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Research paper

Differences in branch hydraulic architecture related to the aridity of growing sites and seed sources of coastal Douglas-fir saplings

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To better understand hydraulic adaptations of coastal Douglas-fir (*Pseudotsuga menziesii var. menziesii* (Mirb.) Franco) to local climate, we examined genetic (G) and environmental (E) responses of branch hydraulic architecture of 7-year-old saplings from dry and wet climates of origin grown at a relatively dry and a relatively wet common garden site in western Oregon. We sampled 2 years of branch growth from three dry-source and three wet-source families grown at both sites (72 branches, total). Overall, only 4 of the 11 traits had significant genetic (G) effects, whereas 9 traits had significant environmental (E) effects ($P < 0.05$). Both dry and wet sources had higher leaf-specific conductance (k_l) at the dry than the wet site, but the values were achieved by different mechanisms and driven by G × E effects for leaf area/sapwood area (A_l/A_s), shoot length (L), specific conductivity (K_s) and leaf-specific conductivity (K_l). Dry sources achieved higher k_l in the dry site through higher K_l (via a lower A_l/A_s and no change in K_s) with no difference in L. Wet sources achieved higher k_l at the dry site through no difference in K_l (via no effect on A_l/A_s, despite decreases in A_l and A_s, and lower K_s) with lower L. Vulnerability to embolism (measured as percentage loss of conductivity at 4 MPa) had no G effect but an E effect, with slightly lower values at the dry site. Specific leaf area had G and E effects, with lower values for the dry sources and site. There were no G or E effects on wood density. The different responses of dry and wet sources to site aridity suggest that populations are differentially adapted to the aridity of growing sites. Population variation in response to aridity should be considered when selecting seed sources for establishing forests for future climates.

Keywords: adaptability, embolism, environmental effects, genetic effects, plasticity.

Introduction

We expect natural selection to give rise to local adaptation to climate, leading to differences in adaptive traits among populations. With rapidly changing climates, however, populations can become maladapted to their native sites (St. Clair and Howe 2007, Lavender and Hermann 2014). The projected increase in frequency and severity of drought in many forested biomes will likely subject trees to conditions to which individuals cannot adjust (Choat et al. 2012, Zhu et al. 2012), probably leading to large-scale tree mortality (Adams et al. 2009, Allen et al. 2010, Rehfeldt et al. 2014, Allen et al. 2015). Moreover, even if relatively dry conditions do not kill trees through physiological limitations, they may pre-dispose the trees to mortality from secondary factors, such as insects and fungi (Desprez-Loustau et al. 2006, Jactel et al. 2012, Kolb et al. 2016, Seidl et al. 2017). Whereas there is much information on interspecific variation in hydraulic strategies in different climates (e.g., Maherali et al. 2004), there is much less information on intraspecific variation (Choat et al. 2018, Rosas et al. 2019, Skelton et al. 2019), and particularly in the degree to which plasticity itself is a genetic trait (Pigliucci 2005). Understanding variation between tree populations in their locally adaptive traits, including their responses to environment, may enhance our options for management, such as assisted migration (Aitken et al. 2008, Williams and Dumroese 2013), under future climates.

This study focused on patterns of variation in hydraulic strategies in coastal Douglas-fir (*Pseudotsuga menziesii var. menziesii*) from relatively dry vs. wet seed sources in relatively dry and wet common gardens. We interpret the results in terms of genetic (G), environmental (E) and G × E effects. In studies of genotypes subjected to different environments, the E effects are termed 'plasticity' (Bradshaw 1965) and the G × E effects are termed 'genetic variation for plasticity' (Pigliucci 2005). We studied the same populations, not the same genotypes, in two environments, and therefore, we do not use the plasticity nomenclature. Instead, any significant E effects are evidence of similar adaptations to the environment of the different populations, and any significant G × E effects are evidence of different adaptations to environment by the different populations. It is particularly important to distinguish between E effects and G × E effects, so we can more accurately predict future phenotypes (e.g., Gugger et al. 2015) as well as the extent to which a population or populations can mitigate environmental variation. However, without experimentation using common gardens, it is impossible to distinguish whether observed phenotypes are influenced more strongly by genetics, environment or genetic variability in plants' response to the environment (Moran et al. 2017).

Nonetheless, comparison of hydraulic strategies of trees in their native sites (rather than in common gardens) gives clues that soil moisture is a selective factor for coastal Douglas-fir (Chauvin et al. 2019). Douglas-fir populations show die-back or death after droughts (e.g., Guarin and Taylor 2005, Williams et al. 2012), reduced growth in relatively dry years and/or on drier sites (Littell et al. 2008, Chen et al. 2010, Eilmann et al. 2013, Sergent et al. 2014*a*, Sergent et al. 2014*b*, Restaino et al. 2016), and increased growth when there is decreased competition for water from other vegetation (Maguire et al. 2009, Gonzalez-Benecke and Dinger 2018).

We consider that branch hydraulic trait values fall on a spectrum from conservative to opportunistic, with more conservative values acting to minimize the risk of hydraulic failure and mortality in branches in low-water environments, and more opportunistic values acting to enhance growth and competitiveness in high-water environments. We expect drier sources to have trait values that are more conservative than those of wetter sources, as is generally observed in gymnosperms (Moran et al. 2017). For the traits examined in this study, we consider the following values as conservative: low specific leaf area (SLA), leaf area per sapwood area (A_l/A_s) and vulnerability to embolism; and high leaf-specific conductivity (K_l) and leaf-specific conductance (k_l, which is K_l divided by shoot length, L). Lower A_l, A_s and L are also more conservative trait values because they are indicative of lower growth rates. We did not judge K_s or K_h along this spectrum because high values would be useful in a low-water environment on the short term by transporting water more quickly, but deleterious on the long-term by depleting soil water more quickly. Common garden studies show evidence of a more conservative hydraulic strategy for drier coastal Douglas-fir provenances. When water is withheld, drier provenances have higher survival than wetter provenances (Ferrell and Woodard 1966, Pharis and Ferrell 1966, Heiner and Lavender 1972). Additionally, seedlings and saplings from drier provenances skew their growth toward earlier in the growing season when water is more plentiful, with earlier dates of budburst (Heiner and Lavender 1972, St. Clair et al. 2005, Gould et al. 2012) and bud-set (White 1987, Gould et al. 2012), and earlier completion of half of the year's stem diameter growth (Gould et al. 2012). When grown on moist sites, seedlings or trees from drier provenances had less height growth (White 1987, Eilmann et al. 2013), deeper roots (Heiner and Lavender 1972), lower cuticular transpiration rate, SLA (Bansal et al. 2015*a*) and root and shoot vulnerability to xylem embolism (Kavanagh et al. 1999).

Two patterns of structural and physiological adjustments have been demonstrated in conifers to maintain water transport to foliage in dry (relative to moist) conditions (Martínez-Vilalta et al. 2004): a drought tolerant strategy in which plants in drought have lower vulnerability to tension-induced embolism, and a drought avoidance strategy in which plants in drier situations develop higher values of K_l. The goal of our research was to learn if branch tips from a drier provenance differ in drought strategy from those from a wetter provenance. We focused on the traits SLA, vulnerability to embolism, K_l and k_l but also investigated which, if any, of several branch architectural and hydraulic traits contributed to differences in K_l and k_l. The examination of traits at more than one scale allows us to identify mechanisms of compensations or exacerbations in hydraulic performance (e.g., Gartner 1991*a*, Gartner 1991*b*, McDowell et al. 2002*a*, Martínez-Vilalta et al. 2009, Meinzer et al. 2009, Barnard et al. 2011, Corcuera et al. 2012, Sterck et al. 2012, Lachenbruch and McCulloh 2014, Hacke et al. 2015, Rosas et al. 2019). Of the two strategies discussed above, the drought tolerant strategy has been reported for 2-year-old coastal Douglas-fir seedlings (Kavanagh et al. 1999), with lower vulnerability to embolism in drier vs. more mesic provenances. However, most comparisons of vulnerability to embolisms in conifers report no, or very small, effects of provenance or site (Stout and Sala 2003, Martínez-Vilalta et al. 2009, Corcuera et al. 2011, Sáenz-Romero et al. 2013, Lamy et al. 2014, Chauvin et al. 2019). In contrast, most studies on conifers from drier provenances or sites show a drought-avoidance strategy, with higher K_l in the relatively drier provenances (López et al. 2016) or sites (e.g., Mencuccini and Grace 1995, López et al. 2016, but also see Sterck et al. 2008 and Hudson et al. 2018). The higher value of K_l is most often driven by lower A_l/A_s in the dry provenance or site (e.g., Mencuccini and Grace 1995, López et al. 2016), although it can be driven by higher K_s (e.g., Peguero-Pina et al. 2011). Lower SLA is another drought

avoidance strategy. Previous studies have shown lower values in drier provenances and sites (Bansal et al. 2015*a*), sites (Reich et al. 1999) and locations within a tree (Fellner et al. 2016).

We studied branch material in part because sampling branches has a minor impact on the remaining plant in long-term studies. Our assumption is that the performance of a branch tip is positively correlated with plant performance during a drought. We make this assumption because conifer branches are less vulnerable to embolism than same-aged bole material (e.g., Domec et al. 2008) and they represent a large portion of the plant's body that interacts with the environment. Drought adaptations, however, involve interacting physical, physiological and life history traits throughout the plant body and throughout life stages (Maherali et al. 2002, Meinzer 2003, Hinckley et al. 2011, Li-Marchetti et al. 2015), and there is little information about the feedback between conifer growth and wood development in the tree in general (Hacke et al. 2015), and even less information on branches compared with the main axis. In *Populus deltoides* Marshall, for example, branches were more drought-sensitive than the bole and were sacrificed under drought to favor the plant's survival (Rood et al. 2000).

We tested the following G, E and G × E hypotheses: (i) Dry sources have lower SLA and higher K_l, and k_l than the wet sources, but both dry and wet sources have similar wood density and vulnerability to embolism. (ii) Plants grown at a dry site have lower SLA and higher K_l, and k_l than those grown at a wet site, but at both sites they have similar wood density and vulnerability to embolism, and (iii) the two populations (dry and wet sources) differ in their hydraulic strategies in the two environments, with the dry sources displaying site differences that appear more conservative than the site differences of the wet sources.

Methods

Selection of test sites and genetic sources

The study used a subsample of saplings in the Douglas-fir Seed-Source Movement Trial (SSMT, Bansal et al. 2015*b*). The SSMT is a reciprocal transplant study to evaluate the progeny of open-pollinated families of coastal Douglas-fir from 12 geographic regions, all grown at nine test sites in western Oregon and western Washington (Gould et al. 2012, Bansal et al. 2015*b*). At each site, there were four replicate blocks of seedlings. Each block contained one plot for each region, and each plot had two individuals from each of 10 families. At the time of this study, trees were 7-years old from seed and had 5 years of growth in the field.

To select two contrasting test sites (of the 9 available), we estimated test-site climates using the online model ClimateWNA (Wang et al. 2012, 2015). The model extracts and downscales the inputs of monthly climate and solar radiation data that are generated by the PRISM model (Daly et al. 2002) with data from the 1961–90 normal period. The model generates scale-free values based on local elevational adjustment for a user-entered latitude, longitude and elevation. Our wet test site (referred to as Nortons in other publications) was in the central Oregon Coast Range (485-m elevation) 35-km west of Corvallis, OR, USA. Our dry test site (at the J. Herbert Stone Nursery) was 270-km south of the wet test site, in a broad inland valley (185-m elevation) near Medford, OR, USA, between the Siskiyou Mountains and the Cascades Range. The dry and wet sites were similar in number of frost-free days but differed in temperature, precipitation and aridity (Table 1). ClimateWNA predicted that on average, the dry site is warmer and receives about one-third the annual and summer precipitation of the wet site. This combination produces a much more arid climate at the dry site, as shown by its 3.9-times higher estimated value of summer heat:moisture index and 2.7-times higher value of aridity, as shown by the Hargreaves climatic moisture deficit compared with the wet site (Table 1).

We elected to use plant material from the geographic region closest to the dry or wet test site, respectively, but still needed to choose which three of the 10 available open-pollinated families per region to study. We used ClimateWNA to characterize the climates at the seed-source locations for each of the families in those two selected regions, then chose the three families per region whose climate of origin were most similar to either the dry site ('dry sources') or the wet site ('wet sources'). Their estimated climate values are similar to those of the dry and wet test sites, respectively (Table 1).

Sampling design

At each site, we sampled two trees from six families (three dry-source families and three wet-source families) from each of three blocks. This experimental design resulted in samples from 18 trees from dry sources and 18 trees from wet sources at both the dry and wet sites (36 samples total, per site), with the same six families represented at both sites.

The sampling of a tree consisted of taking a branch tip. We generally sampled the largest primary branch at the tree's 5-year-old whorl (Figure 1) but selected an alternate branch if the largest branch was forked or its distal end was shaded within the canopy of a neighboring tree. Branches were harvested after pre-dawn, and after terminal buds had set and most or all of the latewood had formed (at the wet site, on 22 August–2 September 2014; at the dry site, on 15 September 2014–9 October 2014). Branches were kept in beakers of water and covered with plastic bags until they were processed, in a random order.

Branch architecture and SLA

We separated each sample into the current-year segment (year n, which included the whorl branches at its base) and the previous segment (year $n - 1$) (Figure 1). The base of the $n - 1$ segment was kept in water throughout processing for later hydraulic assessments. We refer to the main branch axis as

Table 1. Geographic and climatic descriptions for two coastal Douglas-fir common garden test sites (dry or wet) and the location of origin for each family ($n = 3$) in each of seed sources tested (dry or wet). The four-digit numbers under seed source are family IDs from the larger study, the Douglas-fir SSMT.

Geography/climate	Test site		Seed source and family							
	Dry	Wet	Dry				Wet			
			Mean	3,094	3,285	3,286	Mean	6,016	8,045	8,524
Latitude (°)	42.349	44.664	42.623	44.642	44.642	44.642	44.642	42.923	42.472	42.475
Longitude (°)	−122.939	−123.687	−123.088	−123.752	−123.752	−123.752	−123.752	−123.030	−123.116	−123.118
Elevation (m)	185	415	471	228	228	228	228	429	491	493
FFP (days)	298	282	297	308	308	308	308	296	297	299
MAT (°C)	13.0	9.7	12.1	10.9	10.9	10.9	10.9	11.6	12.3	12.3
MWMT (°C)	22.4	15.9	21	17.2	17.2	17.2	17.2	19.9	21.5	21.5
MAP (mm)	535	1711	826	2,653	2,653	2,653	2,653	1,041	713	725
MSP (mm)	87	236	120	346	346	346	346	155	101	103
SHM	259	67	183	53	53	53	53	128	212	208
CMD (mm)	809	303	640	243	243	243	243	543	690	686

Abbreviations: FFP, frost-free period; MAT, mean annual temperature; MWMT, mean temperature of the warmest month; MAP, mean annual precipitation; MSP, mean summer precipitation (May–September); SHM, summer heat-to-moisture index (MWMT/(MSP/1000)); CMD, aridity (Hargreaves climatic moisture deficit, Hargreaves and Samani 1982). All data were obtained from ClimateWNA (Wang et al. 2012).

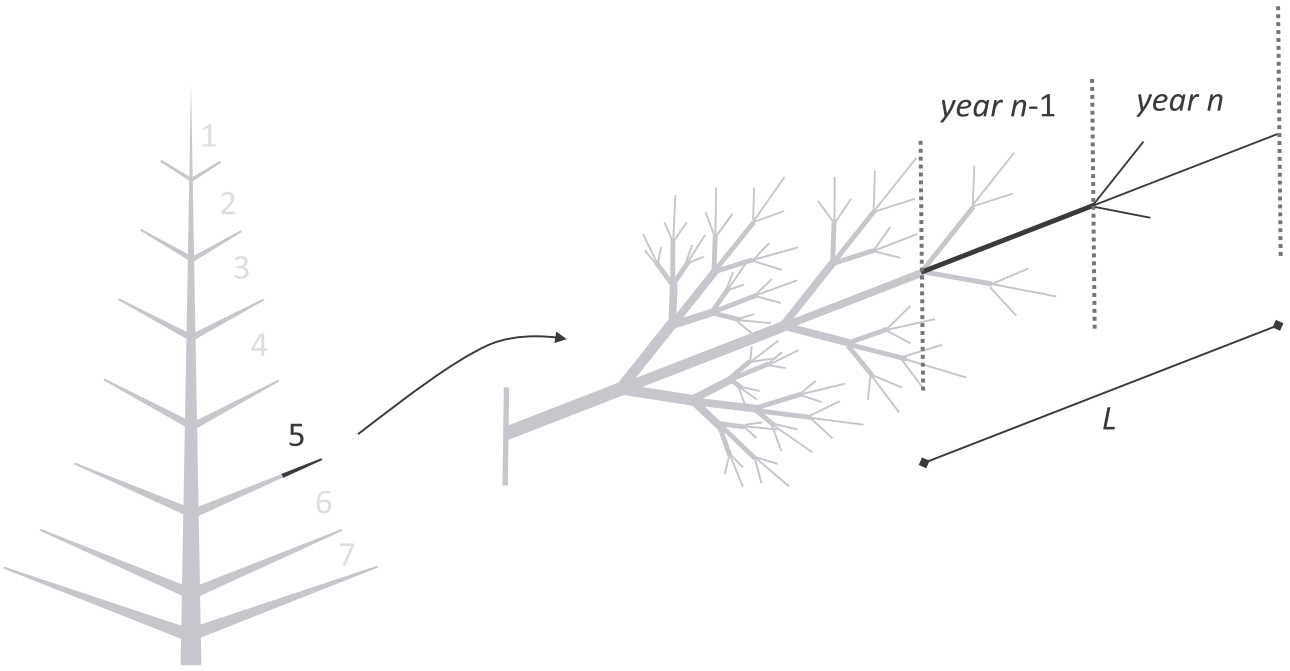

Figure 1. Sampling locations on the tree. Left: Location of 5-year old branch. Right: Schematic of branching pattern on the sampled branch; not all branches per whorl are shown. Hydraulic measurements were made on the year $n - 1$ segment. Leaf area included foliage in both segments (including whorl branchlets of year n). Shoot length was the branch length of both years.

the secondary branch, and the branches off it as the branchlets. Shoot length (L, m) was the length of secondary branch in year n and year $n - 1$ (Figure 1). The cross-sectional area of the shoot (A_s) was taken from the hydraulic measurements of the year $n - 1$ segment.

To estimate fresh leaf area (A_l) for year n and year $n - 1$ of each sample, we first removed all the sample's needles and placed them in four compartments: branch needles for year n and year $n - 1$, and branchlet needles for year n (if branchlets were present) and year $n - 1$ (which were mostly the whorl branchlets). We oven-dried (90 °C) and weighed the branchlet needles for the 2 years separately, then estimated their area using the year n or year $n - 1$ SLA calculated for the branch needles (below).

For the branch needles, we selected 20 fresh needles from year n and from year $n - 1$, then discarded the remaining needles. We estimated their pooled area (separately by year) using ImageJ version 1.51 e5 (Rasband, W.S., ImageJ, U. S.

National Institutes of Health, Bethesda, MA, USA, https://imagej.nih.gov/ij/, 1997–2016) and then oven-dried and weighed them to calculate SLA (fresh area per dry weight, $cm^2\ g^{-1}$) and average needle area. We estimated the number of needles that had been borne directly on the year n or year $n - 1$ branch by counting needle scars visible from one side and multiplying by two. Our goal was to estimate the needle area produced, rather than the area that remained after abscissions. Needles were abscised on an ongoing basis, and its timing likely varied between sites and seed sources. Branch needle area was calculated as branch leaf number multiplied by weight/needle, for each year separately. Total leaf area (A_l) was the sum of branch and branchlet leaf areas for year n and year $n - 1$. Leaf area/sapwood area was A_l divided by A_s. For treatment comparisons (below), we averaged the SLA of the 2 years.

Hydraulic measurements

We estimated K_h, K_s, vulnerabilty to embolism, K_l and k_l of the 2-year-old branch wood of the samples described above, as follows. Using clippers, we removed an 11-cm-long section of 2-year-old wood (year $n - 1$, Figure 1), avoiding the basal 1 cm of stem because of its pronounced curvature and compression wood in some samples. After removing the bark, we affixed a label with a rubber band and submerged the sample in distilled water acidified with KCl to pH 2.0 to prevent microbial growth (Sperry et al. 1988). The submerged samples were held under vacuum to remove embolisms until their mass stabilized, 2–7 days, replacing the acidified water daily. Studies in our lab have shown that small-diameter coastal Douglas-fir samples can be maintained in acidified water and/or in refrigeration for up to 21 days with no decrease in their transport properties (e.g., Domec 2002, Dunham 2006).

To estimate the initial K_h, we followed McCulloh et al. (2015), with one exception. For air injection for vulnerability to embolism studies, we needed to remove the bark, but for hydraulic assessment, we needed to wrap samples in Parafilm ™ (leaving cut ends exposed for measurements). After trimming both ends, we recorded segment length (l, m), fitted the ends with connectors and attached the upstream connector to a filled tube leading from an elevated reservoir of filtered (to 0.22 μm) acidified water. We recorded the height of the reservoir above the sample, about 0.650 m, to the nearest mm. After attaching the downstream connector to an empty pipette marked in 0.01 or 0.05 mL increments, we opened the upstream valve, then recorded the time at which the meniscus passed 3–5 successive markings on the pipette. Afterward, we removed the connectors and Parafilm™ and placed the sample in fresh acidified water for assessment of vulnerability to embolism.

We assessed vulnerability to embolism using the air-seeding method (Sperry and Saliendra 1994) with a double-ended pressure chamber (PMS Cavitation Chamber, model 1505D-EXP). Our protocol came from pilot studies that first identified how long to hold the samples at a pressure and how long to equilibrate them after pressurization. In these studies, we fit numerous branch samples from a dry- and a wet-source family into the double-ended pressure chamber and subjected the sample to an overpressure of 1–6 MPa for 30 s, 45 s, 1 min or 2 min. Afterward, we wetted the sample, patted it with paper towel, weighed it and submerged it in acidified water. We then timed how long it took for the overpressure to equilibrate as shown by a decrease or cessation of air bubbles from the cut ends, while periodically removing the sample from the water, patting it with paper towel, weighing it and returning it to the water. After a 30-s pressurization, samples equilibrated within 1 hour, but at 45-s pressurization, they needed many hours to equilibrate, and at 1- or 2-min pressurization, some samples needed more than 24 hours. Also, at equilibration periods over 1 hour, many samples gained weight. We therefore chose pressurization for 30 s and equilibration of 1 hour.

Next, we needed to choose a pressure at which to assess samples. If possible, we wanted one pressure at which there was substantial sample-to-sample variability but also substantial loss of K_h. We constructed vulnerability curves for three branch samples from both a wet source and site, and a dry source and a site (harvested pre-dawn on 5 August 2014 and 14 August 2014, respectively) using pressures of 1–7 MPa in 1-MPa steps. After each equilibration and before the next K_h measurement, we re-trimmed sample ends, measured l and wrapped the sample with Parafilm™. We then removed the Parafilm™ for pressurization. Percent loss of K_h was calculated as the percent difference between initial K_h and the K_h after pressurization at specific pressure and subsequent equilibration, divided by the initial K_h (see K_h calculation below). Because the vulnerability curves had similar shapes for the two subsamples and because they showed the most marked separation mid-curve, at 4–5 MPa (Figure 2), we chose to assess vulnerability to embolism at 4 MPa, which we called PLC@4. This same value was used by Rosner et al. 2007. Therefore, for the current study, we pressurized samples to 4 MPa for 30 s and allowed them to equilibrate for 1 hour before assessing final K_h using the same methods as for initial K_h.

We cut the sample at its mid-point for sapwood area (A_s, under bark, excluding pith) which we estimated with image analysis using a Keyence VHX-1000 Digital Microscope (Itasca, IL). For hydraulic calculations, the pressure gradient (MPa/m) was the pressure at the upstream end of the sample, calculated as reservoir height (m) times 0.01 MPa/m divided by l (m). We converted the water volume (ml) to mass (kg) and then calculated hydraulic conductivity (K_h, kg m s^{-1} MPa^{-1}) as the mass flow rate divided by the pressure gradient that induced the flow. We calculated xylem-area specific conductivity (K_s, kg m^{-1} s^{-1} MPa^{-1}) as K_h divided by A_s. Percent loss of conductivity at 4 MPa (PLC@4) was calculated as the percent difference between the initial and final K_h values divided by the initial

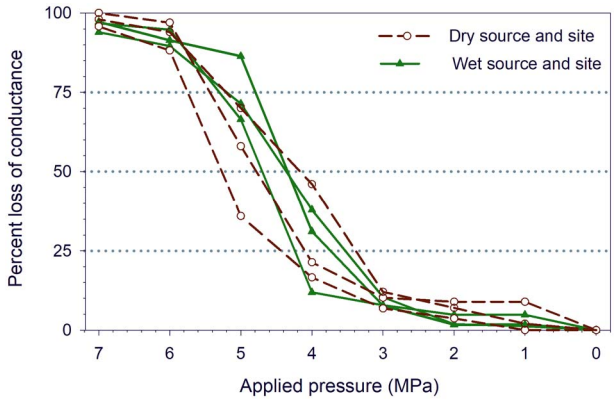

Figure 2. Vulnerability to embolism curves of year $n - 1$ branch segments from a dry genetic source grown at the dry site ($n = 3$) and a wet genetic source grown at the dry site ($n = 3$) for coastal Douglas-fir. This relationship was used to select 4 MPa as the test pressure (see text for details).

value. Leaf specific conductivity (K_l, kg m^{-1} s^{-1} MPa^{-1}) was calculated as K_h divided by A_l, and leaf-specific conductance (k_l) (kg m^{-2} s^{-1} MPa^{-1}) was calculated as K_l divided by shoot length (L).

Wood density

After we finished a sample's hydraulic measurements, we estimated its wood density (dry mass/green volume) because it is simple to measure, and in some studies, its values are positively correlated with resistance to embolism (e.g., Hacke et al. 2001) and/or negatively correlated with K_s (e.g., Bucci et al. 2004). These correlations can make wood density a simple proxy measurement, even though the structural characteristics that combine to make wood density do not necessarily confer these hydraulic values (Lachenbruch and McCulloh 2014). We sawed a 2.0-mm-thick disk from the mid-section of each sample, then let the disks air dry. The samples were X-rayed at INTA, San Carlos de Bariloche, Argentina, after first orienting them so that potential compression wood was always in the same radius. They were X-rayed across two perpendicular diameters (four radii) of 0.5-mm width (Polge and Nicholls 1972). Following Dalla-Salda et al. 2014, WinDENDRO was used to produce densities along three radii that did not include compression wood, and the data from the three radii were then averaged.

Data analysis

We used a linear mixed model (LMM) to test the effect of source (dry vs. wet), site (dry vs. wet) and their interaction for each of the 11 plant traits. Each trait was a dependent variable, source and site were categorical variables and family within sources was a random effect as part of the error term. We report the F- and P-values for the main effects and their interaction. We then used a second LMM to make multiple comparisons of the four combinations of source type (dry or wet) and site type (dry or wet), including family as a random effect. This second model allowed us to characterize the nature of the interactions (e.g., at which site(s) were the genetic effects significant, in which source types were the site effects significant, and what were the relative mean values of each site/source combination). All statistical analyses were done with STATGRAPHICS Centurion 18 (v. 18.1.11, StatGraphics Technologies, 1982–2018, The Plains, VA).

Results

Main effects and their interactions

Fewer of the traits showed significant G effects than E effects at $P < 0.05$ (4 vs. 9 traits, respectively, Table 2). At $P < 0.10$, 5 traits showed significant G effects and all 11 of the traits showed significant E effects (Table 2). The significant genetic effects were in SLA, A_l, A_l/A_s and k_l. Four traits had significant G × E interactions: A_l/A_s, L, K_s and K_l (Table 2). The most integrative trait, k_l, whose calculation includes A_l/A_s, L and K_s, showed significant G and E effects but no G × E interaction.

Following our definition that the more conservative trait value is the one that leads to a lower risk of a branch's hydraulic failure and mortality in low-water environments, then all of the significant effects had more conservative values in the dry than the wet sources, and at the dry than the wet site (Table 2).

Multiple comparison tests: leaf and branch architecture

For SLA and A_l, mean values were significantly lower for the dry than wet sources at both sites and were significantly lower at the dry than the wet site (Figure 3A and C). For wood density, there were no significant differences among the four treatment combinations (Figure 3B). For A_s, the only significant pairwise comparison was between the sites for the wet sources, which had lower values at the dry than the wet site (Figure 3D). For A_l/A_s, the dry sources had lower values than the wet sources at both sites, and the dry sources (but not the wet ones) had a lower mean value at the dry site than the wet site (Figure 3E). For L, the dry sources had no site effect but the wet sources had much lower values of L at the dry site than at the wet site (Figure 3F).

In all the significant comparisons, the trait values were more conservative in the dry sources than the wet sources, and at the dry than the wet site (Figure 3).

Multiple comparison tests: branch hydraulics

For PLC@4 MPa, there were no significant differences in the four treatment combinations except that the dry sources at the dry site had lower mean values than wet sources at the wet site (Figure 4A). The main effects analysis above (Table 2) found a significant E effect ($P = 0.03$) that is not seen for the wet or dry sources individually (Figure 4A). The traits K_h and K_s followed the same pattern as L (Figure 3F), with the dry sources

Table 2. Genetic, environmental and G × E effects on leaf or branch architecture and branch hydraulic traits from Douglas-fir families at two common garden sites (Values in bold font are significant at $P < 0.05$).

Trait[a]	Genetic effects				Environmental effects				G × E effects	
	Dry sources mean	Wet sources mean	*F*-value	*P*-value	Dry site mean	Wet site mean	*F*-value	*P*-value	*F*-value	*P*-value
Leaf or branch architecture										
SLA ($cm^2\ g^{-1}$)	57.8	63.5	58.27	**0.0016**	57.4	63.9	30.48	**0.0000**	0.03	0.8744
Wood density ($g\ cm^{-3}$)	0.493	0.487	0.22	0.6660	0.483	0.497	3.00	0.0882	0.10	0.7534
A_l (m^2)	0.067	0.100	73.12	**0.0010**	0.062	0.106	39.58	**0.0000**	0.61	0.4364
A_s ($\times 10^{-5}\ m^2$)	2.32	2.51	1.43	0.2976	2.04	2.78	10.44	**0.0019**	1.20	0.2768
A_l/A_s ($m^2\ m^{-2}$)	3,053	4,106	48.61	**0.0022**	3,173	3,986	16.29	**0.0001**	5.00	**0.0289**
L (m)	0.57	0.65	2.68	0.1767	0.52	0.70	34.37	**0.0000**	16.92	**0.0001**
Branch hydraulics										
PLC@4	21.7	29.6	2.88	0.1648	20.8	30.6	4.91	**0.0302**	1.12	0.3566
K_h ($\times 10^{-5}\ kg\ m\ s^{-1}\ MPa^{-1}$)	1.53	1.88	3.57	0.1317	1.36	2.06	10.09	**0.0023**	2.366	0.1290
K_s ($kg\ m^{-1}\ s^{-1}\ MPa^{-1}$)	0.636	0.713	3.62	0.1299	0.644	0.706	3.96	0.0510	5.73	**0.0196**
K_l ($\times 10^{-4}\ kg\ m^{-1}\ s^{-1}\ MPa^{-1}$)	2.39	1.81	6.69	0.0609	2.29	1.91	4.27	**0.0427**	8.94	**0.0039**
k_l ($\times 10^{-4}\ kg\ m^{-2}\ s^{-1}\ MPa^{-1}$)	4.22	2.98	33.06	**0.0045**	4.40	2.80	34.78	**0.0000**	2.62	0.1105

[a]Abbreviations: SLA (specific leaf area), K_s (specific conductivity), PLC@4 (percent loss of conductivity at 4 MPa), A_l (leaf area), A_s (sapwood area), A_l/A_s (sapwood area/leaf area), L (shoot length), K_h (hydraulic conductance), K_l (leaf-specific conductivity), k_l (leaf-specific conductance).

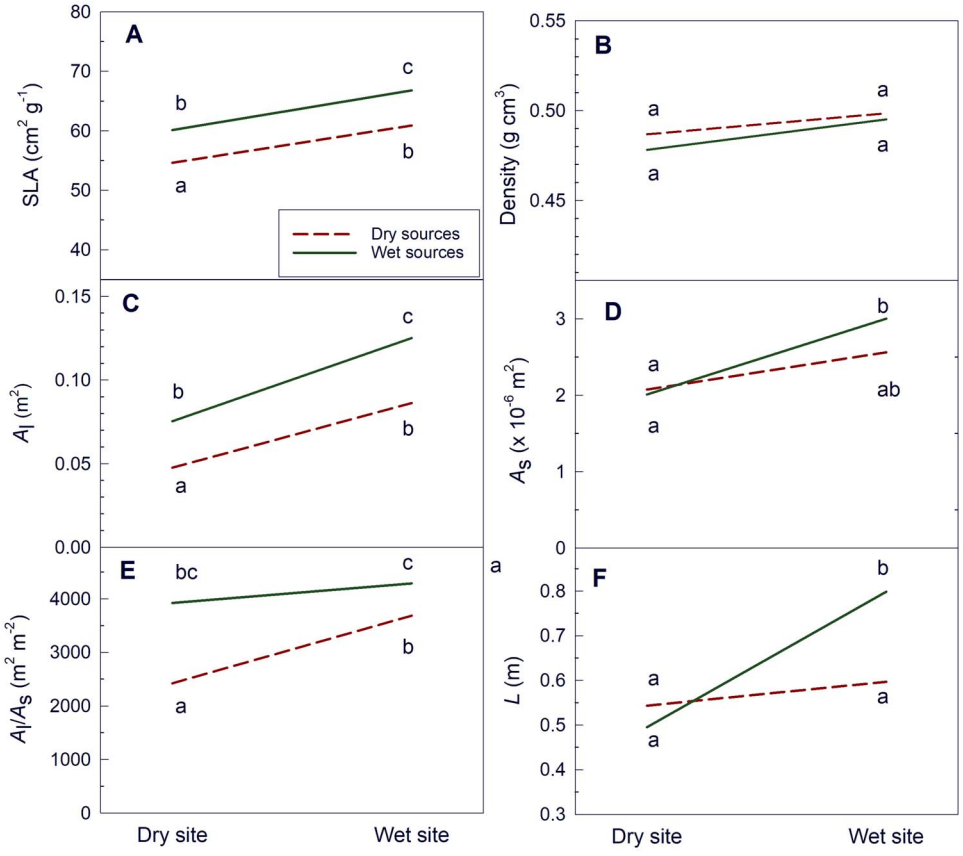

Figure 3. Effects of environment (dry vs. wet site) on genetic material (dry vs. wet sources) for estimated leaf and branch architectural traits of coastal Douglas-fir: (A) specific leaf area (SLA), (B) wood density, (C) leaf area (A_l), (D) sapwood area (A_s), (E), leaf area/sapwood area (A_l/A_s) and (F) shoot length (L). Means and significance are from multiple comparison tests ($n = 18$ for each data point). For each trait, values denoted by the same letter are not significantly different at $\alpha = 0.05$.

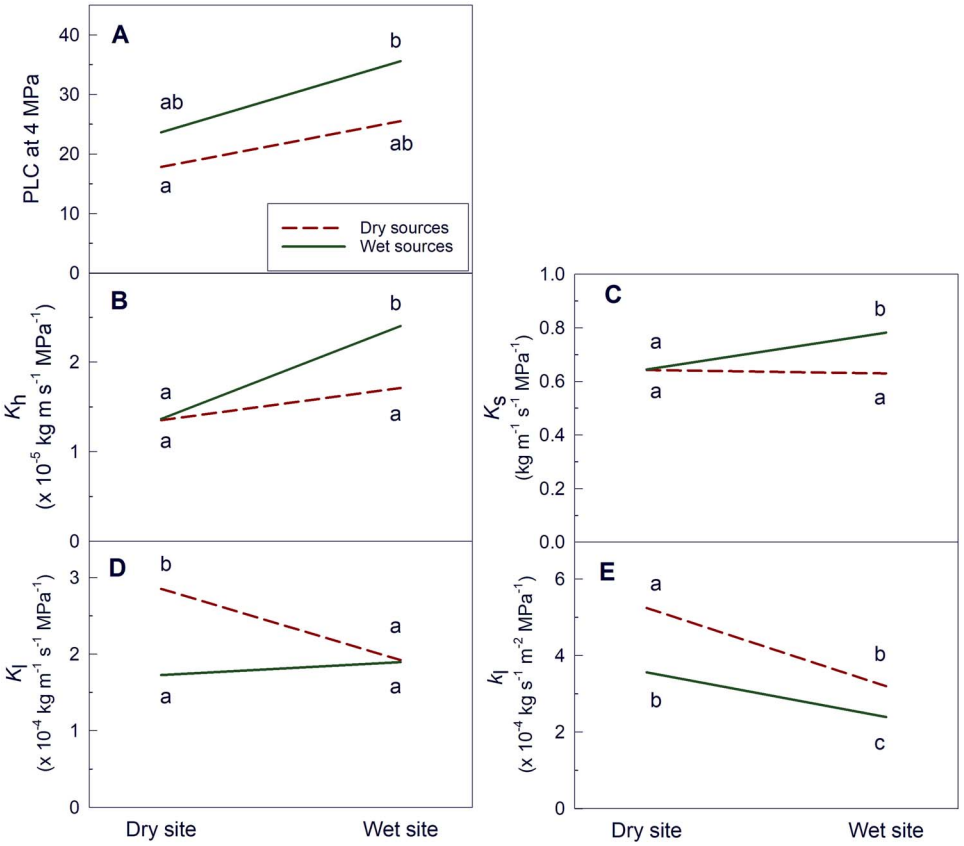

Figure 4. Effects of environment (dry vs. wet site) on genetic material (dry vs. wet sources) for estimated branch hydraulic traits of coastal Douglas-fir: (A) percent loss of conductivity at 4.0 MPa (PLC@4), (B) hydraulic conductivity (K_h), (C) specific conductivity (K_s), (D) leaf-specific conductivity (K_l) and (E) leaf-specific conductance (k_l). Means and significance are from multiple comparison tests (n = 18 for each data point). For each trait, values denoted by the same letter are not significantly different at α = 0.05.

showing no significant site difference, whereas the wet sources had lower values at the dry than the wet site (Figure 4B and C). For K_l, the dry sources had higher values at the dry than wet site, whereas the wet sources had no site effects (Figure 4D). The most integrative trait, k_l, had higher values in the both source-types at the dry site than at the wet site and higher values in the dry sources than the wet sources (Figure 4E).

We did not evaluate the values of K_h or K_s for degree of conservatism (see Introduction), but for both traits, there were no source effects at the dry site, but at the wet sit, dry sources had lower values (Figure 4B and C). In all other significant comparisons, the trait values were more conservative in the dry sources than the wet sources, and at the dry than the wet site (Figure 4).

Discussion

We examined site and source effects on hydraulic architecture of branches of coastal Douglas-fir seedlings to gain insights into strategies and adaptation of provenances from relatively dry or wet climates of origin when grown on dry or wet sites. This study found a greater effect of environment than genetics on phenotype (Table 2), as has been shown in most studies on Douglas-fir (e.g., Gould et al. 2012). The first and second hypotheses were mostly supported: the dry sources grown at dry sites had lower SLA, K_l and k_l than the wet sources grown at the wet site. Also as hypothesized, there were no significant source or site differences in wood density or source effects on vulnerability to embolism. Contrary to hypothesis, the environmental effect on vulnerability to embolism was significant. As expected in the third hypothesis, the two populations (wet and dry sources) differed in their hydraulic strategies in the two environments, but contrary to the hypothesis, the dry sources did not show larger conservative shifts between sites. The results are discussed below.

Leaf and architectural effects

Of the six leaf and architectural traits studied, only wood density showed no genetic or environmental effects (Table 2, Figure 3). Numerous studies have shown no wood density differences between wet and dry sources in the wood grown in common gardens. For example, when Nabais et al. (2018) combined wood density data from numerous provenance trials

with estimates of the climatic conditions for each provenance, they detected a significant effect of aridity in only 5 of the 13 gymnosperm species evaluated. Their study included 10 provenance trials and 43 provenances of Douglas-fir, but the single provenance trial identified as containing only coastal Douglas-fir (rather than other varieties or combinations of varieties) showed no correlations between climate variables and wood density.

We also found no significant effect of site aridity on wood density ($P = 0.08$, Table 2), as was also shown in several other conifers (e.g., *Pinus edulis* Englem. or *Juniperus monosperma* Englem. (Sarge.), Hudson et al. 2018; *Pinus sylvestris* L., Martínez-Vilalta et al. 2009; *Pinus pinaster* Aiton, Corcuera et al. 2011; *Pinus ponderosa* Douglas ex. C. Lawson, Anderegg and HilleRisLambers 2015). Survival studies, however, report an advantage of higher wood density during drought. Individual trees with higher wood density (either overall or within a specific xylem zone, depending on the study) had higher survival after a severe drought, both in coastal Douglas-fir (Martinez Meier et al. 2008, Dalla-Salda et al. 2009, 2011, Britez et al. 2014) and *Picea abies* (L.) Karst. (Rosner et al. 2014). The higher density was associated with higher embolism resistance (Dalla-Salda et al. 2009, Rosner et al. 2014).

As expected, SLA showed both genetic and environmental influences (Table 2), with lower values in the dry sources and for plants at the dry site (Figure 3A). This result is consistent with Bansal et al. (2015*a*), which reported on a larger sample of sources and sites from the same study we used, the SSMT, but sampled trees when they were 2 years younger. Lower SLA appears adaptive for a plant's water economy by presenting a low evaporative surface area per leaf mass, but at the potential loss of light capture and productivity (Grace 1990). The low SLA in the dry sites and sources is consistent with a survey of more than 100 species across six biomes, in which, for a given leaf life span, SLA declined with increasing aridity (Reich et al. 1999).

There were significant G, E and G × E effects on A_l/A_s. The G and E effects showed as lower values in the dry sources than the wet sources and at the dry site rather than the wet site (Table 2, Figure 3E). Lower A_l/A_s can provide more water per leaf area, but at the cost of less leaf area and productivity (Callaway and DeLucia 1994). The pattern of lower values of A_l/A_s, although not universal (e.g., not seen in *P. menziesii var. glauca* or *P. ponderosa* growing in dry hillsides and wetter riparian areas, Stout and Sala 2003), has been commonly reported in gymnosperms for drier sources (e.g., *P. sylvestris*, Martínez-Vilalta et al. 2009; *P. ponderosa*, Callaway and DeLucia 1994 and *Pinus canariensis* C. Sm., López et al. 2016) and drier sites (*P. sylvestris*, Mencuccini and Grace 1995, Martínez-Vilalta et al. 2009; *P. ponderosa*, Maherali et al. 2002, Anderegg and HilleRisLambers 2015; *P. sylvestris* and *P. edulis* Hudson et al. 2018). The report of lower A_l/A_s in relatively taller individuals of coastal Douglas-fir and *P. ponderosa* (McDowell et al. 2002*b*) may be similar to the site effect.

There was also a significant G × E interaction for A_l/A_s (Table 2, Figure 3E): the dry sources had lower A_l/A_s at the dry than the wet site, but the wet sources had no significant site differences. This source difference resulted from A_l, having G and E effects, but A_s having only E effects. For the dry sources, A_l was lower at the dry than the wet site (Figure 3C), but A_s did not differ (Figure 3D), resulting in lower A_l/A_s at the dry than the wet site. In contrast, for the wet sources, although A_l was lower in the dry than the wet site (Figure 3C), A_s was also lower at the dry site and by about the same proportion (Figure 3D), resulting in no difference in A_l/A_s at the two sites (Figure 3E). A different environmental response by wet and dry sources (a G × E interaction) in A_l/A_s was also suggested from common garden experiments with *P. ponderosa* (Maherali et al. 2002) and *P. canariensis* (López et al. 2016).

Shoot length (L) also showed a significant G × E interaction (Table 2, Figure 3F). At the dry site, L showed no G effect, but at the wet site, L was higher (shoots were longer) for the wet sources but not the dry sources. The higher L for the wet sources at the wet compared with the dry site shows opportunistic growth and contrasts with the conservative lack of difference in L between sites for the dry sources. Assuming L is positively correlated with height growth, then the site effect for the wet sources is consistent with studies showing a decrease in height growth during drought years in plantations of Douglas-fir in Germany (Rais et al. 2014). Most Douglas-fir growth studies, however, report radial growth, which is lower on dry sites than wet sites (Littell et al. 2008, Montwé et al. 2015, Restaino et al. 2016).

Branch hydraulic effects

Similar to the architectural traits, this study found that more hydraulic traits had significant E effects than G effects (Table 2). There was no G effect on vulnerability to embolism even though, if provenances have no trait differences that modulate stem water potential (e.g., capacitance, Meinzer et al. 2009; architecture, Mencuccini and Grace 1998; or phenology, Barnard et al. 2011), it would appear adaptive for sources from drier climates of origin to evolve lower vulnerability. Consistent with our findings, most intraspecific studies report little or no variability in vulnerability to embolism with the aridity of the climate of origin (e.g., *P. sylvestris*, Martínez-Vilalta et al. 2009; *Pinus hartwegii* Lindl., Sáenz-Romero et al. 2013; coastal Douglas-fir, Chauvin et al. 2019; *P. pinaster*, Lamy et al. 2014), although some studies report lower vulnerability for more arid provenances (*P. pinaster*, Corcuera et al. 2011; *P. canariensis*, López et al. 2016). Kavanagh et al. (1999) reported lower vulnerability in a drier provenance in coastal Douglas-fir, but in that study, the plant material was 2-year-old seedlings as opposed to the 2-year-old branches on 7-year-old saplings in the current

study. This difference likely resulted from the fact that hydraulic properties in gymnosperm wood are often affected strongly by cambial age and tissue position in the plant (Domec and Gartner 2001, Dunham et al. 2007, Domec et al. 2008, Lachenbruch et al. 2011).

In contrast to the lack of G effect, there was a significant E effect on vulnerability to embolism, with lower vulnerability at the dry than the wet site (Table 2). The literature contains reports of both lower vulnerability to embolism in drier sites (*P. canariensis*, López et al. 2016) and a lack of effect (e.g., *Pinus pinaster*, Lamy et al. 2014; *P. edulis* and *J. monosperma*, Hudson et al. 2018). The mechanism for this apparent environmental signaling is unclear. If we understand correctly that the structures of root, xylem and leaf responsible for embolism formation are already developed before most of the embolisms are formed, then the signal to develop resistant wood in arid sites must derive from conditions experienced in a previous year.

Neither K_h nor K_s exhibited significant G effects (Table 2). Similarly, López et al. (2016) found no provenance difference in K_s for *P. canariensis*. Other studies, however, have reported lower K_s for drier than wetter provenances (e.g., coastal Douglas-fir, Chauvin et al. 2019, *P. pinaster*, Corcuera et al. 2011). In contrast to the G results, K_h (and K_s, at $P = 0.051$) showed E effects, with lower values at the dry site (Table 2). Lower values of K_s in drier sites have also reported for coastal Douglas-fir (Anekonda et al. 2002, Chauvin et al. 2019) and other coniferous species (*P. pinaster*, Corcuera et al. 2011; *P. canariensis*, López et al. 2016; four *Cedrus* spp., Ladjal et al. 2005; *P. ponderosa*, Anderegg and HilleRisLambers 2015; *P. edulis* and *J. monosperma*, Hudson et al. 2018), but some studies have shown no site effects (e.g., *P. sylvestris*, Mencuccini and Grace 1995). In the current study, K_s also showed a different response of the two sources (a G × E interaction), with no environmental effects for the dry sources but lower values of K_s at drier sites for the wet sources (Table 2, Figure 4C).

Neither K_h nor K_s directly control how much water a branch tip receives. When K_h is normalized by the leaf area it supplies, however, the quotient, K_l (equivalent to K_s normalized by A_l/A_s), is an estimate of the rate at which water arrives at a unit area of leaf surface for a given pressure gradient through the stem. Leaf-specific conductance (k_l, which is K_l divided by L) is even more relevant to the water delivery to the branch tip because it takes into account the length of the path. A higher K_l or k_l indicates that the architecture and/or conductivity combine to provide, inter alia, more water to the branch tip.

We saw no G effect for K_l (although it was significant at $P = 0.06$, Table 2), but a significant E effect (Table 2). As we hypothesized, values were higher at the dry than the wet site. Higher K_l on drier sites was also reported for *P. sylvestris* (Mencuccini and Grace 1995, Martínez-Vilalta et al. 2009), *P. ponderosa* (Maherali et al. 2002) and *P. canariensis* (López et al. 2016), but the opposite pattern was reported for *J. monosperma* and *P. edulis* (Hudson et al. 2018). Maherali et al. (2002) reported lower K_l in drier sites but surmised that this resulted from a tree-height effect, with lower K_l in shorter trees, and shorter trees in drier sites. We also saw a G × E interaction for K_l, with the drier sources showing higher K_l at the dry site, but the wetter sources showing no site effect (Figure 4D).

The most integrative measure in this study, k_l, showed both G and E effects, with no interaction (Table 2, Figure 4E). Both sources had higher k_l at the dry than the wet site, and the dry sources had higher values than the wet sources at both sites. The fact that the wet sources showed higher k_l at the dry than the wet site, but that they had similar K_l at both sites, underscores the important role shoot length can play in water relations (Mencuccini 2003).

Conservative vs. opportunistic responses in the dry vs. wet sources

We hypothesized that if the dry sources differed from the wet sources in their responses to the environment, they would do so in the direction of having more conservative responses, defined as having trait values that are more likely to aid in branch survival during water stress. The most integrative measures in this study were SLA and k_l, and so they are the best indicators of drought performance in the current study. Both SLA and k_l showed environmental responses in the conservative direction for both sources. Through inspection of the reaction norm plots (Figures 3A and 4E), the responses were not appreciably larger in the dry than wet sources. Therefore, the data do not support this hypothesis.

However, a comparison of the conservativeness of trait values of the dry and wet source at each site, separately, supports the hypothesis that the dry sources are adapted to conservative growth relative to the wet sources and that the wet sources are adapted to opportunistic growth relative to the dry sources. At the dry site, dry sources had more conservative values than the wet sources for SLA, A_l, A_l/A_s, K_l and k_l, suggestive of adaptations of the dry sources (relative to the wet sources) for the tolerance of the dry conditions but at a cost of growth and competitiveness. At the wet site, the dry sources having more conservative values of SLA, A_l, A_l/A_s, L and k_l than the wet sources is suggestive of adaptations of the wet sources (relative to the dry sources) for opportunistic growth in the wetter environment.

Moreover, at one or both sites, we observed trait values that were more conservative in the dry sources than the wet sources, as follows: at the dry site only (for K_l), at the wet site only (for L) and at both sites (for SLA, A_l, A_l/A_s and k_l). In the main effects analysis, vulnerability to embolism (measured as PLC@4 MPa) showed more conservative values at the dry than the wet site for both sources, although the effect was not significant for either source type individually. In no cases, did the wet sources display more conservative trait values than the dry sources. Thus, for

all the traits except wood density, which showed little genetic or environmental variation, the direction of the trait values at one or both sites suggested adaptive variation of the different sources toward water conservation for the dry sources and toward opportunistic water use in the wetter sources. Trees often change their hydraulic properties as they grow (Hinckley et al. 2011, Lachenbruch et al. 2011). The current study did not include tree size in analyses, but it would be valuable for future research to ask the extent to which slow growth contributes to a conservative hydraulic strategy.

Implications for forest management

This project demonstrated that within coastal Douglas-fir, two populations differed in their hydraulic architectural response to the water availability in the environment in which they grew. Just as phenotypic plasticity expands a plant's developmental and physiological repertoires in response to environment (Bradshaw 1965), this phenotypic variability of populations expands a population's repertoires of responses to different environments. In our branch studies in common gardens, the drier sources exhibited lower SLA, A_l/A_s and k_l. This finding means that the dry sources have a strategy of delivering more water per unit of leaf area, but at the potential cost of lower productivity both because of the lower SLA and the lower A_l/A_s. In all measured cases, the differences of the dry sources in the dry vs. wet sites were in the direction expected for averting the risk of water stress, thus ensuring survival. In contrast, the wet sources exhibited behaviors in the direction expected for taking advantage of higher water availability in the wet site, thus enhancing branch growth and competitiveness.

The drier vs. wetter populations arrived at higher water delivery at the dry site through different strategies. The dry sources achieved higher K_l and k_l at the dry site via lower A_l/A_s, driven by lower A_l with no significant change in K_s or L. The wet sources achieved the higher k_l at the dry site via shorter shoots (L) and lower K_s, with no significant change in A_l/A_s. Therefore, different provenances may show different architectural responses to a site's aridity. These architectural responses could, in turn, impact a plant's reaction to factors that decrease leaf or sapwood area, such as pests, pathogens, fires or ice storms. Further research on provenance differences may help us better match seed sources to habitats for establishing future forests.

Conclusions

This study provides evidence for differences that appear adaptive in the hydraulic strategies of two sources of coastal Douglas-fir and emphasizes that at the population level, plant material can have different adaptations. It will be useful in future research to sample more populations and traits to learn if the trends demonstrated here will be supported with a larger sample.

Wood density was the only trait that showed very little difference by source or site. Vulnerability to embolism showed no genetic effect, but at the dry site, its value tended to be lower than at the wet site. SLA, A_l and A_l/A_s were lower in the dry than the wet sources, all of which, inter alia, will result in less water loss from a shoot. By maintaining similar A_s but decreased A_l, the dry sources had lower A_l/A_s at the dry than the wet site. In contrast, by reducing A_s and A_l by the same proportion, the wet sources had similar A_l/A_s at the wet and dry sites. The combination of A_l/A_s, K_s (or K_h) and L provided the plants from dry sources higher k_l in both the dry and wet site. If the trait values between dry and wet sources differed, the direction of the difference was toward a more conservative hydraulic architecture in the dry sources than the wet sources. Thus, natural selection appears to have resulted in different hydraulic strategies that will contribute to populations' survival during drought.

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Conflict of interest

None declared.

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Authors' Contributions

B.L. designed and carried out the field and lab work, including proposing the hydraulic function hypotheses and experimental design, collecting and analyzing data, supervising student workers and drafting the manuscript. J.B.S.C. and C.A.H. designed and installed the field trial, helped choose families and sites for study, helped with experimental design, climate analysis and preliminary data analysis, interpretation and writing of the paper.

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