

Fuel treatment effects on soil chemistry and foliar physiology of three coniferous species at the Teakettle Experimental Forest, California, USA

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Abstract A full factorial design crossing overstory (O) and understory (U) thinning and prescribed burning (B) was started at Teakettle Experimental Forest, California, in 2001 with the aim of achieving shifts in species composition to favor fire-resistant pines over fir. The goal of the present study was to evaluate the use of metabolic changes as early indicators for predicting the effects of these treatments on species-specific growth and long-term productivity of *Pinus jeffreyi*, *Pinus lambertiana*, and *Abies concolor*. Foliar polyamines, amino acids, soluble proteins and chlorophyll were quantified and related with foliar and soil chemistry. Most changes in soil chemistry occurred only with combined treatments (BU or BO). Changes in foliar metabolism were not driven by soil chemistry. In general, the pines were more sensitive to water stress as compared to fir as indicated by proline content. Understory thinning had no effect on any species. Both O and BO had species-specific effects on foliar amino acids, chlorophyll, soluble proteins, and inorganic ions.

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In addition, both O and BO were the most extreme thinning treatments for pines as they greatly increase the time needed to replenish carbon stocks. With the exception of some amino acids, B by itself had no major effects on foliar inorganic ions, chlorophyll content, and polyamines for any of the three species while BU caused a decrease in chlorophyll in white fir, suggesting a decline in photosynthetic capacity. These data point to BU as the best management option to specifically decrease the growth of fire-sensitive white fir without a major impact on pines.

Keywords Understory thinning · Overstory thinning · Jeffrey pine · Sugar pine · White fir · Prescribed burn

Abbreviations

Con	Control
B	Burn only
U	Understory thin
O	Overstory thin
BU	Burn + understory thin
BO	Burn + overstory thin
Chl	Chlorophyll
Put	Putrescine
Spd	Spermidine
Spm	Spermine
GABA	γ -Aminobutyric acid

Introduction

Forested lands in the United States can serve as a large sink for terrestrial carbon (C) (Woodbury et al. 2007) and these C stocks are directly affected by land use and fire management practices (Hurtt et al. 2002). In many areas of western North America where long-term fire suppression

practices can lead to intense stand-replacing forest fires, management practices often focus on decreasing fuel loads to reduce fire intensity and severity. There are three main fuel reduction practices: mechanical thinning, prescribed fire, and a combination of both. In the long-term, these practices may lessen C loss from combustion if the treated forest is burned by wildfire (Hurteau and North 2008; North and Hurteau 2011; Stephens et al. 2009). Since forests play an important role in reducing global warming via this C sequestration, it becomes a challenge for forest managers to choose the right combination of thinning and prescribed fire that minimizes the release of C into the atmosphere and yet maximizes long-term net productivity.

Nitrogen is considered the most limiting nutrient in natural forest ecosystems. Therefore, it requires special consideration when managing fire, particularly in N-deficient ecosystems (Maars et al. 1983). Of all nutrients, nitrogen is most easily vaporized and lost from the forest during fire, followed by sulfur and phosphorus (McNabb and Cromack 1990). While total N decreased as a result of combustion leading to a decrease in soil C:N ratio, there was a temporary increase in plant available N, particularly NH_4^+ -N, due to increased mineralization by soil microbes (Neary et al. 2008 and references therein). This causes misleading short-lived increases in plant growth and productivity. Smith et al. (2008) showed that in a spruce-dominated boreal forest, burning with or without harvesting caused an increase in soil available NO_3^- and NH_4^+ within the first year of treatment. De Luca and Zouhar (2000) reported a short-term increase in bacterial biomass N, extractable NH_4^+ and NO_3^- , and soluble sugars when thinning was combined with prescribed burning treatment in a study that compared three second-growth ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forests growing within the vicinity of each other in western Montana. Most of these changes were transient and were not observed 2 and 11 years post-treatment. Long-term effects of these treatments on site productivity were not clear even after 11 years post-treatment. These authors recommended that the loss of N from the ecosystem should be considered along with stand mortality and yield when assessing the potential sustainability of forest management strategies. Changes in N availability have been shown to regulate cellular N metabolites, especially those that play a specific role in growth and stress responses (Bauer et al. 2004; Minocha et al. 2000).

Changes in the levels of chlorophyll in foliage have been used as important ecophysiological parameters to evaluate photosynthetic activity and changes in the ratio of chlorophyll *a/b* have been used as an indicator of abiotic stress in plants (Larcher 1995). It provides an indirect measure of leaf nitrogen (since chlorophyll contains nitrogen in its structure) and in turn nutrient status. Thus,

chlorophyll and nitrogen measurements are being used as key drivers of photosynthetic capacity in most current gross primary productivity models (Ollinger and Smith 2005; Smith et al. 2002).

Cellular polyamines [putrescine (Put), spermidine (Spd), and spermine (Spm)] and several amino acids act as N storage compounds and can lessen the toxic effects of excess N in plants. Polyamines are also required for cell growth and development (Evans and Malmberg 1989). A threshold amount of Put is required for growth which varies with species, and an increase above this threshold often indicates physiological stress stemming from a variety of factors such as excess N, Ca deficiency and pathogen infections. The breakdown of polyamines produces precursors to the tri-carboxylic acid (TCA) cycle (Suppl. Fig. 1). Thus, any effects in their levels are indicative of changes in related C and N metabolites within the cells such as amino acids. Cellular amino acid concentrations have also been shown to depend on several factors including N (Ericsson et al. 1993).

Sierra Nevada forests contain over 50 % of California's herbaceous taxa as well as a high number of rare endemic species (Shevock 1996). Over time, large fire-resistant pines at this site have mostly been replaced by fire-sensitive white fir and incense-cedar due to fire suppression policies. With the aim of achieving shifts in species composition to favor fire-resistant pines over fir, a study was initiated in 1997 to evaluate the effects of thinning and prescribed fire treatments on reductions in forest fuels, species-specific ecosystem functions, and site productivity at the Teakettle Experimental Forest (hereafter referred to as Teakettle) in the southern Sierra Nevada region of California. Innes et al. (2006) reported a marked decrease in fine and coarse woody debris within the initial 3 years of fuel reduction treatments. Treatments increased variability in ground and canopy microclimate conditions (Ma et al. 2010; Rambo and North 2009), which in turn were associated with increases in species richness and the extent of herbaceous coverage in the understory plant community (Wayman and North 2007). Burning reduced shade-tolerant species such as white fir and incense-cedar while increasing more fire-resistant species such as Jeffrey pine, thus indicating that burning was an effective treatment to regenerate fire-resistant coniferous species (North et al. 2007; Zald et al. 2008). Thinning in combination with prescribed fire decreased understory stem densities and shrub cover (Gray et al. 2005; North et al. 2007). Decreases in stem densities associated with thinning can increase soil moisture availability (Haig et al. 1941), and this change in available moisture in turn can cause changes in the soil respiration rate (SRR) (Concilio et al. 2006) which plays a vital role in carbon cycling (Schlesinger and Andrews 2000). Hurteau and North (2009, 2010) reported in detail

the effects of these treatments at Teakettle on C stocks. Overall results from the Teakettle experiment suggest many processes and forest structural conditions were most effectively restored with the combined understory thinning and prescribed fire treatment, possibly due to the high amount of heterogeneity it produced in forest microclimate and habitat conditions (North et al. 2007; Wayman and North 2007; Zald et al. 2008).

No investigations have been conducted at Teakettle to evaluate the effects of prescribed treatments on the physiology of the remaining trees. Along with providing a mechanistic understanding of how fire and/or thinning affects cellular metabolism, the measurement of changes in some metabolites can be used as stress indicators in trees to help evaluate forest health and stand productivity (Minocha et al. 2000; Minocha et al. 2010). The goal of this study was to evaluate the long-term effects of forest management on species-specific physiology of Jeffrey pine, sugar pine, and white fir. Currently, this forest is dominated by thin-bark, fire-sensitive white fir. The objectives of the present study were to determine the effects of thinning, prescribed burning, and thinning combined with prescribed burning 8–9 years post-treatment on the cellular levels of: (1) free polyamines; (2) free amino acids; (3) soluble proteins and chlorophyll in the foliage; (4) soil and foliar cations; and (5) soil and foliar total C and N. We hypothesize that the relatively long-term (9 years post-treatment) changes observed in a few chosen metabolites from the present study can serve as indicators to predict changes in species-specific growth responses. The results of this study would aid in further evaluating the best possible combination(s) of treatments that promote the pine population while suppressing the fir population.

Materials and methods

Study area

The Teakettle Experimental Forest (Teakettle) is a 1,300 ha old-growth forest located in the Sierra National Forest on the western slope of the southern Sierra Nevada Mountains, California. The area typically experiences hot dry summers and mild moist winters with mean of 75 ± 25 cm of precipitation per year (Balch Power House, nearest climate station, average of 1950–2012) mostly in the form of snow between November and April. However, the precipitation average during the years of our collections and a year prior to that (2007–2009) was only 40 ± 25 cm. Elevation in the study area ranges from 1,900 to 2,200 m. Soil pH is approximately 5.4 (Meyer et al. 2007b). The Teakettle mixed-conifer forest includes Jeffrey pine (*Pinus*

jeffreyi), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), red fir (*Abies magnifica*), incense-cedar (*Calocedrus decurrens*), and black oak (*Quercus kelloggii*). The dominant shrub is whitethorn ceanothus (*Ceanothus cordulatus*), a nitrogen fixer.

In 1998, 18 permanent 4 ha plots (200×200 m [with a 50 m buffer between plots]) were established at Teakettle. Variogram analysis was used to estimate an area sufficiently large enough per plot to include the range of variable forest conditions that exist at this site. Pre-treatment analysis found no differences in forest structure and composition among plots (North et al. 2009). Three replicates of six treatments were randomly applied using a full factorial design with two levels of burning (burn and no burn) crossed with three levels of thinning including understory (following California Spotted Owl, or CASPO, guidelines), overstory (shelterwood), and no thinning. Following common thinning practices in the Sierra Nevada, harvested trees were de-limbed and branches were left on site and the noncommercial top (<6 in. diameter) was skidded to the landing, piled, and burned 1 year later. Thinning treatments were applied in the fall of 2000 to the plots that were to be thinned and burned, and in the early spring of 2001 to the plots that were to be only thinned. The prescribed fire treatment was applied in the fall of 2001, after fuels had a year to dry (North et al. 2002). Thermocouples were not deployed before prescribed burns. However, percent ash cover and flame char heights on tree boles were recorded for each plot. These values were 14.2 % and 0.4 m, respectively, for burn only plots; 36.4 % and 1.1 m for burning combined with understory thinning; and 48.1 % and 1.6 m for burning combined with shelterwood thinning. Variability with prescribed burning was high, ranging from areas without any burn to 100 % ash and 5.4 m bole char. Overall variability decreased with thinning intensity (i.e., more fuel means more uniformly intense fires). These indirect measures suggest that fire temperature increased with thinning intensity. See <http://teakettle.ucdavis.edu> for more site and treatment information.

Soil sample collection and analyses

In 2008 (8 years after the start of treatments), three soil cores were taken from each of the nine permanent sample grid points (50×50 m spacing) within each treatment plot using an AMS standard 5.8 cm soil auger. The litter layer was removed before taking soil samples. Each of the three samples from each grid point were subdivided by depth into 0–10 cm (topsoil) and 10–30 cm (subsoil) layers, kept on ice for no more than 10 h, and air-dried to constant mass. A total of 27 individual soil samples were collected

for each soil depth. Soils were passed through a 2-mm sieve and then analyzed by the ANR analytical laboratory at the University of California, Davis. Total carbon and nitrogen were analyzed using a flash combustion method (SOP 320.02). Ammonium and NO_3^- were extracted in KCl from 12 out of 27 samples (4 samples from each of 3 replicate plots per treatment for each soil depth) and quantified via a flow injection system (SOP 312.02). Exchangeable calcium (Ca) and magnesium (Mg) (SOP 360.02), DTPA-extractable manganese (Mn) (SOP 380.02), and KCl-extractable aluminum (Al) (SOP 392.01) were all quantitated by inductively coupled plasma atomic emission spectrometry (ICP-AES). Phosphorous (P) was analyzed using the Bray method (SOP 355.02). See <http://anlab.ucdavis.edu> for further details on procedures.

Foliar sample collection and processing

In July 2008 and 2009, foliar samples of Jeffrey pine, sugar pine, and white fir were collected from the mid to upper canopy by shotgun. Visually healthy needles from these trees (50–70 m height) were collected from 5 randomly selected trees of the 3 species from each plot, making a total of 15 trees per species per treatment for the six treatments [control = Con, burn only = B, understory thin = U, overstory thin = O, burn + understory thin = BU, burn + overstory thin = BO]. With few exceptions, the same individuals were sampled for both years. Foliage from 270 trees was collected in each year. Using only current-year foliage from a single branch, a pool of approximately 500 mg of sample was collected from each tree and finely chopped using scissors. The clippings were mixed, and two sub-samples were taken for biochemical analyses. The first sub-sample, weighing approximately 200 mg fresh weight (FW), was placed in a pre-weighed 2-mL microfuge tube with 1 mL of 5 % perchloric acid (PCA); the remainder of the sample was placed in a separate dry tube. On the day of collection, all samples were collected and transported on ice and stored at -20°C until further analysis. The samples in PCA were weighed, frozen and thawed 3 times, mixed thoroughly, and then centrifuged at $14,000\times g$ for 8 min (Minocha et al. 1994). The supernatant was used for the analyses of PCA-extractable (free) polyamines (PAs), amino acids (AAs), and soluble inorganic ions. The set of dry samples were used for soluble proteins and total chlorophyll (Chl) analyses. Samples from each tree were analyzed separately for each parameter. Besides C and N samples which were analyzed only from the 2008 collection, all foliar analyses were conducted individually on each of the 90 foliar samples per species per year for 2008 and 2009.

Foliar total C, total N, and inorganic ions analyses

For the total percentage of C and N, needle samples were pooled from five trees per plot for each of three plots per treatment, dried at 70°C and analyzed by a CHNS analyzer (Thermo Scientific CE Elantech Flash EA1112 Soil) using a method developed and distributed by the EPA (EPA-144). National Institute of Standards and Technology (NIST, Gaithersburg, MD, USA) standards 1,515 (apple foliage) and 1,547 (peach foliage) were used for procedure verification.

Soluble inorganic ions (in 5 % PCA) were quantified using a simultaneous axial inductively coupled plasma emission spectrophotometer (Vista CCD, Varian Inc., Palo Alto, CA, USA) and Vista Pro software (Version 4.0), following appropriate dilutions of the PCA extracts with deionized water (Minocha et al. 2010).

Foliar biochemical analyses

For the analyses of soluble polyamines and amino acids, a fluorescent tag (dansyl group) was attached to the samples (supernatants of the PCA extracts) using dansyl chloride and the derivatives were quantified by HPLC (Perkin Elmer Inc., Waltham, MA, USA) according to Minocha and Long (2004). The reaction was terminated using L-asparagine (Asn) ($50\text{ }\mu\text{L}$ of 20 mg mL^{-1} in water) rather than with alanine as described in the original method. Following this protocol, the separation of Arg and Thr was not always complete. For their quantitation, the concentrations of these two amino acids were added together for each standard to formulate a combined calibration curve; at equal concentrations arginine (Arg) contributed most of the combined peak area.

For Chl analysis, 1 mL of 95 % ethanol was added to 10 mg of thawed needles. Samples were then incubated in the dark in a 65°C water bath for 16 h, centrifuged ($13,000\times g$ for 5 min), and the supernatants were scanned for absorbance ranging from 350 to 710 nm using a spectrophotometer (Hitachi Ltd, Tokyo, Japan). Chlorophyll was quantitated according to Minocha et al. (2009).

For soluble proteins, 0.25 mL of extraction buffer [100 mM Tris-HCl, 20 mM MgCl_2 , 10 mM NaHCO_3 , 1 mM EDTA, and 10 % (v/v) glycerol, pH 8.0] was added to 50 mg of thawed needles. Samples were then frozen and thawed three times and the supernatant was used for protein analysis according to Bradford (1976).

Statistical analyses

The data were evaluated with a hierarchy of repeated measures (for years 2008 and 2009) ANOVA analyses were conducted to examine what treatment and species

factors were most significantly associated with changes in foliar chemistry. Our goal was to identify how samples should be combined or stratified for statistical testing to help identify factors associated with differences in foliar chemistry. The data for each dependent parameter were first subjected to analysis using repeated measures ANOVA with species (three levels: Jeffrey pine, sugar pine, and white fir) as the main factor. *F* tests revealed significant differences between species ($P \leq 0.05$). Thus from there on, data for each species were analyzed individually. Data for each dependent parameter were subjected to analysis using repeated measures ANOVA with two main factors: prescribed burning (two levels: burn and no burn) crossed with thinning (three levels: no thinning, understory, and overstory). Since several dependent variables in the data showed significant interaction between thinning and burning ($P \leq 0.05$), we decided to conduct repeated measures ANOVA with treatment as the main factor. In cases where the *F* test was significant, Tukey's test was conducted to determine differences between Con and treatments. Comparison of B with BU and BO was only conducted where there was no significant interaction between thinning and fire treatments. Pearson correlation coefficients were used to assess the significance of relationship between various parameters studied. Analyses were done using SYSTAT Version 10.2 for Windows (SYSTAT, Richmond, CA, USA) and Microsoft Excel (Version 2007). $P \leq 0.05$ (*) indicates significant differences unless specified otherwise.

Results

Soil chemistry

When compared with the Con, total N and total C did not change in response to any of the treatments while a decrease in C:N was observed with BU and BO in both soil depths (Table 1). The ratio of C:N also increased with O in topsoil. Nitrate (NO_3^-) increased in O and BO in the topsoil and only with BO in the subsoil. Ammonium (NH_4^+) decreased with B only in subsoil. Other than a decrease in Al with BU and BO in topsoil and BO in the subsoil, no other significant changes in nutrient concentrations were observed in response to all treatments (Suppl. Table 1).

Compared to B, BU and BO treatments had lower C:N in both soil depths. In comparison with B, BU had higher N in both depths and BO in the subsoil only. Calcium and total C were also higher in BU in the subsoil, and BO had higher NO_3^- in both soil depths and decreased Al in the subsoil (Suppl. Table 1). Total N, C, C:N and NH_4^+ N were different between the topsoil and subsoil (Table 1). All

other soil parameters did not change between the two soil depths (Suppl. Table 1).

Foliar chemistry and metabolites

Comparisons of concentrations among the three species: as expected, concentrations of inorganic ions and metabolites in the foliar tissues of untreated trees from Con plots were species-specific (Table 2). Total N, total C, C:N, Al, Arg + Thr, glycine (Gly), valine (Val), isoleucine (Ile), tryptophan (Trp), phenylalanine (Phe), ornithine (Orn) and lysine (Lys) concentrations were within a similar range among all species. The dominant amino acid was glutamic acid in pines and γ -aminobutyric acid (GABA) in fir. Proline was 5–6 times higher in pines compared to fir. Calcium, Mg, and Mn were highest in sugar pine. While P was highest in Jeffrey pine, K was highest in white fir (Table 2). Species-specific changes with treatments are described below.

Jeffrey pine Total N decreased with O (Fig. 1a). Besides an increase in Mn with U and O (Fig. 1b) and Mg with O (Fig. 1c), no significant changes were observed for total C and other nutrients. However, a marginal increase in C:N ratio was observed with O in Jeffrey pine ($P = 0.059$) (data not shown). None of the treatments had any effect on soluble proteins, total chlorophyll (Chl), Chl *a*, *b* and *a/b* ratio (data not shown). Among polyamines and amino acids only one amino acid changed significantly; Arg + Thr decreased with B, U and BO treatments (Fig. 1d).

Sugar pine A significant inter-annual variation in foliar Ca and Mg data between 2008 and 2009 was observed with all treatments (individual year's data not shown). The Ca levels for all treatments in 2008 were higher than that in 2009 for all samples. In contrast, the Mg levels were higher in 2009 than 2008 for all the samples. For all other ions analyzed in sugar pine as well as Ca and Mg in the other two species, we did not find variations in the data collected over 2 years (data not shown). This variation cannot be attributed to instrumental or technical error, since all other ions analyzed from the same samples did not show this variation in raw ICP data.

No changes were observed in total C, total N, C:N, and other nutrients with any of the treatments (data not shown). While none of the treatments had any effect on soluble proteins, Chl *b*, and *a/b* ratio (data not shown), total Chl and Chl *a* decreased significantly with BO (Fig. 2a, b). As for polyamines and amino acids, only Glu decreased with BU (Fig. 2c).

White fir No changes were observed in total C, total N, and C:N with any of the treatments (data not shown). Among the other nutrients tested, only Mn decreased with O and BU treatments (Fig. 3a). While Ca did not change

Table 1 Total nitrogen and total carbon in soils that were subjected to prescribed thinning, burning, or both treatments combined. Data presented are mean $\pm$ SE for an n size of 27 for C and N, and 12 for ammonium and nitrate ions

Treatments	Control (Con) Burn (B) Con B	Understory thin (U) Burn + Understory thin (BU) U BU	Overstory thin (O) Burn + Overstory thin (BO) O BO
Topsoil (1–10 cm depth)			
Total C (mg kg ⁻¹)	435 $\pm$ 47a 403 $\pm$ 21	512 $\pm$ 37 507 $\pm$ 62	438 $\pm$ 37 361 $\pm$ 0.19
Total N (mg kg ⁻¹)	18.2 $\pm$ 2.0a 17.3 $\pm$ 1.0	21.4 $\pm$ 1.4 24.3 $\pm$ 2.6 [¶]	16.7 $\pm$ 1.3 17.3 $\pm$ 1.4
Total C:N	24.3 $\pm$ 0.6a 23.8 $\pm$ 0.6	23.9 $\pm$ 0.5 20.8 $\pm$ 0.6* [¶]	26.4 $\pm$ 0.7* 21.7 $\pm$ 0.5* [¶]
NH ₄ ⁺ N (mg kg ⁻¹)	4.53 $\pm$ 0.97a 3.28 $\pm$ 0.28	4.25 $\pm$ 0.43 5.39 $\pm$ 0.99	7.58 $\pm$ 1.82 8.41 $\pm$ 2.46
NO ₃ ⁻ N (mg kg ⁻¹)	0.73 $\pm$ 0.26a 0.36 $\pm$ 0.07	2.13 $\pm$ 0.69 1.96 $\pm$ 0.64	3.56 $\pm$ 0.96* 5.24 $\pm$ 1.17* [¶]
Subsoil (10–30 cm depth)			
Total C (mg kg ⁻¹)	221 $\pm$ 27b 183 $\pm$ 10	224 $\pm$ 24 239 $\pm$ 17 [¶]	233 $\pm$ 20 228 $\pm$ 15
Total N (mg kg ⁻¹)	8.4 $\pm$ 1.0b 7.2 $\pm$ 0.5	9.0 $\pm$ 0.9 10.4 $\pm$ 0.8 [¶]	8.9 $\pm$ 0.7 9.8 $\pm$ 0.8 [¶]
Total C:N	26.6 $\pm$ 1.0b 26.1 $\pm$ 0.7	24.8 $\pm$ 0.6 23.2 $\pm$ 0.7* [¶]	26.0 $\pm$ 0.7 23.6 $\pm$ 0.4* [¶]
NH ₄ ⁺ N (mg kg ⁻¹)	2.30 $\pm$ 0.27b 1.45 $\pm$ 0.15*	2.31 $\pm$ 0.36 2.07 $\pm$ 0.18	3.71 $\pm$ 0.81 2.46 $\pm$ 0.48
NO ₃ ⁻ N (mg kg ⁻¹)	0.19 $\pm$ 0.07a 0.08 $\pm$ 0.04	0.61 $\pm$ 0.26 0.26 $\pm$ 0.06	1.00 $\pm$ 0.43 1.08 $\pm$ 0.24* [¶]

Soil samples were collected in 2008. * $P \leq 0.05$ denotes significant differences between control and other treatments. [¶] $P \leq 0.05$ denote significant differences for burning with and without thinning (B and BU or B and BO). Letters a and b denote significant differences between topsoil and subsoil from control plots only ($P \leq 0.05$)

for any of the treatments compared to Con it was significantly lower in BU compared to B (Fig. 3b). Soluble proteins increased in BO in comparison with Con and B (Fig. 3c). Tot Chl, and Chl *b* decreased in both BU and BO compared to Con (Fig. 3d, f) while Chl *a* decreased only with BO (Fig. 3e). Polyamines did not respond to any of the treatments (data not shown). However, among amino acids Glu, Gly, and GABA responded to one or more treatments (Fig. 3g–i); both B and BO caused a decrease in Glu while GABA decreased only in response to BO (Fig. 3g, i). Glycine increased with O (Fig. 3h).

Discussion

Relatively long-term (8–9 years post-treatment) effects of burning and/or thinning treatments on foliar chemistry and physiology at Teakettle were species-specific. While U treatment did not have any pronounced effects on these parameters and B negatively affected one or two amino acids in Jeffrey pine and white fir, O and/or BO had several negative effects on all species including a decline in Chl content. Of all the treatments, because of its negative

impact mainly on white fir physiology, we predict BU will be most effective in reducing the white fir population at Teakettle. Most foliar changes with treatments were not driven by soil chemistry changes. This indicates that soil chemistry was not responsible for any additional growth-limiting factors. Absolute comparison of these data with other previously published work is difficult due to differences in forest stand age and composition, site climate and chemistry, study designs such as type and duration of prescribed treatments, and most importantly, the lack of data on biological responses of trees from such studies. Review of fire science-related literature clearly shows a critical need for making long-term observations with the same study design being replicated at multiple sites. However, we have made an attempt to make comparisons with other published studies. Besides providing baseline data for several biochemical parameters of the three conifer species growing at Teakettle, a specific goal of the present study was to evaluate the use of metabolic changes as early indicators for predicting the effects of prescribed burning and/or thinning on species-specific growth and long-term productivity. These predictions would later be validated with subsequent reliable growth data.

Table 2 Comparison of foliar N, C, soluble ions, chlorophyll, soluble/free polyamines and amino acids concentrations among Jeffrey pine, sugar pine, and white fir growing in control (unburned and unthinned) plots

	Jeffrey pine	Sugar pine	White fir
Foliar C and N (mmol g ⁻¹ DM)			
Total C	51.6 ± 0.2a	49.0 ± 0.2a	48.1 ± 0.3a
Total N	1.51 ± 0.02a	1.22 ± 0.04a	1.45 ± 0.05a
C:N	34.2 ± 0.5a	40.2 ± 1.6a	33.2 ± 1.3a
Foliar chemistry (μmol g ⁻¹ FM)			
Ca	11.5 ± 0.9a	19.8 ± 2.9b	14.2 ± 1.2a,b
Mg	14.6 ± 1.4a	33.6 ± 3.3b	6.56 ± 0.28c
Mn	1.06 ± 0.10a,b	1.17 ± 0.11a	0.83 ± 0.09b
K	31.6 ± 1.4a	25.9 ± 1.3b	39.4 ± 1.5c
P	10.6 ± 0.7a	6.07 ± 0.43b	8.25 ± 0.37c
Al	1.73 ± 0.12a	1.78 ± 0.31a	1.42 ± 0.07a
Soluble proteins (mg g ⁻¹ FM) and chlorophyll (μg g ⁻¹ FM)			
Soluble protein	0.86 ± 0.09a	0.87 ± 0.11a	0.42 ± 0.07b
Total Chl	871 ± 53a	955 ± 33a	325 ± 19b
Chl a	615 ± 34a	679 ± 22a	241 ± 14b
Chl b	256 ± 20a	276 ± 12a	84.1 ± 5.0b
Chl a/b	2.55 ± 0.09a	2.50 ± 0.05a	2.88 ± 0.04b
Polyamines (nmol g ⁻¹ FM)			
Put		95.3 ± 9.6b	78.3 ± 9.9b
Put + unknown peak	185 ± 24		
Spd	93.3 ± 3.4a		78.3 ± 9.9b
Spd + unknown peak		75.2 ± 2.5	
Spm	17.4 ± 1.0a	15.1 ± 0.9ab	12.8 ± 1.0b
Spd/Put	0.76 ± 0.10a	0.96 ± 0.07a	1.35 ± 0.09b
Amino acids (nmol g ⁻¹ FM)			
Glu	768 ± 54a	771 ± 42a	153 ± 11b
Gln	121 ± 38a	46.6 ± 9.7a,b	15.1 ± 4.8b
Ser	114 ± 10a	83.9 ± 7.8b	104.2 ± 7.6a,b
Arg + Thr	1095 ± 461a	680 ± 246a	172 ± 39a
Gly	10.6 ± 2.8a	21.9 ± 5.7a	21.6 ± 3.2a
Ala	296 ± 20a	232 ± 14b	102.0 ± 7.0c
Pro	138 ± 13a	156 ± 13a	24.4 ± 2.2b
GABA	287 ± 31a	163 ± 13b	504 ± 26c
Val	38.7 ± 4.2a	39.8 ± 3.1a	41.0 ± 5.7a
Met	3.26 ± 0.97a	0.90 ± 0.34b	4.00 ± 0.63a
Ile	17.8 ± 2.7a	19.4 ± 1.7a	14.8 ± 2.3a
Leu	9.23 ± 0.96a	9.88 ± 1.03a	5.11 ± 0.95b
Trp	85.3 ± 21.9a	73.4 ± 14.1a	94.6 ± 29.3a
Phe	21.3 ± 1.4a	20.5 ± 1.3a	22.6 ± 4.4a
Orn	15.78 ± 5.62a	9.09 ± 1.96a	5.25 ± 1.04a
Lys	24.4 ± 5.5a	16.7 ± 1.8a	17.9 ± 5.4a
His	0.00 ± 0.00a	0.00 ± 0.00a	62.1 ± 12.5b

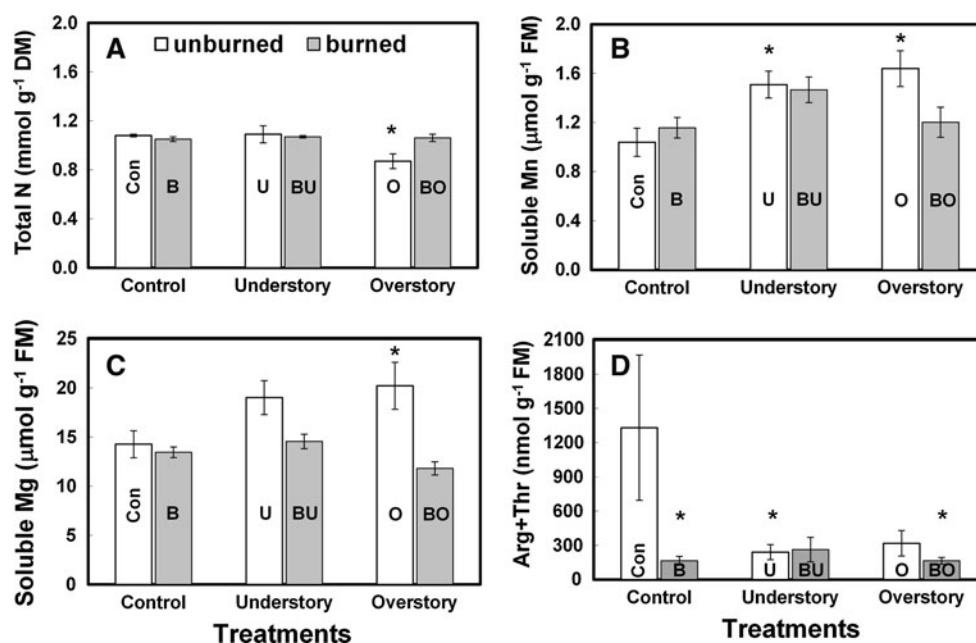
Data are mean ± SE from 30 trees; 15 each collected in 2008 and 2009. Letters a, b, c denote significant differences between species ($P \leq 0.05$)

Soil chemistry

Most of the literature available to date is on early changes in soil processes driven by fire and thinning. Neary et al. (1999) suggested that fire may either kill vegetation and/or oxidize organic C, both of which are sources of C for

heterotrophic microbes thus reducing the abundance of microbes and ultimately leading to changes in the soil C:N ratio. At Teakettle, with one or two exceptions, neither thinning (U, O) nor B had an effect on soil chemistry 8 years post-treatment. However, both BU and BO decreased C:N in both soil depths accompanied by an

Fig. 1 Foliar nitrogen (a), soluble Mn (b), soluble Mg (c), and amino acids arginine + threonine (d) concentrations in Jeffery pine trees that were subjected to prescribed thinning, burning, or both treatments combined. Data presented are mean $\pm$ SE of three replicates (where samples from five trees collected in 2008 were pooled into each replicate) for C and N; and of 15 replicates for soluble ions and amino acids. Each of the 15 replicates is an average of 2008 and 2009 data. * $P \leq 0.05$ denotes significant differences between control and other treatments. Foliar parameters that showed significant differences with treatments are the only ones presented here



increase in total C and total N in either one or both soil depths. Previously published research on the Tahoe National Forest in the central Sierra Nevada region that is dominated by Jeffrey pine showed losses of C and N along with nutrients such as P, K, Ca and S from the forest floor within 1 year after a thinning plus burning treatment (Johnson et al. 2008). Similar results were also reported from the Gondola wildfire site in the Lake Tahoe basin 1 year post-burning (Murphy et al. 2006). Fire is known to have variable effects on soil chemistry depending upon intensity. Higher temperatures and longer burn durations such as those that occurred in the Gondola wildfire often volatilize more N and C than low-intensity conditions that most prescribed burns strive to achieve. Therefore, fire intensity is an important variable to consider when comparing the responses of different sites. Monleon et al. (1997) reported an increase in total C, total N, and C:N in the surface (0–5 cm) soils shortly after burning in a ponderosa pine forest that was thinned 20–30 years prior to prescribed burning. This increase was followed by a decrease after 5 years and no notable difference from the control after 12 years. Driscoll et al. (1999) conducted a study in sub-boreal spruce forests of British Columbia that revealed that the N level was restored to pre fire levels 14 years after treatment. At Teakettle, there was no change in total N in both soil depths (Wayman and North 2007) 2 and 8 years post-B treatment suggesting that N may rebound rapidly to return to pre-treatment levels.

An increase observed in soil NO_3^- ions with BO in both types of soil samples and O in the topsoil after 8 years could have resulted from accelerated soil nitrification. DeLuca and Zouhar (2000) reported an increase in the levels of extractable soil NH_4^+ and nitrate NO_3^- ions with

harvest plus prescribed burn within 1 year at one of three sites in Western Montana (no long-term data were collected in this study). Covington and Sackett (1986) also reported higher NH_4^+ concentrations in burned plots of a ponderosa pine forest within 1 and 2 years; however, data collected after 5 years showed no difference in NH_4^+ ions between the control and burned plots. Soil N mineralization and nitrification rates were reported to be higher in thinning plus burning treatments 3 years after fire treatment in a western study site in the Klamath National Forest, CA (Forman and Boerner 1981). However, in the present study the NH_4^+ content in subsoil was still low 8 years post-burning. Data from these other studies indicate burning or thinning plus burning caused changes in soil NH_4^+ and NO_3^- , but the duration of the change varied with study design, site chemistry and stand composition.

Simard et al. (2001) reported higher concentrations of extractable soil Ca in mineral soil of three spruce-dominated sites in a Quebec boreal forest 20 years after burning or thinning. The increase in soil NH_4^+ and essential cations such as Ca^{2+} indicates a rise in the soil cation-holding capacity (David 1977). Arocena and Opio (2003) suggested that displacement of Al^{3+} from soil colloids often increases the concentration of essential cations such as Ca^{2+} , Mg^{2+} and K^+ over time. However, in the present study the decrease observed in soil Al^{3+} with BU and BO was not accompanied by any change in Ca (Suppl. Table 1).

Foliar chemistry

C and N A marginal increase was observed in C:N ratios in Jeffrey pine ($P = 0.059$) only with O treatment which was probably due to a decrease observed in foliar N with this

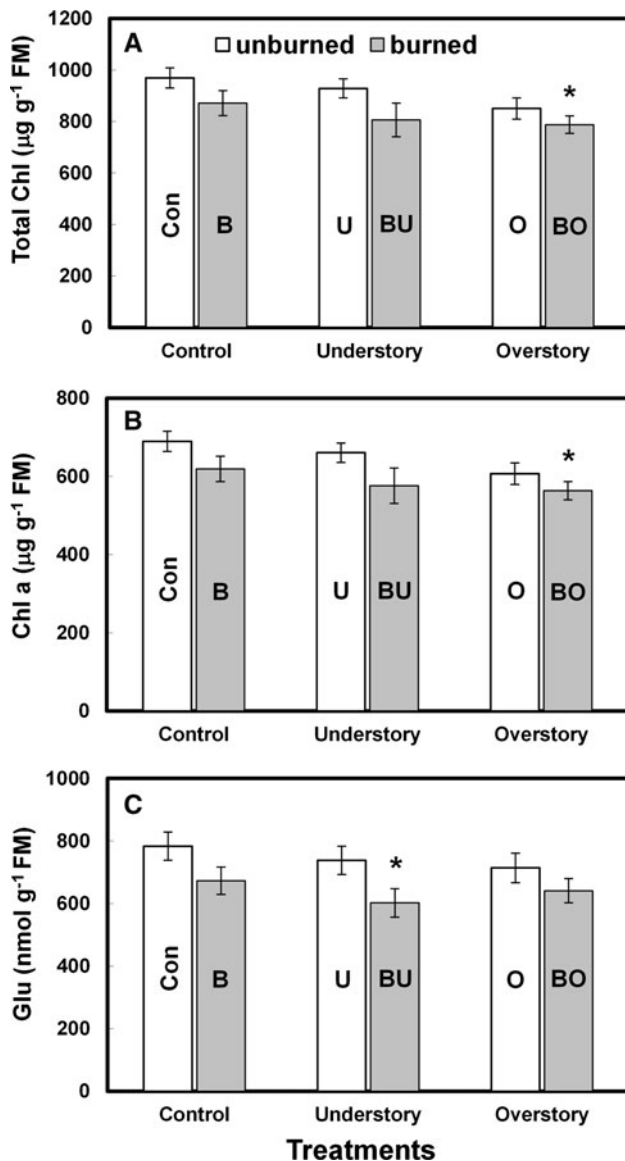


Fig. 2 Total chlorophyll (a), chlorophyll a (b) and foliar glutamic acid (c) concentrations in sugar pine trees that were subjected to prescribe thinning, burning, or both treatments combined. Data presented are mean $\pm$ SE of 15 replicates for chlorophyll and glutamic acid. For more details see legend to Fig. 1

treatment (data not shown). Soil C:N in the topsoil was also higher in the O plots (although not accompanied by any significant change in C or N) indicating that Jeffrey pine may be sensitive to this change. In a study in the Tahoe National Forest in the Sierra Nevada region, thinning or burning increased foliar C and N losses after 1 year in a forest dominated by Jeffrey pine (Johnson et al. 2008). Unlike our study, this study looked only at relatively short-term effects.

Inorganic elements With the exception of a few species, threshold concentrations of essential nutrients in foliage necessary for growth and maintenance are not known at present. At Teakettle, no decreases in P, K, Mg, and Al

were observed in three conifer species with any of the treatments, suggesting no additional limitation on growth were caused by these nutrients. However, a decrease in Mn and Ca was observed with different treatments in white fir. But not knowing the species-specific threshold concentrations of these nutrients needed for growth makes it hard to relate changes in nutrients with growth patterns. Jonard et al. (2006) reported a decrease in N, P, and K concentrations in Norway spruce needles 30 years after a thinning treatment. On the other hand, an increase in N and P concentrations was observed in green pine needles within 3–4 months post-fire treatment in an unmanaged pine forest (Gillon et al. 1999). In yet another study, concentrations of foliar N, P, K and Ca were significantly higher in fire-restored short-leaf pine-hardwood stands 1 year following a prescribed fire (Liechty et al. 2005). It is difficult, however, to make meaningful comparisons among these studies that were not only conducted in very different ecosystems, but also lack long-term observations.

Chlorophyll content and soluble proteins

Chlorophyll measurements can be taken as a proxy for no effects of the treatments on photosynthetic capacity independent of the total canopy biomass (Minocha et al. 2009). Recent investigations on the evaluation of the impacts of crown scorch on Chl content in a long leaf pine (*Pinus palustris*) forest (Fort Gordon, Georgia, USA) reported significant reductions in leaf Chl within 1–3 years after treatment, which in turn increased tree mortality (O'Brien et al. 2010). Chlorophyll pigments decreased 1–3 months following a prescribed thermal pruning experiment in corsican pine (*Pinus laricio*) needles from 10- to 12-year-old trees in the Valdu Niellu Forest in Northwest Corsica (Cannac et al. 2007). These authors have suggested that monitoring the levels of Chl pigments could be used as bioindicators of stress for short-term response of *Pinus laricio* needles to thermal pruning. While Cannac et al. (2007) focused on short-term effects in relatively young trees, our study reports on the effects of thinning and/or burning 8 years post-treatment in mature pines. No treatment effects were seen on total Chl content, Chl a and Chl b, Chl a/b ratios and soluble protein in the foliage of Jeffrey pine after 8 years. However, in sugar pine, total Chl and Chl a content decreased with BO, indicating a possible decrease in photosynthetic capacity due to physiological stress. In white fir, BU and BO resulted in low Chl pigment levels and an increase in soluble protein content (with BO alone), both of which are often interpreted as a stress response. This response in white fir may in part be due to greater evaporative demand in the high-light environment produced by these treatments (Royce and Barbour 2001; Zald et al. 2008).

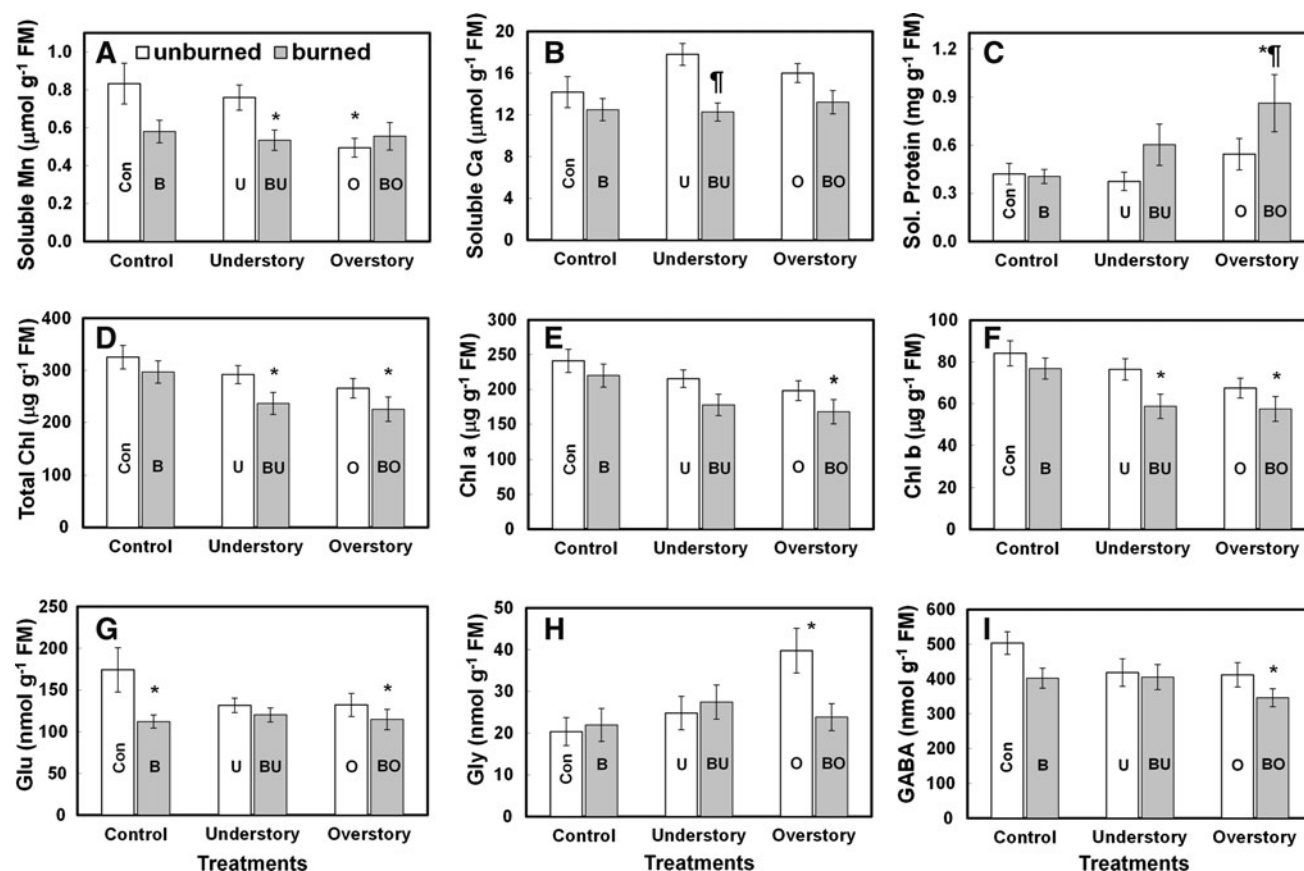


Fig. 3 Foliar soluble Mn (a) and soluble Ca (b), soluble proteins (c), total chlorophyll (d), chlorophyll a (e), chlorophyll b (f), and free amino acids glutamic acid (g), glycine (h), and GABA (i) concentrations in white fir trees that were subjected to prescribed thinning, burning, or both treatments combined. Data presented are mean $\pm$ SE

of 15 replicates for soluble ions, soluble proteins, chlorophyll and amino acids. * $P \leq 0.05$ denotes significant differences between control and other treatments $^{\dagger}P \leq 0.05$ denote significant differences for burning with and without thinning (B and BU or B and BO). For more details see legend to Fig. 1

Polyamines

Besides playing a critical role in growth and development, polyamines modulate stress responses and also detoxify cells from excess ammonia and store this excess N as N reserves. Significant changes in soil and foliar elemental concentrations, such as Ca, Al, and N from stand fertilization or natural pollution have been shown to cause related changes in foliar polyamine concentrations in conifer and hardwood trees (Minocha et al. 2000; Minocha et al. 1997; Schaberg et al. 2011; Wargo et al. 2002). Cellular foliar polyamines did not change in all three species with any of the treatments (data not shown). These data suggest lack of any symptoms of excess N and/or any other nutritional imbalances in the foliar tissues of these conifers at Teakettle.

Amino acids

The dominant free amino acid for both pine species was Glu, while for white fir it was GABA. Differences in the

dominant free amino acid between different species were also observed among sugar maple, yellow birch and American beech growing at the Hubbard Brook Experimental Forest, NH (Minocha et al. 2010). In forest soils which are typically N-limited, an efficient mechanism is required for the assimilation, storage, mobilization, and recycling of all forms of N. In the interconversion between Arg and the amides, Gln and Asn play a key role in N metabolism of conifers (Cánovas et al. 2007). Under similar environmental conditions, each tree species often has one or more specific N metabolites that are used for storing N reserves such as Put and Arg (Minocha et al. 2010). Changes in the concentrations of dominant N metabolites with changes in stress level indicate major shifts in metabolism which are known to take place without an accompanying change in foliar total N. Therefore, such metabolites are good candidates for use as indicators to predict long-term growth changes. Proline was shown to accumulate in plants under water stress (Barnett and Naylor 1966; Chen et al. 1964). In the Sierra Nevada mixed-conifer forests, growth and mortality is largely

regulated by soil moisture availability (Stephenson 1988). Species with reduced drought tolerance are predicted to be at a competitive disadvantage as climate change is predicted to produce longer and more severe droughts for much of California (Battles et al. 2008). Proline levels were 5–6 times higher in the pines as compared to the fir indicating that the pines are more sensitive to water stress than fir at Teakettle. A species-specific decrease in a few amino acids (Glu, GABA, and Arg + Thr) with some treatments in our study indicates a decrease in N reserves with respective treatments. However, this change in amino acids was not linked with soil and foliar N status. Changes in cellular N partitioning with or without a change in soil and total foliar N indicates that cells are capable of making adjustments in its N metabolites according to changes in their immediate environment, such as changes in the availability of Ca (Bauer et al. 2004; Minocha et al. 2010).

Evaluation of foliar physiology per unit mass, as reported in the present study, is a very effective tool for detecting the presence of stress in trees before visual symptoms appear. Factors such as N saturation or nutritional deficiencies with well-defined physiological stress responses have been linked to the decline of some tree species (Bauer et al. 2004; Minocha et al. 1997; Wargo et al. 2002). Thus, species-specific changes in metabolites may hold the potential to also serve as indicators for predicting changes in growth and productivity with forest management practices. On its own, foliar physiology expressed as per unit mass does not allow one to easily make predictions on growth rates and forest productivity except when used in conjunction with early changes in relative growth such as carbon stocks per plot as measured by Hurteau and North (2010) post-treatment.

Conclusions

Understory thinning (U) did not affect the foliar physiology of any of the species. In white fir, a decrease in the Chl content with BU indicated lower photosynthetic ability that could negatively impact growth and physiology of the fir species at this site. Based on these data, we suggest BU as the best management option for the reduction of white fir from these mixed-conifer stands. Burning with understory thinning will allow for the maintenance of a sizable inventory of large pines with little negative impact on their physiology. Both O and BO treatments had negative effects on both pine species and white fir. Hurteau and North (2010) suggested that these treatments led to a considerable loss in carbon that would take a long time to replenish. Other Teakettle studies have also found a negative response to the BO treatment in small mammal abundance (Meyer et al. 2007a), soil respiration rates (Soung-Ryoul

et al. 2009) and microclimate variability (Ma et al. 2010). Thus, BO may not be the best management solution. Preliminary post-treatment evaluation of percent composition data for Teakettle published by North et al. (2007) have thus far indicated no significant changes in species composition with any of the treatments though some trends were visible. Ten-year re-measurement of the Teakettle plots is currently underway and will be repeated at 5-year intervals. We will use these long-term data, which include growth and mortality assessments, to evaluate our physiology-based predictions on how the three tree species used in this study respond to widely used fuel reduction treatments.

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