Does Thinning Improve the Soil Water Balance and Vegetation Health of Southern Californian Forest?

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Project Objectives

Extensive tree mortality occurred in Southern California forests between 2002-04 leading to an estimated 4.6 million trees dying over 375,000 acres of land (Walker et al., 2006). Minnich (2007) states that this surpassed the combined tree mortality in this region over the last century. This forest mortality event added to a persistent decline in Southern California’s forests that has been attributed to air pollution, stem densification, and drought (Savage, 1994). The original objective of this study was to examine if thinning improved forest water balance and, therefore, forest health. However, objectives were modified to examine how plant water availability impacts forest health more broadly. This study uses 3 modified objectives to understand how plant water availability impacts forest health in the San Jacinto Mountains of Southern California. Objective 1 was to characterize the spatial patterning of tree mortality along an elevation gradient. Landscape scale patterns help attribution and are relevant to management. Objective 2 was to determine the role that climate and water availability played in structuring mortality patterns along this elevation gradient. We investigated the mechanisms by which seasonal drought reduces plant carbon assimilation at different elevations. Objective 3 was to understand how plant soil water availability and atmospheric demand control interannual variation in the seasonality of forest productivity over three climatically different years. These objectives provide insight into the ways climate impacts soil moisture availability and vegetation health.

The San Jacinto Mountains are situated near the southerly US extent of mixed conifer forest and are at the edge of their climatic range. Climate changes considerably over the mountain elevation gradient allowing us to observe the role of climate, and more specifically, plant-water availability, on forest function. Other factors affecting forest function are less pronounced in these mountains, allowing us to control for the effects of plant-water availability. Air pollution is low over this portion of Southern California’s mountains and fire has not burned recently.

Approach and Procedures

This study was designed to address both spatial patterns and mechanisms of vegetation health in the San Jacinto Mountains using spatial surveys, physiological measurements, and climate data. We used timescales ranging from seconds to years to address the above stated objectives.

Spatial Survey: 300 m long belt-transects spaced 400 ft in elevation spanned an elevation gradient from 4250 to 9850 ft. Transects were located along the NW aspect of the San Jacinto mountains. We recorded cover along each transect by species for live and dead vegetation. Standing dead-trees retained ~0.25 inch branches. Tree decay indicated that these dead trees died in 2002-03. Standing dead tree cover was used to quantify mortality over elevation.

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Seedlings were counted and the diameter at breast height of all trees >137 cm tall were recorded in 10 (10 by 10 m) subplots equally spaced along each transect.

**Physiological Mechanisms:** Predawn water potential (a measure of plant soil water availability), midday water potential, and leaf gas exchange were measured on major components of the Southern California mixed conifer forest (White Fir [*Abies concolor*], Sugar Pine [*Pinus lambertiana*], Coulter Pine [*Pinus coulteri*], Incense Cedar [*Calocedrus decurrens*], Canyon Live Oak [*Quercus chrysolepis*], and Black Oak [*Quercus kelloggii*]) at monthly intervals over 2009 at the University of California James Reserve. Leaf area index was measured using the Licor LAI2000 at the James Reserve and correlated with MODIS satellite Enhanced Vegetation Index (EVI) to give a 16 day 250 m resolution of leaf area. Dendrometers recorded tree diameter growth. Net ecosystem exchange of carbon and water were measured using eddy covariance at the James Reserve. These measurements provided the temporal pattern for plant physiology and plant-water relationships. Predawn and midday water potentials, leaf level gas exchange, and twig hydraulic conductance were measured early (June-July) and late (Aug-Oct) in the growing season at 8 plots along the elevation gradient for White Fir, Sugar Pine, and Coulter Pine in 2009. These measurements provided the spatial pattern for plant physiology and plant-water relationships. We determined xylem vulnerability curves for White Fir, Sugar Pine, and Coulter Pine.

**Climatic variables:** Remote automated weather stations (RAWS) provided spatial precipitation data for 2009. Historic precipitation and snow depth records obtained from the Western Regional Climate Center (WRCC) gave long-term climatic patterns for the region. Water fluxes measured at the James Reserve using eddy covariance provided evapotranspiration (ET) over 2007, 2008, and 2009. Evapotranspiration was spatially extrapolated to the large landscape using the Penman-Monteith approach. Data required to calculate the Penman Monteith ET were measured at the James Reserve eddy covariance tower and assumed to be the same over the whole mountain, except for temperature and pressure. Miramar radiosonde temperature recorded at the same altitude as the eddy covariance tower showed very similar values and patterns to temperatures measured by the eddy covariance tower giving us confidence that radiosonde temperature profiles provided reasonable spatial patterns of temperature over elevation. Eddy covariance data combined with Miramar radiosonde temperature and pressure were used to determine the elevational pattern of ET over the mountain.

**Results**

**Objective 1: Spatial patterning of tree mortality along an elevation gradient.**

Species covered discreet elevation ranges (Figure 1). The lower conifer tree line was 4600 ft on NW aspects of the San Jacinto Mountains. The total amount of tree mortality from 2002-03 was greatest between 5500-8000 ft in elevation (Figure 2). A greater proportion of conifers died at the low elevation of the total conifer distribution (Figure 3). Mid-conifer species showed the highest mortality and died at the low end of their species’ range (Table 1). This pattern of
mortality led to a skew in species’ distributions upslope (Figure 4). There was no evidence of seedling recruitment above a species’ elevation range.

Figure 1: Species’ fraction cover (sum of species cover/ length of belt transect) rises and falls over the elevation gradient.
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Figure 2: Fraction cover of live and dead mid-elevation conifers (White Fir, Sugar Pine, Jeffrey Pine, Ponderosa Pine, Coulter Pine, Incense Cedar) and high-elevation conifers (Limber Pine and Lodgepole Pine) show the highest amount of mortality occurred between 5500ft and 8000ft.

Figure 3: Higher proportions of conifers died at lower elevations in 2002-03 (p-value < 0.01). Proportion Dead = dead conifer fraction cover/total conifer fraction cover.
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Table 1: Mid-elevation conifers (abco= White Fir; cade=Incense Cedar; pico = Coulter Pine; pila = Sugar Pine; piyel = Ponderosa Pine + Jeffrey Pine) died at the lower portion of their range. DD = mean elevation of dead cover, AL = mean elevation of live cover, and TOT = mean elevation of dead and live cover. DD-TOT mean is −581 +/- 409 ft and is significantly different from 0 (mean +/- 95% CI; p=0.05).

<table>
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<th>Species</th>
<th>TOT (ft)</th>
<th>AL (ft)</th>
<th>DD (ft)</th>
<th>DD-TOT (ft)</th>
<th>AL-TOT (ft)</th>
<th>Fraction Dead</th>
<th>Number Transects</th>
</tr>
</thead>
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<td>7716</td>
<td>7870</td>
<td>7204</td>
<td>-512</td>
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<tr>
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<td>5850</td>
<td>-1369</td>
<td>38</td>
<td>0.03</td>
<td>8</td>
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</table>

Figure 4: Mortality at low elevations of a species’ range leads to an upslope lean in species distribution. Each mid-elevation conifer species’ distribution was centered with the belt transect nearest the mean elevation of the species set equal to 0. Belt transects above the mean elevation are positive and belt transects below the mean elevation are negative. The fraction cover for each species was added.
Objective 2: Role played by climate and water availability in structuring mortality patterns along this elevation gradient.

Climate means show that precipitation increases to approximately 4000 ft and then remains constant above 4000 ft in Southern California mountains (Figure 5). This pattern appears consistent each year along the west face of the San Jacinto Mountains, including 2009. Precipitation amount does not vary over the conifer elevational distribution, which ranges from 4600 ft to the top of the mountain (10,800 ft). Snow line is ~4000 ft and the proportion of precipitation coming as snow increases linearly above 4000 ft. More precipitation comes as snow in the conifer zone. In 2009, evapotranspiration declined with increasing elevation (Figure 6). Plant soil water availability increased with elevations in 2009 (Figure 7).

The conifer species studied showed stomatal closure at predawn water potential values below -1.5 MPa and water potentials rarely went below -2.5 MPa (Figure 8). Xylem vulnerability curves indicate that White Fir, Sugar Pine, and Coulter Pine do not experience large declines in hydraulic conductance until ~ -3 MPa (Figure 9). Leaf level carbon assimilation and stomatal conductance declined with decreasing elevation particularly during late summer in 2009 (Figure 10, 11). White Fir specific hydraulic conductance declined with decreasing elevation during late summer (p< 0.01) but Sugar Pine and Coulter Pine did not show a change with elevation. All species together did not show a change in hydraulic conductance over elevation.

Figure 5: Long term precipitation mean (+/- 1 stdev) from San Jacinto, San Bernardino, and San Gabriel Mountains obtained from WRCC. RAWS data is from 2009.
Figure 6: Evapotranspiration (ET) determined by Penman-Monteith declined with elevation in 2009.

Figure 7: Predawn water potential (WP), a measure of plant-water availability, increases with elevation particularly in late summer. Data include White Fir, Sugar Pine, and Coulter Pine.
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**Figure 8:** Stomatal conductance \((g)\) declines with decreasing predawn water potential. Data include White Fir, Sugar Pine, and Coulter Pine.

**Figure 9:** White Fir \((abco)\), Sugar Pine \((pila)\), and Coulter Pine \((pico)\) xylem vulnerability curves do not show substantial loss in twig hydraulic conductance \((k)\) until \(\sim 3\) Mpa. Fraction Loss = \((k(\text{initial}) - k) / k(\text{initial})\).
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Figure 10: Stomatal conductance (mean +/- 95% CI) shows a strong decline with decreasing elevation in late summer. Data include White Fir, Sugar Pine, and Coulter Pine.

Figure 11: Midday carbon assimilation (mean +/- 95% CI) shows a strong decline with decreasing elevation. Data include White Fir, Sugar Pine, and Coulter Pine.
Objective 3: Plant soil water availability and atmospheric demand controls interannual variation in the seasonality of forest productivity.

Net Ecosystem Exchange (NEE) peaked in June-July (Figure 12). Plant water availability was highest between December and June coinciding with precipitation (Figure 13). Stomatal conductance and leaf level assimilation rates were highest during this period (Figure 14). Predawn water potentials declined over summer and stomatal conductance declined. Leaf area was highest in June to September (Figure 15). Peak NEE and water fluxes corresponded with high leaf area and high leaf level assimilation rates. Late season drought and high vapor pressure deficits corresponded with low leaf-level assimilation rates, NEE, and water fluxes. The lowest precipitation year, 2007, showed dramatic reductions in NEE and water fluxes early in the season (Table 2). Typical precipitation led to higher NEE and water fluxes later into the summer (eg., 2008).

Figure 12: Net ecosystem exchange showed peak forest uptake in June-July (negative values are fluxes from the atmosphere to the forest). Data were filtered for friction velocity > 0.2 and PAR > 1000 micromole m^2 s^−1.
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**Figure 13:** Midday leaf level carbon assimilation (A$_{\text{max}}$; mean +/- 95% CI) measured over 2009 in the eddy covariance footprint. Data include White Fir, Sugar Pine, Coulter Pine, Ponderosa Pine, Incense Cedar, Canyon Live Oak, and Black Oak (qukel).

**Figure 14:** Predawn water potential (WP; mean +/- 95% CI) measured over 2009 in the eddy covariance footprint. Data include White Fir, Sugar Pine, Coulter Pine, Ponderosa Pine, Incense Cedar, Canyon Live Oak, and Black Oak.
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Table 2: Precipitation (P), summer temperature (Temp; Celsius), and summer Vapor Pressure Deficit (VPD) mean (standard deviation) for 2007, 2008 and 2009 measured at the James Reserve eddy covariance tower. P is from Oct. 1 the previous year to Sep. 30 the stated year. Summer is from day 150 to day 250.

<table>
<thead>
<tr>
<th>Year</th>
<th>P (in)</th>
<th>Temp</th>
<th>VPD (kappa)</th>
<th>east (kappa)</th>
<th>e (kappa)</th>
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<td>2007</td>
<td>8.9</td>
<td>23.3 (4.3)</td>
<td>2.21 (0.62)</td>
<td>2.93 (0.57)</td>
<td>0.71 (0.33)</td>
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<td>2008</td>
<td>24.2</td>
<td>22.6 (3.6)</td>
<td>1.94 (0.64)</td>
<td>2.80 (0.55)</td>
<td>0.86 (0.35)</td>
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<tr>
<td>2009</td>
<td>18.3</td>
<td>21.8 (5.1)</td>
<td>1.92 (0.80)</td>
<td>2.71 (0.71)</td>
<td>0.78 (0.27)</td>
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<tr>
<td>mean</td>
<td>24.5+/-1</td>
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</tr>
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</table>

Figure 15: Leaf Area Index (LAI) time series at James Reserve was highest between June and September. LAI was determined from using the MOD13Q1 EVI 250m resolution product. The relationship between LAI and EVI was found to be LAI = 5.07*EVI + 0.0416 (p-value = 0.01).
Discussion

**Objective 1: Spatial patterning of tree mortality along an elevation gradient.**

Widespread forest mortality may be increasing globally (Allen, 2010). An increase in baseline mortality rates in the Western US has been attributed to climate (van Mange and Stevenson, 2007). Southern California forests underwent widespread forest mortality between 2002-2004 with peak mortality occurring between 2002-03 (Walker et al., 2006; Minnich 2007). The resultant snags and fallen dead trees pose both a safety and fire risk.

Allen and Brashear’s (1998) documented a rapid upslope shift in the acetone boundary between Ponderosa Pine forests and Pinion-Juniper woodland. Kelly and Goulden (2008) showed that 9 of the 10 most widely distributed species shifted upslope in Deep Canyon. Moreover, they found that the entire species’ distributions leaned upslope, meaning that species distributions became skewed toward the higher portion of their elevation range but failed to recruit individuals above their range. Our data confirm that high mortality at low elevations, rather than decline alone, was a primary factor in creating the species’ upslope lean. We also found no seedling recruitment above the species’ range. These findings support Kelly and Golden’s results and expand their results to the larger geographic region. These data show that this lean can happen very rapidly and can drive species’ distribution shifts within a short few years.

This has direct repercussions for the management of species distributions. High proportions of conifer mortality below 5000 ft, high amounts of total dead cover between 5500-8000 ft, and a lack of recruitment above 9000 ft for mid-elevation conifers point to specific concerns for land management (Table 2). For example, if management is concerned for land cover type changes, mortality of a high fraction of a species is important and an approach that protects vulnerable species at their low elevations would be important. However, if management’s main concern is to reduce fire or falling dead trees, a focus on mid-elevation stands where the greatest amount of trees will die may be more appropriate. Furthermore, a rapid retraction of a species’ distribution without lower elevation species recruiting into these regions creates uncertainty about the future of key ecotone.

**Objective 2: Role played by climate and water availability in structuring mortality patterns along an elevation gradient.**

Determining which aspects of climate influence forest mortality is critical under climate change. This study provides insights into the ways that precipitation and plant evapotranspiration interact with plant physiological mechanisms to impact plant water availability and vegetation health. Precipitation did not vary over conifer species’ distribution. However, evapotranspiration increased with decreasing elevation over the conifer distribution. Plant water availability declined with decreasing elevation during late-season drought. Therefore, elevational patterns in plant-water availability must be driven by evapotranspiration. Precipitation and/or soil water holding capacity may dictate the seasonal timing and extent of this spatial pattern.

Mueller-Dubois (1988) outlined an overarching theoretical basis for our understanding of widespread forest mortality. Predisposing factors, such as stem densification or air pollution,
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leave forests vulnerable to mortality. A precipitating factor, such as drought, weakens forests further leaving them vulnerable to modifying agents, such as bark beetles. However, why trees die and the mechanisms that predispose certain trees to die remain unclear. McDowell et al. (2008) propose that trees die from carbon starvation or catastrophic xylem cavitations. Carbon starvation requires that carbon demand exceeds carbon supply. Carbon demand is produced by maintenance respiration, growth, export to symbiotic/pathogenic associations, exudation of carbon to the surrounding environment, and construction of defensive compounds, such as oleoresins in pine species. Carbon supply comes from photosynthesis and mobile carbon stored in the plant. Cavitations is the introduction of air into the water conducting xylem, which disrupts the transport of water from the soil to parts of the tree. Catastrophic xylem cavitation leads to a dramatic decline in the tree’s water transport. Adams et al. (2009) argue that carbon starvation is the likely mechanism in Pinyon Pine mortality. Sala (2009) argues that carbon starvation is possible but other mechanisms might be more important, e.g. inadequate carbon allocation.

Our comparison of xylem vulnerability curves and stomatal response to drought stress provides no evidence for cavitation driven mortality in White Fir, Sugar Pine, or Coulter Pine. Furthermore, we do not see large changes in hydraulic conductance over an elevation gradient, which would be expected if cavitation was the driving mechanism in the decline of carbon assimilation at lower elevations in 2009. We did not, however, investigate cavitation in roots or soils, which could be important. In contrast, stomatal conductance does decline at lower elevations and in late summer drought conditions. Stomatal control apparently prevents sufficiently low water potentials that cause extensive cavitation even in the most drought stressed regions of these species’ ranges. In an extreme and prolonged drought, such as in the early 2000’s, stomatal closure would lead to reduced carbon assimilation, increase dependency on stored carbon, and threaten a decline in carbon supply. Furthermore, low elevation trees are exposed to higher temperatures that lead to higher respiration rates and an increase in carbon demand. Trees could reduce growth in order to reduce C demand in an attempt to balance their carbon budget. However, growth reduction is limited. An increased carbon demand combined with a decrease in carbon supply indicates that carbon limitation was likely in 2002-03 tree mortality in the San Jacinto Mountains and contributed to the elevational pattern in tree mortality.

The proximate cause of 2002 conifer tree mortality was bark beetle attack. Conifers use defensive compounds to defend against bark beetle attacks. For example, pines use oleoresin contained in specialized ducts within the bark to defend against attacking beetles. Carbon limitation may have strained carbon allocation to oleoresins. We performed a preliminary test to determine if sap exudation varied over elevation in 2009 by damaging Coulter Pine and Sugar Pine boles with a 0.5 in. punch and collecting exuded sap. We did not find differences in oleoresin exudation amount over elevation in 2009. This may be for several reasons. For example, 2009 was not as deep of a drought year as compared to 2002 and trees may have produced ample carbon for their oleoresin needs. The chemical composition of the resins may have differed leading to different carbon costs for the exuded resin. The test did not carefully control for bark thickness, which was the dominant signal and this may have outweighed an elevational signal. A more thorough investigation is required.

Evapotranspiration, rather than precipitation, limits plant available water at lower elevations in the conifer zone. The conifer species studied showed stomatal closure far before xylem cavitation would occur, ruling out catastrophic xylem cavitation as a main factor in 2002-03
conifer mortality. Most 2002-03 dead trees died due to bark beetle attack. Rather than strictly carbon starvation, reductions in carbon supplies may have limited carbon allocation to insect defenses, leading to reduced bark beetle resistance. Climatic trends over elevation coupled with plant physiological traits show that low elevation conifers are most susceptible to tree mortality, which is consistent with observed tree mortality patterns.

**Objective 3: Plant soil water availability controls on interannual variation in the seasonality of forest productivity.**

Understanding the biological and environmental controls on ecosystem-scale carbon exchange are critical aspects of understanding how ecosystem function will respond to climate change. Climate models predict a northward migration of the storm track. This is predicted to bring less precipitation to Southern California, which may enhance soil moisture stress on vegetation. We investigated the seasonality and interannual variations in seasonality using multiple measurements to understand the biological and environmental controls on mixed conifer forest net ecosystem carbon exchange (NEE).

Leaf area and leaf level assimilation rates were important in controlling the seasonal pattern of NEE in mixed conifer forests. Late summer NEE declined with reduced leaf level assimilation rates. Leaf level assimilation rates declined with reductions in soil moisture availability and high VPD. Lower NEE rates observed in winter were attributable to lower leaf area. Herbaceous growth and Black Oak leaf-out occurred around June-July, which led to a large increase in LAI. Carbon assimilation rates remained high in early summer and, coupled with high LAI, generated peak NEE around June-July. Leaf-out coincided with rising minimum temperatures. More intense drought years (e.g., 2007) led to earlier reductions in NEE and water fluxes that can remain low for the entire summer. It appears that low precipitation is important in setting an early decline in NEE.

We addressed the Kearney Foundation’s 2006-2011 Mission with our three modified objectives. We used multiple spatial and temporal scales to address how plant water availability contributes to the mechanisms and spatial patterning of forest health and mortality. These findings are directly applicable to forest management under changing climate scenarios.
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References


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