

Variation in water relations characteristics of terminal shoots of Port-Orford-cedar (*Chamaecyparis lawsoniana*) seedlings

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Summary We measured water relations attributes of the terminal shoots of 3-year-old Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) seedlings that represented its geographic range. Pressure–volume curves were developed and osmotic potentials at full (ψ_{sf}) and zero turgor (ψ_{sz}), relative water content at zero turgor, and an index of tissue elasticity (IE) were calculated for 38 families during early, mid- and late summer at an inland nursery, and for 12 of these families during mid- and late summer at a coastal nursery. Compared with other conifer species, ψ_{sz} was high (–1.4 to –1.5 MPa) and declined in seedlings at both nurseries as the season progressed. Both IE and osmotic amplitude ($\psi_{sf} - \psi_{sz}$) increased during the season. Osmotic potential at zero turgor was lower and osmotic amplitude greater in seedlings at the inland nursery than at the coastal nursery. Correlations of water relations attributes with geographic location of the seed sources were weak and usually not significant. High elevation southern sources exhibited smaller differences in ψ_{sz} between nurseries than low elevation northern sources. The small differences in water relations attributes among sources and between nurseries suggest that some may be of marginal physiological importance; however, sources that produced larger seedlings appeared to be less desiccation tolerant. We conclude that, when moving genotypes during reforestation, decisions based on patterns in tree size and timing of growth will account for these small differences in water relations.

Keywords: desiccation tolerance, genetic variation, osmotic potential, phenotypic variation, relative water content, seasonal variation, tissue elasticity.

Introduction

Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) trees are valued for their timber, aesthetics and their function in the ecosystem (Zobel et al. 1985). Compared with most conifers, the species grows well on ultramafic substrates (soils derived from serpentinite and peridotite rocks). It has an unusual combination of high tolerance to fire when mature, and high shade tolerance. It is the only shade-tolerant conifer on most ultramafic substrates within its range in southwestern

Oregon and northwestern California, and provides much of the tree cover along streams on ultramafics. But Port-Orford-cedar's role in forest ecosystems is threatened and management of the species is complicated by the presence of the introduced fungus *Phytophthora lateralis* Tucker and Milbrath, which causes a fatal root rot (Zobel et al. 1985). Replacement of populations decimated by root rot is a high priority in the region. A search for genotypes resistant to root rot began in the 1970s (Hansen et al. 1989). Recent intensive selection and disease-resistance screening of populations from throughout the range of Port-Orford-cedar, by Oregon State University, the USDA Forest Service and USDI Bureau of Land Management, have produced candidate genotypes for use in breeding root-rot-resistant stock for planting (E.M. Hansen, Oregon State University and R.A. Sniezko, personal communication).

There is good reason to believe that variation in adaptive traits exists within Port-Orford-cedar. Genetic variability in color and form within the species has produced over 200 named varieties (Zobel et al. 1985). It has moderate to high variation for allozymes (Millar and Marshall 1991) and growth rate (Kitzmiller and Sniezko 2000). A recent study of the phenology of 54 seedling sources indicated significant genetic variability (Zobel et al. 2002; but see Zobel 1983). Stomatal responses of nursery seedlings from an inland and a coastal seed source varied within sources but not consistently between sources (Zobel and Liu 1980). However, the closely related yellow-cedar (*C. nootkatensis* (D. Don) Spach) exhibits substantial genetic variability in water relations and other adaptive characteristics (Russell 1998).

The number of Port-Orford-cedar genotypes resistant to root rot appears to be small and limited to certain portions of the geographic range (E.M. Hansen and R.A. Sniezko, unpublished data), suggesting that planting of resistant stock will require moving genotypes outside their seed zone of origin. Deciding where specific resistant genotypes can be used requires information about variation in traits associated with survival and growth. Port-Orford-cedar is sensitive to summer drought because of its late germination time (Zobel 1990) and long duration of shoot elongation—up to 6 months annually for native saplings (Zobel 1983)—suggesting that differences in sensi-

tivity to dry summer conditions may be important when choosing whether and where to plant resistant genotypes. In addition, Port-Orford-cedar grows more slowly in height than most of the conifers with which it is associated (Zobel et al. 1985), which may result in suppression of expensive, planted resistant stock.

Here we report measurements of two parameters that control tissue water status during drought—osmotic potential and tissue elasticity. We measured these characteristics in terminal shoot tissue, which is responsible for height growth, and which varies genetically in the amount of growth accomplished late in the season (Zobel et al. 2002). We selected seedlings from mother trees that represented the geographic distribution of the species and included genotypes of both high and low apparent resistance to damage by *P. lateralis*. Measurements were made in plant beds in contrasting inland and coastal locations during a hot dry summer.

Materials and methods

Raised bed study design

A subsample of 36 of the original 298 families from a range-wide study of seedling growth (Kitzmilller and Sniezko 2000) was selected for study of water relations, with plants from two other families used to substitute for missing plants within two of the original 36 families (Table 1). (A family represents all seedlings grown from seed from one parent tree.) The subsample of families was chosen to represent all the major watersheds where the species grows and the range of performance in two tests of resistance to the pathogen that causes Port-Orford-cedar root disease, *Phytophthora lateralis* (E.M. Hansen and R.A. Sniezko, unpublished data).

Seedlings were grown at the Dorena Tree Improvement Center, near Cottage Grove, OR, at 240 m elevation and 100 km from the ocean, and at Humboldt Nursery, McKinleyville, CA, at 76 m elevation and 3 km from the ocean. At Dorena, mean monthly maximal temperatures were 28.9, 29.6 and 26.6 °C for July, August and September 1998, respectively. At the coastal weather station nearest Humboldt Nursery (Eureka, elevation 18 m, 12 km south), the corre-

sponding mean monthly maximal temperatures were 17.5, 17.7 and 17.4 °C. These temperatures encompass the normal range of summer temperatures that prevail in the natural habitats of Port-Orford-cedar seedlings (Zobel and Hawk 1980).

Seedlings were grown for a year in containers at a nursery in Korbelt, CA, and then transplanted to Dorena and Humboldt. At Dorena, the experimental design was six randomized, complete blocks with seed lots arranged in 3-tree family row plots. All six blocks were artificial raised beds with organic rooting medium 40 cm deep over a gravel base. During the 2-year study of growth (Kitzmilller and Sniezko 2000), three of the blocks were shaded with 47% shade-cloth from April 15 to October 15 and three blocks were unshaded. At Humboldt, the design was similar, except that only three of the blocks were raised beds (HN-RB); the other three blocks were conventional nursery beds about 20 m away (HN-NB). At Humboldt, all blocks had native mineral soil and seedlings were transplanted 1 month later than at Dorena. In addition, HN-RB blocks were sheltered from wind and partially shaded by a mature spruce canopy, whereas the HN-NB blocks were fully exposed to sun and wind. Thus, treatments at Humboldt represented two contrasting microenvironments, confounding differences in exposure to wind, sun and temperature extremes. Initial spacing of trees was 210, 204 and 160 cm² per seedling, respectively, in the Dorena, HN-NB and HN-RB blocks. All trees were irrigated and fertilized.

Pressure–volume curve measurements

Following the final measurements for second-year height growth (Kitzmilller and Sniezko 2000), plant beds were thinned to allow more even exposure of trees to sunshine. Use of shade cloth at Dorena was discontinued. All non-sample trees in rows adjacent to the selected sample families were removed, but all trees in the second row away from the sample trees were left to provide protection. Tall, thin trees were staked to prevent their collapse after thinning.

From the 298 families available, three sets of 12 families each were selected for water relations measurements, each set representing the geographic range and the range of pathogen resistance; the first set was measured at both nurseries,

Table 1. Subsample sizes and locations by watershed of the Port-Orford-cedar populations.

Regional watershed	No. of stands	No. of trees ¹	Elevation range (m)	Latitude range (°)	Longitude range (°)
Trinity	2	2 (1)	1585–1615	41.090–41.130	122.472–122.529
Sacramento	3	4 (1)	1143–1585	41.220–41.250	122.400–122.460
Klamath	2	3 (1)	1006–1351	41.319–41.820	123.471–123.760
Smith	2	5 (4)	431–1494	41.724–41.912	123.663–124.069
Illinois	1	2 (0)	1067	42.034	123.552–123.553
Applegate	2	3 (1)	701–1372	42.133–41.172	123.279–123.352
Rogue	3	4 (1)	975–1097	42.524–42.666	123.732–124.150
Sixes and Elk	1	4 (1)	190–207	42.780–42.782	124.432–124.441
Coquille	5	7 (1)	183–792	42.828–43.140	123.780–124.080
Dunes	2	4 (2)	30–53	43.340–43.440	124.252–124.340

¹ Number of parent trees; number in parentheses is for Humboldt Nursery.

whereas the other two sets (24 families) were sampled only at Dorena. Four of the six blocks at each nursery were selected, including two of each type at Humboldt. Four trees of each sample family, one from each block, were measured at each location during each of three sample periods. For the early sampling, all 36 families at Dorena were measured from June 29 to July 17, 1998. For the middle sampling, 12 families were measured at Dorena on July 20–24 and the same families were measured at Humboldt from July 26 to August 1; the other 24 families at Dorena were measured on August 3–14 to complete the middle sampling. For the late sampling, the same 12 families were measured at Dorena from August 17–21 and at Humboldt from August 23–28; the additional 24 families at Dorena were measured between August 31 and September 11. Trees of two additional families were sampled to supplement families with too few trees available to complete the sampling, giving a total of 38 families.

Measurements were made by the same two persons at all times and locations; each operator measured half the trees in each family during each sample period. Order of sampling of families and choice of trees within a family and block were randomized within each sample location and period.

Measurements of osmotic potential at full and zero turgor and an index of elasticity were calculated from pressure-volume curves produced by the bench drying (free transpiration) technique (Pallardy et al. 1991); two pressure chambers (Model 600, PMS Instrument Co., Corvallis, OR) were used to construct the curves. The morning before or after sample collection, predawn water potential (ψ) was measured on a lower lateral branch of each sample seedling. Predawn ψ varied from -0.07 to -0.27 MPa (mostly -0.1 to -0.2 MPa) at Dorena and -0.16 to -0.51 MPa (mostly -0.16 to -0.30 MPa) at Humboldt. The afternoon before measurement, samples were collected, recut under water and placed with the cut surface in water in a dark, humid environment overnight. The terminal portion of the main stem, including all branches, was selected for measurement, down to the first branch that had begun to flatten into the normal frond-like form of mature Port-Orford-cedar twigs. Samples collected were large enough to allow removal of the tissue immersed during rehydration. Measurements of tissue mass and balance pressure ($-\psi$) were repeated at 10-min intervals for the first few measurement times, with intervals lengthening with time. Twelve to 19 (usually 16–19) sets of measurements were made for each sample. Sample dry mass was determined after drying at 75°C for 24 h. Relative water content (RWC) was computed for each sample time, the inverse of balance pressure was plotted against RWC, and analysis of the curve for osmotic potential values was completed as described by Pallardy et al. (1991). To calculate the index of elasticity (IE), all values of pressure potential above zero were plotted against RWC; the slope of a linear regression line through these points was used as IE. The succulent tissue of branches of the growing leaders of Port-Orford-cedar occasionally broke during repeated handling; in this case, the broken portion was weighed separately both wet and dry, and calculations were adjusted to account for the loss.

Statistical analysis

Statistical analyses were made on an individual tree basis with the MIXED procedure of SAS Version 6.12 Win95 (SAS Institute Inc., Cary, NC) for two models. (1) All 38 Families and three Periods at Dorena only, with Periods as the fixed effect (the Residual variance was Trees within Period \times Family (Set)). (2) The 12 Family subset and two Periods that were common across both Nurseries, with Periods, Nurseries, and Nursery \times Period as fixed effects (the Residual pooled variance was the 3-way interaction plus Trees within that interaction). Least square means and standard errors were estimated for fixed effects and were predicted (using Best Linear Unbiased Prediction) for Family and Nursery \times Family random effects. The MIXED procedure also estimated degrees of freedom, synthesized F -tests from expected mean squares for fixed effects, and computed variance components and Z -tests for random effects. Significance of random effects with 35 or fewer degrees of freedom was calculated by chi-square of the calculated likelihood ratio statistic (Littell et al. 1996). Correlation analyses among water relations traits and between water relations traits and seedling size were based on seedling values, whereas correlations with geographic variables were based on family means.

Results

Comparison among periods at Dorena

For the 36 families sampled at Dorena, osmotic potentials at full and zero turgor (ψ_{sf} and ψ_{sz} , respectively) and IE differed with sampling period (Tables 2 and 3). Blocking (i.e., plant bed), shading, and set of families had no significant effects on any of the water relations characteristics. Within sets, family differences were significant or nearly significant ($P = 0.029$ – 0.055) for all attributes (Table 2). Sets performed differently during different periods for ψ_{sf} , ψ_{sz} and relative water content at zero turgor (RWC_z). Other interactions were not significant.

In comparisons among individual sampling periods, IE increased (i.e., tissue elasticity declined) as summer progressed (Table 3). Both ψ_{sf} and ψ_{sz} were higher during the early sam-

Table 2. Effects of sampling period, set of families and family on water relations attributes of seedlings growing at Dorena. Abbreviations: osmotic potential at full turgor (ψ_{sf}), osmotic potential at zero turgor (ψ_{sz}), osmotic amplitude ($\psi_{sf} - \psi_{sz}$), index of elasticity (IE) and relative water content at zero turgor (RWC_z). Differences among blocks (plant bed locations) were not significant. Error df = 308.

Source	df	ψ_{sf}	ψ_{sz}	$\psi_{sf} - \psi_{sz}$	IE	RWC_z
Period	2	0.0475	0.0251	0.2988	0.0001	0.8848
Set	2	0.3937	0.9999	0.2809	0.4917	0.9999
Family (Set)	35	0.0550	0.0350	0.0290	0.0380	0.0550
Period \times Set	4	0.0150	0.0010	0.4686	0.9999	0.0400
Period \times	68	0.3630	0.9999	0.9999	0.3243	0.3261
Family (Set)						

Table 3. Effect of sampling period on water relations attributes of seedlings growing at Dorena. Abbreviations: osmotic potential at full turgor (ψ_{sf}), osmotic potential at zero turgor (ψ_{sz}), osmotic amplitude ($\psi_{sf} - \psi_{sz}$), index of elasticity (IE) and mean relative water content at zero turgor (RWC_z). Standard errors are given in parentheses. Within each column, means with different letters differ significantly ($P < 0.05$) according to Tukey's studentized range test.

Period	ψ_{sf} (MPa)	ψ_{sz} (MPa)	$\psi_{sf} - \psi_{sz}$ (MPa)	IE (MPa)	RWC_z (%)
Early	-1.12 (0.02) a	-1.38 (0.02) a	0.26 (0.01) a	5.24 (0.13) a	80.1 (0.5) a
Middle	-1.21 (0.02) b	-1.48 (0.02) b	0.27 (0.01) a	5.68 (0.16) b	80.2 (0.5) a
Late	-1.23 (0.02) b	-1.51 (0.02) b	0.28 (0.01) a	6.04 (0.16) c	80.5 (0.5) a

pling period than during the middle and late sampling periods, but values during the middle period did not differ from those during the late period.

Comparison among nurseries during the middle and late periods

At both nurseries during the middle and late sampling periods, the patterns of variation differed among the five response variables (Tables 4 and 5). Osmotic potential at full turgor (ψ_{sf}) was lower during the late sampling period than during the middle sampling period. Osmotic potential at zero turgor (ψ_{sz}) and osmotic amplitude ($\psi_{sf} - \psi_{sz}$) differed between nurseries (seedlings at Dorena had lower ψ_{sz} and greater osmotic amplitude than seedlings at Humboldt) and between sampling periods (ψ_{sz} was lower and osmotic amplitude was greater at the late sampling period than at the middle sampling period).

Table 4. Analysis of effects on water relations attributes of nursery location, sampling period, and family. Abbreviations: osmotic potential at full turgor (ψ_{sf}), osmotic potential at zero turgor (ψ_{sz}), osmotic amplitude ($\psi_{sf} - \psi_{sz}$), index of elasticity (IE), and relative water content at zero turgor (RWC_z). Error df = 153.

Source	df	ψ_{sf}	ψ_{sz}	$\psi_{sf} - \psi_{sz}$	IE	RWC_z
Nursery	1	0.9522	0.0119	0.0001	0.0762	0.8677
Family	11	0.9999	0.9999	0.1645	0.3630	0.0666
Nursery \times Family	11	0.0405	0.0070	0.9999	0.2291	0.9999
Period	1	0.0101	0.0001	0.0034	0.4656	0.0667
Period \times Family	11	0.9999	0.9999	0.2545	0.9999	0.3948
Nursery \times Period	1	0.3380	0.4125	0.0128	0.4537	0.3010

Table 5. Mean water relations attributes by nursery location and sampling period. Abbreviations: osmotic potential at full turgor (ψ_{sf}), osmotic potential at zero turgor (ψ_{sz}), osmotic amplitude ($\psi_{sf} - \psi_{sz}$), index of elasticity (IE), and mean of relative water content at zero turgor (RWC_z). Standard errors are in parentheses.

Nursery	Period	ψ_{sf} (MPa)	ψ_{sz} (MPa)	$\psi_{sf} - \psi_{sz}$ (MPa)	IE (MPa)	RWC_z (%)
Dorena	Middle and late	-1.24 (0.21)	-1.50 (0.19)	0.26 (0.12)	5.93 (0.13)	80.7 (0.4)
Humboldt	Middle and late	-1.24 (0.21)	-1.43 (0.19)	0.19 (0.12)	6.27 (0.13)	80.6 (0.4)
Dorena and Humboldt	Middle	-1.22 (0.18)	-1.41 (0.16)	0.20 (0.13)	6.05 (0.12)	81.1 (0.4)
Dorena and Humboldt	Late	-1.27 (0.18)	-1.52 (0.16)	0.25 (0.13)	6.15 (0.12)	80.2 (0.4)
Dorena	Middle	-1.20 (0.25)	-1.46 (0.22)	0.25 (0.16)	5.82 (0.17)	81.3 (0.5)
Dorena	Late	-1.28 (0.25)	-1.55 (0.22)	0.28 (0.16)	6.03 (0.17)	80.0 (0.5)
Humboldt	Middle	-1.23 (0.25)	-1.37 (0.22)	0.14 (0.16)	6.27 (0.17)	80.8 (0.5)
Humboldt	Late	-1.26 (0.25)	-1.49 (0.22)	0.23 (0.16)	6.27 (0.17)	80.4 (0.5)

Family behavior in both ψ_{sf} and ψ_{sz} differed between nurseries. Only osmotic amplitude showed an interaction between sampling period and nursery, with a much greater difference between sampling periods at Humboldt than at Dorena. Index of elasticity and RWC_z did not differ significantly between nurseries for the last two sampling periods (Table 4).

Although ψ_{sz} of all families was higher at Humboldt than at Dorena, the magnitude of the difference was related to location of seed source; southern high-elevation sources showed little difference, whereas large differences were observed for northern low-elevation seed sources (Figure 1).

Correlation among water relations attributes

Most water relations attributes were significantly correlated with each other (Table 6); only osmotic amplitude and RWC_z varied independently of each other at both nurseries. The relationship between ψ_{sf} and ψ_{sz} was strong, but most other correlation coefficients were 0.5 or less. As RWC_z increased, osmotic potentials and IE increased. A high osmotic amplitude was associated with high ψ_{sf} and low ψ_{sz} .

Correlation of water relations attributes with geographic origin and tree size

Correlations between water relations attributes and seed source location for a family were generally not significant. At Dorena ($n = 38$), RWC_z was correlated with longitude ($r = 0.32, P < 0.05$), and osmotic amplitude was correlated with elevation and latitude ($r = 0.33$ and -0.38 , respectively, $P < 0.05$). At Humboldt ($n = 12$), only RWC_z was correlated with elevation and latitude ($r = 0.79$ and -0.87 , respectively, $P < 0.01$), and longitude ($r = 0.60, P < 0.05$). All other correlations

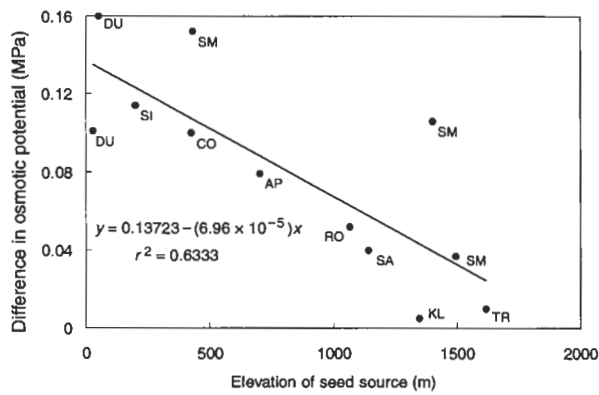


Figure 1. Difference in osmotic potential at zero turgor (ψ_{sz}) between Humboldt and Dorena nurseries for 12 families measured at both nurseries. The two-letter label for each data point is the first two letters of the name of the watershed from which the seed was derived; see Table 1 for the list of watersheds.

with geographic variables were nonsignificant (values not shown).

Some water relations parameters were related to tree size (Table 7). The strongest and most consistent relationships were those between tree size and loss of turgor at high RWC_z and between tree size and less elastic tissue (high IE). At Dorena, large trees also lost turgor at low ψ_s and had a large osmotic amplitude ($\psi_{sf} - \psi_{sz}$), but these relationships were not significant at Humboldt. Osmotic potential at full turgor did not differ with tree size.

Timing of shoot growth (Zobel et al. 2002) was related to the average water relations attributes among the 29 families at Dorena for which data were available. As the proportion of growth that occurred after late August increased, RWC_z and IE increased ($r = 0.432$, $P = 0.019$, and $r = 0.447$, $P = 0.015$, respectively), but ψ_{sz} became more negative ($r = -0.381$, $P = 0.042$). Among the 12 families measured at both nurseries, the correlation between the proportion of late growth and RWC_z was also significant ($r = 0.605$, $P = 0.037$).

Discussion

Adaptation of Port-Orford-cedar seedlings to summer drought

Port-Orford-cedar grows primarily on sites that are not prone to severe soil water deficits. Most native Port-Orford-cedar

seedlings have their lowest predawn water potentials at or above -1.1 MPa, which is less than for some co-occurring conifers (Zobel and Hawk 1980). In the few places where predawn water potentials are less than -1.1 MPa (-1.8 to -2.3 MPa), fog is a common occurrence. Populations that grow in a dry atmosphere are usually found on soils with a consistently high water table. High availability of water during summer appears to be necessary for establishment of Port-Orford-cedar seedlings (Zobel 1990), and for continued seedling growth (Zobel et al. 1985). However, the species does have some control over water loss, because its diurnal change in water potential is often less than that of co-occurring conifers (Zobel and Hawk 1980).

According to Lambers et al. (1998), desiccation tolerance is associated with low water potential at turgor loss (more negative ψ_{sz}), low relative water content at turgor loss (low RWC_z), and high tissue elasticity (low IE). We used these criteria as a basis for interpreting (1) the relative drought tolerance of our geographic sources, (2) the changes in drought tolerance during the growing season, and (3) the effects of nursery environment on drought tolerance.

Direct comparison among the three indicators for drought tolerance showed a consistent relationship at both nurseries: as RWC_z rose, ψ_{sz} became less negative and tissue elasticity decreased; i.e., resistance to desiccation decreased. Although the correlations were mostly significant, they were not particularly strong ($r = 0.14$ to 0.63 ; Table 6). Furthermore, a significant correlation of RWC_z to IE would be expected based on our method of calculating IE.

Only RWC_z varied with location of seed source. At both nurseries, populations from farther west had higher RWC_z , and thus lower drought tolerance. At Humboldt, RWC_z also increased as the seed source moved to the north and to lower elevations. The interaction between nursery and family for ψ_{sz} indicated a relationship to seed source location. Thus, there was little difference in ψ_{sz} between nurseries for southern interior families from the Sacramento, Trinity and Klamath watersheds (Figure 1), whereas the difference between nurseries for northern coastal provenances (Dunes, Coquille, and Sixes and Elk watersheds) was ≥ 0.1 MPa. This suggests that, compared with southern interior sources, coastal sources have a greater ability to modify osmotic potentials as climate changes.

At Dorena, larger seedlings had lower ψ_{sz} , suggesting that they had greater drought tolerance than smaller seedlings. In contrast, larger seedlings had higher IE and RWC_z at both nurseries (Table 7), suggesting that they are less drought-tol-

Table 6. Correlation coefficients among water relations attributes. Values for Dorena are in bold; values for Humboldt are in italics. At Dorena, $n = 324$ and at Humboldt, $n = 95$. Significance values: * = significant at $P < 0.05$, and ** = $P < 0.01$.

Attribute	ψ_{sf}	ψ_{sz}	$(\psi_{sf} - \psi_{sz})$	IE	RWC_z
ψ_{sf}	1.000	0.877**	0.315**	-0.343**	0.320**
ψ_{sz}	<i>0.711**</i>	1.000	-0.180*	-0.232*	0.318**
$(\psi_{sf} - \psi_{sz})$	<i>0.464**</i>	<i>-0.294**</i>	1.000	-0.245**	0.027
IE	<i>-0.459**</i>	<i>-0.135</i>	<i>-0.453**</i>	1.000	0.625**
RWC_z	<i>0.384**</i>	<i>0.514**</i>	<i>-0.126</i>	<i>0.518**</i>	1.000

Table 7. Correlation coefficients of water relations attributes with plant size, based on individual tree data for both Dorena and Humboldt, for all periods. Height and diameter were measured at the beginning of the measurement growing season. At Dorena, $n = 324$ and at Humboldt, $n = 95$. Significance values: * = significant at $P < 0.05$, and ** = $P < 0.01$.

Nursery	Attribute	Height	Diameter
Dorena	ψ_{sf}	-0.119	-0.097
	ψ_{sz}	-0.230*	-0.214*
	IE	0.293**	0.239**
	$(\psi_{sf} - \psi_{sz})$	0.210*	0.223*
	RWC _z	0.275**	0.254**
Humboldt	ψ_{sf}	0.150	0.081
	ψ_{sz}	0.104	0.035
	IE	0.246*	0.188
	$(\psi_{sf} - \psi_{sz})$	0.073	0.066
	RWC _z	0.381**	0.224*

erant than smaller seedlings. Seedling size was maximal in genotypes from the northwestern part of the range at low elevations (Kitzmillier and Sniezko 2000). Both RWC_z and IE increased with the proportion of stem elongation completed late in the season, which was also maximal in genotypes from the northwest coast (Zobel et al. 2002). This suggests that seedlings that grow later into the season (and thus become the largest) are less desiccation-tolerant than smaller trees that exhibit little growth late in the season.

We obtained conflicting data on the seasonal change in drought tolerance. Thus, at Dorena, IE increased during the season but ψ_{sz} declined (Table 3). The finding that ψ_{sz} was lower in seedlings at Dorena than at Humboldt (Table 5) suggests that seedlings grown at Dorena had greater drought tolerance than seedlings grown at the Humboldt location.

Comparison with other conifers

The Port-Orford-cedar seedlings had relatively elastic tissue and high osmotic potentials compared with most conifers. The high tissue elasticity suggests high desiccation tolerance, whereas the high osmotic potentials suggest low desiccation tolerance. Water relations measurements of several other Cupressaceae, including *Chamaecyparis obtusa* (Sieb. et Zucc.) Endlicher saplings (Mizunaga 1988) and rooted cuttings of *C. nootkatensis* grown in long days (Arnott et al. 1993), have yielded osmotic potentials at turgor loss (ψ_{sz}) about 0.2–1.0 MPa lower than the values we determined at Dorena on comparable dates. (Rooted cuttings of *C. nootkatensis* grown in a 9-h photoperiod had similar ψ_{sz} to our samples). Russell (1998) reported that osmotic potential of *C. nootkatensis* varied among seed sources, being lower before drought in the case of seedlings from a more xeric site than in the case of seedlings from a more mesic site. For other North American Cupressaceae, ψ_s values are all lower than our values, some by >1 MPa (Abrams 1988, Grossnickle 1993, D.B. Zobel, unpublished data). In contrast, ψ_{sz} values for *Cupressus torulosa* D. Don in the Himalayas (S.P. Singh,

S.C. Garkoti and D.B. Zobel, unpublished data) were 0.2–0.5 MPa higher during the summer monsoon season and fall than the values we report.

Generally, ψ_{sz} values in other conifers (Yoder 1984, Abrams 1988, Zobel 1996) are lower than the values we measured in Port-Orford-cedar at Dorena and much lower than the values at Humboldt. High ψ_{sz} was found in *Pinus roxburghii* Sarg. during the summer monsoon season in the Himalayas (S.P. Singh, S.C. Garkoti and D.B. Zobel, unpublished data). We cannot determine whether the differences between our values and those in the literature are attributable to differences among species or to our use of leader tissue. We believe that the leader was the appropriate tissue to measure, because our primary objective was to determine the capacity for continued height growth in Port-Orford-cedar seedlings during the dry season. The extended period of growth allows this relatively slow-growing tree to compete with associated Pinaceae, which grow faster and begin growing earlier in the growing season (Zobel 1983).

The high osmotic potentials may be associated with the well-watered conditions in which the seedlings were grown. Even when exposed to hot, dry atmospheric conditions at Dorena, seedling water potentials recovered each night to values above -0.3 MPa. Although these predawn ψ values were higher than those found in naturally established seedlings, predawn ψ values above -0.5 MPa are common at some sites during summer (D.B. Zobel and G.M. Hawk, unpublished data).

Osmotic potential also varies among populations of other conifers (Yoder 1984, Pallardy et al. 1995). Similar to our finding of low ψ_{sz} in fast-growing sources of Port-Orford-cedar at Dorena, fast-growing genotypes of black spruce (*Picea mariana* (Mill.) B.S.P.) develop lower shoot osmotic potentials under osmotic stress than slow-growing genotypes, and osmotic adjustment is positively associated with root growth in ponderosa pine (*Pinus ponderosa* Dougl.) (Pallardy et al. 1995). In contrast, fast-growing varieties of the grand fir-white fir complex (*Abies grandis* (Dougl. ex D. Don) Lindl.–*A. concolor* (Gordon & Glend. ex Hildebr.) Lindl.) had higher osmotic potentials than slow-growing varieties (Yoder 1984). There seems to be little loss of growth caused by temporary use of solutes for osmotic adjustment (Tan et al. 1992, Kramer and Boyer 1995).

Our IE values are not directly comparable with most published values of elastic modulus, because we used a different method of calculation. However, we note that IE for lateral branchlets of *Cupressus torulosa* in the Himalayas during the growing season was half the value we measured (S.P. Singh, S.C. Garkoti and D.B. Zobel, unpublished data), indicating that *C. torulosa* has highly elastic tissue. For Port-Orford-cedar seedlings, a low IE (relative to most conifers) may be required to maintain turgor during hot, dry summer weather, because maximal turgor is limited by high ψ_s .

Physiological significance of the data

The physiological significance of some of the statistically significant differences that we report is difficult to evaluate be-

cause the differences were sometimes small and the relationships inconsistent. Responses of our seedlings, which were grown in a nursery with optimal watering, an artificial or deep substrate, and fertilization, probably differ from those of naturally established seedlings growing in habitats with low fertility, native soil biota, irregular water supply, and competition. Nevertheless, comparisons with field survival indicate the importance of considering water relations in management. Trees from the same seed sources as used in the Kitzmiller and Sniezko (2000) study were planted in four field locations. At two plantations, first-year survival (Jay Kitzmiller, unpublished data) was related to the water relations parameters that we derived for comparable seedlings representing the same watersheds. At plantings at Althouse in interior southern Oregon (mean survival 24%), mean survival from a watershed was correlated with mean values of IE and RWC_z ($r = -0.80$, $P = 0.006$ and $r = -0.72$, $P = 0.033$, respectively). At Trinity Lake near the southern interior end of the species' range (mean survival 81%), survival by watershed was also related to RWC_z ($r = -0.68$, $P = 0.030$). In both areas, plants with predicted high drought tolerance, based on the criteria of Lambers et al. (1998), survived better than seedlings with predicted low drought tolerance.

Because the water relations differences among seed source locations showed a similar pattern to that of growth and phenology, selection of seed sources for planting, based on variation in amount and timing of growth, may accommodate any important differences in water relations. However, based on our finding of the influence of nursery location, we conclude that caution is needed if seedlings from coastal nurseries are planted immediately before the onset of the dry season.

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