FOREST TREATMENT EFFECTS ON WOOD PRODUCTION IN PONDEROSA PINE

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ABSTRACT. Forest treatments reduce wildfire risk and can promote the vigor and production of remaining trees, but they are also a disturbance. Understanding the type, timing, and longevity of tree response to treatment, as well as the potential for interactive effects of treatments and drought, could help managers plan and evaluate forest management practices. Environmental drivers, biological modifiers, and tree capacity to respond to prior disturbances were concurrently tested to predict ponderosa pine basal area increment (BAI) in a lowland and upland dry pine forest in south central Oregon, USA. Environmental drivers included current year and lags or running averages of a drought index, SPEI, and the sum or count of growing degree days $> 0°C$ or $10°C$. Biological modifiers of environmental drivers considered pre-treatment response to disturbance, tree vigor, and tree-to-tree competition. A model was developed to predict BAI in both topographic positions for applicability to the landscape level, and then was used to test for specific differences in BAI between paired forest treatments differing by one treatment. Forest treatments tested included no management (NM), undercut and even spacing harvest (HE), prescribed fire (Rx), and their combinations. HE significantly increased BAI shortly after treatment. Post-harvest, one or two Rx did not provide additional BAI benefits, nor in the absence of HE, did 2Rx vs. 1Rx treatment. The 1Rx treatment was imposed between multi-year droughts; BAI significantly increased after the treatment and was resistant to droughts. Upland trees were affected by a single year of drought; lowland trees responded only after sequential drought years. A single treatment, HE or 1Rx appeared to be as effective as multiple or mixed treatments in improving BAI in dry pine forest stands. HE appeared to generate the largest effect. Timing of forest treatments relative to site water balance may affect short term (decadal) wood production.

1. INTRODUCTION

Forest treatments reduce susceptibility to stand-replacing wildfires (Johnston et al. 2021) and are also expected to promote vigor and productivity of remaining trees. The effects of drought and hot droughts on wood production and tree survival have been of particular interest (Trugman et al. 2021; C. D. Allen et al. 2010). Basal area increment (BAI) is an ideal metric for evaluating stress effects, as carbon allocation to bole growth is a sensitive response indicator as well as economically important (e.g., wood production). Lloret et al. (2011) and others (Serra-Maluquer et al. 2018) proposed the following definitions of tree response to stress: *resistant* trees have no growth reduction or increased growth during the stress; *resilient* trees have decreased growth in response to the stress but have the capacity to return to pre-stress growth rates; tree *recovery* is one where growth is lower during the stress and increases afterwards but not necessarily to pre-stress levels. Within this framework, we evaluated BAI response to forest treatments within the context of site water balance.

In mid-elevation, complacent trees[1], there is significant plasticity of tree physiology and growth (Grulke 2010), and it can be difficult to demonstrate that a population of trees has or has not experienced physiological stress. Because the trees are not necessarily stressed in mid-age, their response to environmental drivers may be muted or temporally lagged. The numbers of trees required to demonstrate response to disturbances in such conditions generally precludes measurements of individual tree physiological drought stress. Although hydrologic drought does not necessarily result in physiological drought stress in trees, specific levels of precipitation have been correlated with measured levels of physiological drought stress in pine at this (Grulke et al. 2020) and other sites (Grulke et al. 2008; Grulke et al. 2002).

Tree carbon allocation to bole growth is the last priority for the allocation of carbohydrates (Rossi et al. 2006; Grulke et al. 1999; Waring 1987), after new foliar growth, new fine root, medium root, branch, coarse root growth and carbohydrate storage. With increasing temperature, respiratory losses of carbon increase and allocation to bole growth is reduced (Duffy et al. 2021). Carbon acquisition is truncated by drought stress (Grulke et al. 2002), by low foliar temperatures in late fall limiting photosynthesis (Ensminger et al. 2006), and low soil temperatures limiting root cell permeability to water ($< 7°C$ Day et al. 1991). BAI reduction can be due to any one of the above factors. Although drought and hot drought impact on carbohydrate reserves (total non-structural carbohydrate) was not found to have a universal role in tree mortality (Adams et al. 2017), carbon allocation to bole growth declines prior to tree death (Cailleret et al. 2017; Manion 1981).

This paper addresses the effect of forest treatments on BAI within the context of hydrological drought in both upland and lowland topographic positions in a dry, ponderosa pine-dominated forest. Evaluation by topographic position was essential as ponderosa pine in lowlands was acclimated to reliable water table access, and upland ponderosa pine likely relied on access to underground springs which may be limited by drought, or on finite pockets of water trapped in weathered bedrock (Hubbert et al. 2001; Rose et al. 2003; Klos et al. 2018). These hydrologic differences are also likely to confound modeled BAI growth when applied across a landscape to evaluate silviculture treatment effects. We systematically evaluated environmental drivers that best explained ponderosa pine BAI including current year and temporally lagged drought index, running average drought index, and growing season length or cumulative heat sum with different base temperatures. We then systematically evaluated potential modifiers of tree response to the selected environmental drivers that best explained ponderosa pine BAI, including different measures of tree vigor, tree to tree competition, and prior response to disturbance to develop a robust model of ponderosa pine BAI in both topographic positions. We asked, how does drought affect BAI in non-treeline forests in different topographic positions (e.g., acclimated to different levels of water availability and reliability)? How do tree characteristics related to tree vigor, or neighborhood competition modify tree response to drought or hot drought? Do prior tree responses to disturbances aid in adapting current tree response to proximate disturbances?

With the same modeling approach, the effects of common forest treatments were statistically explored comparing ponderosa pine BAI response in untreated (no management, NM) vs. thinned (undercut and density reduction with increased tree spacing, HE) or prescribed fire (Rx), as well as treated stands varying by one additional treatment (e.g., HE vs. HE1Rx, or 1Rx vs. 2Rx) in lowlands. We asked, within dense stands

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[1]A *complacent* tree has low variation in annual ring width

unmanaged previously or decades (non-plantation), how do forest treatments such as prescribed fire (Rx), thinning (HE), and their combination affect BAI, and what is the duration of a change in BAI? Did the treatment confer resistance or resilience to drought? Lastly, do treatments implemented during hydrologic drought affect the trees' capacity to respond to the treatment? A better understanding of BAI response to concurrent disturbances, and how endogenous tree characteristics or tree competition modify response could help inform management decisions and the timing of their implementation.

2. METHODS

2.1. **Study Description.**

2.1.1. *Study area.* Allocation to ponderosa pine bole growth was investigated in a dry, pine-dominated forest in the Modoc Plateau and the East Cascades Ecoregions of south-central Oregon, U.S.A. The study area was in the upper Sycan River Watershed (HUC 6), in the in the headwaters of the Klamath Basin, on the divide between the Great Basin and the Klamath Basin. The study area is bounded by the coordinates: NW: 42°5244.96N, 121°1104.55W; NE: 42°5242.41N, 121°0636.44W; SE: 42°5233.62N, 121°0935.19W; SW: 42°5238.52N, 121°1404.46W (Fig. 1.) On-site annual precipitation is 47cm averaged over the last 20 years (hydrologic year, Oct 1 Sept 30), with 90% of the total falling between November through June (from modeled precipitation, PRISM, Daly et al. (1994); Fig. 2). Mean annual air temperature is 5.6°C. Soil type in the forested lowlands adjacent to Sycan Marsh is andesite-derived clayey loam. The most common soil type is Andyfan (60-64A), followed by Andyfan - Shakecreek series (66A-67A) (Bienz et al. 2020).

Historically, forested areas in the study area consisted of a ponderosa pine-dominated forest that averaged 12 trees per ha, with ~ 24% of the trees in clusters of more than 15 trees, and ~ 20% as isolated trees. Within-clump tree spacing averaged 6m on center, and the single-storied stands had small openings between clumps. The average tree diameter was > 68cm diameter at breast height (1.37m; DBH). The natural fire interval ranged from 3 to 37 yr, with a median of 11 yr over the past 400 years (Bienz et al. 2020). Currently, stands are dominated by ponderosa pine and secondarily by lodgepole pine (*Pinus contorta* Dougl. Ex. Loud). There are small inclusions of aspen (*Populus tremuloides* Michx.), juniper (*Juniperus occidentalis* Hook.), and Jeffrey pine (*Pinus Jeffreyi* Grev. & Balf.). Lodgepole pine is co-dominant in two of the lowland stands reported on here, one with no management (1LNM), and one with prescribed fire (L1Rx). There is no evidence of a stand-replacement fire in the last 200 years at this site (Bienz et al. 2020).

2.1.2. *Stand and tree selection.* We investigated tree responses in stands with no management (NM), undercut and even spaced harvest (HE, litter scattered and piled), prescribed burns (1Rx, 2Rx), and combinations of the two (Table 1). The objective of the HE treatment was to restore stands to historic conditions by reducing densities and shifting species composition to pine dominated stands. The average target basal area was approximately 16m^2/ha, but ranged from 0-38 m^2/ha across the units. The following stands were investigated, with the number of trees sampled for BAI analysis given in each: 1LNM (28); 2LNM (36); LHE (29); LHE2Rx (26); L1Rx (32); L2Rx (27); 1UNM (36); 2UNM (38); and 3UNM (33). Locations of stands are indicated in Fig. 1, and stand metrics are given in Grulke et al. (2020) and Table 1 below. In short, all mature black bark pine (furrowed dark brown to black bark, no plates present; Willits 1994) greater than 2.5m distance from another of the same were selected along a 20m wide transect,
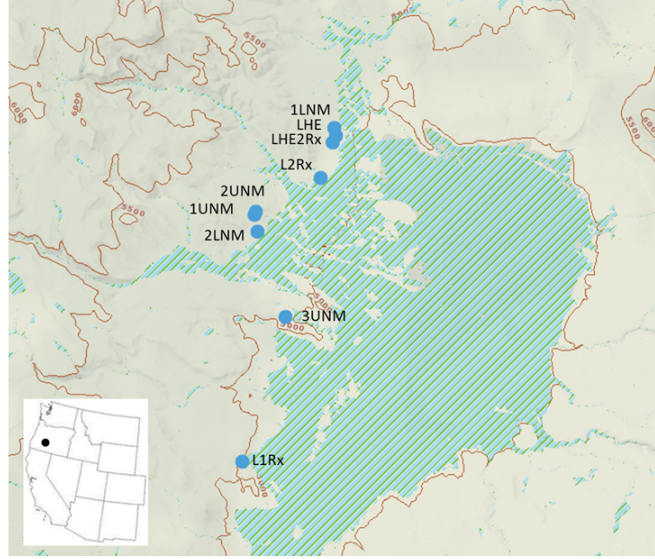
FIGURE 1. Site locations west of Sycan Marsh (blue hatched area) in south central Oregon. Upland stands with no management are denoted by UNM, with replicates 1, 2, and 3. Lowlands stands (L) include no management (NM, 2 replicates), undercut below and increased tree spacing (HE), one and two prescribed fires (1Rx, 2Rx).

with length determined by accumulating at least 30 trees in each stand. Mature black bark pine that were < 2.5m from another of the same were skipped. A starting point for transects in each stand was chosen as representative of the whole stand using Google Earth imagery. Some trees succumbed to the drought in south central Oregon (2013-2015) between transect establishment (2014) and this assessment (late 2016), reducing the number of cores available for analysis. In Grulke et al. (2020), patchy harvest (HP) stands were harvested in 2016. In this paper, basal area increment (BAI) prior to 2016 was analyzed, and these (to become) HP stands were treated as replicates of NM (cross referenced here as: LNM = 1LNM; LHP = 2LNM; UNM = 1UNM; 1UHP = 2UNM; 2UHP = 3UNM). Treatment dates and stand metrics are given in Table 1.

2.2. **Tree response metrics.**

2.2.1. *Basal area increment.* Carbon allocation to annual wood production was determined by measuring ring widths and calculating BAI. BAI was calculated from radial growth r_t in year t by

$$\text{(1)} \qquad \text{BAI}_t = \pi r_t^2 - \pi r_{t-1}^2.$$

Cores (0.635cm) were extracted with increment borers within 10cm of diameter at breast height (DBH, 1.37m), avoiding irregular bark or bole imperfections to tree center in mid- to late October, 2016. Not all trees bored yielded measurable cores due to rot or excessive resin. Cores were mounted on blocks and sanded to 400 grit. Annual ring widths

stand	n	AGE	DBH cm	BAI cm^2	PIPO TPH	Spp TPH	PIPO BA m^{2}ha^{-1}	Spp BA m^{2}ha^{-1}	CZD cm^{2}m^{-1}	RC	SDI	HE	1Rx	2Rx
UNM	91	87 ±4	26 ±2	16 ±9	117 ±64	450 ±188	13 ±6	22 ±1	36 ±2	362	192	-		-
LNM	64	91 ±4	27 ±2	12 ±2	134 ±41	1362 ±607	14 ±6	28 ±9	27 ±2	240	285	-		-
LHE	29	86 ±3	32 ±1	32 ±2	85 ±37	170 ±59	9 ±4	11 ±4	31 ±3	150	147	2005		-
LHE2Rx	26	85 ±4	36 ±2	35 ±4	94 ±16	156 ±29	11 ±1	20 ±9	18 ±1	283	179	2005	2006	2013
L1Rx	32	91 ±4	24 ±2	9 ±2	52 ±16	505 ±98	6 ±1	13 ±2	95 ±55	148	123	-	2008	
L2Rx	27	88 ±3	46 ±2	32 ±3	66 ±43	156 ±28	9 ±6	31 ±9	27 ±2	402	149	-	2006	2013

TABLE 1. Stand treatments, sample size, and mean $\pm$ 1 S.E. of tree age, diameter at breast height (DBH), basal area increment (BAI), number of trees per hectare (TPH) for ponderosa pine (PIPO) and all species (Spp); basal area (BA), competitive zone density (CZD, the average of DBH/distance of four neighboring mature black bark trees NE, SE, SW, and NW of the target tree to 20m distant to the focal tree). Individual tree resilience capacity (RC) and stand density index (SDI) is given post-treatment.

were measured to 0.001mm (Velmex, Inc., 2009; using program J2x, Voor Tech Consulting, 2008), and checked for missing rings (Yamaguchi 1991) based on cross-correlation with a regional chronology (Hagmann et al. 2019).

Cross dating accuracy was evaluated with COFECHA (version 6.06P; Holmes 1983; Grissino-Mayer 2000). Potential dating errors were identified by visual inspection, remeasuring, or re-collecting the core as necessary. For cores that did not intersect the pith, we estimated the number of rings to pith geometrically (Applequist 1958), projected for not more than 4 years or tree was re-sampled or omitted. Cores from 275 trees were successfully sampled.

2.3. **Environmental drivers.**

2.3.1. *On-site environmental data.* Daily precipitation was collected on-site from 1998 to present and was totaled monthly through the hydrologic year (10/1 to 9/30). Snow and sleet were melted and included in daily totals. The focus of our analysis was 1980-2015, and on-site data was insufficient for our analysis. We tested the relationship between local meteorological stations to test whether on-site data could be temporally extended. Monthly meteorological data was assembled from Chiloquin, Klamath Falls, and Lakeview, OR (65km, 88km, and 100km distant from Sycan Marsh). Among the 4 sites, the correlation was poor for both temperature and precipitation for overlapping time periods.

We used modeled meteorological data, PRISM (Parameter-elevation Regressions on Independent Slopes Model; Daly et al. 1994), for our analyses. PRISM data was extracted from a 4km^2 pixel (42.8751, -121.1555, 1601m) that included 1LNM, LHE, LHE2Rx, L2Rx; 2LNM, 1UNM, and 2UNM were contained on 42.8409, -121.2016, 1606m; and 3UNM and L2Rx were contained on another pixel, 42.7977, -121.1730, 1528m. There was little difference in the modeled monthly temperature and precipitation among these pixels. On-site precipitation was available for Sycan Preserve from 1998 through 2019. The correlation between on-site and PRISM annual summed precipitation was moderate ($\rho = 0.71$). Also, PRISM overestimated on-site temperature by 2.9°C. Daily PRISM data was used to determine the role of annual growing degree days, summed or counted in
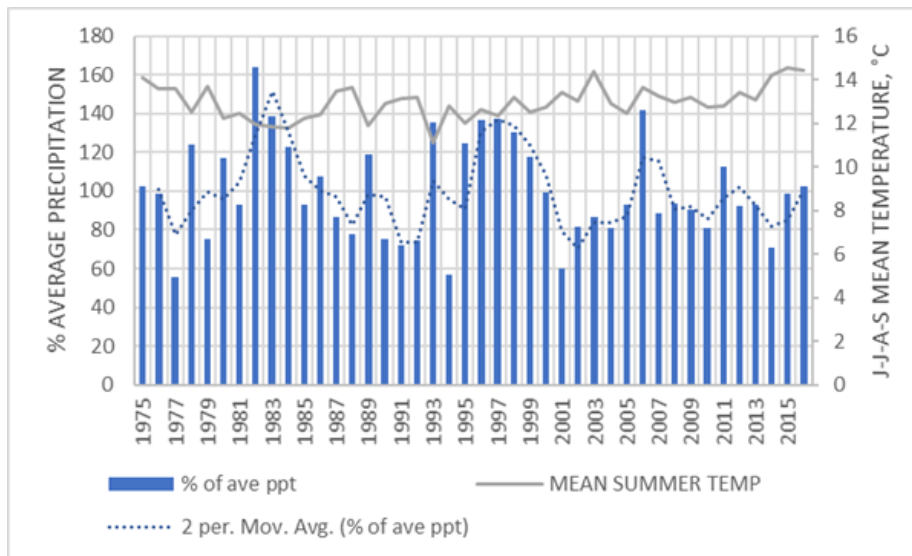
FIGURE 2. Annual % of average precipitation (bars), summertime (June, July, August, September) mean air temperature (grey line), and 2-yr moving average precipitation (dotted line). Data is from PRISM.

exceedance of either > 0°C or > 10°C, as well as monthly summed precipitation (Fig. 2). Potential evapotranspiration (PET) was calculated using Thornthwaite's (1948) approach, as the Penman-Monteith calculations are preferred in more moist environments (Stannard 1993; R. G. Allen et al. 1998). The drought index, SPEI (Vicente-Serrano et al. 2010) was expressed annually for the hydrologic year, 10/1 of the previous year through 9/30 of the current year (i.e., 12 months, h for hydrologic year: SPEI12h). Both temporal lags (1-, 2-, 3-, and 4-yr; SPEI12h_1, SPEI12h_2, SPEI12h_3, SPEI12h_4), and running averages (2-, 3-, and 4-yr) of SPEI12h were tested for inclusion in the predictive models of BAI. SPEI12h, the 2-yr running average of SPEI12h, the percent average precipitation (based on 1977 to 2016) and summertime average temperature (June, July, August, September) for the western edge of Sycan Marsh, south central Oregon are available at https://github.com/asherlevin/SYCANDATA.

We performed two checks on the effectiveness of SPEI12h as a primary environmental driver. First, we tested the correlation between SPEI12h and annual outflow from the Sycan River headwaters (million m^3 water; C. Bienz, unpubl. data) from 1980 to present. Second, we tested NDVI (Normalized Difference Vegetation Index) as a measure of vegetation response to meteorological conditions. Normalized Difference Vegetation Index (NDVI) is a measure of vegetation response to environmental and meteorological conditions, where NDVI = (NIR - RED)/(NIR + RED), NIR is near-infrared light, and RED is visible red light. NDVI was extracted from 2/18/2000 to 9/29/2020 from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS) aboard Terra and Aqua satellites. The MOD13Q1 product was used, which has a spatial resolution of 250m, is corrected for atmospheric and illumination effects, and is produced using 16 day composite periods. NDVI values during snowy and cloudy conditions which precluded observation

of the vegetation were removed, and the response was smoothed using the cloud computing platform Google Earth Engine (Gorelick et al. 2017). The number of pixels representing stands were 4, 5, 3, 3, 5, and 2 for LNM, UNM, LHE, L1Rx, L2Rx, and LHE2Rx, respectively. Values of NDVI were summed for the periods where the mean temperature averaged over a 2-wk period was > 0°C (or 10°C) based on PRISM-derived temperature, from mid-February (date when photoperiod is conducive to growth when not limited by temperature, Sloan 1991; change in date with latitude, Dougherty et al. 1994) to end of the growing season, as defined by mean temperature < 0°C (or 10°C), generally occurring by the end of November to mid-December (for 0°C) or mid to end of October (for 10°C) , similar to that used by Strachan et al. (2017).

2.3.2. *Biological Modifiers of Environmental Drivers.*

2.3.3. *Potential Tree Traits Affecting Response to Environmental Drivers.* Tree traits associated with vigor, lifetime patterns of BAI, and those suggesting resilience and recovery from prior disturbance were tested to determine whether they were significant modifiers of tree response to environmental drivers (listed in Appendix A). Resistance prior to treatments could not be reliably tested because occurrence of a disturbance could not necessarily be assigned if no response was observed. Three variables representing tree vigor were tested, (1) a measure of pre-existing rate of wood production: [barkless DBH] / [tree age at DBH] as an average rate of tree growth in 1980, the start of our analysis (DBH_ AGE80); (2) RANK, based on needle length and color, branchlet length and diameter, needle retention on the branch as well as within a needle age class, frequency of pathogens and insect attack, and whole tree phenology changes indicative of drought (Grulke et al. 2020); tree vigor was recorded as above-average (1), average (2), or low vigor (3) and averaged over 3 yrs of observation in the latter half of August (2014-2016); and (3) percent live crown retained (length of live crown from crown top to point of attachment of lowest live primary branch) divided by tree height ×100), as branch and needle retention is correlated to wood production (Sheppard et al. 1986).

Prior to forest treatments in 2005, tree response (accelerations and de-accelerations in BAI over a disturbance-relevant time period) to some disturbance (neighborhood tree loss, periods of drought, or favorable water status as per historical PRISM record) was apparent in approximately one third (LNM), one half (LHE, L1Rx, L2Rx), and three quarters (UNM, LHE2Rx) of the trees. Roughly 5% of the trees exhibited BAI responsiveness in each decade centering on 1960, 1970, 1990, and 2000. In the 1980s, 22% of the trees responded to a disturbance. Response in the 2000 decade coincided with modeled (PRISM) and measured water deficits (onsite precipitation and Sycan River watershed outflow). Increased BAI growth during unfavorable meteorological conditions was coded as resistant. Recovery was defined as increased BAI after disturbance.

2.3.4. *Potential Exogenous Effects on Tree Response to Environmental Drivers.* The importance of spatial configuration at multiple landscape scales has been assessed for ecological functions of large trees (Hatcher et al. 2017; Hessburg et al. 2015; Hessburg et al. 2019; Lehmkuhl et al. 2015; Lundquist et al. 2013). In each stand, measures of individual tree-level, forest structural attributes such as neighborhood tree density and basal area were assessed; they included variable-radius plots (VRP), resilience capacity (RC), competitive zone density (X4CZD), and number of trees in a cluster (NO.CLUST), described below. The VRP sampling scheme selects sample trees with probability proportional to basal area (BA; BA factor 10) determined at DBH (Avery et al. 2015; Husch et al. 2002). Since wood volume is proportional to a squared power of DBH, and large trees

usually occur less frequently than small trees, this approach greatly improves sampling efficiency and produces unbiased inventory estimates (Packard et al. 2007). For this metric, tree age and dominant height were used in preference to site index. For ponderosa pine, the estimated SDI_{MAX} for the study area is 1100 (Kimsey et al. 2019). RC is SDI for an individual tree, with a lower value reflecting lower tree resilience due to increased tree-to-tree competition from neighboring trees (Contreras et al. 2011; Vernon et al. 2018). Four measures of CZD (Shaw 2017) were tested: DBH / distance (m) to the nearest single neighboring live tree >10cm at DBH ((1) conspecific and (2) any tree species) within 20m; and the average of DBH / distance of the nearest single neighboring live tree > 10cm DBH within 4 pie-shaped quadrats (NE, SE, SW, NW), radius 20m, of all conspecific (3, X4CZD) or any tree species (4). NO.CLUST was the number of trees in a cluster around the target tree (a count of the number of trees and stumps projected to be > 10cm at DBH (determined with stand-specific regressions) within radius 6.0m.

2.3.5. *Approach to statistical analyses.* Generalized additive mixed models (GAMM; Wood 2004; Wood 2011) fit to upland and lowland stands were used to explore relationships among environmental drivers and biological modifiers of BAI response. After selecting variables based on the LNM and UNM unmanaged stands (described in Appendix A), we used the resulting model to compare treatments.

3. RESULTS

3.1. **Hydrological and biological tests of PRISM-parameterization effectiveness.** Watershed outflow from the Sycan Marsh was used an independent test of PRISM-parameterization of SPEI12h. There was a high correlation between total watershed outflow and current year SPEI12h ($\rho = 0.94$). This correlation supported our use of modeled meteorological data to calculate local drought index for our analysis of BAI. The correlation between outflow and 1-yr lagged SPEI12h was $\rho = 0.34$. The correlation between SPEI12h and the 1-yr lagged SPEI12h was $\rho = 0.20$.

Summed site-specific NDVI over the growing season (variable number of 2-wk points depending on growing season length) and August average (2, 2-wk points) were a second independent test of PRISM-parameterization of SPEI12h, as NDVI reflects the inferred productivity of the forest and accompanying vegetation responses to favorable and unfavorable environmental conditions (Wang et al. 2004; Pompa-García et al. 2021). The correlation coefficients between growing season sum and August summed NDVI to SPEI12h for the nine stands ranged from -0.17 to -0.36, and so could not be used to verify PRISM-parameterized SPEI12h with high stand-to-stand differences in stand density and patchy understory cover.

3.2. **Model selection.** We developed a generic generalized additive mixed model (GAMM) to describe the response logarithm of BAI using environmental drivers and tree-level covariates. Letting S_1, S_2 denote two distinct stands, and letting $j(i)$ be the stand of tree i,

we considered models of the following form:

$$
\begin{aligned}
\log(\mathrm{BAI}_{i,t}) = {}& \beta_{T,1} x_{i,1} + \cdots + \beta_{T,n_1} x_{i,n_1} && \text{tree-level} \\
& + \beta_0 + \beta_{S_2} I_{\{j(i)=S_2\}} && \text{stand-level} \\
& + s_1(t) I_{\{j(i)=S_1\}} + s_2(t) I_{\{j(2)=S_2\}} && \text{stand-level smooths } t \\
(2)\qquad & + \beta_{E,1} y_{t,1} + \cdots + \beta_{E,n_2} y_{t,n_2} && \text{time-varying var.} \\
& + \beta_{E,1,S_2} y_{t,1} I_{\{j(i)=S_2\}} + \cdots + \beta_{E,2,S_2} y_{t,n_2} I_{\{j(i)=S_2\}} && \text{interactions} \\
& + B_{0,i} + B_{1,i} t && \text{random eff. for tree} \\
& + \varepsilon_{i,t} && \text{random error}
\end{aligned}
$$

Here, $I_{j(i)=S_2} = 1$ if tree i is in stand S_2, and takes the value 0 otherwise. The random variables $\{B_{k,i}\}$ are i.i.d. centered Gaussians. The random effect for tree i is $B_{0,i} + B_{1,i} t$. The variables $x_{i,k}$ are measurements on trees, and the variables $y_{t,k}$ are environmental drivers.

We evaluated the role of all like-variables in predicting tree BAI in lowland and upland stands. Details on the variable selection process are described in Appendix A. Of the seven drought index metrics tested (SPEI12h and its lag by up to 3 prior years, and 2-, 3-, and 4-yr running averages), we retained SPEI12h and SPEI12h_1, the one-year lag of SPEI12h. Of the four growing degree day metrics (two temperature thresholds, summed and counted), the count of growing degree days $> 10°C$ provided the largest marginal decrease in AIC. Increasing values of RANK was assigned to decreasing crown vigor (Grulke et al. 2020), and was associated with a decrease in predicted BAI growth. An initial higher rate of bole growth (DBH_AGE80) had a stimulatory effect on predicted BAI. Of the seven metrics of tree-to-tree competition, X4CZD (DBH/distance of four conspecific neighboring trees) was selected (but was marginally significant in only one paired treatment comparison, L1Rx vs. L2Rx). See Appendix A for details of variable selection. Of the competition metrics tested here, only VRP, stand density from the perspective of the target tree, was correlated to whole stand metrics (with TPH, $\rho = 0.767$; with BA/ha, $\rho = 0.854$) but was not a significant explanatory of BAI. All other comparisons had a $\rho < 0.5$. None of the BAI lifetime growth patterns, pre-treatment responsiveness to (any) disturbance, pre- to post-disturbance changes in BAI growth rates, or metrics suggesting prior capacity to respond to disturbance significantly affected BAI and were not included in the model.

The final model obtained was

$$
\begin{aligned}
\log(\mathrm{BAI}_{i,t}) = {}& \beta_{\mathrm{RANK}} \mathrm{RANK}_i + \beta_{\mathrm{DBHAGE}} \mathrm{DBH\_AGE80}_i + \beta_{\mathrm{X4CZD}} \mathrm{X4CZD}_i \\
& + \beta_0 + \beta_{S_2} I_{\{j(i)=S_2\}} \\
& + s_1(t) I_{\{j(i)=S_1\}} + s_2(t) I_{\{j(2)=S_2\}} \\
(3)\qquad & + \beta_{\mathrm{SPEI12h}} \mathrm{SPEI12h}_t + \beta_{\mathrm{SPEI12h\_1}} \mathrm{SPEI12h}_{t-1} + \beta_{\mathrm{CGDD10}} \mathrm{CGDD\_10}_t \\
& + \beta_{\mathrm{SPEI12h},S_2} \mathrm{SPEI12h}_t I_{\{j(i)=S_2\}} + \beta_{\mathrm{SPEI12h\_1},S_2} \mathrm{SPEI12h}_{t-1} I_{\{j(i)=S_2\}} \\
& + B_{0,i} + B_{1,i} t \\
& + \varepsilon_{i,t}
\end{aligned}
$$

The fitted model for LNM/UNM is summarized in Table 2. Effect plots are shown in Fig. 3. In each, the predicted log(BAI) is plotted against each variable, setting the remaining variables at their mean values.

	Value	Std.Error	DF	t-value	p-value
β_0	2.0677	0.1871	6047	11.05	0.00
$\beta_{SPEI12h}$	0.0018	0.0007	6047	2.47	0.01
β_{UP}	0.1235	0.0746	168	1.65	0.10
$\beta_{SPEI12h\_1}$	0.0051	0.0006	6047	8.11	0.00
β_{DBH_AGE80}	2.8464	0.2240	168	12.71	0.00
β_{RANK}	-0.1697	0.0608	168	-2.79	0.01
β_{X4CZD}	0.0031	0.0111	168	0.28	0.78
β_{CGDD_10}	-0.0028	0.0006	6047	-5.14	0.00
$\beta_{SPEI12h,UP}$	-0.0003	0.0008	6047	-0.37	0.71
$\beta_{SPEI12h\_1,UP}$	-0.0014	0.0008	6047	-1.83	0.07

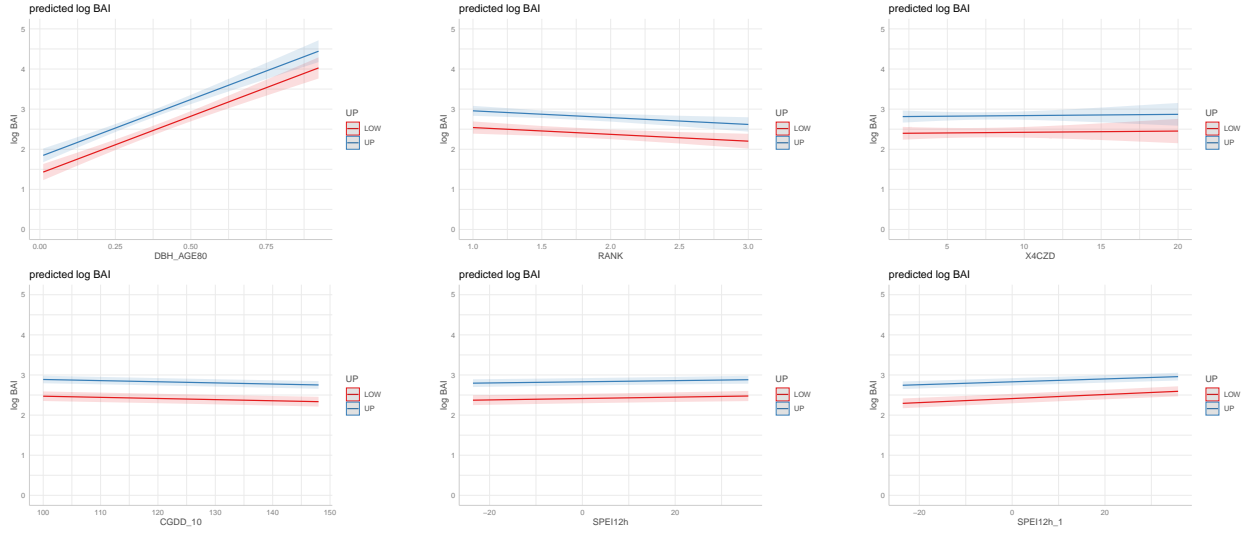TABLE 2. Fitted no-treatment GAMM model for log(BAI) in unmanaged upland (UNM) and lowland (LNM) topographic positions.

FIGURE 3. Effect plots for covariates for unmanaged upland (UNM) and lowland (LNM) stands. Predicted log(BAI) is shown when setting all other variables to their average values.

3.3. **BAI variability within a stand.** We analyzed BAI from 1980 to 2015. Within-stand variability in tree BAI was high in all stands, but the range was similar for most (log(BAI), 0 to 4, but see 2LNM (1-4) as shown in Fig. 4). In model (3) fit to the upland and lowland unmanaged stands (so S_1 = LNM and S_2 = UNM), the standard deviation of the tree-effect $B_{0,i}$ was estimated to be 0.46, while the residual standard deviation of the error term $\varepsilon_{i,t}$ was estimated at 0.41. Thus, tree-to-tree variability was similar in size to the residual error in these non-treeline stands. Three of the stands (1LNM, 1UNM, 2UNM) had at least one tree with lower-than-average BAI. Trees in 3UNM had a similar decline in BAI to the 2001-2004 drought as in the other stands, but two groups of trees were apparent post-drought, one with higher bole growth rate than the other (average log(BAI), 3.8 vs. 2.5; Fig. 4).
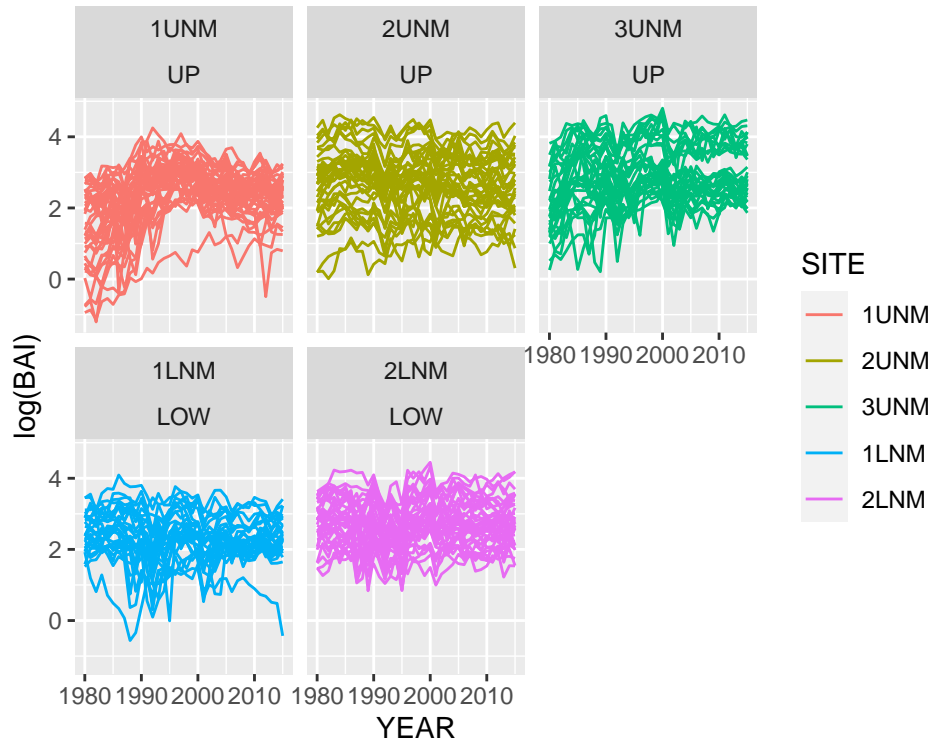
FIGURE 4. Traces of log(BAI) trees in lowland and upland no management stands (LNM, UNM).

3.4. **Paired comparisons of forest treatments.** The BAI of forest treatments were compared where only one aspect of the treatment differed. The paired comparisons considered were: (LNM, UNM), (LNM, LHE), (LNM, 1Rx), (L1Rx, L2Rx), (L2Rx, LHE2Rx), and (LHE, LHE2Rx), as upland stands had not been treated at the time of our analysis.

Over the 35 years of analysis in this study, the predicted BAI response of all trees exhibited some accelerations of BAI growth, as well as resistance, recovery, and resilience to water deficits as well as subsequent treatments. At the beginning of our analysis period (1980), trees in UNM stands had much lower predicted BAI than that in LNM stands, likely due to extremely low precipitation in 1977 and 1979 prior to our analysis period (58%, and 79% of average precipitation, -22cm and -14.1cm annual water deficit, respectively; Fig. 2). The analysis was not extended earlier to capture this due to a change in accuracy of PRISM before 1980. Upland trees (UNM) showed recovery from 1 yr of extreme drought (1977) prior to our period of analysis, and resistance to subsequent multi-year droughts (1987, 1989-1992, 1994; 2001-2004, 2013-2015). Lowland trees (LNM) were resistant to multiyear droughts, except for the mid 1990's when water deficits were < -12cm in 4 out of 5 years, and of those, < -22cm in 1994 (Fig. 5 and Fig. 2). Trees in both topographic positions showed resistance to the 2013-2015 hydrological drought with measured physiological tree drought stress (Grulke et al. 2020).

Model (3) was used in each treatment comparison with the variables selected using the LNM and UNM stands. The effect plots are shown in Fig. 3; each plot shows the
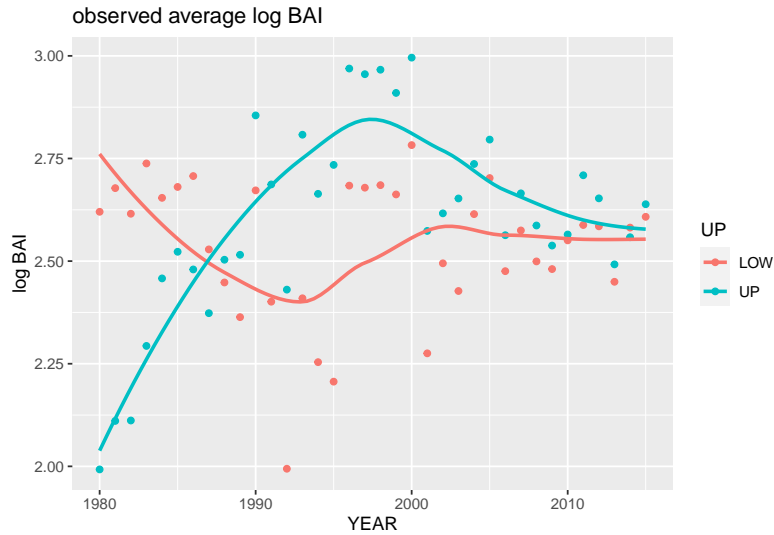
FIGURE 5. Observed average log(BAI) for upland (UNM) and lowland (LNM), no management stands with smooth spline.

Stands		index		interaction	
S_1	S_2	β_{SPEI12h}	$\beta_{\text{SPEI12h\_1}}$	$\beta_{\text{SPEI12h},S_1}$	$\beta_{\text{SPEI12h\_1},S_2}$
LNM	UNM	0.01	0.00	0.71	0.07
LNM	LHE	0.00	0.00	0.00	0.47
LNM	L1Rx	0.00	0.00	0.09	0.20
L1Rx	L2Rx	0.04	0.00	0.00	0.57
L2Rx	LHE2Rx	0.00	0.00	0.03	0.16
LHE	LHE2Rx	0.00	0.00	0.48	0.69

TABLE 3. p-values for test of $\beta = 0$ for SPEI12h and its interactions. See also Fig. 3 for effect sizes.

predicted log(BAI) as a function of a single variable, assuming that all other variables are set to their mean values.

In each treatment comparison, the marginal effect of YEAR, setting all other variables to their mean values, is shown in Fig. 6(b) - 6(f). This allowed us to estimate the impact of treatments over time, controlling for all other variables included in the model, in particular water balance (SPEI12h, SPEI12h_1, current and 1 yr lagged) and variability in tree characteristics (e.g., tree vigor, tree-to-tree competition).

(a) LNM vs. UNM   LNM and UNM, SPEI12h

(b) LNM vs. LHE   LNM and LHE, SPEI12h

(c) LNM vs. L1Rx   LNM and L1Rx, SPEI12h

(d) L1Rx vs. L2Rx   L1Rx and L2Rx, SPEI12h

(e) L2Rx vs. LHE2Rx   L2Rx and LHE2Rx, SPEI12h

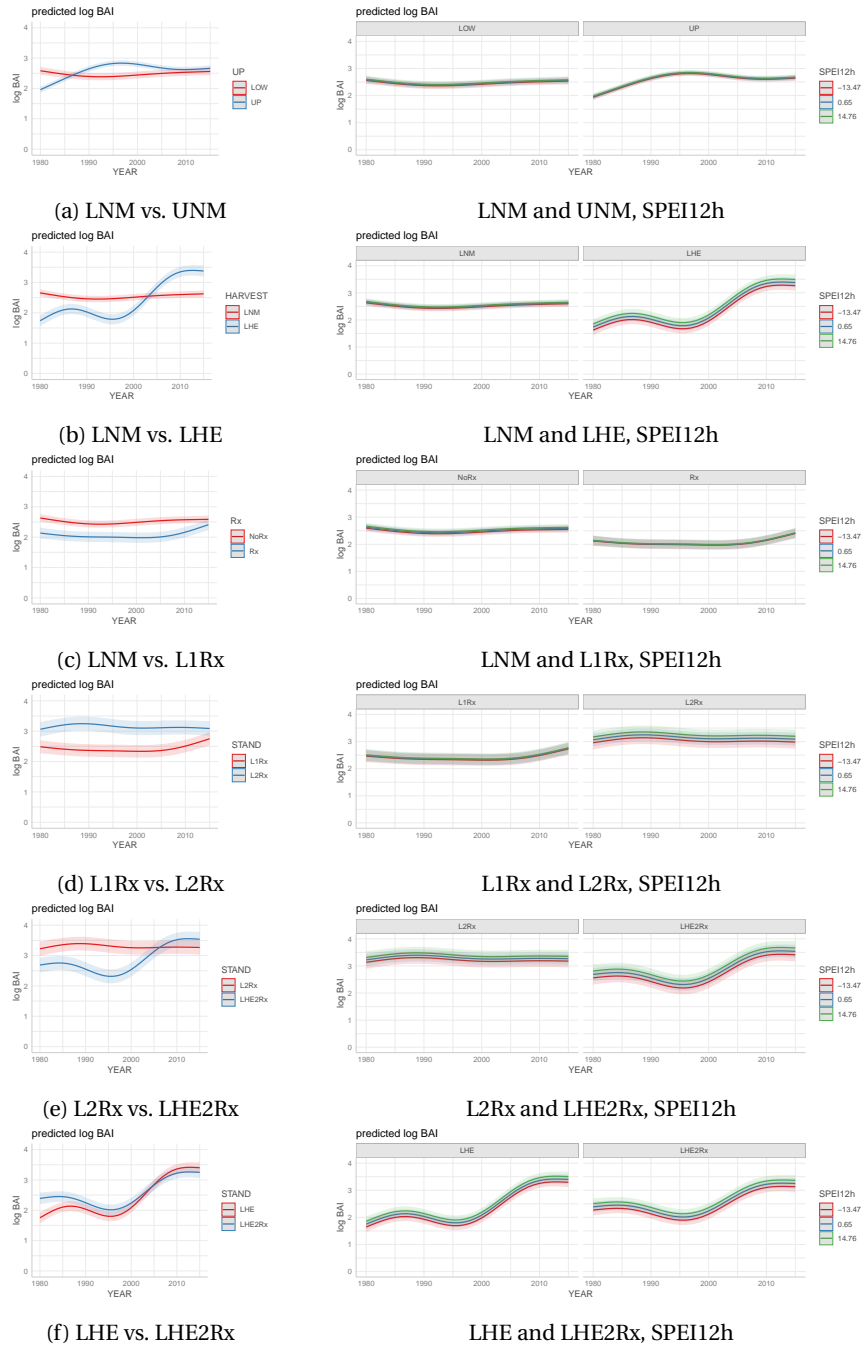(f) LHE vs. LHE2Rx   LHE and LHE2Rx, SPEI12h

FIGURE 6. Paired comparisons between predicted BAI of (a) lowland unmanaged (LNM) and upland unmanaged (UNM) trees; (b) LNM and lowland even harvest trees (LHE); (c) LNM and lowland one prescribed fire trees (L1Rx) (d) lowland one and two prescribed fire trees (L!Rx, L2Rx) trees; (e) L2Rx and LHE2Rx; and (f) LHE and LHE2Rx trees.

The harvest treatment in 2005 had a clear impact on BAI. While the smoothing functions in GAMM responses (Fig. 6(b)) precluded precise temporal interpretations of the observed responses, a piece-wise linear model with a jump discontinuity at 2006 allowed for more precise estimation of the impact of harvest treatment. Specifically, we fit the following model:

$$
\begin{aligned}
\log(\mathrm{BAI}_{i,t}) = {} & \beta_{\mathrm{RANK}}\mathrm{RANK}_i + \beta_{\mathrm{DBH\_AGE}}\mathrm{DBH\_AGE80}_i + \beta_{\mathrm{CZD}}\mathrm{X4CZD}_i \\
& + \beta_0 + \beta_1 t + \beta_H I_{\{j(i)=\mathrm{HVST}\}} + \beta_{H,t}\, t I_{\{j(i)=\mathrm{HVST}\}} \\
& + \beta_{J,t} I_{t>2005}(t-2005) \\
& + \beta_{J,H} I_{t>2005} I_{\{j(i)=\mathrm{HVST}\}} + \beta_{J,H,t} I_{t>2005}(t-2005) I_{\{j(i)=\mathrm{HVST}\}} \\
& + \beta_{\mathrm{SPEI12h}}\mathrm{SPEI12h}_t + \beta_{\mathrm{SPEI12h\_1}}\mathrm{SPEI12h}_{t-1} + \beta_{\mathrm{CGDD\_10}}\mathrm{CGDD\_10}_t \\
& + \beta_{\mathrm{SPEI12h},S_2}\mathrm{SPEI12h}_t I_{\{j(i)=S_2\}} + \beta_{\mathrm{SPEI12h\_1},S_2}\mathrm{SPEI12h}_{t-1} I_{\{j(i)=S_2\}} \\
& + B_{0,i} + \beta_{1,i} t \\
& + \varepsilon_{i,t}
\end{aligned}
$$

(4)

The parameter $\beta_{J,H}$ is the size of the jump. The slope of t was allowed to change in both stands. The estimated value $\beta_{J,H}$ is 1.11 with a standard error 0.054; thus, the estimate is significantly different from 0 and the effect size is large. Fig. 7 (left) shows the predicted response in LHE as a function of time, setting all other variables to their mean values, and for high, average, and low SPEI12h.
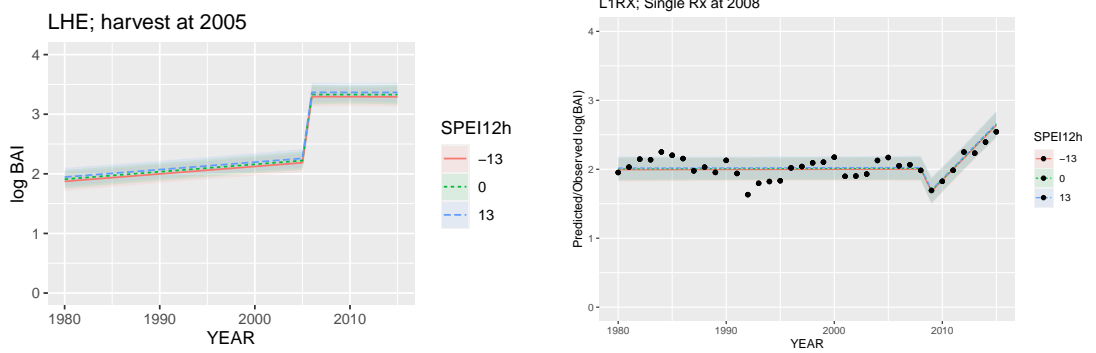

FIGURE 7. Piecewise linear models. Left: Predicted log(BAI) at LHE to show response to treatment without smoothing. Right: log(BAI) for piecewise linear model (lines). The dots represent the **observed** average log(BAI) in L1Rx. In both graphs SPEI12h has average value 0, and standard deviation ∼ 13.

Trees in LHE, harvested in 2005, initially had lower bole wood production than those in LNM. The fitted model predicted that post-treatment, trees will respond positively at all levels of water availability (as captured by SPEI12h) (Fig. 6(b) for the smooth model; Fig. 7 for the piecewise linear model). In particular, note that the predicted responses conditioned on the value SPEI12h equal to one standard deviation above or below average do not change much.

Similar to that of LHE, trees in L1Rx also had lower initial wood production than those in LNM. Post-treatment (after 2008), the model predicted accelerated bole growth in L1Rx (Fig. 6(c)). The predicted effect of water deficits were also small compared to the

treatment effect (right-hand plate, Fig. 6(c)). Trees in L1Rx were less productive than that of LNM, but by the end of the analysis period, there was no difference in estimated growth rate between the trees in the two stands. As with the harvest treatment, we also considered a piecewise linear model with a discontinuity at 2009 (the year after the prescribed fire) for L1Rx. A plot of the predicted log(BAI), holding all other variables fixed at their mean values and for low, average, and high SPEI12h is shown in Fig. 7 (right); also shown is the observed average log(BAI) in L1Rx. Note the jump is negative at 2009; this may represent immediate decrease in wood production after fire (heat shock on cambium?), although this may be random fluctuation. Post-Rx, there is continued increase in wood production through two periods of drought (the observed log(BAI) in Fig. 7). The model also predicted a small effect of SPEI12h both pre and post Rx.

We estimated little response to prescribed fire in L2Rx (Fig. 6(d)), suggesting resistance to treatment. There may be several reasons for this. One may be that trees in L2Rx were larger, DBH was already increasing at a maximum rate, and thus was resistant to drought or treatment. Another possibility is that the implemented prescribed fire itself differed from others (e.g., lower intensity). The predicted increase in BAI due to SPEI12h was slightly larger in L2Rx than in L1Rx (Fig. 8). Bole scorch height was lower in L1Rx than in L2Rx (2.0m vs. 3.6m, respectively; Grulke, unpublished data), and the percent circumference burned was similar (83% vs. 87%, respectively). L1Rx had the highest tree-to-tree competition (X4CZD) (Table 1) and L2Rx had the greatest stand basal area (all species) among the treated stands. Tree-to-tree competition was a significant covariate only in the L1Rx-L2Rx comparison, with depressive effects on BAI. In L2Rx, individual trees had higher DBH, many of the trees in this treatment had resinous or checked centers, and a lower number of trees were evaluated. L1Rx trees were loosely, but consistently clumped throughout the stand. L2Rx trees grew in stringers of clumped trees, interspersed with dry, sparse meadow rich in forbs on the edge of the Sycan Marsh.
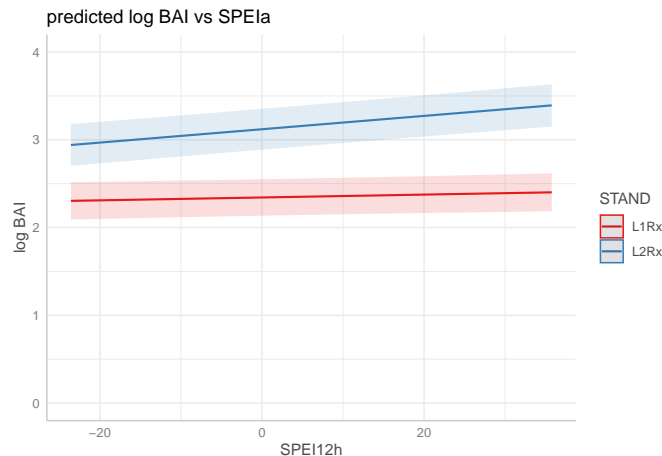

FIGURE 8. Interaction of SPEI12h with stand in L1Rx vs. L2Rx comparison. The coefficients of SPEI12h were significantly different at the two sites; L2Rx was more responsive to SPEI12h.
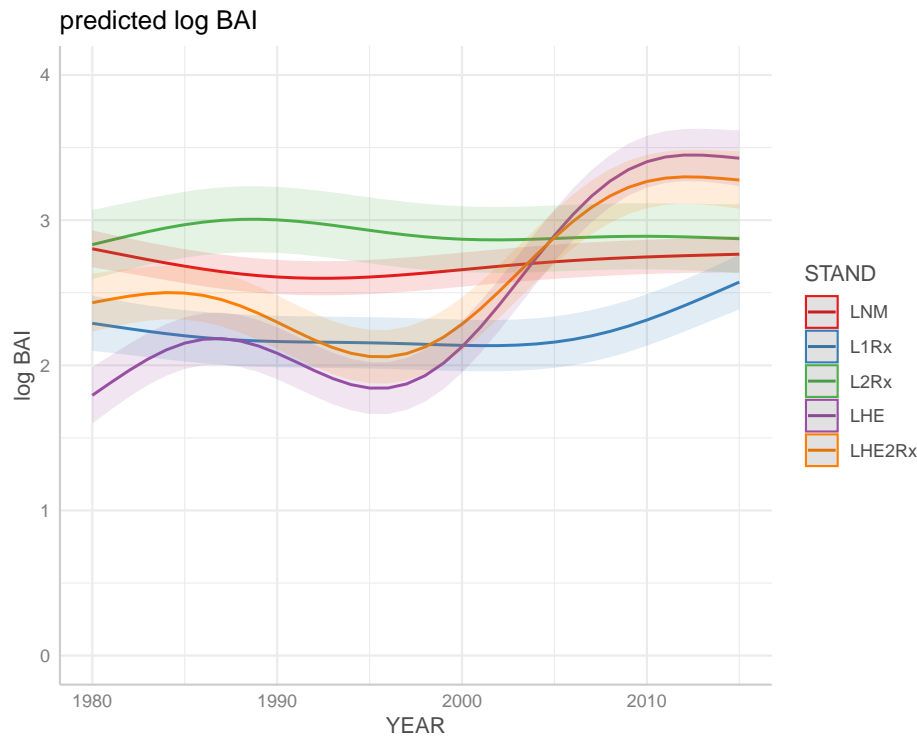
predicted log BAI

FIGURE 9. Predicted values of BAI for all lowland stands.

Trees in the stand that was to become LHE2Rx were less productive pre-treatment than those in L2Rx. Post harvest, there was no difference between the two treatments (Fig. 6(e)). In the comparison of pre-treatment trees in LHE and LHE2Rx, BAI was similar. The model showed a treatment effect of HE in both stands, but there was no difference between predicted BAI of trees in L2Rx and LHE2Rx post 2005, and no difference between predicted BAI of trees in LHE and LHE2Rx post 1988 (right plate, Fig. 6(e)). Bole scorch height and percent bole circumference scorched suggested that L2Rx was more severe (3.6m, 90%, respectively) than that in LHE2Rx (2.5m, 47%, respectively).

An additional model was fit to concurrently compare all treatment stands. Fig. 9 shows predicted BAI when all covariates are set to their mean values; estimated coefficients are showin in Table 4. HE treatment increased predicted BAI, and there was little if any effect of 2Rx on predicted BAI after HE. The predicted BAI of trees in L1Rx prior to treatment was among the lowest of the stands. In this model, tree-to-tree competition was not a significant covariate. Except in L1Rx, the interaction term with SPEI12h is significant, with a positive coefficient. Thus, with the exception of L1Rx, treatment enhanced response to water availability. Compare the dependence on SPEI12h in L1Rx and L2Rx in the right-hand plate in Fig. 6(d), and also Fig. 8.

4. DISCUSSION

We evaluated the relative roles of environmental drivers (drought index, lagged drought index, running average of drought index, and sum or count of growing degree days),

	Value	Std.Error	DF	t-value	p-value
β_0	2.6886	0.1806	6284	14.89	0.00
β_{L1Rx}	-0.4607	0.1027	172	-4.49	0.00
β_{L2Rx}	0.2226	0.1361	172	1.64	0.10
β_{LHE}	-0.2363	0.1077	172	-2.19	0.03
β_{LHE2Rx}	-0.0915	0.1089	172	-0.84	0.40
$\beta_{SPEI12h}$	0.0022	0.0006	6284	3.54	0.00
$\beta_{SPEI12h\_1}$	0.0051	0.0006	6284	9.26	0.00
β_{CGDD_10}	-0.0018	0.0005	6284	-3.78	0.00
β_{X4CZD}	-0.0134	0.0110	172	-1.22	0.23
β_{RANK}	-0.2517	0.0634	172	-3.97	0.00
β_{DBH_AGE80}	1.5892	0.1735	172	9.16	0.00
$\beta_{L1Rx,SPEI12h}$	-0.0017	0.0010	6284	-1.65	0.10
$\beta_{L2Rx,SPEI12h}$	0.0043	0.0011	6284	3.96	0.00
$\beta_{LHE,SPEI12h}$	0.0061	0.0010	6284	5.86	0.00
$\beta_{LHE2Rx,SPEI12h}$	0.0071	0.0011	6284	6.44	0.00
$\beta_{L1Rx,SPEI12h\_1}$	-0.0012	0.0010	6284	-1.24	0.21
$\beta_{L2Rx,SPEI12h\_1}$	-0.0005	0.0010	6284	-0.52	0.60
$\beta_{LHE,SPEI12h\_1}$	0.0007	0.0010	6284	0.70	0.48
$\beta_{LHE2Rx,SPEI12h\_1}$	0.0012	0.0010	6284	1.16	0.25

TABLE 4. Estimated coefficients of the GAMM for All lowlands combined.

and tree vigor and competition characteristics that may modify tree response to the selected environmental effects. We focused on factors that might improve or depress bole wood production, BAI, with the idea that more vigorous trees may ultimately be more resistant, resilient, and or recover from disturbance, whether that disturbance was drought, hot drought, or the forest treatments themselves. The annual drought index (SPEI12h) calculated over the hydrological year for our site was highly correlated to the annual water basin river outflow, supporting relevancy of modeled meteorological parameterization for this site. However, neither summed NDVI over the growing season or over just August was significantly correlated to current year SPEI12h, likely due to uneven within and between stand tree density and understory cover in these dry, pine-dominated forests.

The use of GAMMs to analyze and compare tree response (BAI) in paired treatments differing by topographic position, or within a topographic position, differing in only one treatment appeared to be a robust means to evaluate the relative roles of environment, crown and bole vigor, and tree-to-tree competition, as was also demonstrated by Johnston et al. (2019) for the effects of burn severity on BAI. As sustaining resilient forest ecosystems are a top priority of land managers, federal and state alike (*Strategic Plan* 2021), the models developed here provide a quantitative demonstration of tree resistance or resilience to, or recovery from disturbance, where the disturbances included hydrologic drought, growing season length, and/or common forest treatments: even harvest, prescribed fire, and their combinations.

Upland ponderosa pine appeared to respond deleteriously to a single, extreme drought year, suggesting a finite resource replenished from precipitation inputs. Lowland ponderosa pine acclimated to accessing a reliable water table were resistant to single drought years, but deleteriously affected by multi-year droughts suggesting prolonged drought effects on depth to water table. Current year and prior year water deficits were persistent, significant explanatories of BAI, as was also reported by Dannenberg et al. (2020). However the effect size of SPEI12h was small to moderate. Fluctuations in predicted BAI when fixing the value of SPEI12h and growing season in unmanaged stands (Fig. 6) and in treatment stands over pre-treatment years suggest the importance of other variables not included in the model for BAI response, likely soil available water content, its location relative to the root mass, and soil temperature (critical for root cell absorption of water; Day et al. 1991). After multiple years of above average precipitation, there was some evidence of decreased BAI in lowland trees adjacent to Sycan Marsh. We suggest this may be due to waterlogging, reducing fine root function and or increasing root mortality (Repo et al. 2020). In all paired treatment comparisons, greater heat load, here the count of days when mean temperature > 10°C (CGDD_10), decreased BAI.

Trees responded shortly (1-3 years) after treatment, and thus analysis of BAI could provide an early evaluation of treatment effectiveness in improving wood production of trees remaining on site. Camarero et al. (2018) suggest that after the physiological challenge of drought, declining and non-declining trees may be identifiable. In the even harvest treatment, treatment effect persisted for 10 yrs, and showed resistance to an extreme multi-year drought. In the single prescribed fire treatment, BAI significantly increased 3 yrs after treatment, and showed resistance to the same drought for at least the following 4 years. Hood et al. (2016) demonstrated treatment persistence for up to 12 yrs in reduced pine mortality to bark beetle. Old growth ponderosa pine exhibited recovery after the extreme 2002 drought in thinned and thinned and burned treatments (Kolb et al. 2007).

Using prior field data on ponderosa pine in southern California (Grulke et al. 2008), not accounting for growing degree days, a single year of < 80% of average precipitation induced moderate physiological drought stress (applying Levitt (1980) criteria), and a single year of < 60% of average precipitation induced severe physiological drought stress (both years were preceded by above-average precipitation years). Percent of average precipitation was presented here with the idea that trees are acclimated to average, on-site water availability and can tolerate low precipitation years up to some threshold. It is possible that the threshold was reached for upland trees but not lowland trees, and/or that lowland trees were buffered from single years of severe water deficits from proximity to the water table underlying the Sycan Marsh. Considering the level of predictive capability of the drought index, it is clear that a better understanding of water availability in uplands is needed to predict wood production.

In this study, the <80% and < 60% of average precipitation equated to approximately < -10cm and < -20cm annual water deficit, respectively. If these values of percent of average precipitation were to be applied to this study, 1979, 1988, 1990-1992, and 2014 would meet the criteria for moderate ponderosa pine drought stress, and 1977, 1994, and 2001 for severe tree drought stress (Fig. 2; Appendix A). At this site, reduced needle elongation and very low needle turgor (< 0.04 MPa) were recorded in August 2014, 2015 and 2016 (Grulke et al. 2020), averaging an -8.2cm water deficit. This provides a quantitative, multiple year 'tipping point' for deleterious tree water balance for this site,

extending that suggested by Huang et al. (2015). This study may contribute to developing a simple non-mechanistic metric for linking hydrological drought, here suggested by water deficit (SPEI12h), to physiological tree drought stress in ponderosa pine, deleterious enough to reduce wood production. However, the role of tree capacity for and speed of adaptation to drought (e.g., rapid reduction in leaf area, branch and branchlet excision, physiological upregulation of osmoregulation, etc.) should be considered in future analyses (Barbeta et al. 2013).

Prior tree responsiveness to disturbance was not predictive of tree response to more recent drought or forest treatment in the 275 trees assessed in this study, but see DeSoto et al. (2020). Crown vigor was a significant accelerator of predicted BAI response in all paired treatment comparisons. Low crown vigor (high value for RANK indicated lower vigor) had negative, significant effects on predicted BAI. At this site, crown vigor can be reliably assessed (low vigor, 77%, not-low vigor, 93% accuracy) using 4-band imagery (Schrader-Patton et al. 2021). In declining Scots pine (*Pinus sylvestrus L.*), resiliency to drought was also lower. In our study, the initial rate of bole growth (DBH / AGE in 1980) had large positive, significant and persistent effects on predicted BAI. Indeed, this variable had the largest effect of any variable considered (Fig. 3): vigorously growing pine were more resilient after disturbance, here drought and forest treatment. Prior year ring width growth alone was a significant explanatory in current year Scots pine bole growth (Ivanova et al. 2021). When stands are harvested, and when there is a choice between comparable trees, leaving the more vigorous trees, here suggested by crown vigor and rate of bole growth, may further improve effects on stand wood production above stand density reduction alone (example given in Grulke et al. (2020)).

Within the context of multiple explanatories, tree-to-tree competition had a borderline significant effect ($p = 0.05$) on predicted BAI only in the paired comparison of L1Rx and L2Rx. The effect size was small (Fig. 3). L1Rx had loose clusters of smaller trees, and tree to tree competition (X4CZD) was higher. L2Rx trees had a patchy distribution of larger trees with lower CZD, with the same order of magnitude as the other stands despite patchy distribution. That tree-to-tree competition was not a significant explanatory in most of the paired comparisons is not in sync with the many reported effects of greater stand density decreasing ponderosa pine growth (Skov et al. 2005), however SDI of these stands was low (123-432) relative to estimated SDI_{MAX} (Kimsey et al. 2019). Ponderosa pine in Arizona, U.S.A. reliant on deep soil water, exhibited a similar seasonal water use pattern regardless of stand density (Kerhoulas et al. 2013). Trees in close proximity to one another increases insect attack rates (Fettig et al. 2019), where a smaller diameter tree in close proximity may be more likely to be attacked than a large, distant tree (Mitchell et al. 1991). Braun (1998) found that increased spacing between trees reduced bark beetle attack specifically due to spacing, but did not increase tree vigor. Tightly clustered conspecific trees may also reduce available water, nutrient and light resources, as well as promote fire contagion. In these dry ponderosa pine forests, leaving patches or clusters of trees may not be conducive for resiliency to disturbance (fire, insects, drought).

Forest managers employ a number of metrics to guide thinning. An example is the upper management zone (UMZ; Cochran 1994) defined as the maximum basal area considering site conditions, likelihood of bark beetle attack (Fettig et al. 2007), and the estimated level of fire risk after a specific time period from shrub re-growth and tree recruitment. Thinning is performed with a number of considerations, including the degree of tree patchiness and proximity to relatively open areas with greater forage cover

(important for ungulate cover), avian nesting, microtine foraging, and public prefer-
ences. Reliant species also may require different aged trees, patch size, or patch density.
Without these important considerations, our analysis suggests vigorous trees respond
effectively to thinning treatments with more even spacing of retained mature trees and
also to a single prescribed fire in dry pine forests. These treatments improved tree resis-
tance or resilience to hydrologic drought.

5. Conclusions

A current year and 1-yr lagged drought index were significant environmental drivers
of BAI, although with modest effect size. A count of the number of growing degree
days exceeding 10°C was also a significant environmental driver of BAI. Tree vigor at-
tributes (crown vigor and point-in-time rate of bole growth) were significant modifiers
of BAI response to the environmental drivers, both accelerating predicted BAI. BAI of
upland trees were deleteriously affected by a single drought year less than -10cm water
deficit. Lowland trees were buffered from single drought years, but multiple years of
water deficit (averaging < -8cm) deleteriously affected predicted BAI. Our generalized
model was effective in comparing upland and lowland tree responses, comparing re-
sponse to different forest treatments, as well as demonstrating resistance or resilience
to environmental stress. A single harvest increasing tree-to-tree spacing effectively in-
creased BAI, yielded resilience to drought, and its effect was persistent for at least 10
years. Post-harvest, one or two prescribed fires did not provide additional BAI benefits,
nor in the absence of the harvest, did two vs. one prescribed fire treatment. Our analysis
suggests that in dry pine forests thinning treatments, if there is a choice between com-
parable trees, leaving more vigorous trees and reducing tree-to-tree competition may
improve tree resistance to drought.

Acknowledgments

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APPENDIX A. LIST OF VARIABLES TESTED FOR PREDICTING BAI

(1) List of environmental drivers:
   SPEI12h, SPEI12h$(t-1)$, SPEI12h$(t-2)$, SPEI12h$(t-3)$,
   SPEI12h(2 yr ave), SPEI12h(3 yr ave), SPEI12h(4 yr ave)
   SGDD_0, Sum growing degree days $> 0°$C
   CGDD_0, Count growing degree days $> 0°$C
   SGDD_10, Sum growing degree days $> 10°$C
   CGDD_10 Count growing degree days $> 10°$ C

(2) External verification of SPEI12h:
   Sycan River, million m^3 water outflow per year
   NDVI for each unmanaged and treated stand per year

(3) BAI patterns
   Type of tree BAI growth pattern: linear, increase plateau, increase variable plateau,
      increase decrease, zigzag
   Exhibits rapid acceleration or de-acceleration of BAI pre-treatment (2005)
   (Post-disturbance [BAI/yr]) / (Pre-disturbance [BAI/yr])
   Sign change in pre- disturbance vs. post-disturbance rate of bole growth

(4) Tree vigor attributes
   RANK, crown vigor
   LIVECROWN, % live crown retained in 2014
   DBH_AGE80: barkless DBH / tree age (at DBH) in 1980

(5) Tree-to-tree competition
   NOCLUST, number of trees in a cluster
   Resilience capacity
   Nearest single neighboring tree, conspecific tree > 10cm to 20m
   Nearest single neighboring tree, all tree species
   X4CZD, DBH / distance to the nearest 4 neighboring trees, conspecific, in the four aspects (NE, SE, SW, NW
   Nearest 4 neighboring trees, all tree species

A.1. **Model selection.** Our variable selection process balanced biological importance with the usual tradeoff between fit and complexity.

To select a model, we used the lowland and upland no treatment stands. We began with a base model including the variables SPEI12h, 1-year lag of SPEI12h, and their interactions with the UPLANDS/LOWLANDS indicator, smooth time-varying terms, and random per tree effects (linear in time):

$$
\begin{aligned}
\log(\text{BAI}_{i,t}) = {} & \beta_{\text{SPEI12h}}\text{SPEI12h}_t + \beta_{\text{SPEI12h}_1}\text{SPEI12h}_{t-1} \\
& + \beta_{\text{SPEI12h,UP}}\text{SPEI12h}_t I_{\{i \text{ in UP}\}} + \beta_{\text{SPEI12h}_1,\text{UP}}\text{SPEI12h}_{t-1} I_{\{i \text{ in UP}\}} \\
& + s_{\text{UP}}(t) I_{\{i \text{ in UP}\}} + s_{\text{LOW}}(t) I_{\{i \text{ in LOW}\}} \\
& + B_{0,i} + B_{1,i} t + \varepsilon_{i,t}
\end{aligned}
$$

(5)

Adding all possible subsets of the vigor variables (RANK, DBH_AGE80, and LIVE-CROWN), we evaluated the Aikake Information Criterion (AIC) (Table 5). The model adding both RANK and DBH_AGE80 minimized AIC among two-variable subsets; adding LIVECRN produced a very small reduction in AIC. We also considered dropping the interactions of the two SPEI12h variables with UPLANDS; this led to a small reduction in AIC but we retained the interactions. Our final model included RANK and DBH_AGE80.

Next, starting with the base model (5), we considered the addition of subsets of the density variables (X4CZD, NOCLUST). The AIC of the resultant models are shown in

added variables	df	AIC
null	14	7292.9
LIVECRN	15	7292.3
RANK	15	7288.2
DBH_AGE80	15	7171.5
LIVECRN, DBH_AGE80	16	7171.4
LIVECRN, RANK	16	7287.1
RANK, DBH_AGE80	16	7166.2
LIVECRN, RANK, DBH_AGE80	17	7165.6
RANK, DBH_AGE80, no SPEI12h:UP interaction	13	7166.4

TABLE 5. AIC for addition of vigor variables.

Table 6. The optimal model among these was the base with X4CZD added, with slightly lower AIC than the base model.

	df	AIC
null	14	7292.9
X4CZD	15	7292.3
NOCLUST	15	7294.6
NOCLUST, X4CZD	16	7293.6

TABLE 6. AIC for addition of density variables.

We then compared the base model (5), the model adding the vigor variables DBH_AGE80 and RANK, and the model adding DBH_AGE80, RANK and the density variable X4CZD. (Table 7.) While the largest model among these (row three in Table 7) had larger AIC than the model in row two, we preferred to include a density covariate and thus retained the larger model.

	df	AIC
null	14	7292.9
RANK, DBH_AGE80	16	7166.2
DBHAGE, RANK, X4CZD	17	7168.1

TABLE 7. AIC for null, null with vigor, and null with vigor/density.

Finally, we evaluated growing degree day metrics: CGDD_0, CGDD_10, SGDD_0, SGDD_10. At this stage, we took as the base model the base model in (5) with the addition of the tree-variables DBH_AGE80, RANK, and X4CZD. The AIC for the resulting models is shown in Table 8. We also considered removing the interaction of SPEI12h variables with UP, and adding in the two-year SPEI12h lag. The optimal model contained CGDD_10, which was included in the final model.

The p-values in the model summary (Table 2) should be interpreted with caution, both because of the implicit multiple hypothesis testing of the selection process, and because of the approximate nature of the Student distribution.

	df	AIC
base	17	7168.059
SGDD_0	18	7076.273
SGDD_10	18	7077.883
CGDD_0	18	7166.568
CGDD_10	18	7073.437

TABLE 8. AIC for heat variables.

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