



Evaluating the effects of nitrogen and sulfur deposition and ozone on tree growth and mortality in California using a spatially comprehensive forest inventory



Mark E. Fenn^{a,*}, Haiganoush K. Preisler^b, Jeremy S. Fried^c, Andrzej Bytnerowicz^a, Susan L. Schilling^a, Sarah Jovan^c, Olaf Kuegler^c

^a USDA Forest Service, Pacific Southwest Research Station, 4955 Canyon Crest Drive, Riverside, CA 92507, USA

^b USDA Forest Service, Pacific Southwest Research Station, 800 Buchanan St., WAB, Albany, CA 94706, USA

^c USDA Forest Service, Pacific Northwest Research Station, 620 Southwest Main, Suite 502, Portland, OR 97205, USA

ARTICLE INFO

Keywords:

Forest monitoring
Air pollution
Carbon sequestration
Forest growth
Tree mortality
Mediterranean climate

ABSTRACT

Although nitrogen deposition and tropospheric ozone have impacted California forests for decades, broad scale studies of these impacts on forest growth and mortality are lacking. Because of the summer-dry climate over most of the state, forest responses to air pollution are expected to differ from more mesic climates. In this study, data from US Forest Service Forest Inventory and Analysis (FIA) permanent (remeasured) plots were combined with modelled atmospheric N and S deposition and an ozone exposure index to evaluate tree growth and mortality responses in California. Seven of 18 species exhibited significantly greater carbon increment (CI) in tree boles as N deposition increased, though the magnitude of the effect was quite small in most California forests. However, increases in CI were substantial in the coastal ecoregions of central and northern California where precipitation and fog exposure are greatest. Redwood (*Sequoia sempervirens* (D. Don) Endl.) trees exhibited the strongest CI response to N deposition. Our model results imply a mean CI increase of $4.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of C per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N deposition statewide versus 13.6 in the Central and Northern California Coast ecoregions, where > 50% of the trees are redwood or tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.). Increased carbon sequestration rates in response to N deposition in these California coastal regions were similar to increases reported for Europe and global estimates. Nitrogen and S deposition significantly increased the odds of top damage and trees with crown damage exhibited higher mortality, although the effect was small. Elevated ozone exposure was associated with significantly larger rates of overall tree growth. However, for ozone-sensitive ponderosa pine at moderate ozone levels (ozone index values of ca. 20–30 ppb) and moderately-elevated N deposition ($15\text{--}25 \text{ kg ha}^{-1} \text{ yr}^{-1}$), CI begins to decline, before increasing at higher pollution levels, presumably because of the fertilizing effect of N deposition; although data are limited for these more polluted conditions. Sulfur deposition in California forests was low, ranging from 0.3 to $3.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$, but was associated with positive growth response in seven coniferous species. The combined effect of N and S deposition and ozone exposure statewide is a net increase in bole CI. However, aridity reduces the stimulatory growth effect of N deposition, and alters the threshold, capacity and sometimes the direction (e.g., S deposition) of the CI response to deposition, factors that need to be considered in global change models.

1. Introduction

Long term N deposition and ambient ozone are the two major pollutants impacting forests in California, USA. Ozone is a phytotoxic secondary gaseous air pollutant observed to cause foliar injury and canopy dieback in some forest tree species, such as ponderosa and Jeffrey pine. Ozone has also been linked to plant injury that does not

immediately result in visible symptoms (Bussotti & Ferretti, 1998). Ozone exposure and N enrichment increase shoot:root ratios in plants, and in *P. ponderosa* in particular (Agathokleous et al., 2016; Grulke et al., 1998; Mills et al., 2016). The N enrichment of trees growing on sites with a high pollution burden in the San Bernardino Mountains in southern California appears to result in increased bole growth (Fenn & Poth, 2001), at least in part because of decreased C translocation to

* Corresponding author.

E-mail address: mark.fenn@usda.gov (M.E. Fenn).

<https://doi.org/10.1016/j.foreco.2020.118084>

Received 16 August 2019; Received in revised form 25 February 2020; Accepted 11 March 2020

0378-1127/ © 2020 Elsevier B.V. All rights reserved.

Table 1
Tree species names, codes and number of trees included in the analysis.

Common Name	Code	Number of Live Trees ¹	Ozone Analysis	Mortality Tree Count	Species Name
Blue oak	QUDO	892	479	65	<i>Quercus douglasii</i>
California black oak	QUKE	2,650	1,145	285	<i>Quercus kelloggii</i>
Canyon live oak	QUCH	3,808	1,516	268	<i>Quercus chrysolepis</i>
Interior live oak	QUWI	571	403	84	<i>Quercus wislizeni</i>
Tanoak	LIDE	3,071	192	202	<i>Lithocarpus densiflorus</i>
Pacific madrone	ARME	1,009	53	101	<i>Arbutus menziesii</i>
Incense-Cedar	CADE	4,079	2,305	284	<i>Calocedrus decurrens</i>
Ponderosa pine	PIPO	7,860	2,137	322	<i>Pinus ponderosa</i>
Sugar pine	PILA	1,510	734	134	<i>Pinus lambertiana</i>
Redwood	SESE	2,087	140	12	<i>Sequoia sempervirens</i>
Singleleaf pinyon	PIMO (mono)	347	347	88	<i>Pinus monophylla</i>
California red fir	ABMA	2,337	2,082	327	<i>Abies magnifica</i>
Douglas-fir	PSME	10,336	1,284	414	<i>Pseudotsuga menziesii</i>
Jeffrey pine	PIJE	3,998	2,425	85	<i>Pinus jeffreyi</i>
Lodgepole pine	PICO	2,519	1,831	107	<i>Pinus contorta</i>
Western juniper	JUOC	1,230	246	8	<i>Juniperus occidentalis</i>
Western white pine	PIMO (mont)	556	335	34	<i>Pinus monticola</i>
White fir	ABCO	10,543	4,431	841	<i>Abies concolor</i>
Total		59,403	22,085	3,661	

¹ Refers to the number of live trees with DBH > 12.7 cm.

roots (Grulke et al., 2001). Enhanced N status of *P. ponderosa* also appears to mitigate some of the negative effects of ozone injury, by increasing N availability for photosynthetic pigments and enzymes (Beyers et al., 1992), which may promote reparation of photosynthetic pigments. On the other hand, increased N availability appears to also increase stomatal conductance and ozone uptake (Grulke, 2003). Likewise ozone and N deposition have been shown to predispose ponderosa and Jeffrey pine trees to increased bark beetle attack and beetle-induced mortality (Jones et al., 2004). Thus, because of increased aboveground growth, exposure of California forests to ozone and elevated N deposition may at first glance appear beneficial, but the health and vigor of trees under co-occurring stressors such as drought, long-term fire suppression and bark beetles is compromised by these additional air pollution stressors (Grulke et al., 2009).

Considering the global-scale anthropogenic alteration of the N cycle (Smil, 2001), an ongoing question is how chronic N deposition affects C sequestration in forests and other ecosystems. Most studies address this issue in temperate and boreal forests, documenting positive effects on C accumulation. For instance, analyses in other European regions (De Vries et al., 2009, 2014b, 2014a; Laubhann et al., 2009; Solberg et al., 2009) indicate that N deposition increases C sequestration in woody biomass. Likewise, a study in the northeastern U.S based on a dataset similar to ours (i.e. remeasured inventory plots from the USDA Forest Service, Forest Inventory and Analysis (FIA) program) found notable differences in tree growth, mortality and C sequestration among the region's 24 most common tree species (Thomas et al., 2010). However, little work has been done in Mediterranean climates similar to California's (but see Ferretti et al., 2014) and few studies have considered the impacts of co-occurring exposure to ozone (De Vries et al., 2014b). Furthermore, many questions remain regarding the sustainability of some forests under the influence of chronic N deposition over time (Ferretti et al., 2014) owing to impacts such as soil acidification and nutrient imbalances (Carter et al., 2017).

Ozone concentrations and N deposition levels vary widely across California's forests. Little is known about the dose-response relationships of tree growth and mortality to the combined exposure to these pollutants in California. An elevated tree mortality event concentrated in California's Sierra Nevada region was estimated to have resulted in > 129 million tree deaths attributed to drought and insects on 3.6 million hectares over a six-year period ending in 2015, with the southern Sierra experiencing the highest mortality rates (Forest Climate Action Team, 2018; USDA Forest Service, 2017). Extended drought, bark beetles and high stand densities resulting from declines in

management intensity, especially on public forests, are considered to be the major factors responsible for the extensive tree mortality (e.g., Stephens et al., 2018). However, the role of air pollution has not been investigated as a potential contributing factor, even though the preponderance of tree mortality occurred in the most polluted portion of the Sierra Nevada.

We analyzed responses of basal area increment (growth), bole C increment and mortality to both ozone exposure and N and sulfur (S) deposition for 18 major tree species, most with broad distribution across California (Fig. A.1). We relied on tree data from FIA inventory plots initially measured in 2001–2005, then remeasured ten years later. While S deposition tends to be low in California (Bytnerowicz et al., 2016), we included it because a recent U.S. study, also using FIA data, reported significant tree growth and mortality responses for some species for both N and S deposition (Horn et al., 2018). We also included a variety of non-pollutant explanatory attributes such as climate, with the goal of controlling for those attributes to better discern the response to air pollution.

2. Materials and Methods

We combined five “panels” of remeasured FIA forest inventory plots (see Appendix B, FIA Sampling Methods for details) with modelled atmospheric N and S deposition to evaluate tree growth and mortality responses across California for 18 forest tree species—the sixteen most common species in the state plus two of particular interest (western white pine and interior live oak) (Table 1). We constructed statistical models that controlled for tree size, site productivity, climate, tree top damage, and competition experienced by each remeasured tree so that we could estimate the significance, magnitude and direction of the effects of N and S deposition on carbon increment (CI), basal area increment (BAI), and mortality odds. The effects of ozone were evaluated separately for a portion of California for which ozone exposure data were available (see Fig. 1c).

2.1. Preparation of the inventory data

Because our target population was trees growing on California's forest lands, we first filtered the inventory data to trees growing on the 3314 remeasured, spatially referenced FIA plots containing conditions (full or partial plots) that were forested at both the initial visit (“Visit 1”) that occurred between 2001 and 2005 and the ensuing re-visit (“Visit 2”) between 2011 and 2015 (Table C.1). All land owner

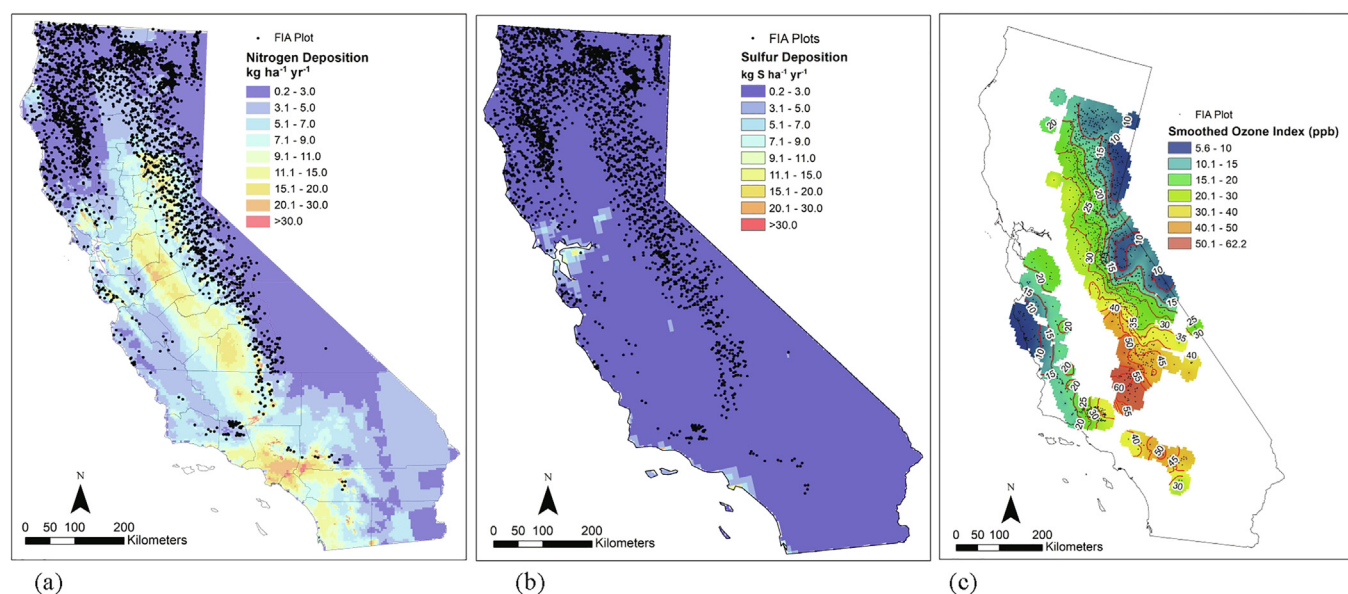


Fig. 1. Annual N deposition (a) in California based on the CMAQ model with values adjusted based on empirical throughfall deposition measurements (see text for details). Annual S deposition (b) is based on the TDEP model. Ozone exposure index values are shown in (c). Black dots in (a) and (b) indicate the location of FIA plots used in the analyses for responses to N and S deposition. Black dots in (c) indicate the location of FIA plots used in the analyses for responses to ozone.

categories are represented, including corporate, family and national forest. Most (72%) of the plots comprise a spatially balanced re-measurement sample of the entire state; the others were established by national forests as a strata-based spatial intensification, primarily to ensure adequate sampling of rare forest types. Modeled pollutant estimates for each plot over a period commensurate with the re-measurement interval between 2001 and 2005 and 2011–2015 (Table C.1) were obtained via spatial overlay.

To calculate the dependent variables (e.g., CI and BAI) used in our models, data for trees > 12.7 cm dbh at Visit 1 and Visit 2 on these forested plots were filtered to exclude trees 1) of species other than the 18 listed in Table 1; and 2) with missing data for one or more explanatory variables (e.g., on site quality), or 3) unsuitable for growth or mortality analyses (e.g., ingrowth trees not observed at Visit 1, the Visit 2 crew noting a dbh or height error made at Visit 1, or the dbh measurement location changing between visits). Models of CI and BAI considered only trees that were alive at both visits; mortality was analyzed for trees live at Visit 1 and live or dead at Visit 2. The ~ 5% of trees recorded as having negative CI, typically owing to bole breakage or imprecision in height measurement, were assigned a zero increment. Ultimately, 87% of all live trees, of the 18 selected species, met the criteria for the growth analysis and 34% of the trees dead at Visit 2 proved suitable for the mortality analysis; many of the dead trees were below the minimum size threshold of 12.7 cm, or no longer measurable as standing trees, owing to fire.

Elemental mass of bole C, the basis of C increment (CI) in our analysis, is not a measurement included with the inventory data. Instead, diameter, height and species, collected with high accuracy and precision thanks to an extensive QA program integral to the inventory (Adams & Christensen, 2012; Melson et al., 2002), are used to calculate volume and biomass for each tree component for each tree by applying allometric equations (See Appendix D). Carbon is then approximated as half of dry woody biomass. We also calculated basal area increment (BAI) as the difference between basal area ($(DBH^2/4) \cdot \pi$) at visits 1 and 2 as an additional growth measurement. BAI is independent of height, and thus avoids the imprecision introduced by tree height measurements. BAI data are also free of potential bias introduced by applying volume equations, which are often estimated from a sample of trees with far more limited geographic extent than the statewide sample represented by the FIA data.

2.2. Pollutant data

Total annual N deposition was estimated with the Community Multi-scale Air Quality (CMAQ) Model for the most polluted two-thirds of the state on a 4-km resolution grid. A 36-km grid resolution (Fenn et al., 2010; Fig. 1a) was used for the relatively unpolluted northern and far southeastern areas (Tonnesen et al., 2007). Total nitrogen deposition was adjusted based on the linear relationship with empirical throughfall data from 36 sites in the Sierra Nevada and southern California (from 2002 – 2014) using the method described in Fenn et al. (2010; See Appendix E.)

N deposition patterns in California correspond to urban and agricultural sources, dominant climate and topography, and are manifest as steep spatial gradients. The 3314 on-grid and spatially intensified FIA plots used for this study sample trees across most of the N deposition gradient, though forests are largely absent where deposition is greatest. N deposition estimates were obtained for each FIA plot via spatial overlay on a GIS layer of throughfall-adjusted CMAQ model predictions. In order to estimate the CI response to anthropogenic N deposition, pre-industrial N deposition was estimated as $0.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$ based on data from Holland et al. (1999) and from the lowest deposition data from CMAQ in this study.

Estimated annual total S deposition ($\text{kg ha}^{-1} \text{ yr}^{-1}$) for the FIA plots (Fig. 1b) was obtained from data provided by NADP Total Deposition Science Committee (TDEP model; Schwede & Lear, 2014) at their website: <http://nadp.slh.wisc.edu/committees/tdep/tdepmaps/>. Gridded data of the variable: “s_tw” (total S deposition) for the year 2015 was downloaded in June 2017 from <ftp://ftp.epa.gov/castnet/tdep/grids> and S deposition estimates assigned to FIA plots via overlay on exact coordinates.

The ozone data or Ozone Index (OI, ppb) used for this study were derived from a continuous prediction surface developed from an extensive active and passive monitoring network in California’s Sierra Nevada Mountains and Transverse Range Mountains in southern California. (See Appendix E.)

2.3. Climate data

Climate data for the FIA monitoring plots used in the analysis were derived from: ClimateWNA (<http://cfcg.forestry.ubc.ca/projects/>

Table 2

Variables retained by the selection criteria as significant explanatories in final models of C increment (CI) and percentage of variability ‘explained’. Model form is specified by Eq. (1) under Statistical Analysis in the Materials and Methods. The table also provides the overall direction of the estimated effect (increasing ↑, decreasing ↓ or variable ↑↓).

Variable	Effects on CI		
	Variability explained	(Ozone) ⁶ %	Effect direction
Site and sampling characteristics	16% ⁷		
Latitude, Longitude	3.6% ⁸		↑↓
Elevation	3.9%		↓
Site quality (mean annual increment) ¹	74%		↑
Tree size category(TPA) ²	3.5%		Medium ↑ Large↓ yes ↑no↓
Plot intensified (yes, no) ³	15.1%		
Tree characteristics	73.4%		
Bole Carbon Mass at Visit 1	4.5%		↑
Crown Ratio at Visit 1	6.0%		↑
Crown Ratio at Visit 2	15%		↑
Tree species	3.8%		↑↓
Basal area of trees larger than this tree	8.5%		↓
Diameter at Breast Height at Visit 1	2.4%		↑
Tree top damage (tree top broken or missing)	60%		↓
Climate	1.4%		
Mean Annual Temperature	33%		↑
Mean Summer Precipitation	22%		↓
Summer heat-moisture index	26%		↓
Number of frost-free days	18%		↓
Pollutants	8.4%	(19%) ⁷	
N deposition ⁴	30%	(28%) ⁸	↑ ↓
S deposition ⁴	70%	(25%)	↑ ↓
Ozone	NA ⁹	(46%)	↑
Disturbances	1.2%		
Basal Area Harvested	26%		↓
Basal Area Killed by Fire	56%		↓
Disturbances present ⁵	18%		↑↓
Total Explained Variability	37%	(39%)	
Sample Size	59,403	(22,085)	

¹ Mean annual increment, derived from field-measured and modeled site index (height of dominant, free-to-grow trees at a species-specific “base age”), accounts for potential productivity driven by site factors such as soil depth, precipitation, elevation, and temperature, independent of the amount and size of vegetation currently present.

² Tree sampling intensity for large (> 61.0 cm dbh) sized trees, sampled on 1 acre (4047 m²) plot areas was six times as great as for medium (12.7–61.0 cm dbh) sized trees sampled on 1/6 acre (674 m²) plot areas, so they are more heavily represented in the tree sample used to build the model.

³ Intensified plots were in addition to the spatially-balanced remeasurement sample of the entire state. They were established by national forests in California as a strata-based spatial intensification, primarily to ensure adequate sampling of rarer forest types.

⁴ Effects and significances for tree species responses to N and S deposition are given in Figs. 2 and 6.

⁵ Disturbances present refers to disturbances not included in the first two categories listed, such as insect pests, diseases, and miscellaneous other disturbances.

⁶ Values in parenthesis in table are for model using subset of data that have ozone measurements.

⁷ Explained variability as a percentage of total.

⁸ Explained variability as a percentage of subtotal in each of the variable categories.

⁹ NA = not applicable.

climate-data/climatebcwna; Wang et al., 2016). Climatic data and indices used included 30-year normals (1981–2010) of the following variables: mean annual temperature (MAT), mean annual precipitation (MAP), mean annual summer precipitation (MSP), summer heat-

moisture index (SHM), number of frost-free days (NFFD), and Hargreaves climatic moisture deficit (CMD). However, MAP and CMD were not significant in the final model as indicated in Table 2.

2.4. Statistical analysis

2.4.1. Model for estimating annual carbon increment (CI) and basal area increment (BAI)

We used a log-normal model to evaluate the effects of the explanatory variables on CI and BAI. We chose a log-normal model, in part to obtain an error distribution closer to Gaussian, but more importantly, because the response variable, growth rate, as we’ve defined it, can only be positive. Therefore, we made the assumption that the expected value of the growth rate can be approximated by an exponential function which is bounded by zero at the lower end. Growth rate is often modeled similarly in the literature, for example, Thomas et al., 2010; Ferretti et al., 2014; Horn et al., 2018. The change in bole C, CI, was estimated as the derivative, $K = dC/dt$, of bole C with respect to time (t), by fitting a regression model to the observed rate of change

$Y = CI = (C2 - C1)/\Delta t$ where Δt = elapsed time (decimal years) between measurements and C1, C2 are the elemental C in the bole at Visit 1 and Visit 2, respectively.

Assuming Y is a random variable with multiplicative error and expected value K such that

$$Y = K \times \varepsilon, \text{ one can model K by}$$

$$K = g_1(\text{Ndep, species}) \times g_2(\text{Sdep, species}) \times g_3(\text{OI, species}) \times g_4(\text{Site characteristics}) \times g_5(\text{Tree characteristics}) \times g_6(\text{Climate}) \quad (1)$$

Where $\varepsilon \sim$ a multiplicative random noise such as log-normal

$g_i \sim$ one or two dimensional spline function

Ndep ~ Nitrogen deposition (see Fig. 1a)

Sdep ~ Sulfur deposition (Fig. 1b)

OI ~ ozone exposure index (Fig. 1c)

Site characteristics include disturbances, such as fire, insects and disease, and treatments that harvest trees, in addition to elevation, site location (latitude and longitude), site quality (as assessed by the potential rate of live tree volume accretion), and stand basal area. Tree characteristics include species, size and crown ratio.

Climate includes mean annual temperature, mean summer precipitation, number of frost free days, and summer-heat moisture index.

Table 2 lists all explanatory variables that proved to be significant predictors in our final model, along with the magnitude and direction of their influence.

Estimation for BAI follows analogously, with Y defined as $BAI = (BA2 - BA1)/\Delta t$.

We used the generalized additive model, gam, in the R-statistical package (R Core Team, 2018) to estimate, for both CI and BAI, the relationships with each of the explanatory variables. Gam uses Generalized Cross Validation (GCV) and Unbiased Risk Estimator (UBRE) for selecting terms and smoothness levels (Craven & Wahba, 1978; Wahba, 1990; Wood, 2017; Wood et al., 2016). Results using GCV or UBRE are similar to those obtained using AIC (Akaike Information Criteria). We used the GCV criteria and the approximate P-values provided by gam to identify candidate variables for selection or removal from the final model. Our final model included only those variables that were selected by the above criteria. Additionally, we provide plots of the partial residuals showing the estimated effects of the pollutant variables (together with ± 2 SE bounds) for each tree species which can be used to identify the species that are significantly affected by the pollutants. The standard errors in these plots are one of the outputs of the gam program and they are based on a Bayesian approach using

penalized maximum likelihood (Marra & Wood, 2012; Nychka, 1988).

2.4.2. Model for estimating probability of tree damage and survival

Our interest was in estimating effects of the pollutants on 1) probability of tree damage (where damage was defined as the top of a tree, either missing or damaged) and 2) probability of tree mortality during the 10 years between measurements.

We used the following semiparametric logistic regression model to estimate these probabilities:

$$\text{Let } Y = 1 \text{ if a tree alive at Visit 1 was damaged by Visit 2} \\ \text{(for damage study) or dead by Visit 2 (for mortality study)} \\ = 0 \text{ otherwise}$$

$$\text{Pr}[Y=1] = p = \{1 + \exp(-\theta)\}^{-1}$$

where the linear predictor, θ = odds = $p/(1-p)$, is given by

$$\theta = \alpha + g_1(\text{Ndep}) + g_2(\text{Sdep}) + g_3(\text{OI}) + g_3(\text{Site characteristics}) \\ + g_4(\text{Tree characteristics}) + g_5(\text{Climate}) \quad (2)$$

and the explanatory variables are as described above. The model for tree mortality distinguished between pollutant effect in the presence and absence of damage to the tree top.

3. Results

The model for predicting annual CI explained 37% (for model without ozone) and 39% (for model with ozone) of the total variance (Table 2). Most of the variability explained by the model was due to tree characteristics (73%), with only 16% explained by site and sampling characteristics. As expected, CI was enhanced in more productive sites, with greater tree vigor (as indicated by crown ratio), and with greater initial tree size (bole C; Table 2). In contrast, top damage and sum of basal area of trees larger than each tree (a measure of competition) were associated with lower CI. Of the variability explained, 8.4% was due to N and S deposition. For a subset of sites where ozone exposure data are available (37% of the FIA plots), the combined effect of all three pollutants explained more than twice as much of the variability in annual C increment at 19% (Table 2). Climate only accounted for 1.4% of the explained variability, likely because climate attributes are already accounted for by site quality, elevation, latitude and longitude, and species.

3.1. Effect of N deposition on annual CI and BAI

Most (> 95%) of California's forested area experiences an N deposition rate of well under $20 \text{ kg ha}^{-1} \text{ yr}^{-1}$, and of the 18 species analyzed, eight species exhibited a statistically significant (P -value < 0.05) growth response within that range of deposition. Seven species exhibited a positive CI response to increasing N deposition: western juniper, incense-cedar, singleleaf pinyon pine, redwood, tanoak, California black oak, and canyon live oak; Lodgepole pine had a negative CI response, albeit over a narrow deposition range (maximum N deposition < $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$; Fig. 2). Seven species exhibited a positive BAI response to N deposition: incense-cedar, singleleaf pinyon pine, California black oak, canyon live oak, white fir, ponderosa pine and Douglas-fir (Fig. 3), and seven species exhibited no response for CI or BAI: California red fir, Jeffrey pine, sugar pine, western white pine, Pacific madrone, blue oak, and interior live oak.

Four species showed a positive response only for CI: western juniper, lodgepole pine, redwood and tanoak; and three only for BAI: white fir, ponderosa pine and Douglas-fir. Differences in responses for CI and BAI may be explained by the greater variability in CI owing to its calculation requiring tree height (a more imprecise measurement than the DBH required to compute BAI) and a species specific volume equation.

Similar to CI, median BAI was greatest in redwood at $30.1 \text{ cm}^2 \text{ tree}^{-1} \text{ yr}^{-1}$, although the increasing response to N deposition was not statistically significant at the 5% level. Of the species with a significant BAI response, median values ranged from 16.5 to $21.2 \text{ cm}^2 \text{ tree}^{-1} \text{ yr}^{-1}$ for Douglas-fir, white fir and ponderosa pine (Fig. 3). For the other four species with a significant response to N deposition, median basal area increment ranged from 3.0 to $9.8 \text{ cm}^2 \text{ tree}^{-1} \text{ yr}^{-1}$.

California consists of a number of ecoregions, or regions of unique ecological characteristics, as defined by McNab et al., 2007 (see Appendix C and Fig. C.1 for further details and a map of the ecoregions of California). Nearly half of the statewide CI increase in response to N deposition above pre-industrial levels (0.16 Tg C) was from the Northern California Coast ecoregion (0.08 Tg C) where > 50% of the trees in the FIA plots were redwoods and tanoak trees, species that responded positively to N deposition. Including both of the two primary ecoregions (Northern California Coast, Central California Coast) where redwood trees were commonly found in the FIA plots accounted for 83% (0.15 Tg C) of the estimated annual statewide CI increase in response to N deposition above pre-industrial levels, but included < 7% of the trees on the FIA plots. The remainder of the CI in response to N deposition was primarily from the following ecoregions, in descending order of CI increase: Southern California Mountain and Valley, Northern California Coast Ranges, Modoc Plateau, Klamath Mountains, and Sierra Nevada Foothills. Three of the ecoregions had negative net C increment in response to N deposition: Northern California Interior Coast Ranges, Southern Cascades and Sierra Nevada. Average CI values for all of the California ecoregions, expressed as $\text{kg ha}^{-1} \text{ yr}^{-1}$ in response to N deposition, are shown in Table 3.

We estimate a 1.7% statewide increase in bole CI per $\text{kg ha}^{-1} \text{ yr}^{-1}$ increase in N deposition based on the eight species that showed a significant response to N. This equates to a statewide mean of 4.2 kg ha^{-1} in the aboveground bole CI per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N deposition. In the Northern California Coast ecoregion, mean CI per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N is much greater— 19.9 kg ha^{-1} .

3.2. Effects of ozone on annual C increment

Based on the subset of FIA plots for which the ozone exposure index was available, CI increased with ozone for three conifer species (lodgepole pine, western white pine and ponderosa pine) and exhibited a bimodal response for California red fir increasing with ozone index to a threshold of 30 ppb, then declining (Fig. 4). For two hardwoods (canyon live oak and California black oak), CI increased with ozone. Blue oak showed decreasing CI with increasing ozone exposure until the ozone index reached a value of 40, after which CI began to increase (Fig. 4).

Potentially confounding effects of ozone and N deposition are presented in Fig. 5a, suggesting that the highest levels of ozone ($\text{OI} > 40 \text{ ppb}$) and N deposition ($> 15 \text{ kg ha}^{-1} \text{ yr}^{-1}$) result in the highest CI responses observed in this study. These results are also confounded with locations, since they only occur in Southern California (see Fig. 1). At lower levels of ozone and N deposition, responses may vary with species. Significant combined effects of ozone and N deposition were evident for only two species in the mixed conifer zone (Fig. 5a), which spans a wide range of ozone and N deposition exposure. At moderate ozone exposure (index values of ca. 20–30 ppb) and N deposition of $15\text{--}25 \text{ kg ha}^{-1} \text{ yr}^{-1}$, CI for ozone sensitive ponderosa pine begins to decline, before increasing again at the highest pollutant levels (Fig. 5a), although data are limited for these highest pollution levels and thus uncertainty is greater. CI for canyon live oak doesn't decline at moderate ozone levels. When considering the response of CI to ozone and N deposition with all species combined, we again see the greatest CI at the highest ozone and N deposition. However, at ozone index values below around 20 ppb, increasing N deposition was generally associated with reduced CI (Fig. 5b).

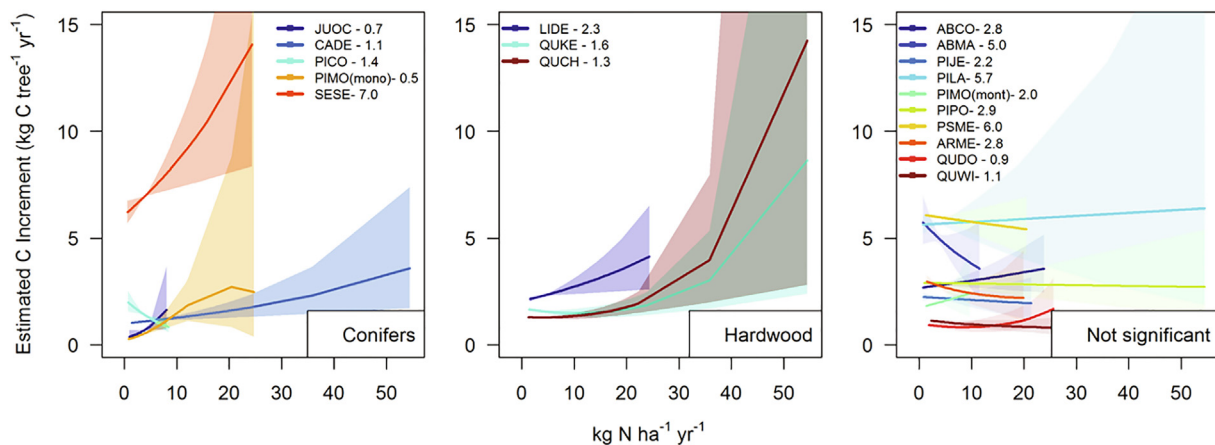


Fig. 2. Effect of N deposition on annual C increment estimated for the 18 tree species listed in Table 1. Values accompanying tree species codes in the legend represent median annual C increment ($\text{kg tree}^{-1} \text{yr}^{-1}$). Displayed values are estimates of the function g_1 (N dep) in Eq. (1). Shading indicates approximate 95% confidence interval bounds for each value of N deposition.

3.3. Effects of S deposition on annual C increment

Estimated S deposition in California forests is low ($0.3 - 3.1 \text{ kg ha}^{-1} \text{yr}^{-1}$), and thus the following growth responses were largely unexpected. For singleleaf pinyon pine and redwood, CI declined as S increased, though for redwood, CI began to increase again when S deposition exceeded $2.3 \text{ kg ha}^{-1} \text{yr}^{-1}$. Pacific madrone and Douglas-fir showed bimodal CI responses, initially increasing, then decreasing above a threshold of 1.5 and $1.9 \text{ kg ha}^{-1} \text{yr}^{-1}$ of S respectively. CI response was positive in seven conifer species (Fig. 6), negative for tanoak and canyon live oak, and not significant for the other four hardwoods (only significant trends shown in Fig. 6).

3.4. Effects of N and S deposition and ozone on tree survival and damage

There was a small but significant increase in the odds of tree mortality in trees with damaged tops until deposition reached $25 \text{ kg ha}^{-1} \text{yr}^{-1}$ of N or $1.5 \text{ kg ha}^{-1} \text{yr}^{-1}$ of S, after which there was no further increase in the odds of mortality (Fig. 7; Table 4). A small but significant N deposition mortality effect on trees with damaged tops was observed for white fir, California red fir, lodgepole pine, western white pine and blue oak. In trees without top damage, N and S deposition didn't significantly impact mortality. Nitrogen and S deposition increased the odds of tree top damage until deposition reached $5 \text{ kg ha}^{-1} \text{yr}^{-1}$ of N or $1.5 \text{ kg ha}^{-1} \text{yr}^{-1}$ of S, respectively, after which there was

no further increase in top damage (Table 4). The effects of increasing N deposition on canopy damage was mostly observed in hardwoods, in particular tanoak, blue oak, California black oak, interior live oak and, to a lesser extent, canyon live oak (data not shown). No effects of ozone on the odds of top damage was observed; however, regardless of top damage, odds of tree mortality decreased with increasing ozone exposure until the ozone index reached a threshold of 30 ppb (Fig. 7, Table 4)

4. Discussion

As in our study, previous studies looking at N or S deposition effects on tree growth and mortality based on FIA data reported a range of responses among different forest tree species (Horn et al., 2018; Thomas et al., 2010). Etzold et al. (2020) reported varying species stem growth responses to N deposition in Europe. Growth of spruce increased linearly, beech showed a non-linear quadratic response with a tipping point at $24 - 34 \text{ kg N ha}^{-1} \text{yr}^{-1}$, while pine and oak did not show a significant growth response to N deposition. However, because of the strong influence of dry deposition in California and the large topographic variation, N deposition can vary greatly over just a few km. Thus, some species in California (lodgepole pine, California red fir, western white pine, western juniper) are exposed to a relatively narrow range of N deposition (e.g., $2 - 12 \text{ kg ha}^{-1} \text{yr}^{-1}$, while others (incense-cedar, canyon live oak, California black oak, sugar pine, ponderosa pine) are

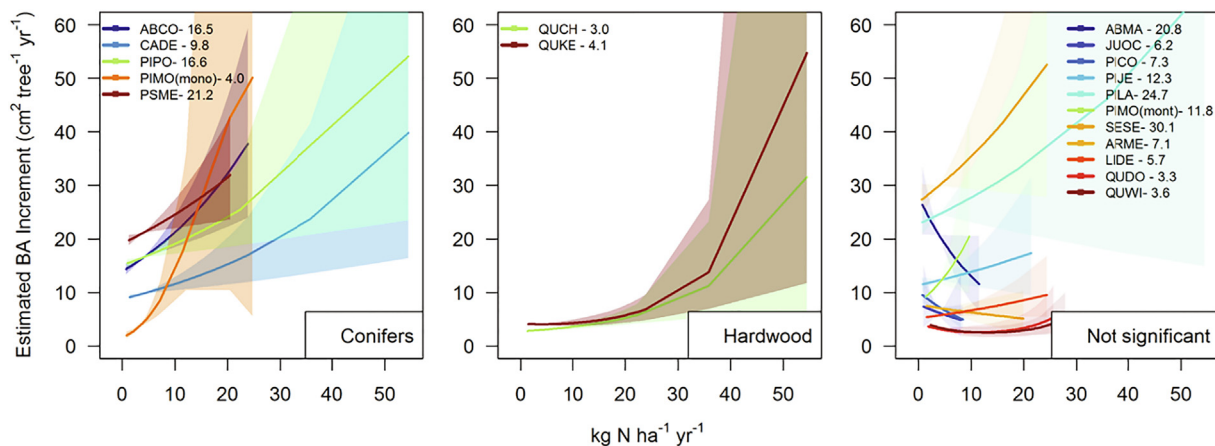


Fig. 3. Effect of N deposition on annual basal area increment per tree for 18 tree species. Numbers in the legend after the tree species codes represent the median annual basal area increment ($\text{cm}^2 \text{tree}^{-1} \text{yr}^{-1}$) for each species. Displayed values are estimates of the function g_1 (N dep) in Eq.1. Shaded areas are approximate pointwise 95% confidence bounds.

Table 3

Average ($\text{kg ha}^{-1} \text{yr}^{-1}$ of C) and total (Tg) C increment in each ecoregion in California in response to N deposition above the pre-industrial background ($0.6 \text{ kg ha}^{-1} \text{yr}^{-1}$). Ecoregions are as defined by McNab et al. (2007). Values account only for the eight tree species for which a significant growth response to N was observed.

Ecoregion Name ¹	Average C increment ($\text{kg ha}^{-1} \text{yr}^{-1}$)	Total C (Tg)	Tree Count	Hectares (x1000)
Northern California Coast	50.83	0.083243	3209	1638
Central California Coast	50.49	0.067183	637	1331
Southern California Mountain and Valley	3.91	0.010760	376	2755
Northern California Coast Ranges	2.54	0.004070	1628	1599
Modoc Plateau	1.87	0.004361	726	2330
Klamath Mountains	1.69	0.006435	2975	3806
Sierra Nevada Foothills	1.54	0.002807	176	1819
Central California Coast Ranges	0.34	0.000855	57	2485
Mono	0.33	0.000559	247	1689
Southeastern Great Basin	0.10	0.000712	189	6932
Northwestern Basin and Range	0.01	0.000102	11	7074
Mojave Desert	0.01	0.000075	3	13,457
Northern California Interior Coast Ranges	-0.19	-0.000139	51	750
Southern Cascades	-2.59	-0.004790	1,215	1848
Sierra Nevada	-3.19	-0.016739	6,474	5253

¹ See Fig. C.1 for the location of these ecoregions.

distributed across a much broader range of N deposition (e.g., $2\text{--}50 \text{ kg ha}^{-1} \text{yr}^{-1}$; Fig. C.2), albeit with much less representation at the highest levels. Likewise for ozone exposure, and to some degree for S deposition, there were fewer trees at the upper range of exposure. Thus the spatial distribution of pollutants and trees resulted in greater uncertainty (and standard error estimates) in the response to N, S and ozone exposure in California's most polluted forests (see Figs. 2–4; 6 & 7).

Nearly 90% of the marginal CI response to N deposition (i.e., relative to a pre-settlement baseline of $0.6 \text{ kg ha}^{-1} \text{yr}^{-1}$ of N) occurs in the coastal ecoregions of central and northern California even though N deposition in these ecoregions only exceeds $10 \text{ kg ha}^{-1} \text{yr}^{-1}$ near the urbanized Bay Area (Fig. 1a). On a per tree basis, the highest mean rates of CI in this study were approximately $14 \text{ kg tree}^{-1} \text{yr}^{-1}$ in redwood trees with N deposition at $25 \text{ kg ha}^{-1} \text{yr}^{-1}$ and also in canyon live oak trees with N deposition of $50 \text{ kg ha}^{-1} \text{yr}^{-1}$. However, as already noted, few trees in the inventory sample were found at such high levels of N deposition. Nonetheless, the stimulatory response to N at

levels above $30 \text{ kg ha}^{-1} \text{yr}^{-1}$ was observed in most of the tree species found in mixed conifer forests typical of mid-elevation locations in southern California and the southwestern Sierra Nevada. Ozone and N deposition levels there are highly elevated by direct exposure to polluted air masses originating from urban and agricultural regions with high nitrogenous emissions (Bytnerowicz et al., 2019; Fenn et al., 2003a,b, 2010).

4.1. Aridity and thresholds for response to N deposition

Redwood trees, which grow in humid, often foggy, coastal settings, exhibited a significant growth response to even low levels of N deposition ($< 5 \text{ kg ha}^{-1} \text{yr}^{-1}$). With the exception of redwood, western juniper and singleleaf pinyon pine, growth responses weren't generally observed until N deposition reached a threshold of $20 \text{ kg ha}^{-1} \text{yr}^{-1}$ or greater. This seems to be especially true for hardwoods. Based on these findings, we hypothesize that the generally more xeric context common in southern California's mixed conifer forests, eastside forests and

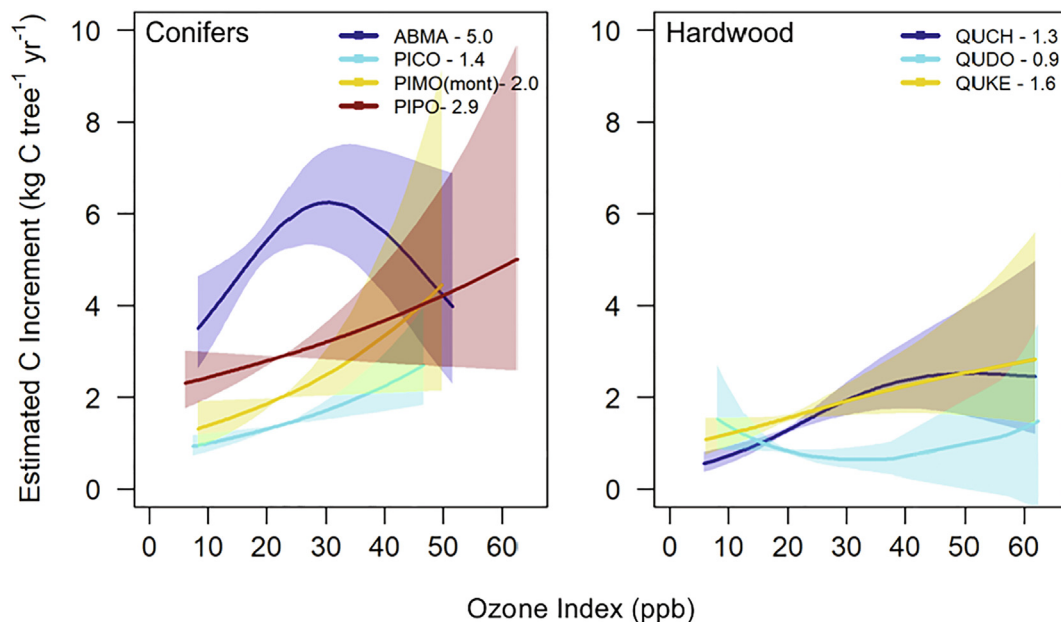


Fig. 4. Effect of ozone exposure on annual change in C increment. Only the tree species with a significant response are shown. Values accompanying tree species codes in the legend represent median annual C increment ($\text{kg tree}^{-1} \text{yr}^{-1}$). This analysis covers a subset of FIA plots where ozone data are available. Displayed values are estimates of the function g_3 (OI) in Eq.1. Shading indicates approximate 95% confidence interval bounds for each value of the ozone index.

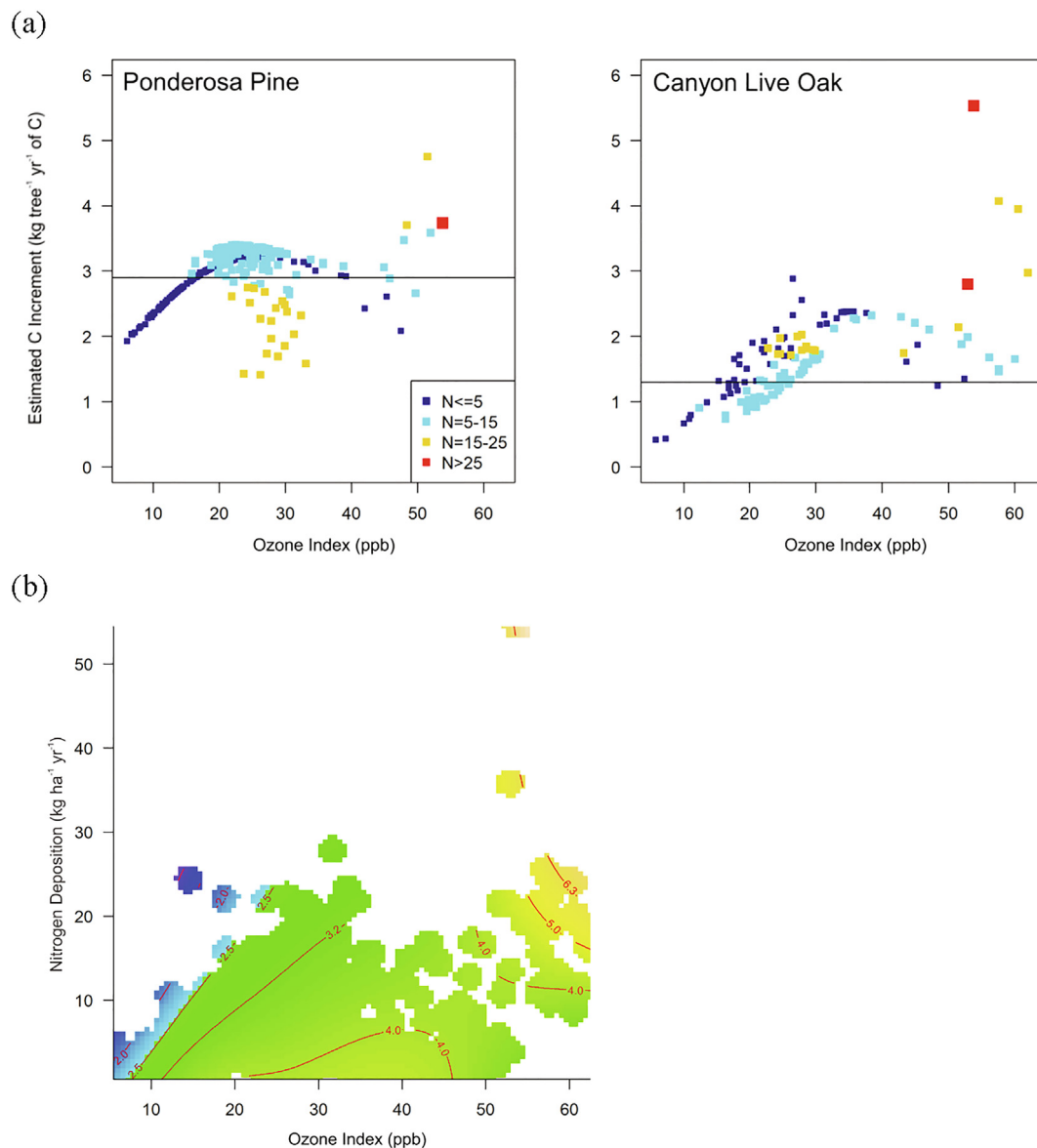


Fig. 5. Plots showing combined effects of N deposition and ozone exposure on C increment per tree. Fig. 5a shows results for ponderosa pine (PIPO) and canyon live oak (QUCH). Marker color indicates annual N deposition range (kg ha⁻¹ yr⁻¹). Horizontal lines represent C increment at the statewide mean ozone index (18 ppb). Fig. 5b shows estimated C increment response (kg C tree⁻¹ yr⁻¹; contour lines and color scale), to ozone (x-axis) and N deposition (y-axis), averaged over all 18 tree species. Displayed values in both plots are estimates of the function $g_1(N \text{ dep}) \times g_3(OI)$ in Eq. (1).

elsewhere, reduces tree response to N deposition for most species. The arid conditions prevalent in California result in greater N retention in the canopy (Avila et al., 2017), but not necessarily foliar uptake or biological assimilation (Padgett et al., 2009; Temple & Miller, 1998). High canopy retention of N and little precipitation during the growing season also results in minimal throughfall moisture and dissolved N flux to the rooting zone in spring and summer. In addition, over most of montane California, the largest precipitation inputs occur in winter when root nutrient uptake is likely temperature limited, whereas dry deposition of N and S pollutants are thought to be greatest during the dry summer season (Bytnerowicz & Fenn, 1996; Fenn & Bytnerowicz, 1997).

The end result of such scenarios in the summer-dry climate of California is a relatively low proportion of atmospherically-deposited N that is available for plant nutrient uptake compared to more mesic environments. All of these factors may contribute to the high N deposition threshold growth response in the inland forests of California. For western juniper and singleleaf pinyon pine, CI responded positively

as N deposition increased from near background levels to 5 or 10 kg ha⁻¹ yr⁻¹, respectively (Fig. 2). Thus, these two species, which are generally found in low elevation highly-arid sites, stand out as exceptions to the coastal, more humid environment hypothesis described above. These are also the two species with the lowest median annual CI (0.5 kg tree⁻¹ yr⁻¹ at the lowest N deposition sites), an order of magnitude lower than for redwood trees. Thus, increases in absolute levels of CI by these species with increased N deposition were not comparable to much faster growing species such as redwood or tanoak. One hypothesis explaining the favorable growth response to low levels of N deposition for singleleaf pinyon pine and western juniper is that the milder winters experienced by these two low-elevation species allows for greater biological availability, physiological uptake and assimilation of N from atmospheric deposition during winter when more favorable moisture conditions generally prevail.

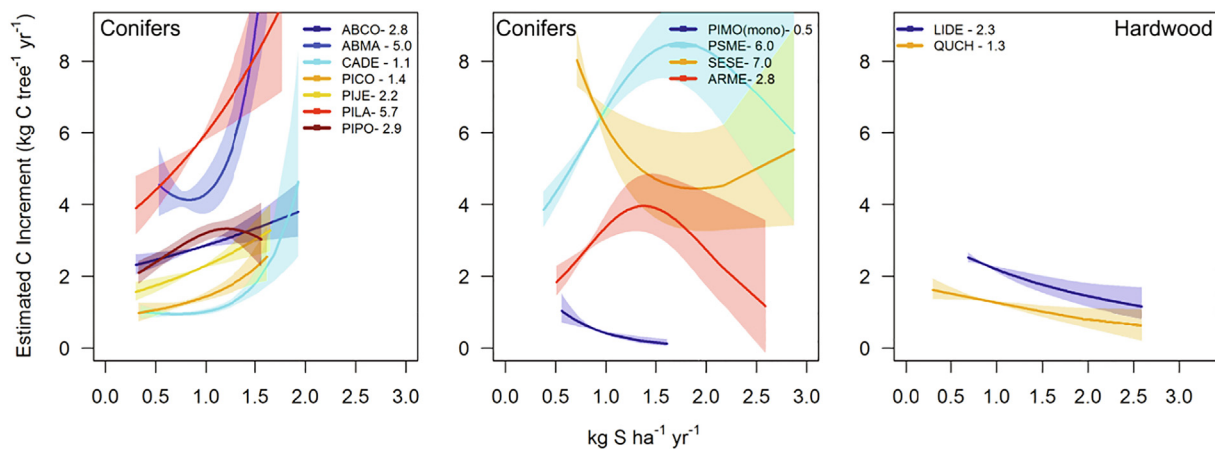


Fig. 6. Estimated effect of S deposition on annual C increment by species, where significant. Values accompanying tree species codes in the legend represent median annual C increment (kg tree⁻¹ yr⁻¹). Displayed values are estimates of the function g_2 (Sdep) in Eq. (1). Shading indicates approximate 95% confidence interval bounds for each value of S deposition.

4.2. Effects of N and S deposition and ozone on annual C increment

The effects of N and S deposition on annual C increment was small but significant, with 2.5% of the overall variance explained due to N deposition. This is similar to the findings in previous studies (De Vries et al., 2014b). Of the effects explained by N and S deposition (8.4%), 30% was attributed to N deposition and 70% to S deposition. The combined effects of N and S deposition and ozone increased the variance explained from 8.4 to 19%. At the sites where ozone exposure data were available, of the effects explained by air pollution, 28% was attributed to N deposition, 25% to S deposition and 46% to ozone exposure. The combined exposure to ozone and N deposition, at sufficiently high levels, appears to cause a synergistic effect on bole growth. The stimulatory effects of ozone on bole growth increased further with increasing N deposition and vice-versa. We hypothesized that such N deposition levels sufficient to affect tree growth would also be reflected in increased N fertility levels. This was confirmed by C:N ratios in soil from the FIA P3 plots showing a negative power function in relation to N deposition (See Appendix F and Fig. F.2).

Nitrogen amendment field studies and physiological studies of the

combined effects of N deposition and ozone in California forests also indicate that ozone and N deposition combined result in greater aboveground growth, presumably because of the reported decrease in C accumulation in fine and coarse roots accompanied by increased carbohydrate levels in the bole (Grulke et al., 2001). Both ozone and increased N fertility result in reduced C translocation to roots, lower fine root biomass and increased shoot:root ratios (Agathokleous et al., 2016; Braun et al., 1999; Grulke et al., 1998, 2001; Mills et al., 2016). Needle and branch growth and woody biomass production were all greatest at sites in the San Bernardino Mountains in southern California where ozone and N deposition were elevated. The authors concluded that “N deposition dominated the ponderosa pine response despite high ozone exposure” (Grulke & Balduman, 1999). Thus, it isn’t unexpected to find a positive aboveground growth response to elevated N deposition and an even greater response to the combined effects of N deposition and ozone exposure, at least at the highest levels of the pollutants. However, as these results suggest, the stimulation of aboveground growth may be at the expense of belowground growth.

Ozone is a known phytotoxicant with clear injury responses to seedlings and saplings fumigated experimentally with ozone, and plant

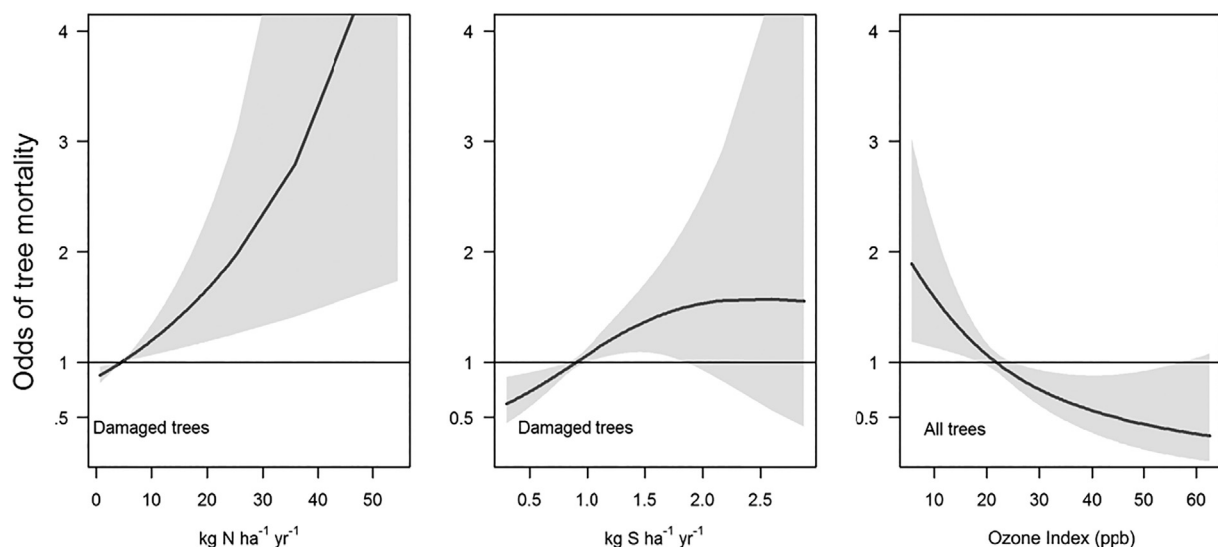


Fig. 7. Estimated odds of tree mortality as a function (see Eq. (2) in Methods for details) of N deposition, S deposition or ozone exposure. For the first two graphs, only trees with top damage are included in the analysis, while for the ozone index graph, all trees are included. For trees with no top damage, effect of N or S deposition on the odds of tree mortality was not significant. All odds are relative to the odds at the mean deposition or ozone exposure value: 4 and 0.7 kg ha⁻¹ yr⁻¹ for N and S deposition respectively, and an ozone index value of 20 ppb for ozone exposure, which is set to one in each instance.

Table 4

Estimated effect on, and standard error of, the change in odds (p/1-p) for tree top damage and for tree mortality¹ associated with the three pollutants: N deposition; S deposition, and Ozone Index, based on the logistic regression model in Eq. (2). See also Fig. 7. The change in odds is evaluated relative to the odds at the mean value of the pollutant. For example, if $p = 0.4$ at N deposition = $5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for mortality of trees with top damage, then the odds are $0.4/(1-0.4) = 0.67$. Therefore, we should expect a 0.1 fold increase in the odds for each $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ increase in N deposition (up to $25 \text{ kg ha}^{-1} \text{ yr}^{-1}$). At N deposition = $25 \text{ kg ha}^{-1} \text{ yr}^{-1}$ this leads to an increase in probability of mortality to 57%² from the assumed 40% at N deposition = $5 \text{ kg ha}^{-1} \text{ yr}^{-1}$.

Pollutant (unit)	Tree Top Damage Pollutant range	Change in odds	Tree Mortality Pollutant range	Change in odds Damaged tops	Undamaged tops
N deposition ($\text{kg ha}^{-1} \text{ yr}^{-1}$)	≤ 5	$+ 0.35 \pm 0.05$ per unit	≤ 25	$+ 0.1 \pm 0.04$ per unit	n.s. ³
	> 5	Plateau ⁴	> 25	Plateau ⁴	n.s.
S deposition ($\text{kg ha}^{-1} \text{ yr}^{-1}$)	≤ 1.5	$+ 2.2 \pm 0.5$ per unit	≤ 1.5	$+ 0.1 \pm 0.04$ per unit	n.s.
	> 1.5	Plateau ⁴	> 1.5	Plateau ⁴	n.s.
				Damaged or undamaged tops	
			≤ 30	$- 0.1 \pm 0.05$ per unit	
Ozone index (ppb)	All	n.s.	> 30	Plateau ⁴	

¹The odds of tree mortality refers to mortality occurring between T1 (the initial site visit) and T2 (the second site visit), which on average was a time interval of 9.9 years.

²Calculated as $\frac{\{0.67 \times [0.1 \times (25 - 5)]\}}{1 + \{0.67 \times [0.1 \times (25 - 5)]\}} = 0.57$.

³n.s. not significant (P-value < 0.05).

⁴Plateau means no further significant increase with increasing pollutant above the specified threshold.

species vary widely in their degree of ozone sensitivity (Miller et al., 1983). However negative effects on tree growth under field conditions are more difficult to determine (Arbaugh et al., 1999; Etzold et al., 2020; Paoletti, 2006) or are not observed (Cailleret et al., 2018; Ferretti et al., 2018; Verryckt et al., 2017). In a recent review of ozone impacts on forest growth in Europe, Cailleret et al. (2018) concluded that ozone effects on growth of forest trees seem negligible for various reasons, including the presence of confounding factors such as drought, N fertilization, past land use and management. They also state that “ozone concentration is usually positively correlated with air temperature and N deposition (see also, De Vries et al., 2014b), which both can be related to increased tree growth”. Furthermore, high levels of N deposition were reported to ameliorate some of the phytotoxic effects of ozone on photosynthetic pigment concentrations in ponderosa pine (Grulke, 1999).

In a study of European forests, Etzold et al. (2020) found that stomatal ozone flux was positively related to stem volume growth for Norway spruce (*Picea abies* (L.) H. Karst) and pine (*Pinus sylvestris* L.), but not for beech (*Fagus sylvatica* L.) and oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.). The authors concluded that the positive response to ozone was likely due to collinearity with temperature and N deposition. However, AOT40 (cumulative ozone exposure above 40 ppb) showed a non-linear relationship in spruce and pine with increased growth up until a threshold, after which growth declined. However, from the statistical models used, ground-level ozone showed little evidence of a generalized relationship with stem volume growth (Etzold et al., 2020). In summary, broad-scale studies in Europe (Cailleret et al., 2018; Etzold et al., 2020) confirm our findings in California of an apparent increased stem growth as ozone exposure increases, although it is difficult to disentangle this response from the effects of co-occurring factors such as increased temperature and N deposition.

For those tree species that are found across a broad range of air pollution exposures (Fig. C.2), which are primarily those associated with the mixed conifer zone in mid-elevation sites, the highest CI responses were observed in FIA plots where maximum values of N deposition and ozone co-occur. At lower ozone levels and with N deposition < $15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ozone reduces C allocation belowground, resulting in greater C accumulation in the bole. As ozone increases (ozone index ca. 20–35 ppb) sensitive species such as ponderosa pine begin to be more negatively affected by ozone, presumably with overall reduced tree growth. Then as N deposition reaches $\geq 25 \text{ kg ha}^{-1} \text{ yr}^{-1}$

CI begins to increase again. This may be because at the highest N deposition levels enough of the deposited N is biologically available to compensate for ozone injury and to cause a greater fertilization effect, resulting in increasing CI. Increased N can also provide added N for reparation of photosynthetic pigments in ozone-damaged foliage (Beyers et al., 1992; Grulke, 2003). However, our statistical model could not formally test for an interaction between ozone and N. Furthermore, Cailleret et al. (2018) concluded that the interdependency among environmental drivers such as climate, atmospheric deposition and biotic stressors, ultimately leads to complex synergistic and antagonistic relationships that are difficult to disentangle and predict. Ozone concentration is usually positively correlated with air temperature and N deposition (De Vries et al., 2014b), which are both related to increased tree growth in various geographical regions (Cailleret et al., 2018).

4.3. Coastal forest responses to N deposition

This study and another FIA-based study looking at 94 species in the continental U.S. (Horn et al., 2018) found that in California, the dominant region of C increment increase in response to N deposition is along the NW coast of California, a region where California redwood and tanoak are common species. Mean CI per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N from atmospheric deposition in the forests of the Northern California Coast ecoregion was $19.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of C, which is nearly five times the statewide average of 4.2. This strong N response in coastal ecoregions likely results from redwood's legendary growth rates and favorable growth conditions (Olson et al., 1990). We offer four plausible explanations for the high level of responsiveness of redwood trees to N deposition.

- (1) Greater humidity likely enhances canopy uptake of atmospheric N via stomata and foliar surfaces (Gessler et al., 2002), twigs, branches and bark (Dail et al., 2009; Earles et al., 2016; Fenn et al., 2013). The more humid coastal environment also enhances the solubility of N compounds within the canopy and within the rooting zone, leading to greater canopy and root utilization of atmospheric reactive N. Simultaneously, the frequent fog exposure during the otherwise dry summer season, in conjunction with high annual precipitation in the northern California coastal regions (as much as 3000 mm), relieves much of the drought stress to which most of California is exposed in spring and summer. Templer et al. (2015)

found that summer fog provides nitrogen for direct canopy uptake and assimilation and increases throughfall canopy drip, providing N for root uptake, especially at the forest edge. Thus summer fog and ocean aerosols (Zinke et al., 1996) provide nutrients and moisture, affecting the physiologic function and growth of redwood trees. The response of redwoods to low levels of atmospheric N may be favored by preferential direct canopy uptake of $\text{NO}_3\text{-N}$ which is common in humid forests of the Pacific Northwest and other mesic and humid regions (Fenn et al., 2013). Coastal species such as redwood may also be predisposed to positive growth response to added N because of the inputs of other macro and micro nutrients, including Mg, S and B (Zinke et al., 1996), from seasalt deposition (Fenn & Kiefer, 1999; Parker, 1983) that may alleviate co-occurring nutrient deficiencies such as potassium or S (Mika et al., 1992; Sardans & Peñuelas, 2015; Schmalz & Coleman, 2011). Precipitation and throughfall are generally influenced by sea salt at sites within approximately 100 km from the coastline (Fenn & Kiefer, 1999; Parker, 1983). European studies have also found that: (1) the forest growth effect of N deposition only becomes apparent when growth-limiting factors other than N, such as light, other nutrients or water are in sufficient supply (Bernhardt-Römermann et al., 2015); and (2) increased tree growth (probably due to elevated CO_2 and N availability) and resulting higher nutrients demands, led to decreasing foliar concentrations, down to levels that are characterized as “low” or “deficient” for P (and sometimes also other nutrients, such as S and Mg) in a number of tree species (Jonard et al., 2015).

- (2) Redwood tree roots are colonized by arbuscular mycorrhizae. The growth of tree species associated with arbuscular mycorrhizal fungi exhibit a stronger growth response to added N than do trees with ectomycorrhizal fungi as symbionts. This has been demonstrated previously in response to N deposition in large scale field surveys using FIA data (Averill et al., 2018; Horn et al., 2018; Thomas et al., 2010) and in other studies (Phillips et al., 2013). Three of the 18 species in this study are colonized by arbuscular mycorrhizae: redwood, western juniper and incense-cedar. All three exhibited a significantly positive CI response with increasing N deposition. Tanoak trees overlap a great deal with redwood but had a lower growth response to N deposition. The lower N response for tanoak could be related to the fact that tanoak is ectomycorrhizal while redwood has arbuscular mycorrhiza. In addition, the range of tanoak extends farther from the coast where the much lower precipitation and fogwater inputs are less favorable to tree growth and utilization of available N compared to the coastal zone to which redwood is restricted.
- (3) Coastal species in California, such as redwood and tanoak grow on soils underlain by sedimentary deposits rich in geologic N that have been shown to foster greater forest growth and soil fertility (Morford et al., 2011; 2016). Moreover, mild winter temperatures in coastal forests are generally less restrictive to biological activity.
- (4) The coastal ecoregions where redwood trees are common are generally located upwind of agricultural NH_3 emissions source areas. As a result, redwood trees are exposed to atmospheric N inputs with much lower $\text{NH}_4\text{-N}:\text{NO}_3\text{-N}$ ratios (Ewing et al., 2009; 2012). Inasmuch as $\text{NH}_4\text{-N}$ deposition has been shown to be more harmful to vegetation than $\text{NO}_3\text{-N}$ deposition (Britto & Kronzucker, 2002; Stevens et al., 2011; Van den Berg et al., 2016), the higher proportion of oxidized N inputs in coastal areas may also contribute to the greater growth response observed. The proportion of wet inorganic N deposition as $\text{NH}_4\text{-N}$ is generally within the range of 70 to 80% in Sierra Nevada foothill and montane sites located to the east of the extensive agricultural emissions source area in the Central Valley of California. In contrast, along western coastal sites not influenced by agriculture and at inland sites remote from major agricultural emissions, the proportion of wet deposition as ammonium is lower at 50–60% (Fenn et al., 2018; Ewing et al., 2009).

However, in fogwater at a coastal Redwood site in Sonoma county in northern California, $\text{NO}_3\text{-N}$ concentrations were 5-fold greater than $\text{NH}_4\text{-N}$ concentrations (Ewing et al., 2009).

4.4. Effects of S deposition on annual C increment

With a few exceptions, the CI response of most conifers to S deposition was positive and for most hardwoods, was negative. This was surprising given that (1) levels of S deposition in the FIA plots (ca. $0.3 - 3.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$) were as low as one tenth those observed in Europe, the eastern U.S. and parts of Asia, and (2) forest soils in California are generally well buffered and thus not predisposed to S-induced acidification. The pattern of greater sensitivity of hardwoods comports with Horn et al. (2018; see their [Supporting Information](#)), which reports a negative response to S deposition in 61% of the hardwoods vs. 39% of the conifers.

Although S is not typically considered limiting to tree growth (Fisher & Binkley, 2000), our analysis suggests S deposition exerts a growth-promoting influence in some California forests. Others (Blake et al., 1990; Mika et al., 1992; Schmalz & Coleman, 2011) have found that S availability limits the maximum growth response of Douglas-Fir, lodgepole pine and ponderosa pine to added N. Lodgepole pine was among the species responding positively to increased S deposition in our study, suggesting that the supposition in a countrywide FIA study (Horn et al., 2018) that S deposition would not increase growth cannot be universally applied, particularly in semi-arid forests less vulnerable to soil acidification impacts.

4.5. Effect of N deposition on C sequestration in CA forests

In European-scale studies basal area increment increased by $1.2 - 1.5\%$ per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N deposition (De Vries et al., 2014b), and averaged across 71 tree species evaluated in the conterminous United States, tree growth showed a net increase of 1.7% per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N deposition (Horn et al., 2018). These are similar to our estimated 1.7% increase in bole CI per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N deposition for eight tree species in California, but lower than a European-wide inventory-based study with an estimated N-enhanced C sequestration in bolewood of 4.4% (De Vries et al., 2006). The average estimated C sequestration response reported for European forests was: 33 kg C/kg N^1 in bolewood (De Vries et al., 2006), 19 kg C/kg N in all woody biomass (stems, woody branches and roots; Solberg et al., 2009), and $21\text{--}26 \text{ kg C/kg N}$ for total forest C uptake (Laubhann et al., 2009). In a meta-analysis of forest fertilization studies, the estimated C sequestration rate in aboveground woody biomass for temperate forests averaged 12.7 kg C/kg N (Schulte-Uebbing & De Vries, 2018), resembling the estimate of 14.4 for C sequestration in aboveground woody biomass determined via stoichiometric scaling (De Vries et al., 2014a). Higher estimates of $34\text{--}61 \text{ kg C/kg N}$ deposition were reported by Thomas et al. (2010) for aboveground biomass in the northeastern U.S. and based on modelling estimates for temperate forests (Thomas et al., 2013). Our estimate of 13.6 kg C/kg N in bolewood for the more humid northern and central coast ecoregions is similar to many of these global and European estimates, but the statewide average for California (4.2 kg C/kg N) is much lower than published estimates. We hypothesize that this is due to the generally arid climate of California as discussed above.

4.6. Effects of N and S deposition on tree survival and damage

In trees with no top damage, N and S deposition did not have a significant effect on tree mortality. However, N and S deposition increased the odds of tree top damage, and trees thus damaged showed a

¹ $\text{kg C/kg N} = \text{kg ha}^{-1} \text{ yr}^{-1}$ of C sequestered per $\text{kg ha}^{-1} \text{ yr}^{-1}$ of N deposition.

marginal but significant increase in the odds of tree mortality with N and S deposition up to a threshold, after which no further mortality was observed. In central Europe forest growth has accelerated in response to increased temperature, extended growing seasons and atmospheric deposition (Pretzsch et al., 2018). Notably, this increased growth is also associated with a simultaneous 8–12% decrease in wood density since 1900. As a result, stem biomass increment increased 9–24 percentage points less compared to volume increment. The authors of the study concluded that tree stability against windthrow, wood strength, energy content and C sequestration are reduced as a consequence of the increased growth rates (Pretzsch et al., 2018). This may explain how atmospheric deposition could contribute to top damage in California.

Horn et al. (2018) confirmed findings of previous studies (Averill et al., 2018; Phillips et al., 2013) that tree species with arbuscular mycorrhizal associations tend to fare better than species with ectomycorrhizal symbionts under added N. For trees with crown damage there was a lower N deposition threshold for increased tree mortality in hardwoods (ca. 5 kg ha⁻¹ yr⁻¹) compared to conifers (ca. 10 kg ha⁻¹ yr⁻¹; data not shown). All six of the species with declining survival with increased N deposition in the nationwide FIA study (Horn et al., 2018) were hardwoods, consistent with our finding of a significant effect of N deposition on the probability of top damage in hardwoods but not conifers. The three species in the current study that are associated with arbuscular mycorrhizae (incense-cedar, redwood and western juniper) are coniferous species and thus part of the group less prone to mortality from low levels of N deposition. In summary, N and S deposition increased the odds of top damage in trees up to a deposition threshold, but did not significantly affect tree mortality in trees with no top damage.

The low levels of S deposition in California are not generally expected to cause detrimental effects. The effects of N and S deposition on tree mortality in trees without top damage in the present study were not significant, as might be expected considering the low levels of S deposition in California forests and the well buffered soils in California forests compared to forests of eastern North America exposed to elevated atmospheric deposition (Horn et al., 2018). Likewise, Horn et al. (2018) reported few instances of negative effects of S deposition on tree survival in California and over much of the Western U.S., although negative responses were much more common in forests in Utah and Colorado. Nonetheless, in the present study there was a small but significant effect of S deposition on survivability of trees that had crown damage. The mechanism for such an effect of low levels of S deposition in California forests is not clear.

4.7. Effects of ozone on tree survival and damage

Considering the phytotoxicity of ozone, the ozone response from the FIA data was unexpected and the mechanism causing the reduction in mortality at low to moderate ozone levels (up to ca. 30 ppb ozone index) is unknown. Based on previous studies we hypothesize some possible mechanisms explaining the ozone responses observed in the present study. Ozone initially stimulated foliar growth in an ozone-sensitive birch clone, but further exposure caused growth reductions (Pääkkönen et al., 1996). This hormetic response, by which low levels of a toxicant (or in some cases high concentrations) stimulate various endpoints or physiological processes, including growth, has been widely demonstrated for plants and other organisms (Calabrese & Blain, 2009), including for the response of plants to low doses of ozone (Agathokleous et al., 2019). It has also been demonstrated in a number of plant species, including pines and other trees, that ozone can induce plant defense mechanisms (Eckey-Kaltenbach et al., 1994; Schraudner et al., 1997), suggesting that a potential cause of reduced mortality at low to moderate ozone exposures could be enhanced disease resistance, but this would require further study.

The ozone sensitivity of plant species, including forest tree species in California, varies widely (Miller et al., 1983). The decreased

mortality with increasing ozone shown in Fig. 7 was observed only when trees from all 18 species, most of which are not ozone-sensitive based on visual injury surveys, were combined to increase the sample size for the analysis. The need for a large sample was implied by the findings of Cailleret et al. (2018) of only negligible ozone effects in European forests at broad scale, notwithstanding the many mechanistic studies showing physiological impacts of ozone in sensitive tree species. This finding may be attributable to confounding factors such as drought, variable land management, N deposition, differences among tree sizes and species.

5. Conclusions

Among the many factors driving tree growth and C increment, N deposition was comparatively minor, but statistically significant, nonetheless. Across all of California, and with the current range of N deposition, we estimate a 1.7% increase in bole C increment per kg ha⁻¹ yr⁻¹ increase in N deposition. Eighty-three percent of the estimated annual statewide N deposition-induced 0.16 Tg C increase in C increment occurred in the Central and Northern California Coast eco-sections (0.15 Tg C), even though these eco-sections account for only 7% of California's trees. Much of this C sequestration was attributed to redwood trees. The relatively arid Mediterranean climate that prevails in California results in a high N deposition threshold (25–30 kg ha⁻¹ yr⁻¹) for a growth response in most species; however, in the typically foggy and humid coastal eco-sections, redwood trees exhibited strong responses even at relatively low N deposition (ca. 2–15 kg ha⁻¹ yr⁻¹).

The effects of N deposition and ozone on aboveground tree growth are intricately linked, with both resulting in increased bole growth at sufficiently high levels. However, data are more limited at the highest ozone and N deposition levels, which increases uncertainty. Although aboveground tree growth tended to increase at high levels of ozone exposure and N deposition, previous studies indicate that these pollutants put trees at greater mortality risk in the face of drought, climate change, bark beetle outbreaks, and increased stand density resulting from long-term fire suppression. The positive and negative growth responses to S deposition were surprising considering the low levels of S deposition across California's forests and because S nutrient deficiency is purportedly rare. Nitrogen and S deposition increased the odds of crown damage and trees with crown damage were more likely to die.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

With gratitude for the dedication, over two decades, of nearly 200 FIA field crew, information management, and analytic staff responsible for collection and quality assurance for this inventory data. Funding for this study has been provided by the USDA Forest Service.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Appendix A

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118084>.

References

- Adams, P.C., & Christensen, G.A. (2012). A National Analytical Quality Assurance Program: Developing Guidelines And Analytical Tools For The Forest Inventory And Analysis Program. In: Will McWilliams & Francis A. Roesch (Eds.). Monitoring Across Borders: 2010 Joint Meeting of the Forest Inventory and Analysis (FIA) Symposium and the Southern Mensurationists (e-Gen. Tech. Rep. SRS-157. pp. 139-145) Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.
- Agathokleous, E., Belz, R.G., Calatayud, V., De Marco, A., Hoshika, Y., Kitao, M., Calabrese, E.J., 2019. Predicting the effect of ozone on vegetation via linear non-threshold (LNT), threshold and hormetic dose-response models. *Sci. Total Environ.* 649, 61–74.
- Agathokleous, E., Saitanis, C.J., Wang, X.N., Watanabe, M., Koike, T., 2016. A review study on past 40 years of research on effects of tropospheric O₃ on belowground structure, functioning, and processes of trees: a linkage with potential ecological implications. *Water Air Soil Pollut.* 227, 33.
- Arbaugh, M.J., Peterson, D.L., Miller, P.R., 1999. Air pollution effects on growth of ponderosa pine, Jeffrey pine, and bigcone Douglas-fir. In: In: Miller, P.R., McBride, J.R. (Eds.), *Oxidant Air Pollution Impacts in the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains*, (Ecological Studies 134. Springer-Verlag, New York, pp. 179–207.
- Averill, C., Dietze, M.C., Bhatnaga, J.M., 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. *Glob. Change Biol.* 24, 4544–4553.
- Avila, A., Aguilau, L., Izquieta-Rojano, S., García-Gómez, H., Elustondo, D., Santamaría, J.M., Alonso, R., 2017. Quantitative study on nitrogen deposition and canopy retention in Mediterranean evergreen forests. *Environ. Sci. Pollut. Res.* 24, 26213–26226.
- Bernhardt-Römermann, M., Baeten, L., Craven, D., De Frenne, P., Hédli, R., Lenoir, J., Verheyen, K., 2015. Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. *Glob. Change Biol.* 21, 3726–3737.
- Beyers, J.L., Riechers, G.H., Temple, P.J., 1992. Effects of long-term ozone exposure and drought on the photosynthetic capacity of ponderosa pine (*Pinus ponderosa* Laws). *New Phytol.* 122, 81–90.
- Blake, J.I., Chappell, H.N., Bennett, W.S., Webster, S.R., Gessel, S.P., 1990. Douglas-fir growth and foliar nutrient responses to nitrogen and sulfur fertilization. *Soil Sci. Soc. Am. J.* 54, 257–262.
- Braun, S., Rihm, B., Schindler, C., Fluckiger, W., 1999. Growth of mature beech in relation to ozone and nitrogen deposition: an epidemiological approach. *Water Air Soil Pollut.* 116, 357–364.
- Britto, D.T., Kronzucker, H.J., 2002. NH₄⁺ toxicity in higher plants: a critical review. *J. Plant Physiol.* 159, 567–584.
- Bussotti, F., Ferretti, M., 1998. Air pollution, forest condition and forest decline in Southern Europe: an overview. *Environ. Pollut.* 101, 49–65.
- Bytnerowicz, A., Fenn, M.E., 1996. Nitrogen deposition in California forests: a review. *Environ. Pollut.* 92, 127–146.
- Bytnerowicz, A., Fenn, M.E., Cisneros, R., Schweizer, D., Burley, J., Schilling, S.L., 2019. Nitrogenous air pollutants and ozone exposure in central Sierra Nevada and White Mountains of California – distribution and evaluation of ecological risks. *Sci. Total Environ.* 654, 604–615.
- Bytnerowicz, A., Fenn, M., Allen, E.B., Cisneros, R., 2016. Atmospheric Chemistry. In: Mooney, H., Zavaleta, E. (Eds.), *Ecosystems of California*. University of California Press, Oakland, California, pp. 107–128.
- Calabrese, E.J., Blain, R.B., 2009. Hormesis and plant biology. *Environ. Pollut.* 157, 42–48.
- Cailleret, M., Ferretti, M., Gessler, A., Rigling, A., Schaub, M., 2018. Ozone effects on European forest growth-towards an integrative approach. *J. Ecol.* 106, 1377–1389.
- Carter, T.S., Clark, C.M., Fenn, M.E., Jovan, S., Perakis, S.S., Riddell, J., Hastings, M.G., 2017. Mechanisms of nitrogen deposition effects on temperate forest lichens and trees. *Ecosphere* 8 (3), e01717. <https://doi.org/10.1002/ecs2.1717>.
- Craven, P., Wahba, G., 1978. Smoothing noisy data with spline functions. *Numer. Math.* 31, 377–403.
- Dail, D.B., Hollinger, D.Y., Davidson, E.A., Fernandez, I., Sievering, H.C., Scott, N.A., Gaige, E., 2009. Distribution of nitrogen-15 tracers applied to the canopy of a mature spruce-hemlock stand, Howland, Maine, USA. *Oecologia* 160, 589–599.
- De Vries, W., Solberg, S., Dobbertin, M., Sterba, H., Laubhann, D., van Oijen, M., Sutton, M.A., 2009. The impact of nitrogen deposition on carbon sequestration by European forests and heathlands. *For. Ecol. Manage.* 258, 1814–1823.
- De Vries, W., Dobbertin, M.H., Solberg, S., Van Dobben, H.F., Schaub, M., 2014b. Impacts of acid deposition, ozone exposure and weather conditions on forest ecosystems in Europe: an overview. *Plant Soil* 380, 1–45.
- De Vries, W., Du, E.Z., Butterbach-Bahl, K., 2014a. Short and long-term impacts of nitrogen deposition on carbon sequestration by forest ecosystems. *Curr. Opin. Environ. Sustain.* 9–10, 90–104.
- De Vries, W., Reinds, G.J., Gundersen, P., Sterba, H., 2006. The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Glob. Change Biol.* 12, 1151–1173.
- Earles, J.M., Sperling, O., Silva, L.C.R., McElrone, A.J., Brodersen, C.R., North, M.P., Zwieniecki, M.A., 2016. Bark water uptake promotes localized hydraulic recover in coast redwood crown. *Plant, Cell Environ.* 39 (2), 320–328.
- Eckey-Kaltenbach, H., Grosskopf, E., Sandermann, H., Ernst, D., 1994. Induction of pathogen defence genes in parsley (*Petroselinum crispum* L.) plants by ozone. In: *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences* 102. pp. 63–74.
- Etzold, S., Ferretti, M., Reinds, G.J., Solberg, S., Gessler, A., Waldner, P., de Vries, W., 2020. Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. *For. Ecol. Manage.* 458, 117762.
- Ewing, H.A., Weathers, K.C., Lindsey, A.M., Templer, P.H., Dawson, T.E., Bradbury, D.C., ...Boukili, V.K.S. (2012). Fog and soil weathering as sources of nutrients in a California redwood forest. In: Richard B. Standiford, Theodore J. Weller, Douglas D. Piirto, John D Stuart (tech. coordinators). *Proceedings of coast redwood forests in a changing California: A symposium for scientists and managers*. (Gen. Tech. Rep. PSW-GTR-238, pp. 265-272). Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- Ewing, H.A., Weathers, K.C., Templer, P.H., Dawson, T.E., Firestone, M.K., Elliott, A.M., Boukili, V.K.S., 2009. Fog water and ecosystem function: Heterogeneity in a California redwood forest. *Ecosystems* 12 (3), 417–433.
- Fenn, M.E., Bytnerowicz, A., 1997. Summer throughfall and winter deposition in the San Bernardino Mountains in southern California. *Atmos. Environ.* 31, 673–683.
- Fenn, M.E., Kiefer, J.W., 1999. Throughfall deposition of nitrogen and sulfur in a Jeffrey pine forest in the San Gabriel Mountains, southern California. *Environ. Pollut.* 104, 179–187.
- Fenn, M.E., Bytnerowicz, A., Schilling, S.L., 2018. *Passive monitoring techniques for evaluating atmospheric ozone and nitrogen exposure and deposition to California ecosystems*. (General Technical Report. PSW-GTR-257). Albany, CA: U.S. Department of Agriculture, Forest Ser. Pacific Southwest Res. Station.
- Fenn, M.E., Ross, C.S., Schilling, S.L., Baccus, W.D., Larrabee, M.A., Lofgren, R.A., 2013. Atmospheric deposition of nitrogen and sulfur and preferential canopy consumption of nitrate in forests of the Pacific Northwest, USA. *For. Ecol. Manage.* 302, 240–253.
- Fenn, M.E., Poth, M.A., Bytnerowicz, A., Sickman, J.O., & Takemoto, B.K. (2003a). Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada. In A. Bytnerowicz, M.J. Arbaugh, & R. Alonso (Eds.), *Developments in Environmental Science, Volume 2: Ozone Air Pollution in the Sierra Nevada: Distribution and Effects on Forests*. (pp. 111-155). Amsterdam: Elsevier.
- Fenn, M.E., Haeuber, R., Tonnesen, G.S., Baron, J.S., Grossman-Clarke, S., Hope, D., Sickman, J.O., 2003b. Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience* 53, 391–403.
- Fenn, M.E., Allen, E.B., Weiss, S.B., Jovan, S., Geiser, L., Tonnesen, G.S., Bytnerowicz, A., 2010. Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. *J. Environ. Manage.* 91 (12), 2404–2423.
- Fenn, M.E., & Poth, M.A. (2001). A case study of nitrogen saturation in western U.S. forests. In J. Galloway, E. Cowling, J.W. Erisman, J. Wisniewski, & C. Jordan (Eds.), *Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection: Proceedings of the 2nd International Nitrogen Conference*, 14-18 October 2001, Potomac, Maryland, USA. (pp. 433-439). Lisse, The Netherlands: A.A. Balkema Publishers, and TheScientificWorld, www.thescientificworld.com. DOI 10.1100/tsw.2001.280.
- Ferretti, M., Baraco, G., Brunialti, G., Confalonieri, M., Cristofolini, F., Cristofori, A., Gottardini, E., 2018. Scarce evidence of ozone effect on recent health and productivity of alpine forests-a case study in Trentino, N Italy. *Environ. Sci. Pollut. Res.* 25 (9), 8217–8232.
- Ferretti, M., Marchetto, A., Arisci, S., Bussotti, F., Calderisi, M., Carnicelli, S., Pompei, E., 2014. On the tracks of nitrogen deposition effects on temperate forests at their southern European range - an observational study from Italy. *Glob. Change Biol.* 20, 3423–3438.
- Fisher, R.F., Binkley, D., 2000. *Ecology and Management of Forest Soils*, 3rd ed. John Wiley & Sons Inc., New York, NY.
- Forest Climate Action Team. (2018). *California Forest Carbon Plan: Managing Our Forest Landscapes in a Changing Climate*. Sacramento, CA.
- Gessler, A., Rienks, M., Rennenberg, H., 2002. Stomatal uptake and cuticular adsorption contribute to dry deposition of NH₃ and NO₂ to needles of adult spruce (*Picea abies*) trees. *New Phytol.* 156, 179–194.
- Gulke, N.E. (1999). Physiological responses of ponderosa pine to gradients of environmental stressors., In: P.R. Miller and J.R. McBride (Eds.), *Oxidant Air Pollution Impacts in the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains* (Ecological Studies, vol. 134.,pp. 126-163). New York: Springer-Verlag.
- Gulke, N.E. (2003). The physiological basis of ozone injury assessment attributes in Sierran conifers. In A. Bytnerowicz, M.J. Arbaugh, & R. Alonso (Eds.), *Developments in Environmental Science, Volume 2: Ozone Air Pollution in the Sierra Nevada: Distribution and Effects on Forests*. (pp. 55-81), Amsterdam: Elsevier.
- Gulke, N.E., Balduman, L., 1999. Deciduous conifers: High N deposition and O₃ exposure effects on growth and biomass allocation in ponderosa pine. *Water Air Soil Pollut.* 116, 235–248.
- Gulke, N.E., Minnich, R.A., Paine, T.D., Seybold, S.J., Chavez, D.J., Fenn, M.E., ... Dunn, A. (2009). Air pollution increases forest susceptibility to wildfires: A case study in the San Bernardino Mountains in southern California. In: A. Bytnerowicz, M.J. Arbaugh, A.R. Riebau, & C. Andersen. (Eds.), *Wildland Fires and Air Pollution*. (Developments in Environmental Science, Volume 8, pp. 365-403), Amsterdam: Elsevier.
- Gulke, N.E., Andersen, C.P., Hogsett, W.E., 2001. Seasonal changes in above- and belowground carbohydrate concentrations of ponderosa pine along a pollution gradient. *Tree Physiol.* 21, 173–181.
- Gulke, N.E., Andersen, C.P., Fenn, M.E., Miller, P.R., 1998. Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California. *Environ. Pollut.* 103, 63–73.
- Holland, E.A., Dentener, F.J., Braswell, B.H., Sulzman, J.M., 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46, 7–43.
- Horn, K.J., Thomas, R.Q., Clark, C.M., Pardo, L.H., Fenn, M.E., Lawrence, G.B., Watmough, S., 2018. Growth and survival relationships of 71 tree species with nitrogen and sulfur deposition across the conterminous U.S. *PLoS ONE* 13, e0205296.

- <https://doi.org/10.1371/journal.pone.0205296>.
- Jonard, M., Fürst, A., Verstraeten, A., Thimonier, A., Timmermann, V., Potocic, N., Rautio, P., 2015. Tree mineral nutrition is deteriorating in Europe. *Glob. Change Biol.* 21, 418–430.
- Jones, M.E., Paine, T.D., Fenn, M.E., Poth, M.A., 2004. Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. *For. Ecol. Manage.* 200, 67–76.
- Laubhann, D., Sterba, H., Reinds, G.J., De Vries, W., 2009. The impact of atmospheric deposition and climate on forest growth in European monitoring plots: an individual tree growth model. *For. Ecol. Manage.* 258 (8), 1751–1761.
- Marra, G., Wood, S.N., 2012. Coverage properties of confidence intervals for generalized additive model components. *Scand. J. Stat.* 39, 53–74.
- McNab, W.H., Cleland, D.T., Freeouf, J.A., Keys, J.E., Nowacki, G.J., & Carpenter, C.A. (2007). Description of ecological subregions: sections of the conterminous United States. (General Technical Report WO-76B), Washington, DC: U.S. Department of Agriculture, Forest Service.
- Melson, S., Azuma, D., & Fried, J.S. (2002). A first look at measurement error on FIA plots using blind plots in the Pacific Northwest. In: R.E. McRoberts, G.A. Reams, P.C. Van Deusen, & J.W. Moser (Eds.), *Proceedings of the Third Annual Forest Inventory and Analysis Symposium* (General Technical Report NC-230, pp. 11–20) St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station.
- Mika, P.G., Moore, J.A., Brockley, R.P., Powers, R.F., 1992. Fertilization response by interior forests: when, where and how much? In: Chappell, H.N., Weetman, G.F., Miller, R.E. (Eds.), *Forest fertilization: sustaining and improving nutrition and growth of western forests*. College of Forest Resources, University of Washington, Seattle, WA, pp. 127–142.
- Miller, P.R., Longbotham, G.J., Longbotham, C.R., 1983. Sensitivity of selected western conifers to ozone. *Plant Dis.* 67, 1113–1115.
- Mills, G., Harmens, H., Wagg, S., Sharps, K., Hayes, F., Fowler, D., Davies, B., 2016. Ozone impacts on vegetation in a nitrogen enriched and changing climate. *Environ. Pollut.* 208, 898–908.
- Morford, S.L., Houlton, B.Z., Dahlgren, R.A., 2016. Direct quantification of long-term rock nitrogen inputs to temperate forest ecosystems. *Ecology* 97, 54–64.
- Morford, S.L., Houlton, B.Z., Dahlgren, R.A., 2011. Increased forest ecosystem carbon and nitrogen storage from nitrogen rich bedrock. *Nature* 477, 78–81.
- Nychka, D., 1988. Bayesian confidence intervals for smoothing splines. *J. Am. Stat. Assoc.* 83, 1134–1143.
- Olson, D.F., Jr., Roy, D.F., & Walters, G.A. (1990). *Sequoia sempervirens* (D. Don) Endl. Redwood. In: R.M. Burns & B.H. Honkala (Eds.), *Silvics of North America*, Vol. 1, Conifers. (Agriculture Handbook 654, pp. 541–551). Washington, DC: United States Department of Agriculture, Forest Service.
- Pääkkönen, E., Vahala, J., Holopainen, T., Karjalainen, R., Kärenlampi, L., 1996. Growth responses and related biochemical and ultrastructural changes of the photosynthetic apparatus in birch (*Betula pendula*) saplings exposed to low concentrations of ozone. *Tree Physiol.* 16, 597–605.
- Padgett, P.E., Cook, H., Bytnerowicz, A., Heath, R.L., 2009. Foliar loading and metabolic assimilation of dry deposited nitric acid air pollutants by trees. *J. Environ. Monit.* 11, 75–84.
- Paoletti, E., 2006. Impact of ozone on Mediterranean forests: A review. *Environ. Pollut.* 144, 463–474.
- Parker, G.G., 1983. Throughfall and stemflow in the forest nutrient cycle. *Adv. Ecol. Res.* 13, 57–133.
- Phillips, R.P., Brzostek, E., Midgley, M.G., 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytol.* 199, 41–51.
- Pretzsch, H., Biber, P., Schütze, G., Kemmerer, J., Uhl, E., 2018. Wood density reduced while wood volume growth accelerated in Central European forests since 1870. *For. Ecol. Manage.* 429, 589–616.
- R Core Team. (2018). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing, <https://www.R-project.org/>.
- Sardans, J., Peñuelas, J., 2015. Potassium: a neglected nutrient in global change. *Glob. Ecol. Biogeogr.* 24, 261–275.
- Schmalz, H.J., Coleman, M.D., 2011. Foliar sulfate-sulfur as a nutrient diagnostic tool for interior Douglas-fir. *West. J. Appl. For.* 26, 147–150.
- Schraudner, M., Langebartels, C., Sandermann, H., 1997. Changes in the biochemical status of plant cells induced by the environmental pollutant ozone. *Physiol. Plant.* 100, 274–280.
- Schulte-Uebbing, L., De Vries, W., 2018. Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate, and boreal forests: a meta-analysis. *Glob. Change Biol.* 24, e416–e431. <https://doi.org/10.1111/gcb.13862>.
- Schwede, D.B., Lear, G.G., 2014. A novel hybrid approach for estimating total deposition in the United States. *Atmos. Environ.* 92, 207–220.
- Smil, V., 2001. *Enriching the Earth: Fritz Haber, Carl Bosch, and the Transformation of World Food Production*. The MIT Press, Cambridge, MA.
- Solberg, S., Dobbertin, M., Reinds, G.J., Lange, H., Andreassen, K., Garcia Fernandez, P., ... de Vries, W. (2009). Analyses of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: A stand growth approach. *For. Ecol. Manage.*, 258(8), 1735–1750.
- Stephens, S.L., Collins, B.M., Fettig, C.J., Finney, M.A., Hoffman, C.M., Knapp, E.E., ... Wayman, R.B. (2018). Drought, tree mortality, and wildfire in forests adapted to frequent fire. *BioScience*, 68, 77–88.
- Stevens, C.J., Manning, P., Van Den Berg, L.J.L., De Graaf, M.C.C., 2011. Ecosystem responses to reduced and oxidised nitrogen inputs in European terrestrial habitats. *Environ. Pollut.* 159, 665–676.
- Temple, P.J., & Miller, P.R. (1998). Seasonal influences on ozone uptake and foliar injury to ponderosa and Jeffrey pines at a southern California site. In: A. Bytnerowicz, M.J. Arbaugh, & S.L. Schilling (Tech. Coord.), *Proceedings of the International Symposium, Air Pollution and Climate Change Effects on Forest Ecosystems*. Feb. 5–9, 1996, Riverside, CA. (General Technical Report, PSW-GTR-166, pp. 221–228) Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.
- Templer, P.H., Weathers, K.C., Ewing, H.A., Dawson, T.E., Mambelli, S., Lindsey, A.M., Firestone, M.K., 2015. Fog as a source of nitrogen for redwood trees: evidence from fluxes and stable isotopes. *J. Ecol.* 103, 1397–1407.
- Thomas, R.Q., Bonan, G.B., Goodale, C.L., 2013. Insights into mechanisms governing forest carbon response to nitrogen deposition: a model–data comparison using observed responses to nitrogen addition. *Biogeosciences* 10, 3869–3887.
- Thomas, R.Q., Canham, C.D., Weathers, K.C., Goodale, C.L., 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nat. Geosci.* 3, 13–17.
- Tonnesen, G., Wang, Z., Omary, M., Chien, C.-J., 2007. Assessment of nitrogen deposition: Modeling and habitat assessment. California Energy Commission, PIER Energy-Related. *Environ. Res CEC-500-2006-032*.
- USDA Forest Service, Office of Sustainability and Climate, Washington, D.C. (2017). *Drought and Tree Mortality in the Pacific Southwest Region*. A synopsis of presentations and work group sessions from the Symposium held July 2017, Sacramento, CA. Science and Management Symposium—Lessons Learned From Extreme Drought and Tree Mortality in the Sierra Nevada: How Can Past Events Inform Our Approach Forward?.
- Van den Berg, L.J.L., Jones, L., Sheppard, L.J., Smart, S.M., Bobbink, R., Dise, N.B., Ashmore, M.R., 2016. Evidence for differential effects of reduced and oxidised nitrogen deposition on vegetation independent of nitrogen load. *Environ. Pollut.* 208, 890–897.
- Verryckt, L.T., Op De Beeck, M., Neiryck, J., Gielen, B., Roland, M., Janssens, I.A., 2017. No impact of tropospheric ozone on the gross primary productivity of a Belgian pine forest. *Biogeosciences* 14, 1839–1855.
- Wahba, G. (1990). Spline Models for Observational Data. CBMS-NSF Regional Conference Series in Applied Mathematics, Soc. Indust. Appl. Math., vol. 59. 161 pp. <https://doi.org/10.1137/1.9781611970128>.
- Wang, T., Hamann, A., Spittlehouse, D., Carroll, C., 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* 11 (6), e0156720. <https://doi.org/10.1371/journal.pone.0156720>.
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction with R*, 2nd edition. Chapman and Hall/CRC Press, Boca Raton, Florida.
- Wood, S.N., Pya, N., Saefken, B., 2016. Smoothing parameter and model selection for general smooth models (with discussion). *J. Am. Stat. Assoc.* 111, 1548–1575.
- Zinke, P.J., Stangenberger, A.G., & Bertenshaw, J.L. (1996). Pattern and process in forests of *Sequoia sempervirens* (D. Don) Endl. In: J.W. LeBlanc (Ed.), *Proceedings of the Conference on Coast Redwood Forest Ecology & Management: June 18–20, 1996*, (pp. 26–38). Arcata, CA: Humboldt State University.