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Influence of fuel-reduction forest thinning on growth of an arboreal forage lichen

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ABSTRACT

Significant differences in microclimate have been found within crowns of dispersed vs. clumped leaf trees resulting from fuels reduction treatments in Sierra Nevada mixed-conifer forest. The question remained whether these differences in abiotic conditions might be biologically significant to arboreal epiphyte communities. The objective of our experiment was to assess growth of transplants of a lichen epiphyte, *Bryoria fremontii*, in relation to differences in within-crown vapor pressure deficits (VPD) among no-thin control, and understory (U-thin) and overstory (O-thin) fuels reduction prescriptions. Transplant annual relative growth ranged from 6.2–11.6%. We expected *Bryoria* growth would be greatest in trees in intact forest of the control and less in the O-thin after treatment, but there was no statistical difference. The control had the highest VPDs and the least growth before thinning. *Bryoria* grew best, both before and after thinning, in trees nearest streams and in the U-thin where VPDs were lowest. Classification and regression tree analysis revealed a positive correlation between *Bryoria* growth and greater basal area (BA) surrounding study trees before thinning, and lower VPDs after thinning. Topographic positions of the study plots confounded within-crown VPDs among treatments and therefore on *Bryoria* growth. The U-thin plot had a lower topographic position that was more affected by a moisture-influenced riparian microclimate than the more upland control and O-thin plots. However, results consistently suggest that greater BA surrounding trees buffers their within-crown microclimate and favors *Bryoria* growth. Fuels treatments that thin from below and leave large, live trees in a clumped pattern may foster *Bryoria*, providing an important food source for the northern flying squirrel and associated arboreal food webs. Stand reconstructions have demonstrated an historical precedent for such a forest spatial pattern.

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1. Introduction

A century of fire-suppression in western U.S. forests has resulted in fuel accumulations and increased fire severities exceeding historic ranges of variability. To mitigate this trend, forest managers have made it a priority to reduce fuels by mechanical thinning. Two such treatments often used are defensible fuel profile zones (DFPZs) and strategically placed area treatments (SPLATs). DFPZs reduce canopy bulk density by thinning the overstory and leaving evenly spaced live trees with separated crowns, while SPLATs thin primarily from the understory, leaving groups of overstory trees in a pattern historically characteristic of many western forests (Bonnicksen and Stone, 1982; North et al., 2004). Although both treatments are now widely used, we know little about their effects on the arboreal environment and its ecological processes. There is particularly little information on the effects of grouped vs. spaced live-tree retention on poikilohydric epiphytes such as lichens and bryophytes that are strongly affected by

moisture and temperature regimes (Proctor, 1982; Kershaw, 1985), and especially sensitive to microclimate changes (Renhorn et al., 1997).

One such epiphyte in the Sierra Nevada is *Bryoria fremontii*, which is directly ecologically linked as forage for the northern flying squirrel (*Glaucomys sabrinus*) and indirectly with three Forest Service Designated Sensitive Species (USDA, 1993), the California spotted owl (*Strix occidentalis occidentalis*), pine marten (*Martes americana*), and American fisher (*Martes pennanti*) (Rambo, 2010). *B. fremontii* was described as being fairly common and locally abundant on the western slopes of the Sierra Nevada from Tulare County north to Modoc County (Hale and Cole, 1988) and common in Calaveras Big Trees State Park (Pinelli and Jordan, 1978). Jovan and McCune (2004) quantified it as occurring in 21% of study plots across the Sierra Nevada, Southern Cascades and Modoc Plateau region, and found it to be a significant indicator of that region. It was the only prominent forage lichen found in a survey of Yosemite, Sequoia and Kings Canyon National Parks and Devils Postpile National Monument (McCune et al., 2007). It is found pendant on twigs and foliage sprays of mainly coniferous trees, and at our site it is strongly associated with red fir (*Abies magnifica*) (Rambo, 2010). Red fir here inhabit a climatic zone that receives greater

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annual precipitation and deeper snow than either lower elevation mixed-conifer or higher subalpine forests (Fites-Kaufman et al., 2007), and are generally found in riparian areas or cooler forest pockets that retain snowpack longer into spring (North et al., 2005).

The objective of our experiment was to assess the growth of *B. fremontii* transplants in relationship to microclimatic differences within crowns of isolated trees vs. trees left imbedded within groups. Significant differences in microclimate were found to exist within tree crowns of those two contrasting patterns of live-tree retention (Rambo and North, 2009), but the question remained whether these differences in abiotic conditions might be biologically significant to arboreal epiphyte communities. Most studies of forest management effects on microclimate and epiphytes investigate contrasting environments among different ages of managed stands or across selective cuts and an uncut control without discriminating between finer scale within-crown differences created between grouped and solitary trees. Very few studies have examined the influence of grouped vs. evenly spaced retained live-trees on microclimate (Heithecker and Halpern, 2006; Ma et al., 2009; Rambo and North, 2009), or on epiphytes (Coxson and Stevenson, 2004; Waterhouse et al., 2007). Campbell and Coxson (2001) and Coxson et al. (2003) studied the effects of group- and single tree-selected thinning prescriptions on canopy microclimate in conjunction with abundances of alectoroid lichens, including *Bryoria* spp., in Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forest canopy, and Stevenson and Coxson (2003) assessed relative growth of *B. fuscescens* in the same forest and silvicultural prescription. However, our study experimentally examines epiphyte growth response in relationship to microclimate in replicate trees in contrasting retention treatments. We tested the null hypothesis that there would be no difference in the relative growth of *Bryoria* transplants within tree crowns among solitary trees, trees embedded within groups, and unthinned forest. Results provide forest managers with information valuable for determining what silvicultural thinning prescription may be most beneficial for *Bryoria* and its associated ecological linkages, and contributes to the need expressed in the Sierra Nevada Ecosystem Project report for acquiring data on ecological functions of Sierra Nevada forest ecosystems (SNEP, 1996).

2. Methods

2.1. Study site

The Teakettle Experimental Forest (36° 58'N, 119° 02'W) is situated in the Sierra National Forest north of the North Fork of the Kings River, approximately 80 km east of Fresno, California. This 1300 ha old-growth forest spans the upper montane red fir and lower montane mixed-conifer ecotone of the southern Sierra Nevada on the west side of the crest. The mixed-conifer overstory consists of white fir (*Abies concolor* var. *lowiana*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*). In a study of 526 post-thinning stumps, these respective species ranged in age up to 332, 397, 403, 407 and 354 years (North et al., 2005), with individuals reaching heights >65 m. Mean tree basal area (BA) is 68 m² ha⁻¹ with 60% canopy cover that is characteristically discontinuous with trees significantly clustered in groups separated by large gaps (North et al., 2004). Representative gap and understory woody plants include manzanita (*Arctostaphylos nevadensis* and *A. patula*), bush chinquapin (*Castanopsis sempervirens*), whitethorn (*Ceanothus cordulatus*), and snowberry (*Symphoricarpos mollis*). Warm, dry summers contrast with much cooler, moist winters in this Mediterranean climate. Annual precipitation averages 112 cm and falls mainly as

winter snow, which usually persists through May. Generally gradual slopes, with an average gradient of 136 m/km (Keeler-Wolf, 1990), give rise to first and second order perennial streams that average summertime widths of 120 cm and depths up to 65 cm.

2.2. Teakettle ecosystem experiment

This research was done within the context of the Teakettle Ecosystem Experiment, which included two different forest thinning treatments in plots 4 ha in area. Analysis of the Teakettle forest structure determined plot size needed to be approximately 4 ha to include the range of composition and stand variability that characterizes the discontinuous canopy cover of southern Sierra mixed-conifer forest (North et al., 2002). Thinning treatments were performed in the summers of 2000 and 2001. The understory-thinned treatment (U-thin) followed California Spotted Owl Report (CASPO) guidelines (Verner et al. 1992) and retained 40% of live BA while removing trees 25–76 cm diameter at breast height (dbh). This treatment left an average of 44 trees ha⁻¹ with a mean dbh of 91 cm often aggregated in groups (see Rambo and North, 2009 for stand visualizations and metrics). Originally designed to minimize impact on Spotted Owl habitat, CASPO guidelines became the standard forest thinning practice in the Sierra Nevada during the 1990s and remain widely used as a fuel reduction treatment (SNFPA, 2004). The overstory-thinned treatment (O-thin) harvested all trees ≥25 cm (dbh) except for 22 large trees ha⁻¹ left regularly dispersed 20–25 m apart (Rambo and North, 2009). This prescription was widely practiced in Sierra Nevada forests prior to CASPO and approximates fuels reduction thinning currently used in defensible space zones where tree crowns are spaced widely to reduce potential for crown fire spread. To determine stand canopy closure, hemispherical images were taken with a gimbal and tripod mounted digital camera from intersecting points on a 50 × 50 m grid established within plots, and analyzed using Gap Light Analyzer software (GLA; Frazer et al., 1999). The Teakettle Experiment also included broadcast burning in half the plots, but this study was restricted to plots that were thinned only. Mean elevations for our U-thin, O-thin, and no-thin plots were 2070, 2097, and 2124 m, respectively.

2.3. Transplants

Six mature trees (three each of red and white fir) were selected from within each of three treatment plots (O-thin, U-thin, control; $n = 18$ total trees; Fig. 1, Table 1). Eight trees were near-riparian (<25 m from perennial streams) and ten were distinctly upland (≥44 m from streams). This grouping was chosen to take advantage of a natural break in distances of study trees from water that kept the comparative groups close in size. That break point coincided with the distance where tree species composition largely transitioned from domination by firs along streams to a more upland composition of mixed-conifers. Study tree selection was constrained by ensuring that individuals were >30 m from treatment plot edges, tree locations were representative of the range of site geographic variation (Fig. 1), and trees could be rigged for climbing. None was selected with any preconceived bias for the presence of *Bryoria*.

Bryoria thalli were harvested from a red fir to be cut in the thinning treatments. Thalli were air-dried using oven-dried reference samples to account for ambient humidity, weighed, and prepared as transplants by attaching individuals to a nylon monofilament loop with silicone sealant (McCune et al., 1996). Initial transplant weights, adjusted for ambient humidity, ranged from 0.074–0.199 g (mean = 0.131 g, st dev = 0.023 g). Eleven transplants were spaced approximately 10 cm apart and hung along a nylon line (Fig. 2) to make 72 sample strings. Four strings were installed in

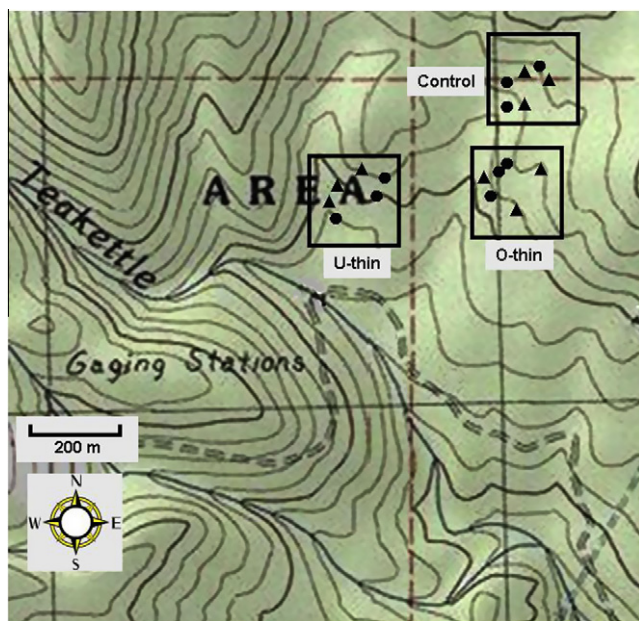


Fig. 1. A portion of the Teakettle Experimental Forest with our no-thin control, understory-thin (U-thin), and overstory-thin (O-thin) 4 ha (200 m × 200 m) plots, and the distribution of study trees within them. ● = red fir, ▲ = white fir.

each fir by spanning their lines between live branches at mid-crown height (mean = 32.4 m) where *Bryoria* abundance was at its peak (Rambo, 2010). This positioning approximated the openness and ventilation to which naturally occurring *Bryoria* thalli were exposed. We considered each study tree as the experimental unit or plot, and the four sample strings as subsamples. Using a split plot design, we installed half the sample strings in a southwest (SW) aspect and half in a northeast (NE) aspect. Transplants were in place for two years prior to treatments (September 1999–2001) to establish pre-treatment growth rates and evaluate any between-treatment or between-tree species differences. Transplants remained in place two more years following treatments (2001–July 2003). Sample strings were removed annually during summers when thalli were physiologically dry and dormant, weighed to assess biomass gain, and returned to their same positions in the canopy. Before returning sample strings, we replaced any thalli that were lost or had negative growth.



Fig. 2. A portion of a sample string of *Bryoria fremontii* thalli in a red fir.

2.4. Environmental variables

Temperature and relative humidity in the red fir were recorded every 30 min by 18 Hobo Pro 8 Data Loggers for one year pre-thinning (July 2000–July 2001) and one year post-thinning (July 2001–July 2002). Sensors were suspended from the branches used for *Bryoria* transplants in the NE and SW aspects in conjunction with those respective pairs of sample strings. These sensors have an accuracy of ±0.2 °C and ±3% relative humidity (±4% in condensing environments). To reduce radiant heating of the sensors, they were enclosed within naturally vented multi-plate shields (however, see Nakamura and Mahrt, 2005).

A heat load index based on latitude, slope and aspect was calculated for each tree (McCune and Mefford, 2004; McCune, 2007), and tree height, dbh and distance from the nearest first or second order perennial stream were measured (Table 1). BA was measured before and after treatments in a 0.1 ha circular plot established around each study tree (Table 1). Digital imaging with a hemispherical lens was used to measure canopy closure from study tree bases in the SW and NE aspects (Table 1). Percent closure was analyzed with GLA software.

Table 1
The 18 study trees with environmental variables: Treat = overstory-thin (O), understory-thin (U), and no-thin (N); Hgt = tree height (m); dbh (cm); Pre- and Post-BA = basal area (m²) in surrounding circular 0.1 ha plot before and after thinning; Pre- and Post-close = % canopy closure before and after thinning; Heat = heat load index; H₂O = distance to nearest perennial stream (m). ABCO = *Abies concolor*, ABMA = *A. magnifica*.

Species	Treat	Hgt	dbh	Pre-BA	Post-BA	Pre-close	Post-close	Heat	H ₂ O
ABCO	O	39	73	6.07	1.40	80.21	76.62	1.04	5
ABCO	O	51	130	7.19	2.90	83.89	73.16	1.03	96
ABCO	O	50	117	6.72	1.28	84.19	62.89	1.05	134
ABCO	U	48	123	3.92	7.38	71.32	71.16	1.01	122
ABCO	U	49	99	7.04	3.12	82.80	78.66	1.01	11
ABCO	U	65	144	11.53	5.64	84.84	80.66	1.00	12
ABCO	N	55	175	6.61	6.61	79.81	79.81	1.05	101
ABCO	N	65	150	8.10	8.10	82.13	82.13	1.02	17
ABCO	N	50	105	10.75	10.75	83.25	83.25	1.01	124
ABMA	O	48	98	5.12	1.46	78.40	72.50	1.06	15
ABMA	O	42	101	4.43	2.96	79.05	69.69	1.06	44
ABMA	O	45	76	5.74	0.66	80.49	74.11	1.06	16
ABMA	U	65	143	9.39	7.83	82.63	79.51	1.00	21
ABMA	U	51	129	11.50	9.65	82.19	80.92	1.04	122
ABMA	U	55	129	8.77	7.38	82.47	77.50	1.02	85
ABMA	N	51	135	4.49	4.49	83.19	83.19	1.04	111
ABMA	N	60	122	6.75	6.75	83.62	83.62	1.00	24
ABMA	N	52	151	7.35	7.35	85.28	85.28	1.04	64

2.5. Data analyses

Mean percent gains in *Bryoria* biomass by trees were compared among and within treatments before and after thinning (SAS 2002–2003). Comparisons of growth before and after thinning were further made between NE and SW canopy aspects, red and white firs, and near-riparian and upland trees. Initial transplant weights had a statistically significant regression fit with their corresponding growth ($P < 0.05$). Therefore, analysis of covariance was used with initial transplant weight as a covariable to test the above differences, with means separated via orthogonal contrasts ($P < 0.05$). Negative growth of thalli was assumed to have resulted from fragmentation or predation by squirrels, and those were excluded. One red fir with outlying high relative weight gain (21.5%, >5.5 st dev) was deleted from an analysis when necessary to make model assumptions acceptable. Analysis of variance (ANOVA) was used to compare GLA canopy closure from study tree bases and string installations among treatments before and after thinning and within treatments between pre- and post-thinning. BA surrounding study trees was also compared among treatments before thinning.

The 30-min observations of temperature and humidity were used to calculate vapor pressure deficit (VPD; kPa), a measure of the drying power of air more biologically significant than relative humidity with respect to condensation and evaporation that are especially important for epiphytic cryptogams (Barkman, 1958). It was assumed that $VPD = 0$ when temperature was ≤ 0 °C. For each year, daily temperature readings across the 18 sensors were averaged and those means were smoothed using a five-day moving average approach (Liu et al., 1998) to determine starting and ending seasonal temperature thresholds. Using thresholds of 0 and 10 °C, the spring temperature period was defined as when daily mean temperatures were 0–10 °C, the summer period when means were consistently >10 °C, and fall when daily means were again 0–10 °C before dropping frequently <0 °C for the winter period (Ma, 2003). Analyses were restricted to the period from the onset of fall through spring (31 August–6 May pre-thin and 7 October–26 May post-thin). In the summer Mediterranean climate of the Sierra Nevada *Bryoria* thalli are nearly always air-dried and physiologically dormant. Most *Bryoria* growth likely occurs during the fall to spring period of hydration (Rambo, 2010). Repeated measures ANOVAs were used to compare VPDs between SW and NE aspects within crowns. Then, because pairs of observations by aspect were not independent of one another, they were averaged within a tree, and compared before and after thinning among and within treatments, and between near-riparian and upland trees (SAS, 2002–2003). If transformation of the response variable could not

adequately achieve homoscedasticity and otherwise satisfy assumptions of normality, nonparametric rank F test analyses were used.

Classification and regression tree (CART) analysis was performed to identify significant environmental variables associated with *Bryoria* growth in red firs within the single years immediately preceding and following thinning when VPD was measured. Other independent variables included tree height and dbh, surrounding tree BA and GLA canopy openness, subsample string height, distance to the nearest perennial stream, the heat load index, and within-crown aspect. We used a minimum group size of six before splitting, a minimum node size of 3 and a minimum node deviance of 0.01 (S-Plus 6, 2001).

Bryoria growth was regressed against GLA closure, surrounding BA, string height, and VPD to assess the relative amount of variation those environmental variables explained. Regression analysis was also used to assess the strength of correlations among GLA closure, surrounding BA, and VPD (SAS, 2002–2003).

3. Results

3.1. Environmental variables

GLA canopy closure estimates were higher than closure estimates for the overall plots (Rambo and North, 2009) because images in this study were taken from the immediate bases of study trees, rather than from the Teakettle study plot grid points, which were just as likely to be in gaps as under trees. Pre-treatment percent closures for the control, U-thin, and O-thin plots in this study were 82.9, 83.0, and 81.0, respectively. There were no statistical differences among treatments before thinning. However, differences in closures among treatments after thinning were significant ($P < 0.05$), as were the differences within the U-thin and O-thin between before and after thinning. Percent closure values after thinning for the control, U-thin, and O-thin were 82.9, 79.5, and 71.5, respectively. Increasing canopy closure was positively correlated with increasing BA surrounding those trees both before and after thinning ($R^2 = 31.6\%$, $P = 0.0151$ and $R^2 = 56.4\%$, $P = 0.0049$, respectively).

Mean within-crown VPDs were higher in SW aspects across all nine red fir before thinning, although the difference was not statistically significant. After thinning, VPD was higher in the SW aspect within control and U-thin trees, but not in O-thin trees. Prior to thinning, VPDs in control plot trees were significantly greater than in U-thin trees ($P = 0.0168$) (Table 2). After thinning, VPDs were significantly higher in control plot trees than in trees of both the

Table 2

Mean percent annual growth of *Bryoria* by treatments for two years before thinning and two years after, and pre- and post-thin vapor pressure deficits (VPD, kPa) in red firs. Different letter or number superscripts within a comparison group indicate significant differences among the means ($P < 0.05$). U-thin and O-thin are understory- and overstory-thin treatments, respectively, ABMA = *Abies magnifica*, ABCO = *A. concolor*, Riparian and Upland = <25 m and ≥ 44 m from streams, respectively.

	Treatments			Tree species		Location	
	No-thin	U-thin	O-thin	ABMA	ABCO	Riparian	Upland
n (growth)	6	6	6	9	9	8	10
n (VPD)	3	3	3	9		4	5
Pre-thin growth	10.38	12.24	10.42	10.57	11.46	11.59	10.55
(st dev)	(2.08)	(1.15)	(1.07)	(1.73)	(1.59)	(1.45)	(1.77)
Pre-thin VPD	0.397 ^a	0.345 ^b	0.366 ^b	0.369		0.359	0.377
(st dev)	(0.419)	(0.384)	(0.402)	(0.402)		(0.397)	(0.406)
Post-thin growth	5.63 ^a	8.57 ^b	6.05 ^{ab}	6.44 ¹	7.05 ²	7.74	5.95
(st dev)	(1.71)	(2.63)	(0.75)	(3.02)	(0.99)	(2.56)	(1.57)
Post-thin VPD	0.382 ^a	0.321 ^b	0.343 ^b	0.349		0.334	0.360
(st dev)	(0.336)	(0.295)	(0.310)	(0.315)		(0.305)	(0.322)
% change growth	−46	−30	−42	−40	−38	−34	−43
% change VPD	−3.7	−7.0	−6.3	−5.4		−7.0	−4.5

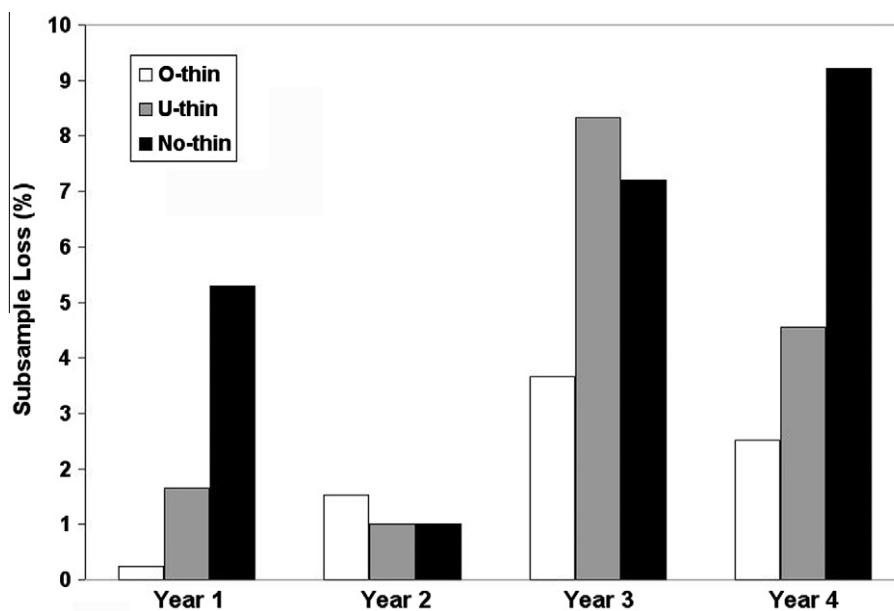


Fig. 3. Mean percent loss of thalli to arboreal squirrels by treatments for two years before and two years after thinning. Logging disturbance occurred between years 2 and 3. $n = 264$ thalli per treatment each year.

U- and O-thin plots ($P = 0.0018$ and 0.0474 , respectively). Within treatments, there were no significant differences between before and after thinning. VPDs were higher in upland trees than in near-riparian trees before and after thinning. Although the difference between the two before thinning was not significant, it was suggestively so after thinning ($P = 0.0888$). There were positive correlations between decreasing VPD and increasing BA and canopy closure before thinning ($R^2 = 31.1\%$, $P = 0.0199$) and ($R^2 = 13.4\%$, $P = 0.0285$), respectively, but not after treatments.

3.2. *Bryoria* growth

Of the 792 transplants installed, obvious squirrel predation caused an average loss of 5.4% across the two years prior to thinning and 17.8% after thinning (Fig. 3). Several entire strings of thalli were nibbled down to the silicone. Another 21.4% and 15.6% (pre- and post-thinning, respectively) lost biomass from apparent simple fragmentation. The remaining transplants with positive biomass gains averaged 11.6% annual relative growth across all 18 study trees in the first year and 10.5% in the second year (Table 2). After thinning, growth averaged 6.2% the first year and 7.4% the second year. The relative decline after thinning, which was significant for all three treatments ($P < 0.05$), did not differ among them. *Bryoria* growth was greatest in the U-thin plot across the two years before thinning (Table 2). Although the differences among treatments were not statistically significant with our small sample size, those between the U-thin plot and the more upland O-thin and N-thin control were strongly suggestive of significance ($P = 0.0501$ and 0.0543 , respectively). After thinning, growth remained greatest in the U-thin. The greater growth was significant in comparison to that in the control ($P = 0.0166$) and suggestively so with respect to the O-thin ($P = 0.0633$). There was no statistical difference in growth between the O-thin and control either before or after thinning. Nor was there any significant difference in *Bryoria* growth between red and white firs before thinning. After thinning, however, *Bryoria* had greater growth in white firs ($P = 0.0239$). There was no difference in *Bryoria* growth by aspect within trees, and though growth was greater in near-riparian than upland trees before and after thinning, the differences were not statistically significant.

Greater *Bryoria* growth positively correlated with increasing BA surrounding the study trees ($R^2 = 22.9\%$, $P = 0.0448$) for the two years prior to thinning but not after. Throughout the study, there was a positive correlation between increasing *Bryoria* growth and decreasing VPD. Vapor pressure deficit accounted for 20.7% ($P = 0.0053$) and 35.5% ($P = 0.0149$) of the variation in growth response for the two years before and after thinning, respectively.

Classification and regression tree analysis demonstrated that the most significant condition associated with *Bryoria* growth prior to forest thinning was the amount of BA surrounding sample trees (Fig. 4a). Trees with $<6.25 \text{ m}^2$ averaged only 7.99% *Bryoria* growth. *Bryoria* growth in trees with surrounding BA $>6.25 \text{ m}^2$ was best differentiated by aspect within tree crowns. Samples installed in NE aspects averaged 12.78% growth while those in SW aspects averaged 10.33%. After thinning, VPD was the most significant condition associated with *Bryoria* growth (Fig. 4b). Growth averaged only 3.49% when VPD was higher ($>0.345 \text{ kPa}$). Under lower VPD conditions, growth was greater (6.52%) when openness was $<29.2\%$, and less (5.62%) when openness was $>29.2\%$.

4. Discussion

The mean annual relative growth of *Bryoria* we observed (6.2–11.6%) was greater than the 2.4–9.1% reported by Stevenson and Coxson (2003) for *B. fuscescens* in Engelmann spruce and subalpine fir forest in British Columbia. This is somewhat surprising because their *Bryoria* thalli were carefully protected within mesh cages to eliminate predation and to collect and include thallus fragments. Our relative growth results were certainly conservative due to predation and loss of fragments. *Bryoria* largely reproduces by simple fragmentation, and in Sierra Nevada mixed-conifer forest it is susceptible to predation and harvest by flying squirrels and other arboreal rodents such as Douglas squirrels (*Tamiasciurus douglasii*), which use lichens in nest construction (Carey, 1991). Because of their pendant growth form, *Bryoria* spp. in general are vulnerable to breakage under the changed environmental conditions that can result from thinning (Stevenson and Coxson, 2003; Muir et al., 2006). The average annual pre- and post-thin transplant losses

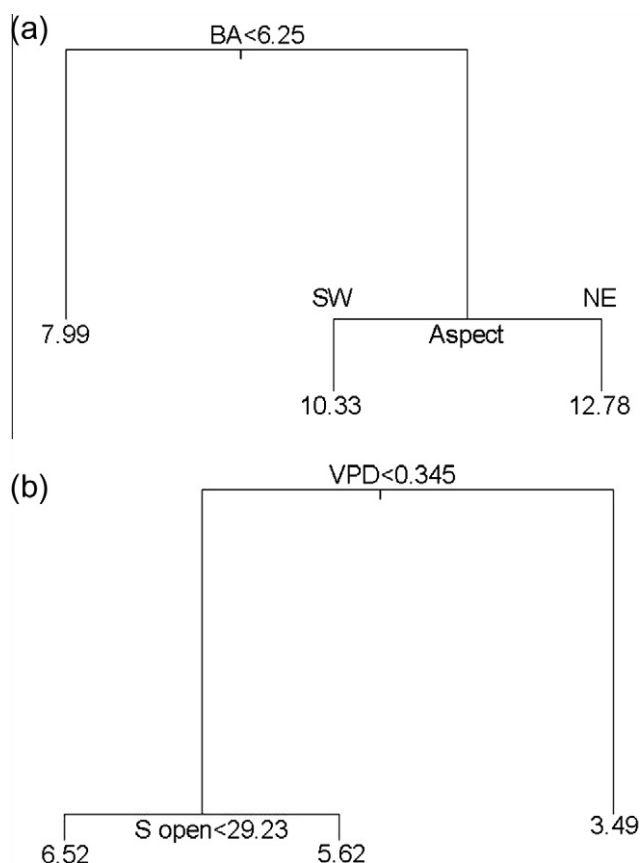


Fig. 4. Classification and regression tree results of site variables associated with *Bryoria* growth before (a) and after (b) mechanical fuels treatments. The length of each vertical branch is proportional to the amount of variance explained. BA = basal area ($\text{m}^2 \text{0.1 ha}^{-1}$), VPD = vapor pressure deficit (kpa), S open = % canopy openness; half of subsamples were in SW aspects and half in NE aspects; terminal nodes are % annual *Bryoria* growth.

we experienced (26.8% and 33.4%, respectively) were in line with an expected potential annual attrition of up to 30% (McCune et al., 1996).

The significant decline in *Bryoria* growth across treatments after the disturbance of the mechanical thinning operations was also likely due to the increased predation on transplants by arboreal squirrels, especially the flying squirrel. Only transplants with negative growth were excluded from analyses, and any that may have had less growth due to predation remained factored into analyses. *Bryoria* populations in the thin plots were negatively impacted by the harvesting of their phorophytes during treatments. At the same time, the mechanical disturbance likely drove squirrels out of thin plots and into surrounding forest and nearby control plots to forage for *Bryoria* that winter. The U-thin showed less decrease in *Bryoria* growth than the O-thin whose canopy was more severely impacted. Our U-thin plot was surrounded by un-thinned forest and separated from any of the Teakettle O-thin plots by some distance. It experienced less of an increase in predation pressure and its *Bryoria* populations were left considerably more intact than those in the O-thin, which were severely reduced by thinning. Our control plot had the greatest decline in *Bryoria* growth. It was nearly adjacent to Teakettle O-thin plots on two sides and more upland Jeffrey pine-dominated forest on a third side, which was much less favorable habitat for both *Bryoria* and flying squirrels. Flying squirrels (Myer et al., 2005) and *Bryoria* (Rambo, 2010) were most strongly associated with red fir in the mixed-conifer composition of the Teakettle Forest. The lack of critical winter forage that *Bryoria* provided could have caused a decline in the

resident flying squirrel population between the first and second post-thin years, which would account for the slight rebound in *Bryoria* growth that second year.

The distribution of *B. fremontii* in North America extends from British Columbia and Alberta south into the Cascade and Sierra Nevada Ranges. In wet-belt forests of British Columbia, near the northerly extent of its range, *Bryoria* appears to be sensitive to periods of prolonged moisture (Goward, 1998; Stevenson and Coxson, 2007). In contrast, near the southerly limit of its range in the drier Sierra Nevada, more moist conditions favor *B. fremontii*. It was positively associated with proximity to streams where VPDs were diminished (Rambo, 2010). Our transplant experiment corroborates those latter findings. Campbell and Coxson (2001) quantified greater abundance of *Bryoria* spp. in clumped trees than solitary trees in north-central British Columbia, and Coxson et al. (2003) reported a significant post-thinning decrease in *Bryoria* abundance in the upper canopies of single- vs. group-selected trees in the same forest. So, we expected *Bryoria* growth would be best in trees in the intact forest of the control and worst in the O-thin after treatment. Our clumped trees of the U-thin did have greater *Bryoria* growth than solitary trees of the O-thin after thinning, but the U-thin plot also had greater growth than the O-thin before thinning. Our control had the lowest growth rates both before and after thinning. The control had the highest VPDs and the U-thin the lowest. Both before and after thinning, *Bryoria* grew best in trees nearest streams and where VPDs were the lowest. Even when *Bryoria* growth significantly declined after treatments, there was an inverse relationship between the relative decrease in growth among treatments and the relative decrease in VPD. The greater the decrease in VPD, the better *Bryoria* fared relative to its growth prior to thinning. The consistent decrease in VPDs across treatments was likely due to inter-annual climate variation.

Topographic positions of the study plots confounded the comparison of within-crown VPDs among treatments and therefore on *Bryoria* growth. The U-thin plot had a lower topographic position that was more greatly affected by a moisture-influenced riparian microclimate than the more upland control and O-thin plots. This gave the U-thin plot and its near-riparian trees an ambient microclimate that moderated within-crown VPDs beyond those in the more upland control and O-thin plot trees (Rambo and North, 2009). This confounding makes it difficult to determine the potential buffering effect of surrounding trees on an individual tree's within-crown VPD. However, before thinning, increasing *Bryoria* growth was positively correlated with increased surrounding BA. After thinning, CART associated the greatest *Bryoria* growth with conditions that combined low VPD with the least amount of canopy openness.

The comparison of VPD between aspects further suggests that increased surrounding BA provides microclimatic buffering within tree crowns. Though not a significant difference, VPD was higher in SW aspects within tree crowns in the intact forest across treatments before thinning and in the post-thin control and U-thin. But in the O-thin after thinning, the forest surrounding study trees was so severely reduced that any buffering proffered by surrounding forest was likely compromised such that within-canopy microclimate differences by aspect were overwhelmed by the general ambient climate. In the same way, mean VPD was diminished in study trees with greater surrounding BA and within the buffering umbrella of greater canopy closure before treatments. CART results associated the best *Bryoria* growth before thinning with greater surrounding BA and then in the NE aspect. Aspect was not a distinguishing factor for *Bryoria* growth in conditions of less surrounding BA. All this suggests that in more open forest before thinning, and after thinning when the forest was mechanically opened, regardless of the method and pattern, the relatively stable atmospheric conditions found in more dense forest were destabilized and

overwhelmed by the pervasive landscape-level climate. The buffering provided by greater BA and canopy closure may have no longer been sufficient to give those study trees significantly diminished VPD.

The abundance of *B. fremontii* has noticeably decreased over the past few decades in nearby Sequoia National Park (N. Stephenson pers. comm. 2003). Several factors may have contributed to this decline. Foremost is the threat of airborne pollutants from California's large population centers and adjacent agricultural Central Valley (McCune et al., 2007). *B. fremontii* is sensitive to air pollution (Tarhanen et al., 2000). *Bryoria* at this latitude may also be susceptible to climate change and warming temperatures since the southern Sierra Nevada approaches the limit of its range (McCune et al., 2007). Warming temperatures in western forests have also been positively correlated with an increasing size, frequency, and severity of crown fires (Miller et al., 2009) that threaten all arboreal species. Fuels reduction strategies that thin from below and leave retained trees in a grouped pattern may help maintain and foster *Bryoria* populations and their important ecological associations. Stand reconstructions have demonstrated that historically such a structural pattern was the norm in western forests prior to the advent of fire suppression management (Bonnicksen and Stone, 1982; North et al., 2007).

Our experiment had two unexpected results that suggest how treatment placement and severity may impact arboreal food webs. Differences in VPD were most strongly correlated with *Bryoria* growth such that thinning had little impact on riparian samples in consistently low VPD conditions, while *Bryoria* growth was significantly less in upland conditions where VPDs were greater. High *Bryoria* predation rates, particularly in the more severe O-thin, suggest that fuels treatments which substantially reduce canopy closure can adversely impact forage availability for some arboreal mammals such as the northern flying squirrel. Though conclusions from this study are insightful, they are necessarily limited by a lack of site replication. It would be beneficial to expand this research regionally so that inferences might be strengthened and more broadly inferred.

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