP(3), FU
4	Klamath (KLA)	BP(4), BQ(4)	BQ(2), BZ, CA, CC, CF, CM
4	Smith River (SR)	GS(4), HG(4)	GH, GM(2), GW(2), GQ, HE(2), HH
6	Sacramento (SAC)	S(4), U(5)	AF, AO(2), AQ, S, U,
6	Trinity (TRN)	AZ(3), BH(3)	AZ, AW, AX, BA, BG, BJ

Parentheses indicate # replicates, no number indicates one replication

## Water Potential

Predawn ( $\Psi_{pre}$ ) and mid-day ( $\Psi_{mid}$ ) water potentials were measured during mid-August, within a one-day period at each provenance plantation. I sampled replicates of the same families within the same block at Althouse and over 4 blocks at Trinity Lake in order to evaluate the change in  $\Psi_{pre}$  over time.

Measurements were taken August 12-13, 2000, at the Althouse outplanting site (42° 03' 31" N Lat, 123° 31' 53" W Long, 916 m elevation), which is located in the Siskiyou Mountains, Josephine County, Oregon. Prior to data collection, rainfall in nearby Cave Junction, Oregon, was 2.2 cm in July and 0.5 cm in August (Southwest Oregon Climate Data Center). Average temperature for the month of August was 21.3 °C. On August 14-15, 2000, water potentials were measured at the Trinity Lake outplanting site (40° 51' 16" N Lat, 122° 50' 20" W Long, 920 m elevation), near Weaverville, California. In Weaverville, average August temperature was 22.2 °C and rainfall was 0.25 and 0 cm, respectively, for July and August (Western Regional Climate Center).

$\Psi_{pre}$  was measured between midnight and 0500 PDT. Branchlets approximately 15 cm long were cut from the southern aspect of each tree, avoiding new growth. Samples were taken ca. ¼ of the way down from the top of each seedling, except for some very small trees at Althouse. Then, the foliage was placed into plastic bags and the air removed. Samples were stored in a cooler no longer than 20 minutes until placed into the pressure chamber for measurement (Model 600, PMS Instrument Co., Corvallis, OR) (Ritchie and Hinckley 1975, Karlic and Richter 1979).  $\Psi_{mid}$  was measured between 1000 and 1400, sampled similarly to and within the same 24-hour period as  $\Psi_{pre}$ .

Trees were sampled randomly at Althouse within Block 1, Set 1. Sampling at Trinity Lake was randomly from within Blocks 1, 2, 3, and 6, which occur over similar topography in Set 1.

### **Statistical Analysis**

Normality of data was checked using the Kolmogorov-Smirnov test statistic. The following transformations were performed in order to use parametric tests: Althouse  $\Psi_{pre}$  (natural logarithm, absolute value), Trinity Lake  $\Psi_{pre}$  (logarithm, absolute value), survival (arcsin of proportion).

The General Linear Model (ANOVA) and Bonferroni's Pairwise Multiple Comparisons test were used to check for differences in  $\Psi$  and survival among the fixed and nested factors - breeding blocks, watersheds, and families (SAS Institute v.8). An unpaired two sample t-test (unequal variances) was used to detect  $\Psi$  differences between plantations. Estimates of variance components were obtained using the proc mixed procedure with the REML estimation method.

## **RESULTS**

### **Field Water Potential**

Trees sampled at the Althouse plantation were drier than trees at Trinity Lake. Average  $\Psi_{pre}$  at Althouse (-1.45 MPa) was significantly lower than at Trinity Lake (-0.90

MPa) (t-statistic = -7.97,  $p < 0.0001$ ). Likewise, the average  $\Psi_{\text{mid}}$  at Althouse (-2.13 MPa) was significantly lower than at Trinity Lake (-1.92 MPa) (t-statistic = -3.51,  $p = 0.0006$ ).

No significant differences among breeding blocks, watersheds, and families occurred for  $\Psi_{\text{pre}}$  at Althouse or Trinity Lake (Table 2.3). Blocks were significantly different for  $\Psi_{\text{pre}}$ , indicating that  $\Psi$  may have been changing over time throughout

Table 2.3. Significant  $p$ -values from ANOVA tables for Predawn and Mid-day Water Potential ( $\Psi$ ) data at Althouse and Trinity Lake.

Factor	df	Althouse		Trinity Lake	
		$\Psi_{\text{pre}}$	df	$\Psi_{\text{pre}}$	$\Psi_{\text{mid}}$
Model	52	0.12	24	0.007	0.02
Blocks	-	-	3	<b>0.001</b>	0.14
Breeding Block	3	0.72	3	0.25	<b>0.04</b>
Watershed	7	0.30	8	0.13	0.05
Family	40	0.16	10	0.11	0.16

**Bold** = significant at  $p \leq 0.05$

the night or that soil water content really was different among the blocks. At Althouse,  $\Psi_{\text{mid}}$  could not be transformed to normality. According to the non-parametric Kruskal-Wallis test, no significant differences were found among breeding blocks, watersheds, and families for  $\Psi_{\text{mid}}$  at Althouse. At Trinity Lake,  $\Psi_{\text{mid}}$  for breeding block 6 was higher (less stressed) than those of breeding blocks 1, 3, and 4 (Table 2.4); the southern interior breeding block 6 had a significantly higher (less stressed)  $\Psi_{\text{mid}}$  by 0.24 MPa [95% CI

0.025 to 0.448] compared to the north coastal breeding block 1 (see Appendix A for watershed and family means). A  $p$ -value of 0.05 showed marginal but insignificant differences among watersheds within breeding blocks for  $\Psi_{\text{mid}}$ .

Table 2.4. Average Mid-day Water Potential ( $\Psi_{\text{mid}}$ ) at Trinity Lake by Breeding Block, August 2000.

Breeding Block	Avg. $\Psi_{\text{mid}}$ (MPa)	(n)	S.E.	MIN (MPa)	MAX (MPa)
1	-1.99	41	0.047	-2.9	-1.5
3	-1.94	8	0.065	-2.2	-1.6
4	-1.93	32	0.046	-2.6	-1.4
6	-1.75	15	0.063	-2.2	-1.2

### 3-Year Survival at Trinity Lake

Sets, breeding blocks, and watersheds at Trinity Lake were highly significantly different (ANOVA,  $p < 0.0001$ ) for 3-year survival. Breeding blocks account for ~ 27% of the variation in the data, while watersheds, families, and residual account for 11, 12, and 50%, respectively. Each set contains mostly different families, so each set constitute a separate experiment (or replication of the study). The interaction between set and breeding block indicates that the selection of families affects the comparative outcome among breeding blocks. Survival in all sets was significantly greater in the southern interior breeding blocks 4 and 6 compared to the north coastal breeding block 1. In sets 2 and 3, survival of breeding block 3 was significantly greater than that in breeding block 1



but less than that in breeding block 6 (Table 2.5, Figure 2.1). Figure 2.2 demonstrates the positive relationship between survival and  $\Psi_{mid}$ .

Table 2.4. Average Survival (%) at Trinity Lake by Breeding block and Set.

Set	BB 1	(n)	BB 3	(n)	BB 4	(n)	BB 6	(n)
1	77 ± 13	25	85 ± 7	16	88 ± 13	38	89 ± 4	19
2	67 ± 15	27	78 ± 11	20	82 ± 8	34	89 ± 5	17
3	56 ± 21	30	69 ± 13	29	78 ± 12	23	90 ± 9	16
Mean	66 ± 2	82	77 ± 1.6	65	83 ± 1.2	95	89 ± 0.9	52

± represent 1 Standard Error

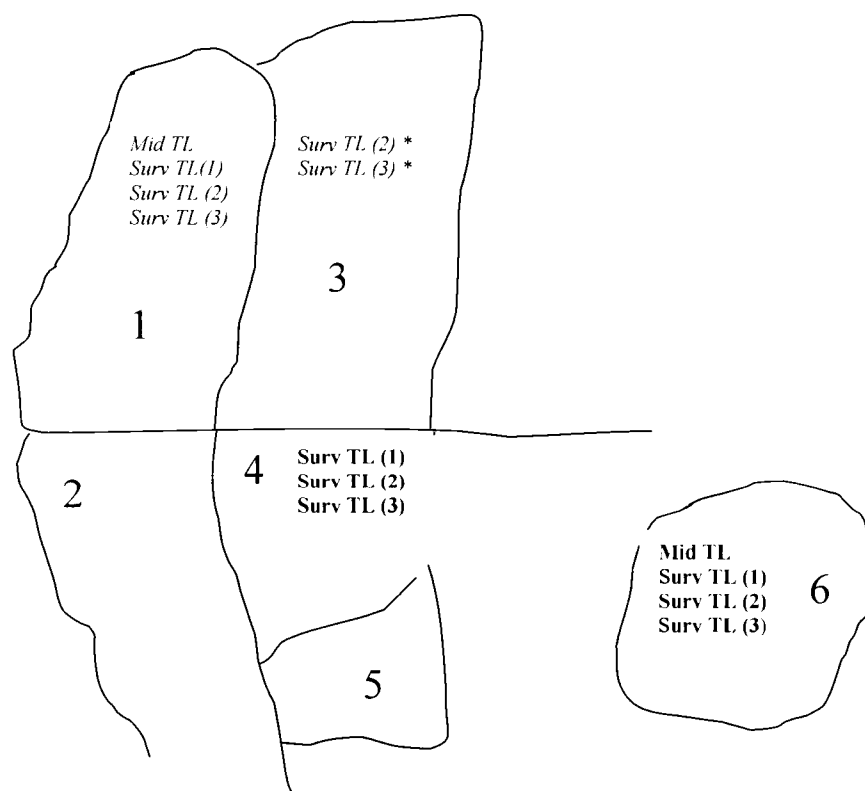


Figure 2.1. Significant Differences Among Breeding Blocks of Port-Orford-cedar for 2000 Summer Water Potential Data and 1998 Survival at Trinity Lake (TL).

\* these factors are < BB 6 but > BB1

MID = Mid-day  $\Psi$

SURV= % survival

**boldface** have greater means than *italicized*

TL = Trinity Lake outplanting

(1) = set number 1, etc.

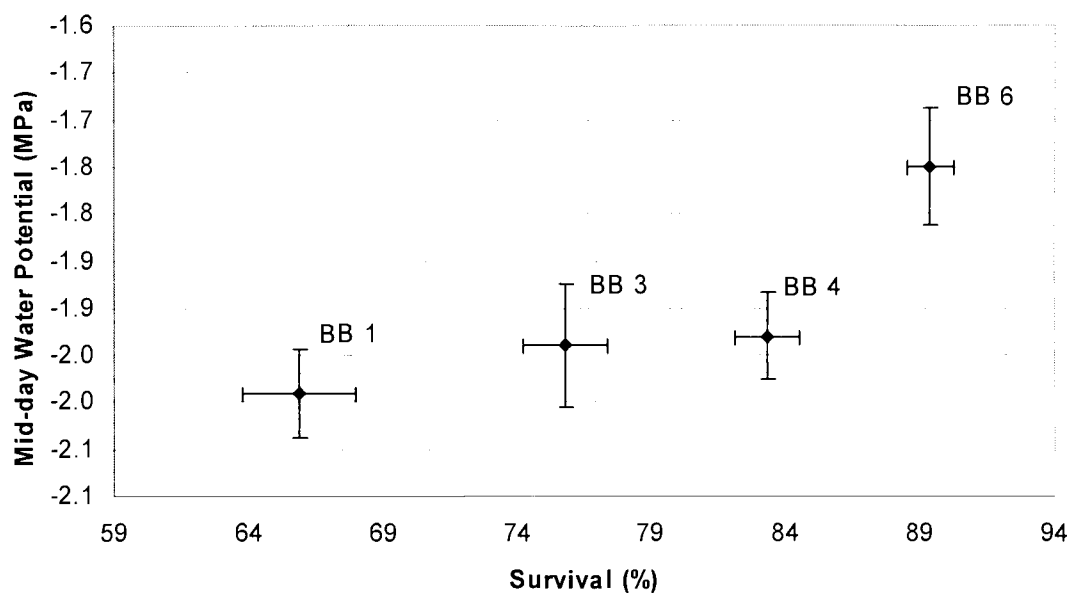


Figure 2.2. 1998 Survival Data at Trinity Lake vs. 2000 Mid-day Water Potential by Breeding Block (BB).  
Error bars = +/- 1 Standard Error

## DISCUSSION

Overall, average  $\Psi_{pre}$  at Trinity Lake during the dry season was not particularly low, compared to field measurements from natural seedlings of Port-Orford-cedar. The  $\Psi_{pre}$  of trees at Althouse, on the other hand, was lower than most reported field values and was similar to values for natural Port-Orford-cedar saplings during mid-August in mixed pine communities (Zobel and Hawk 1980).

Greater overall mortality at the Althouse site (50%) versus the Trinity Lake site (~20%) suggested that it is a less favorable environment. Significantly lower water

potential ( $\Psi$ ) indicated that the trees at Althouse are drier during mid-day than the trees at Trinity Lake. Likewise, on average the trees at Althouse had lower predawn water potentials than the trees at Trinity Lake, indicating lower soil water potential at Althouse. The reason for drier conditions and higher mortality at Althouse compared to Trinity Lake is unclear given that rainfall was higher at Althouse compared to Trinity Lake. Water potentials, however, are low enough to expect that mortality from drought might have occurred when the seedlings were first planted. Harsher site conditions at Althouse are supported by an earlier attempt and failure as a plantation site for Douglas-fir (Rod Stevens, Roseburg, OR, BLM, personal communication). Certain environmental factors at Trinity Lake may lessen transpiration in the high-elevation environment and contribute to higher  $\Psi$  and greater survival of Port-Orford-cedar. For example, cool air drainage or persistent fog may facilitate establishment of Port-Orford-cedar in drier areas such as Trinity Lake (Don Zobel, Oregon State University, personal communication).

Family representation of watersheds was limited at Althouse due to the extreme mortality; therefore, only the Trinity Lake site will be discussed in detail. The genotypes sampled at Trinity Lake showed slightly significant differences among watersheds and breeding blocks for their ability to control mid-day  $\Psi$ . The inland, high elevation breeding block 6 had significantly greater control over  $\Psi_{\text{mid}}$  compared to the north coastal breeding block 1. This result is consistent with other studies that have found significant differences between these two areas (Kitzmilller and Sniezko 2000, Zobel et al. 2002), which represent the two extremes of environment for Port-Orford-cedar. Higher elevation areas may provide a refuge for Port-Orford-cedar from drier, lower elevation regions in the southeastern portion of its range.

Similar to the high elevation breeding block 6, survival in breeding block 3 was significantly greater than breeding block 1. The seed sources tested in breeding block 3, the northernmost interior breeding block, have a lower average elevation (495 m) than those in breeding block 6 (1477 m). Seedling physiology may be similar between these two zones because increases in latitude may compensate for decreases in elevation (Morgenstern 1996). Millar and Marshall (1991) found that interior zones in California had lower genetic diversity than coastal sources. The comparison between interior and coastal breeding blocks in northern Oregon may differ from that in California, however, because populations in breeding block 3 are less isolated and may have greater gene flow from the coastal regions than the disjunct, southern interior populations. Coastal sources also may have less desiccation tolerance than inland genotypes (Zobel et al. 2001).

Overall, northern, coastal genotypes appear to have less control over mid-day  $\Psi$  and experience greater mortality at Trinity Lake, compared to southern genotypes that occur at higher elevations. Lower mid-day water potentials in lower elevation families in breeding block 1 support the hypothesis that they may not control  $\Psi$  as well as higher elevation families in breeding block 6.

Consideration should be given to the short-term nature of this study and to its use of 5-year-old seedlings for  $\Psi$  data and 3-year outplanting survival data. Although most seedling mortality is expected in the first year after planting, atypical droughts over longer time intervals could confound or alter these conclusions.

**CHAPTER 3 – SEASONAL ROOT GROWTH POTENTIAL AND  
CHLOROPHYLL FLUORESCENCE FOLLOWING DROUGHT IN PORT-  
ORFORD-CEDAR (*CHAMAECYPARIS LAWSONIANA*)**

**By Jodie M. Sharpe, and Donald B. Zobel**

**ABSTRACT**

Root growth potential (RGP) of 1-0 greenhouse grown Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl., Cupressaceae) seedlings was measured during two seasons. Winter RGP assessment, under non-stress conditions at the time when seedlings are typically outplanted, examined 25 families representing the natural range of Port-Orford-cedar. Low-elevation, coastal families had greater root growth (RGP) than inland, high elevation sources. Greater variation in the data was accounted for by families than by breeding blocks, indicating little regional specialization in RGP across the species' range. Following an experimental drought during late summer, RGP was measured on 9 families that represent the environmental extremes of the range. Average predawn water potential ( $\Psi_{pre}$ ) of seedlings following the drought was -1.46 MPa. Both north coastal and southern interior families showed decreased root growth following the drought in summer, compared to the winter, non-stress conditions. Despite significantly higher  $\Psi_{pre}$  in inland, high elevation families, lower elevation coastal families produced significantly more roots. Change in chlorophyll fluorescence yield measured on foliage before and after the drought treatment increased with greater water stress; however, change in yield was not a sensitive predictor of  $\Psi_{pre}$  ( $R^2 = 0.06$ ) at the

levels used in this study. Lower levels of  $\Psi$  may be necessary to produce sufficient stress to severely damage Port-Orford-cedar foliage.

## INTRODUCTION

Ecological races may occur within a tree species due to adaptation to local environments (Turesson 1922, Bongarten and Teskey 1987, Kruckeberg 1995, Morgenstern 1996, Tognetti et al. 1997, Haas and Kuser 1999, Rowland 2001, Sorenson et al. 2001). Breeding blocks are used by managers to differentiate genetically dissimilar populations and are delineated by population responses to a common environment (Campbell and Sugano 1993). Managing a species with ecological races requires knowledge of the pattern of variation among populations. Differences in drought and frost tolerance, for example, will determine how far and to what extent genotypes can be moved among breeding blocks (Grossnickle et al. 1997, Balduman et al. 1999).

Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl., Cupressaceae) is a conifer species in the Pacific Northwest noted for its wide ecological amplitude within a small geographic range (Zobel et al. 1985, Jimerson 1994). Disjunct stands occur at high elevations in the southeastern corner of its range, indicating possible refugia for a species that has become coastally restricted since the Tertiary period (Edwards 1983). Over its small range, restricted within 2° latitude and longitude, populations of Port-Orford-cedar are threatened by an exotic root pathogen, *Phytophthora lateralis* Tucker and Milbrath. Present in the Pacific Northwest since the 1920's, this fungal-like oomycete thrives in the

wet areas where this tree grows. The pathogen spreads via flowing water and mud moved by vehicles and animals, leaving dead Port-Orford-cedar along many creeks and roadsides (Hansen et al. 2000). Few trees escape this disease, due to physiological factors that restrict this species to sites with continuous summer moisture (Zobel 1990, Zobel et al. 2002).

Federal and state agencies joined efforts due to concern over the effects of this disease and the ecological damage that may occur if local populations of Port-Orford-cedar are reduced or eradicated. Since 1997, potentially resistant trees from across the range have been selected by the USDI Bureau of Land Management and the USDA Forest Service and screened for resistance by Oregon State University (Bower et al. 2000). These efforts have produced ~1100 trees to be used in a breeding program to increase disease resistance. Of these clones, < 1% display high resistance to the pathogen (Hansen et al. 2000, Sniezko and Hansen 2000, Sniezko et al. 2000). Two tests, a stem dip and a root dip test, give opposing results regarding the geographic origin of more resistant trees. A few trees, however, do well on both tests and are considered highly resistant (E.M. Hansen, Oregon State University, personal communication). The U.S. Forest Service has established an operational containerized seed orchard to produce resistant Port-Orford-cedar seed; those with the highest level of resistance, however, are from the coastal, breeding block 1 (USDA Forest Service 2002). In contrast, populations of Port-Orford-cedar range from sea-level to 1950 m (6400 ft), and occur in some dry interior climates.

Its wide ecological amplitude, and cultivar differences in color, size, and foliar morphology, indicate genetic diversity within Port-Orford-cedar. Given its small range,

Port-Orford-cedar appears to have moderately high levels of allozyme variability among stands. Millar and Marshall (1991) found an expected heterozygosity of 15% among nine populations of *Ch. lawsoniana* in California, compared to values ranging from 0 in western redcedar to 33% in widespread Douglas-fir.

Genetic adaptation to field conditions has been studied in common garden plantings of Port-Orford-cedar (Table 2.1). Two hundred ninety-eight “families” (groups of seedlings that originate from seed from the same parent tree), collected from 52 stands from 11 watersheds across the range, were evaluated at an inland and a coastal nursery (Kitzmilller and Sniezko 2000). Families of Port-Orford-cedar differed significantly in height; southern, high elevation families grew less than those from northern, low elevation seed sources. In addition, low elevation, coastal families had a higher proportion of growth in late season than high elevation, inland families (Zobel et al. 2002). Lower elevation populations of Port-Orford-cedar may be genetically more variable and differ more across soil types than inland and higher elevation populations (Millar et al. 1991, Millar et al. 1992).

Despite the root disease, very little work has focused on the root biology of Port-Orford-cedar. In this study, root growth potential (RGP) was evaluated at two critical times of the year, to indicate this species’ ability to recover from drought. Re-initiation of root growth is important for subsequent water uptake following a drought period. The objective was to study the pattern of RGP among genotypes of Port-Orford-cedar and to correlate it to previous data on field water potential and survival (Chapter 2). RGP as a measure of drought resistance will ultimately need to be corroborated by field measurements of seedling survival. Three-year survival data exist from the plantation



sites where water potential was collected (Jay Kitzmiller, USDA Forest Service, Chico CA, unpublished data).

A mid-winter RGP assessment was used to determine what differences exist among genotypes under non-stress conditions when seedlings are typically outplanted. A late summer assessment of RGP following an imposed drought simulated the potential for root growth following a dry season. If RGP is indicative of drought resistance, then it will provide a relatively quick and easy test for determining if resistant stock from low-elevation, coastal sources can be moved to drier, inland areas.

Measurements of RGP have implications regarding general morphology of root systems as well as seedling survival and water uptake. Root growth potential, commonly defined as the number of roots (>1 cm) initiated in a given time period under favorable conditions, has been widely used to evaluate tree seedling quality at the time of planting (Stone 1955, Burdett 1979, Feret and Kreh 1985, McCreary and Duryea 1985, Palmer and Holen 1986, Binder et al. 1988). Rapid new root growth is important for establishment and drought resistance of newly planted seedlings (Grossnickle & Reid 1984, Nambiar 1984, Sands 1984, Girard et al. 1997). Root growth re-establishes root/soil contact and increases the area for water absorption, especially at the root tips (Satoo 1956, Lauenroth et al. 1987, Sponchiado et al. 1989, Arnott et al. 1993, Kavanagh & Zaerr 1997, Tinus et al. 2000).

RGP is correlated with stress resistance and has been used to detect the degree of drought stress in conifers, as well as cultivar differences in drought resistance of tall fescue (Burdett 1979, Ritchie 1985, Ritchie and Tanaka 1990, Tinus 1996, Huang and Fry 1998). Periods of high RGP correlate with the period in which species are most

tolerant to desiccation (Hermann 1967, Ritchie and Dunlap 1980, Larson 1984, Ritchie and Tanaka 1990). In fact, the correlation between growth chamber measurements of root growth and actual field survival may be stronger for plants whose RGP is measured after they are stressed rather than for non-stressed plants (McCreary and Duryea 1985). The July/August RGP test, following an experimental drought, mimics the time of year when Port-Orford-cedar would be drought stressed in the field.

Most studies indicate that new root growth occurs at the expense of recently synthesized photosynthate, unless photosynthesis is inhibited for a substantial time (Ritchie and Dunlap 1980, Van den Driessche 1987). Since there was no stress imposed on the Port-Orford-cedar seedlings in our February/March RGP test, we hypothesize that low elevation genotypes are likely to have greater RGP than high elevation genotypes, because they probably have more photosynthesis. Mild stress, as imposed in the summer RGP test, may initially stimulate root growth in coastal genotypes (Huang and Fry 1998, Villar-Salvador et al. 1999); as water potential declines, however, root growth may become lower as a consequence of increased stress (Girard et al. 1997, Tinus et al. 2000). Inland genotypes may lose less water or have a higher root/shoot ratio and, thus, they may be less affected by drought than coastal genotypes (Sharpe unpublished data). Coastal genotypes, therefore, may be expected to display little to no root growth under water stress compared to interior genotypes.

The shoots of high elevation populations of Port-Orford-cedar grow less late in the growing season than lower elevation, coastal populations (Zobel et al. 2002). Root growth, therefore, may be innately higher in the high elevation genotypes during late summer as shoot and root growth rarely compete for photosynthate (Oleksyn et al. 2000).

Low elevation genotypes may be continuing their shoot growth, thus limiting resources available for root growth.

During the summer drought test, measurements of chlorophyll fluorescence yield were used as a second assessment of stress and seedling vigor (Lichtenthaler and Rinderle 1988, Mohammed et al. 1995, Eastman and Camm 1995). Havaux and Lannoye (1985) found that the slow transient kinetics of chlorophyll fluorescence were strongly reduced in drought-sensitive cultivars of wheat. Similarly, a drought-sensitive species of *Populus* showed depressed electron transport rates following drought (calculated from measurements of chlorophyll fluorescence), compared to a more drought tolerant species (Li and Kakubari 2001). Some seedlings may display no root growth due to a lethal threshold of water stress (Hawkins and Binder 1990); therefore, fluorescence yield may be useful in quantifying stress levels experienced by the shoot, rather than by the root, in these seedlings.

Differences in leaf chlorophyll concentrations among plant genotypes could result in innate differences in fluorescence yield (Lichtenthaler et al. 1986). Observing the change, rather than absolute values, in chlorophyll fluorescence yield from non-stress to stressed conditions should alleviate any confounding effect of differences in chlorophyll content among genotypes.

## **MATERIALS AND METHODS**

### **Establishment of Plant Material**

All seed for root growth potential (RGP) testing was soaked for 24-hours in 1% H<sub>2</sub>O<sub>2</sub>. After draining, the seed was soaked in water for an additional 24-hours and then stratified for 21 days at 1.7 °C. Seeds were sown into supercells (Ray Leach Single Cell System, 164 ml) containing media consisting of peat:vermiculite:composted fir bark:perlite:pumice (40:30:10:10:10) on March 14, 2000, at the USDA Forest Service Dorena Tree Improvement Center, Cottage Grove, OR. Fertilization treatments were once per week and consisted of a pre-sow application of controlled release fertilizer (18-6-8) into the plugs (60 g/rack). During the late stages of germination, a conifer starter fertilizer (7-40-17) was applied at 75 ppm. Then, a nitrate fertilizer containing Ca and Mg was alternated with medium to high nitrate balanced fertilizer at 75 ppm for 6 to 8 weeks following completion of germination. During the growing season, high urea fertilizer was alternated with high nitrate fertilizer (both balanced) at 100 ppm. At the end of the growing season, a conifer finisher (4-25-35) was applied at 75 ppm to harden off the trees by reducing shoot growth and stimulating root growth (Landis et al. 1989). Overhead sprinklers were used to irrigate the plants for 30 minutes in the greenhouse, 5 times per week.

### **Measurement of Root Growth Potential**

Two root growth tanks of dimensions 118 cm x 62 cm x 100 cm deep were utilized and kept within a climate-controlled, well-insulated building at the Dorena Tree

Improvement Center. Mistlers in the bottom of the tanks sprayed tap water onto the seedling roots for ~ 14 seconds every 5 minutes. An exterior water heater and piping system in the bottom of the tanks maintained tank air temperature at 20-21 °C.

Two Vita-lite full-spectrum 40 Watt fluorescent lights (122 cm length) were maintained at 47 cm above each tank. Plants were exposed to a light regime of 12:12 hours (light:dark) in the winter and 16:8 hours (light:dark) in the summer RGP test. Potting mix was removed from the plant roots and rinsed away with warm water before placing the seedlings into the tanks. Wooden planks 3.8 cm thick (standard 2 x 2) covered the tops of the tanks and seedlings were placed between the plank edges, which were lined with plastic foam. Within each RGP test, two tanks were used, each containing 6 rows (2 edge rows and 4 middle rows). Seedlings were completely and randomly assigned to tanks and to middle and edge rows.

The total number of new root tips (Troots) was assessed and classified by a subjective root length category. "B" class roots were ~0.5-2 cm long, "C" class roots were ~2-4 cm long, and "D" class roots were >4 cm long. Greater overall root growth in the non-stressed winter run made counting of "A" (<0.5 cm) roots difficult, so they were measured only in the summer RGP test. Calculations of root proportions in each size category were made. "Bprop" is the proportion of "B" class roots, "cprop" is the proportion of "C" class roots, and "dprop" is the proportion of "D" class roots.

Total active root length (TARL) is an estimate of new root growth, characterized by white, unuberized tissue, and is usually highly correlated to Troots (Ritchie 1985, Burr et al. 1987, Rietveld 1986). TARL was estimated by multiplying the number of roots in each category by the median length of each size category. Five centimeters was

used as the average length for “D” roots. Root diameter, although not measured, was observed to be greater with increasing length and from B to D root categories. The presence or absence of “surface” and “sinker” root systems was also noted for each seedling. The majority of new roots in the “surface” root system originated in the upper one-third of the root system and were longer and of larger diameter than a normal root system. Large diameter roots that originated and extended downward beyond the main root mass characterized “sinker” root systems.

Most RGP studies have compared different tree species using from 5 to 24 replicates (Stone et al. 1962; Burdett 1979, Larson 1984; Johnson-Flanagan and Owens 1985; Ritchie 1985, Kaushal and Aussenac 1989, Ritchie and Tanaka 1990, Arnold and Young 1991, Graham 1995). One study compared six families of loblolly pine using 60 replicates, the standard required by seedling testing laboratories; however, 20 replicates would have been sufficient (Rose 1992, Robin Rose, Oregon State Univ., personal communication 1999). Sixteen replicates per family of Port-Orford-cedar were used in this test.

### **Winter RGP Test**

For the winter RGP assessment, 25 families of Port-Orford-cedar 1-0 seedlings representing 13 watersheds from across its range were evaluated (Table 3.1). Two 3-week testing periods were used. Average elevation of breeding blocks represented at the Trinity Lake outplanting sites and of the families represented in the

winter RGP increases as one moves south and inland across the range of Port-Orford-cedar (Table 3.2).

The first winter RGP test was initiated February 5, 2001. Approximately one-third of the seedlings were loaded into the tanks on that day, with the remainder loaded on Feb. 7 and 8. The second RGP test was initiated March 1- 4, 2001. Height was measured as the seedling was placed into the RGP tank and assessment of root growth was made exactly 3 weeks later. Almost no root pruning (excision of active root tips) was necessary because root growth was not occurring when the experiment began. Air temperatures and relative humidity within the chamber where the tanks were kept ranged from 3.3-16.7° C and 30-100% over both runs, respectively, with air temperature dropping down to 0° C for 3 hours during the first RGP run.

Following the testing periods, plant material was dried in an oven at 65° C and then destructive sampling was taken for seedling root and shoot masses.

**Statistical Analysis (Winter RGP)** - Normality of data was checked using the Kolmogorov-Smirnov test statistic. The following transformations were performed in order to use parametric tests: Troot, TARL (square root), cprop, dprop (logit), root/shoot ratio ( $\text{Log}_{10}$ ).

The General Linear Model and Bonferroni's Pairwise Multiple Comparisons test were used to check for breeding block, watershed, and family differences (SAS v.8), with all factors being fixed and breeding block, watershed, and family as nested variables.

Estimates of variance components were obtained using the proc mixed procedure with the REML estimation method.

Table 3.1 Replicates for Winter and Summer RGP Tests, by Breeding block, Watershed, and Family Code.

Breeding Block	Watershed	Family	Winter (n)	Summer (n)
1	Umpqua	CU	16	-
1	Umpqua	CV	16	-
1	Coos	IF	16	15
1	Coos	IG	16	-
1	Elk	LF	16	15
1	Elk	LP	16	15
1	Dunes	MF	16	15
1	Dunes	MH	16	16
3	Cow Creek	OH	16	-
3	Cow Creek	ON	16	-
3	Coquille	PB	16	-
3	Coquille	PG	16	-
4	Klamath	BP	16	-
4	Klamath	BQ	16	-
4	Klamath	BP	16	16
4	Illinois	FU	16	-
4	Applegate	EU	16	-
4	Applegate	EX	16	-
4	Smith River	GS	16	-
4	Smith River	GW	8	-
4	Smith River	HJ	8	-
6	Sacramento	AI	16	15
6	Sacramento	S	16	16
6	Trinity	BH	16	-
6	Trinity	AZ	24	16



Table 3.2. Average Elevation of Families in Winter Root Growth Potential Assessment, by Breeding Block.

<i>Breeding block</i>	<i>(n)</i>	<i>Average Elevation (m)</i>
1	9	276
3	4	476
4	7	1237
6	5	1481

### Summer RGP Test

Because of logistics required by droughting the trees prior to the summer RGP test, it was decided to include all test families within one RGP testing period. In order to do this, nine families, representing the two extreme breeding blocks of the range of Port-Orford-cedar, were evaluated (Table 3.1). Five months prior to the test, all 1-0 seedlings were transplanted from super cells into 10 cm square by 36 cm deep, 2.83 L pots (Tall One Treepot, Stuewe & Sons, Corvallis, OR) in March 2001. A soil mix of grower grade peat moss, coarse vermiculite, unscreened pumice, aged fine fir bark, and coarse perlite (40, 30, 10, 10, 10 %) was used. All pots were placed according to their random assignment into one of three pallet boxes for holding purposes. Seedlings were kept outside and irrigated by overhead sprinklers for 1.5 hours, three times per week until the start of droughting, at which time they were brought into the greenhouse. Following the non-stress measurement of fluorescence (see below), seedlings were watered to field capacity and then droughted withholding water for ~ 3 weeks. Temperatures in the greenhouse ranged 11-47 °C during the droughting period. Day-length was natural.

**Chlorophyll Fluorescence** - Chlorophyll fluorescence was measured before the drought treatment on June 12, 2001, using an OS5-FL Modulated Chlorophyll Fluorometer (Opti-Sciences, Tyngsboro, MA). The fluorescence signal was detected using a 660 nm short pass filter. The intensity of this modulation source was 65. A 35 Watt halogen lamp with 690 nm short pass filter provided a high light source to saturate the plant's photosystems. Saturation intensity was 110. Actinic intensity from a 685 nm solid state source was 125. Detector amplitude was 75.

Fluorescence yield was measured between 1000 and 1400 hours PDT to mitigate the effects of daily fluctuations in photosynthesis and their effects on fluorescence (Mohammed et al. 1995). Measurements were performed in the greenhouse under 35% shade cloth and only on clear days, to mitigate the effect of changing Photosynthetically Active Radiation (PAR) levels. The flattened sprays of Port-Orford-cedar leaves were clamped under an open body PAR cuvette and the tops of the foliage were illuminated. Use of the cuvette allowed similar leaf areas to be analyzed. For each seedling, fluorescence readings were taken at three positions: top third, middle third, and lower third of the seedling. In order to evaluate seasonal or innate changes in fluorescence, a set of well-watered control plants was also kept in the greenhouse beside the experimental, droughted plants.

Chlorophyll fluorescence was again measured following the droughting period on both control and experimental plants, July 9, 2001. Predawn water potentials ( $\Psi_{pre}$ ) were measured using a pressure chamber (Model 600, PMS Instrument Co., Corvallis, OR) on experimental plants, 0300 to 0500 hours, July 13, 14, and 15, 2001. After predawn water potential was measured, seedling roots were washed free of soil with warm water and

placed into the RGP tanks. On July 18, the experiment was terminated without data collection because the trees died, due to a failure in the water delivery system.

On June 2, 2001, non-stress level chlorophyll fluorescence was measured in the greenhouse on control and experimental seedlings for a second set of plants. Prior to this measurement, the seedlings had remained outdoors. Chlorophyll fluorescence yield measurements were lower and the foliage yellower than seedlings in the first RGP test. The second set of seedlings likely experienced more stress prior to the experiment than the seedlings in the first test, as temperatures increased into the growing season. On July 7, 2001, seedlings were moved into the greenhouse and watered to field capacity before the droughting began.

Beginning July 24, 2001, average  $\Psi_{pre}$  of seedlings was  $-1.46$  MPa.  $\Psi_{pre}$  was measured for pallet 4 on July 25, 2001, and the seedlings subsequently loaded into the RGP tanks. The remaining two pallets were measured for water potential and loaded into the tanks July 26 and 28. Average seedling height was 66.6 cm; seedling tops were tied with string to keep them upright in the RGP tanks. Air temperatures around the tanks varied from 17.8-26.7 °C during the second summer RGP run. Relative humidity around the shoots varied from 40-95%. Seedlings remained in the tanks 3 weeks and were then assessed for root growth on August 15, 16, and 18, using the same criteria as in the winter RGP assessment.

**Statistical Analysis (Summer RGP)** - Normality of data was checked using the Kolmogorov-Smirnov test statistic. The following transformations were performed in order to use parametric tests:  $T_{root}$  ( $\text{Log}_{10}$ ),  $\Psi_{pre}$  (square root, absolute value).

The General Linear Model (ANOVA) and Bonferroni's Pairwise Multiple Comparisons test were used to check for differences in  $\Psi$  and survival among the fixed and nested factors - breeding blocks, watersheds, and families (SAS Institute v.8).

## RESULTS

### Winter RGP

All root variables differed among breeding blocks, watersheds, and families, except that only breeding blocks were significantly different for the proportion of "C" roots (cprop) (Table 3.3). Families accounted for more variation in the root data than either watersheds or breeding blocks, although the unexplained variation is much higher than any of these geographic variables (Table 3.4). The north coastal breeding block 1 had significantly more Total roots (Troots) than the southern interior, breeding block 4 (Table 3.5). Similarly, northern breeding blocks 1 and 3 had significantly greater Total Active Root Length (TARL) compared to breeding block 4 (see Appendix B for watershed and family means). On a per unit shoot height basis, however, breeding block 6 has significantly more roots than breeding blocks 1 and 4. The proportion of "B" roots was significantly greater in breeding block 1 than in zone 3 ( $p=0.01$ ), while the proportion of "C" roots was significantly greater in breeding block 6 compared to breeding block 1 ( $p=0.002$ ).

Forty-two percent of the seedlings tested from the interior breeding blocks 3 and 6 had sinker root systems while only 14-20% of the seedlings in breeding blocks 1 and 4 had sinker root systems.

Table 3.3. Significant *p*-values from Analysis of Variance for Total Roots, Total Active Root Length (TARL), Root/Shoot Ratio, and Proportion of “b”, “c”, and “d” Roots, Winter Root Growth Potential Test.

<b>Factor</b>	<b>df</b>	<b>√Troot</b>	<b>√TARL</b>	<b>Rt/Sht</b>	<b>bprop</b>	<b>cprop</b>	<b>dprop</b>
Run	1	0.47	0.0001	<0.0001	<0.0001	0.005	<0.0001
Tank	2	<0.0001	<0.0001	0.01	0.03	0.02	<0.0001
Day	4	0.003	0.004	0.32	0.03	0.67	0.02
Tank(Row)	19	0.05	0.07	0.44	0.005	0.14	0.04
Breeding Blk	4	0.004	0.0003	0.01	0.006	0.002	0.005
Watershed	9	0.0004	<0.0001	<0.0001	0.0002	0.16	0.01
Family	11	<0.0001	<0.0001	<0.0001	<0.0001	0.06	<0.0001
Model	50	<0.0001	<0.0001	<0.0001	<0.0001	0.0005	<0.0001
<b>R<sup>2</sup></b>	-	<b>0.40</b>	<b>0.40</b>	<b>0.49</b>	<b>0.33</b>	<b>0.23</b>	<b>0.46</b>

Table 3.4. Percentage of Data Variation Accounted for by Breeding Blocks, Watersheds, Families and Residual for Total Roots, Total Active Root Length, and Root/Shoot Ratio in Winter Root Growth Potential Test.

<b>% of Variation Accounted for by:</b>	<b>√Troot</b>	<b>√TARL</b>	<b>Rt/Sht</b>
Breeding Block	2	3	0
Watershed	0	0	1
Family	14	17	29
Residual	84	80	70

Table 3.5. Mean Root Variables by Breeding Block (BB) in Winter Root Growth Potential Test.

BB	(n)	Troots	TARL	Rt/Sht †	bprop	cprop	dprop
1	143	65 ± 2.2	139 ± 5	0.61 ± 0.02	0.62 ± 0.01	0.25 ± 0.01	0.13 ± 0.01
2	8	55 ± 6.6	126 ± 26	0.65 ± 0.02	0.58 ± 0.07	0.30 ± 0.04	0.12 ± 0.05
3	63	64 ± 3.3	153 ± 8	0.62 ± 0.03	0.53 ± 0.03	0.28 ± 0.02	0.19 ± 0.02
4	103	55 ± 2.5	117 ± 5	0.62 ± 0.02	0.61 ± 0.02	0.26 ± 0.01	0.13 ± 0.01
6	64	56 ± 2.5	126 ± 7	0.74 ± 0.04	0.59 ± 0.02	0.30 ± 0.01	0.12 ± 0.01

+/- represents standard error

† n-values are 85, 7, 38, 69, and 38 respectively.

Troots and TARL were highly correlated ( $p < 0.0001$ ,  $R^2 = 0.74$ , Figure 3.1).

Although both variables were analyzed, we will discuss primarily Troots.

Plant size (Troots, shoot mass) declined moving farther east and south across the range of Port-Orford-cedar and as elevation increased. Root/shoot ratio was highest in the short seedlings of the southeast, but was not significantly correlated to elevation. Taller plants had larger shoots (Figure 3.2) and roots, but lower root/shoot ratios (Table 3.6).

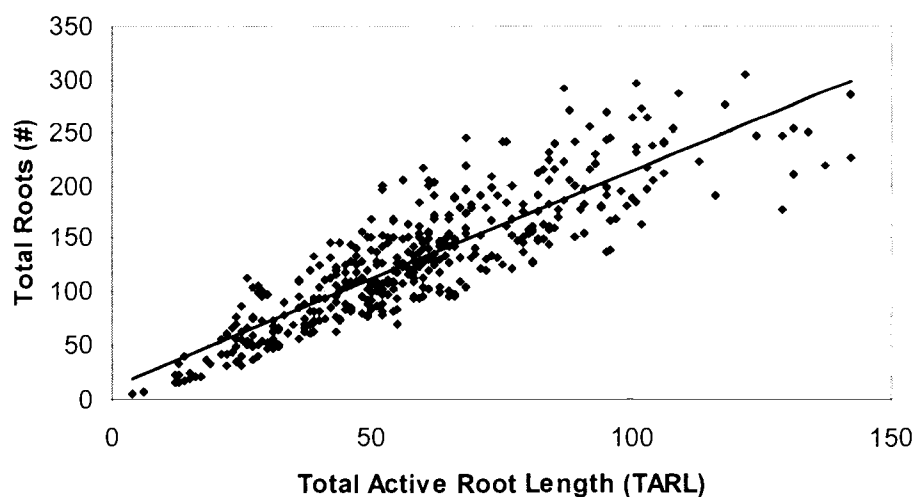


Figure 3.1. Total Roots vs. Total Active Root Length (TARL) for Winter Root Growth Potential.

$$\sqrt{\text{Roots}} = 4.3906 + 0.0240(\text{TARL}) \quad p < 0.0001, R^2 = 0.74$$

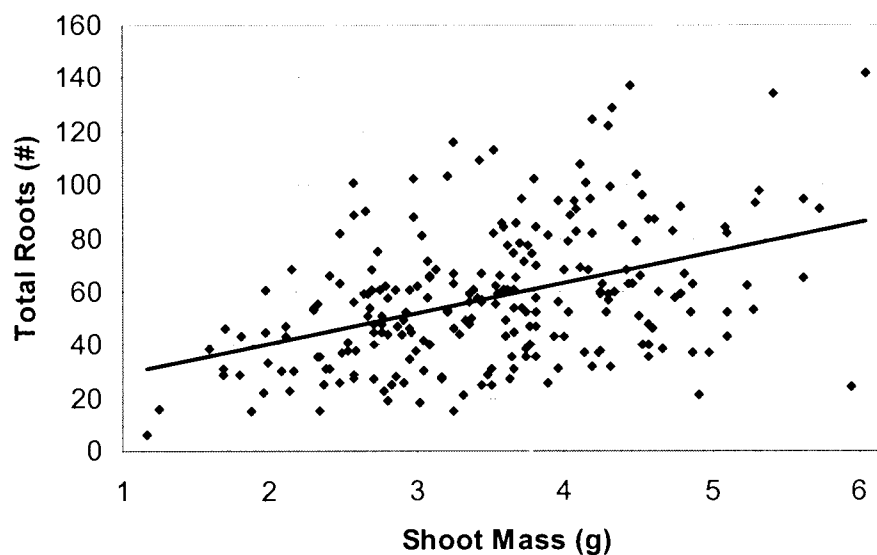


Figure 3.2. Shoot Dry Mass vs. Total Roots for Winter Root Growth Potential.  
 $\sqrt{\text{Roots}} = 4.7639 + 0.759(\text{Shoot Mass in grams}), \quad p < 0.0001, R^2 = 0.18$

No significant relationships were found between bprop or dprop and root/shoot ratio, shoot and root mass, latitude, longitude, elevation, and average summer rainfall. The proportion of “C” roots increased with elevation and declined with summer rainfall and seedling height (Table 3.6); however, these regressions have low  $r^2$  values and significance is mostly due to the isolated, high elevation populations in California.

Table 3.6. Simple Linear Regression Correlations for Total Roots, Proportion of “c” Roots, Root/Shoot Ratio, and Shoot Mass, Winter Root Growth Potential.

Dependent Variable	Independent Variable	<i>p</i> -value	R <sup>2</sup>	Sign of Correlation
Roots	Root Mass (g)	< 0.0001	0.18	+
	Shoot Mass (g)	< 0.0001	0.18	+
	Root/Shoot	< 0.0001	0.13	*
	Height (cm)	< 0.0001	0.09	+
	Longitude	0.002	0.03	+
	Latitude	0.0003	0.03	+
	Elevation	0.0003	0.03	-
Cprop	Elevation	0.006	0.02	+
	Summer Rain †	0.0002	0.05	-
	Height	< 0.0001	0.06	-
Root/Shoot	Height	0.002	0.04	-
	Longitude	0.03	0.02	-
	Latitude	0.004	0.03	-
Shoot Mass	Elevation	0.001	0.05	-
	Latitude	< 0.0001	0.07	+
	Longitude	< 0.0001	0.11	+

\* polynomial fit

† sum of rain in June, July & August as calculated by the Prism model (Daly et al. 1994)

### Summer RGP

**Chlorophyll Fluorescence Yield** – Chlorophyll fluorescence yield (“yield”) did not change significantly in the control plants (paired t-test, t-statistic= -1.45, df=89,  $p=0.15$  [95% CI -0.05 to 0.01]), but did decrease significantly in the experimental plants during the 23-day drought (t-statistic=9.66, df=248,  $p< 0.0001$ , [95% CI 0.05 to 0.08]). Yield decreased over time as the drought progressed and from low to high positions on the seedling (Table 3.7).



Table 3.7. Average Chlorophyll Fluorescence Yield of Droughted Plants, Summer Root Growth Potential.

<i>POSITION</i>	<i>(n)</i>	<i>Avg. Yield (pre-stress)</i>	<i>S.E.</i>	<i>(n)</i>	<i>Avg. Yield (stressed)</i>	<i>S.E.</i>
TOP	201	0.65	0.006	192	0.59	0.007
MID	200	0.72	0.005	191	0.66	0.008
LOW	200	0.77	0.004	191	0.73	0.005

**Predawn Water Potential** – Following the experimental drought, average  $\Psi_{pre}$  of seedlings was  $-1.46 \text{ MPa} \pm 0.81$  (S.D.) (min= -3.4, max= -0.15). Breeding blocks ( $p=0.002$ ) were significantly different for  $\Psi_{pre}$  when tree size (height) was used as a covariate. Southern interior breeding block 6 had a significantly higher (less stressed)  $\Psi_{pre}$  compared to north coastal breeding block 1 (Table 3.8). Breeding block 4 was under represented in the summer RGP. As  $\Psi_{pre}$  declined, Troots increased (Figure 3.3) and change in fluorescence yield increased (Figure 3.4).

Table 3.8. Average Predawn Water ( $\Psi_{pre}$ ) Potential after the Drought Period, by Breeding block, Summer Root Growth Potential.

<b>Breeding block</b>	$\Psi_{pre}$ (MPa)	S.E.	(n)	min	max
1	-1.78	0.08	73	-3.4	-0.35
4	-1.90	0.18	15	-3.0	-0.50
6	-0.76	0.08	47	-2.5	-0.15

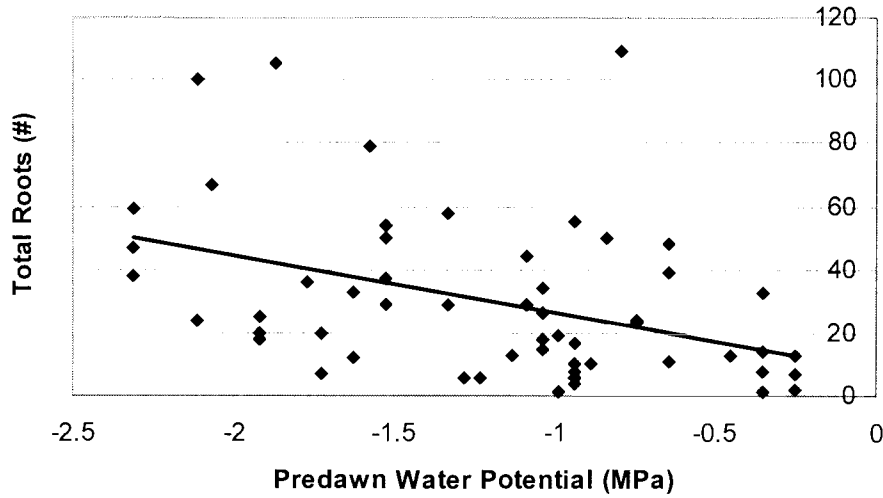


Figure 3.3. Predawn Water Potential ( $\Psi_{pre}$ ) vs. Total Roots, Summer Root Growth Potential.

$$\text{Log}_{10} \text{ Troots} = 1.9979 - 0.8289(\Psi_{pre} \text{ MPa}), \quad p = 0.0003, R^2 = 0.22, n = 55$$

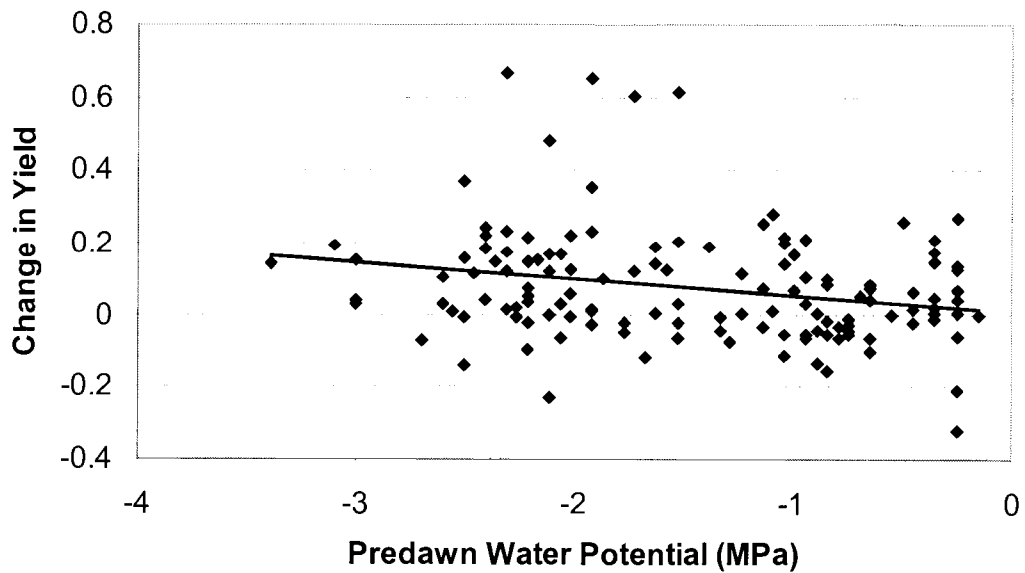


Figure 3.4. Change in Fluorescence Yield vs. Predawn Water Potential ( $\Psi_{pre}$ ), Summer Root Growth Potential.

$$\text{Change in Yield} = -0.0426(\sqrt{|\Psi_{pre} \text{ MPa}|}) + 0.10308$$

$p = 0.005, R^2 = 0.06, n = 131$

**Root Growth Potential** - Total Active Root Length (TARL) and Total roots (Troots) were related by a quadratic regression ( $p < 0.001$ ,  $R^2 = 0.74$ ,  $n = 55$ ,  $\text{Log Troots} = 2.1837 + 0.0315(\text{TARL})^2$ ). Significant differences among breeding blocks ( $p < 0.0001$ ) and watersheds ( $p = 0.01$ ) were found for Troots ( $p = 0.0004$ ,  $R^2 = 0.66$ ). Breeding block 1 had significantly more roots than breeding block 6, following the experimental drought (Table 3.9) (see Appendix B for watershed differences). Likewise, seedling height was

Table 3.9. Average Total Roots by Breeding Block, Summer Root Growth Potential.

<b>Breeding block</b>	<b>Avg. Troots</b>	<b>S.E.</b>	<b>(n)</b>	<b>min</b>	<b>max</b>
1	18.03	3.17	73	0	109
4	12.07	4.61	15	0	55
6	3.68	1.05	47	0	33

positively correlated to Troots ( $p = 0.0003$ ,  $R^2 = 0.23$ ) (Figure 3.5). If Total roots is divided by seedling height, however, breeding blocks 1 and 4 have significantly more roots per unit height than breeding block 6, the opposite result from the winter RGP test.

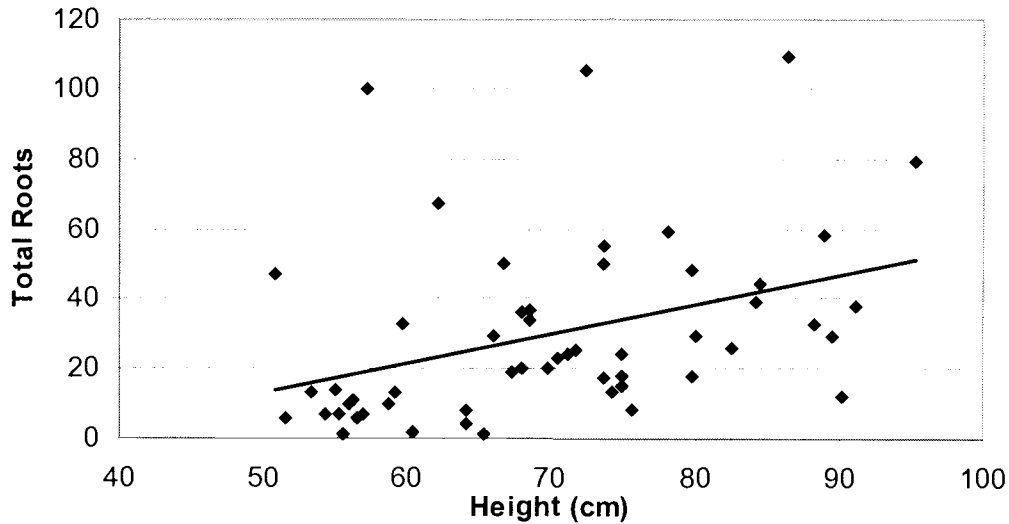


Figure 3.5. Seedling Height vs. Total Roots, Summer Root Growth Potential.  
 $\text{Log}_{10} \text{ Troots} = 0.0179 + 0.0424(\text{height})$ ,  $p=0.0003$ ,  $R^2=0.23$ ,  $n=53$

Some seedlings, both experimental and control, displayed zero root growth and were eliminated from the analyses where the logarithmic transformation was used. The percentage of experimental seedlings with no root growth was greater than 50% and similar across all breeding blocks. Breeding blocks 1, 4, and 6 had 55, 60, and 64% zero root growth, respectively. This result differs from that in the winter root growth potential test, where all seedlings produced root growth.

The proportion of roots in each length category could not be analyzed due to non-normal data. Overall, the average sum of b, c, and d roots was significantly higher by 46.3 [95% CI: 41.4, 51.2] in the winter compared to the summer RGP test (t-statistic= -18.67,  $p < 0.001$ ). If the average sum of b, c, and d roots by family in the summer is subtracted from the sum of these in the winter, there does not appear to be a large difference in the seasonal pattern in root production among families and over elevations

(Table 3.10). The Dunes watershed families, in particular family MH, may have been most affected by the summer drought. Other coastal families, however, like those in the Elk watershed, seem affected similarly to higher elevation, interior families like those in the Sacramento and Trinity watersheds.

Table 3.10. Comparison of Average Total Roots in the Winter and Summer Root Growth Potential Test.

Breeding Block	Watershed	Family	Avg. Winter Roots	Avg. Summer Roots	DIFF	Max Troot (summer)	ELEV (m)
1	COOS	IF	70.6	16.43	54.17	82	30
1	DUNES	MF	51.63	2.71	48.92	31	47
1	DUNES	MH	80.25	4.47	75.78	29	53
1	ELK	LP	60.88	10.2	50.68	50	201
1	ELK	LF	55.88	18.8	37.08	54	207
6	SACRAMENTO	AI	48.31	2.13	46.18	9	1143
4	KLAMATH	BP	62.38	6.07	56.31	30	1311
6	SACRAMENTO	S	56.31	0.38	55.93	6	1478
6	TRINITY	AZ	64.92	1.31	63.61	10	1615

An informal study was conducted in order to determine the lethal  $\Psi$  of Port-Orford-cedar. Approximately 30 seedlings were droughted to  $\Psi_{pre}$  ranging from  $-1.5$  to  $-4.0$  MPa. After droughting for  $\sim 2$  weeks, the foliage was yellow and non-turgid. Upon rewatering, however, all seedlings returned to a  $\Psi_{pre}$  of  $-0.2$  to  $-0.3$  MPa and foliage appeared green and turgid.

## DISCUSSION

### Winter RGP

This study identified a genetic component to root growth; lower elevation, coastal families had greater root growth compared to inland, high elevation sources. Kitzmiller and Sniezko (2000) found that north coastal families of Port-Orford-cedar had greater height than southern interior families. Coastal families of Port-Orford-cedar may have overall greater photosynthate and greater RGP in order to support a larger shoot and subsequent greater transpiration. Conifer genotypes capable of greater photosynthesis, or with surplus stored carbohydrate, are likely to have higher RGP than genotypes with lower photosynthetic rates or less storage (Van den Driessche 1987, Kozlowski 1992).

The two northern breeding blocks in Oregon, 1 and 3, as represented by the families in this study, have significantly higher Total Active Root Length than breeding block 4. Breeding block 3 is similar to the north coastal zone in total root numbers, but similar to the southern interior breeding block 6 in root morphology. Sinker roots, more common in breeding blocks 3 and 6, are long, thick roots that extend downward beyond the main root system. These roots may aid in water uptake by penetrating deeper into soils than fine roots of the main root system.

Southern interior families had a larger proportion of long roots and fewer short, fine roots than families in the north coastal breeding blocks. In addition, it was observed that longer roots were generally larger in diameter. Root morphology and size distribution will likely differ among genotypes of a species (Theodorou & Bowen 1993), especially in Port-Orford-cedar given its wide ecological amplitude (Zobel et al. 1985,

Zobel 1998). Roots with a high specific root length (SRL) (length: dry weight ratio) absorb water and nutrients more efficiently than roots with a lower SRL (Silberbush and Barber 1983, Eissenstat 1992). In the wetter climates of the northern breeding blocks where low-elevation Port-Orford-cedar genotypes occur, higher turnover of small roots may be more adaptive in a competitive environment; large-diameter roots may be more beneficial than fine roots over the long-term in low nutrient, rocky soils, developed on serpentine and peridotite (Ryser and Lambers 1995). Longer and smaller diameter roots were associated with enhanced competitiveness for the uptake of water and nutrients in several weed species (Wright et al. 1999). For two woody and three herbaceous species, hydraulic conductivity increased with decreasing root diameter.

Several trade-offs exist, however, between having fine versus coarse roots. Radial resistance to water flow, for instance, is less in large-diameter roots and construction costs are lower than those of small-diameter roots. Large roots typically persist longer than fine roots and may be more advantageous in exploring coarser soils (Fitter 1996, López et al. 1998). Species with large-diameter roots are thought to be associated with mycorrhizae more often than those with smaller-diameter roots, so this investment may help compensate for loss in absorption capacity (Eissenstat 1992).

In this study, inland seedlings from the southern portion of the range had higher root/shoot ratios than north coastal seedlings. Elevation, however, showed no relationship with root/shoot ratio. Greater root mass compared to shoot mass may be adaptive in the drier interior environment.

Although almost all seedling measurements and seed source location data are significantly correlated to Total Roots, they are poor predictors, with  $R^2$  values only 0.02-

0.18. In general, taller seedlings with greater root and shoot mass had higher total root numbers; however, a low, large-scale genetic component is suggested by the low correlation between Troots and geographical seed source data. A stronger correlation does exist between shoot mass and latitude and longitude, indicating that north coastal families generally have greater shoot mass than southern, interior families. This relationship shows the same pattern as Kitzmiller and Sniezko (2000), that north coastal families are taller than southern, interior families. The relationship found in this study, however, has high variability and may only be significant due to the two extremes of the range of Port-Orford-cedar, the north coastal and the southern interior. Environmental conditions and their effect on the shoot may be stronger determinants of field root growth than genetics. Phenotypic plasticity in roots is common and highly controlled by variable environmental factors like soil temperature (Tryon and Chapin 1983).

In the winter RGP test, more variation in the measured root variables is accounted for by family differences than by breeding blocks, indicating little regional specialization across the range of Port-Orford-cedar. Management decisions that consider winter root growth potential in Port-Orford-cedar should be made based on the family, rather than the breeding block, responses. It should be noted, however, that none of these variables accounted for a high proportion of variation in the root data. Furthermore, winter RGP did not correlate with measurements of field survival. Winter root growth potential, however, may be a good predictor of field survival among different genotypes of Port-Orford-cedar when analyzed on a per unit height basis. In this study, conclusions regarding breeding block 2, the coastal zone in California, are limited due to under representation in this study.



## Summer RGP

Chlorophyll fluorescence yield (“yield”) followed the expected pattern and decreased with droughting, indicating less electron transport as a result of lowered photosynthetic activity. The pattern of increasing yield from top to bottom of the seedling follows the general observation that shade leaves have less chlorophyll and show higher levels of chlorophyll fluorescence than sun leaves (Mohammed et al. 1995); however, the measurement may be confounded by lower PAR levels reaching the bottom leaves due to shading effects.

Although confounded by season, a contrast between the winter and summer RGP tests was done; however, no conclusions can be drawn regarding the relative effects of the experimental drought on different genotypes. In the summer test, seedling root growth was less than in winter but remained proportional to seedling size. Families of Port-Orford-cedar appear similarly affected from the winter to the summer RGP tests; families from both breeding blocks 1 and 6 produced fewer roots after being droughted compared to the winter test. That some control seedlings had zero root growth in the summer test suggests that some factor other than drought treatment decreased root growth.

North coastal families had both significantly more roots and lower  $\Psi_{pre}$  than southern interior families. The prediction that high elevation populations have greater root growth as a consequence of less shoot growth late in the growing season (compared to coastal populations) was not supported. Earlier studies indicated that low elevation, coastal genotypes have less control over mid-day water potential and experience greater

mortality at interior outplanting sites, compared to southern genotypes that occur at higher elevations (Chapter 2).

Root growth potential in the summer may not be a good indicator of stress suffered by field seedlings. First, many seedlings, both droughted and control, produced no roots in the RGP test. Also, although a general reduction in root growth occurred, the pattern in root growth in the summer test was similar to that of the winter RGP test. The drought was not sufficient to alter root growth patterns among families substantially, despite the fact that some families had lower water potentials than other families. These results suggest that either the range in water potential in this study produced more or less the same effect on root growth for all families or that the differences in stress cannot be detected by measuring root growth potential. The number of roots per unit height displayed a pattern contrary to the differences in  $\Psi_{pre}$ ; breeding block 1 had lower  $\Psi_{pre}$  but more roots per unit seedling height than breeding block 6. This pattern in roots per unit height was opposite that in the winter RGP test and may be a consequence of mild stress stimulating root growth in coastal genotypes (Huang and Fry 1998, Villar-Salvador et al. 1999).

The low correlation between chlorophyll fluorescence yield and  $\Psi_{pre}$  indicates that the drought may not have been severe enough to produce major differences among genotypes of Port-Orford-cedar shoots. At mild levels of  $\Psi$ , yield was not a sensitive indicator of water stress in *Ziziphus rotundifolia*, a fruit tree considered tolerant of drought (Corlett 1993). More severe  $\Psi$  may be necessary in order to produce stress in Port-Orford-cedar shoots, as indicated by the informal experiment in which seedlings recovered completely from  $\Psi_{pre}$  as low as

-4 MPa. Significantly lower root growth potential in coastal genotypes as compared to southern interior genotypes may occur at water potentials below those measured here.

## CHAPTER 4 – GENERAL DISCUSSION AND CONCLUSIONS

Water potentials in this study were within the range of those reported for native Port-Orford-cedar. The predawn water potentials ( $\Psi_{pre}$ ) measured on 5-year-old seedlings at the outplanting sites are comparable to those found in natural stands, although those at Althouse are on the low end, similar to Port-Orford-cedar in mixed pine communities (Zobel and Hawk 1980). Although genotypic differences in stress were not indicated by measurements of chlorophyll fluorescence and root growth potential (RGP), the average  $\Psi_{pre}$  on 1-0 seedlings following the experimental drought was the same as that measured on 5-year-old seedlings at Althouse, where 50% mortality had occurred during seedling establishment. The preliminary experiment to estimate lethal  $\Psi$  levels suggested that, overall, Port-Orford-cedar as a species tolerates lower  $\Psi$  than used in this study or typically measured in the field. Given the well-watered, wet conditions where Port-Orford-cedar usually grows and the low survival at Althouse, however, some factor besides seedling water potential may limit the distribution of this species. One explanation for its limitation to wet sites is its late germination in June (Zobel 1990). This explanation does not, however, explain the lower survival at Althouse, where seedlings were planted. Repeated stress in the field during the dry season may lower the vigor of seedlings more susceptible to drought. Differences in frost tolerance may also contribute to lower survival of coastal genotypes planted at high elevations.

In general, families with greater shoot growth had greater root growth but lower  $\Psi_{mid}$  and lower survival at the outplanting sites. Variation patterns among Port-Orford-

cedar families in the winter root growth potential (RGP) data were different from those in field  $\Psi$ , and opposite the survival data. This finding is not consistent with studies that show greater survival in seedlings with greater RGP (Stone 1955; Burdett 1979; Feret and Kreh 1985; McCreary and Duryea 1985; Palmer and Holen 1986; Binder et al. 1988).

Similar to the winter data, summer RGP data from the two extremes of the range, the north coast and the southern interior, differed from patterns of field  $\Psi$  and survival. Despite lower  $\Psi_{\text{pre}}$  and lower outplanting survivals, north coastal families produced significantly more roots than southern interior families following the drought. Induced root growth may be a good indicator of survival at time of planting for seedlings of a specific stock; however, RGP differences among families may not relate to measurements of field stress due to genetic differences among genotypes, such as shoot size.

In my study, root growth appears tightly coupled to shoot growth, with a positive correlation between Total roots and both seedling height and shoot mass. If Total root values in the winter test are divided by seedling height, then breeding block 6 has significantly more roots per unit height than breeding blocks 1 and 4, corresponding to field measurements of  $\Psi$  and survival. Following the summer drought, however, this pattern reversed, possibly a consequence of the drought affecting and stimulating root growth in coastal seedlings more than those from the southern interior (Huang and Fry 1998, Villar-Salvador et al. 1999). The  $\Psi_{\text{pre}}$  of experimentally-droughted seedlings in breeding block 4 was lower than that of breeding block 1, a pattern that was not seen in the field data.

One might expect higher  $\Psi$  and survival from seedlings with more roots per unit foliage. In this study, we used height as an estimate for shoot size. On a per unit height

basis, the RGP data in the winter test correlates with field survival, while the pattern from the summer test does not. Caution should be exercised when interpreting RGP data from among genotypes of a particular species. Unless evaluated on a per unit height basis, RGP differences among genotypes may be misleading due to innate genetic variability. Furthermore, zero root growth from some of the non-droughted, summer controls suggests that there may be inherent problems with testing RGP at this time of year. The low correlation between chlorophyll fluorescence yield and  $\Psi_{pre}$  suggests that, perhaps, chlorophyll fluorescence is also not a sensitive test of drought resistance (Corlett 1993), at least at the  $\Psi$  levels in this study.

No conclusions regarding field levels of  $\Psi$  can be made for breeding block 3 due to no sampling at the outplanting sites. Survival information was measured for breeding block 3; in general, survival across all breeding blocks increases as one moves inland and south across the range of Port-Orford-cedar. Our data suggest that Port-Orford-cedar from breeding block 3 differs from other zones, being similar to the north coastal breeding block 1 in root numbers (possibly indicating greater shoot growth capabilities) but similar to breeding block 6 in interior California in its root system morphology. Sinker root systems were more common in breeding blocks 3 and 6, compared to other breeding blocks, possibly an adaptation to the drier inland environment.

RGP test duration varies among species (Rietveld and Tinus 1990). The standard two week period was too short for RGP testing in Port-Orford-cedar. Because my seedlings began root growth later than expected in the winter test, root growth was insufficient for measurement after 2 weeks, so the testing period was lengthened to 3 weeks. Similarly, my seedlings were slow to put on roots following the drought, so 3

weeks was also necessary in the summer RGP test. Grossnickle et al. (1988), in contrast, found that 7-14 days was a suitable test length for western redcedar.

The most significant differences in Port-Orford-cedar survival and  $\Psi$  occur between the north coastal breeding block 1 and the southern interior breeding block 6, at least as represented by the families in this study. At the Trinity Lake outplanting site, low elevation families from the north coast had lower  $\Psi_{\text{mid}}$  and lower survival than families in the southern interior. These results support the conclusions from pressure-volume curve analysis that found large Port-Orford-cedar seedlings from north coastal sources to be less tolerant of desiccation (Zobel et al. 2001). In general, this study shows that as one moves inland and south across the range of Port-Orford-cedar, outplanting survival at stressful sites increases as seedling size decreases. Characteristics such as waxy formations on leaf surfaces, fewer stomata, and sunken stomata (Grossnickle 1993, Miller et al. 1995) may enable inland genotypes to survive in harsher, drier conditions and may help explain their limited growth compared to coastal sources (Kitzmilller and Sniezko 2000, Zobel et al. 2002).

Resistant stock from low-elevation, coastal breeding block 1 may not survive well if outplanted to higher elevation, drier, inland areas like breeding block 6. Adaptive traits related to the drier inland environment may allow greater control over  $\Psi_{\text{mid}}$  and subsequent greater survival for inland rather than coastal families. Seedlings from breeding block 6 are likely distinct genetically, compared to seedlings from other breeding blocks, due to their geographic isolation and the selection pressures from the high elevation, interior environment. This population may represent an ecotype that is both physically and genetically separated from the main range of Port-Orford-cedar. At

least some of interior genotypes' adaptive advantage appears to be associated with their sinker-root morphology and their greater control of mid-day  $\Psi$ .



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**APPENDICES**

**APPENDIX A –  
WATERSHED AND FAMILY AVERAGES FOR MID-DAY WATER  
POTENTIAL AT TRINITY LAKE OUTPLANTING, AUGUST 2000.**

Table A.1. Watershed and Family Means for  $\Psi_{mid}$  at the Trinity Lake Outplanting Site, August 2000.

<b><u>Watershed</u></b>	<b><u><math>\Psi_{mid}</math> (MPa)</u></b>	<b><u>(n)</u></b>
APPLEGATEe (APP)	-1.98	9
COOS (COOS)	-1.89	8
COQUILLE (COQ)	-1.94	8
DUNES (DUN)	-2.15	8
ELK (ELK)	-1.89	8
ILLINOIS VALLEY (ILV)	-1.92	8
KLAMATH (KLA)	-1.76	8
ROGUE (ROG)	-1.84	7
SACRAMENTO (SAC)	-2.04	8
TRINITY (TRN)	-1.66	6
UMPQUA (UMP)	-2.10	10

<b><u>Family</u></b>	<b><u><math>\Psi_{mid}</math> (MPa)</u></b>	<b><u>(n)</u></b>
AZ	-1.76	3
BH	-1.56	3
BP	-1.73	4
BQ	-1.80	4
CU	-2.18	6
CV	-1.99	4
CY	-1.94	8
DH	-1.82	3
DJ	-1.86	4
ES	-1.76	5
EX	-2.20	4
FO	-1.92	8
GW	-2.08	4
HG	-2.00	4
IF	-1.94	4
IZ	-1.85	4
LN	-1.91	4
LT	-1.87	4
MF	-2.26	4
MH	-2.04	4
S	-1.60	4
U	-1.97	5



**APPENDIX B–  
FAMILY AND WATERSHED COMPARISONS FOR ROOT DATA, WINTER  
AND SUMMER ROOT GROWTH POTENTIAL.**

Table B.1. Significant Family Means Comparison for Winter Total Roots (Troots).

<u>Family</u>		<u>Mean</u>
IG	a	89.6
MH	ab	80.3
GW*	abc	79.9
IF	abcd	70.6
PG	abcd	70.6
OH	abcde	67.2
ON	abcde	65.4
AZ	abcde	64.9
BP	abcde	62.4
HJ*	abcde	55.1
LP	bcde	60.9
CU	bcde	60.3
DQ	bcde	57.9
EU	bcde	57.7
S	bcde	56.3
LF	bcde	55.9
CV	bcde	55.7
EX	bcde	55.1
GS	bcde	53.6
PB	bcde	51.9
MF	cde	51.6
AI	cde	48.3
BH	cde	42.0
FU	de	45.4
BQ	e	40.5

*\* conclusions limited based on these families due to smaller sample sizes*

*Means with the same letter do no differ significantly at  $p=0.05$ , according to the Bonferroni Multiple Comparisons Test.*

Table B.2. Significant Watershed Means Comparison for Winter Total Roots (Troots).

<u>Watershed</u>		<u>Mean</u>
COOS	a	80.4
COW CREEK	ab	66.3
DUNES	ab	65.9
COQUILLE	b	61.6
SMITH RIVER	b	60.6
TRINITY	b	59.2
ELK	b	58.4
UMPQUA	b	58.0
ROGUE	b	57.9
APPLEGATE	b	56.4
SACRAMENTO	b	52.3
KLAMATH	b	51.4
ILLINOIS VALLEY	b	45.4

*Means with the same letter do not differ significantly at  $p=0.05$ , according to the Bonferroni Multiple Comparisons Test.*

Table B.3. Significant Watershed Means Comparison for Winter Total Active Root Length (TARL).

<u>Watershed</u>		<u>Mean</u>
COOS	a	181.5
COQUILLE	ab	159.5
COW	ab	147.2
TRINITY	abc	139.2
ELK	bc	134.8
DUNES	bc	128.4
APPLEGATE	bc	127.1
UMPQUA	bc	124.7
SMITH RIVER	bc	124.5
ROGUE	bc	117.2
KLAMATH	c	114.4
SACRAMENTO	c	112.6
ILLINOIS VALLEY	c	90.1

*Means with the same letter do no differ significantly at  $p=0.05$ , according to the Bonferroni Multiple Comparisons Test.*

Table B.4. Significant Family Means Comparison for Winter Total Active Root Length (TARL).

<b>Family</b>		<b>Mean</b>
IG	a	196.9
OH	ab	172.2
PG	abc	169.4
MH	abcd	165.2
AZ	abcd	156.8
IF	abcd	165.2
GW*	abcde	163.1
PB	abcde	148.9
LF	abcde	144.2
CU	abcde	139.5
HJ*	abcde	126.4
EX	bcde	128.3
BP	bcde	126.0
EU	bcde	125.9
LP	bcde	125.4
S	bcde	125.3
ON	bcde	122.2
DQ	bcde	117.2
CV	bcde	109.9
GS	cde	104.6
BQ	de	102.7
AI	de	99.9
BH*	de	86.5
MF	e	91.7
FU	e	90.1

*\* conclusions limited based on these families due to smaller sample sizes*

*Means with the same letter do no differ significantly at  $p=0.05$ , according to the Bonferroni Multiple Comparisons Test.*

Table B.5. Significant Watershed Means Comparison for Summer Total Roots (Troots).

<u>Watershed</u>		<u>Mean</u>
COOS	a	27.36
ELK	a	25.67
KLAMATH	ab	12.07
DUNES	ab	5.62
TRINITY	b	3.94
SACRAMENTO	b	3.55

*Means with the same letter do not differ significantly at  $p=0.05$ , according to the Bonferroni Multiple Comparisons Test.*