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The Role of Fire in California’s Landscapes Across Spatial and Temporal Scales

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By

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Committee in charge:

Professor Scott L. Stephens, Chair
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Abstract

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The role of fire in California's landscapes has dramatically changed in recent centuries with the arrival of European cultures and later by the influence of rapid climate change. Novel challenges face land and fire management in the forms of invasive species, human encroachment, severe fuel loads, and fire regime shifts. Because fire is a critical land management tool and natural process in California ecosystems, reintroducing prescribed fire to our ecosystems is increasingly necessary, but also more challenging than ever. It is now of utmost importance that we investigate and seek to understand the modern role of fire in historic, modern, and future ecosystems at multiple scales.

First, I investigate the micro-scale effects of fire in an invaded ecosystem to elucidate how novel plant community dynamics in the face of fire. Studying fire-use related plant species interactions at the 1-m scale informs how we can expect plant communities to shift due to fire in the face of invasive species. This technique is a useful tool for managers and scientists to experiment with variations in fire-use to find ideal fire regimes in novel communities, and to prepare for fire-effects on plant communities.

Second, I investigate prescribed fire effects across an invaded site of a similar plant community knowledge using information gained from these micro-scale investigations. Here I implement the knowledge gained from the micro-scale study, while incorporating more diverse investigations of fire effects, including soil nutrient and seedbank dynamics. This exploration allows for a more holistic understanding of fire-ecosystem interactions in these novel communities. The use of these intensive monitoring techniques on prescribed fire empower adaptive management by informing scientists and land managers of prescribed fire effects, and allowing for informed adjustments to practices based on results.

Finally, I study the role of fire at a much larger scale through an investigation of seasonal conifer xylogenesis. By better understanding annual cambial development of California's common mixed conifers, we can more accurately interpret fire scars and, in turn, California's fire history. We can then also use this information to look to the future and inform decisions regarding management of our landscapes and firescapes in the face of rapid climate change.

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Chapter 1: Prescribed Fire Effects on Population Dynamics of an Annual Grassland

Abstract

Medusahead (*Elymus caput-medusae* (L.) Nevski) is a highly damaging invasive annual grass in California rangelands. While it has been shown that prescribed fire can be a successful tool in controlling medusahead populations, fire treatments are not always successful. Given the sociological and economic constraints of prescribed fire use, it is critically important that we maximize likelihood of treatment success. We conducted experimental investigation of population dynamics of competing species from different functional groups: invasive annual medusahead, naturalized but forageable non-native wild oat (*Avena spp.* Pott ex Link), and native perennial purple needlegrass (*Stipa pulchra* (Hitchc.) Barkworth). We observed population dynamics at the 1-m^2 scale before and after treatments of prescribed fire and seed-limitation (weed whipping in a 1-m buffer area). We asked: 1) what is the role of seed dispersal from burn edges on subsequent medusahead poplation size, and 2) how does density and fecundity of the dominant species respond to fire? Results showed that 1) seed-dispersal is an important factor in recovery dynamics, and 2) wild oat fecundity significantly increases in the year after fire while medusahead and needlegrass fecundity seem minimally affected. Ultimately, managers should consider fire as a preferable first-entry tool, and should thoroughly consider shape and size of planned burns, as well as what vegetation is present to play a role in post-treatment seed-dispersal dynamics.

1. Introduction

Medusahead (*Elymus caput-medusae* (L.) Nevski) is one of the most damaging invasive plants in North American rangelands. Over 400,000 hectares of the western United States have been invaded by medusahead, and its range is increasing at an average rate of 12% per year (Duncan et al. 2004). An annual grass, medusahead propagates efficiently, and can quickly approach densities of 1 000 to 2 000 plants per square meter after initial establishment (Mangla et al. 2011). Mature plants are unpalatable to livestock; in invaded areas, grazing capacity can be reduced by 75-90% (Hironaka, M. 1961). Medusahead invasion has also been shown to significantly reduce species richness and diversity on the landscape (Davies and Svejcar 2008), an effect believed to lead to an overall reduction of ecosystem services (Walker et al 1999).

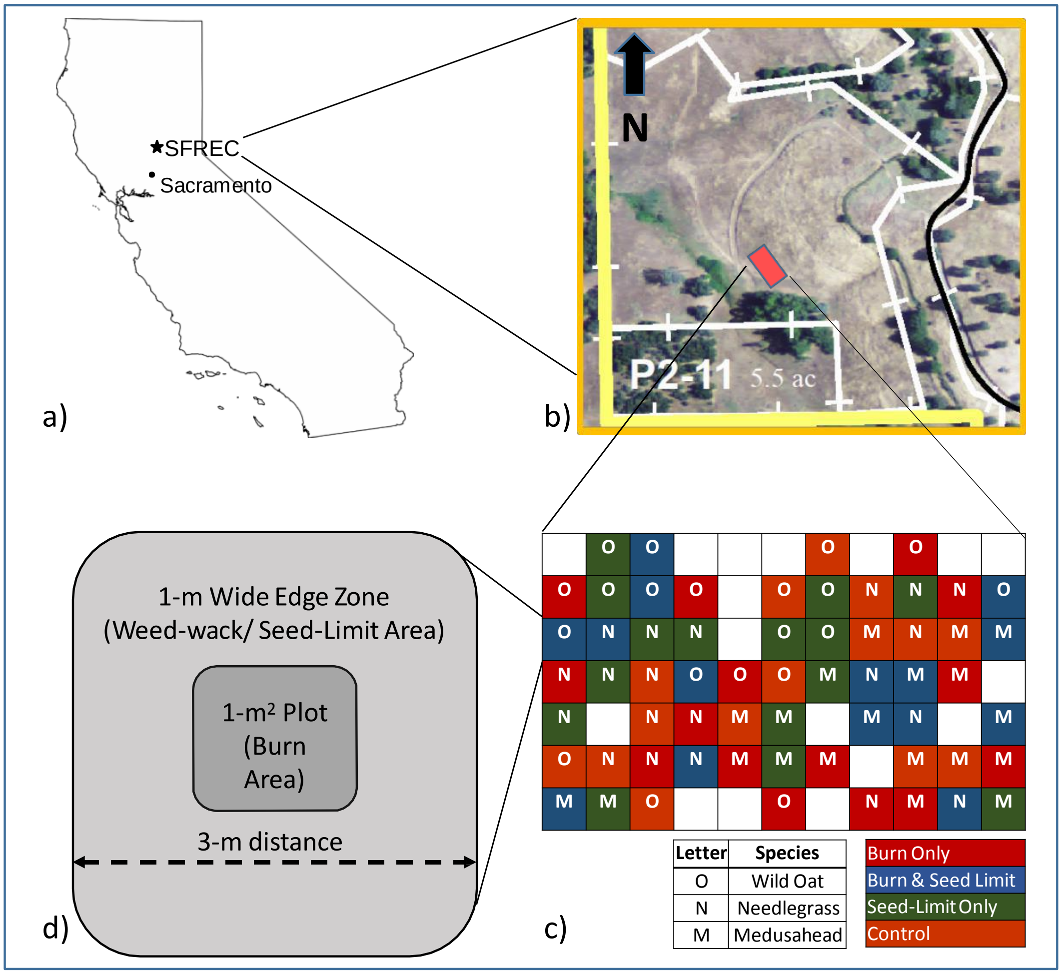
Although most past research has shown that prescribed fire can reduce medusahead populations, some results have shown much less success (DiTomaso et al. 2007, Kyser et al. 2008). Given the environmental, social, and economic constraints on using prescribed fire (Quinn-Davidson and Varner 2011), it is important to maximize its effectiveness if fire is to be a successful management tool. Understanding the effects of prescribed fire on key aspects of medusahead population dynamics, and relative species densities will guide public and private land managers about more effective ways to efficiently improve rangelands. Previous research on fire effects on medusahead indicated that burns should be timed when seed heads are ripe and doughy, but not yet dispersed (DiTomaso et al. 2005; Sweet 2005). Because medusahead has a later seasonal phenology than other grassland species, carefully timed prescribed fire can expose medusahead seeds to maximum heat, after other species' seeds have already dropped, escaping the heat of the fire and remaining viable on the soil surface. However, even with this timing, burns are not always successful (Kyser et al. 2008). A hitherto unexplored factor that may influence the effectiveness of prescribed burns is burn-size and the influence of treatment edges. If burns are conducted with high populations of medusahead surrounding burn edges, medusahead could quickly reinvade from burn edges even when the burn successfully treated medusahead within the burn. Another aspect needing more research is how the density of medusahead within the treatment unit affects fire impact. Finally, the post-fire fecundity responses of rangeland focal species are also unknown.

We evaluated the recovery dynamics of an annual rangeland treated with prescribed fire targeting reduction of medusahead. Specifically, we address the following questions: 1) what is the role of seed dispersal from burn edges on subsequent medusahead poplation size, and 2) how does density and fecundity of the dominant species respond to fire. We expect a burn-edge interaction in burn plots with low initial within-plot medusahead populations and undisturbed medusahead presence in plot edges. This information can be applicable at larger spatial scales to help guide decisions regarding how land managers approach medusahead management.

2. Methods

2.1 Study Area

The study was conducted at Sierra Foothills Research and Extension Center (SFREC), a University of California owned property located 97 km northeast of Sacramento in Browns Valley, California (Figure 1a and 1b). The project site is an annual rangeland characterized by Mediterranean climate, with cool, wet winters and hot, dry summers. Weather data from the California Irrigation Management Information Systems station in Browns Valley shows that, since 1962, annual precipitation varies from 23–132 cm per year, with a mean of 71-cm, and air temperatures range from an average of 4°C minimum in winter and 32°C maximum in summer. Total precipitation during both years of the experiment was below average. Precipitation from September to May leading up to the experiment in 2013 totaled 52-cm, with most occurring in December 2012. Precipitation the year following treatments totaled to 44-cm, with most occurring in February and March of 2014 (California Irrigation Management Information System). The soil is mapped as Sobrante-Timbuctoo Complex, primarily composed of a moderately deep and well drained gravelly loam (Lytle 1998). Cattle graze this pasture site every year but for the two years preceding this study were excluded from the project area.



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Letter	Species
O	Wild Oat
N	Needlegrass
M	Medusahead

🟥 Burn Only
🟦 Burn & Seed Limit
🟩 Seed-Limit Only
🟧 Control

Figure 1. a) Location of study site at the Sierra Foothills Research and Extension Center (SFREC), Browns Valley, California. b) Expanded view of pasture at SFREC, red block indicates study area. c) Layout of the experimental units – each color represents a different treatment, each letter shows a different dominant species category pre-treatment (O = wild oat, N = needlegrass, M = medusahead). d) layout of experimental plot with 2x2 factorial design of treatments: burned or unburned, and seed-limited or not-seed-limited.

2.2 Experimental Design and Data Collection

We studied population dynamics and prescribed fire treatment effects on three rangeland species dominants, their associated communities, and their interactions. These species were purple needlegrass (*Stipa pulchra* (Hitchc.) Barkworth) as a native perennial, wild oat (both *Avena barbata* and *Avena fatua*; hereafter grouped as *Avena spp.*) as a non-native forage grass, and medusahead as a non-native invasive species targeted for removal. These species were chosen because they are prevalent, high-abundance species on annual grasslands high-impacts on rangeland ecosystems (DiTomaso et al. 1999, 2005, 2007, Kyser and DiTomaso 2002, Blondel

2003, Bartolome et al. 2007, Kyser et al. 2008, Sweet et al. 2008). Our study was conducted at small spatial scales (1-m^2), focusing on the influence of edges, providing key insights that are scalable to the role of fire as a restoration tool in annual rangelands with similar species composition.

For project setup, 80 3 x 3 m experimental units were laid out in a grid and categorized into one of three categories by relative dominance of focal species: wild oat, needlegrass, or medusahead. Dominance was determined by ocular estimate of >50% cover. Medusahead was present in every unit. Of these, sixty units were randomly selected for study – twenty from each dominance category (O = wild oat dominated units, N = purple needlegrass dominated units, M = medusahead dominated units). (Fig. 1c) – based on naming each unit within each category and using a randomizer in excel. The center one-square-meter of each unit was designated as the fixed-area study plot; a 1-m wide surrounding space was designated as the plot buffer to examine the influence of seed dispersal. Plots were split in a 2 x 2 factorial design: burned and unburned (1-m^2 burn boxes), seed-limited (by cutting current year's growth in the 1-m plot buffer) and non-seed-limited (Fig. 1d).

In May 2013, we measured pre-treatment density and fecundity of the dominant grass, density of the other two focal species, and ocularly-estimated percent-cover of all species in every plot. Pre-treatment percent cover was also collected for every species within a half meter distance on each side of the 1-m^2 plot; this data identified the species composition of most-likely seeds dispersing into the plots post-treatment. Wild oat and medusahead density were measured in a 10 x 40 cm randomized subplot; needlegrass density was measured as number of bunches in the entire plot as well as circumference of each individual bunch. Fecundity was measured for each of the three focal species according to highest correlation methods (Spotswood, unpublished data, 2013); these correlated measurements were number of glumes, length of seedhead, and number of stalks for oat, medusahead, and needlegrass, respectively. Fecundity measurements were taken for 20 random individuals of each species per plot. All above measures were repeated exactly one year later post-treatment.

Burn and seed-limitation (cutting with a weed-whipper) treatments were implemented on plots according to treatment assignment the morning of May 23rd, 2013. Temperature was 24°C, relative humidity ranged from 27–35 %. Average wind speed was 5.6-kph with gusts of 13.7 kph from the South and Southwest. Soil and grass average percent moisture during the burn was 4.4% and 20.5%, respectively. All burn boxes were lit with a backing fire to consume all fine fuels. Burns were timed for the end of spring to best match existing recommendations for burning to control medusahead (Kyser et al. 2008). In plots used as controls for fire treatment, vegetation within the 1-m^2 was left intact. For seed-limitation treatments, a 1-m wide strip of the current year's growth was cut and removed on all four sides of the plots. For control plots of the limitation treatment, this 1-m wide strip surrounding the center 1-m^2 was left intact as reseeding potential.

Immediately post-treatment, seed rain traps made from 8-cm diameter petri dishes spread with a thin layer of an adhesive insect glue were set. Nine were placed in each plot, distributed in a 3x3 grid pattern. These were left for the duration of the summer to estimate seed rain into the plot area post-treatment. In late September 2013, seed rain traps were collected and seeds were identified to species and counted.

Underneath the center seed rain trap we collected surface seeds, which consisted of seeds that fell into the plot soil surface pre-treatment or were not consumed during the burn. Surface seeds were identified to species, tallied, and then planted in the greenhouse to determine germinability. This germination experiment was carried out in the Oxford Tract Greenhouse in Berkeley, California, from October 2012 to May 2013. Percent cover, fecundity and stemcount measurements were taken again in May 2014 to assess change to plots post-treatment, and better understand how plant and seed dynamics are linked in a management perspective.

2.3 Analytical Methods

Surface seeds collected and germinated in the greenhouse were analyzed for percent germinability across burn treatment. Medusahead seed-rain into plots were tallied and compared across burn and seed-limiting treatments, as well as focal species' stem counts and fecundities. All tests were performed with analysis of variance (ANOVA) for pre- and post- burn using *R* statistical software. Where significant differences occurred ($p < 0.05$), comparisons between means were performed using Tukey's HSD multiple comparison test with the 'agricolae' package in *R*. To account for random effects of unique plot baseline variations and for the effect of yearly variation, GLMER models run using the 'poisson' statistical family were generated using *R*'s 'lme4' package. This strengthened statistical outputs by isolating for fixed effects of treatments on focal species densities.

Shifts in plant vegetation types and indicator species were investigated using cluster analysis in PC-ORD (McCune and Mefford 1999), which creates a dendrogram based on Bray-Curtis similarity values. Percent cover data were square-root transformed. Both community analyses based on percent cover data and stemcount analyses were analyzed and included because they approach the burn impact at different scales of effect. Community analyses look more generally at how plots shift or do not shift through time and what causes these changes or lack thereof. Stemcount analyses show the specific effect of the treatments on a subset of focal species densities.

3. Results

3.1 Treatment Effects on Seeds

First, we tested our hypothesis that the burn effectively reduced medusahead populations. Seeds collected from plot surfaces and germinated in the greenhouse estimated survivability of seeds after the prescribed fire treatment. Of the 425 medusahead seeds that were collected at the end of the summer, only 4 were germinable (.01%). This is compared to the germination rate from the control units, which was 182 out of 207 germinated (88%). Fire had less impact on wild oat, with 23 out of 89 (26%) germinating in the burn units, and 65 out of 81 (80%) in the controls (Figure 2). No needlegrass seeds were found in the germination experiment.

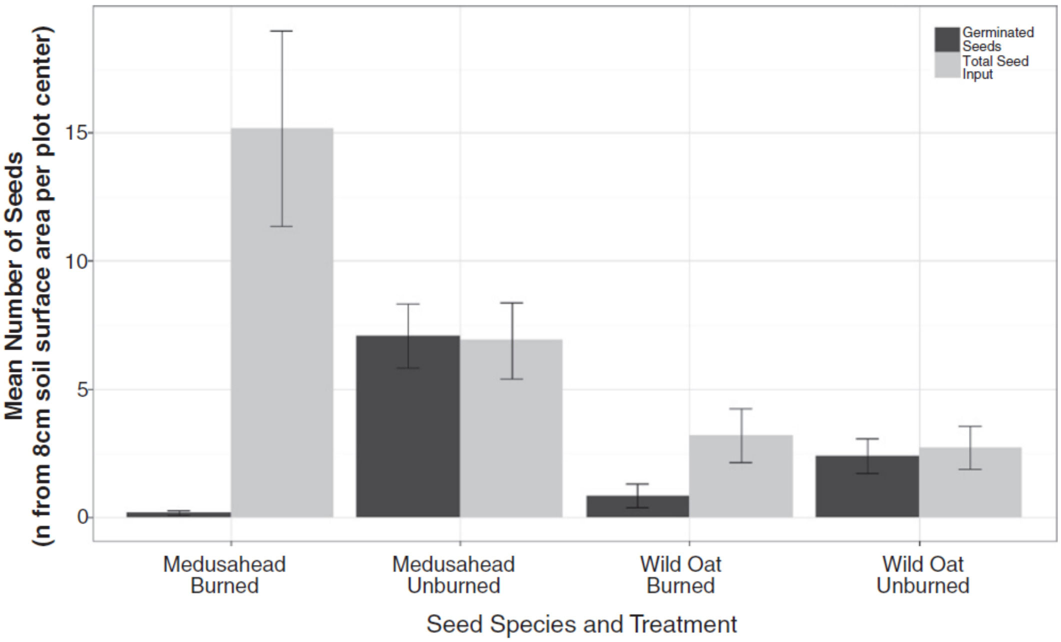

Figure 2. Mean per-plot surface seed germinability of medusahead and wild oat in burned versus unburned plot treatments (from 8-cm area at plot center). Treatment had a significant impact on medusahead germinability.

Medusahead seed-rain in M plots was influenced by treatment (Figure 3). Spread of seed-rain count data in unburned plots M plots was narrow compared to burned plots. Burned M plot seed-rain counts ranged from zero to well above those of unburned M plots. Highest seed-rain counts occurred in M plots that were burned but not seed-limited. ANOVA analyses showed that there were statistically significant differences across treatment groups. Seed-limited plots resulted in the lowest seed-rain counts (p = .05). Not treating plots (controls) resulted in a slightly higher seed-rain count than plots that were seed-limited (p = .05), but these treatments were not significantly different from each other. Burning alone yielded the highest seed-rain counts (p = .009), and was in its own statistically significant group from other treatments. Burning combined with seed limitation fell into its own group with only slightly higher seed-rain counts than the control, but there was also less statistical confidence that this difference was due to more than random chance (p = .089).

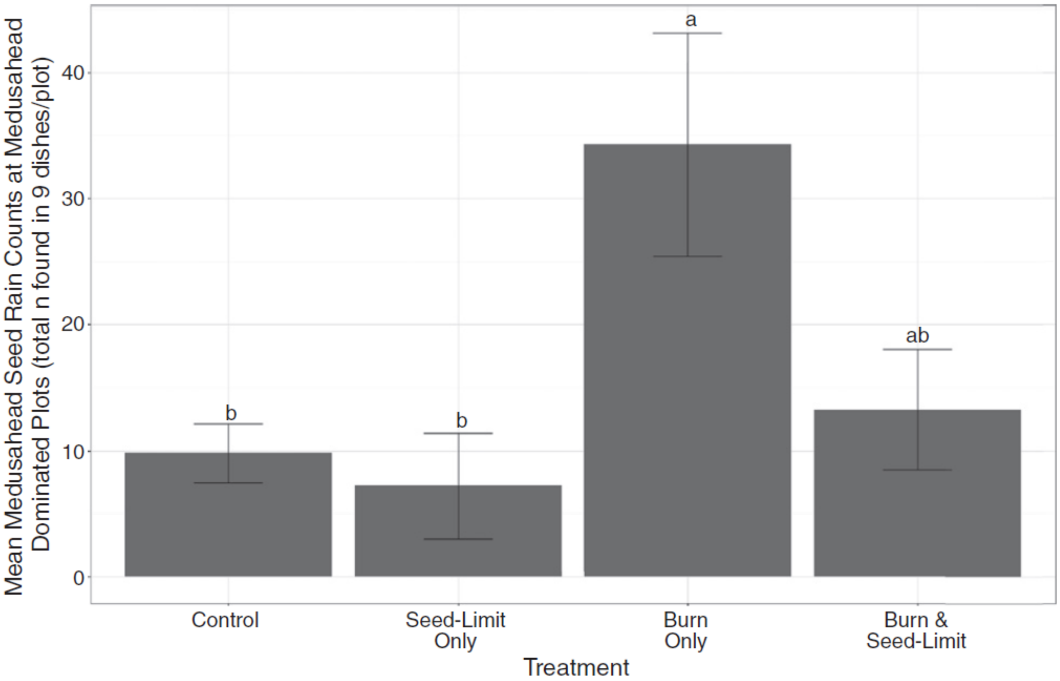

Figure 3. Effects of burning and edge removal on medusahead seed-rain into 9 8-cm dishes per plot in medusahead dominated plots. ANOVA results show that each treatment result was statistically significantly different from the control.

3.2 Treatment Effects on Focal Species Density

ANOVA and Tukey's HSD was used to determine significance differences in medusahead densities across treatment groups before and after treatment (Figure 4). Results indicate that treated groups were significantly different from groups that were not treated (both control and pre-treatment). GLMER modeling medusahead stemcounts from all plots, with random effects of plot and year accounted for, found treated groups were distinct from controls (p = <.0001). The mean expected baseline value for the control group was 19 stems. For this model, the seed-limit treatment group was not significantly different from the control. However, the burn only group and the combination burn and seed-limit group were highly significantly different from the control, with ~8 fewer stems (p = <.0001) and ~16 fewer stems (p = <.0001) expected due to treatments, respectively. When running GLMER on medusahead stemcounts in M plots only, seed-limit does become a treatment that is significantly different from the control with ~2 more stems expected due to seed-limitation beyond the ~46 stem mean expected stemcount in the control group. GLMER results for treatment effects on medusahead stemcounts in O and N plots were not as statistically significant, but followed similar trends to models for all plots and M plots. GLMER results for treatment effects on needlegrass bunch-counts and wild oat stemcounts showed that treatment was not a significant factor for difference from control groups (p = .8155 and p = .399, respectively).

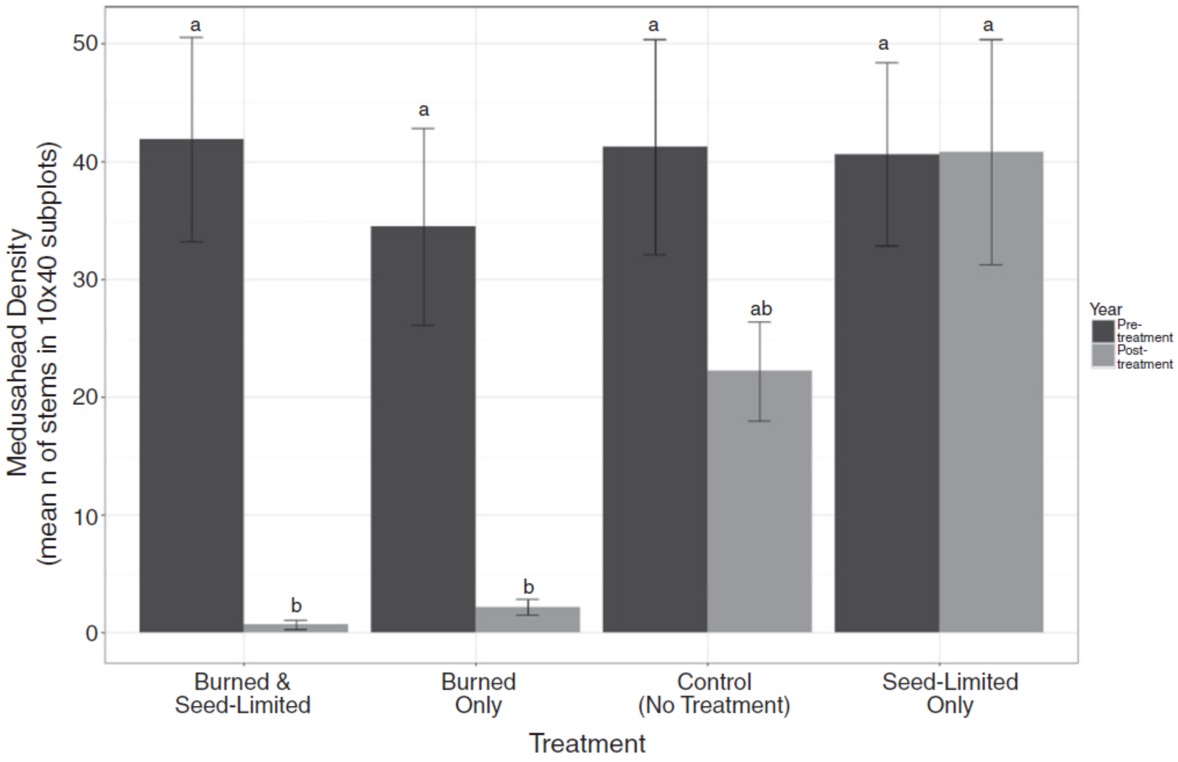

Figure 4. Treatment effects on mean medusahead densities from 10x40-cm sub plots. Burning was significant different from the control group in all cases, but the effect size increased with medusahead pre-treatment dominance and further again with seed-limitation. Seed-limitation where medusahead dominated increased its own stemcount.

3.3 Fecundity Responses to Treatments

Burning had a significant effect on wild oat and needlegrass fecundities, but had no significant impact on medusahead fecundity (Figure 5). The post-treatment standing crop fecundity for these two species were significantly different from year one's standing crop. Specifically, burning wild oat led to a significant increase in wild oat fecundity of an average 5 glumes higher than the control (p = 0.015). Needlegrass showed decreased fecundity from burning that was slightly statistically distinct from the unburned (p = 0.069).

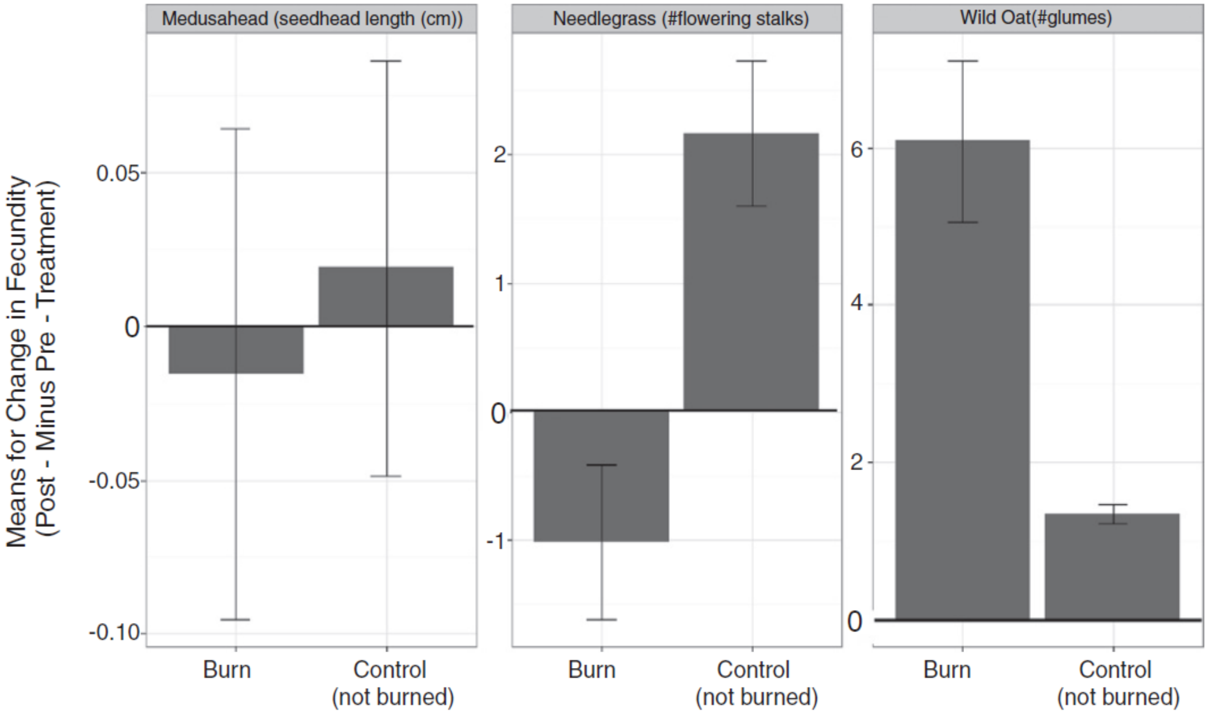

Figure 5. Changes in Mean Fecundity by Dominant Species (1) Treatment had no significant effect on medusahead fecundity (mean seed-head lengths from 10x40-cm subplot), (2) Burning reduced needlegrass fecundity (mean n flowering stalks per bunch per 1-m plot) while unburned needlegrass saw increased fecundity that year, and (3) Burning significantly increased oat fecundity (mean n of glumes per individual from 10x40-cm subplot) with a statistically significant difference from not burning.

3.4 Community Analysis of Vegetation Types and Drivers of Change

Analyses in PC-ORD resulted in determination of four vegetation types. Of these four pretreatment vegetation types identified; three of these had one clear indicator species: filaree (*Erodium spp*.), wild oat, and medusahead. The fourth vegetation type identified had multiple significant indicator species (needlegrass mix). The strongest indicator species in this vegetation type was needlegrass, but six others – four forbs and two grasses, all non-native – were identified as significant species for community identification (p<0.05) (Table 1). Three of these four vegetation types found through Bray Curtis community analysis matched the initial ocular dominance categorizations. The fourth, filaree, was not used as a dominance categorization because it was in the understory and therefore less notably dominant in the first year, and because our study was focusing on the dominant grasses. Community states of plots before and after treatment showed that all plots went through one of five possible shifts, or showed no change (Table 2).

4. Discussion

4.1 Treatment Effects on Seeds and Focal Species Densities

The germination rates of burned medusahead seeds compared to unburned medusahead seeds and burned seeds of other species indicate a fundamental level of burn success, as the objective of the burn was to specifically negatively impact medusahead populations while having a less limiting effect on other more desirable species. However, burning alone was not as successful a treatment as when combined with seed-dispersal limitation. While fire successfully killed seeds (Sweet et al. 2008), dispersal in from plot edges will eventually limit treatment effectiveness. This is further shown in our seed-rain measurements, where accumulations were highest in burned plots that were not seed-limited.

While treatments had a strong limiting effect on medusahead population densities, they had no notable effect on population densities of wild oat or needlegrass in the first year after treatment. An important area for future research would be to study potential effects of these treatments on all three focal species at this scale in proceeding years, as this study was limited to first year after treatment, and delayed effects on population dynamics are possible. For instance, the increased wild oat fecundity observed in the first year after treatment may correlate with an increase in wild oat densities two years after treatment. Both this and the longevity of such a population boost should be investigated. The lack of treatment effect on needlegrass densities in the first year after treatment indicates that using prescribed fire where needlegrass and medusahead coexist for restoration could be a responsible treatment option, as the impact on needlegrass is similar with or without treatment, yet treatment strongly negatively impacts medusahead. In addition, other studies have previously shown that prescribed fire can have a delayed positive impact on needlegrass population dynamics (Dyer 2003), which would create a beneficial inverse effect of treatments improving needlegrass populations while limiting medusahead populations.

Specific effects of treatments on medusahead population densities showed that burning had a significant negative effect. Dispersal limitation further increased burn effects by reducing seed-input from surrounding areas. Where plots were burned but not seed-limited, the highest seed-rain inputs were seen, counteracting some of the beneficial effects of the fire by creating openings for new invasion.

Needlegrass, wild oat, and medusahead in control plots showed reduced stemcounts in year two. These data and weather data suggest that year two of the experiment was likely a low productivity year in general for grasses, based on drought. The abiotically driven tendencies of annual rangeland in California further support this contention (Bartolome et al. 2007). However, seed-rain data in medusahead dominated plots indicates that medusahead stemcount reduction is a result of more than just annual weather variation. Medusahead seed-rain in untreated medusahead dominated plots was significantly lower than in burned plots where space had been cleared due to fire. This is a result of a dense medusahead thatch layer which seems to prevent seeds from reaching the soil surface and similarly prevents seeds from establishing, based on seed rain trap data.

In medusahead dominated plots, the seed-limitation treatment – reducing propagule pressure from the plot buffer area – without the combined effect of fire, resulted in an increased stemcount. Through increased availability of resources such as light and water, more seeding stems were produced and survived through the thatch. More research is needed to determine whether these came from an increase in the number of germinated seeds or an increase in the number of flowering stems per seed. Burning and seed-limiting resulted in the biggest reduction in medusahead stemcount, due to removal of medusahead seed from edges. This highlights the importance of considering edge effects when planning treatment units.

The spread of seed-rain count data was narrow in plots that were not burned, but much wider in burned plots. This may be explained by medusahead's thatching tendencies. Medusahead litter decomposes more slowly than most other species due to its high silica content (Bovey et al. 1961). Based on seed-rain counts, it seems that medusahead's tendency to form dense mats of undecomposed litter might result in fewer seeds arriving at the soil surface. Seed-rain data under untreated thatch combined with observed reduced stemcounts in untreated patches suggest that medusahead becomes self-limiting once it reaches dense populations, but more research is needed to determine this distinctly from the possibility that observed trends were merely due to plant plasticity in fecundity or stemcount.

Burning reduced medusahead populations beyond the reduction seen in controls in all treatment groups, but to different extents. Adding one extra meter of seed-limitation surrounding the plot strongly reduced the availability of seeds to the treated area, indicating that treatments will be most effective where they exceed medusahead's relatively short dispersal distances to limit invasion from treatment edges (likely only slightly larger than 9-m^2, the size of the seed-limited & burned areas in this study). However, this effective 1-m buffer used in our study comes from a site where cattle grazing was excluded. This dispersal distance changes with cattle grazing, where seeds have been found to travel up to 160-m on cattle (Chuong et al. 2016). Effective prevention of reinvasion will depend on the available seedstock outside a planned treatment area and on grazing presence and pressure (Monaco et al. 2005; Davies and Sheley 2007; Davies 2008).

4.2 Fecundity Responses to Treatments

The null hyposthesis was that the fecundities of focal species would not be changed significantly by fire treatment. Previous research on other annual grass species has shown varying levels of plasticity for fecundity in response to environmental conditions (Volis 2009). Our results suggest the null hypothesis only held true for medusahead fecundity. Wild oat fecundity responded very positively to fire with a highly significant correlation to treatment, likely due to nutrient release. Needlegrass showed slight fecundity reduction where it was burned. Previous anecdotal studies show this fecundity reduction to be expected, but is limited to one or two years after the burn and is followed by a surge of needlegrass germination (Menke 1992), but more thorough research investigation is needed to confirm this.

4.3 Plot Vegetation Types, Shifts, and Important Drivers

Four clusters, or vegetation types, became apparent for plots in each year one and year two in the analysis of the percent cover data. The life history traits of needlegrass (Bartolome and Gemmill 1981) result in open space around bunches to be inhabited by other species, and a diverse array of indicator species found in this community. These plots transitioned to a filaree type when burned due to filaree's typical strong response to fire (DiTomaso et al. 2005), and removal of thatch. In these plots, filaree is not replacing needlegrass, but the low stature rosettes approach 100% cover. According to Menke (1992), this could be of concern in future years as this dense understory can negatively impact germination of needlegrass. Filaree plots also had high medusahead or wild oat presence, so many of these moved to a medusahead or wild oat dominated states if left untreated. This is expected as filaree is a disturbance adapted plant, showing significant increases in germination where openings are created by activity (Schiffman 2011). Therefore, where there is a lack of disturbance, other species are likely to become more dominant over time. Wild oat's increased fecundity after fire caused the observed shifts from filaree to wild oat dominance. The adverse effect of the fire treatment on medusahead seed germinability, combined with filaree's strong response to fire caused the transition of all medusahead plots to filaree. This is consistent with George et al. (1992) that shows filaree as a competitive forb after fire in annual rangeland due to its drought tolerance and fast-growing tap root.

4.4 Implications

In Early Detection Rapid Response (EDRR) scenarios (Brooks 2008), managers may try a targeted approach, treating entire medusahead patches. Managers should also ensure that treatment scale is significant enough to minimize seed encroachment from treatment edges by considering what species occur in the boundaries and their invasibility.

Medusahead fecundity did not respond to changes in resource availability associated with burning, while wild oat had a significant positive response. This suggests that where managers use fire on medusahead infested pastures with a wild oat seedbank, they have the ability to promote this more desirable species as a side effect. Further research can identify what other species have strong fecundity responses to fire timed at reducing medusahead populations.

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Chapter 2: Using Prescribed Fire to Restore a Medusahead Invaded Northern California Coast Range Grassland

Abstract

After over a century of overgrazing and accelerated impacts of invasive species and land conversion in recent decades, protection and restoration of California's rangelands are critical in order to preserve their intrinsic value and the vast array of ecosystem services they provide. In a coastal rangeland in Sonoma County, California, prescribed fire, targeted grazing and native grass seeding are being combined to restore degraded annual rangelands within an organic ranching framework. Restoration goals are to reduce invasive plant species, particularly medusahead (*Elymus caput-medusae*), improve forage quality and quantity within an organic ranching framework, enhance soil resources, and increase both remnant and planted native grasses and forbs. Baseline data collection and post-restoration monitoring have been implemented to inform ongoing adaptive management. Using these data, this study addressed four questions: a) did prescribed fire used as site preparation prior to native seeding reduce medusahead abundance; b) did prescribed fire differentially affect native and nonnative plant species richness or diversity c) how did prescribed fire impact seedbank dynamics and does seedbank species composition reflect overstory species composition; and d) are soil carbon and nitrogen levels associated with the overstory vegetative community? We found that a) burning reduced medusahead and other exotic grass; b) species richness and Shannon diversity increased due to burning and drill-seeding, with native forbs, native grasses, and exotic forbs all increasing in cover while exotic grass decreased; c) while exotic grass and forb presence in the seedbank matched the changes seen in the cover populations, native grass and forbs shifted slightly in the opposite direction, both decreasing in the seedbank; and d) medusahead dominated overstory was associated with low soil carbon and nitrogen levels, suggesting that either medusahead grows more easily where nutrient levels are low, or that the presence of medusahead can result in reduced nutrient levels over time. Ongoing monitoring will be conducted to determine long-term restoration success.

1. Introduction

Rangelands encompass much of California's last undeveloped landscapes, incorporating California's watersheds, biodiversity, recreational land, cultural heritage, and beauty (Brunson and Huntsinger 2008, Kroeger et al. 2010). Rangelands contain 40% of California's native plant species (Schiffman 2007), and 90% of the species listed in the Inventory of Rare and Endangered Species in California (Skinner and Pavlik 1994). Rangelands are critical habitat for and provide forage for wildlife and livestock (Guisti et al. 1996, Jackson and Bartolome 2007). Finally, rangelands can potentially sequester carbon (Schuman et al. 2002, Booker et al. 2007), though this dynamic is particularly variable across space and time and requires site-specific monitoring to interpret local processes.

California's grasslands have changed over time, but most dramatically in the last 200 years with the arrival of Europeans, their livestock, and the plant species that came with them

(Spiegal et al. 2014). In recent decades, human population growth has impacted rangelands with pressures of development and over-use (Stromberg and Griffin 1996, Gelbard 2003); these changes pose novel challenges to land-management (Bartolome and Spiegal 2014). With increasing threats and the diminishing presence of this valuable resource, protection and restoration of rangelands is critical.

Restoration of California grasslands focus primarily on the reduction of exotic species (Bartolome et al. 2007a), often in conjunction with increasing native species abundance and diversity (Seabloom et al. 2003, Bartolome et al. 2004, Stromberg et al. 2007, Lulow 2008). Additional objectives include improvement of wildlife habitat, soil stability, and for rangelands specifically, forage production (Huntsinger et al. 2007). The high ecological variability of California rangelands has led to correspondingly variable success of restoration efforts (Bartolome et al. 2007b & 2009, Wilson et al. 2011). Rangeland species composition varies spatially and temporally (George et al. 1992, Jackson and Bartolome 2002, Spiegal et al. 2014) and is primarily influenced by annual abiotic variation, such as temperature and rainfall patterns (Bartolome 1987), combined with influences of topography, edaphic characteristics, disturbance, management actions, and other factors. Restoration and related management practices can alter biotic processes toward increased biodiversity and improved ecosystem services (Huntsinger and Hopkinson 1996, Huntsinger et al. 2007, Barry 2011). The implementation of a targeted strategy that continuously investigates its efficacy and effects is needed (Wossink and Swinton 2007), and adaptive management is the framework that can guide managers to best achieve this objective.

Adaptive management is a science-based feedback method available to managers to assess and refine landscape management actions. The 6-step approach involves 1) assessing the problem, 2) designing a plan and setting objectives, 3) implementing the plan through management actions, 4) monitoring plan implementation and effectiveness, 5) evaluating results, and 6) adjusting plans and practices based on what was learned to loop back into Step 1 (Spiegal et al. 2014). This approach directs feedback to the manager, resulting in improved long-term management.

At a working preserve in the foothills of Sonoma Mountain, North Coast Range, California, we implemented a monitoring protocol to assess restoration effectiveness and to inform adaptive management. We chose a Coast Range Grassland rangeland meadow with low native grass abundance and high medusahead (*Elymus caput-medusae*) abundance as the site of this restoration project, which serves as a pilot project to evaluate strategies for continued restoration across the property. Medusahead is an exotic invasive particularly known for its slow decomposition hindering nutrient cycling, creation of monocultures (Mangla et al. 2011), and its negative effects on forage quality and quantity (Hironaka 1961), species richness and biodiversity (Davies and Svejcar 2008), and other ecosystems services (Walker et al. 2011). Use of properly timed prescribed fire is a commonly successful management tool for reduction of medusahead (DiTomaso et al. 2005, Sweet 2005, Sweet et al. 2008).

General goals of this project are to 1) reduce dominance of exotic grasses, particularly medusahead, and manage the presence of exotic forbs, and 2) increase abundance and diversity of native grasses and maintain or increase presence of existing native forbs. Restoration methods included prescribed fire, drill-seeding of a nine-species native grass mix, and targeted livestock grazing. The monitoring protocol was designed to assess the effectiveness of the restoration relative to goals described above, the duration of restoration impact, and the need for adjustments to management or monitoring approaches.

Specifically, we asked four questions to assess initial impact of our applied restoration approach at this site: a) did burning affect medusahead abundance; b) did burning affect species richness, and were responses by native forbs and grasses different than those of non-native forbs and grasses; c) what were the effects of burning on seedbank dynamics and did seedbank species composition reflect overstory species composition; and d) are overstory vegetative communities associated with particular soil carbon and nitrogen levels? While the complete treatment on the site was a three-step approach of grazing, burning, and seeding, the aspects of restoration analyzed here are specifically assessing the impacts of the prescribed fire, with some initial impacts of drill-seeding incorporated, but not the entire drill-seeding effect due to the early stage of restoration. Drill-seeding impacts will be fully analyzable three to five years after seeding when grasses have fully established.

We hypothesized that treatments would reduce medusahead and increase richness and diversity. We expected the seedbank would hold more species richness potential or might express species not seen in the overstory due to competitive effects, and that fire might release some of these species. Finally, we hypothesized there would be a correlation between vegetative cover and soil nitrogen and carbon levels, either by these nutrients creating an environment that favored one community over another, or by different communities drawing down soil nutrients to different levels. While questions a) through c) aim to assess the success of restoration strategies, question d) the determination of soil nutrient – overstory composition relationships, aims to understand the underlying dynamics involved in restoration treatments, and therefore allow for adjustments to ongoing restoration management activities.

2. Methods

2.1 Study Area

The Mitsui Ranch is a 256 ha property on Sonoma Mountain in the coast mountains of Sonoma County, California (Figure 1). The climate is characterized as Mediterranean at an overall average temperature of 22 °C, with cool, wet winters with a minimum temperature of 2 °C and hot, dry summers with a maximum temperature of 36 °C (Santa Rosa RAWS station data, June 2012 – June 2015). Rainfall in 2014 was 58 cm and in 2015 was 52 cm; average rainfall for this area is 63 – 150 cm. Elevations range from 603 – 730 m a.s.l. The Mitsui Ranch is a mosaic of annual and perennial grasslands, oak woodlands, wetlands, forest groves, ponds, and creeks, and approximately 85% of the property is comprised of annual grasslands. Restoration efforts studied in this project were carried out on a 4 ha grassland parcel named Corral Meadow.

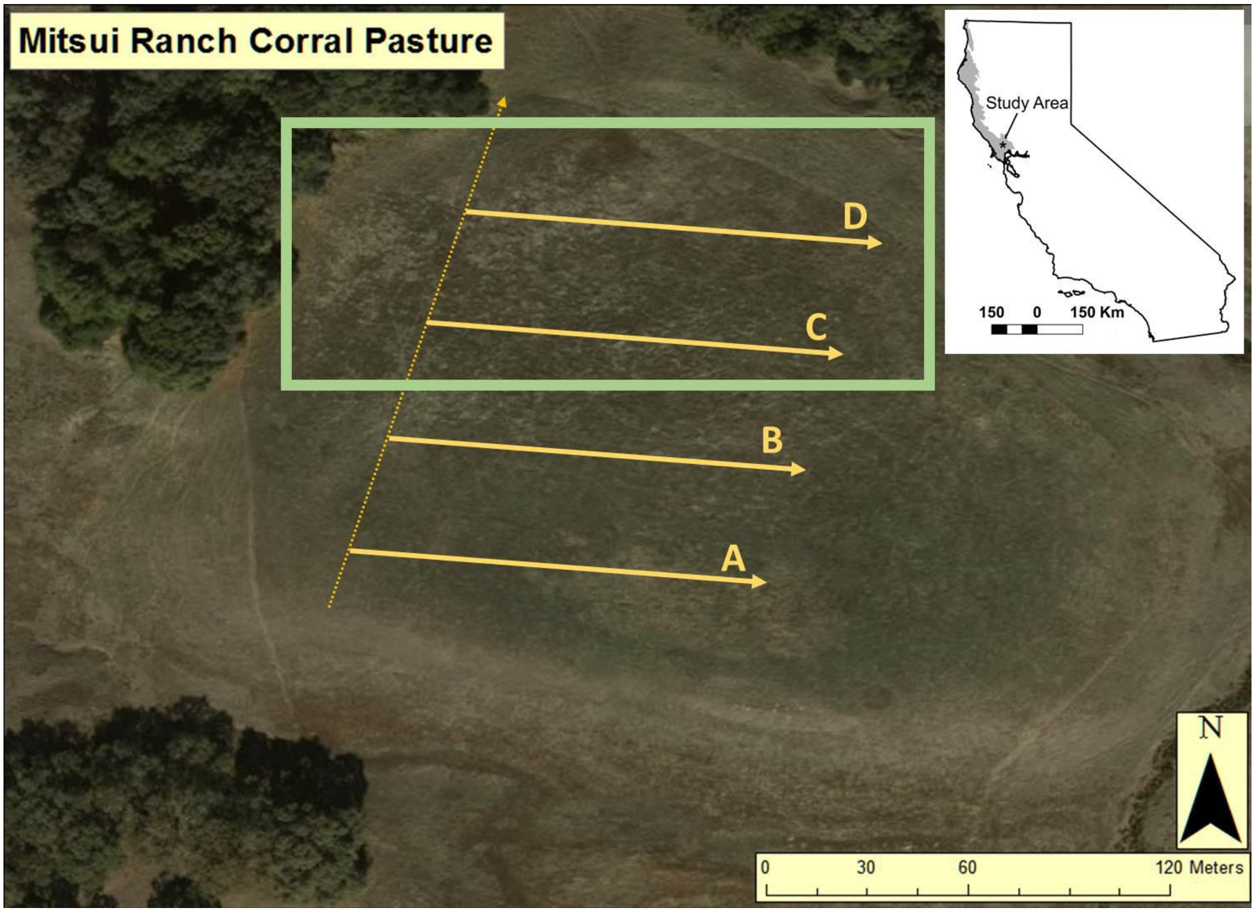


Figure 1. Study area within the Northern California Coast Ecoregion (gray), with grassland survey transects identified in the Corral Meadow. Box identifies the prescribed burn unit, which was followed by drill seeding of a native grass seed mixture and continued targeted grazing.

2.2 Site History

The Mitsui property has been grazed by cattle since at least 1844 when General Mariano G. Vallejo obtained the land as part of his Rancho Petaluma land grant. Dairy heifers were stocked on site from the 1960s-1980s, with a switch to cow-calf pairs since then. The Mitsui Ranch is similar in ecology and history to most other rangeland sites in this region of Northern California, and has been invaded by the typical suite of non-natives, including medusahead, which was first recorded on site in 1996. In 2012 and 2013, an average of 87 cow-calf pairs grazed on 89 ha, including the Corral Meadows site, over about four months. In 2014, this grazing period was shortened to two months due to drought and the decision to conduct a prescribed burn to prepare the Corral Meadow site for native planting. The burn was conducted in collaboration with a local fire department on June 25th, 2014, and a mixture of eight perennial native bunchgrass species and one native annual grass (Table 1) was drill-seeded at an approximate rate of 31-36 kg/ha in half of the pasture on January 7th, 2015. The pasture was then grazed again in March 2015 using a high stocking rate and short duration.

Species	Common Name	% by weight
Elymus trachycaulus ssp. trachycaulus	Slender wheatgrass	25
Danthonia californica	California oatgrass	18.75
Elymus glaucus	Blue wildrye	12.5
Stipa pulchra	Purple needlegrass	12.5
Bromus carinatus	California brome	8.33
Hordeum brachyantherum	Meadow barley	8.33
Elymus triticoides	Creeping wildrye	6.25
Melica californica	California melicgrass	4.17
*Festuca microstachys**	Small fescue	4.17

*annual grass; all other species are perennial

Table 1. Native grass species and relative proportions used in drill-seeding treatment.

2.3 Data Collection for Monitoring of Treatment Effects

2.3.1 Species Composition

In 2013, four permanent, parallel transects were established across the site. Ten permanent 1 m^2 plots were laid out along each transect at 10 m intervals to serve as vegetation monitoring units (Figure 1). Of these 40 plots, six were located outside the burn area, while 34 were within the burn area. All 40 plots were grazed; the six unburned plots serve as a control to specifically test the effect of the prescribed fire where grazing impact is held constant. Foliar percent cover by species was visually estimated in cover classes using the Daubenmire method in each plot at peak standing crop in 2013, 2014, and 2015 (two years pre-burn and pre-seeding, one year post-burn and post-seeding) (Daubenmire 1959).

2.3.2. Seedbank

Soil seedbank sampling and processing was conducted generally following established protocol (Matzek and Hill 2012, Rayburn et al. 2016). Soil seedbank samples were collected from a randomized subset of the 1 m^2 monitoring plots, with 21 samples – one per plot – collected for each one year pre-burning and one year post-burning but pre-seeding. Samples to 2 cm depth were collected in the fall of 2013 and 2014, just prior to the onset of germinating rains, using a slide hammer soil corer with a 6 cm diameter. Each sample was planted in a unique pot and combined with 50% added sterile potting soil. Seeds germinated in the UC Berkeley Oxford Greenhouse from November to May in each of the two sample years. Germinated seeds were identified to genus or species, counted, and discarded to prevent interference with other sample seeds. Seedlings that could not be identified were transplanted and grown in a separate pot until they could be identified.

2.3.3. Soil Nutrients

To determine the correlation between overstory plant composition and soil carbon and nitrogen, we collected soil samples stratified across four main cover types found at Corral

Meadow: unburned naturalized annual grass, unburned medusahead dominated, unburned remnant native perennial bunchgrass dominated, and burned and seeded sites previously dominated by annual grass, now dominated by forbs in the family Brassicaceae. These cover types for soil analyses were chosen because they represented widespread communities of unrestored rangeland including both invasive annual grass (medusahead dominated) and naturalized annual grass (forage-species dominated), as well as fully restored (remnant native bunchgrass dominated) and restoration in progress (burned site and seeded). We consulted Natural Resources Conservation Service soil maps (UC Davis California Soil Resource Lab) first to ensure a uniform soil type. In March 2015, within each cover type, ten sample locations were randomly selected and samples were taken at two depths, 0 – 15 cm and 40 cm to depth at impermeable layer, using a 6 cm wide soil auger. We hypothesized that carbon and nitrogen at deeper soil depths would be consistent across cover types, serving as a control for examining the correlation between shallower soils and cover types. Soil samples were dried and ground before analysis for texture, total carbon and total nitrogen using the dynamic flash combustion system method coupled with a gas chromatographic (GC) separation system and thermal conductivity detection (TCD) system at the UC Davis Soil Analytics Lab (AOAC Official Method).

2.4 Analysis

Percent cover was used to evaluate treatment effects on species composition. Medusahead abundance, plot richness, and Shannon diversity were analyzed using a before-after control-impact (BACI) approach (Smith 2002). These vegetative assessment metrics are reported for 2013 – 2014 from control and treatment plots, prior to treatment. These two years of data serve as a baseline for BACI analysis pre-treatment. Results reported for 2014 – 2015 show shifts occurring from pre- to post-treatment, serving the "after" portion of BACI analysis.

Significance of treatment effects on these metrics was tested using analysis of variance (ANOVA) in program R (R Core Team, 2014). Medusahead abundance was represented by the percent cover of medusahead in each plot. Richness was the number of species in each plot. Shannon diversity index is an assessment of the combined abundance and evenness of the species present within each plot. The independent variables in all BACI ANOVAs were control (plots unburned, n=6) and treatment (plots burned, n=34). Each of these analyses was followed up with a linear mixed effect (LMER) or generalized linear mixed effects (GLMER) model analysis in order to account for the random effects of plot and year variation and to isolate for effects of burning as a treatment. For these models, all plots pre-treatment were used as controls, and only plots that were burned are considered treated. To determine if there was a significant difference between control and burned, ANOVA of the LMER and GLMER models was used, for which the *p*-values were reported for significance of differences between groups.

Seedbank measurements from control plots were not used for comparison in statistical analysis due to limited sample size, and instead, pre-burn treatment samples were compared to post-burn treatment samples (before-after comparison of impact samples). To compare seedbank composition to above-ground vegetation, germination counts were converted to relative abundances so that each sample totaled to 100% (Rayburn et al. 2016). Since cover data was already out of 100% per plot, this standardized data for analysis. Next, abundance-weighted Jaccard dissimilarity indices were computed using the vegdist function of the vegan package (Oksanen et al. 2013) to determine whether treatment elucidated species that had been dormant in the seedbank and changed the strength of the seedbank reflection in the overstory community.

Soil nutrient data was analyzed first using ANOVA to determine significance of vegetative category and soil core depth, followed by Tukey's honest significant difference (HSD) test to determine what groups are significantly different from each other if the ANOVA first detected a significant difference.

3. Results

3.1 Ecological Effects of Treatments

3.1.1 Vegetative Cover Dynamics

A total of 20 species were found in vegetation monitoring plots pre-burn. Of these, six were exotic grass species (88.1% of total cover across plots), 12 were exotic forb species (9.9%), and two were native forb species (2.6%). In plots post-burn, 28 total species were identified. These included nine exotic grass species (comprising 16.6% of total cover), twelve exotic forb species (74.1%), four native forb species (7.3%), and native grass species due to direct seeding which were not yet identifiable to species level at the early seedling stage (3%).

In cover plots pre-burn, the most common species – in order of abundance – were the non-native grasses wall barley (*Hordeum murinum*), ripgut brome (*Bromus diandrus*), soft chess (*Bromus hordeaceus*), and medusahead, with Italian ryegrass (*Festuca perennis*) at lower but still abundant levels (Table 2). Native forbs identified pre-burn were primarily small flowered fiddleneck (*Amsinckia menziesii*) and low abundances of annual lupine (*Lupinus bicolor*).

Post-burn, exotic forbs occurred in far higher abundances than grasses. The most abundant of these were rose clover (*Trifolium hirtum*), broadleaf filaree (*Erodium botrys*), and various mustards (*Brassica nigra*, *Sysimbrium officinale*, and *Raphanus raphanistrum*). For native forbs, abundance of both the small flowered fiddleneck and annual lupine increased by one percent each, while three additional species appeared: wild hyacinth (*Dichelostemma capitatum*), harvest brodiaea (*Brodiaea elegans*) and summer lupine (*Lupinus formosus*). Native grass seedlings were also found in cover plots post-burn as a result of direct seeding and comprised 1.5% of total cover across all plots in the first spring after seeding, but most individuals were not yet identifiable to species level.

Top Eight Most Abundant Cover Species Pre- and Post-Burn					
Rank	**Abundance**	**Pre/Post**	**Scientific Name**	**Common Name**	**Group**
1	37%	pre-burn	*Hordeum murinum*	wall barley	EG
2	25%	pre-burn	*Bromus diandrus*	rip-gut brome	EG
3	19%	pre-burn	*Bromus hordeaceous*	soft-chess brome	EG

4	13%	pre-burn	*Elymus caput-medusae*	medusahead	EG
5	3%	pre-burn	*Amsinckia menziesii*	fiddleneck	NF
6	3%	pre-burn	*Trifolium hirtum*	rose clover	EF
7	2%	pre-burn	*Festuca perennis*	Italian ryegrass	EG
8	2%	pre-burn	*Erodium botrys*	filaree	EF
1	31%	post-burn	*Trifolium hirtum*	rose clover	EF
2	21%	post-burn	*Erodium botrys*	filaree	EF
3	12%	post-burn	*Brassicaceae mix**	non-native brassicas*	EF
4	4%	post-burn	*Amsinckia menziesii*	fiddleneck	NF
5	3%	post-burn	*Festuca perennis*	Italian ryegrass	EG
6	3%	post-burn	*Bromus diandrus*	rip-gut brome	EG
7	2%	post-burn	*Bromus hordeaceous*	soft-chess brome	EG
8	2%	post-burn	*Lupinus bicolor*	annual lupine	NF

* non-native mustard-family species (comprised of *Brassica nigra*, *Sysimbrium officinale*, and *Raphanus raphanistrum*)

Table 2. Top eight most abundant (total percent cover across all plots) species in pre- and post-burn vegetative cover. (In column “Group”: EG = exotic grass, EF = exotic forb, NF = native forb)

3.1.2. Medusahead Abundance

Between 2013 and 2014, ANOVA analyses show medusahead cover decreased by 15% in control plots, and by 2% in pre-treatment plots, and the difference between these groups was not statistically significant ($p = 0.08$, Figure 2a). However, post-treatment (from 2014 to 2015), medusahead cover increased in control plots by 15%, and yet continued to decrease in treated plots by another 8%, and the difference between groups was statistically significant ($p = 0.01$). Using a LMER model to account for variation in plot and year, the model predicted 4.5% medusahead cover without burning (no treatment), whereas only 1.7% is predicted where burn treatment is applied, a statistically significant difference ($p = 0.02$).

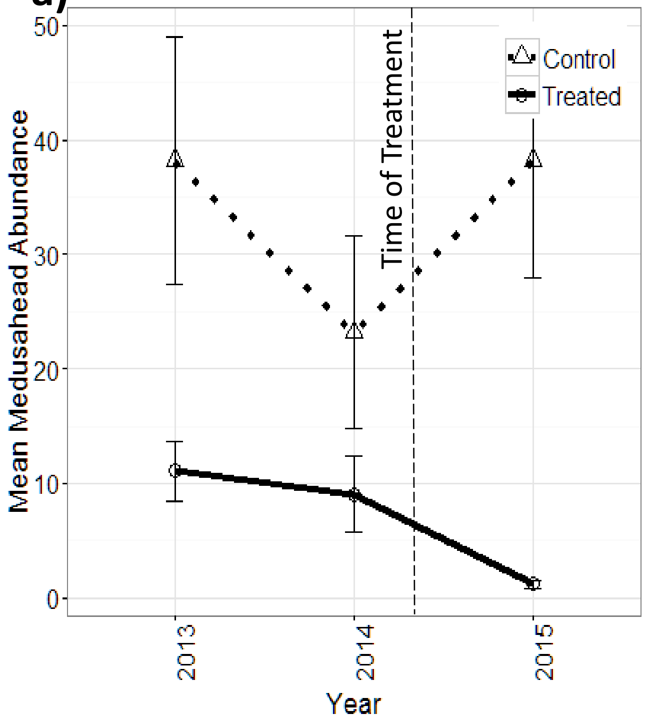
3.1.3. Plot Richness

From 2013 to 2014, richness remained unchanged in control plots at 12 species, but decreased in pre-treatment plots by 2, from 10 to 8 species, and the difference between these groups was statistically significant ($p = 0.05$) (Figure 2b). Post-treatment (2014 to 2015), richness decreased in control plots by 3, from 12 to 9 species, and increased in treated plots by 4, from 8 to 12 species, and the difference between groups was statistically significant ($p < 0.0001$). When the effect of burn on richness was analyzed with a GLMER using the Poisson family, and the effects of plot and year were accounted for, the estimated magnitude of the difference between groups was 3 species more with treatment ($p = 0.0009$), with 9 species estimated in the controls versus 12 species estimated with burn.

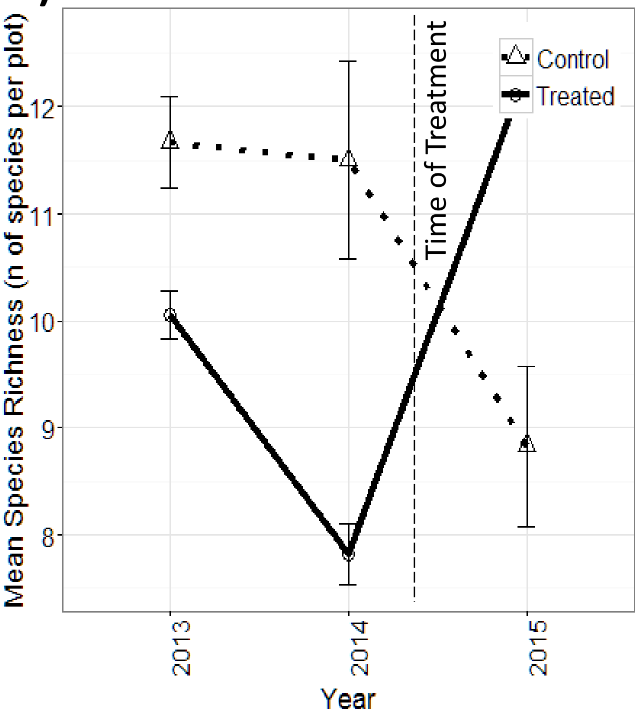
3.1.4 Shannon Diversity

Shannon diversity decreased from 2013–2014 in both the control and pre-treatment plots (Figure 2c). In control plots, this decrease averaged 0.06 (from 1.8 to 1.74) and in pre-treatment plots this decrease averaged 0.38 (from 1.86 to 1.48), and the difference between these groups was not statistically significant ($p = 0.07$). Post-treatment (from 2014 to 2015), Shannon diversity continued to decrease in control plots by 0.32, and yet increased in treated plots by 0.24, and the difference between groups was statistically significant ($p = 0.002$). Using LMER to isolate for effects of treatment, a Shannon diversity that is 0.25 higher is expected due to treatment in the burn group ($p = 0.04$), with 1.61 estimated in control versus 1.86 in the burn group.

a)


Mean Medusahead Abundance
50
40
30
20
10
0
Time of Treatment
Control
Treated
2013
2014
2015
Year

b)


Mean Species Richness (n of species per plot)
12
11
10
9
8
Time of Treatment
Control
Treated
2013
2014
2015
Year

c)

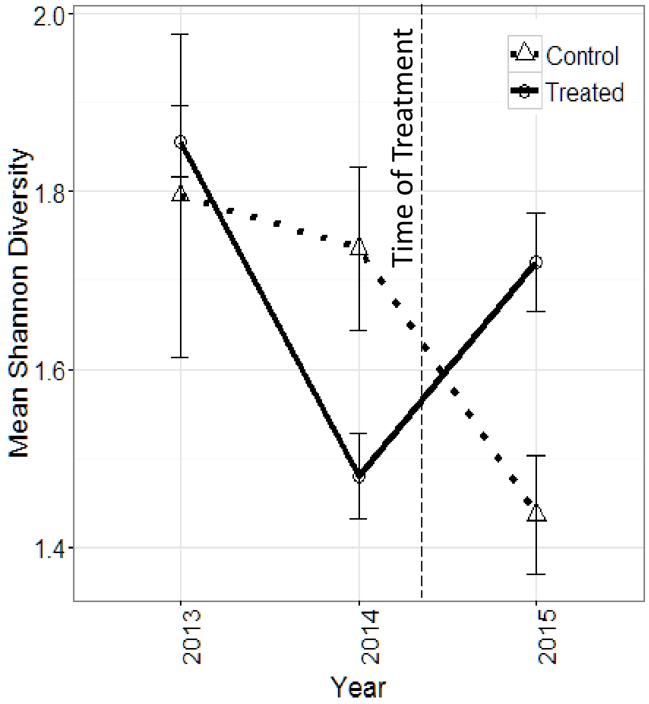

Mean Shannon Diversity
2.0
1.8
1.6
1.4
Time of Treatment
Control
Treated
2013
2014
2015
Year

Figure 2. Treatment effects based on percent cover differences between years for three metrics: **a)** Medusahead Abundance in Plots; **b)** Plot Richness; **c)** Plot Diversity.

3.1.5 Seedbank Dynamics and Cover Comparisons

A total of 19 species germinated in pre-burn seedbank samples. Of these seven were exotic grasses species (76.2% of total germination), eight exotic forb species (8.7%), three native forb species (13.6%), and one native sedge species (1.5%). No native grass species germinated in seedbank samples in either year. In post-burn samples, 17 species total germinated. These included six exotic grass species (comprising 15.8% of germination), eight exotic forb species (63%), and three native forb species (21.2%). No native sedges were found in post-burn samples.

In seedbank samples pre-burn (totals pooled across all samples), the most common grass species were Italian ryegrass at 76 individuals (ind), seaside barley (*Hordeum marinum*) at 35 ind, soft chess at 28 ind, medusahead at 19 ind, and ripgut brome at 16 ind (Table 3). Twenty-four ind of the native forb, bittercress (*Cardamine oligosperma*) germinated. Other native forbs seen were three climbing bedstraw (*Galium porrigens*), and one annual lupine.

Post-burn, no grass species germinated in higher quantity than seven ind (Table 3). Although no non-native brassica species germinated in the pre-burn seedbank samples, post-burn samples from the same areas germinated 101 ind of the aforementioned brassica species group. Ten ind of rose clover germinated in post-burn samples, but no more than two ind germinated of any other exotic forb species. For native forbs in post-burn samples, 28 ind of bittercress germinated, as well as 11 ind of California everlasting (*Pseudognaphalium californicum*) and one annual lupine.

Top Five Most Abundant Seedbank Species Pre- and Post-Burn					
Rank	**n ind.**	**Pre/Post**	**Scientific Name**	**Common Name**	**Group**
1	76	pre-burn	*Festuca perennis*	Italian ryegrass	EG
2	35	pre-burn	*Hordeum marinum*	seaside barley	EG
3	28	pre-burn	*Bromus hordeaceous*	soft-chess brome	EG
4	19	pre-burn	*Elymus caput-medusae*	medusahead	EG
5	16	pre-burn	*Bromus diandrus*	rip-gut brome	EG
1	101	post-burn	*Brassicaceae mix**	non-native brassicas*	EF
2	28	post-burn	*Cardamine oligosperma*	Western bittercress	NF
3	11	post-burn	*Pseudognaphalium californicum*	California everlasting	NF
4	10	post-burn	*Trifolium hirtum*	rose clover	EF
5	7	post-burn	*Festuca perennis*	Italian ryegrass	EG

* non-native mustard-family species (comprised of *Brassica nigra*, *Sysimbrium officinale*, and *Raphanus raphanistrum*)

Table 3. Top five most abundant (total number germinated across all samples) species in pre- and post-burn seedbank. (In column "Group": EG = exotic grass, EF = exotic forb, NF = native forb)

When comparing changes in relative abundance of vegetative groups between seedbank and vegetative cover, ANOVA showed that vegetative grouping was significantly correlated with variance between groups (*p* = <0.0001) (Figure 3a). According to Tukey's HSD, exotic grass in cover (EG_C) and seedbank fell into one group (ΔEG_C = -71.1% ± 3.2%, ΔEG_S = -58.3% ± 10.5%). Exotic forbs in cover (EF_C) and seedbank (EG_S) also fell into one group (ΔEF_C = 64% ± 3.9%, ΔEF_S = 61.2% ± 7.5%). Native forbs and native grasses for both seedbank (NF_S, NG_S) and cover (NF_C, NG_C) samples all fell into the third group (ΔNF_C = 47.7% ± 2.3%, ΔNF_S = -1.2% ± 7.6%; ΔNG_C = 2.3% ± 0.7%, ΔNG_S = -1.7% ± 1.3%).

For treatment-caused change in richness of vegetative groups between seedbank and vegetative cover, ANOVA showed that both sample type (vegetative cover vs. seedbank) and vegetative grouping were significant variables for variance between groups, as well as their interaction (Sample Type: *p* = <0.0001; Grouping: *p* = <0.0001; Interaction: *p* = 0.0006) (Figure 3b). According to Tukey's HSD, richness of exotic forb and native grass in the cover data increased similarly (ΔEF_C = 1.4 ± 0.3, ΔNG_C = 1.4 ± 0.3). Change in exotic forb richness in seedbank samples resembled exotic grass and native forb richness change in the vegetative cover (ΔEF_S = 0.8 ± 0.3, ΔEG_C = 1.1 ± 0.3, ΔNF_C = 0.8 ± 0.2). Native forb and native grass richness in seedbank samples changed similarly (ΔNF_S = -0.1 ± 0.2, ΔNG_S = -0.1% ± 0.1). Finally, exotic grass from the seedbank fell into its own grouping for change in richness (ΔEG_S = -1.9 ± 0.6).

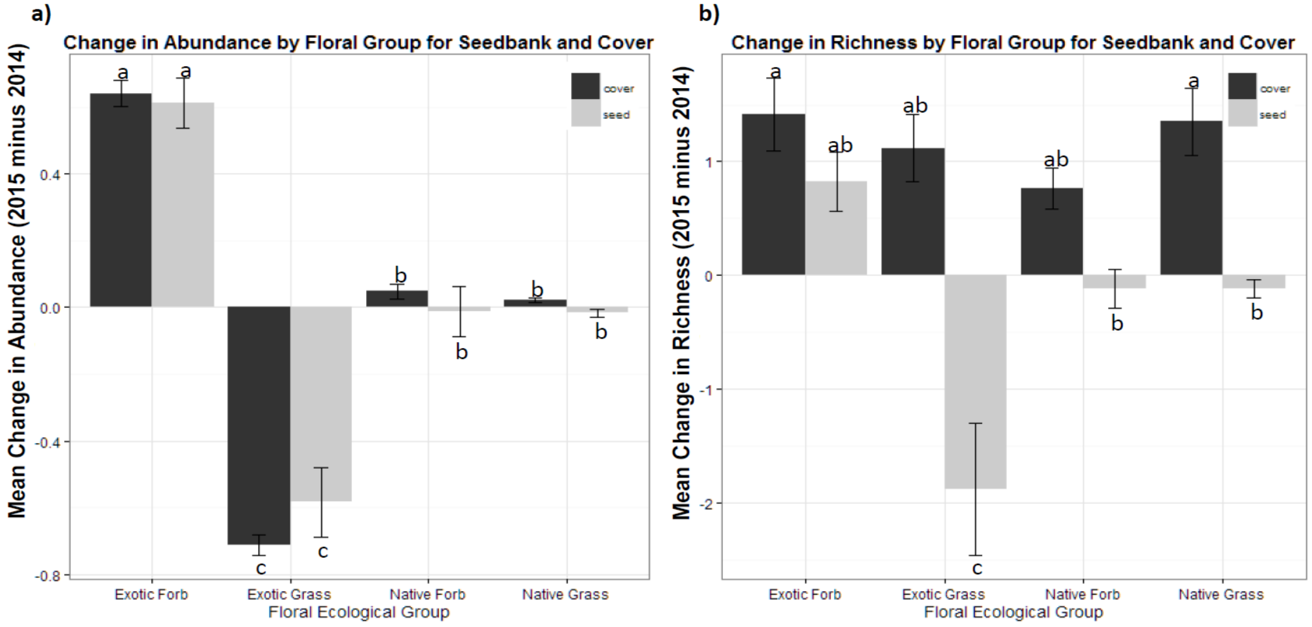


Figure 3. Mean change in **a)** abundance and **b)** richness by vegetative group for percent cover compared to seedbank.

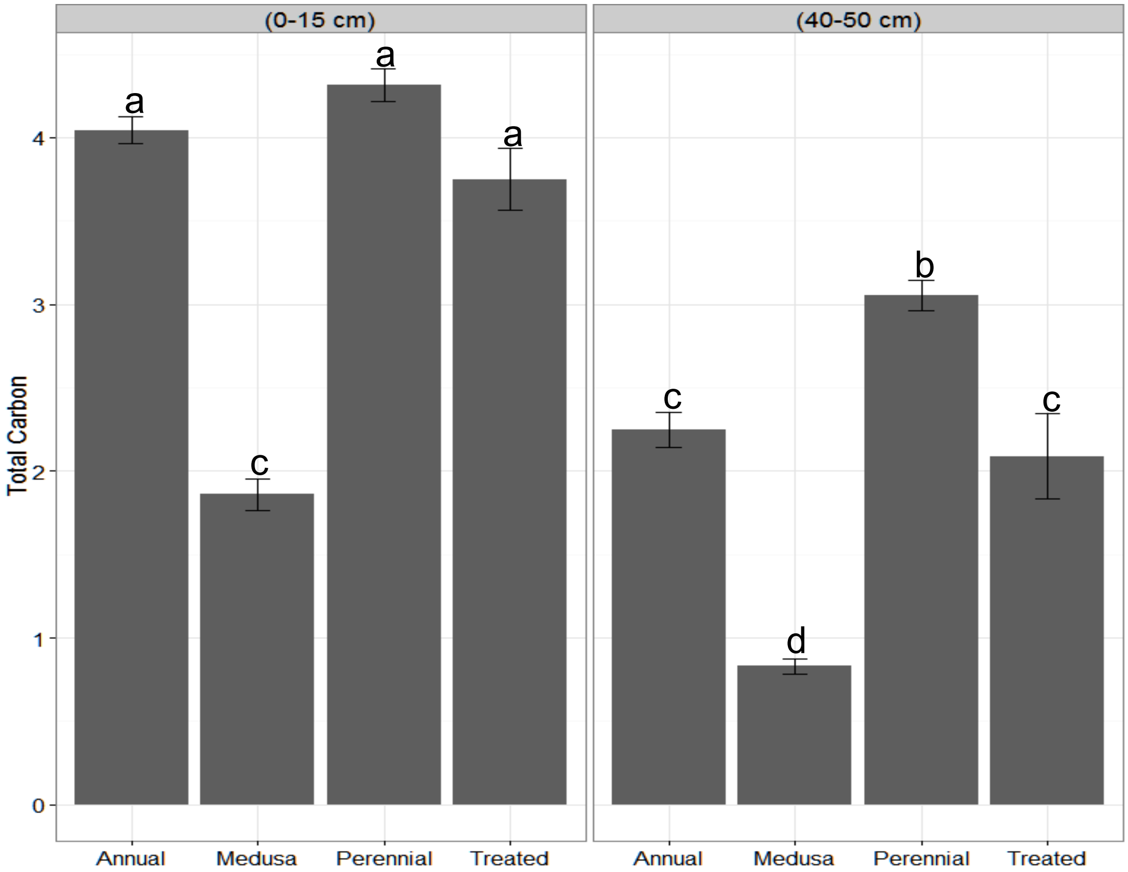
Jaccard index test results for dissimilarity in treatment plots between cover and seedbank pre- and post-burn determined that cover and seedbank dissimilarity did not change between years (Jac_{pre} = 0.888 ± 0.006, Jac_{post} = 0.893 ± 0.006).

3.2 Soil Nutrient Analysis

Overall, shallow soils (0 – 15 cm) had higher quantities of nitrogen and carbon than their paired deeper soils (40 cm to depth at impermeable layer), and these trends were seen in the different plant community types. For both nitrogen and carbon levels, soils under medusahead had statistically lower amounts of these elements than for soils under other vegetative covers.

For total carbon (C) composition of soils by category, both vegetative cover category and core depth were statistically significant (category: p = <0.0001; depth: p = <0.0001). The interaction of these variables was not significant (p = 0.07). Tukey's HSD test found four distinct groups: shallow soil samples from the annual, perennial and treated cover groups fell into one category, while shallow medusahead soils shared a group with deep soil annual and treated cover groups. Deep soils under medusahead and perennial cover types each had their own distinct groups (Figure 4a).

For total nitrogen (N) composition of soils by category, both vegetative cover category and core depth were statistically significant (category: p = <0.0001; depth: p = <0.0001), and the interaction of these variables was also significant (p = 0.03) (Figure 4b). Tukey's HSD test found three distinct groups for N composition: shallow soil samples from the annual, perennial and treated cover groups fell into one category, while shallow medusahead soils shared a group with deep soil N in annual, perennial and treated cover groups. Deep soil under medusahead cover was in its own distinct group.


(0-15 cm)
(40-50 cm)
Total Carbon
0
1
2
3
4
a
c
a
a
c
d
b
c
Annual
Medusa
Perennial
Treated
Annual
Medusa
Perennial
Treated

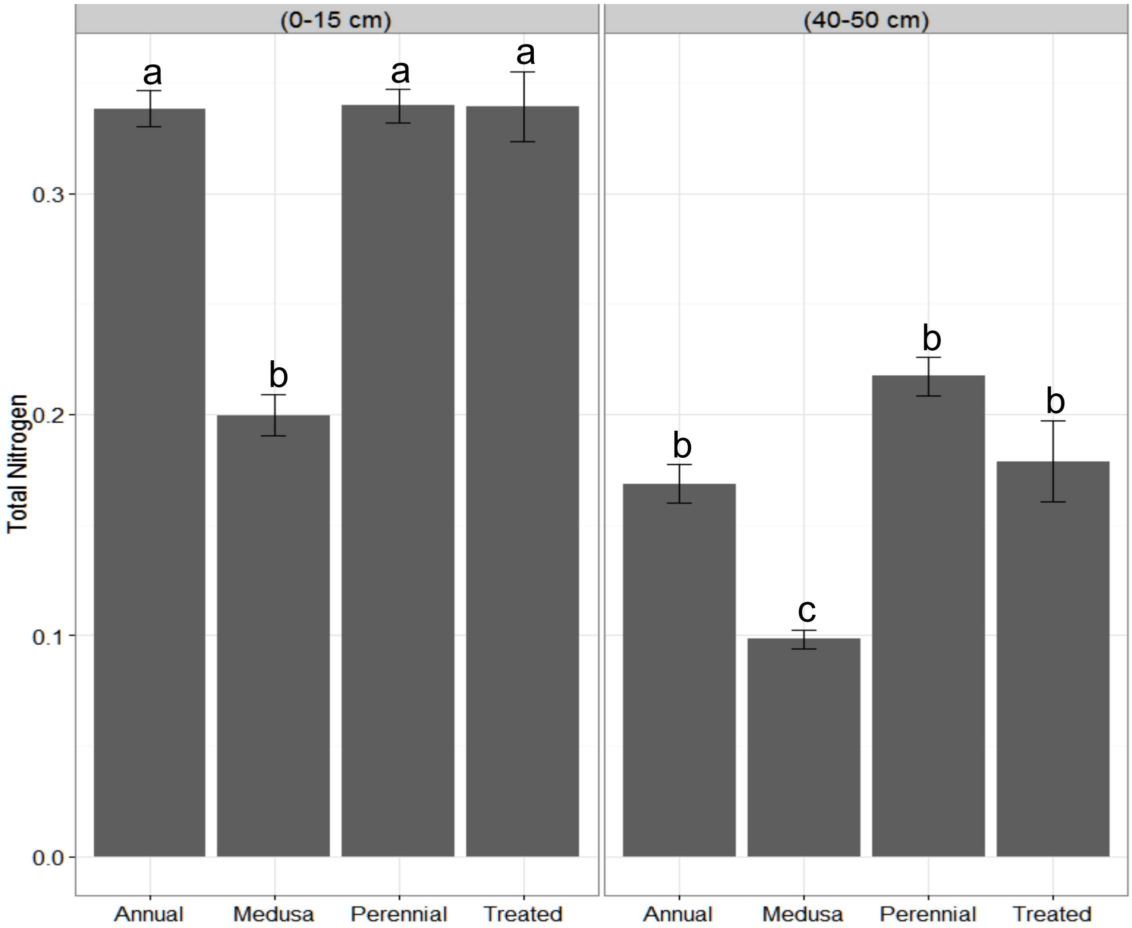

(0-15 cm)
(40-50 cm)
Total Nitrogen
0.0
0.1
0.2
0.3
a
b
a
a
b
c
b
b
Annual
Medusa
Perennial
Treated
Annual
Medusa
Perennial
Treated

Figure 4. a) Percent total carbon in soil by vegetative category and sample depth.
b) Percent total soil nitrogen by category and sample depth.

4. Discussion

Because California's grasslands are temporally and spatially variable, use of adaptive management is crucial. Incorporation of a scientific monitoring feedback loop informs managers of practices that achieve, or fail to achieve, intended goals. Abiotically driven long-term variation in species compositions necessitates the maintenance of these feedback loops across time. This long-term monitoring allows managers to continue acting in the best interest of the landscape as changes occur. Results presented here are only for the first year post-restoration, and therefore only show initial outcomes. The results are presented in that light, with the understanding that these results inform the success or shortcomings of our treatments now, and that adjustments to management practices may be needed in future years based on continued analyses.

4.1 Ecological Effects

Implementation and analysis of monitoring plots at the Corral Meadow confirmed that the site was dominated by medusahead and other exotic species, as observed over several years of field observations. Exotic plant dominance has been shown to negatively impact native species and ecosystems in general (Vitousek et al. 1997, Wilcove et al. 1998). Specifically, medusahead has been shown to degrade rangeland forageability, species diversity and richness, and other ecosystem services (Hironaka 1961, Mangla et al. 2011, Walker et al. 2011). We investigated the efficacy of rangeland restoration – targeted grazing, prescribed fire, and drill seeding – at this site. Through continued monitoring and analysis of collected data across years before and after treatment, it is evident that short-term goals were accomplished in the reduction of medusahead and increase in native species diversity and presence.

Prescribed fire profoundly altered vegetation in the first year after treatment. Fire caused decreased medusahead abundance while increasing overall species richness and Shannon diversity. By functional group, prescribed fire led to a reduction of exotic grass in both the seedbank and cover, while increasing exotic forbs in both. Native forbs increased in cover and seedbank due to fire, while native grass increased in cover due to fire combined with seeding for native grass, but was never present in seedbank analyses due to seedbank collection prior to drill-seeding. This is consistent with prior research showing that medusahead can be treated with properly applied prescribed fire (McKell et al. 1962, Pollak and Kan 1998), that fire can promote germination of native species that were previously rare or dormant (D'Antonio et al. 2002, Gillespie and Allen 2004), and that fire preferentially promotes forbs, generally both native and non-native (D'Antonio et al. 2002).

We ultimately found that dissimilarity between seedbank and percent cover richness was slightly reduced with treatment, but this was not statistically significant. Seedbank and percent cover vegetation were already similar prior to treatment, suggesting that conditions in the field are not strongly limiting germination of certain species. However, California everlasting was only seen germinating in greenhouse plots, suggesting that seedbank investigation is shedding light on additional native species that exist in the seedbank yet were not present in percent cover measurements due to field conditions (Rayburn et al. 2016).

4.2 Soil Nutrient Analysis

Both soil carbon and nitrogen levels were significantly lower where medusahead was dominant. We offer two potential hypotheses for this correlation: 1) medusahead causes a reduction in soil nutrients, or 2) medusahead more successfully invades areas where soil nutrients are low. Past research indicates that the first hypothesis is likely. Medusahead responds positively to nitrogen enrichment (Kay and Evans 1965, Harris 1967) and is limited by reduction of available nitrogen in soils (Young et al. 1998). This suggests medusahead favors environments where available nitrogen is high. However, medusahead's high silica content results in a particularly slow decomposition rate (Torell et al. 1961). This thatch accumulation over time could tie up carbon, nitrogen, and other nutrients in dead plant material above the soil surface, ultimately reducing nutrient levels in the soil. However, if medusahead is tying up soil nutrients in its thatch, then the established ability of prescribed fire to restore nutrients from thatch back into the soil (Wan et al. 2001) is particularly critical in restoration of these medusahead-infested sites, in addition to its role in medusahead control, furthering the importance of fire-use in future restoration projects.

4.3 Adaptive Approach

Continued monitoring of these plots over time will allow for a determination of the duration of the fire-caused transition to exotic forb dominance with increased native forb presence and overall species diversity. Continued monitoring in coming years will also reveal the magnitude of drill-seeding influence and whether direct seeding can, in combination with targeted grazing, further shift this meadow to a native grass dominated rangeland. We expect that the effects of fire as an initial site preparation method will ultimately improve drill-seeding restoration impact at our site, based on the parallels in success of our first-year impacts at our site with established studies of our methodology from previous studies (DiTomaso 2000). Native perennial bunchgrasses are likely most strongly limited in competition against annual grasses at the seedling stage because annual exotic grasses germinate at higher densities and earlier in the season (Dyer and Rice 1997, Hamilton et al. 1999, DiVittorio et al. 2007). The fire-caused shift away from exotic annual grass dominance in the Corral Meadow should give the drill-seeded native grasses a competitive advantage as they transition from seedling to adult stage in the first few years (Dyer et al. 1996, Stromberg and Kephart 1996, Corbin et al. 2004, Moyes et al. 2005). This advantage in the reduced presence of exotic annual grasses is partly due to higher soil-moisture availability to the seeded perennials, as many forbs do not compete directly with most native bunchgrass seedlings for the same soil-water due to their deeper root formations (Moyes et al. 2005). While the effect of fire as a shift away from exotic grasses is likely temporary (Seabloom et al. 2003), mature native grasses are expected to successfully compete with and persist in the presence of exotic annual grasses (Stromberg et al. 2001, Seabloom et al. 2003b, Corbin and D'Antonio 2004, Lulow 2006) and the effects of fire give these drill-seeded plants this temporal boost. This interaction will be a key determination of future monitoring in the coming years.

Additionally, the competition created by drill-seeding may further hinder medusahead reinvasion in years to come compared to where drill-seeding did not occur (James et al. 2015). Published results on this interaction between native and invasive annual grass competition are inconclusive, however, and often do not extend beyond the second year after treatment; this points to the importance of continued monitoring of our seeded and unseeded plots over time for determining the results of this interaction. Continued limitation of annual exotic grasses is important to the restoration objectives of this site for the maintenance of increased biodiversity, native species presence, and ecosystem services (Abraham et al. 2009).

Targeted grazing has been shown to reduce exotic forb abundance after fire (D'Antonio et al. 2002), and can successfully reduce medusahead dominance when applied during a specific two-week window (Lusk et al., 1961, Young et al., 1970). However, improperly timed short-term grazing of medusahead could lead to increased seed production as a compensatory response (Gornish and James 2016). Therefore, continued targeted grazing in Corral Meadow combined with analysis of effects is important to ensure quick adaptation of management strategies in response to feedback.

California's native bunchgrasses are adapted to coexist with fire (Moyes et al. 2005) particularly where grazing is an incorporated process (D'Antonio et al. 2002), and fire has been shown to successfully limit exotic annual grass at this site many others across the state. Therefore, future management should also include continued prescribed burning of the Corral Meadow after the bunchgrasses have reached maturity in order to minimize competition from exotic species. This should be conducted in conjunction with continued monitoring and analysis of treatment effects to inform management and determine impacts.

4.4 Implications

Restoration efforts consisting of prescribed fire, drill seeding, and targeted grazing were implemented in a degraded Coast Range rangeland in Sonoma County, California. Monitoring protocols were established to inform adaptive management. These included 1-m^2 cover plots and seedbank potential investigations. Soil nutrient – vegetative overstory relationship investigations were conducted to assess underlying challenges to restoration. Fire reduced medusahead abundance and nonnative grasses in general, while increasing exotic forb presence and richness in both the cover and seedbank. Native forb richness and presence increased due to fire, while slightly decreasing in the seedbank. Native grass presence and richness increased in the cover population due to drill seeding, but decreased slightly in the seedbank. Medusahead was associated with low soil nutrient levels relative to soils found under mixed annual grass, perennial native grass, or burned treatment area previously dominated by mixed annual grass. This suggests that medusahead either dominates more easily where soil nutrient levels are low, or that medusahead can cause a decrease in soil nutrient levels. Further research is needed to determine the dynamics of this system but these results may be important when considering future restoration projects aiming to mitigate medusahead populations.

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Chapter 3: Developing Data-Driven Models Predicting Annual Variations in Xylogenesis to Improve Fire Scar Chronologies in Sierran Mixed Conifer Forests

Abstract

The study, located at University of California Blodgett Forest Research Station in the north-central Sierra Nevada, cored 90 trees equally represented by the five mixed conifer species common to the region: white fir (*Abies concolor*; WF), sugar pine (*Pinus lambertiana*; SP), incense-cedar (*Calocedrus decurrens*; IC), ponderosa pine (*Pinus ponderosa*; PP) and Douglas-fir (*Pseudotsuga mensziesii*; DF). These trees were cored bimonthly over the course of the growing season for three years (2009 – 2011); then, those cores were measured in the lab for earlywood and latewood ring development. Using these measurements and weather data on-site summarized by time intervals between core dates, we aimed to answer the following questions: 1) what were common earlywood and latewood initiation dates, correlated weather variables, and implications of these results for fire-scar interpretations and future climate change impacts; 2) what were incremental growth rates for each species, correlated weather variables, and implications of these results for fire-scar interpretations and future climate change impacts; and 3) is latewood in these species developed from earlywood cells, or is latewood grown as new differentiated cells at the end of the season? Key findings were: 1) minimum air temperature and maximum air temperature correlated most significantly with earlywood and latewood initiation, respectively; 2) for incremental growth of both earlywood and latewood, average soil temperature was the most significantly correlated temperature variable, with the interaction of precipitation being the most significant at moderate precipitation levels (1-49 mm) for earlywood and high precipitation levels (50+ mm) for latewood; and 3) latewood is likely both developed and grown in these tree species, with some proportions of each varying with and influences by annual weather patterns. These results can directly inform fire-scar interpretations for these species in this region of the Sierra Nevada, and can be used with climate change models to predict likely climate change impacts on these species and, therefore, inform future management.

1. Introduction

As climate changes and the fire season in California expands after over a century of fire suppression, threats to our forests are increasing (Millar and Woolfenden 1999). Mixed conifer forests of the Sierra Nevada cover 3.2 million ha (7.8%) of California's total land base (CDF, 2003). They are a commercially important forest type, and a critical source of biodiversity (Battles et al. 2001). The five species common to Sierra Nevada mixed conifer forest included in this study were white fir (*Abies concolor*; WF), sugar pine (*Pinus lambertiana*; SP), incense-cedar (*Calocedrus decurrens*; IC), ponderosa pine (*Pinus ponderosa*; PP) and Douglas-fir (*Pseudotsuga mensziesii*; DF).

Assessment of intra-annual scar position has been common methodology for determination of historic fire seasonality in North American conifer forests for many years (e.g., Ahlstrand 1980, Dieterich and Swetnam 1984, Caprio and Swetnam 1994, Stephens and Collins 2004, Moody et al. 2006, Fry and Stephens 2006). These studies state broadly that scars positioned in the earlywood are from growing season fires, those in latewood are from late growing season fires, and scars in the ring boundary indicate dormant season fires occurring in late fall or early winter (Caprio and Swetnam 1994). Besides inferring the approximate time of year a fire has occurred from our understanding of tree growth, the timing has been determined for particular fires using several methods. For example, historical newspaper reports on a wildfire impacting a town in the southern Klamath Mountains in 1887 (Fry and Stephens 2006), and fire-scar collection capturing a reported wildfire in the Sierra San Pedro Martir in 2003 (Stephens et al. 2010). In general, these studies categorize early, late, and dormant season fires based on fire scar position within annual rings, although there has not been a systematic study of xylogenesis and environmental factors influencing these species to determine when these time periods specifically occur. As we might expect growing season and fire season to shift in the face of rapid climate change, a more complete understanding of xylogenesis in these ecologically and financially valuable species is pertinent, and can inform better management and planning in the future.

Studies in other species and other locations have aimed to investigate weather correlations with ring development using a variety of other methods. One study assessed climate correlations on Corsican pine ring section development using pointer years in chronologies (Lebourgeois 2000); another study used dendrometer hooks and a dial caliper to assess cambial development in four other Sierra Nevada species not used in our study (Royce and Barbour 2001). Many studies have used dendrometer bands to assess cambial development. These devices not only measure irreversible secondary growth, but also stem water fluctuations (Drew and Downes 2009). However, all of these methods they lack direct observation and study of earlywood and latewood development. Recent studies from Austria, Italy and Spain have used similar microcore methodologies (Rossi et al. 2006, Camarero et al. 2010, Oberhuber et al. 2014), and have demonstrated that microcores provide finer scale analysis opportunity for investigation of xylogenesis, and therefore the microcore method was used here as well.

Xylogenesis is the formation of wood through the growing season, specifically the onset, rate, and duration of cell differentiation (Wodzicki 1971, Uggla et al. 2001, Deslauriers et al. 2003). Studies on a wide varieties of tree species have shown that the regulation of this process is complex, and can be impacted by a suite of factors including genetics (e.g. Hertzberg et al. 2001, Schrader et al. 2004), hormones (e.g. Uggla et al. 1998, Schrader et al. 2003), and the environment (e.g. Denne 1976, Savidge 1996). Looking ahead, as climate and seasonality change from historical norms, the specific ways in which annual xylogenesis will be affected are unknown. Improving our understanding of how these species grow, and how xylogenesis correlates with climate can be used to better understand historic fire seasonality from fire scars and how we may expect these species to react in the face of climate change.

Specifically, this study aims to answer the following questions: 1a) what are annual earlywood and latewood initiation dates for the five conifer tree species in a Sierran mixed conifer forest: PP, SP, DF, IC and WF and 1b) what weather variables correspond with initiation of xylogenesis, and 1c) what could these initiation-weather correlations imply for fire-scar interpretations and future climate change impacts; 2a) what are rates of growth by species over the course of xylogenesis and 2b) what weather variables are associated with this incremental growth; 3) is latewood developed from earlywood cells, or is latewood grown as new differentiated cells at the end of the season?

2. Methods

2.1 Study Area

Data for this study were collected from University of California Blodgett Forest Research Station, located in the north-central Sierra Nevada approximately 20 km east of Georgetown, California (38°54’N, 120°39’W). The 1214 ha station has an altitude range of 1188 – 1410 m, and is divided into management compartments ranging 8 – 80 ha each. Forest stands used in the study generally had gentle slopes; slopes of individual tree locations ranged from 3 – 13°. Precipitation averages 160 cm annually with most occurring between September and May (Stephens and Collins 2004), with summer and fall being hot and dry. For our study years 2009 – 2011, cumulative precipitation was 132, 196, and 127 cm, respectively. Average January temperatures average 0 – 8°C, while August temperatures average between 10 – 29°C (Stephens and Collins 2004). For our study years, January temperatures averaged 7°, 5°, and 7°C, respectively, and August temperatures averaged 21°, 19°, and 21°C, respectively.

2.2 Project Design

Three trees of each species were selected from each of six research compartments at Blodgett for a total of 90 trees. Compartments were selected to capture some range of slope and aspect, without dramatically changing site types; drainages and mesic sites were avoided. All six compartments were thinned from below between 2000 and 2008 (R. York, personal communication 2016). Individual tree selection criteria included 90+ years of age, dominant or codominant crown class, no major crown defects, greater than 40% crown ratio, and no visible disease nor evidence of insect defoliation. Trees that met these initial criteria were cored. Trees showing exceptionally small sample rings were excluded from the study, as these exceptionally small rings suggest stress, poor health and low vigor, adding growth variables we aimed to exclude. After all study-trees were selected, on-site meta-data were collected, including tree height, DBH, aspect and slope, and if a tree was dominant or co-dominant. On-site climate data were also obtained from the weather station at Blodgett for 2005 – 2012 (Blodgett Weather

Station). This included a series of “temperature variables” comprised of daily air and soil temperature (°C; minimum, maximum, and average) and daily cumulative precipitation (mm).

From April 2009 to October 2011, these 90 trees were cored at breast height bi-monthly during the growing season (April – October, Table 1), using quarter rotations around the tree with slight horizontal (+/- 10 degrees) and vertical (+/- 30 cm) offsets to prevent re-coring of damaged areas. For 2011 growth, a subset of trees was cored through January 2012 in order to capture potential dormant-period changes. Cores to a depth of 2 – 4 cm were extracted to allow determination of cambial radial growth and decadal increment growth. Cores and bark were placed in uniquely labeled paper straws and sent to the lab for processing.

2009	Ordinal Date	2010	Ordinal Date	2011	Ordinal Date
1-May	121				
11-May	131	15-May	135		
25-May	145	28-May	148	20-May	140
5-Jun	156	12-Jun	163	5-Jun	156
22-Jun	173	25-Jun	176	20-Jun	171
7-Jul	188	10-Jul	191	1-Jul	182
17-Jul	198	23-Jul	204	18-Jul	199
3-Aug	215	6-Aug	218	4-Aug	216
14-Aug	226			19-Aug	231
2-Sep	245	8-Sep	251	10-Sep	253
26-Sep	269	28-Sep	271	30-Sep	273
25-Oct	298			20-Oct	293
		8-Nov	312	12-Nov	316
				22-Dec	356
				18-Jan	383

Table 1. Core dates during the three years of study. The last two core dates of 2011 came from only a subset of study trees.

2.3 Data Processing

In the lab, cores were removed from paper straws, mounted and labeled, and sanded to a smooth surface. Earlywood and latewood measurements of all present annual rings and current year’s cambial development were measured in micrometers (0.0001 mm) using a sliding stage (Velmex Inc., Bloomfield, NY, USA) and recorded in the computer software Measure J2X (Voortech Consulting, Holderness, NH, U.S.A 2005). Earlywood and latewood differentiation were determined using qualitative aspects of cells (darkening) (Lebourgeois et al. 2010, Makinen and Hynynen 2012, Zhao et al. 2015). To minimize measurement bias and inconsistency, all tree-ring measurements were recorded by one individual, and were determined through a microscope cross-hair to keep assessment location within the scope consistent, so that wood measurements were always recorded as they passed through this specific point.

The earliest available growth year on all cores was 2008. To accommodate for inherent variation in ring widths around tree circumference (due to common phenomenon such as compression wood and root-resource variability) and boring-angle variability, all measurements for growth on each core in subsequent years were converted to ratios against growth from the same core in 2008 (growing-year ring width measurement from one core divided by measurement of 2008 ring width). This standardization allowed for cross-comparisons between cores with variability across cores accounted for. These ratios provided total growth to date for cambial development. For analyses, ratio-growth was then further adjusted for "incremental growth", defined as the differences between sequential core growth ratios on each tree within each year (current core ratio-growth minus previous core ratio-growth on same tree).

For climate data 2009 through January 2012, air and soil temperature data (average, minimum, and maximum) and average precipitation were summarized for analytical use by interim periods between each core date (10 – 20 days, generally two weeks). Cumulative precipitation was summarized by two week intervals prior to each core date to remove the effects of variations in length of interim period. To understand the relationship between multiple variables, precipitation was classified into three categorical levels of cumulative precipitation, termed "precipitation level", per two-week period: none (<1 mm), moderate (1 – 49 mm), and high (>50 mm).

2.4 Statistical Analysis

The first summary analysis included a histogram for earlywood and latewood initiation dates. For this study, earlywood and latewood initiation are defined as the first signs of earlywood or latewood presence in the growing season for a particular growing year. First, data were organized by counts of trees to begin earlywood or latewood growth for each core date by species and year. By organizing by counts of trees to initiate growth at a given core date, surges of growth became apparent and the surges in initiation could be assessed for correlations with weather variables. The second form of summary analysis assessed earlywood and latewood growth and development trends and correlating weather trends over the course of each study year. These data were organized by averaging growth ratios across replicate trees of each species for earlywood and total ring width (earlywood plus latewood) growth over the course of each year. These data were then plotted over average daily temperature and precipitation to show growth and climate trends.

All statistical analyses for this study were performed in R Version 3.3.1 (R Core Team 2016). First, we tested for the overall effects of variables "species" and "compartment". Next, for determination of weather correlations with earlywood and latewood initiation, data were summarized by "count", defined as counts of trees that began growing earlywood or latewood on any particular core date (separated by species and core year). These counts were then sorted into two groups: less than three trees versus three or more trees. This split at three trees was the winning model based on the results of an AIC competition relating weather variables to counts of trees at a variety of split levels (one tree through six trees were tested as the split determination). Of these models, the split at three trees had the lowest AIC.

Statistical models were run using the binomial family in the "glm()" function for generalized linear models in the R base-package "stats" (R Core Team 2016). We tested and compared a series of models, each including one temperature variable and its interaction with precipitation grouping, on the dependent variable "count group". A series of levels for count group were tested in this competition ranging from a split at one tree, to a split at six trees, to determine what count level per core date had the strongest correlation with weather variables. For earlywood and latewood each, this AIC competition was run for model selection (Burnham and Anderson 2002); for this method, Akaike information criterion (AIC, Akaike 1974) was used to assess model fit, and the model with the lowest AIC was chosen. Using results from these models, we then predicted probabilities of earlywood and latewood growth initiation for each precipitation level as temperatures increase.

The "rpart" package (Therneau et al. 2015) in R was used to build classification trees showing expected correlations of cumulative precipitation and most strongly associated temperature variable on count grouping (more or less than three trees per species per year). For analysis of weather correlations with earlywood and latewood incremental growth, the linear mixed-effects model "lme()" function of the nlme package was used (Pinheiro et al. 2016). This allowed for incorporation of the nested random effects "core year", "compartment" and "sample tree" in the models. First, temporal autocorrelation had to be accounted for. To do this, an overall model which included all weather variables was run with temporal autocorrelation coefficients including autoregressive, differing, and/or moving averages where parameters for moving average (q) and autoregressive order (p) were 0 and 1. Then, all combinations of autocorrelation structure were tested and the model with the lowest AIC was selected for further analysis, which was where the temporal autocorrelation structure had an order of one ("corAR1()"). To determine which of the many temperature variables had the strongest correlation to growth, we then created reduced models, one for each temperature variable, compared the models' AIC values, and selected the model with the lowest AIC. Next, precipitation level was added as an interaction term to the winning temperature variable from each AIC competition (earlywood and latewood) to determine effects of the lead temperature variable and precipitation level on earlywood and latewood incremental growth.

For incremental growth, though "species" was not significant as a main effect, it was significant in some cases as an interaction term. This means that, overall, the species identity of a tree was not expected to influence average incremental growth rates; however, in some cases, the way "species" interacts with weather variables is significant for resulting incremental growth (i.e. there are some species differences in the way weather variables correlate with incremental growth). Since species differences are of ecological interest, even though "species" is not a significant main effect for growth, a second set of models was run incorporating "species" as an a third interaction term (with precipitation level and the winning temperature variable) to determine differences in effects by species. Finally, we used these two models for earlywood and latewood each (models with and without species interaction with climate variables) to estimate the expected incremental growth of earlywood and latewood for increasing temperatures at each precipitation level and their 95% confidence interval. For the earlywood incremental growth models, only earlywood measurements obtained before latewood initiation were used. This way, weather variable correlations with incremental growth of earlywood were only investigated where earlywood was not yet influenced by latewood growth or development.

To address the question of whether latewood is developed from earlywood versus added on, a model was run on all earlywood incremental growth (pre- and post-latewood) to test the independent variable latewood presence/absence had a statistically significant effect on measured earlywood width. For this model, "lme()" function of the nlme package was used again for the same reasons as described above.

3. Results

For all of the analyses described below, statistically significant differences were never found for factors "species" and "compartment" overall, meaning these factors were not meaningful influences of variation in growth characteristics. This suggests that compartments used in the study performed well as replicates, and that the five conifer species we studied grew similarly to each other and were associated with similar weather variables.

3.1 Summary Statistics

In all three years of our study, WF and DF showed stronger surges of earlywood initiation (more trees initiating growth within a given core period) and began earlywood growth earlier than IC, SP, or PP (Figure 1a). In all three years of study, earlywood initiation in WF and DF began between May 25th and June 5th (ordinal dates 145 – 156), a much tighter grouping of initiation suggesting a potential correlation with day of year or length of day that overrides specific annual climatic drivers. IC, PP, and SP were slower to initiate, but typically earlywood was found on some individuals between June 5th and June 12th (156 – 163), with SP being the slowest to respond with earlywood initiation. For all species in all three years, highest rates of earlywood initiation occurred between June 5th and June 25th (156 – 176). The latest common initiation dates for earlywood were July 1st (182) for WF and July 23rd (204) for IC, PP, and SP, with DF between these two dates.

WF and DF also consistently showed earlier signs of latewood at higher frequencies than the other three species. Overall, timing of latewood initiation (Figure 1b) was more variable by year, with initial flushes of latewood typically occurring between July 7th and July 23rd (188 – 204), and peak frequencies occurring typically between August 4th and September 10th (216 –

253). Peak initiation frequencies occurred earlier in 2009, with all five species peaking between July 7th and September 2nd (188 – 245). Start date surges were by far the highest in 2010, with all species but DF peaking strongly on September 8th (251). In 2009, almost all trees had begun latewood development by September 9th (252). However, in 2010 and 2011, it wasn't until around September 30th (273) that most trees had begun latewood development.

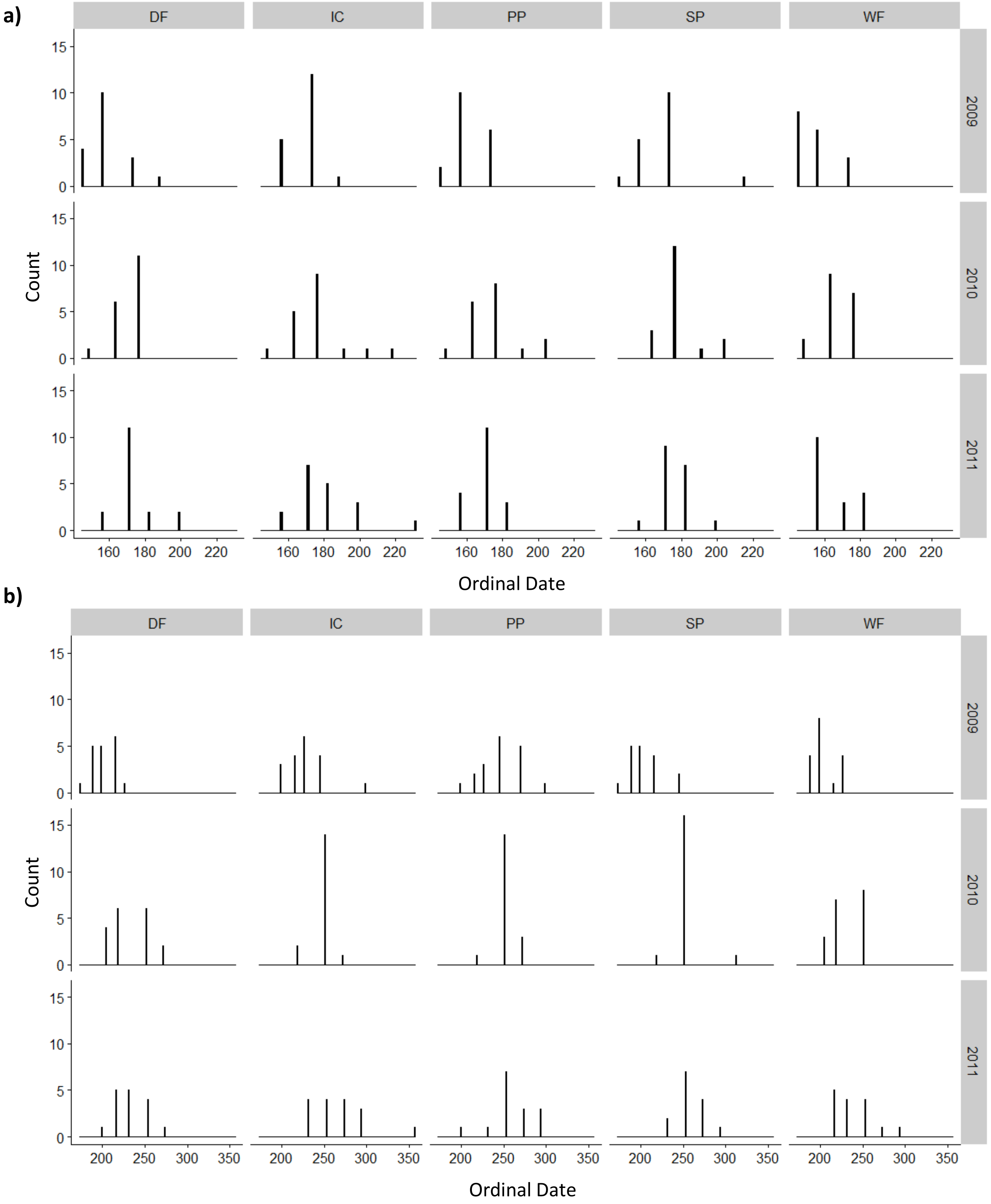


Figure 1. Histograms of earlywood (a) and latewood (b) actual initiation dates (in ordinal date) for all trees grouped by species and year.

Overall, 2011 had the largest total growth of the three study years (Figure 2). A dramatic dip in earlywood growth ratio appears at the time of latewood initiation in most cases. In all three years, measureable precipitation increase is noted within two weeks before the initiation of earlywood growth (Figure 2a). Latewood initiations are first noted shortly after average daily air temperatures begin to peak (Figure 2b).

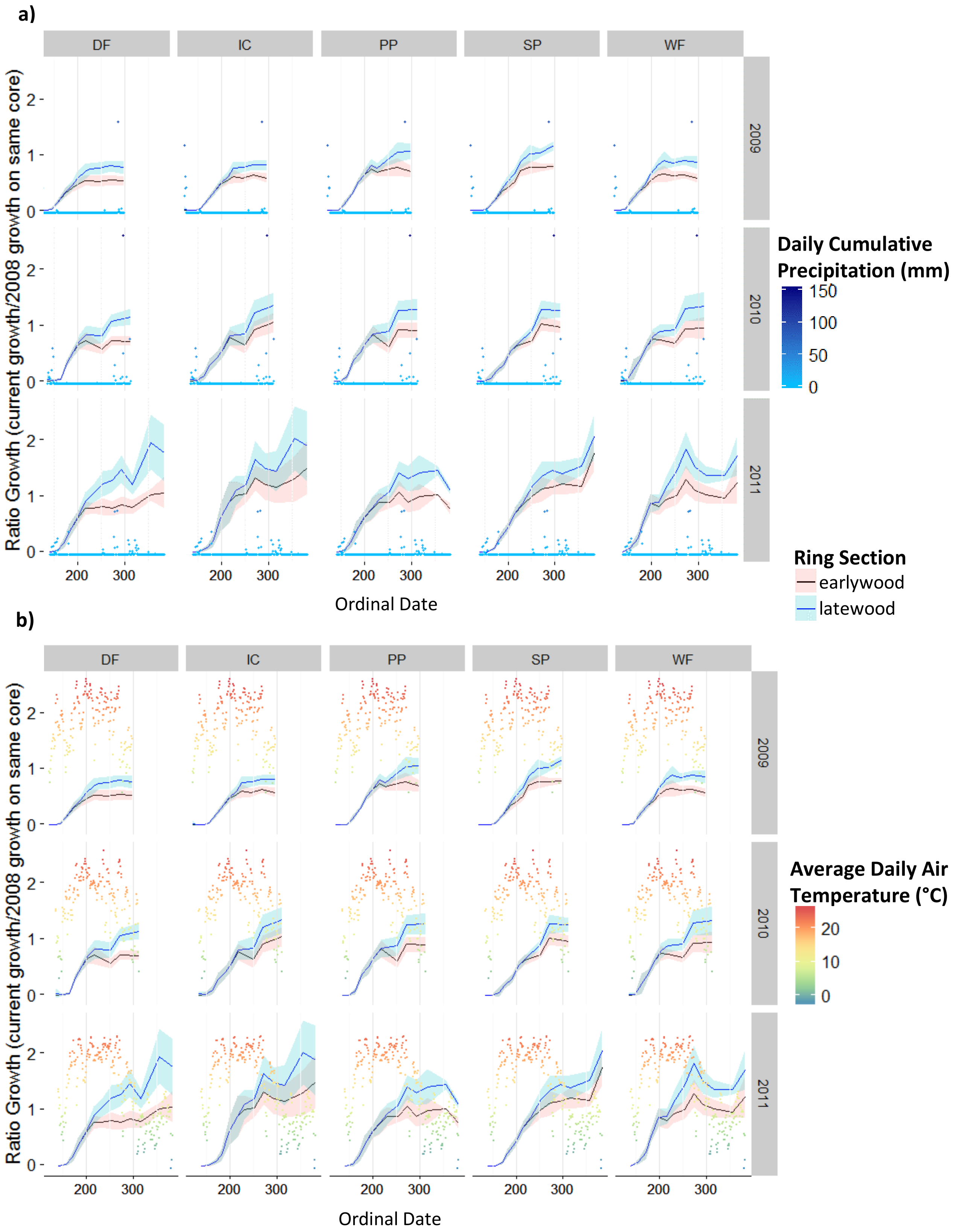

a)
DF
IC
PP
SP
WF
2009
2010
2011
Ratio Growth (current growth/2008 growth on same core)
0
1
2
200
300
Ordinal Date
Daily Cumulative Precipitation (mm)
150
100
50
0
Ring Section
earlywood
latewood
b)
Average Daily Air Temperature (°C)
20
10
0

Figure 2. Averaged growth ratios across species and year, showing earlywood and total ring widths (with space between representing proportional latewood). Shaded regions represent 95% confidence intervals. Daily cumulative precipitation overlaid (a) and daily average air temperatures overlaid (b) to show growth trends with corresponding climatic trends.

3.2 Growth Initiation and Related Weather Variables

For both earlywood and latewood, AIC competition determined that three or more trees initiating growth on a given core date was the count at which the most meaningful correlation with weather variables became apparent. Using this count grouping for growth initiation, weather variable relationships were determined as follows:

Minimum air temperature had the most significant correlation of the temperature variables with earlywood initiation. The classification tree for earlywood initiation (Figure 3a) shows that air temperature below -0.5°C is associated with a delay in earlywood development, and an earlier initiation is observed with air temperatures between -0.5°C and 0.28°C. At temperatures above 0.28°C (above freezing), cumulative precipitation becomes an important variable. Cumulative precipitation greater than or equal to 47 mm at temperatures above 0.28°C correlates with low frequency of earlywood initiation. However, where precipitation is 2 – 46 mm and temperatures are above 0.28°C, high frequency of earlywood initiation is expected. Where cumulative precipitation is less than 2 mm, a temperature range of 5.44 – 5.94°C is expected to correlate with high frequency of earlywood initiation. However, at this precipitation level, a temperature outside this range will have low frequency of earlywood initiation.

Using a generalized linear model with the binomial family, there is a significant correlation between high frequency of earlywood initiation and minimum air temperature with moderate precipitation (odds ratio = 2.22; log-odds estimate = 0.8, p <0.01); in other words, high frequency of earlywood initiation is twice as likely as minimum air temperature increases (above 0°C) at moderate precipitation levels (1 – 49 mm) (Figure 3b).

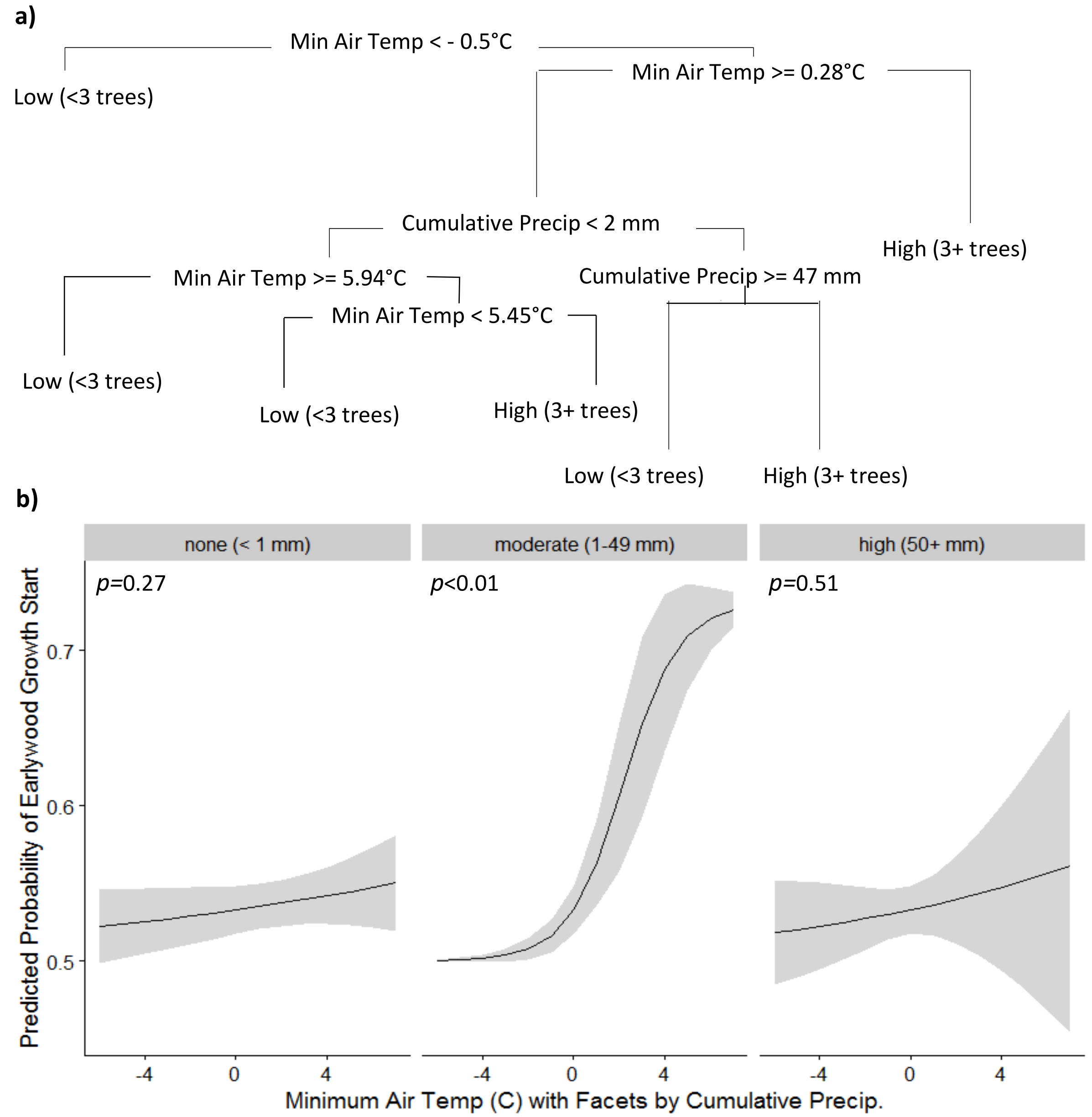


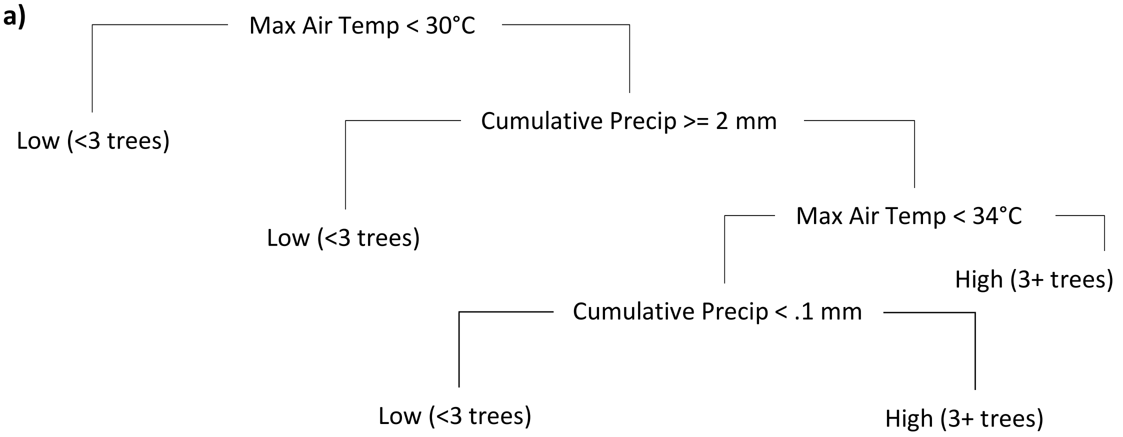
Figure 3. Classification tree (a) and earlywood growth-initiation predicted probabilities (b) for the influence of maximum air temperature (°C) and cumulative precipitation (continuous mm for tree; categorical for probability model) on latewood initiation (grouped as <3 or 3+ trees; all species combined).

For latewood, maximum air temperature had the most significant correlation with the initiation date. The classification tree (Figure 4a) shows that latewood initiation was uncommon when maximum air temperatures was below 30°C. Above the 30°C threshold, cumulative precipitation became an important climate factor. Where maximum temperatures reached above 30°C and cumulative precipitation was above or equal to 2 mm, latewood initiation was later. Where maximum temperatures reached above 34°C and cumulative precipitation was below 2 mm, high frequency of latewood initiation was expected. At a maximum temperature range of 30 – 34°C, a cumulative precipitation less than 0.1 mm correlated with low frequency of latewood initiation (less than three trees), while a precipitation range of 0.1 – 2 mm correlated with high latewood initiation (three or more trees).

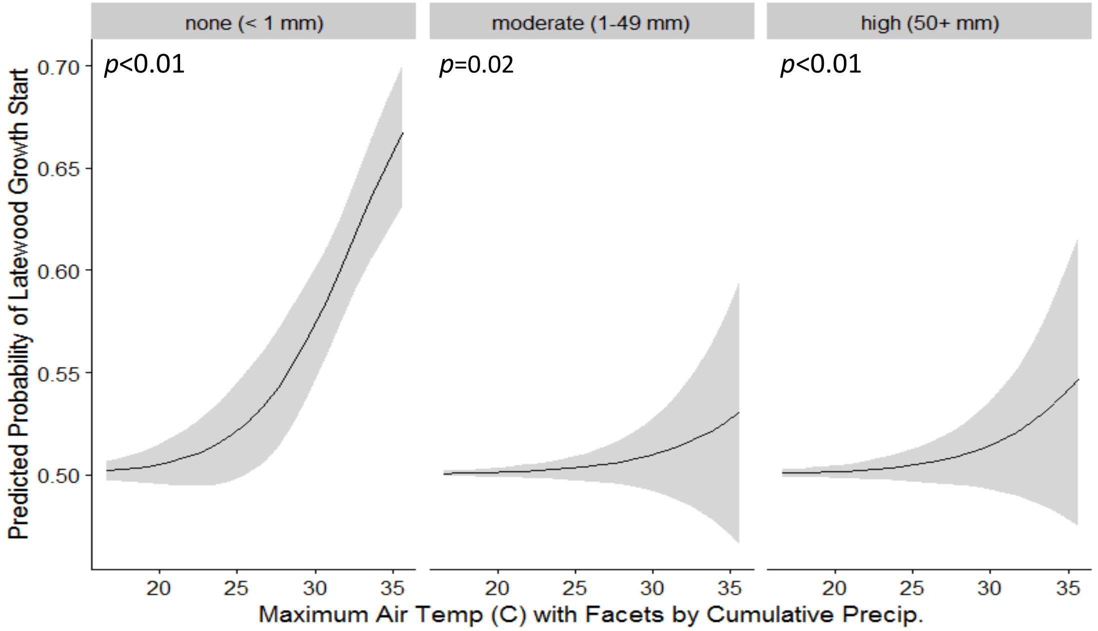
Using generalized linear models, significant correlation between high frequency of latewood initiation and maximum air temperature was found at all precipitation levels, though the less than 1 mm precipitation had the highest significance level and the largest predicted probabilities. When precipitation was less than 1 mm, the odds ratio of latewood initiation for each unit of maximum air temperature increase is 1.35 (log-odds estimate = 0.3, p <0.01); in other words, high latewood initiation is 1.35 times more likely as maximum air temperature increases at very low precipitation levels (<1 mm). At moderate precipitation levels (1 – 49 mm), latewood growth initiation is 1.25 times more likely as temperatures increase (log-odds estimate = 0.2, p =0.02). At high precipitation levels (50+ mm), latewood growth initiation is 1.27 times more likely as temperatures increase (log-odds estimate = 0.2, p <0.01). The corresponding graph of latewood initiation predicted probability (Figure 4b) shows a near exponential increase in probability of latewood initiation around 29°C when precipitation level is very low (<1 mm).

For latewood, unlike earlywood, species was a significant third interaction term along with temperature and precipitation, and including species as an interaction explained the significance of latewood initiation at moderate and high precipitation levels. When remodeled with species incorporated as an interaction term, it becomes apparent latewood initiation predictions are only significant for ponderosa pine at moderate precipitation levels, and for incense-cedar and ponderosa pine at high precipitation levels (Figure 4c). For ponderosa pine, latewood initiation becomes 1.33 times more likely at moderate precipitation levels as maximum temperatures increase (log-odds estimate = 0.3, p <0.01). For all other species, there is no significant correlation with the variable maximum temperature at moderate precipitation. At high precipitation levels, both ponderosa pine and incense-cedar are 1.31 times more likely to have latewood initiation for each °C increase in maximum temperature (log-odds estimate = 0.3, p <0.01). There was no significant correlation with maximum temperatures at high precipitation levels for any other species.

a)


Max Air Temp < 30°C
Low (<3 trees)
Cumulative Precip >= 2 mm
Low (<3 trees)
Max Air Temp < 34°C
High (3+ trees)
Cumulative Precip < .1 mm
Low (<3 trees)
High (3+ trees)

b)


none (< 1 mm)
moderate (1-49 mm)
high (50+ mm)
p<0.01
p=0.02
p<0.01
Predicted Probability of Latewood Growth Start
0.70
0.65
0.60
0.55
0.50
20
25
30
35
Maximum Air Temp (C) with Facets by Cumulative Precip.

c)

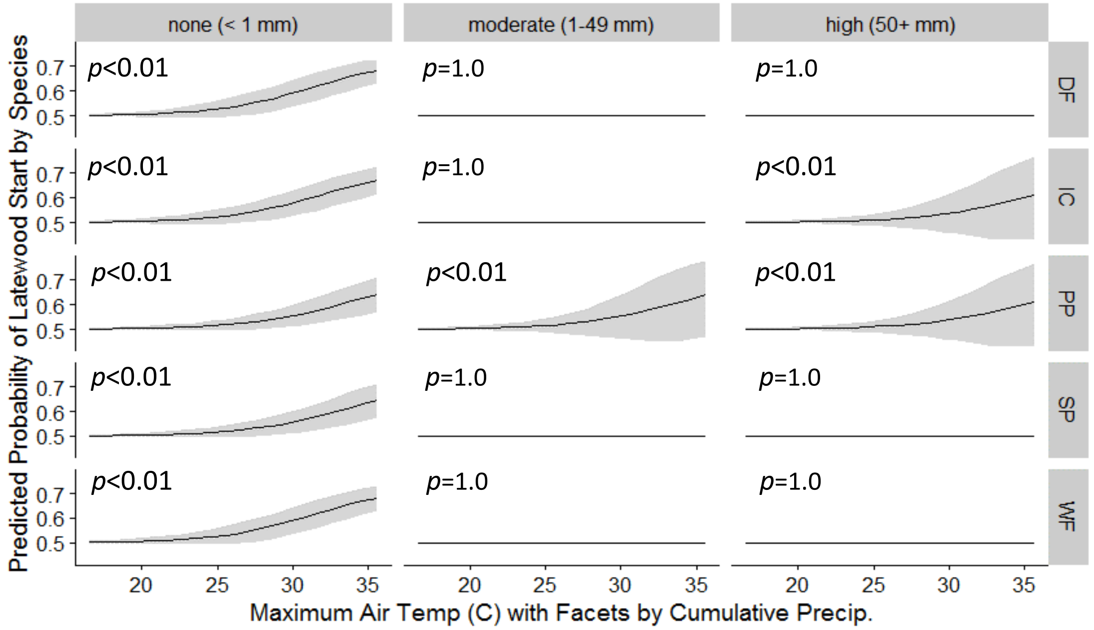

none (< 1 mm)
moderate (1-49 mm)
high (50+ mm)
p<0.01
p=1.0
p=1.0
DF
p<0.01
p=1.0
p<0.01
IC
p<0.01
p<0.01
p<0.01
PP
p<0.01
p=1.0
p=1.0
SP
p<0.01
p=1.0
p=1.0
WF
Predicted Probability of Latewood Start by Species
0.7
0.6
0.5
20
25
30
35
Maximum Air Temp (C) with Facets by Cumulative Precip.

Figure 4. Classification tree (a), predicted overall probabilities of initiation (b) and probabilities by species (c) for influence of maximum air temperature (°C) and cumulative precipitation (continuous precipitation (mm) for classification tree; categorical by none/moderate/high precipitation for probability model) on latewood initiation (grouped as <3 or 3+ trees).

3.3 Incremental Growth and Weather Variable Associations

For both earlywood and latewood incremental growth, AIC competitions determined that average soil temperature was the most significant factor. Incremental growth is shown as the difference in ratio-growth between consecutive core samples, with ratio-growth being current growth on a core divided by 2008 growth on the same core for standardization. For earlywood pre-latewood, the range of incremental growth was -0.883 – 1.671. These fluctuations in values that include negative measurements of growth are explained by the high frequency of coring as development is occurring, as tree cells go through phases of development, initially lacking structure, but eventually becoming more rigid and tightly packed as cell walls are developed. For latewood, the range of incremental growth was -0.767 – 0.789. The overall effects of soil average temperature on earlywood incremental growth is an expected 0.014, 0.015, and 0.010 increase in incremental growth for each °C increase in temperature for the three precipitation levels (none, moderate, and high), respectively (all $p<0.01$). A regression tree for earlywood initiation weather variable associations determined a threshold for soil average temperature where at temperatures below 14°C trees would only be expected to grow by a total increment of 0.027. However, at and above 14°C, incremental growth was expected to surge to an estimated 0.174. For latewood incremental growth, for each unit increase in temperature, we expect a 0.004 ($p<0.01$), 0.002 ($p=0.05$), and 0.006 ($p<0.01$) increase in incremental growth for “none”, “moderate” and “high” precipitation levels, respectively.

When incorporating species as a third interaction term along with precipitation and temperature, slight differences arise (Figure 5a). For earlywood, when there is no precipitation, as soil average temperature increases, IC, DF, and SP are all expected to increase incremental growth by 0.014, whereas PP is only expected to increase by 0.013 and WF is expected to increase by 0.015 (all $p<0.01$). At moderate precipitation levels, for each unit increase in soil average temperature, IC and SP are expected to increase incremental growth by 0.011, whereas PP, DF, and WF are expected to increase incremental growth by 0.012, 0.015, and 0.020, respectively (all $p<0.01$). Finally, at high precipitation levels, for each °C increase in soil average temperature, incremental growth is expected to increase by 0.008 for DF (though only marginally significant at $p=0.07$), by 0.009 for WF and PP ($p=0.03$ and $p=0.04$, respectively), by 0.010 for SP ($p=0.02$), and by 0.012 for IC ($p<0.01$). It should be noted however, that while these estimates are still considered statistically significant, they are not as strong as estimates for lower precipitation levels.

For latewood (Figure 5b) at the no precipitation level, IC, SP and PP are all expected to have 0.004 incremental growth increase for each °C increase in soil average temperature, whereas DF and WF are estimated at 0.005 (all $p<0.01$). At moderate precipitation, only PP had a significant estimate with an expected 0.003 incremental growth increase as soil temperatures increase ($p<0.01$). At high precipitation, IC was estimated with 0.004 incremental growth increase as soil temperatures rise, with DF estimated at 0.006, and SP and PP estimated at 0.008 (all $p<0.01$). The estimate for WF was not significant.

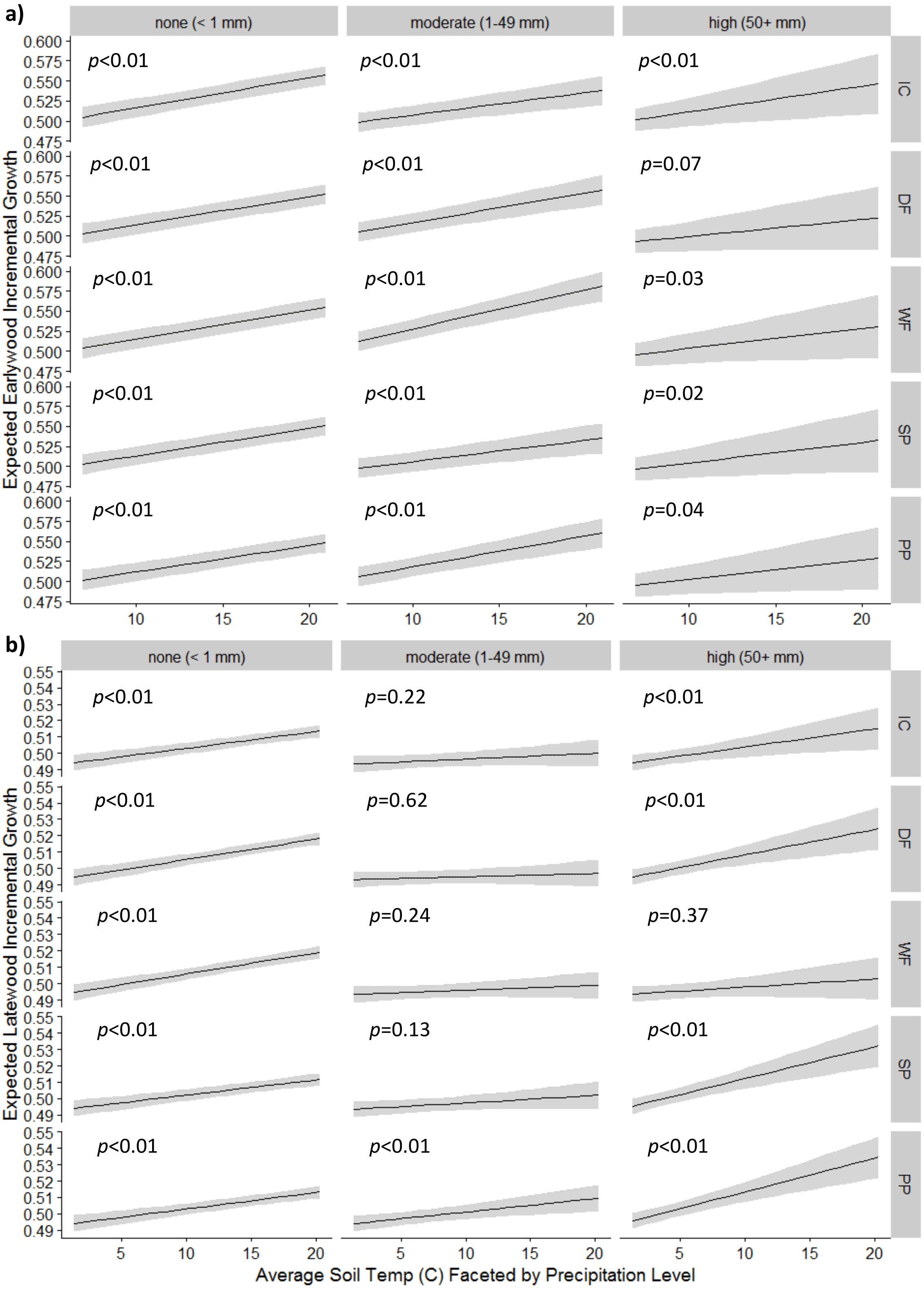


Figure 5. Incremental growth estimates for earlywood (a) and latewood (b) by species for each cumulative precipitation level by average soil temperature.

3.4 Latewood Development vs. Growth

Where latewood was not yet present, earlywood had a statistically significant positive incremental growth (value = 0.11, p <0.01). Where latewood was present, earlywood had a statistically significant negative incremental growth (value = -0.08, p <0.01).

4. Discussion

4.1 Growth Initiation and Weather Correlations – Implications for Fire Scar Interpretations and Climate Change

Overall, these earlywood and latewood start dates suggest a slightly earlier growing season for WF and DF than for IC, PP, and SP. Initiation of earlywood and latewood determined by this study allow us to more thoroughly interpret fire seasonality from mixed conifer forests in similar climates. Fire scars positioned in earlywood likely represent fires that may have occurred anytime between end of May and beginning of July in WF and DF, and anytime between beginning of June and end of July for IC, PP, and SP. Due to high variability by individual trees and year in latewood development, scars positioned within latewood may represent fires that occurred in a much broader range of dates, potentially initiating as early as mid-July, particularly in WF and DF, and extending through the end of the calendar year. While we have estimates for growing season dates in these years, climate variability may have caused a shift in growing season since the time of many fires that are analyzed in fire history studies. Looking ahead, rapidly shifting climate in the present and foreseeable future make our understanding of climatic variability on annual xylogenesis of even more importance in understanding historical, present and future fire seasonality.

Earlywood and latewood initiation were temperature driven, as is commonly found for other Mediterranean conifer species (Camarero et al. 2010). The most significant weather correlation for earlywood initiation was minimum air temperatures at the moderate precipitation level. In general, above freezing air temperatures, particularly co-occurring with moderate rain, trigger high frequencies of growth initiation. The most significant climatic triggers for latewood initiation were maximum air temperatures where no precipitation occurred. Specifically, maximum air temperatures above 34°C, but as low as 30°C correlated with high frequency of latewood initiation. When modeled, PP and IC differed from this generalization. PP latewood development overall is expected to begin at high maximum temperatures regardless of precipitation levels, while IC is not expected to begin latewood at moderate precipitation, but is likely to begin latewood development at high precipitation. These data suggest that if Sierra Nevada summers become warmer and drier and shift into this state earlier in the year, latewood may begin to form on more trees earlier in the summer season. This translates well to annual ring width knowledge that drought years cause narrower annual rings, as earlywood growth would be stunted as weather variables shift latewood formation earlier in the year.

4.2 Growth Trends and Associated Weather Variables – Implications for Fire Scar Interpretations and Climate Change

Both earlywood and latewood incremental growth were driven by average soil temperatures. Effect sizes of these variables were much larger on earlywood than on latewood, likely because overall growth rates are much higher in earlywood. Effect size of soil temperature on earlywood was highest at moderate precipitation levels, which corresponds with the significance of precipitation on initiation date, but all levels of precipitation were significant. A soil average temperature threshold was found for earlywood incremental growth, with growth increments surging at or above of 14°C. Effect size of soil temperature on latewood was highest at high precipitation, which is explained by latewood development occurring during late fall and through winter. This is in stark contrast to the relationship of latewood start to cumulative precipitation, which occurs during the driest and hottest part of the year. A soil average temperature threshold was found for latewood incremental growth, with growth increments surging between 16°C and 18°C.

4.3 Latewood Development vs Growth

Previous research has indicated that unlike conifers of temperate climates, conifers in Mediterranean regions can exhibit bimodal xylogenesis (Camarero et al. 2010). This growth pattern is a reflection of bimodal rainfall, with earlywood growing quickly with spring rains, summer drought causing a slowing or a cessation of growth, and fall rains initiating a secondary surge of growth for latewood. Furthermore, this bimodal xylogenesis is a demonstration of plasticity to spatio-temporal variability of Mediterranean climates, and is expected to fluctuate with annual climatic variation, further supporting our expectation that these dynamics are precipitation driven. In years with higher fall precipitation, a surge of cell production in latewood might be expected. Conversely, in years where fall rains are scarce, latewood may be preferentially developed from earlywood cells to some extent. This is further supported by our visual assessment that in many cases, latewood had not fully developed by the end of the coring survey for that year. Particularly, in years with low rainfall, latewood development seemed to begin within the annual ring rather than at the external edge, with maximum darkening of cells beginning as a stripe through the earlywood portion, and over time filling in toward the outer edge of the annual ring.

The presence of latewood had a statistically significant negative effect on earlywood increment. This reflects the visible dip in earlywood ratios at the start of latewood in the raw data (Figure 3). We offer two possible hypotheses for this interaction, which may each be responsible for some proportion of the observed dynamic. First, latewood may be formed in part or in whole by development of earlywood cells into latewood cells after their formation. If this is the case, a larger proportion of the annual ring would be initially be recorded as earlywood, with the tree adding compounds to outer layers of cells when triggered by hot and dry climate conditions. Second, latewood may be compressing earlywood cell layers around the tree circumference, causing a recorded reduction in earlywood measurement. Based on observations of raw data from this study, it seems likely that a combination of these processes is occurring. In some cases, total annual ring width continued to increase after latewood was present, which suggests that trees continue to add new cells as latewood in addition to early cell development when climatic conditions suit. Our raw data suggest that these conditions may be precipitation driven, as continued increase in total annual ring widths seem correlated with high levels of fall rains.

4.4 Future Research

A next step is to undertake cellular level analysis under a high-power microscope to determine cellular quality, ideally combined with the use of a latewood differentiating stain. This method could more specifically determine latewood transition, by allowing for measurements of cell wall thickness, cell shape, structure variability and cellular change/development over time. These fine-tuned measurements could then be correlated back to climate to further understand how these processes affect ring development.

Another area for future research is whether and how tree age/size and management history interact with variability in climate on annual ring initiation and incremental growth. For this study, all trees were 90+ years of age, had dominant and codominant crown status, and came from stands with similar management histories. It is possible that trees in this size and age class interact with their environment differently from single species stands or younger trees, as was found in one study from Austria (Oberhuber et al. 2014) where large trees were more influenced by precipitation, but small trees seemed to grow independently of weather variables. Management histories effecting resource availability may also dramatically change tree sensitivity to weather variables by modifying competition for resources. In the face of climate change, understanding the repercussions of our management actions could be critical to understanding best practices. While this study sets a solid baseline for mixed conifer forest tree growth in this region where productivity is high, and where the management objective is primarily forest ecology research and timber production, understanding the range of variation for these interactions would be an important consideration for future investigation.

Finally, using results from this study, it would be interesting to use existing climate change models (e.g. Williams et al. 2013) in combination with our weather-growth relationships to predict xylogenesis expectations as climates change. Using this climate modeling approach, at risk species, resilient species, and further implications for management may become apparent. Knowledge that could result from such a study could become particularly useful for decisions regarding the potent seeding of certain mixed conifer species outside their range and may inform where we might expect certain species to perform well (Millar et al. 2007). For example, this study shows that WF and DF respond to weather differently from the other mixed conifer species, with less variation in their growth start dates, which might translate to less overall plasticity in its growth-weather relationship. This might indicate that these species may not be expected to do as well in the face of climate change as the other mixed conifer species. If this is true, focusing on the movement of the other mixed conifers may be a better investment in our future, although other challenges facing pines such as pathogenic threats are other important considerations.

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