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Stand Structure and Composition Affect the Drought Sensitivity of Oregon White Oak (*Quercus garryana* Douglas ex Hook.) and Douglas-Fir (*Pseudotsuga menziesii* (Mirb.) Franco)

Ze'ev Gedalof *  and Jennifer A. Franks

Department of Geography, Environment and Geomatics, University of Guelph, Guelph, ON N1G 2W1, Canada; jennifer.anne.franks@gmail.com

* Correspondence: zgedalof@uoguelph.ca

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Abstract: Due to a suite of environmental changes, Oregon white oak (*Quercus garryana* Dougl. ex Hook; called Gary oak in Canada) associated ecosystems at many North American sites are being encroached upon by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and other conifer species. Alteration of stand structure and composition is causing substantial changes in the dynamics of these ecosystems, creating an environment in which Oregon white oak is not thriving. In this study we used dendrochronology to investigate the competitive dynamics between Oregon white oak and Douglas-fir in a mixed forest stand on Southern Vancouver Island. Significant species-specific differences in radial growth sensitivity to drought were found between Oregon white oak and Douglas-fir. Oregon white oak trees growing at high densities, or competing with Douglas-fir for moisture were found to be more sensitive to drought and more sensitive to growing conditions during the prior year. The response of Douglas-fir to drought was less variable, possibly due to the relatively low conifer densities at our study site, as well as the species' ability to root graft, its higher shade tolerance than Oregon white oak, and its rapid growth rates that allow it to achieve a more dominant canopy position. The non-stationary response to climate exhibited by Oregon white oak provides insights into the mechanisms by which Oregon white oak savannas are being converted to coniferous woodland, but also suggest that tree-ring reconstructions of climate need to explicitly address changes in stand dynamics that could influence the growth–climate relationship

Keywords: dendroecology; competition; oak savanna; global change; forest conifer encroachment; uniformitarian principle

1. Introduction

Anthropogenic activity and environmental changes have the potential to alter intra- and inter-specific competitive interactions in many forest ecosystems [1,2]. For any given species, traits such as shade tolerance, drought resistance, growth rate and form, affect its competitive status within a forest environment [1]. Environmental site conditions such as slope, aspect, soil depth, radiation influx, and soil moisture also influence climatic sensitivities and patterns of forest dynamics [3,4]. Changes to the biotic and abiotic factors affecting individual trees may therefore differentially affect competitive interactions between neighboring trees. In turn, changing competitive interactions over time may influence stand trajectories, structure, and composition, potentially affecting disturbance dynamics [5] and biodiversity [6].

While the effects of changing stand structure and composition on disturbance regimes, soil properties and erosion are reasonably well understood, the role of competition in both mediating

and driving these changes is less well understood. Relative differences in the diameter growth of trees can be used to interpret the competitive status of individuals within a stand [2,7]. Diameter growth represents a low priority of a tree's annual carbon allocation [8], so relative annual ring-width increment should provide a good gauge of an individual tree's competitive status [9]. The connection between annual growth and performance provides an opportunity to investigate stand dynamics at an annual resolution over the length of a tree's life. Such a fine resolution cannot feasibly be achieved by any other recognized method. To date, few studies have used tree-ring analyses for investigating competitive interactions between species (but see [2,10,11]).

Dendroclimatologists normally strive to use dominant trees to reconstruct past climates because radial growth of these trees is assumed to be less influenced by environmental effects such as competition and thus mostly influenced by climatic factors. Yet, trees are long-lived species and, as stand structure and composition change over time, growth patterns of dominant individual trees or species of trees may include past signals of competition apart from the climate signal [2]. Thus, the effects of competition may influence radial growth to a greater extent than is generally appreciated in dendroclimatology studies and warrants further investigation.

Oregon white oak savannas of the Pacific Northwest offer an ideal model system to test the effects of competition on growth–climate associations. Like most temperate oak savannas, Oregon white oak ecosystems throughout their range in Western North America are stressed or disturbed by a number of factors such as fragmentation, climatic change, changes in land management practices, fire exclusion, and invasive species [12–16]. Prior to European settlement, fire-tolerant oak stands were sustained by the setting of prescribed low-lying fires by native communities to keep their camas plots free of weeds and brush [17–19]. With the end of regulated prescribed fires, starting at ca. 1850, Oregon white oak ecosystem dynamics were altered [16,20].

Fire exclusion is often associated with a slow invasion of other species [2,21,22], and, particularly on moist sites, Oregon white oaks tend to be out-competed by faster-growing conifers if not maintained by disturbance [16,23]. On Vancouver Island, British Columbia, many Oregon white oak stands are being encroached upon by Douglas-fir [13,17]. Changes in stand dynamics of Oregon white oak ecosystems in this region are well documented over the last century [16,20,24] making this area well suited for analyzing the effects of competition on limiting climatic factors in varying stand structures and compositions.

The purpose of this analysis is to evaluate whether changing stand structure and composition in a mixed Oregon white oak (*Quercus garryana* Douglas ex Hook.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco *i*) stand has affected their climatic limiting factors, and by extension their competitive status within the stand. Specifically, we tested the following hypotheses (stated as predictions):

1. Douglas-fir and Oregon white oak trees growing at the same site will exhibit different relationships to climate.
2. Trees growing at high densities will be more sensitive to climatic variability than will trees growing at low densities.
3. Trees with broad crowns and large lower limbs (characteristic of an open canopy at the time of establishment and early growth) will exhibit different relationships to climate than will trees with narrow crowns and few lower branches (characteristic of closed canopy environments).
4. Trees competing with conspecifics for resources will exhibit different relationships to climate than trees competing with heterospecifics.

2. Materials and Methods

2.1. Study Site

The investigation was conducted at a site near the northernmost limit of the range of Oregon white oak, in a region with few previous dendroecological studies. The study site, located at Canadian Forces Ammunition Depot Rocky Point, near the town of Metchosin, on the southern tip of Vancouver

Island ($48^{\circ}37' \text{ N}$, $123^{\circ}72' \text{ W}$), Canada (Figure 1), consists of open grassland, scattered oak trees, oak woodland, mixed oak conifer woodland, and dense conifer forest. The stand dynamics and fire history of the site are described in Gedalof et al. (2006; ref [16]): prior to 1850 oak trees were present only at very low densities. Following the cessation of burning oak tree density increased rapidly with peak recruitment occurring at ca. 1900. Conifer establishment (primarily Douglas-fir, with a small component of lodgepole pine (*Pinus contorta* var. *contorta*) and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) has occurred continuously since 1860 but has peaked since 1950. A few madrone (*Arbutus menziesii* Pursh) trees are present at the site, but could not be dated due to concerns regarding the annularity of rings.

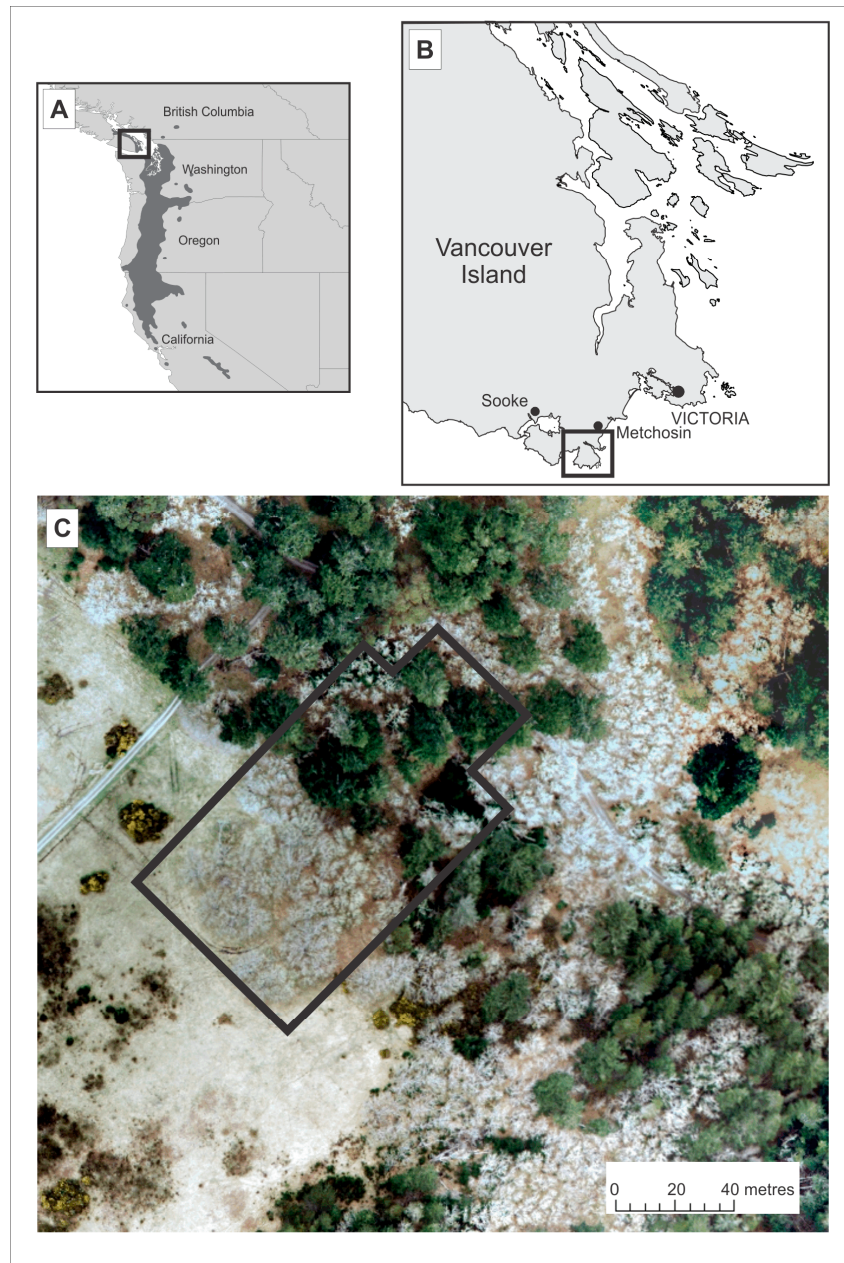


Figure 1. (A) The distribution of Oregon white oak in western North America. (B) Southern Vancouver Island. Rocky Point is located in the boxed area indicated. (C) A March, 2004, orthophoto of Rocky Point, and the approximate location of the study site. The oak has not leafed-out and appears much lighter in colour and less dense than the conifers toward the northeastern portion of the study area. North is oriented upwards. (After Gedalof et al. 2006; ref [16]).

The most common tree species at the site are Oregon white oak, Douglas-fir, and grand fir. Exotic grasses dominate the understory, which consists mainly of orchard grass (*Dactylis glomerata*), colonial bentgrass (*Agrostis capillaries* L.), sweet vernal grass (*Anthoxanthum odoratum* L.), and bracken fern (*Pteridium aquilinum* (L.) Kuhn). Scotch broom (*Cytisus scoparius* (L.) Link) and gorse (*Ulex europaeus* L.) are also present in scattered patches [13]. A more detailed cultural and ecological history of the site is described in [1].

Southern Vancouver Island is characterized by a Mediterranean-like environment with mild wet winters and warm dry summers, with a mean annual temperature of 9.3 °C and mean annual precipitation of 1505 mm [25]. Drought conditions tend to extend from June through August but may lengthen throughout May and September [25]. The long dry summers this zone experiences play a major factor in its ecology, as the soils in this region are gravel loams or gravel sandy loams developed on young, non-homogeneous parent material that do not readily retain moisture.

2.2. Chronology Development

Ring-width chronologies were developed using subsets of the trees cored at the study site by Gedalof et al. (2006; ref [16]) in summer of 2001. In that study, the site was divided into a sampling grid of 10m by 10 m quadrats. Each tree (dbh > 10 cm) in every quadrat was cored as near to the base as possible and trees were identified by the quadrat in which they were located. For this analysis, chronologies were developed from cross-dated sample data and used to develop seven pairs of chronologies representative of the total Douglas-fir and Oregon white oak populations, high and low densities of both species, closed- and open-grown individuals of both species, and different species compositions at this site. The categories are defined as follows:

1. Species Chronologies: all Oregon white oak; all Douglas-fir
2. Stand Density Chronologies: Stem density was defined based on the total basal area index (BAI) within each quadrat. The upper and lower quartiles of BAI were used to distinguish quadrats of high- and low-densities respectively. All trees of a given species (i.e., Oregon white oak or Douglas-fir) within that quadrat were included in the subset used to generate the chronology.
3. Morphology Chronologies: The morphology of each overstory tree was classified into two categories: open-grown (trees exhibiting large lower branches, a wide crown and a deep canopy); and closed-grown (trees exhibiting few lower branches, a narrow, tall crown and a generally erect posture). Chronologies for each species were developed for each of the two morphology types. While there is some overlap between the stand density chronologies and the morphology chronologies there were sufficient differences to merit analyzing them separately. For Oregon white oak, of the 57 cores that contributed to the closed-grown chronology 14 were also included in the high-density chronology, accounting for 64% of the high density chronology. For the open-grown chronology 7 of the 10 cores were also in the low-density chronology, accounting for 32% of that chronology.
4. Intra- and Inter-Competitive Dynamics Chronologies: Separate chronologies were developed using cores from quadrats containing only a single species (i.e. only Oregon white oak or only coniferous) and quadrats containing a mix of species.

In developing these chronologies all snags and stumps were included in both the density and competition analyses as they presumably contributed to both categories in an important way throughout a large portion of the study timeframe (1941–2001). This decision was based on the recent mortality dates calculated for two Oregon white oak snags, which were 1999 and 2001 [16]. Grand fir and lodgepole pine were counted as Douglas-fir in determining stand density values for the analysis of density- and competition-effects but were not used in the development of any of the chronologies.

Individual core measurement series were standardized using the software program ARSTAN [26]. A cubic smoothing spline with a 50 percent frequency cut-off of 75 years [27] was used to remove age-related growth trends and other non-climatic signals. Mean chronologies were calculated using autoregressive and moving average modelling [28,29], and a robust mean [30]. Descriptive statistics were calculated for each residual chronology including the percentage of missing rings, mean sensitivity, and the common variance among trees in each chronology (\bar{r}), and expressed population signal [31,32].

2.3. Assessing Growth–Climate Associations

We quantified the direction, magnitude, and seasonality of growth–climate associations at Rocky Point using the Palmer Drought Severity Index (PDSI) [33,34]. The PDSI has been found to be more strongly related to tree growth in many regions, presumably due to its integration of both temperature and precipitation into a single index of moisture availability (e.g. [35–37]).

PDSI data were taken from Shabbar and Skinner [38] for the gridpoint closest to Rocky Point for the years 1941–2001. These data are available at a monthly resolution, but for this analysis seasonal, semi-annual, and annual averages were used. The seasonal drought categories used were defined as: Spring (March–May; spring3 hereafter); Summer (June–August; summer3); Fall (September–November; fall3); and Winter (December–February; winter3). A second grouping of semi-annual seasons was also used to reflect the Mediterranean climate of the study site location, more strongly characterized by a rainy season and a dry season: the winter half-year (October–March; winter6) and summer half-year (April–September; summer6). Water year totals (October–September) were also used for the same reason. As climate in the preceding growing season often influences tree growth the following year [31], the tree-ring chronologies were also correlated against these same climatic variables for the prior year. Climatic variables from the prior year are indicated using the notation (−1); e.g., Summer3 (−1) refers to June, July and August of the year prior to growth.

2.4. Analyses and Interpretation

Significant growth–climate associations between each of the chronologies and the PDSI data were identified using the Pearson product moment correlation. Statistically significant differences in the strength of the correlations between pairs of chronologies were determined using an equality of correlations test [39]. Insights obtained from the effects of stand structure and composition on growth–climate associations were then used to characterize the competitive interactions between Oregon white oak and Douglas-fir. Lastly, the observed differences in the growth–climate associations related to stand structure and composition were assessed for their implications for dendroclimatology-based climate reconstructions.

3. Results

A total of 123 trees were cored, cross-dated, and measured. The statistical properties of the derived chronologies indicate that they are all of good quality, and most are very good (Table 1). In four chronologies, the number of trees contributing was lower than ten. This small sample size may have affected the quality in three of these chronologies: Open-grown Douglas-fir; Low-density Douglas-fir; and Intra-specific Douglas-fir (expressed population signal values for 1950–2000 range from 0.71 to 0.78).

3.1. Growth–Climate Associations

The results of the growth–climate associations for all chronologies at the site are shown in Figure 2 Figure 3 Figure 4 Figure 5 Figure 6 Figure 7 Figure 8. Analyses of monthly data were also undertaken, but are not shown since they reveal no patterns not also shown by the seasonal variables. Similarly, separate analyses of temperature and precipitation are consistent with the results of the PDSI data (i.e. generally negative correlations to temperature and generally positive correlations to precipitation) and are not shown here.

Table 1. Selected properties of the tree-ring chronologies developed for comparison to the Palmer Drought Severity Index (PDSI) data and to each other from Rocky Point, British Columbia, Canada.

Chronology	N cores	Max age	Mean age	Mean r-bar	EPS	Lag-1 ACF	Mean S
All Douglas-fir	33	136	100	0.419	0.951	0.429	0.152
All Oregon white oak	90	277	116	0.478	0.987	0.528	0.244
Open-grown Douglas-fir	6	123	119	0.302	0.706	0.393	0.175
Open-grown Garry oak	10	277	140	0.533	0.922	0.561	0.244
Closed-grown Douglas-fir	13	136	86	0.292	0.803	0.458	0.153
Closed-grown Oregon white oak	57	148	114	0.485	0.982	0.543	0.180
High Density Douglas-fir	8	133	110	0.574	0.906	0.195	0.211
Low Density Douglas-fir	8	123	79	0.224	0.717	0.443	0.182
High Density Oregon white oak	23	145	113	0.398	0.943	0.566	0.165
Low Density Oregon white oak	22	140	114	0.534	0.953	0.425	0.193
Heterospecific Competition Douglas-fir	17	129	91	0.494	0.951	0.388	0.167
Heterospecific Competition Oregon white oak	22	148	112	0.422	0.955	0.603	0.190
Conspecific Competition Douglas-fir	8	136	118	0.292	0.787	0.484	0.162
Conspecific Competition Oregon white oak	43	277	120	0.485	0.972	0.520	0.244

r-bar is the mean correlation coefficient among series contributing to the chronology; EPS is the expressed population signal, a measure of how well the sample represents a theoretically infinite population; Lag-1 ACF is the correlation between the chronology and itself lagged by one year; Mean S is the mean sensitivity, a measure of the year-to-year variation in ring width (see [40]).

3.2. Species Chronologies

The analyses of the growth climate associations of Oregon white oak and Douglas-fir indicate that growth of both species is significantly limited by moisture availability, and that the two species exhibit slightly different associations to climate (Figure 2). Growth of Douglas-fir is significantly correlated to drought during all seasons analyzed, during both the year of growth and during the prior year. Growth of Oregon white oak is limited by moisture availability only during the current growth season and the immediately preceding wet season. The equality of correlations tests indicates that the sensitivity of Douglas-fir to drought during the prior year is significantly larger than the response of Oregon white oak. There are no current year radial growth response differences between the two species.

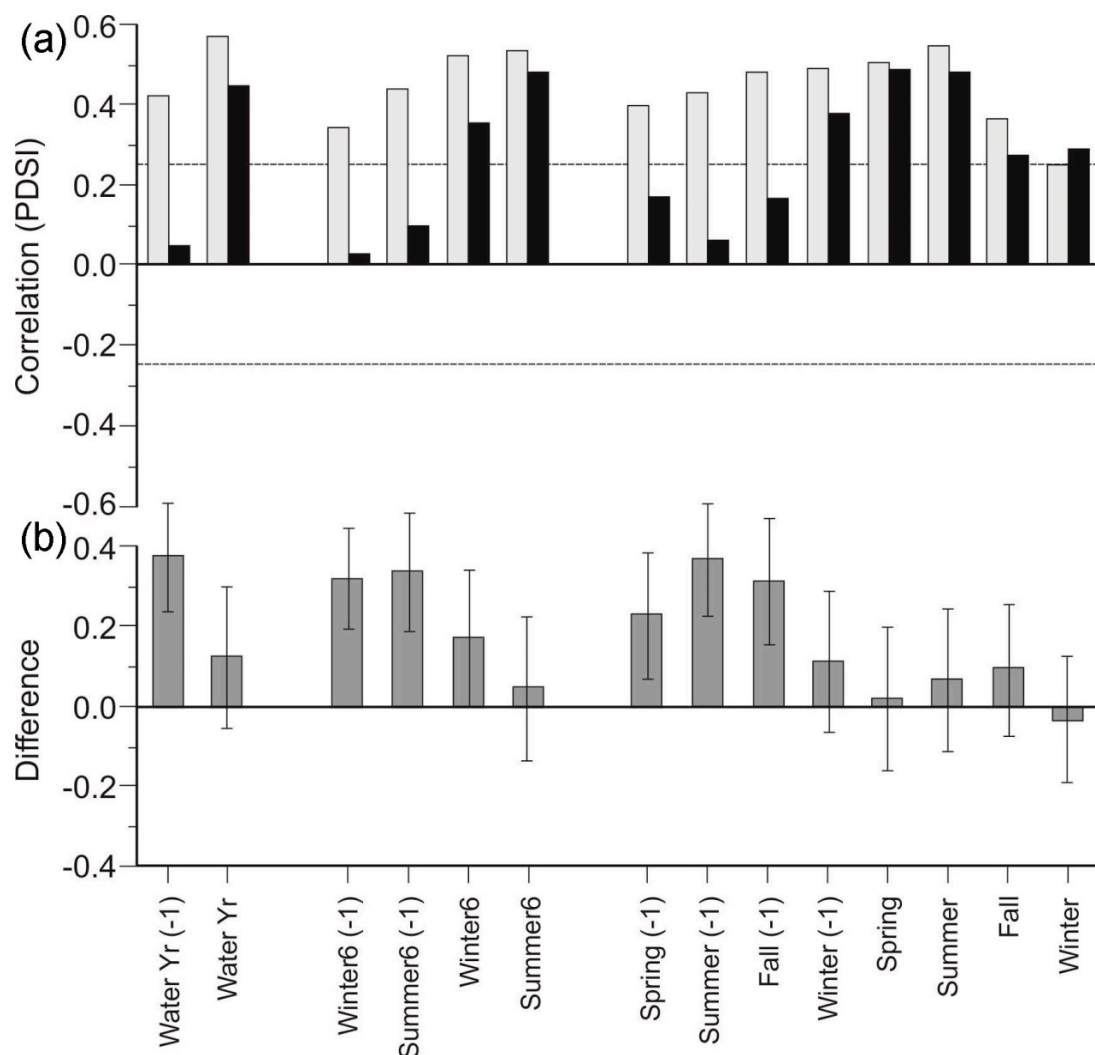


Figure 2. (a) Correlations between radial growth index of Douglas-fir (light gray) and Oregon white oak (solid) and seasonal values of the PDSI (see text for time windows). The horizontal dashed lines indicate the threshold for significance at the 95% confidence level. (b) Growth–climate response differences for the two species. Positive values indicate that Douglas-fir is more positively correlated to PDSI than Oregon white oak during that season. The error bars indicate the 95% confidence limit on the difference.

3.3. Stand Density Chronologies

Results of this study suggest that while density does not affect the growth–climate associations of Douglas-fir at this site (Figure 3) Oregon white oak growing at high densities are more limited by drought than Oregon white oak growing at low densities (Figure 4). Douglas-fir trees growing at both high-density and low-density are significantly positively correlated to PDSI during most seasons of the previous and current year but not to current fall and winter or winter6 (−1). Oregon white oak trees growing at high-density show greater sensitivity to drought in spring and summer of the prior year than Oregon white oak trees growing at low-density. The equality of correlations tests indicates that during the prior year the sensitivity to drought of Oregon white oak growing at high-density, as indicated by radial growth, is significantly different from the response of Oregon white oak growing at low density. There are no current year radial growth/drought association differences between the two subsets of trees.

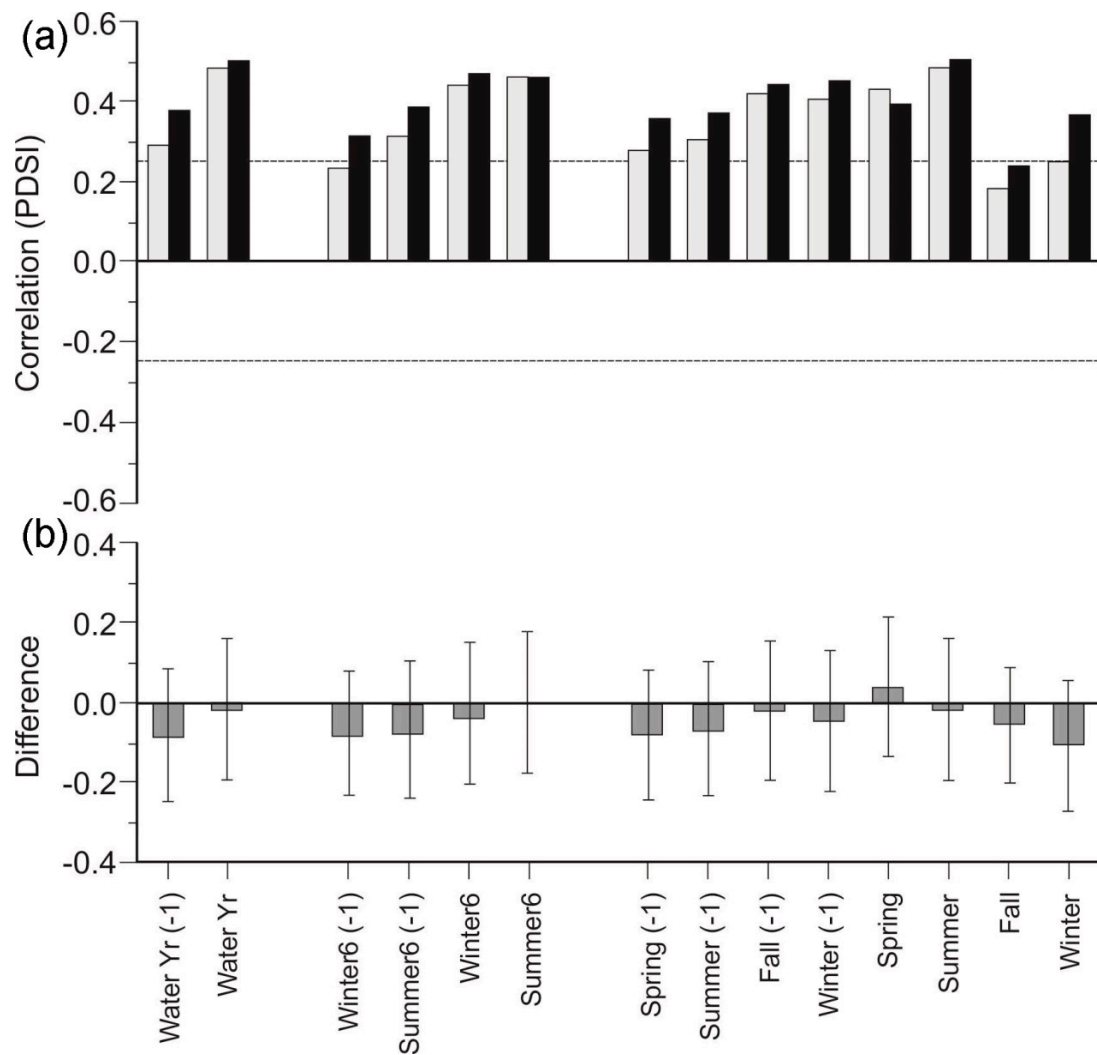


Figure 3. (a) Correlations between radial growth index of Douglas-fir growing at high density (light gray) and low density (solid) and seasonal values of the PDSI (see text for time windows). Significance levels and confidence limits are indicated as in Figure 2. (b) Growth–climate response differences for the two chronologies. Positive values indicate that Douglas-fir growing at high density are more positively correlated to the PDSI than Douglas-fir growing at low density during that season. The error bars indicate the 95% confidence limit on the difference.

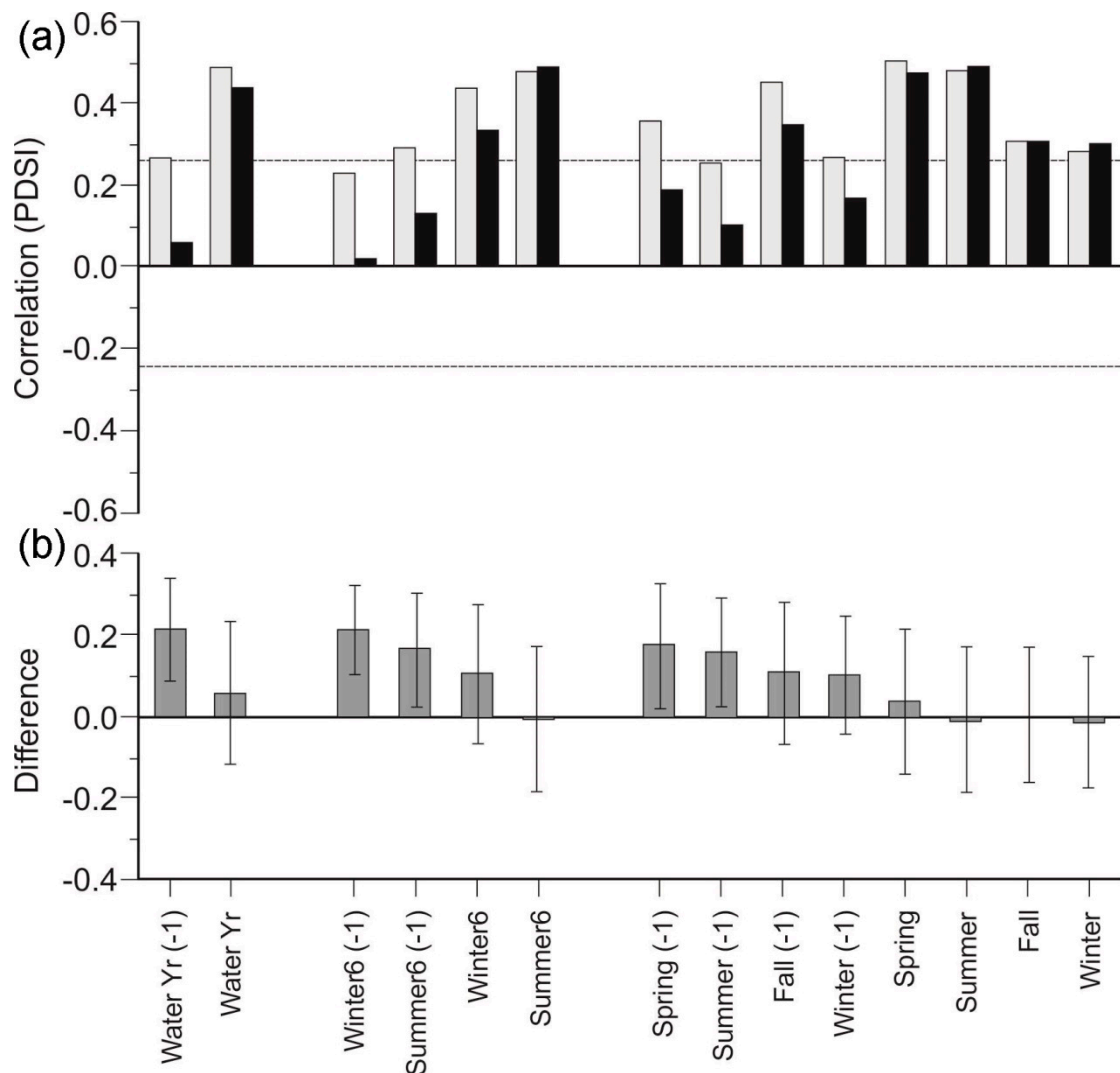


Figure 4. (a) Correlations between radial growth index of Oregon white oak growing at high density (light gray) and low density (solid) and seasonal values of the PDSI (see text for time windows). Significance levels, and confidence limits are indicated as in Figure 2. (b) Growth–climate response differences for the two chronologies. Positive values indicate that Oregon white oak growing at high density are more positively correlated to the PDSI than Oregon white oak growing at low density during that season. The error bars indicate the 95% confidence limit on the difference.

3.4. Canopy Morphology Chronologies

Whereas the growth–climate associations of Douglas-fir are not affected by morphological characteristics at our site (Figure 5), Oregon white oak trees with open-grown crown morphologies exhibit different associations to climate than Oregon white oak with closed-grown crown morphologies (Figure 6). All open-grown and closed-grown Douglas-fir show significant positive correlations to drought during all seasons analyzed except fall during the year of growth. Open-grown Oregon white oak are less sensitive to drought than closed-grown Oregon white oak in both the prior and current year. Closed-grown Oregon white oak exhibit more significant positive correlations to drought than open-grown Oregon white oak, with significant positive correlations to summer6(-1), spring3(-1), fall3(-1), winter3(-1), and to all of the current year seasons. Open-grown Oregon white oak exhibits significant positive correlations to drought in current year summer6, spring3, and summer3. The equality of correlations tests indicates that the sensitivity of open-grown Oregon white oak radial

growth to drought during both the prior and current year is significantly weaker than the response of woodland- type Oregon white oak to drought during all seasons analyzed.

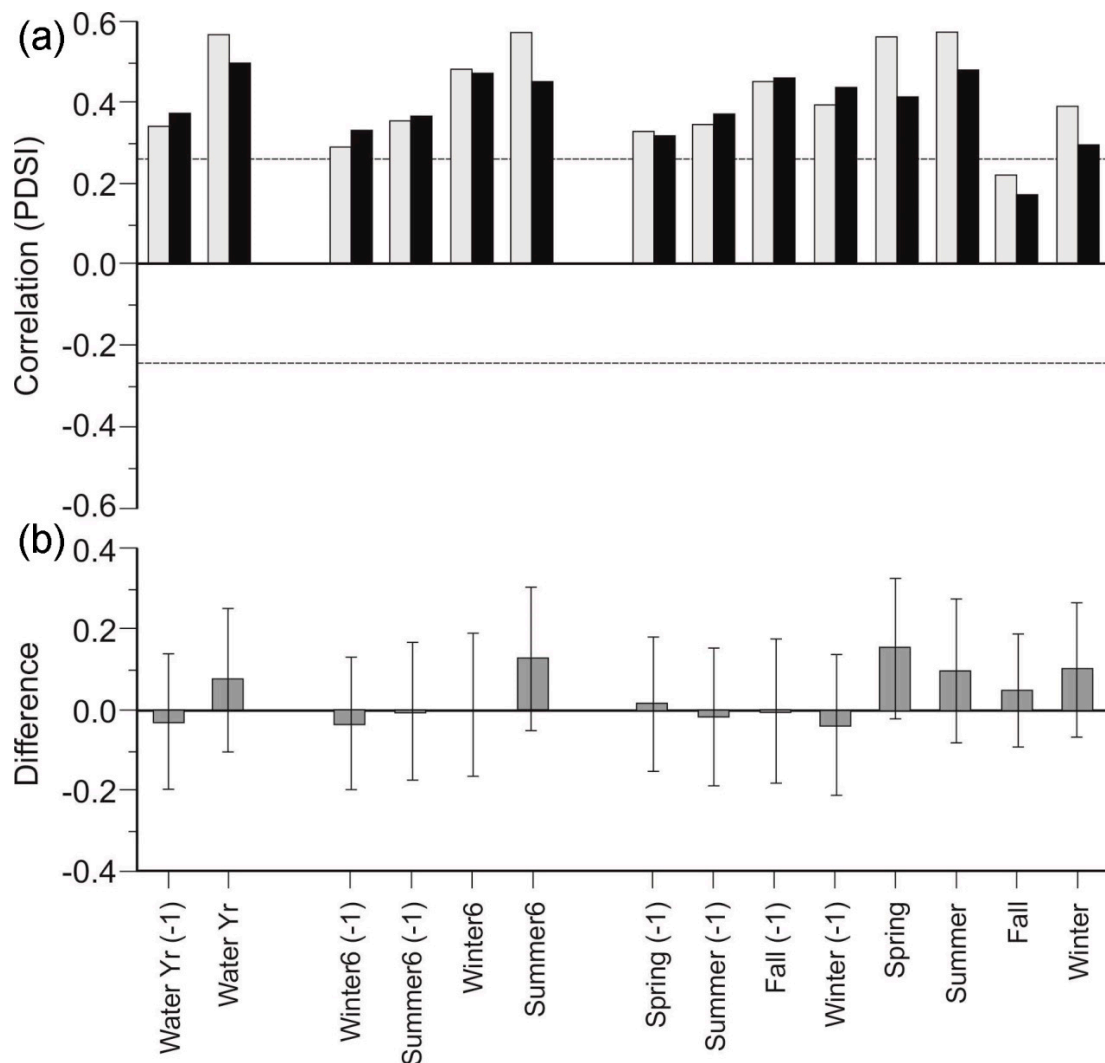


Figure 5. (a) Correlations between radial growth index of open-grown Douglas-fir (light gray) and closed-grown Douglas-fir (solid) and seasonal values of the PDSI (see text for time windows). Significance levels and confidence limits are indicated as in Figure 2. (b) Growth–climate response differences for the two chronologies. Positive values indicate that open-grown Douglas-fir are more positively correlated to the PDSI than closed-grown Douglas-fir during that season. The error bars indicate the 95% confidence limit on the difference.

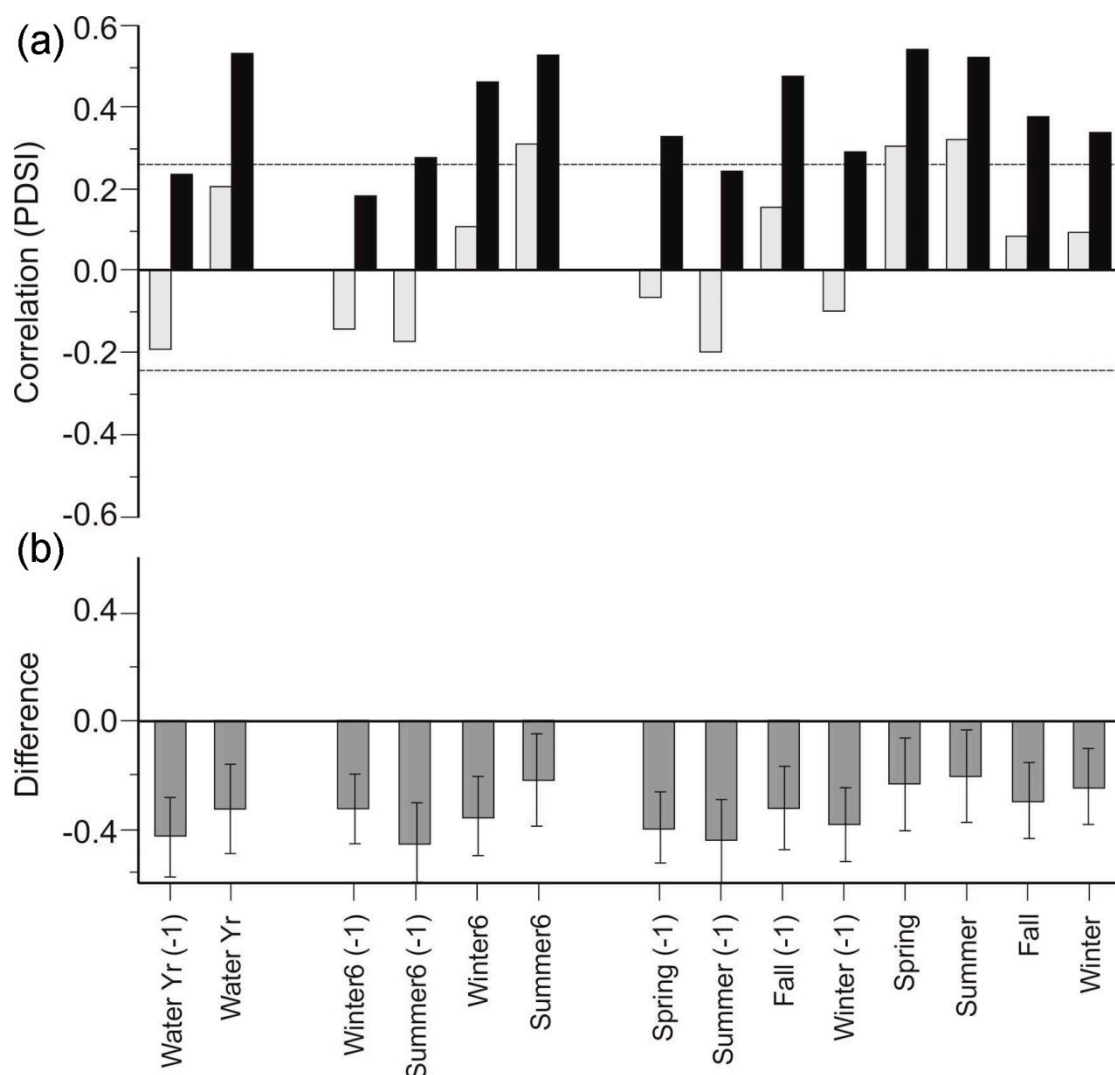


Figure 6. (a) Correlations between radial growth index of open-grown Oregon white oak (light gray) and closed-grown Oregon white oak (solid) and seasonal values of the PDSI (see text for time windows). Significance levels and confidence limits are indicated as in Figure 2. (b) Growth–climate response differences for the two chronologies. Positive values indicate that open-grown Oregon white oak are more positively correlated to the PDSI than closed-grown Oregon white oak during that season. The error bars indicate the 95% confidence limit on the difference.

3.5. Stand Composition Chronologies

The growth–drought relationships of Douglas-fir growing adjacent to Oregon white oak are not significantly different from the growth–drought relationships of Douglas-fir growing adjacent to conspecifics (Figure 7). Our analysis indicates that Oregon white oak competing with conspecifics for resources exhibit different relationships to climate than Oregon white oak competing with heterospecifics (Figure 8). Oregon white oak competing with Douglas-fir are more sensitive to drought than Oregon white oak competing with conspecifics. Significant positive correlations between radial growth and drought for Oregon white oak growing adjacent to conspecifics occur in previous year fall3 and current year water year, summer6, winter6, spring3, and summer3. Significant positive correlations between radial growth and drought for Oregon white oak growing adjacent to fir occur in all previous year seasons excepting winter6 and summer3 and all current year seasons. The equality of correlations tests indicates that the radial growth sensitivity to drought of Oregon white oak growing among

heterospecifics is significantly higher than the radial growth sensitivity to drought of Oregon white oak growing among conspecifics in all prior year seasons with the exception of fall3.

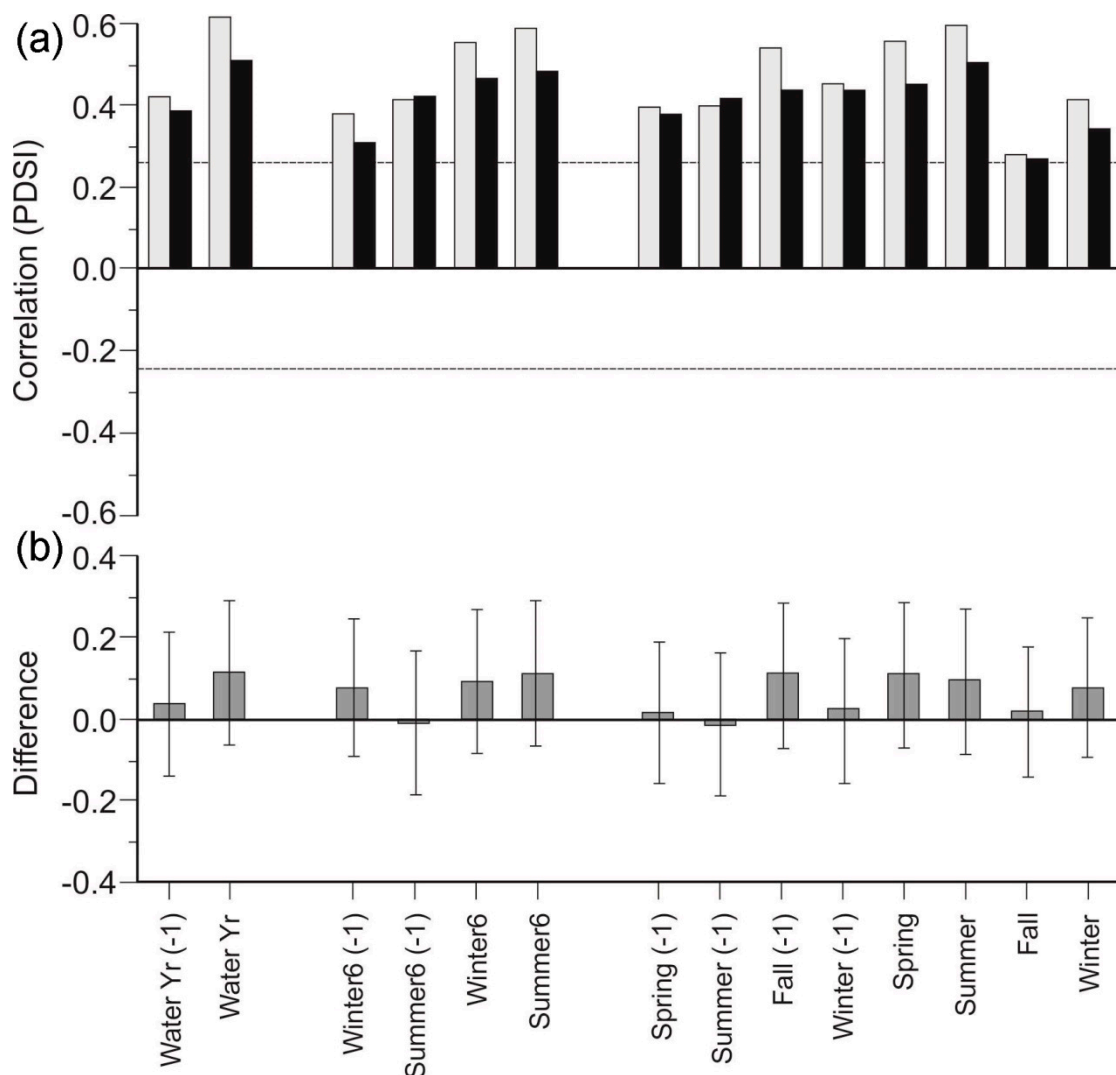


Figure 7. (a) Correlations between radial growth index of Douglas-fir growing among conspecifics (light gray) and heterospecifics (solid) and seasonal values of the PDSI (see text for time windows). Significance levels and confidence limits are indicated as in Figure 2. (b) Growth-climate response differences for the two chronologies. Positive values indicate that Douglas-fir growing among conspecifics are more positively correlated to the PDSI than Douglas-fir growing among heterospecifics during that season. The error bars indicate the 95% confidence limit on the difference.

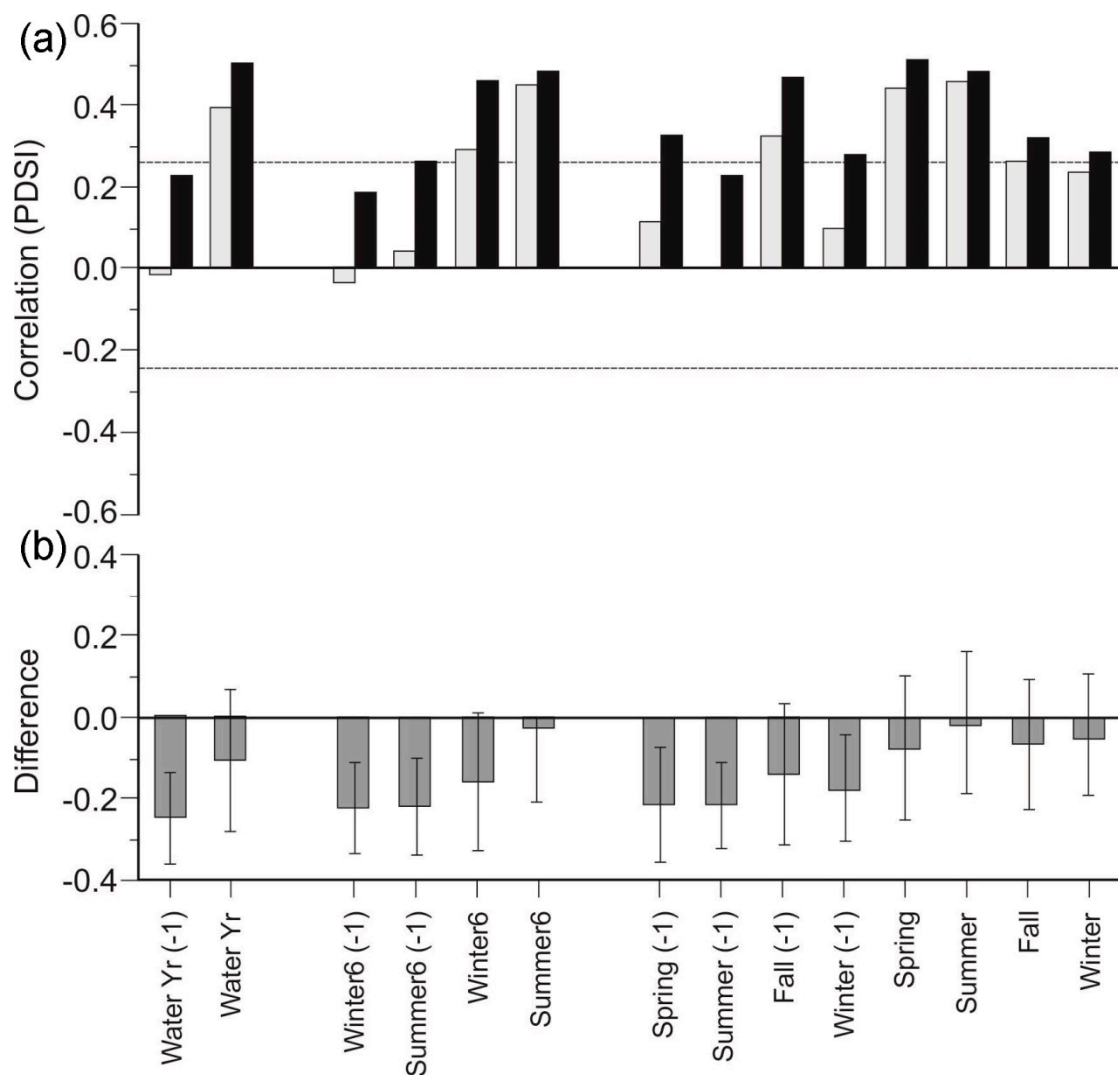


Figure 8. (a) Correlations between radial growth index of Oregon white oak growing among conspecifics (light gray) and heterospecifics (solid) and seasonal values of the PDSI (see text for time windows). Significance levels and confidence limits are indicated as in Figure 2. (b) Growth–climate response differences for the two chronologies. Positive values indicate that Oregon white oak growing among conspecifics are more positively correlated to the PDSI than Oregon white oak growing among heterospecifics during that season. The error bars indicate the 95% confidence limit on the difference.

4. Discussion

Lack of soil moisture can act as a limiting factor affecting tree growth in regions that experience prolonged dry conditions, especially during the growing season [41–43]. Our results show that annual summer drought conditions on southern Vancouver Island limits tree growth at Rocky Point. However, our results also suggest that the sensitivity of tree-ring growth to climate is affected by both stand composition and stand structure.

4.1. Species-specific Responses to Drought

The results of this analysis indicate species-specific differences in growth response to seasonal drought (Figure 2). The Pearson correlations between seasonal PDSI and radial growth index illustrate the differences between the two species and can be interpreted in terms of ecophysiological adaptations to the specific site conditions on southern Vancouver Island.

Current year radial tree growth is often influenced by the prior year's climatic conditions, especially in conifers [31,44,45]. At this site, Oregon white oak is not as sensitive to drought during the previous year as is Douglas-fir. Whereas oak responds positively to moisture increases beginning in the winter preceding the growth year, Douglas-fir shows positive responses throughout the entire previous growing season. Shoot growth of Douglas-fir is determinate, so its growth in the current spring and early summer is comprised of the enlargement of cells that were initiated during the previous late summer and fall [46]. Maximum needle area and thus the maximum conducting area in wood are also preset through conditions of the past year(s) as needles are retained for many years [47]. Although deciduous trees are normally dependent on carbon storage from previous years to promote bud break, the growth of Douglas-fir seems to be much more dependent on prior growth than is the growth of deciduous oak [48].

Our results suggest that Douglas-fir trees are more limited by drought conditions than are collocated Oregon white oak. Significant correlations between radial growth and drought for current summer occur in both species but extend for a longer period for Douglas-fir. Oak xylem anatomy allows for the rapid transport of water through large diameter earlywood vessels when soil moisture is readily available, but conductance occurs mainly through narrower, late-wood vessels during drought—reducing the likelihood of cavitation [49]. Oaks also tend to maintain a higher rate of photosynthesis at low leaf water potentials and high vapor pressure deficits than co-occurring species of other genus types [49]. This adaptation is typical for Mediterranean species [50]. Douglas-fir, on the other hand, is not as well adapted to drought conditions and physiological activity will continue throughout the driest months as this species depends on summer moisture to increase carbon storage that can be mobilized in the following year [51]. Sustained cambial activity in Douglas-fir can increase the risk of cavitation during prolonged drought periods [52]. If the climate becomes drier and hotter in British Columbia, as is predicted over the next half century [53], the ability of Oregon white oak to conduct sap through latewood vessels during drought conditions could favor the growth of this species over the growth of Douglas-fir.

The positive response correlation to PDSI in the previous winter exhibited by both species may be related to the fact that these species both rely on winter precipitation to recharge soil water for the next growing season. However, winter moisture can also have a direct positive effect on root growth. White oak (*Quercus alba* L.) have been reported to grow fine roots even in winter if the soil temperature is above 0 °C [54]. The majority of precipitation on Southern Vancouver Island falls between October and March, and mean monthly soil temperatures rarely drop below 0 °C making root growth in winter a possibility at this site. Root growth in winter may be important for species growing in climates that experience significant summer drought [50].

The response to PDSI is generally significantly positive in the current growing season for both species. In the summer months, increasing temperatures are assumed to lead to increasing drought by increasing evapotranspiration. There are no differences between Oregon white oak and Douglas-fir in their correlations to PDSI during the period beginning in the winter prior to growth.

4.2. Stand Density and Responses to Drought

There are no obvious differences in the response to drought of Douglas-fir trees growing at high density to that of Douglas-fir growing at low density at the study site (Figure 3). This result differs from previous studies [(cf examples in [46]) that have noted Douglas-fir growing in high density stands respond more severely to drought than trees in open stands. Our results may reflect the common occurrence of root grafting in Douglas-fir stands [55]. Root grafting can cause a more equal distribution of resources among all trees interconnected by their roots thus muting density-specific climatic effects within a single site. Alternatively, the stand sampled may not contain the full range of stand densities tolerated by Douglas-fir, and so the high-density chronology may still be of sufficiently low density that additional moisture stress is not induced.

In contrast to Douglas-fir, Oregon white oak growing at high stand densities exhibit significantly greater sensitivity to drought than Oregon white oak growing at low densities (Figure 4). These results probably reflect the fact that more dense stands will deplete soil moisture more rapidly during the growing season, causing trees growing at higher densities to rely more on deep soil water that is recharged during the wet season. When encroached upon by Douglas-fir, Oregon white oaks have a competitive disadvantage as they generally grow slowly in both height and diameter. In contrast to the open-grown trees that have short boles bearing large crooked branches that form dense rounded crowns, Oregon white oak growing at higher densities, even at 70 to 90 years old, have slim, straight boles, fine side branches, and narrow crowns [17].

Because the majority of Douglas-fir are located in the denser north-east portion of this site, the low density Douglas-fir chronology (including those individuals growing at densities of less than $0.0071 \text{ m}^2/\text{m}^2$) are actually growing at a higher density than the high density Oregon white oak (greater than $0.0066 \text{ m}^2/\text{m}^2$). The fact that Oregon white oak is affected by competition at a far lower density than Douglas-fir testifies to its poorer competitive status.

4.3. Morphological Responses to Drought

Oregon white oak is more strongly influenced by morphology type than is Douglas-fir (Figure 4; Figure 5). A reason for this may simply be that Douglas-fir is more dominant than Oregon white oak at this site and does not show any signs of stress from competition. Other reasons may include the tendency for the roots of Douglas-fir to graft together readily, often leading to a system of interconnected roots [56] allowing them to share nutrient and water resources regardless of morphology type [55,56]. This adaptation makes it difficult to distinguish morphology-based competitive ability in this species [57]. The relatively small number of Douglas-fir trees in each chronology may also affect the strength of the expressed population signal in our results.

In Oregon white oak, morphology plays a more substantial role in the sensitivity of tree-ring growth/climate associations. The greater radial growth/drought sensitivity of closed-grown morphology than open-grown morphology can perhaps be interpreted as a greater sensitivity to increased competition from Douglas-fir. Most notably, the greater sensitivity to drought in previous year spring3 in closed-grown Oregon white oak could be a result of Douglas-fir drawing on soil moisture stores before the deciduous trees commence their growing season [17,51]. Perhaps due to increased competition for water resources and light, this specific morphology type of Oregon white oak is affected by drought conditions more readily than trees with wider crowns and deeper canopies. Possibly because of reduced photosynthesis closed-grown Oregon white oak are not able to allot as much stored carbon to radial growth [58]. There is substantial, but not complete, overlap between the low-density and open-grown chronologies, and the high-density and closed-grown chronologies, respectively. The different associations seen between the two sets of chronologies may be a response to early development stages. Some of the open-grown trees occurred in plots with high density, but may be better able to tolerate drought due to their wide crown which precludes subsequent establishment by other seedlings and their associated extensive root extent [17].

Given that the species (i.e., stand-wide) chronology of Oregon white oak does not exhibit a strong dependency on the prior year's climate, it is surprising that woodland-grown Oregon white oak demonstrates such strong correlations to the previous year's PDSI. As the size of the root system in trees is often related to the size of its crown rather than its bole, there should be evidence of differences in below-ground resource use between open-grown morphology and closed-grown trees [59]. The root biomass of Oregon white oak is probably greater in open-grown trees than in closed-grown trees. The total proportion of root biomass decreases with age in Douglas-fir, and as the trees at this site are still young, it is likely that the majority of Douglas-fir trees in this study still nearly 50% of their total biomass in roots, and have achieved their near maximum rooting depth [51]. With a large percentage of root biomass still intact, and a larger and more dominant crown position, Douglas-fir at this site should be a dominant competitor for soil moisture.

4.4. Competitive Interactions and Responses to Drought

Through the investigation of intra- and inter-specific growth–climate relationships of Douglas-fir and Oregon white oak, our results suggest that while the radial growth of Oregon white oak is reduced in the presence of Douglas-fir—probably due to competition for moisture—the presence of Oregon white oak does not reduce the radial growth of Douglas-fir. This result supports the proposition that Douglas-fir is the dominant competitor between these two species at this site and that the presence of Oregon white oak does not interfere with its uptake of available resources.

Oregon white oak competing with Douglas-fir exhibit stronger and more statistically significant correlations to drought than do Oregon white oak competing with conspecifics (Figure 8). The significant increase in the sensitivity of Oregon white oak growth rates to drought during the seasons preceding the year of growth imply that current radial growth of Oregon white oak is more influenced by previous year carbon allocation when growing in the presence of Douglas-fir.

4.5. Competitive Interactions and Climate Reconstructions

The finding that changes in stand structure and composition can affect the growth–climate relationships of trees has implications for reconstructing past climates and predicting future vegetation patterns using dendrochronological techniques. In dendroclimatology James Hutton’s principle of uniformitarianism is often used to support the assumption that tree growth–climate relationships are stable over time. This assumption enables tree-ring scientists to infer the nature of past climate from statistically derived calibrations between ring-width index chronologies and climate in the more recent past [31]. Few studies have directly tested this assumption, although there have been several observations of changes in the response of tree growth and/or a reduction in tree sensitivity to climate over the past 40 or 50 years [60–62], as well as age-related variability in the growth response of trees [63]. Our results suggest that changes in stand structure and composition may also be a factor in the alteration of the climate signal recorded by tree rings as a result of competitive dynamics. If competition and stand density affect the climatic signal recorded by a tree ring, trees may not show a stationary response to climate at a location where these factors have changed over the tree’s life. The reconstruction of past stand composition and structure should therefore play an important role in the reconstruction of past climates. Changes in stand dynamics of this sort, due to fire exclusion, cattle grazing, and pest control efforts over recent decades, are probably widespread in stands sampled for dendroclimatic reconstructions. Naive interpretations of tree-ring reconstructions of climate may therefore be problematic.

5. Conclusions

This study has provided insights both into the dynamics of Oregon white oak ecosystems and into the effects of competition on limiting factors. Dendroecology proved to be an effective tool for identifying differences in species growth–climate relationships under various stand compositions and structures within a mixed Oregon white oak–Douglas-fir forest. Encroachment of the Oregon white oak savanna by Douglas-fir appears to increase the sensitivity of Oregon white oak to drought and increases its reliance on carbon reserves from previous years. Douglas-fir may have a competitive advantage over Oregon white oak due to root grafting, greater shade tolerance, and foliage that is retained over multiple years. The results of this study are geographically- and species-specific; therefore, it would be scientifically valuable to replicate this analysis in other geographic locations with the same species, and between other groups of species to assess the transferability of our findings.

The oak savanna at Rocky Point has undergone dramatic changes over the past 300 years: Scattered oak savanna transitioned to oak woodland between ca. 1750 and 1850, and then subsequently to mixed oak-conifer woodland. The understory is now dominated by exotic grasses that were likely introduced during the early- to mid-twentieth century [16]. These changes have the potential to alter the growth–climate associations over time as competition for resources changes. This finding challenges

the common assumption of stationarity in the growth–climate relationships of tree-ring chronologies, and speaks to the importance of understanding stand history and the effects of competition when developing reconstructions in closed canopy forests, particularly those with uneven age structures and mixed species composition.

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