

**Relative Effects of Fog, Competition and Tree Size on Coast
Redwood Growth in Strawberry Canyon, Berkeley, California**

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ABSTRACT

Climate change is reducing the amount of fog across the California coast, which encompasses all of the native habitat of Coast Redwood (*Sequoia sempervirens*). In order to explore the potential impacts of diminishing fog levels on redwood growth, I investigated the effects of fog, intraspecific competition, and tree size on redwood radial growth to quantify the relative importance of each factor. My study site was an even-aged, planted stand with a strong summer fog gradient in Berkeley's Strawberry Canyon. I compared the relative effects of competition, the summer and winter fog hours in which each tree was inundated, and the size of each tree on relative growth rate. I investigated whether the intensity of intraspecific competition in redwoods differed over a gradient of water stress, as measured by differences in fog levels, in order to test the Stress Gradient Hypothesis, and investigated whether lower fog levels correlated with less radial growth. I found that fog hours and intraspecific competition accounted for very little of the variation in growth, but that tree size described a significant amount of the variation in growth. Size and summer fog were the only significant factors in the best-fitting regression model. Additionally, crown competition may play a role. I found no connection between fog amounts and intraspecific competition, which does not provide evidence for the Stress Gradient Hypothesis. These results show a lack of fog stress in this stand, which is a good sign for the species in the context of climate change.

KEYWORDS

Stress Gradient Hypothesis, Inverse Distance Weight (IDW), Hegyi competition index, intraspecific competition, radial growth

INTRODUCTION

Water availability is widely considered to be the most important physical input factor in the growth of terrestrial plants, and is often considered to be the limiting resource that determines the geographical regions and ecosystems that different terrestrial plants can or cannot inhabit (Odum 1971). Adaptations to alleviate water stress, such as the ability to take in water through leaves in addition to roots (Dawson 1998), are often important morphological features of plants. These adaptations have evolved over hundreds of thousands of years as climates, ecosystems, and the organisms within them change. However, current anthropogenically-caused climate change is changing ecosystems at a faster rate than ever before (Visser 2008), thus heavily affecting the environments in which plants evolved. These changes substantially impact water stocks and cycles worldwide (Arnell 1999) and consequently water available to plants. In the context of climate change, water stress is now an even more important factor in plant growth and mortality, and is leading to rapid changes in the distribution of many plant species (Kelly and Goulden 2008).

Climate change also influences the relative importance of other factors that affect plant growth, including plant competition. In general, competition is considered a negative interaction between plants: it decreases growth and fecundity in and reduces overall fitness of all organisms involved (Freeman 2011). It's so powerful an ecological factor that species evolve unique niches primarily to avoid competition (Grace and Tilman 1990). Knowledge about the effects of changing levels of stress on competition, especially those affected by climate change, will be crucial in coming years to inform conservation and restoration efforts. Therefore, it is of special importance to conduct research on species that both rely on resources threatened by climate change and currently undergo competitive interactions that may be particularly altered by climate change. Coast Redwood (*Sequoia sempervirens*) is one such species: they rely heavily on fog water, which accounts for up to 45% of total transpiration (Dawson 1998), and rely even more heavily on fog in years of below-average precipitation (Dawson 1998). They are also sensitive to drought, due to poor control of stomatal closure (Burgess and Dawson 2004). Additionally, they often grow clumped near each other and thus have a high degree of intraspecific competition (Dagley 2007). Unfortunately, since the early 20th century, fog frequency has declined as much as 33% across their range on the West Coast as a result of climate change (Johnstone and Dawson 2010). Redwood's need for fog leads to an exceptionally small habitat range in terms of both area and

elevation (Farjon 2005). These factors combine to potentially increase water stress in redwoods across their already-limited range. However, it's currently unknown how much these factors are affecting redwood growth: they are experiencing reduced fog levels, which may lead to increased water stress (Dawson 1998), but it is unclear as of yet whether the climate-change induced increases in fog levels are affecting their growth or their level of competitive stress.

Unlike water stress, stress from competition may actually be alleviated by the effects of climate change: increased resource stress resulting from climate change may mean a decrease in competition. The Stress Gradient Hypothesis (SGH) predicts that as stress increases, competition decreases and shifts to facilitation (Bertness and Callaway 1994). According to the SGH, species tend to interact competitively during periods of relatively low stress, which harms the organisms involved. During periods of higher stress, species tend to shift to facilitative relationships that do not harm, and benefit at least one of, the organisms. Although supported widely (Callaway 2007), the SGH has primarily investigated interspecific competition, as opposed to intraspecific competition (Garcia-Cervigon et al., 2013). This makes for an incomplete hypothesis by disregarding the potential effects that changes in stress have on intraspecific competition. Therefore, the SGH should also be tested on species that are both sensitive to climate change and that are affected heavily by intraspecific competition, making them a priority for conservation research.

Though it has been both hypothesized (Oberlander 1956, Azevedo and Morgan 1974, Libby 1996) and shown (Dawson 1998, Burgess and Dawson 2004) that fog makes up an important part of redwoods' water budget, an experiment quantifying the effects of fog on individual tree growth is novel. In order to be able to compare effects of fog and competition on redwood growth not only with each other, but with a sort of baseline, I chose to also examine the effects of tree size, a factor known to have a large effect on tree growth. In this study, I examine the relative effects of these three factors—tree size, competition and fog levels—on redwood growth, in order to determine the potential impact that the reduction in fog may have on future redwood growth and health. I also ask whether the SGH applies to intraspecific as well as interspecific competition, and if redwood intraspecific competition is affected by differential fog levels. Because fog is a resource that is not exhausted by redwoods, changes in fog levels may not greatly affect competition. By examining relative growth, hours spent inundated with fog, individual tree sizes and levels of competitive stress, I will test the relative importance of each factor to growth, and will

investigate whether the SGH holds intraspecifically in redwoods affected by climate-change induced changes in fog levels. Additionally, I will quantify the the effects of different fog levels on individual redwood growth, to further elucidate their need for and use of fog water.

METHODS

Study site

This site is an even-aged, planted Coast Redwood (*Sequoia sempervirens*) grove in the UC Berkeley-affiliated Strawberry Canyon Ecological Study Area. Being in Berkeley, the site has a Mediterranean climate and receives little summer rainfall, but receives significant amounts of summer fog. The site was planted sometime in the 1930s, making the trees between 74 and 83 years old. However, redwoods often sprout clones from their bases, so there may be some younger trees resulting from clonal sprouts as well. Compared to a natural redwood forest, the trees are somewhat sparsely packed in the grove, but it has a high degree of canopy cover. No significant understory is present. The average slope of the grove is 15 degrees, with a northwest aspect. I studied 2 plots within the grove, one near the bottom of the grove, which I refer to as the lower plot, and one near the top, which I refer to as the upper plot. The upper plot is approximately 100 meters away from the lower plot, up the slope of the grove. These plots were established by John Battles in 2007 (John Battles, *unpublished data*). The lower plot (Figure 1) is 1600 m² (40 m x 40 m) and the upper plot is 1200 m² (40 m x 30 m). In total, there are approximately 170 trees in the two plots, 139 of which I was able to identify and measure (75 trees in the lower plot and 64 trees in the upper plot).

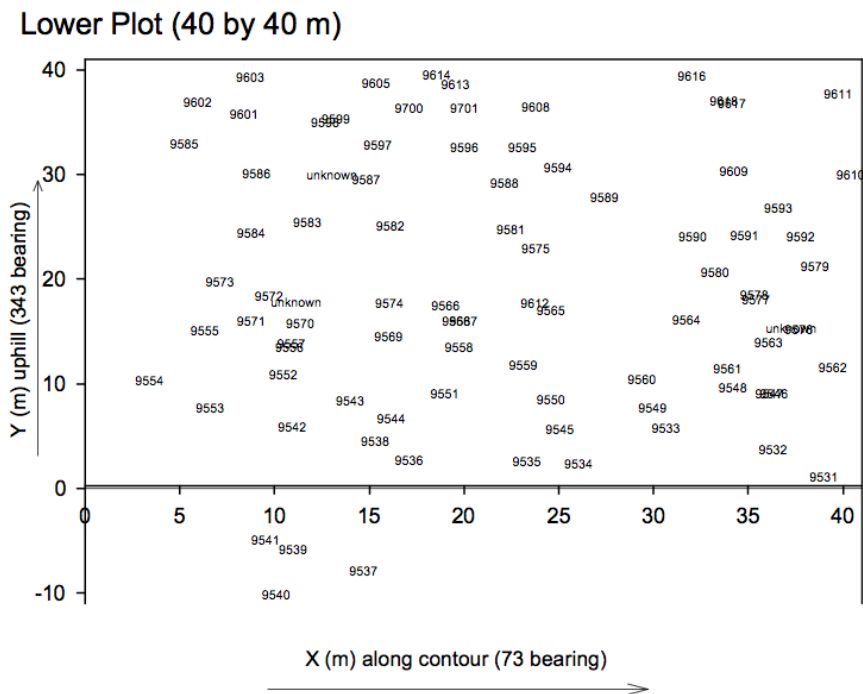


Figure 1. Map of all trees in the lower plot. Each tree was assigned a 4-number code and tagged accordingly by John Battles' undergraduate students in 2007. Trees were mapped according to their x and y distances in meters from a reference point at (0,0) (John Battles, *unpublished data*).

Data collection

Because competition is difficult to quantify (Körner 2003), I chose to define it as the amount of hours spent inundated in fog, according to the idea that less fog hours would equate to more stress. To relate amounts of fog received to competition and growth, I collected data on fog hours received throughout the plot, on tree radial growth, and on tree competition. I measured fog received throughout the grove as total hours spent inundated in fog for a period of 66 days during the summer and 44 days during the winter. To determine the hours spent inundated in fog, I collected continuous relative humidity readings every 39 minutes at 5 locations in the grove from June 3rd-August 27th, the most fog-heavy months in the Berkeley hills (Oberlander 1956), using an iButton Hygrochron DS1923 data logger. These 5 locations were along the elevation gradient of the grove: one at the top of the grove, one in the middle of the upper plot, one each at the top and bottom of the lower plot, and one at the bottom of the grove. To account for potential differences in winter fog patterns, I also collected relative humidity readings every 39 minutes from January

4th to February 17th, but this time placed all sensors within the two plots: 3 sensors in the upper plot and 2 sensors in the lower plot.

To calculate each tree's relative growth rate and Competition Index, or CI (a measure of competitive stress for each tree), I collected the DBH (diameter at breast height, approximately 1.37 m from the ground) of each tree, and used both maps of the trees in the two plots in conjunction with a distance tape and compass to find the distances between each tree and its neighbors (John Battles, *unpublished data*).

Data processing

I characterized the presence of fog as a sensor reading at or above a specific relative humidity. This relative humidity percentage, or fog threshold percentage, was different for each of the 5 sensors, ranging from 94% to 96.3%. I found each sensor's fog threshold percentage by placing all the sensors in the same place with a known relative humidity of 100%, verifying that the relative humidity was 100% with a sling psychrometer. I used this data to find each fog threshold percentage by observing the lowest reading each sensor logged out of approximately 50 readings each sensor took at 100% relative humidity. I then applied this threshold to my data to find the number of times the sensors logged the presence of fog over the course of data collection, which I refer to as fog counts. Since the readings were taken every 39 minutes, I defined each reading that indicated the presence of fog, or fog count, as 39 minutes of fog inundation.

In order to convert fog inundation data into more easily understood units, I converted from fog counts to fog hours. To do so, I multiplied the fog counts by 39/60, or 0.65 (the number of 39-minute intervals in an hour). To account for the longer time spent collecting summer fog data compared to winter fog data, I then multiplied the winter fog hours by the number of days spent collecting summer data divided by the number of days spent collecting winter fog data (66/44, or 1.5).

To obtain a fog hour reading for each tree in the two plots, I used surface interpolation in ArcGIS to interpolate each tree's hours spent in fog based on the tree's relative proximities to the 5 sensors in the grove and on the hours of fog logged by each sensor (ESRI 2012). I did so by using an IDW, or inverse distance weighted, interpolation, to model the fog hours received in different areas of the grove (Croft and Burton 2006). This model assumes a linear decay function,

which means that fog hours will change linearly as the distance from the sensors also changes linearly. I created two separate IDWs, one each for the summer and winter fog campaigns.

I found radial growth over the past 7 years by subtracting the current DBHs from the DBHs of the same trees measured 7 years ago (John Battles, *unpublished data*). Then, to convert radial growth to relative growth, I used the following formula: $RGR = (DBH_1 - DBH_0) / DBH_0$, where RGR = relative growth rate, DBH_1 = the current DBH of the tree, and DBH_0 = the DBH of the tree in 2007. I assumed that no trees had shrunk over the course of the experiment, and set any negative growth rates in the dataset (which occurred when their measured diameter was smaller than the diameter in the previous data set) to zero.

To calculate distance between each tree for CI, I used the x and y locations of a map of field-recorded tree locations (see Figure 1) loaded into R (R Development Core Team 2010) and R Commander (Fox et al. 2011). To calculate CI, I used Hegyi's formula (Hegyi 1974): $CI = \sum e_{ij} D_j / D_i (Dist_{ij} + 1)$, where e_{ij} = a linear expansion factor, D_j = DBH of competitor tree, D_i = DBH of subject tree, and $Dist_{ij}$ = distance between the two trees. I imported DBH data and distance between each tree into a function in R (Natalie Solomonoff Van Doorn, *unpublished data*) to find a CI for each tree. I included competitor trees within a 10-meter radius around each subject tree (Natalie Solomonoff Van Doorn, personal communication).

I used parabolic volume as the metric for tree size, which takes into account height and DBH and models the tree as a three-dimensional parabola, according to the following formula: $Parabolic\ Volume = (\pi/2) \times height \times (diameter/2)^2$. Parabolic volume was measured in cubic meters (m^3).

Data analysis

In order to find the relative significance of each hypothesized factor as they affected relative growth, I created 5 multiple regression models that included progressively fewer factors. The factors tested were tree size, competition, summer and winter fog (considered separately), site (upper or lower plot), and various interactions between two of these variables. All the models tested relative growth as a function of the various independent variables. To determine which model best described relative growth, I tested each multiple regression analysis with Akaike information criterion (AIC) analysis, which penalizes models with more parameters in order to

adjust for their inherent prediction superiority, and gives a score based on each model's goodness of fit to the data, relative to the other models. To look for a relationship between fog stress and competition, I used linear regression with fog hours received by each tree as the independent variable and CI of each tree as the dependent variable.

RESULTS

Fog data and interpolation

There was a substantial gradient of summer fog hours occurring across the grove. Total summer fog hours ranged from 140 hours to 898 hours, with a median of 345 hours (corrected for differences in sensors). Monthly summer fog hours ranged from 64 hours to 394 hours, with a median of 160 hours. Over the summer, the top of the grove and the upper plot received the most fog hours, the site under the lower plot received the median number of fog hours, and the lower plot and bottom of the grove received the fewest fog hours (Figures 2 & 4). Over the course of the summer, the sensor in the upper plot logged 898 fog hours, while the sensor in the lower plot logged 280 hours (Figure 2).

Winter fog hours, measured just within the two plots, varied less: they ranged from 370 hours to 571 hours, with a median of 460 hours (corrected for differences in sensors and collection time) (Figure 3). Monthly winter hours ranged from 169 hours to 260 hours, with a median of 202 hours. Winter fog hours in the upper and lower plots did not differ significantly. The winter fog hours did not follow the same increasing trend along the elevation gradient, or any strong trend in general.

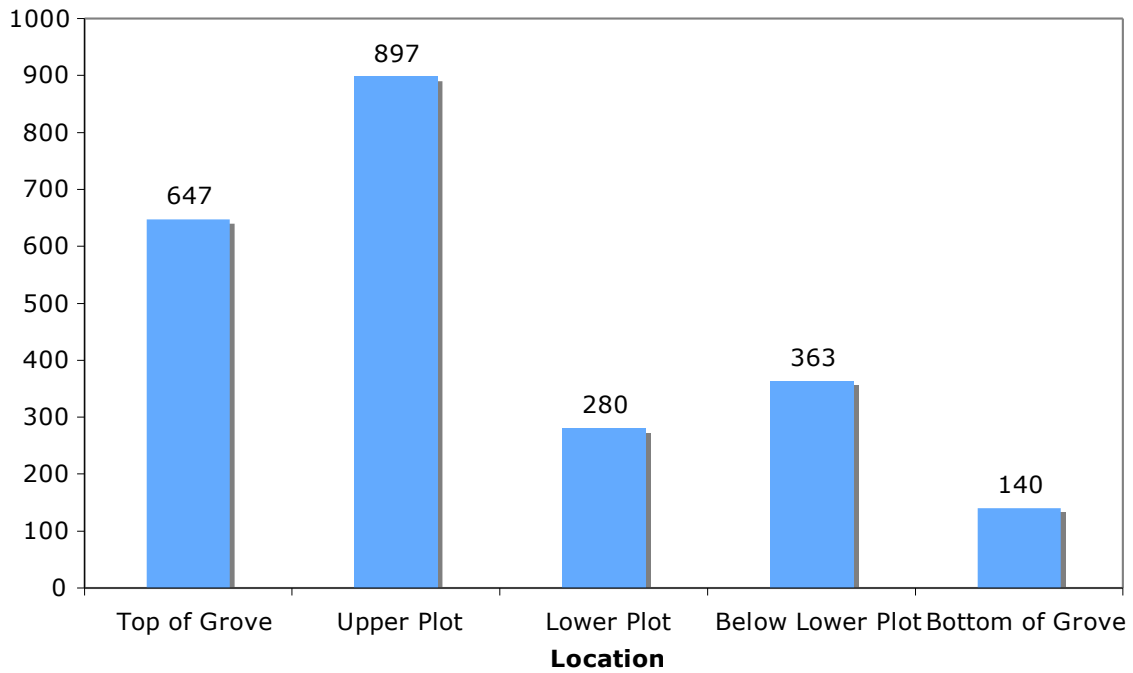


Figure 2. Total summer fog hours. These are organized in order of decreasing elevation from top of grove to bottom of grove. Fog inundation hours were highest within the upper plot and were drastically lower in the lower plot and bottom of the grove.

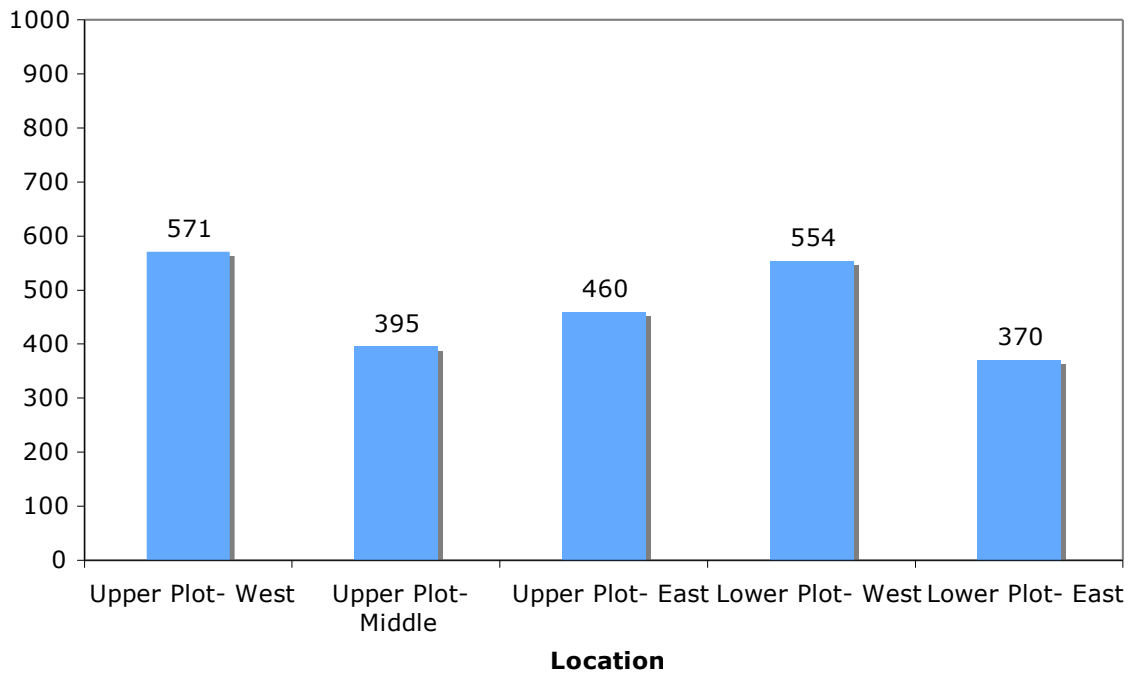


Figure 3. Total winter fog hours. These are organized in order from west to east of upper plot and from west to east of lower plot. Compared to summer fog patterns, there is no significant variation between the two plots, and no fog gradient following the elevation gradient.

The inverse distance weight (IDW) interpolation model developed in ArcGIS to estimate the total number of fog hours received by each tree is summarized in Table 1. The most important aspect of the model was simply that it showed the large difference in summer fog between the two plots and across the grove as a whole, with fog hours increasing along with elevation. Though the winter fog hours varied more inside of the plots, the winter fog hours in both plots are not significantly different (Table 1).

Table 1. Summary of fog hour statistics resulting from ArcGIS IDW fog interpolation across entire grove. All units are fog hours. These winter fog data are corrected to account for differences in winter and summer fog data collection times. Differences in fog hours between plots are substantial during the summer, with the upper plot receiving far more fog inundation, but are insignificant during the winter.

Season	Plot	Range	Median
Summer	Lower	280 - 407	326
Summer	Upper	795 - 897	864
Winter	Lower	370 - 554	457
Winter	Upper	394 - 571	449

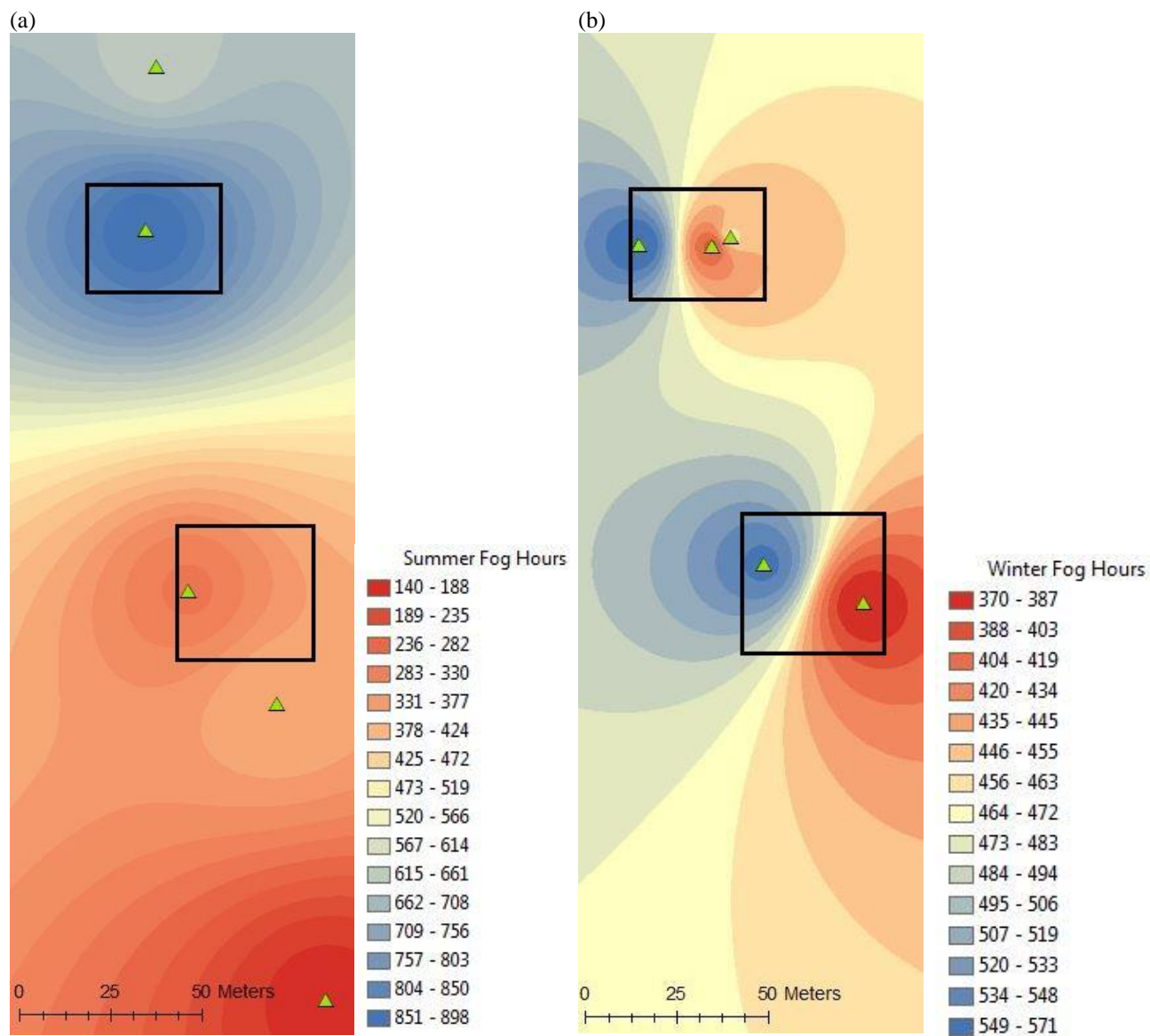


Figure 4. ArcGIS-created IDW model of total summer fog hours (a) and winter fog hours (b) across the full grove. Blue colors indicate more fog hours, and red colors indicate fewer fog hours. Sensor locations are represented by green triangles. Note that the two models have different scales, shown on the lower right of each model. Upper and lower plot boundaries are represented by black lines. After creating the model pictured here, I multiplied the resulting interpolated winter fog data by 1.5 before using them in analysis, to correct for the shorter amount of time spent collecting winter fog data.

Competition indices

Overall, CIs throughout the grove had an average of 1.98 ± 1.17 . As CI is calculated as a ratio, this is a relative, unitless number. In general, there did not seem to be an association between tree size and CI. CIs did not differ significantly between the two plots.

Relative growth rates

Overall relative growth rates ranged from 0 to 15.3%, with a median growth rate of 2.3%. 35% of the trees in the grove did not grow measurably. Average growth rates in the upper and lower plot did not vary significantly. A t-test showed that the trees that didn't grow were significantly smaller than the trees that did grow, in terms of parabolic volume ($t = 4.9465$, $df = 27$, $p\text{-value} = 3.5 \times 10^{-5}$).

Relationships between fog, competition, size, and growth

Results of the multiple regressions showed that tree size was by far the most significant factor affecting growth. The best-fitting model as determined by AIC analysis, Model 1 ($R^2=0.49$, $p=1.2 \times 10^{-12}$), included as parameters summer fog, tree size, competition, and site (Table 2). However, of those variables, the only significant ones were tree size ($p=1.3 \times 10^{-14}$) and competition ($p=0.018$), with size being much more significant. In fact, in every model, tree size and competition were the only significant parameters, with one exception: every parameter in Model 4, which only included summer fog, competition and tree size, was significant. Tree size alone accounted for 41% of the variation in growth ($p=4.9 \times 10^{-12}$), compared to all the parameters the best-fitting model (including size), which together accounted for 49% of the variation in growth ($p=1.2 \times 10^{-12}$).

Table 2. Summary of statistics of the 5 best-fitting multiple regression models. Lower AIC values (i.e., more negative) indicate a better fit. AIC values only indicate relative, not absolute, goodness of fit. Models with more parameters were penalized in their AIC value so as to account for their inherent superiority of prediction. The best fitting model, Model 1, had summer fog, tree size, competition and site as parameters, and accounted for 49% of relative growth.

Model Number	All Parameters	AIC value	R ²	p-value
1	Summer fog, tree size, competition, site.	-334.80	0.490	1.2x10 ⁻¹²
2	Summer fog, winter fog, tree size, competition, site.	-333.51	0.488	4.4x10 ⁻¹²
3	Summer fog, size, competition, site, site-summer fog interaction.	-333.20	0.486	5.1x10 ⁻¹²
4	Summer fog, size, competition.	-333.02	0.474	1.17x10 ⁻¹²
5	Summer fog, winter fog, size, competition, site, site-summer fog interaction.	-331.67	0.483	1.9x10 ⁻¹¹

DISCUSSION

Overall, these findings indicate that while many factors and mechanisms are likely affecting tree competition, growth, and resulting interactions in this grove, tree size was by far the most important variable measured in terms of predicting relative growth. While it's clear that growth is a function of a myriad of biotic and abiotic factors, the fact that tree size accounted for 41% of the variation in growth is significant. My results saw no correlation between water stress and competition, which does not provide evidence for the SGH. However, these results are somewhat inconclusive, as the lack of a correlation between fog and growth seems to imply a lack of fog stress.

Fog and relative growth

Given the extensive support of a correlation between fog belt and redwood habitat in the literature (e.g., Oberlander 1956, Azvedo and Morgan 1974, Libby 1996, Dawson 1998, Johnstone and Dawson 2010), the lack of correlation between fog and redwood growth was surprising. The most likely reason for this lack of correlation is that fog is not the limiting factor for growth in this

stand. If the trees are indeed getting more fog than they need, additional fog water will not necessarily lead to greater growth; growth will instead be limited by another variable.

This finding implies that the coastal fog present across the redwoods' range provides a threshold for the tree's water budget: the trees require a minimum input of fog water, but is not the sole driver of their growth. This is in line with the idea that fog may partially benefit redwoods by lowering the evaporative potential and vapor pressure deficit of the surrounding air and thus lowering evapotranspiration and water stress (Dawson 1998), thus helping to mitigate water lost by redwood's "leaky" stomata (Burgess and Dawson 2004). It also implies that the trees are not under a great deal of water stress, as if they were, an input of even a small amount of water would likely have a large affect on growth.

Additionally, although there were large differences in summer fog hours (the upper plot spent approximately 38% of the measured time inundated with fog, compared to approximately 23% in the lower plot), which are thought to be more ecologically significant (Dawson 1998, Oberlander 1956), the fog levels in one single year over such a small area may not necessarily be an accurate indication of larger trends in fog distribution over time.

Competition, size and radial growth

Intraspecific competition in this population had little effect on growth, accounting for less than 1% of the observed variation. Although Hegyi's competition index (Hegyi 1974) has undergone rigorous testing (Biging and Dobbertin 1992), these results are an indication that there are situations in which diameter-based competition indices do not predict growth well, especially in established systems.

In an ecological example of the "rich getting richer," growth over the course of the observed data is most correlated simply with the size of the trees. These results support the idea that tree size is one of the most important factors in radial growth (Piutti and Cescatti 1996). This growth trend is likely for a variety of reasons: taller trees with larger DBHs have greater access to sunlight due to their height and a greater surface area of foliage with which to take in fog water, due to redwood's demonstrated ability for both foliar water uptake and foliar fogdrip accumulation (Dawson 1998). It seems that smaller trees had already been outcompeted by the time data was gathered, and as a result had not been and were not growing. These results are consistent with the

grove's relatively low tree density and the age of the trees, indicating that the grove is in a late stem exclusion phase, exemplified by the low competition (Oliver 1981).

It's particularly noteworthy that the competition index, which included diameter and spacing parameters, was not correlated with relative growth, while parabolic volume (the metric for tree size), which included diameter and height parameters, was significantly correlated with relative growth. This seems to illustrate the fact that tree height was an important factor in determining growth. The importance of height suggests that this population is more limited by crown competition and thus sunlight competition than by growing space competition, which also fits in with the lack of correlation between fog hours and growth.

Fog and competition: the Stress Gradient Hypothesis

These results suggest that competition is not associated with fog stress. However, it's difficult to determine whether there is evidence in support of, or against the SGH; as noted above, the lack of correlation between fog hours and growth indicate that this population is not fog-stressed. Thusly, it would seem that trees are not competing for fog: rather, they're competing for a different resource, which makes using fog hours as a metric for stress, and directly comparing fog hours to tree competition, somewhat problematic. Ultimately, while these results seem inconclusive, they agree with some previous literature, including a 2005 meta-analysis of 26 SGH experiments by Maestre et al., which found that competition under stress did not significantly affect plant growth at either low stress or high stress (Welden 1988, Maestre et al. 2005, 2009). Furthermore, it's been shown that experiments done in the similar sites but using different metrics representing stress and competition can have contrasting results (Pugnaire and Luque 2001, Maestre et al. 2005, Beduschi and Castellani 2013). For this reason, the choice of metrics for stress and competition may have had a large effect on these results regarding the SGH.

One potentially important difference between this study and most experiments refuting the SGH is the ecosystem in which it was performed: most other studies refuting the SGH have been done in arid or semi-arid ecosystems which have clear extremes of water stress (e.g., Maestre et al. 2005, 2009). This study was conducted in a moist, Mediterranean climate, where fog makes up a large part of the ecosystem's water budget (Dawson 1998). Additionally, I used a measure of stress (fog) that isn't necessarily limited as a resource by the amount of organisms that use it: more

trees in a foggy zone likely won't reduce the amount of fog as it drifts towards the next patch of trees. In fact, increased redwood density has been shown to increase moisture levels in the surrounding environment (Dawson 1996), suggesting facilitative effects. For this reason, the plant interactions when using water as a resource that can be "used up" may differ fundamentally from interactions in environments with more finite type of water resources.

Limitations and future directions

Lacking fog data for each tree led to the need for a model to interpolate fog amounts, which is inherently less accurate than actual measured climate data. Most of this study's limitations stemmed from lack of fog data. Limited undergraduate research funding lead to a small number of fog sensors. These few fog sensors meant less precise fog data within the plots, as they had to cover the entire grove. Additionally, interpolations such as IDWs become less accurate as the number of initial point values to base the model on drops (Bolstad 2005). Because the fog hours were involved with a majority of my data testing, a potentially inaccurate model would have a large influence on my results.

Another limitation stems from the nature of the study site. It is both a planted grove, which may limit the ability to extrapolate the study's results to natural redwood forests with larger diversity in both age and spatial patterns, especially of the latter. Additionally, though this grove is inside of the native range of redwoods, it is at the southern end of the range. The difference in climate between this site and more northern California may limit the ability to extrapolate these results to redwoods growing substantially further north up the California coast, where the bulk of redwood habitat is.

Future studies that can obtain fog hours for each tree measured individually, and factor in more precise differences in microclimate and topography, would help to confirm or reject these results. Similarly, repeating this study in a naturally occurring site with greater spatial heterogeneity would help to confirm whether these results also apply to natural, uneven-aged stands. In addition, it would be worthwhile to test the SGH again in a moist redwood ecosystem, but to instead choose a different metric of stress against which to compare competition, preferably one that is affecting trees more strongly. Lastly, it could prove highly useful to include leaf area data, since redwoods are known for their foliar uptake of fog water (Dawson 1998).

Broader implications

Given the climate-driven change increases in stress on plants in a myriad of ecosystems, the most important implication of this study is the lack of fog stress. On an individual level, the redwoods in this study seem to be growing well with the amount of fog they are currently experiencing. Though I'm cautious to extrapolate these results to the entirety of redwood habitat, this sign of forest health in the face of a reduction in fog hours bodes well for the species in the context of climate change.

From a management perspective, Coast Redwood is often the vastly dominant tree species in the forests in which it grows, which highlights the importance of intraspecific competition and spacing in redwood management, restoration and reforestation, both in planted and natural groves. Additionally, these results show that smaller redwoods may potentially be outcompeted to the point of zero growth well within 70-80 years of planting, germinating, and/or sprouting, which can inform redwood silviculture. Finally, these results can be taken as an indication of the complexity of forest ecology, plant-plant and plant-environment interactions: even with the wealth of literature supporting the effects of water stress and competition on forest growth, other factors, too, can play unexpectedly important roles.

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