Adaptation to Climate Change? Moving Coast Redwood Seedlings Northward and Inland[1]

Christa M. Dagley,[2] John-Pascal Berrill,[2] Forrest T. Johnson,[2] and Lucy P. Kerhoulas[2]

Abstract

Insight into genetic variation in trees may provide opportunities to select for genotypes that are better adapted to new locations and future climate conditions. We established a field test at two sites in Humboldt County, California to study the performance of coast redwood (*Sequoia sempervirens* (D. Don) Endl.) under assisted migration. Both test sites were near the eastern (inland) limit of coast redwood's range and had no naturally occurring redwood. Seed were collected from redwood trees on dry, hot ridges and upper slopes from the southernmost populations, and combined with redwood seed from Mendocino County and seed and tissue culture clones from Humboldt County. A total of 34 different clones, open-pollinated families, and commercial seedlots were planted in 27 replicates at each test site using an interlocking hexagonal design. Health, instances of damage, and total height of every seedling was recorded annually since planting in 2010. Caliper (basal diameter) was also measured annually three times beginning in spring 2014, giving basal diameter increment for each tree. Water stress was assessed for each young tree ($n \approx 2000$ trees) in the summer of 2015 using a pressure bomb. Performance of progeny planted at each test site varied among regions-of-origin, forest-of-origin, and among families of seedlings from individual open-pollinated parent trees. Results were counter to our expectation that seedlings originating from parents located at the warmer and drier southern extremes of redwood's range would perform best on the more extreme test site (higher elevation, no fog) in Humboldt County. However, high variances within families and clones suggested that genetic effects may have been obscured by other sources of variability at this early age.

Keywords: assisted migration, climate change adaptation, forest restoration, genetics, reforestation, seed collection

Introduction

Insight into genetic variation in trees informs forest conservation, restoration strategies, and assisted migration efforts in the face of a changing climate. Investigators have measured genetic variation through the use of molecular markers and analysis of data from common garden experiments in an attempt to divide phenotypic variability into genetic and environmental components. Genetic variation is hierarchical. Tree-to-tree variation among trees in the same stand is usually a major source of genetic variation. Many tree species also exhibit geographic variation among provenances, especially among distant populations in widespread species that occupy different climates (White et al. 2007).

Genetic variation among provenances may be a result of natural selection acting on local populations, making them adapt to local conditions. O'Brien et al. (2007) found that traits of jarrah (*Eucalyptus marginata* Sm.) varied over geographical scales; their findings suggested seed transfer from high to low rainfall sites would be accompanied by increased mean growth rate for the site. However, under drier conditions the high growth rates may be unsustainable and result in increased mortality over longer time intervals. This suggested that seed sourced from different locales may be better or worse suited for conservation and/or restoration projects. Millar and Libby (1989, 1991) also

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[2] Department of Forestry and Wildland Resources, Humboldt State University, 1 Harpst Street, Arcata, CA 95521. Corresponding author: pberrill@humboldt.edu.

noted the importance of considering the environmental conditions and provenance variability in conservation planning and restoration activities.

Coast redwood (*Sequoia sempervirens* (D. Don) Endl.) is a species with restricted natural range. The current geographic range is confined to a relatively narrow coastal strip from the southwestern corner of Oregon (42°09’ N. latitude) to Monterey County in central California (35°41’ N. latitude) (Burns and Honkala 1990). In general, along this north-to-south gradient, rainfall declines and potential evapotranspiration increases, yet trees of similar size can grow at similar rates in tall forests (Sillett et al. 2015). Less coastal fog and warmer growing season temperatures are found inland, further away from the Pacific coast, creating another potential evapotranspiration gradient. Throughout this range, redwoods are found with different assemblages of associated species and different upper limits of stand density in terms of leaf area index and total live above-ground biomass (Van Pelt et al. 2016). For example, the northern redwood forests of Del Norte and Humboldt counties often have coast redwood, coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh), and Pacific madrone (*Arbutus menziesii* Pursh). In comparison, the drier southern redwood forests often comprise a mix of redwood, Douglas-fir and hardwoods including California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.), coast live oak (*Quercus agrifolia* Née), and tanoak (Olson et al. 1990, Zinke 1988). Redwood forms a more continuous belt north of the Sonoma-Mendocino County line, and becomes more isolated in its disjunct populations further south (Douhovnikoff and Dodd 2011).

Unknown is the genetic variation within or among coast redwood populations that make them better or worse adapted to different climates. For example, if drought tolerance and water-use efficiency are found to be heritable traits, we can select for these characteristics and raise seedlings for reforestation on marginal sites or in areas where adverse changes in climate are forecast. Most conifers have only 20 to 24 chromosomes. However redwood has 66 chromosomes making it hexaploid (Saylor and Simons 1970, Sclarbaum and Tsuchiya 1984). As a result, within a single individual it is possible for allelic variation to occur (alternative forms of the same gene). The wide variation of within-family genetic variability was clearly demonstrated by Rogers (1994) by showing gametes to have one, two, or in some cases three different alleles of a gene coding for a particular enzyme. Therefore, any redwood provenance might be capable of adapting to new sites and climates.

We implemented a large field experiment to determine if progeny of redwood trees growing in the hottest/driest parts of their natural range may be better-adapted to hot, dry conditions and hold promise for restoration and resistance to climate change. We designed this study to answer the following questions about the progeny of coast redwoods originating from different climates: 1) Do progeny growing at test sites differ in growth and/or water stress, and 2) Do progeny exhibit differences between and within regions of origin in terms of growth and/or water stress? When planting redwood on an extreme site (hot, dry summers; cold winters), we hypothesized that progeny originating from the southernmost populations where redwoods experienced hotter and drier summers would outperform seedlings or clones originating from the more northern, moister coastal locations. Conversely, we expected seedlings adapted to moister locales to outperform the southern redwoods moved northward and planted on a northern site with some coastal fog. This paper describes the implementation of the experiment and presents preliminary data on tree size, growth, and water stress at two test sites for redwood propagules from different regions, forests, and open-pollinated families.

Methods

Coast redwood seed cones were collected from southern and inland locations where redwood experiences hotter and drier conditions (fig. 1). These southern redwoods were mixed with shrubs or hardwoods and showed characteristics of thick, flaking bark with sparse crowns. In the autumn of 2009, shallow increment cores were taken from candidate parent trees of dominant or co-dominant crown position exhibiting favorable form characteristics (i.e., straight, without excessive forking; small horizontal branching). A subset of these trees had increment cores exhibiting favorable radial growth and wood properties, defined as relatively wide growth rings (rapid growth), darker heartwood coloration, and higher density (resistance of core sample to fingernail pressure). These superior trees were selected for seed collection.

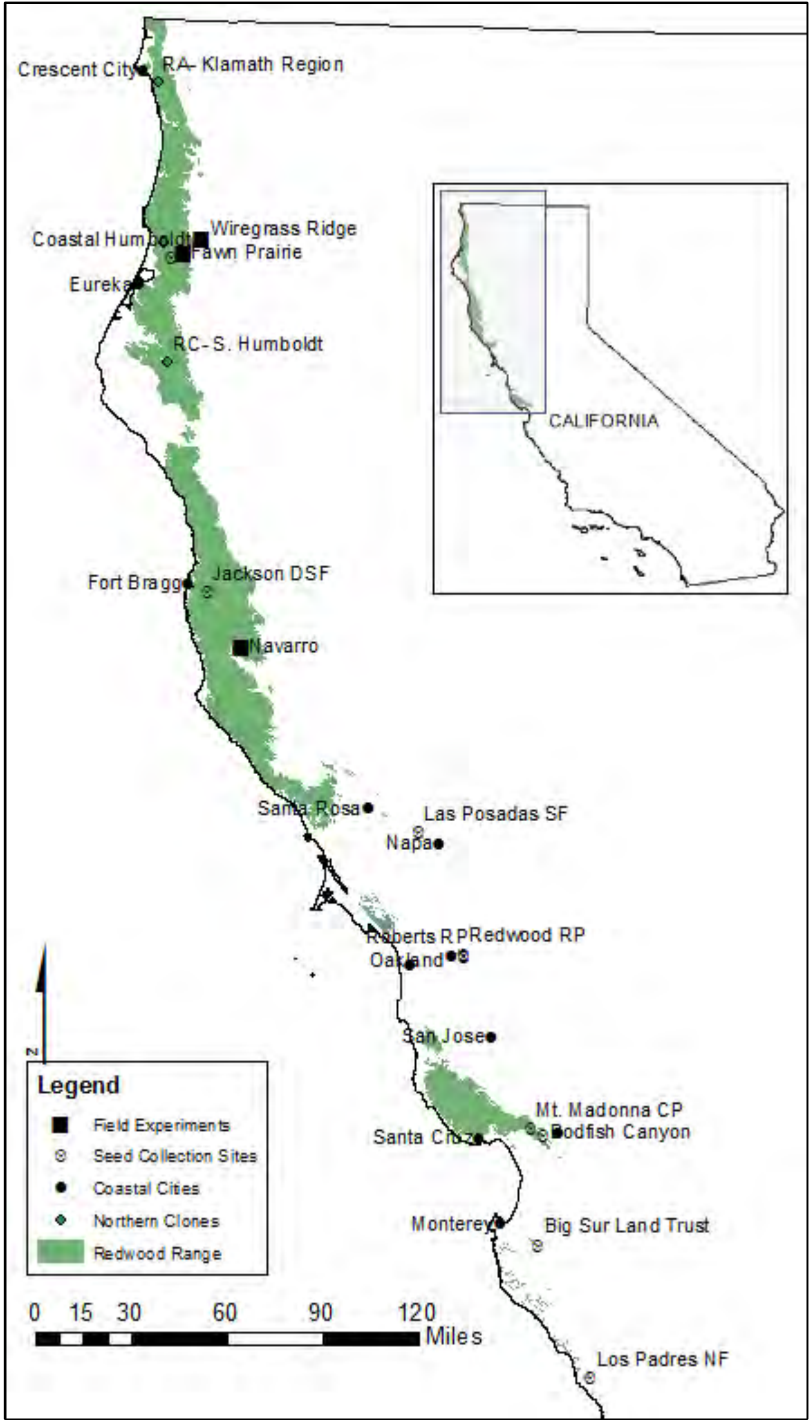

Figure 1—Location of seed cone collection locations, clone origins, and field test sites.

Cones were concentrated at the tops of the selected trees. Tree climbers used pole pruners to clip branchets bearing clusters of cones. Individual trees yielded 3 to 18 liters of cones with each cone having up to 50 seeds. Seed cones from each parent tree were kept separate. The cones were processed by the CAL FIRE L.A. Moran Reforestation Center. Open-pollinated families (separate seedlot for each parent tree) were tested for germination rate, cold stratified for 1 month, and planted at a rate of four seeds per styro-15 container. Seed from a commercial seed collection (multiple open-pollinated families) on Jackson Demonstration State Forest in Mendocino County were also sown in styro-15 blocks at the same time and location. The 1-0 seedlings were raised in a commercial nursery at a hot, dry location outside of redwood's natural range at Cottage Grove, Oregon. Additional planting stock for the field tests were open-pollinated seedlings and tissue culture clones from Humboldt County, raised in styro-15 containers at Green Diamond Resource Company's Korbell Nursery, Humboldt County, California.

The seedlings from Mendocino and Humboldt counties and tissue culture clones from Humboldt County were labelled and planted in winter 2010-2011 at two test sites in Humboldt County using the replicated interlocking hexagonal experimental design of UC Berkeley Professor Emeritus William J. Libby (fig. 1). Both test sites were Douglas-fir/tanoak sites with no naturally occurring redwood and were approximately 20 km (12.5 miles) from the Pacific coast, near the eastern (inland) limit of coast redwood's range. The first test site, Fawn Prairie (FP), is at 560 m (1,847 ft) elevation and receives some summer fog. The second test site, Wiregrass Ridge (WG), is on an exposed ridge at 1000 m (3,269 ft) elevation. We considered the WG test site to be the more extreme test site because it does not receive coastal fog and soon after planting was covered by 30 cm of snow. The following year, a third test site was established at a hot dry site near Navarro in Mendocino County. This site suffered drought and was abandoned due to widespread mortality in the first growing season.

The experimental area at each test site covered 1.2 ha (2.7 ac) and included 980 planted seedlings. A total of 34 genotypes were planted at each test site which included 27 replicates (nine replicate blocks with three replicates within each block), each containing the 34 genotypes. Two outside border rows surrounded the experimental area at each test site. The hexagonal design provides for two future thinning operations (each removing one of the three complete replicates, i.e., cut 33 percent of the trees at each thinning) that preserve even spacing between neighbors. Site preparation included spraying tanoak stumps and/or sprouts with triclopyr. Manual weeding in the vicinity of each planted redwood was undertaken annually.

Health, instances of damage, and total height to the nearest centimeter (cm) were recorded for every seedling annually since planting in 2010. Health status was coded as healthy, sick, moribund, or dead based on visual assessment. Instances of damage recorded included deer browsing, dead tops, or broken tops. Early in the spring of 2014, a form pruning on seedlings with multiple stems and/or basal sprouting occurred. At this time, basal diameter (termed 'caliper') was also measured to nearest 0.1 mm using digital calipers immediately above any swelling associated with the root collar. Caliper was re-measured at end of the 2014 and 2015 growing seasons. The difference between repeat measurements gave annual growth in terms of caliper increment. Converting caliper data to cross-sectional stem area gave basal increment.

Data were sorted and summarized by test site, forest-of-origin and region-of-origin, and by open-pollinated family or individual clone. Assuming that the slowest growing trees had problems such as poor genetics, poor establishment, or damage, we excluded from the analysis the shortest 25 percent of trees from each family or clone based on height in 2016.

Water potential was measured using a Scholander pressure bomb during the dry summer months of 2015. Samples were taken repeatedly throughout the day. Water potential data were plotted to demonstrate how water stress changed over the course of a day at the test sites inside and outside redwood's range.

Results and Discussion

Regional differences were examined based on the average tree height after five full growing seasons (hereafter referred to as age-5 years), and 2-year caliper increment and basal increments for both test sites. Growth was much lower on average (41 percent, 28 percent, and 55 percent less in height, caliper increment, and basal increment, respectively) at the more extreme test site (WG) versus FP (table 1).

Table 1—Regional averages of age-5 height, and 2-yr caliper increment and basal increment, for Fawn Prairie (FP) and Wiregrass Ridge (WG) test sites (standard deviation in parentheses)

Test Site	Region	Height (cm)		Caliper increment (mm yr^{-1})		Basal increment (cm^2 yr^{-1})	
FP	Humboldt	243.2	(80.8)	11.52	(5.1)	7.81	(7.9)
FP	Mendocino	233.0	(89.3)	12.70	(6.3)	8.67	(6.3)
FP	Southern	232.4	(79.4)	12.15	(6.5)	8.12	(7.7)
WG	Humboldt	136.7	(52.4)	9.49	(4.7)	4.12	(3.1)
WG	Mendocino	140.6	(41.4)	8.42	(5.0)	3.52	(3.4)
WG	Southern	137.7	(52.9)	8.25	(4.7)	3.42	(3.5)

As a group, clones and seedlings from the northern region (Humboldt) that were planted at FP showed slightly better performance in height, however, the central region (Mendocino) had better performance in caliper and basal increment. When the redwoods were planted on the harsher test site (WG) the opposite result occurred; the central region seedlings showed the best performance in height and the northern region had the highest caliper and basal increment (table 1).

Table 2—Fawn Prairie test site showing averages of age-5 height, and 2-yr caliper increment and basal increment, and top rankings in basal increment (standard deviation in parentheses)

Forest	Height (cm)		Caliper increment (mm yr^{-1})		Basal increment (cm^2 yr^{-1})		rank
GD Clone (N. Humboldt)	228.5	(65.6)	13.07	(4.3)	8.80	(5.0)	
Central Humboldt Seedlot	238.8	(71.1)	11.40	(4.4)	6.43	(5.1)	
GD Clone (C. Humboldt)	245.9	(84.2)	12.96	(5.2)	9.13	(5.9)	3
GD Clone (S. Humboldt)	265.0	(102.2)	12.88	(6.7)	9.70	(9.0)	1
Mendocino Seedlot (JDSF)	233.0	(89.3)	11.52	(6.3)	7.81	(7.9)	
Inland Napa (Las Posadas SF)	228.8	(78.7)	8.79	(4.2)	4.80	(4.4)	
Roberts Park (Oakland Hills)	243.7	(81.1)	12.67	(6.9)	9.35	(9.1)	2
Redwood Park (Oakland Hills)	238.8	(57.6)	12.39	(6.2)	8.00	(7.0)	
Mount Madonna (Watsonville)	229.3	(76.4)	13.13	(6.5)	8.70	(7.0)	
Gilroy (Bodfish Canyon)	243.3	(90.0)	12.63	(7.3)	9.07	(8.7)	4
Big Sur Land Trust	219.6	(89.5)	13.12	(6.6)	8.46	(7.1)	
Los Padres National Forest	204.6	(71.8)	10.58	(4.9)	5.77	(5.3)	

Table 3—Wiregrass Ridge test site showing averages of age-5 height, and 2-yr caliper increment and basal increment, and top rankings for basal increment (standard deviation in parentheses)

Forest	Height (cm)		Caliper increment (mm yr^{-1})		Basal increment (cm^2 yr^{-1})		rank
GD Clone (N. Humboldt)	140.6	(49.0)	8.99	(5.0)	3.84	(3.2)	
Central Humboldt Seedlot	129.7	(67.5)	7.26	(4.0)	2.90	(2.4)	
GD Clone (C. Humboldt)	137.1	(48.6)	8.50	(4.2)	3.51	(2.7)	
GD Clone (S. Humboldt)	135.4	(53.7)	8.21	(5.3)	3.46	(3.9)	
Mendocino Seedlot (JDSF)	140.6	(41.4)	9.49	(5.0)	4.12	(3.4)	2
Inland Napa (Las Posadas SF)	134.3	(53.6)	6.57	(3.0)	2.41	(1.9)	
Roberts Park (Oakland Hills)	143.4	(54.0)	8.39	(5.2)	3.55	(3.9)	4
Redwood Park (Oakland Hills)	148.7	(53.8)	10.12	(4.7)	4.59	(3.8)	1
Mount Madonna (Watsonville)	145.6	(54.8)	8.89	(4.9)	3.96	(3.7)	3
Gilroy (Bodfish Canyon)	133.4	(56.0)	7.91	(4.3)	3.17	(3.3)	
Big Sur Land Trust	125.5	(35.7)	7.75	(4.7)	2.99	(3.2)	
Los Padres National Forest	121.3	(43.6)	6.71	(4.1)	2.30	(2.5)	

Two year averages in basal increment and caliper increment, along with 5 year height averages were summarized for both test sites based on forest-of-origin. Basal increment rankings varied for both test sites showing differences in seedling performance when planted in different climates. Clones that were collected from southern Humboldt County showed the highest basal increment when planted at FP (table 2). In contrast, when planted at the more extreme site (WG), the greatest growth came from seed collected further to the south in Redwood Park, an area in the Oakland Hills (table 3).

Individual family or clone averages were also summarized for height, caliper increment, and basal increment at the test sites (tables 4 and 5). The two test sites showed differences in top performers within all three categories; however the high variances within families and clones suggested that genetic effects may have been obscured by other sources of variability at this early age.

Table 4—Redwood clones and O-P families (n = 32) listed in order of their place of origins from north to south and planted at Fawn Prairie (FP) test sites showing means and top rankings for age-5 height, and 2-yr caliper increment and basal increment (BI) (standard deviation in parentheses)

Clone*/	Height			Caliper increment			Basal increment		
family	(cm)		rank	(mm yr^{-1})		rank	(cm^2 yr^{-1})		rank
RA20*	215.9	(54.1)		14.53	(3.5)	4	10.08	(5.0)	
RA38*	192.5	(75.6)		8.21	(3.6)		3.99	(2.1)	
RA60*	273.7	(39.6)	2	14.70	(3.1)	1	10.57	(4.4)	
O92**	238.8	(71.1)		11.40	(4.4)		6.43	(5.1)	
RB1*	215.5	(86.9)		13.76	(4.9)		9.22	(4.3)	
RB2*	266.1	(78.1)		12.27	(5.1)		9.00	(5.9)	
RB54*	259.1	(85.8)		12.86	(6.1)		9.18	(7.8)	
RC59*	234.5	(66.7)		11.22	(5.0)		6.37	(3.4)	
RC64*	298.5	(126.0)	1	14.54	(8.0)	3	13.03	(11.6)	1
C**	233.0	(89.3)		11.52	(6.3)		7.81	(7.9)	
E3	228.8	(78.7)		8.79	(4.2)		4.80	(4.4)	
D1	256.4	(67.5)		13.68	(6.3)		9.55	(6.5)	
D2	248.4	(86.4)		12.67	(7.8)		10.34	(11.0)	
D3	215.9	(104.3)		12.80	(7.5)		10.05	(10.7)	
D5	266.2	(78.1)		14.14	(8.0)		10.83	(10.9)	3
D6	234.0	(62.1)		10.00	(4.5)		5.97	(5.1)	
R1	232.5	(72.5)		12.57	(7.6)		8.02	(8.6)	
R2	246.3	(50.8)		12.52	(5.1)		8.74	(6.4)	
R4	238.2	(47.8)		12.05	(5.8)		7.25	(5.9)	
M1	230.0	(78.6)		14.09	(6.2)		9.16	(5.9)	
M2	230.0	(74.0)		12.34	(5.3)		7.42	(5.2)	
M3	227.9	(80.2)		12.86	(8.0)		9.49	(9.6)	
B1	249.1	(94.6)		14.69	(8.7)	2	11.14	(10.8)	2
B2	241.1	(80.3)		12.05	(7.6)		7.99	(8.5)	
B3	268.2	(82.9)	4	14.51	(6.4)		10.59	(8.6)	4
B5	185.2	(85.6)		9.62	(6.3)		5.86	(6.8)	
B7	270.5	(86.8)	3	12.31	(7.3)		9.81	(8.4)	
BSL1	219.6	(89.5)		13.12	(6.6)		8.46	(7.1)	
LP1	209.1	(74.6)		11.06	(2.8)		5.66	(3.0)	
LP2	180.8	(80.7)		10.80	(6.2)		6.24	(6.7)	
LP3	200.4	(62.5)		8.89	(5.5)		4.96	(6.8)	
LP4	227.6	(66.2)		11.73	(4.8)		6.38	(4.3)	

**Seedlot from multiple parent trees in Humboldt County 092 seed zone or Jackson Demonstration State Forest (C).

Table 5—Redwood clones and O-P families (n = 31) listed in order of their place of origins from north to south and planted at Wiregrass Ridge (WG) test sites showing means and top rankings for age-5 height, and 2-yr caliper increment and basal increment (standard deviation in parentheses)

Clone*/	Height			Caliper increment			Basal increment		
family	(cm)		rank	(mm yr^{-1})		rank	(cm^{2} yr^{-1})		rank
RA20*	154.4	(57.73)		11.16	(5.0)	2	5.52	(4.0)	2
RA38*	140.8	(42.49)		8.77	(2.1)		3.56	(3.1)	
RA60*	127.9	(49.04)		7.23	(4.4)		2.57	(2.0)	
O92**	129.7	(67.54)		7.26	(5.1)		2.90	(2.4)	
RB1*	137.6	(53.37)		9.01	(4.3)		3.94	(2.7)	
RB2*	115.8	(37.66)		6.14	(5.9)		2.14	(2.0)	
RB54*	155.8	(48.66)	4	9.83	(7.8)		4.12	(2.9)	
RC59*	131.5	(55.06)		7.74	(3.4)		3.14	(4.0)	
RC64*	138.7	(54.75)		8.63	(11.6)		3.74	(3.9)	
C**	140.6	(41.36)		9.49	(7.9)		4.12	(3.4)	
E3	134.3	(53.63)		6.57	(4.4)		2.41	(1.9)	
D1	151.3	(51.38)		9.41	(6.5)		4.03	(4.0)	
D2	131.7	(50.53)		7.37	(11.0)		2.97	(3.4)	
D3	140.4	(65.05)		8.63	(10.7)		3.81	(5.2)	
D5	157.1	(43.54)	3	7.68	(10.9)		3.10	(2.0)	
D6	137.8	(58.74)		8.76	(5.1)		3.77	(4.5)	
R1	169.2	(59.99)	1	11.22	(8.6)	1	5.55	(4.6)	1
R2	145.3	(42.73)		9.51	(6.4)		4.36	(3.3)	4
R4	131.3	(52.30)		9.63	(5.9)	4	3.80	(3.5)	
M1	132.1	(42.74)		8.72	(5.9)		3.72	(3.4)	
M2	167.0	(63.18)	2	10.20	(5.2)	3	4.80	(4.2)	3
M3	138.0	(52.62)		7.83	(9.6)		3.38	(3.3)	
B1	146.4	(46.66)		9.18	(10.8)		3.98	(3.3)	
B2	136.9	(51.40)		7.82	(8.5)		3.20	(4.1)	
B3	129.3	(55.42)		7.87	(8.6)		2.86	(3.5)	
B5	115.5	(58.37)		6.93	(6.8)		2.60	(2.7)	
B7	139.6	(67.34)		7.73	(8.4)		3.27	(3.0)	
BSL1	125.5	(35.74)		7.75	(7.1)		2.99	(3.2)	
LP1	117.0	(50.67)		6.00	(3.0)		1.87	(1.9)	
LP2	122.4	(37.82)		8.09	(6.7)		3.23	(3.5)	
LP3	124.3	(42.86)		6.09	(6.8)		1.85	(1.6)	

**Seedlot from multiple parent trees in Humboldt County 092 seed zone or Jackson Demonstration State Forest (C).

Water potential samples taken repeatedly throughout the day during the summer months of 2015 revealed how water stress changed over the course of a day. Both test sites were found to be more similar in midday values than anticipated (fig. 2). The FP test site showed slightly more relaxed predawn values, although midday values were similar to WG, which suggested that stomata were conservatively regulating plant water status by controlling the rate of water loss to the atmosphere. This implied that redwoods were water-use efficient (i.e., exhibit isohydric stomatal regulation). In contrast, Ambrose et al. (2015) described redwood as relatively anisohydric. This conclusion was reached in part because they found redwood seedlings exposed to severe drought conditions to reach below -5.3 MPa during the daytime. Their study took place in a greenhouse where they had control over soil moisture conditions and could impose a severe drought condition. In our field tests, we found redwood stomatal closure preventing daytime water potential from going below -2.5 MPa. Our findings may differ simply because neither of our sites reached a severe drought state during the sampling period.

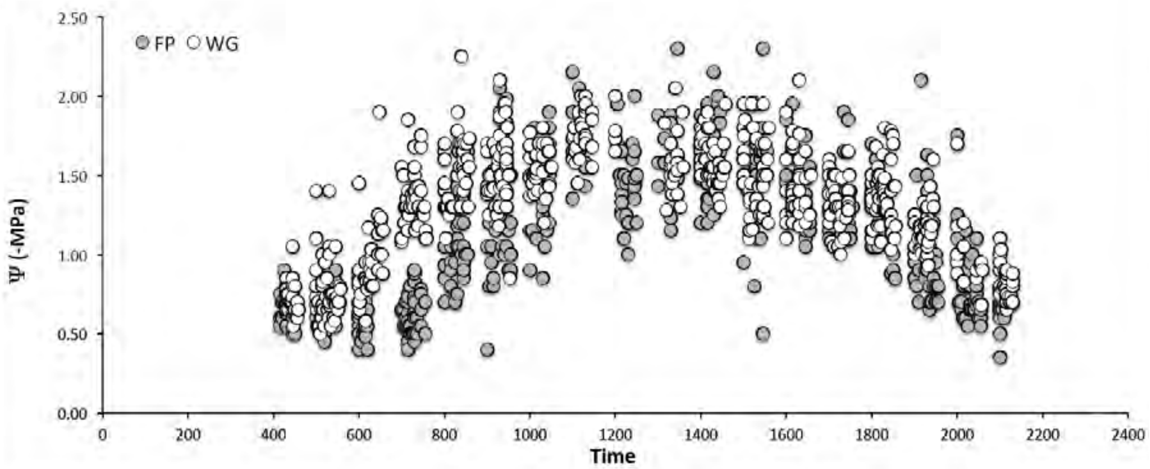

Figure 2—Diurnal water potential for redwood seedlings at two study sites Fawn Prairie (FP) and Wire Grass (WG) in mid-summer. Values show similar midday values at both sites.

Our next step is to analyze the summer 2015 water potential data we collected for every young redwood at both test sites (n ≈ 2000 trees) for among-region, among-forest, and among-family or among-clone differences in water stress. Ambrose et al. (2015) found no significant differences in water potential, hydraulic function, or growth and only minor differences in leaf gas exchange among redwood seedlings from Del Norte, Mendocino, and Santa Cruz counties. However, Anekonda et al. (1994) reported significant differences in metabolic response to temperature among redwood populations. Unlike these experiments performed under controlled conditions, our field test of seedlings from different populations appeared to have suffered from confounding environmental variations (e.g., microsite effects causing variability within families) which may dissipate with advancing age. Our preliminary findings appear to mirror field tests of redwood clones planted far outside its range (in New Zealand), where Meason et al. (2016) found no strong trends between growth, provenance, or provenance site characteristics. Therefore, we recommend continued monitoring and analysis of genetic variation in growth of our open-pollinated seedlings and tissue culture clones at field tests inside and outside redwood’s range.

Conclusions

Progeny of some southern redwood families had high-ranking performance at both test sites. Different clones performed well at each test site. However high variability in growth among progeny from the same parent tree and progeny from the same forest suggested that other factors (e.g., microsite effects, weed competition) within each test site may have overshadowed genetic differences. Therefore, we recommend repeatedly re-measuring trees to later ages to get estimates of increment that may reveal within- and among-family differences in redwood performance after assisted migration northward onto different sites experiencing different climates.

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