

Physiological variation among western redcedar (*Thuja plicata* Donn ex D. Don) populations in response to short-term drought

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Abstract

• Variation in the ability of western redcedar (*Thuja plicata* Donn ex D. Don) populations to withstand water stress may exist because this species is found in coastal and interior biogeoclimatic subzones representing the full range of precipitation regimes in British Columbia, Canada.
• Seven western redcedar populations from locations in British Columbia, representing a wide range of habitat types, were assessed for their gas exchange and water relations response to controlled drought.
• Before drought, population variation occurred in stomatal conductance, net CO₂ assimilation rate and intrinsic water use efficiency and the relative water content at turgor loss point. During drought, populations had different responses of net CO₂ assimilation to decreasing predawn shoot water potential. After drought, populations differed in stomatal conductance and intrinsic water use efficiency, plus osmotic potential at turgor loss point, osmotic potential at saturation and apparent cuticular transpiration. Western redcedar populations from drier-inland habitats had a lower osmotic potential at turgor loss point, lower relative water content at turgor loss point and lower apparent cuticular transpiration in response to drought than populations from coastal origin with temperate maritime habitat.
• Reduction of cuticular water loss and adjustments of cellular water relations in response to drought was found to occur among seven western redcedar populations originating along a precipitation gradient while; there were minimal population differences in the gas exchange response to drought.

Résumé – Variations physiologiques dans des populations de thuyas géants (*Thuja plicata* Donn ex D. Don) en réponse à une sécheresse courte.

• Les variations de capacité à résister au déficit hydrique dans des populations de thuyas géants (*Thuja plicata* Donn Ex D. Don) apparaissent parce que cette espèce se rencontre dans les sous-zones biogéoclimatiques côtières et de l'intérieur représentant l'éventail complet de régimes de précipitations en Colombie britannique (Canada).
• Sept populations de thuyas géants issues de sites de Colombie britannique, représentant un large éventail des types d'habitats, ont été évaluées pour leurs échanges gazeux et leurs relations hydriques en réponse à une sécheresse contrôlée.
• Avant la sécheresse, une variabilité existait entre populations pour la conductance stomatique, l'assimilation nette de CO₂, l'efficacité intrinsèque d'utilisation de l'eau et la teneur relative en eau au point de perte de turgescence. Pendant la sécheresse, les populations ont présenté des réponses différentes de l'assimilation nette de CO₂ à la baisse du potentiel hydrique de base. Après la sécheresse, les populations différaient en conductance stomatique et efficacité intrinsèque d'utilisation de l'eau, mais également en potentiel osmotique au point de perte de turgescence, en potentiel osmotique à saturation et en transpiration cuticulaire apparente. Les populations de thuyas géants des habitats intérieurs les plus secs présentaient un plus faible potentiel osmotique au point de perte de turgescence, une plus faible teneur en eau au point de perte de turgescence et une plus faible transpiration cuticulaire apparente en réponse à la sécheresse que les populations d'origine côtière avec un habitat maritime tempéré.
• Une réduction des pertes d'eau cuticulaires et des ajustements des relations hydriques cellulaires en réponse à la sécheresse ont été trouvés parmi sept populations de thuyas géants originaires de sites se trouvant le long d'un gradient de précipitations, alors qu'il n'y avait que de faibles différences entre populations pour la réponse des échanges gazeux à la sécheresse.

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1. INTRODUCTION

Western redcedar (*Thuja plicata* Donn ex D. Don) is a tree species that occurs over a wide geographic range in British Columbia, Canada. It spans from coastal regions where it is most productive in the moist maritime environment of the coastal western hemlock (CWH) zone, the wetter soil water regimes of the coastal Douglas-fir (CDF) zone, and it is also found in interior regions where it is a dominant species of the interior cedar-hemlock zone (ICH) (Ketcheson et al., 1991; Nuszdorfer et al., 1991). It is also found in valley basins of the very dry interior Douglas-fir zone (IDF) (Hope et al., 1991). With access to the water table, it can also occur in areas that are too dry for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Minore, 1990). Such adaptation observations potentially infer genetic variation which is systematic with respect to environmental parameters.

The occurrence of western redcedar in both coastal and interior biogeoclimatic subzones represents the full range of precipitation regimes in British Columbia. This suggests that populations from various habitats may differ in their ability to withstand water stress. Such adaptation may depend on genetic variation among populations of western redcedar (Rehfeldt, 1994). Studies have documented genotypic variation in gas exchange (e.g., Aspelmeyer and Leuschner, 2004; Johnsen and Major, 1995; Monson and Grant, 1989) and water relations (e.g., Abrams, 1988; Aspelmeyer and Leuschner, 2004; Johnsen and Major, 1999; Parker and Pallardy, 1985) of tree species in relation to their habitat of origin. Although widely distributed in the region under sharply contrasting environmental conditions, western redcedar has been found to vary little genetically in isozymes (e.g., Yeh, 1988), while there is reported population variation in microsatellites (O'Connell et al., 2001). Significant family variation has been shown for western redcedar in growth rates (Russell et al., 2003; Wang and Russell, 2006) and population variation in physiological and morphological traits (Fan et al., 2008; Grossnickle et al., 2005; Rehfeldt, 1994). Some adaptive genetic variation is known to exist between western redcedar populations (Rehfeldt, 1994), though information on the amount and pattern of this variation in relation to precipitation gradients and soil water regimes is minimal.

This study was part of a larger program investigating the adaptive physiology of seven western redcedar populations originating along a precipitation gradient (from east to west) from various biogeoclimatic zones in British Columbia. The overall program objective was to define the physiological and morphological response of these western redcedar populations to summer time soil and atmospheric water conditions. In companion papers, Grossnickle et al. (2005) reports on the gas exchange response and summer-time water use efficiency of the same populations to atmospheric demand under summer time field conditions, while Fan et al. (2008) reports on the morphological development and inherent water-use efficiencies of these populations under long-term moderate drought. The objective of this trial was to describe gas exchange parameters, plus drought tolerance and avoidance parameters of seven western redcedar populations in response to short term

drought. Intended application of program findings was to define physiological variables that could be used to assess western redcedar populations when developing a sound gene resource management strategy.

2. MATERIALS AND METHODS

2.1. Plant material

Western redcedar (*Thuja plicata* Donn) seeds came from six populations representing zonal associations within biogeoclimatic variants (Pojar et al., 1991) from the west coast to interior wet belt climatic zones at $\sim 49^\circ$ north latitude and spans from 116° to 125° west longitude (Tab. 1). In addition, a population collected near Prince Rupert ($\sim 54^\circ$ N Lat.) from the coastal cedar-western hemlock biogeoclimatic zone was included in the study. Open-pollinated seeds were collected from five trees within each of the seven populations. Each population assessed in this study came from a combination of four of the five open-pollinated families. Population descriptor data were obtained from Meteorological Service of Canada: 1961–1990 average monthly precipitation data for British Columbia that had been mapped on a 2.5° by 2.5° grid using the PRISM climate analysis system and a digital elevation model (Daly et al., 1997).

Seedlings were grown as 1+0 container (planted in April in a 415B styroblock™ format; 108 cc volume cavities) stocktype at Cowichan Lake Research Station ($48^\circ 49' N$ Lat. $124^\circ 10' W$ Long., 200 m elevation) under standard cultural practices to ensure rapid development. Seedlings were then placed outdoors in September and treated with a fall watering, fertilization, daylength and temperature regime to allow for fall/winter acclimation. These seedlings were grown under a standard container-nursery cultural regime used in British Columbia, Canada (Van Eerden and Gates, 1990). All populations were grown as part of a homogeneous nursery crop population and had statistically similar height, diameter, shoot and root dry weight, before trial initiation (Fan et al., 2008).

2.2. Testing environment

In late winter, each test seedling was potted in a two-litre milk carton. Cartons had two eight mm diameter drainage holes at their base, and were filled with a 1:1 peat:sand mixture, selected for its slow, even drying pattern. After potting, seedlings were placed in a controlled environment room ($22 \pm 3^\circ C$ air temperature, $35 \pm 5\%$ relative humidity, 2.3 ± 0.05 kPa vapour pressure deficit, ambient CO_2 conditions ≈ 400 ppm, 16-h photoperiod at $600 \mu mol m^{-2} s^{-1}$ at seedling height). Seedlings from all populations were randomly positioned and maintained under well-watered conditions for two weeks and the initiation of shoot growth was started before commencement of the experiment.

Test populations (each population = 50 seedlings or 10 to 12 per family) were divided in half for two watering regimes: (1) continuously well-watered; or (2) exposed to two drought/recovery cycles, consisting of a first dry-down cycle followed by a ten-day well-watered period and then a second dry-down cycle. Dry-down cycles ended for each population when mean predawn shoot water potential (Ψ_{pd}) was -1.2 MPa for the first dry-down cycle and -1.8 MPa for the second dry-down cycle (i.e., typically a 10 to 16 d timeframe). Thus, populations were removed from the drought regime one at

Table I. Description of the site of origin for seven western redcedar populations in British Columbia Canada, including the biogeoclimatic (BEC) subzone and variant.

	2	4	11	12	16	19	23
Population number	Yellowpoint	Nicolium	Garibaldi	Kennedy lake	Oliver lake	Gilpin	Creston
Population name ¹	50	320	400	50	65	1200	635
Elevation (m)							
Latitude	49° 03'	49° 22'	49° 57'	49° 01'	54° 17'	49° 02'	49° 10'
Longitude	123° 48'	121° 20'	123° 10'	125° 35'	130° 15'	118° 20'	116° 20'
BEC subzone and variant ²	CDFmm	CWHds1	CWDds1	CWHvm1	CWHvh2	IDFxb1	ICHmw2
Precipitation regime ³	Moist (m)	Dry (d)	Dry (d)	Very moist (vm)	Very wet (vw)	Very dry (x)	Moist (m)
Actual moisture regime ⁴	Medium-dry (md)	Fresh (f)	Fresh (f)	Very moist (vm)	Very moist (vm)	Very dry (vd)	Fresh (f)
[MAP] Mean annual precipitation (mm) ⁵	1097	1681	1960	3327	3102	677	654
[MSP] Mean summer precipitation (mm) ⁶	185	355	372	606	879	260	224
[ADI] Annual dryness index ⁷	1.10	0.58	0.49	0.35	0.34	1.28	1.27
[SDI] Summer dryness index ⁷	10.78	5.17	4.78	2.84	1.78	7.11	8.14
[MAT] Mean annual temperature (°C) ⁵	9.6	6.4	6.2	9.2	7.6	4.8	4.2
[MTWM] Mean temperature of coldest month (°C) ⁵	2.7	-3.6	-2.5	4.6	3.2	-6.4	-7.5
[MTCM] Mean temperature of warmest month (°C) ⁵	17.3	16	15.5	15	13.5	16.1	15.9
Continentality (MTWM-MTCM) ⁸	14.6	19.6	18	10.4	10.3	22.5	23.4
[SUMAVE] Average summer temperature (°C) ⁵	15.06	13.44	12.78	13.18	11.5	13.02	12.72
[SUMMAX] Average maximum temperature (°C) ⁵	20.62	19	18.1	16.92	14.88	20.46	20.02

¹ Populations 2 through 16 are from coastal biogeoclimatic (BEC) zones, while populations 19 and 23 are from interior biogeoclimatic zones.

² A descriptions of the biogeoclimatic (BEC) zone classification system for British Columbia can be found in Meidinger and Pojar (1991).

³ Five PR categories have been identified by Pojar et al. (1991a) for British Columbia: (1) very dry (x); (2) dry (d); (3) moist (m); (4) wet (w); (5) very wet (vw).

⁴ Actual moisture regime is determined on site using indicator species as described by Lloyd et al. (1990), and Green et al. (1984).

⁵ Derived from the PRISM climate analysis system and a digital elevation model (Daly et al., 1994, 1997).

⁶ For the months of April through to September, inclusive.

⁷ Indices have been defined by Guy and Holowachuk (2001).

⁸ Continentality is the mean temperature of warmest month – the mean temperature of coldest month.

a time. During the recovery period, seedlings from both watering regimes were fertilized with 250 mL of Plant Products™ 20-20-20 at 150 ppm N.

2.3. Measured parameters

2.3.1. Gas exchange

Net CO₂ assimilation rate (A), foliar conductance of water vapour (g_{wv}) and intrinsic water-use efficiency (WUE_i) (i.e., ratio of A to g_{wv}) were determined using a LI-6400 (LI-COR Inc., Nebraska USA) portable photosynthesis system with the standard sample chamber. Gas exchange was measured on eight seedlings per population and water regime. A section approximating 6 cm² of foliage area on the upper surface of the third branch from the top of each seedling was tagged for gas exchange measurements. All meristem tips within this foliage section were excised to prevent a change in sample surface area during the experiment, and a non-toxic rubber compound was used to identify the boundary of this sample section. This allowed for repeated measurements on the same foliage section throughout the experiment. Trial measurements did not commence until two weeks after the preparation of this sample area to allow cut tips to heal. At the end of the study, this branch section was removed and the sample's foliage silhouette area was determined with a LI-3000 (LI-COR Inc., Nebraska USA) area meter. Surface area was calculated by multiplying the foliage area value by two.

2.3.2. Predawn shoot water potential

Predawn shoot water potential (Ψ_{pd}) monitored the progression of drought in each population during dry-down cycles. At each measurement period, two gas exchange seedlings and three seedlings from the general population of each family were randomly selected and Ψ_{pd} measurements were made on excised lower branches. These Ψ_{pd} measurements were made using a pressure chamber (Soil Moisture Corp. Model 3005) before lights were turned on.

2.3.3. Water relations parameters

Osmotic potential at turgor loss point (Ψ_{tlp}) and at saturation (Ψ_{sat}), relative water content at turgor loss point (RWC_{tlp}), and modulus of cell wall elasticity (ϵ_{max}) were determined using the pressure-volume shoot-transpiration method with the pressure-volume curves analyzed following procedures of Schulte and Hinckley (1985). Drought avoidance was determined by the rate of water loss from needles after apparent stomatal closure on shoot samples used in the above described pressure-volume analysis (Vanhinsberg and Colombo, 1990). Foliage was separated from the stem portion of each sample after oven-drying to determine dry weight. The rate of water loss in mg per hour per g foliage dry weight was determined for each sample. Water loss during the first hour after zero-turgor was defined as apparent transpirational flux density cuticular water loss ($TFD_{cuticular}$). Stomata theoretically close during zero-turgor (Schulte and Hinckley, 1985), thus water loss after zero-turgor was assumed to be primarily through the cuticle.

2.4. Experimental design and data analysis

Seedlings from each population (four of the five open-pollinated families as replicates for each population) were placed on light tables in a complete randomized design. Measurements were conducted under well-watered conditions during the day before commencement of dry-down cycles ($N = 8$ seedlings per population). Measurements were made frequently during first dry-down cycle ($N = 26$ to 32 paired Ψ_{pd} and gas exchange measurements per population across the dry-down cycle). Each measurement period during the first dry-down cycle consisted of measurements made on two randomly selected seedlings from eight seedlings tagged for gas exchange in each population. On the fifth day of recovery from the second drought, measurements were once again taken on the sample population ($N = 8$ seedlings per population). For the assessment of water relation parameters pre-trial measurements were made on seedlings (one per family, five per population) before dry-down cycles commenced and at the end of the ten day recovery period after exposure to two dry-down cycles.

Means and standard errors were calculated for each parameter. One-way analysis of variance was conducted for all parameters to determine population (P) differences before dry-down cycles commenced, and a two-way analysis of variance assessed the fixed effect of drought (i.e., $D =$ well-watered vs. water stress), and the random effect of population on all parameters measured during the second recovery period using SYSTAT Statistical Package, version 9v (SPSS, Inc.). A one-way analysis of variance defined population differences of RWC_{tlp} , ϵ_{max} , Ψ_{sat} , Ψ_{tlp} and $TFD_{cuticular}$ (i.e., measured before the drought and only on drought-treated seedlings after two dry-down cycles). If analysis of variance indicated significance, Fisher's least significant difference determined how population means differed. Covariant analysis determined if populations differed in their A , g_{wv} and WUE_i response to changing Ψ_{pd} during the first dry-down cycle. A test for homogeneity of slopes of shifting gas exchange parameters in response to Ψ_{pd} was conducted on log linear values of the above gas exchange parameters, and where slopes differed between populations (P), nonlinear regression analysis modeled these responses. Pearson's product moment correlation coefficient assessed possible relationships between physiological parameter means and various biogeoclimatic site environmental descriptors (defined in Tab. I) for the seven western redcedar populations.

3. RESULTS AND DISCUSSION

3.1. Measured parameters before drought

The seven western redcedar populations had A that ranged from 3.63 to 5.30 $\mu\text{mol m}^{-2} \text{s}^{-1}$, g_{wv} that ranged from 72.6 to 90.5 $\text{mmol m}^{-2} \text{s}^{-1}$ and WUE_i from 0.048 to 0.055 $\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$ under well-watered conditions (Fig. 1). These gas exchange values are comparable to reported values for western redcedar under field conditions (Grossnickle, 1993; Grossnickle et al., 2005). There was variation ($P > 0.05$) in the gas exchange response for various populations. The Gaibaldi population (#11) had the greatest and the Kennedy Lake (#12) the lowest A and g_{wv} , while the Nicolum population (#4) had the greatest, with Yellowpoint (#2) and Creston (#23) the lowest WUE_i . Fan et al. (2008) reported these western redcedar populations to have no variation in g_{wv} and WUE_i .

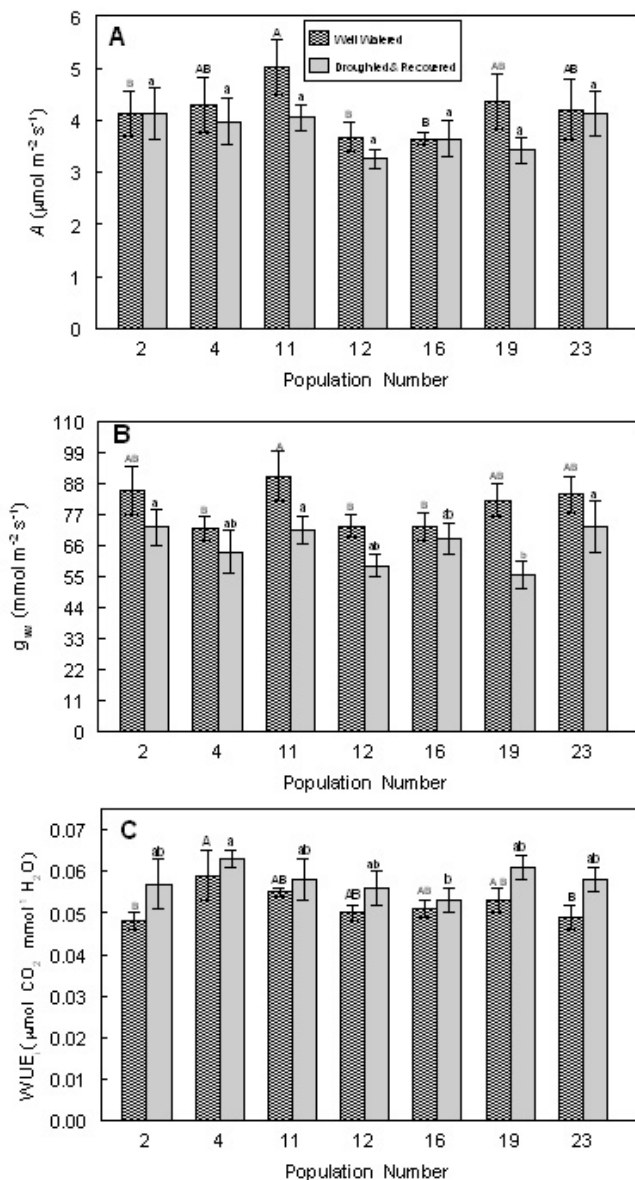


Figure 1. Mean (SE) for net CO_2 assimilation (A), stomatal conductance of water vapour (g_{wv}) and intrinsic water use efficiency (WUE_i) for well-watered seedlings and well-watered seedlings after two dry-down cycles from seven western redcedar populations. Population means for each parameter that do not share the same letter (uppercase for well-watered & lower case for drought recovery) are significantly different ($P < 0.05$ Fisher's LSD test). See Table I for population details.

under well-watered conditions, while under forest site conditions the two populations from Vancouver Island (Yellowpoint #2 & Kennedy Lake #12) had greater A and g_{wv} , across a full range of vapor deficit conditions (Grossnickle et al., 2005). Varying gas exchange response patterns for the same western redcedar populations under a range of test conditions indicates that instantaneous gas exchange parameters are not a definitive means to define population performance differences.

Water relations parameters had the following range of values: 81.9% to 86.8% for RWC_{tlp} , 6.1 MPa to 8.8 MPa for ϵ_{max} , -1.235 MPa to -0.995 MPa for Ψ_{sat} and -1.456 MPa to -1.336 MPa for Ψ_{tlp} (Tab. II). The ranges of these water relation parameters are comparable to reported values for actively growing western redcedar under field conditions (Grossnickle, 1993). Population differences were detected only in RWC_{tlp} , with the Nicolum population (#4) having greater RWC_{tlp} than all other populations, except Gilipin (#19).

3.2. Gas exchange during drought

During drought, A (Fig. 2) and g_{wv} (not shown) declined with decreasing Ψ_{pd} . This is a typical gas exchange pattern for western redcedar to decreasing soil water under field conditions (Grossnickle, 1993). Analysis of gas exchange response to decreasing Ψ_{pd} indicated that the seven populations differed in their A response ($P \leq 0.05$) to changing Ψ_{pd} , with the Garibaldi population (#11) having the least change in A and the Kennedy Lake population (#12) having the largest decline in A to decreasing Ψ_{pd} . Genetic variation in the response of A to changing plant water status has been found to be a common occurrence (e.g., Grossnickle and Fan, 1999; Major and Johnsen, 1996; Russell, 1993). All populations were similar in their g_{wv} and WUE_i response to decreasing Ψ_{pd} (not shown). Fan et al. (2008) reported a similar pattern of g_{wv} and WUE_i response for these same populations under long-term moderate drought, with a similar lack of genotypic variation in these gas exchange parameters reported for other tree species (Major and Johnsen, 1996; Parker and Pallardy, 1991).

3.3. Post drought gas exchange

After drought, all populations had a similar A response during recovery from drought (Fig. 1). Population differences were detected for g_{wv} (Yellowpoint [#2], Garibaldi [#11] and Creston [#23] which were greater than Gilpin [#19]) and WUE_i (Nicolum [#4] was greater than Oliver Lake [#16]). Fan et al. (2008) reported that the same western redcedar populations had comparable gas exchange patterns under drought due to the overall suppression effect of drought. Thus, western redcedar populations express minor variation during actual drought conditions, though they can express variation in instantaneous gas exchange response during recovery from drought.

3.4. Water relations after drought

Western redcedar populations showed a change in water relations parameters in response to drought; RWC_{tlp} , Ψ_{tlp} and Ψ_{sat} decreased, while ϵ_{max} remained relatively unchanged (Tab. II). This is a typical pattern of increased drought tolerance for western redcedar in response to drought (Major et al., 1994). Osmotic adjustment was greatest in the Creston and Gilpin populations (#23 & #19, respectively) for Ψ_{tlp} , and the

Table II. Mean (SE) of relative water content, osmotic potential at turgor loss point, osmotic potential at saturation, modulus elasticity at saturation and cuticular transpiration of seedlings from seven western redcedar populations before and after drought. Population means for each parameter that do not share the same letter are significantly different ($P < 0.05$ Fisher's LSD test). See Table I for population details.

Population number	Population name	2	4	11	12	16	19	23
(RWC_{ip})	Relative water content at turgor loss point (%)	Yellowpoint	Nicolum	Garibaldi	Kennedy lake	Oliver lake	Gilpin	Creston
	<i>Before drought</i>	83.6a (0.6)	86.8b (1.1)	81.9a (0.7)	82.5a (1.4)	83.4a (0.9)	83.8ab (1.3)	82.2a (1.2)
	<i>After drought</i>	80.1a (1.5)	79.2a (1.1)	79.6a (2.2)	81.3a (0.9)	82.9a (1.0)	79.9a (0.9)	78.4a (1.2)
(Ψ_{ip})	Osmotic potential at turgor loss point (MPa)							
	<i>Before drought</i>	-1.357a (0.030)	-1.456a (0.077)	-1.336a (0.069)	-1.348a (0.037)	-1.365a (0.065)	-1.419a (0.050)	-1.396a (0.039)
	<i>After drought</i>	-1.697ab (0.65)	-1.597b (0.071)	-1.765ab (0.149)	-1.576b (.103)	-1.713ab (0.058)	-1.894a (0.024)	-1.899a (0.107)
(Ψ_{sat})	Osmotic potential at saturation (MPa)							
	<i>Before drought</i>	-1.073a (0.023)	-1.235a (0.087)	-0.995a (0.093)	-1.054a (0.067)	-1.082a (0.076)	-1.145a (0.053)	-1.106a (0.017)
	<i>After drought</i>	-1.195b (0.067)	-1.204ab (0.061)	-1.25ab (0.044)	-1.126b (0.104)	-1.409a (0.053)	-1.251ab (0.071)	-1.368a (0.059)
(ϵ_{max})	Modulus of elasticity at saturation (MPa)							
	<i>Before drought</i>	6.7a (0.5)	8.8a (0.8)	6.1a (0.6)	6.6a (0.8)	7.1a (0.6)	7.0a (0.4)	6.9a (0.4)
	<i>After drought</i>	5.5a (0.4)	6.0a (0.5)	7.2a (0.8)	7.5a (0.5)	8.0a (0.6)	7.0a (0.9)	7.0a (0.7)
(TFD _{cuticular})	Cuticular transpiration ($mg\ h^{-1}\ gdw^{-1}$)							
	<i>Before drought</i>	78a (7)	122a (19)	78a (8)	97a (21)	67a (7)	86a (14)	82a (8)
	<i>After drought</i>	118ab (22)	98ab (11)	95ab (26)	165b (13)	134ab (17)	108ab (17)	61a (14)

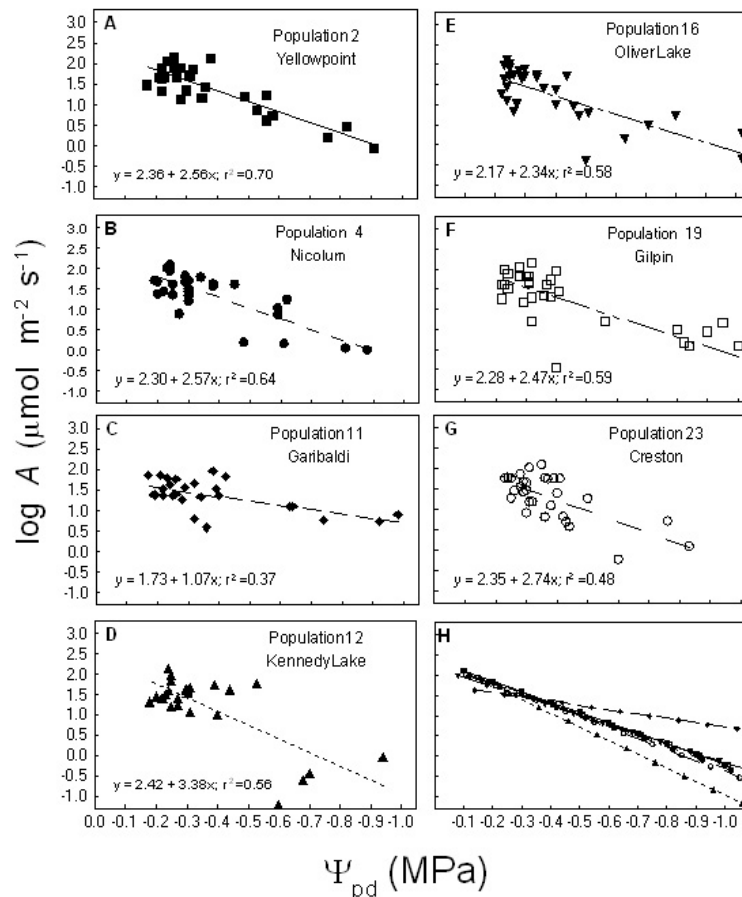


Figure 2. The relationship between log transformed net CO₂ assimilation (A) and predawn shoot water potential (Ψ_{pd}) for seven western redcedar seedling populations during drought. Individual populations are shown in sections A to G, and all populations are shown together in section H. See Table I for population details.

Creston and Oliver Lake populations (#23 & #16) for Ψ_{sat} . There were no population differences for RWC_{tlp} and ϵ_{max} in response to drought. Genetic variation in osmotic adjustment within a species can occur in response to drought (e.g., Abrams, 1988; Aspelmeier and Leuschner, 2004; Johnsen and Major, 1999; Russell, 1993). In the current study, western redcedar populations provided evidence of genetic variation in drought tolerance to short-term drought.

Drought avoidance was determined by measuring apparent cuticular water loss. Cuticular transpiration ($TFD_{cuticular}$) increased across all populations by $\sim 25\%$ after drought (Tab. II). The supposition was that $TFD_{cuticular}$ should decline in tested western redcedar populations after exposure to drought because of the increase in wax structures that can occur on western redcedar foliage after drought (Krasowski and Owens, 1991). However, cuticular water loss increases during shoot elongation (Grossnickle and Folk, 2007; Vanhinsberg and Colombo, 1990) and though these western redcedar seedlings were being exposed to drought, they did show continued shoot growth during the trial (data not shown). For $TFD_{cuticular}$ the Creston population (#23) had the lowest values while the Kennedy Lake population (#12) had the highest values. Ge-

netic variation in $TFD_{cuticular}$ has been detected in other tree species (Grossnickle and Folk, 2007).

3.5. Physiological adaptations to habitat

Gas exchange parameters measured on these western redcedar populations had few significant correlations with climatic indices (Tab. III). The exception to this was with WUE_i that showed a relationship to continentality (Fig. 3) after exposure to drought. In contrast, correlations were found with climatic indices for these western redcedar populations and a number of the water relation parameters after seedlings were exposed to drought (i.e., RWC_{tlp} , ϵ_{max} , Ψ_{tlp} and $TDF_{cuticular}$). Continentality was significantly correlated with the greatest number of water relations parameters (Tab. III and Fig. 3) such that populations from more interior locations had greater drought tolerance (RWC_{tlp} , Ψ_{tlp}), drought avoidance ($TDF_{cuticular}$) and greater water use efficiency (WUE_i) than coastal populations. Water relations parameters for these western redcedar populations were also related to site precipitation characteristics (i.e., mean annual precipitation (MAP) and

Table III. Pearson's correlation coefficient for all pre-drought and post-drought measured gas exchange, water-use, and water relations parameters against elevation and various indices of temperature and precipitation for the location of origin of seven western redcedar populations. One, two or three asterisks indicate significance at the 0.10, 0.05 and 0.01 level of probability. See Table I for more details about locations of populations and descriptors of the site of origin for the western redcedar populations.

	Elevation (m)	(MAP) Mean		(MSP) Mean		(SDJ) Summer dryness index	Continentality (MTWM-MTCM)	Average summer temperature (°C)
		annual precipitation (mm)	summer precipitation (mm)	(ADI) annual dryness index	(SUMAVE)			
(A) Net CO ₂ assimilation (μmol m ⁻² s ⁻¹)								
Well-watered seedlings	0.44	-0.51	-0.59	0.23	0.32	0.62	0.15	
Droughted seedlings	-0.13	-0.51	-0.52	0.30	0.57	0.39	0.34	
Log linear slope of A to decreasing Ψ _{pd}	-0.15	0.13	0.09	0.12	0.02	-0.21	0.19	
(g _{wv}) Stomatal conductance of water vapour (mmol m ⁻² s ⁻¹)								
Well-watered seedlings	0.33	-0.58	-0.64	0.50	0.61	0.45	0.30	
Droughted seedlings	-0.42	-0.15	-0.14	0.05	0.32	-0.01	0.10	
Log linear slope of g _{wv} to decreasing Ψ _{pd}	0.64	-0.46	-0.21	0.54	0.28	0.34	0.08	
(WUE _i) Intrinsic water-use efficiency								
Well-watered seedlings	0.20	0.02	-0.01	-0.33	-0.32	0.30	-0.16	
Droughted seedlings	0.64	-0.62	-0.66	0.44	0.37	0.76**	0.33	
Log linear slope of WUE _i to decreasing Ψ _{pd}	-0.36	0.46	0.48	-0.25	-0.34	-0.48	-0.08	
(RWC _{tip}) Relative water content at turgor loss point (%)								
Before drought	0.04	-0.08	-0.02	-0.08	-0.06	-0.15	0.13	
After drought	-0.57	0.90***	0.95***	-0.72*	-0.77**	-0.87***	-0.50	
(Ψ _{tip}) Osmotic potential at turgor loss point (-MPa)								
Before drought	-0.28	-0.15	-0.35	0.03	0.43	0.11	0.52	
After drought	0.70*	-0.66*	-0.32	0.53	0.29	0.72*	-0.29	
(Ψ _{sat}) Osmotic potential at saturation (-MPa)								
Before drought	0.30	-0.33	-0.20	0.25	0.12	0.42	0.10	
After drought	0.41	-0.34	0.08	0.28	0.02	0.38	-0.56	
(ε _{max}) Modulus of elasticity at saturation (MPa)								
Before drought	0.02	-0.08	0.01	-0.07	-0.09	0.20	0.02	
After drought	-0.15	0.61	0.85**	-0.52	-0.79**	-0.39	-0.94***	
(TFD _{cuticular}) Cuticular transpiration (mg h ⁻¹ gdw ⁻¹)								
Before drought	0.03	-0.03	-0.23	-0.12	-0.05	0.24	0.29	
After drought	-0.47	0.81**	0.65	-0.61	-0.58	-0.84**	-0.07	
Number of significant correlations	1	3	2	1	2	4	1	

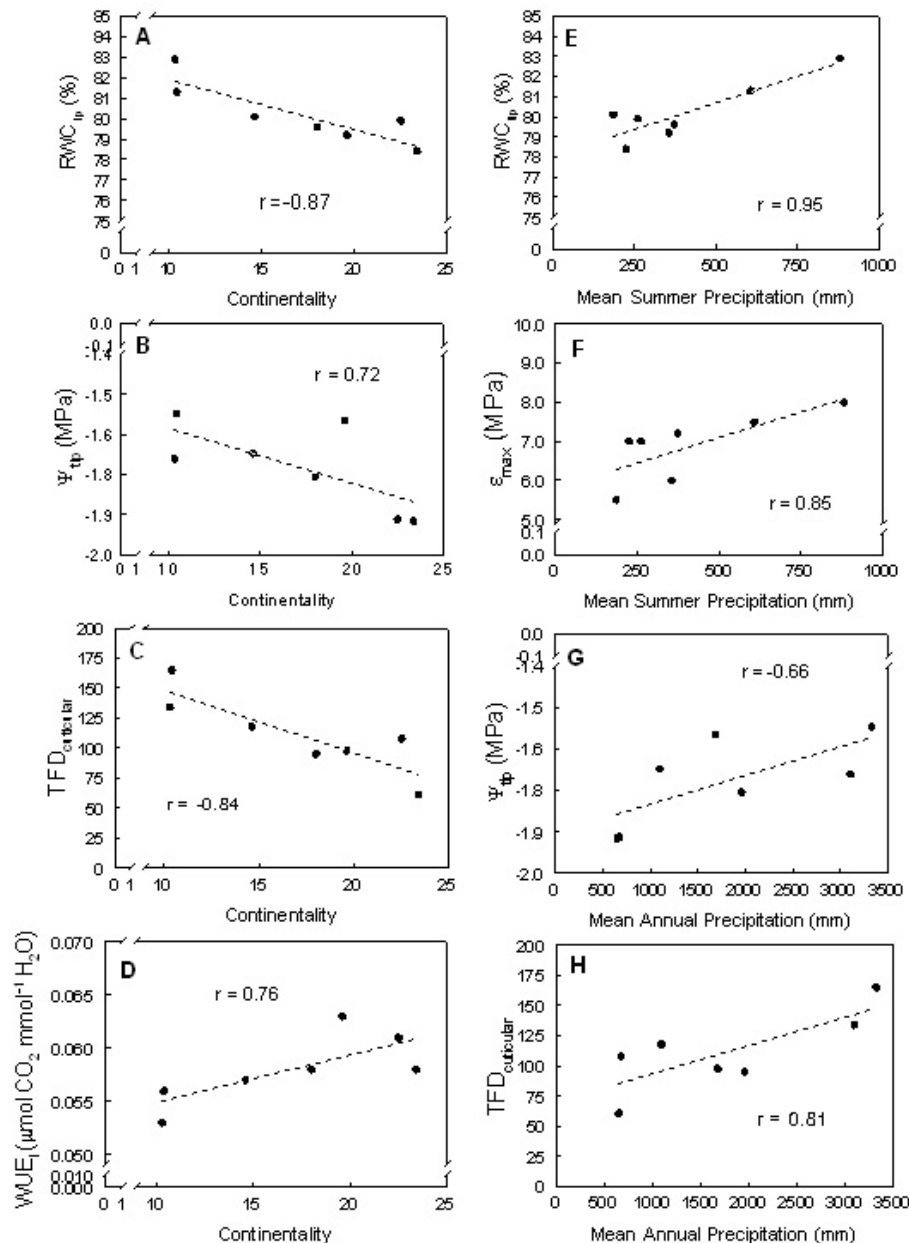


Figure 3. Relationship of seven western cedar populations after exposure to drought with continentality (A) relative water content at turgor loss point (RWC_{tlp}), (B) osmotic potential at turgor loss point (Ψ_{tlp}), (C) cuticular transpiration ($\text{TFD}_{\text{cuticular}}$) and (D) intrinsic water use efficiency (WUE_i); mean summer precipitation with (E) relative water content at turgor loss point (RWC_{tlp}) and (F) modulus elasticity at saturation (ϵ_{max}); annual precipitation with (G) osmotic potential at turgor loss point (Ψ_{tlp}) and (H) cuticular transpiration ($\text{TFD}_{\text{cuticular}}$). The r is Pearson's correlation coefficient, and the line provides a visual assessment of qualitative trends in the data. Table 1 describes more details of environmental indices.

mean summer precipitation); with populations from drier sites having a lower RWC_{tlp} , higher ϵ_{max} , more negative Ψ_{tlp} and lower $\text{TDF}_{\text{cuticular}}$ compared to populations from wetter sites. Genetic variation in gas exchange and water relation parameters can be related to habitat from which a tree species have originated (e.g., Aspelmeier and Leuschner, 2004; Parker and Pallardy, 1985). This trial shows that western redcedar populations from drier-inland habitats had greater development of

drought tolerance, avoidance as well as water use efficiency in response to drought than populations from coastal origin with temperate maritime habitats.

Plants respond to environmental variability through physiological adaptation (Bazzaz, 1996) and genetic adaptability to drought can be expressed by a plants ecophysiological response. By defining the physiological response of a species to site environmental conditions, one provides a means to

understand the biological basis for the adaptability of tree species to site (Dickmann, 1992). A series of trials were conducted to define the response of a group of western redcedar populations originating from coastal to interior biogeoclimatic subzones where summer time environmental conditions can impose a range of drought conditions. Combined results of these trials have found that western redcedar populations from more interior sites with drier summer habitats tended to have greater capability to develop drought tolerance, drought avoidance and instantaneous water use efficiency in response to short term drought (current trial). However, these western cedar populations did not show adaptation to summer climatic conditions related to long term water use efficiency and summer seasonal gas exchange response to vapor pressure deficit (Grossnickle et al., 2005), as well as growth under a range of extended soil water conditions (Fan et al., 2008).

Substantial shifts in potential forest tree species habitats under current climate change predictions may result in more favorable ecosystems that can support western redcedar (Hamann and Wang, 2006). As well, climate-based seed transfer is currently being implemented in British Columbia (O'Neill et al., 2008) and assisted migration will most likely become more important to ensure future resilient forests. Western redcedar population movements beyond both current seed transfer guidelines and present species distribution can benefit from a sound gene resource management program that entails both long-term field trials as well as controlled-environment studies such as reported in this paper. Information from this and other studies will help to identify important western redcedar population adaptation patterns to present and future selection pressures.

4. CONCLUSIONS

Development of drought tolerance and avoidance capability, in response to drought, was found to occur among seven western redcedar populations originating along a precipitation gradient (from east to west) from various biogeoclimatic zones in British Columbia. In contrast, there were minimal population differences in the gas exchange response to drought. Combined results from a series of trials on the same western redcedar populations found that water relations parameters were a better physiological measure than growth, gas exchange response and long term water use efficiency to identify population adaptability to summer climatic conditions. Physiological response patterns of this wide array of western redcedar populations can provide information for developing a sound gene resource management strategy that includes gene conservation, seed movement and tree breeding.

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