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Changes in forage lichen biomass after insect outbreaks and fuel reduction treatments in the Blue Mountains, Oregon

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Abstract: Forage lichens are pendulous, hairlike species eaten by a wide range of mammals. Our overall goal was to estimate losses of *Bryoria,* a genus of ecologically important forage species, in forests subjected to disease and fuel reduction treatments at Starkey Experimental Forest in the Blue Mountains of northeastern Oregon. Specific objectives were to (1) estimate *Bryoria* biomass in stands decimated by insects and disease, (2) compare *Bryoria* biomass in untreated stands with those treated by mechanical fuels reduction and prescribed fire, and (3) estimate the range of pre-insect outbreak *Bryoria* biomass using historical data. Our general approach was to estimate tree-level *Bryoria* biomass on a sample of trees, regress estimates against tree size and species using nonparametric multiplicative regression (NPMR), then predict stand-level biomass by applying NPMR to tree size and density data. For live trees, logarithm of dbh was a strong predictor *of Bryoria* biomass (cross validated $R^2 = xR^2 = 0.83$). Biomass on dead trees showed a similar but weaker pattern ($xR^2 = 0.45$); including *Abies grandis* as an indicator variable substantially improved the model ($xR^2 = 0.52$). Current *Bryoria* biomass is clearly much lower

than the potential biomass for forests of this type. Based on our prediction of pre-outbreak *Bryoria* biomass and benchmarks from related studies, we conclude that the biomass in intact, mature forests should be about 0.5 - 2.0 T/ha. This means insects and disease caused a loss of about 50-80% of starting *Bruoria* biomass, and fuel reduction treatments removed roughly another 10%. How long it will take for the biomass to recover is unknown, but we assume that *Bryoria* recovery will keep pace with structural recovery of the canopy. Even though small, young trees individually supported very low *Bryoria* biomass, their combined contribution to standing biomass will soon be appreciable due to high regeneration density.

Key **words:** *Abies grandis,* advance regeneration, *Bryoria fremontii,* epiphytes, fire, forest management, kernel smoother, *Larix occidentalis,* lichenized fungi, nonparametric multiplicative regression, NPMR, Pacific Northwest, *Pinus ponderosa,* prescribed fire, *Pseudotsuga menziesii,* ungulate forage, western spruce budworm.

Introduction

Forests of the intermountain West are facing an onslaught of disturbances and stressors: logging, fire, insect and disease epidemics, fuel reduction treatments, and climate change. Federal agencies are studying how they can best manage disturbance regimes to restore and enhance ecosystem health. Although many attributes of these forests are actively being studied, an important but largely neglected component of these forests is the forage lichens.

Forage lichens are pendulous, hairlike species, eaten by a wide range of mammals (McCune et al. *2007). Bryoria* (Fig. 1) and other forage lichens are an important component of winter diets of ungulates, thought to improve digestibility of poorer forage and enhance their energy balance (Rochelle 1980; Jenks and Leslie 1988, 1989; Gray and Servello 1995). Mule deer (or black-tailed deer, *Odocoileus hemionus)* and elk *(Cervus elaphus)* eat *Bryoria* litterfall, particularly in winter (Ward 1999, Ward and Marcum 2005). Based on exclosure studies, these authors found winter consumption of *Bryoria* to be 6.5 - 8.2 kg/ha. Forage lichens were also eaten by Native Americans (Brodo and Hawksworth 1977, Brodo et al. 2001). Aside from food, many animals use pendulous lichens for nest materials (Sharnoff and Rosentreter 1998). Northern flying squirrels and Douglas squirrels use *Bryoria* for nest material, in addition to eating it (Hayward and Rosentreter 1994, Rambo 2004).

The most conspicuous species of *Bryoria* at low to mid elevations in the intermountain West is *Bryoria fremontii,* forming massive dark brown beards on conifers (Fig. 1). Abundant in the Pacific Northwest and northern Rocky Mountains, where it can achieve a biomass over 1 T/ha dry weight, this species becomes increasingly rare southward and eastward in drier habitats. The palatability of *Bryoria fremoniii* is notable because, unlike most forage lichens, *B. fremontii* virtually lacks the secondary chemicals that commonly defend lichens against herbivory. Considering its ecological importance in western North America, studies of factors affecting its local distribution and abundance are surprisingly rare (e.g. Lehmkuhl 2004 , Ward 1999, Ward and Marcum 2005).

Bryoria fremontii (henceforth *"Bryoria")* is particularly abundant throughout Starkey Experimental Forest in the Blue Mountains of Oregon, where it is the dominant epiphyte. Our overall goal was to estimate losses of *Bryoria* biomass in forests subjected to disease and fuel reduction treatments. Specific objectives were to

Figure 1. *Bryoria* forms dark brown beards on conifers in western North America. *Bryoria fremontii* in a mixed conifer forest in Starkey Experimental Forest, northeastern Oregon.

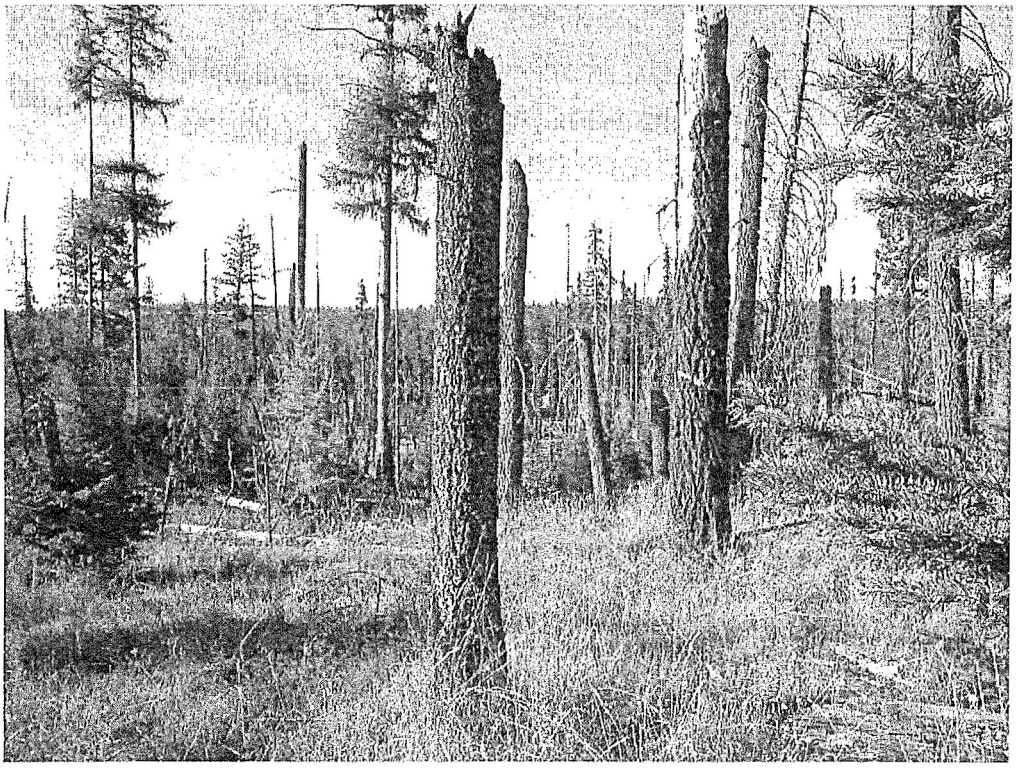

Figure 2. Mixed conifer forest where the *Pseudotsuga menziesii* and *Abies grandis* have been decimated by western spruce budworm. Photo from Starkey Experimental Forest, northeastern Oregon.

(1) estimate biomass of *Bryoria* in stands decimated by insects and disease (Fig. 2), (2) compare *Bryoria* biomass in untreated stands with those treated by mechanical fuels reduction followed by prescribed fire, and (3) estimate the range of pre-outbreak *Bryoria* biomass in these forests. We estimated stand-level *Bryoria* by applying regressions of biomass against characteristics of individual trees.

We found no nearby intact stands for comparison (within a 20-30 km radius). Sampling in distant stands of the same habitat type (sensu Pfister and Arno 1980) would be of questionable relevance to our study area, because epiphyte distribution and abundance appears discordant with vascular plant communities (McCune and Antos 1981a, b, 1982). As an alternative, we applied epiphyte biomass models to historical data on stand structure, allowing us to reconstruct stand-level *Bryoria* biomass from mature, intact stands, similar to what existed prior to the insect and disease outbreak.

Study Area

All study sites were in the Starkey Experimental Forest (Rowland et al. 1997), northeast of La Grande, Oregon. This rolling upland is weakly dissected by drainages, underlain by basalt, and covered by soils with a large component of volcanic ash. Annual precipitation averaged 548 mm from 1986 to 1995, with about 60% falling as snow. Mean annual temperature (1989-1995) was 6.6°C, (U.S. Forest Service, unpublished data in Clark et al. 2000) while mean annual maximum (August) and minimum (December) temperatures in the same period were 25.4 and -7.2°C, respectively.

Abies grandis, Larix occidentalis, Pinus ponderosa, and *Pseudotsuga menziesii* are dominant tree species in the Experimental Forest (Table 1). Stand density varies from open grasslands to closed forests, but all six sites that we studied were formerly closed forests, apart from a few grassy, thin-soil inclusions. Each of these sites had been selected at random for an exclosure experiment involving different densities of elk and cattle (C. Parks and B. Endress, unpublished study plan, 2004). The lichen data reported here were collected within two years after the exclosures were built, but before grazing treatments began. Each 7-ha exclosure site was partitioned into seven 1-ha paddocks, plus an additional i-ha reference area outside the exclosure. We sampled *Bryoria* on trees in each of the 42 paddocks and each of the six associated reference areas.

Forests at all six sites had incurred heavy mortality from insect and disease outbreaks (Fig. 2), apparently initiated by the western spruce budworm, *Choristotieura occidentalis,* beginning in the early 1980s (Rowland et al. 1997). This, exacerbated by drought, resulted in very high mortality, often > 90%, of the mature *Pseudotsuga* and *Abies,* beginning in the late 1980s and continuing well into the 1990s. Half of our study sites were subjected to mechanical fuel reduction treatment, including some tree removal followed by prescribed fire, while half received no treatments.

Methods

Treatments

Three sites had fuels reduction treatments in 2001 and 2002. These consisted of stand-scale mechanical fuels removal, followed by prescribed fire, both in the same year. This included partial cuts of mainly dead overstory trees and removal of fuels (downed wood) in the understory. Prescribed fires combined slash pile burning and broadcast burning. Control stands received no silvicultural treatments in the past 40 years, although they too experienced very high levels of tree mortality from insects and disease.

Bryoria biomass

Our general approach was first to estimate tree-level *Bryoria* biomass on a sample of trees. We then regressed *Bryoria* biomass against tree size and species, then used these relationships to scale up to the stand level using tree size and density data (C. Parks and B. Endress,

Table 1. Site and stand characteristics for trees > 20 cm dbh; biomass of *Bryoria*. All stands had heavy mortality from insects and disease. Treated stands had mechanical fuels reduction followed by prescribed fire. *Larix* is *Larix occidentalis*; *Pseudotsuga* is *Pseudotsuga menziesii*. *Bryoria* biomass (kg/ha) is expressed as mean, median, and standard deviation among paddocks. Eight paddocks were sampled per site.

						Bryoria biomass, kg/ha			
Site	Coordinates, decimal deg.	Elevation, m	Dominant tree species	Current basal area (m^2/ha)	Treated	Mean	S. Dev.	*n*	Median
Bally Camp	45.280 -118.574	1402	*Pinus contorta, P. ponderosa*	8.17	Yes	122	85	8	118
Half Moon	45.237 -118.591	1460	*Larix, Pseudotsuga*	9.61	Yes	236	117	8	201
Louis Spring	45.303 -118.577	1395	*Larix, Pinus ponderosa*	4.18	Yes	110	58	8	99
Bee Dee	45.287 -118.571	1402	*Larix, Pseudotsuga*	6.38	No	216	71	8	213
Doug Prairie	45.293 -118.578	1366	*Larix, Pseudotsuga*	4.51	No	214	82	8	210
Kaenta Spring	45.196 -118.538	1463	*Pinus ponderosa, Larix*	6.30	No	522	574	8	234
					Overall	237	271	48	192

unpublished data, 2007). A total of 5508 individuals > 1 cm dbh (diameter breast height) were included in the tree data.

During 2004-2006 we sampled trees for *Bryoria* biomass at a subset of plots arrayed along transects in each paddock that were sampled for vascular vegetation (C. Parks and B. Endress, unpublished study plan, 2004). We stratified our sample into young vs. remnant trees, the latter group defined as being at least 24 years old (i.e. established before 1980). Young trees and snags less than 2 m in height were excluded because they supported so little *Bryoria* biomass. At each sample point we visually estimated *Bryoria* biomass and measured dbh of a remnant tree and young tree, choosing the tree in each category that was nearest to tagged angle-iron stakes that marked the vascular plant plots. Snags were sampled if they were the nearest trees to the stake. Our objective was to sample nine live remnants and nine live young trees for each paddock. We began by sampling at every odd-numbered plot but often included some even-numbered plots at random until we met the sampling objective. Trees were re-sampled if they happened to be the nearest individual to multiple plots. In total we estimated *Bryoria* biomass on 1062 trees.

We estimated *Bryoria* biomass on individual trees using an approach similar to the visual scoring methods of Rosso et al. (2000), Berryman and McCune (2006), and Armleder et al. (1992). We took several steps to assure accuracy of the observations. First, before conducting surveys, we practiced scoring *Bryoria* biomass on five branches of varying size. We

visually estimated biomass, took photos of branches for use in future calibration efforts, then removed and weighed the lichen. Observer estimates were reasonably correlated with measurements (adjusted r^2 = 0.85 and 0.81 for primary surveyor and a second observer, respectively). Weighed *Bryoria* was stored in transparent plastic bags and frequently referenced by the field worker throughout biomass surveys. Photos of tree canopies with known weights of *Bryoria* (Armleder et al. 1992) were also employed to help re-calibrate during surveys.

Since branches were used for calibration, we scored individual tree branches or whorls of branches when estimating biomass of live trees with large canopies. The estimate of total canopy biomass thus consisted of summed branch scores plus biomass estimated for the tree trunk. For smaller trees with low branches, we estimated and summed biomass of individual *Bryoria* clumps. The canopy biomass of each tree was often scored several times from a variety of vantage points. Calibration and between-observer comparisons showed that the accuracy of this approach was sufficient to detect large differences in biomass (i.e. differences spanning half an order of magnitude or more). Numerous trees scored by independent observers showed consistent results (r = 0.94, n = 189).

Historical Bryoria biomass

To estimate the *Bryoria* biomass in intact forests before the insect and disease outbreaks, we used historical tree data from a nearby area in Starkey Experimental Forest. In 1991 a full census of both live and dead trees > (3 inches) dbh was made in 39, 17-m radius circular plots in the Syrup Creek area (B. Dick, unpublished data; methodology of B. Coleman and B. Bobowski, 1991, unpublished Forest Service document). At the time of sampling, the insect outbreaks were in progress but the stands were still relatively intact. Using only stems > 10 cm dbh, on average the stands had 23.6 m^2/ha oflive basal area and 10.0 m^2/ha of dead basal area. Plots averaged 461 and 383 trees/ha for live and dead trees, respectively. Of the live-tree basal area, *Pseudotsuga menziesii* had 39% of the live basal area, *Abies grandis* 30%, *Pinus ponderosa* 15%, *Larix occidentalis* 15%, and *Pinus contorta* 1%. *Pinus ponderosa* and *Larix occidentalis* had much lower proportion of dead trees than the other species.

Data Analysis

Model building

We regressed $\log_{10}$ of *Bryoria* biomass on individual trees against tree characteristics for the 1062 trees we sampled. Individual trees were treated as sample units. Predictors included: tree species (as a series of binary indicator variables, one per species, and as a single multistate categorical variable), dbh (cm), $\log^{10}$ (dbh), status (live vs. dead), cohort (remnant vs. young), and site (categorical).

We used nonparametric multiplicative regression (NPMR; McCune 2006) with a local linear estimator and Gaussian kernel function (Bowman and Azzalini 1997) to model *Bryoria* biomass. We chose NPMR over multiple linear regression to avoid making distributional assumptions about the data and to accommodate a wide range of response surface shapes. Model building sought the best possible combination of predictors of *Bryoria* biomass. The standard deviation (tolerance) of the kernel function was optimized by maximizing the cross-validated coefficients of determination (xR^2), the statistic used to evaluate model quality. Interpretation of xR^2 is similar to the usual R^2, except that it is penalized by leave-one-out cross-validation. Tolerances define how broadly the estimate for a given point is based on the surrounding sample space. Host tree species were used as binary predictors with tolerance = 0, meaning that categories for predictors must match for a data point to contribute to an estimate. Sensitivities are given only for quantitative predictors. A sensitivity of 1.0 means that nudging a predictor results in a response of equal magnitude, when expressed as proportions

of the variable ranges (McCune 2006). The average neighborhood size, *N*,* is the average sum of weights applied to individual data points. This is the average amount of data bearing on the estimate of the response variable at each point. To apply these nonparametric regression models to new data points, NPMR interpolates from the original data sets on *Bryoria* biomass and tree size, which are available from the first author.

We used the software HyperNiche (McCune and Mefford 2004) to find the best model for each number of possible predictors. We selected the most parsimonious model beyond which the inclusion of additional predictors provided minimal improvement in fit. Preliminary models showed live and dead trees had different relationships to the strongest predictor of *Bryoria* biomass, and different degrees of variability, so we constructed separate regressions for live and dead trees. In each case, we specified a minimum average neighborhood size of 5% of the sample size. The final models were evaluated with a randomization test using 1000 permutations of the response variable in relation to the predictors.

We used the final regression models to estimate biomass on each of the 5508 trees measured by the vegetation crew. Biomass predictions were back-transformed using the same approach as McCune (1993), applying the regression model to each tree. To eliminate the systematic underestimation of biomass caused by back-transforming fitted values from a regression model, we generated random numbers from normal distributions to serve as errors for each prediction. Normal distributions were defined using standard deviations of the NPMR residuals, SD = v'(SSR/(n-1)), where SSR is the sum of squared residuals. We defined two normal distributions, one for live trees (SD = 0.59 log kg) and one for dead trees (SD = 1.15 log kg). Back-transformation was accomplished as follows:

$$\hat{y}^* = \exp\left(\hat{y} + \mathrm{N}(0, \mathrm{SD})\right)$$

where y is the estimate of the log of *Bnjoria* biomass (log kg), y^* is the back-transformed estimate of *Bryoria* biomass (kg), and N is a normally distributed random number with mean = 0, and SD = standard deviation of the residuals. Biomass estimates were then scaled up to kg/ha for each paddock by first summing across all sampled trees in the paddock. This total was then multiplied by the ratio of paddock area to the area within the tree plots.

Bryoria biomass was compared between treated and untreated sites, and between sites within treatments, using ANOVA. Biomass was first log transformed to reduce the strong positive skew. Treatment was analyzed as a fixed factor, while stand was a random factor, with paddocks nested within sites. Variance due to treatment was tested against site-to-site variance. Variance among sites within treatments was tested against variance among paddocks within sites.

Historical data

To estimate the biomass of *Bryoria* in the Syrup Creek plots censused in 1991, we used HyperNiche (McCune and Mefford 2004) to apply our nonparametric regressions of biomass against tree characteristics to individual trees. We then aggregated tree-level estimates to the plot level. To reduce the bias associated with back transformation, we reintroduced the regression error before back transforming, as described above. A frequency distribution was constructed using a probability density function made with a Gaussian kernel smoother. We used Bowman and Azzalini's (1997) cross-validation method for optimizing the smoothing parameter.

Results and Discussion

Bryoria biomass in relation to tree characteristics

For live trees, the best NPMR model identified a single strong predictor of *Bryoria* biomass, log (dbh). This yielded a cross-validated xR^2 = 0.82 (tolerance = 0.098, sensitivity =0.82; N* = 141). None ofthe 1000 randomizations of the

data produced a value this high or higher ($p < 0.001$). Beyond this single-predictor model, the variable that improved the model the most was tree species, coded as a multi-state categorical variable. Because this predictor increased xR2 only slightly (to *0.86),* it was not retained in the final model.

Bryoria biomass on live trees increases with live tree diameter, but in a nonlinear way (Fig. 3). The importance of tree dbh for accumulation of forage lichens relates to two factors not directly measured in this study, tree age and surface area. Older trees, besides having more substrate available for colonization, have had a longer time to accrue *Bryoria* biomass. Other related factors may also be important, such as changing moisture, light, and temperature conditions in the expanding tree crown. No data on changing environmental conditions with tree size are available for this environment.

Tree species differed slightly in their relationships between diameter and *Bryoria* biomass (Fig. 4). No single species stood out strongly from the others, as evidenced by the failure of individual tree species coded as binary variables to enter the model. *Abies qrandis* did, however, appear to have accumulated more *Bryoria* for a given size in the smaller diameter trees, but large trees had about the same *Bryoria* biomass, regardless of species (Fig. 4).

Dead trees showed a similar pattern of *Bryoria* biomass and tree size (Fig. 3), except that the relationship fell apart in the larger diameters (> 18 cm dbh), with many trees having much lower biomass than would have been expected for a live tree of similar diameter. This accords with our field observation that snags consistently held much less biomass than their live counterparts. Some recently dead trees, however, *had Bryoria* biomass similar to live trees. Time since death is likely an important predictor since lichens are shed along with bark and branches after the tree dies. Lichens also experience a dramatic change in microclimate following needle loss from the dead crowns but it is unclear whether this change

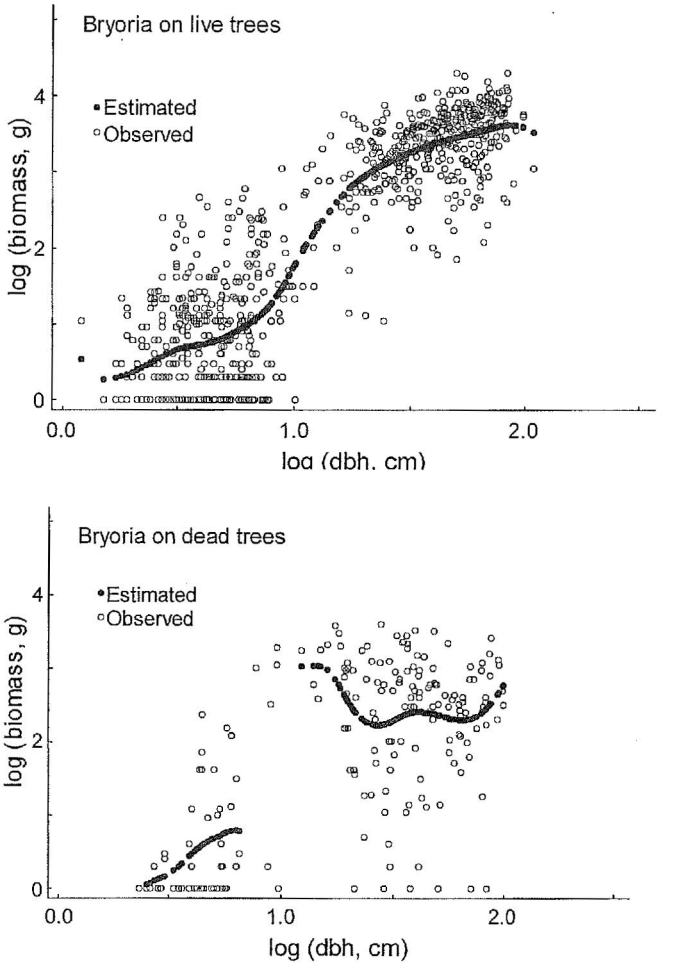

Figure 3. Scatterplots of $\log_{10}$-transformed *Bryoria* biomass vs. tree dbh for live trees (upper, n = 868 trees, xR^2 = 0.83) and dead trees (lower, n = 194 trees, xR^2 = 0.52). Log(dbh) was the only predictor for the live tree model; log(dbh) and the binary variable "*Abies grandis*" were predictors for the dead tree model.

would promote or diminish *Bryoria.* Growth rates may be promoted in portions of the crown experiencing moderate light and moisture increases but diminished in others where a microclimatic shift is more extreme. Perhaps more important is mechanical loss of substrate from the dead tree as well as greater exposure to wind, causing a more rapid flux of *Bryoria* biomass from the canopy into the litter pool (Fig. 5).

Including Abies *grandis* as an indicator variable improved the regression model for dead trees from xR^2 = 0.445 *to* xR^2 = 0.522 (N-* = 19; log (dbh) tolerance = 0.082, sensitivity = 0.88). As with the live trees, small *Abies grandis* tend to have somewhat higher biomass of *Bryoria* than similar sized trees of other species (Fig. 4, lower panel). *Abies grandis* both occurs in and creates more sheltered conditions than the other tree species. Because of its shade tolerance, small individuals are often older than their size would suggest. Both of these conditions would lead to more *Bryoria* biomass on small *Abies grandis* than on small individuals of other species.

Stand -level biomass

We estimated that stand-level *Bryoria* biomass ranges from 99-234 kg/ha (median = 192 kg/ha), based on median values from the eight paddocks sampled in each of the six stands. These low biomass values largely resulted from devastation of the canopy by insect and disease outbreaks. Snags have lower *Bryoria* biomass than intact trees, gradually shedding branches and lichens into the litter. Although tree regeneration has been strong in some areas, the younger cohort is still too small to support much epiphyte biomass.

The fuels reduction treatment (cutting, piling, and burning of slash piles) appears to have also had a small negative effect on epiphyte biomass. We do not have before-and-after data, although biomass *of Bryoria* averaged somewhat lower (median 99-201 kg/ha) in the three treated areas than in the three untreated areas (median 210-234 kg/ha; Fig. 6, Table 1). Although p = 0.11 for

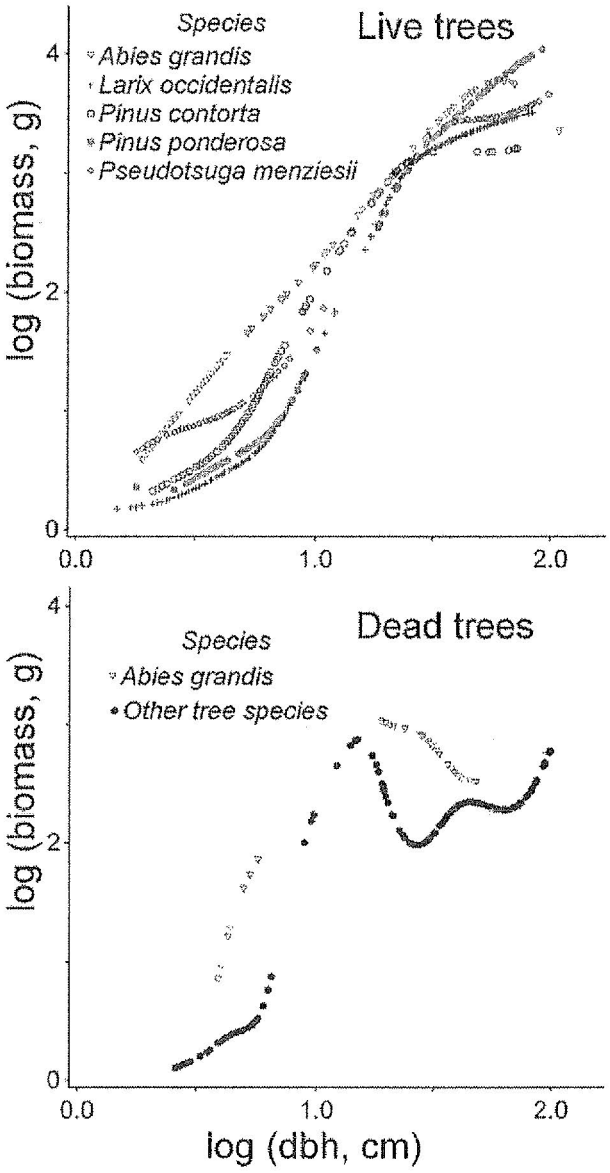

Figure 4. Estimates of *Bryoria* biomass by species and log(dbh). Upper panel: live trees (xR^2 = 0.83). Lower panel: dead trees (xR^2 = 0.52).

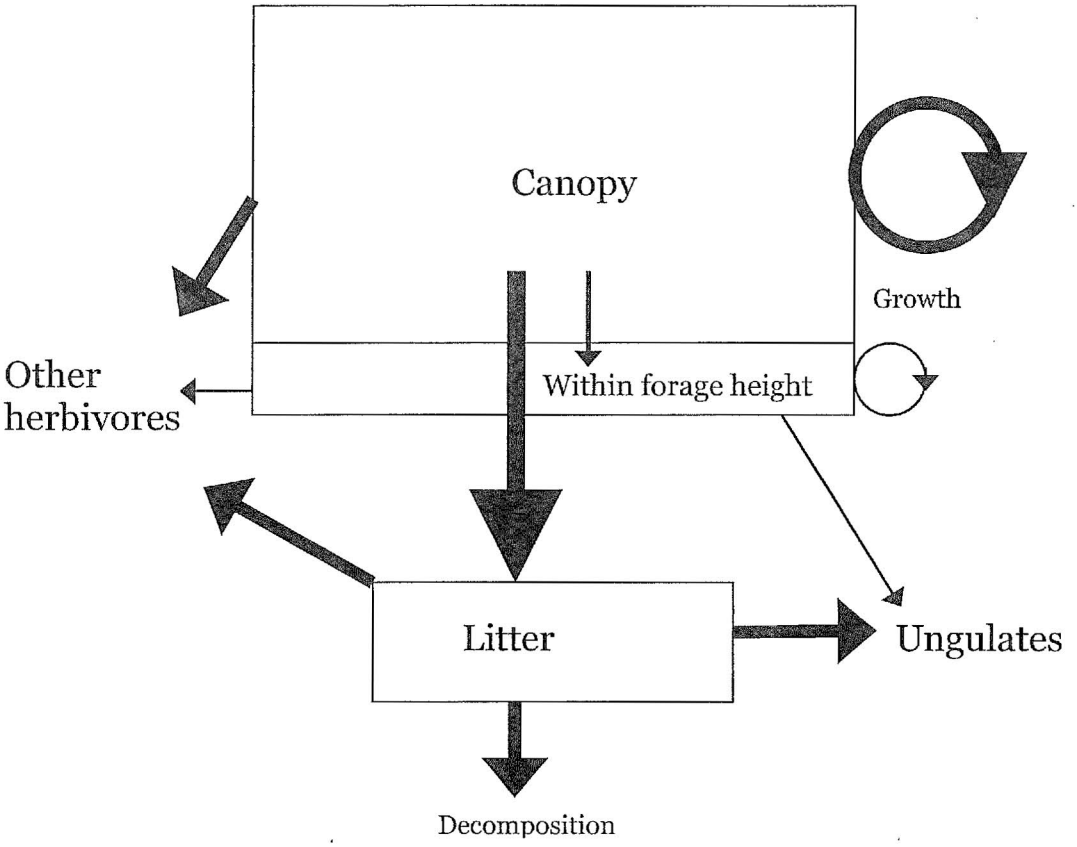

Figure 5. Conceptual model for forage lichen (*Bryoria*) biomass fluxes (arrows) and pools (boxes). The width of the arrow roughly indicates the size of the flux, but data on these fluxes are extremely limited.

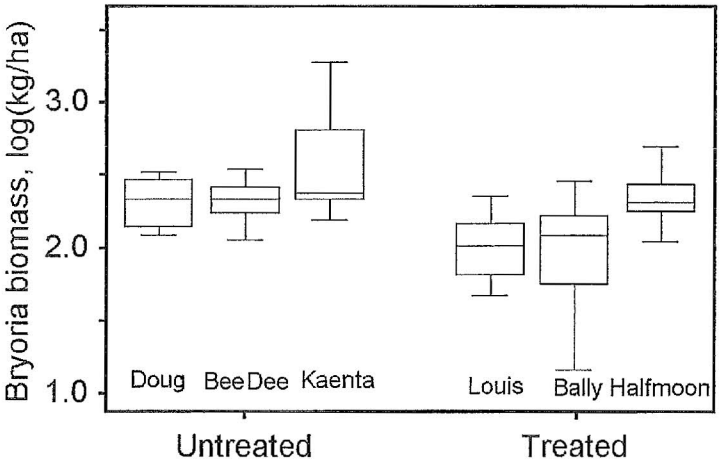

Figure 6. Estimated *Bryoria* biomass in 8 paddocks at each of 6 sites. Treated sites had removal of some residual trees and broadcast burning, the treatments over 10 years after insect and disease epidemics. Boxes show the median, 25th, and 75th percentiles. Whiskers show the range of values.

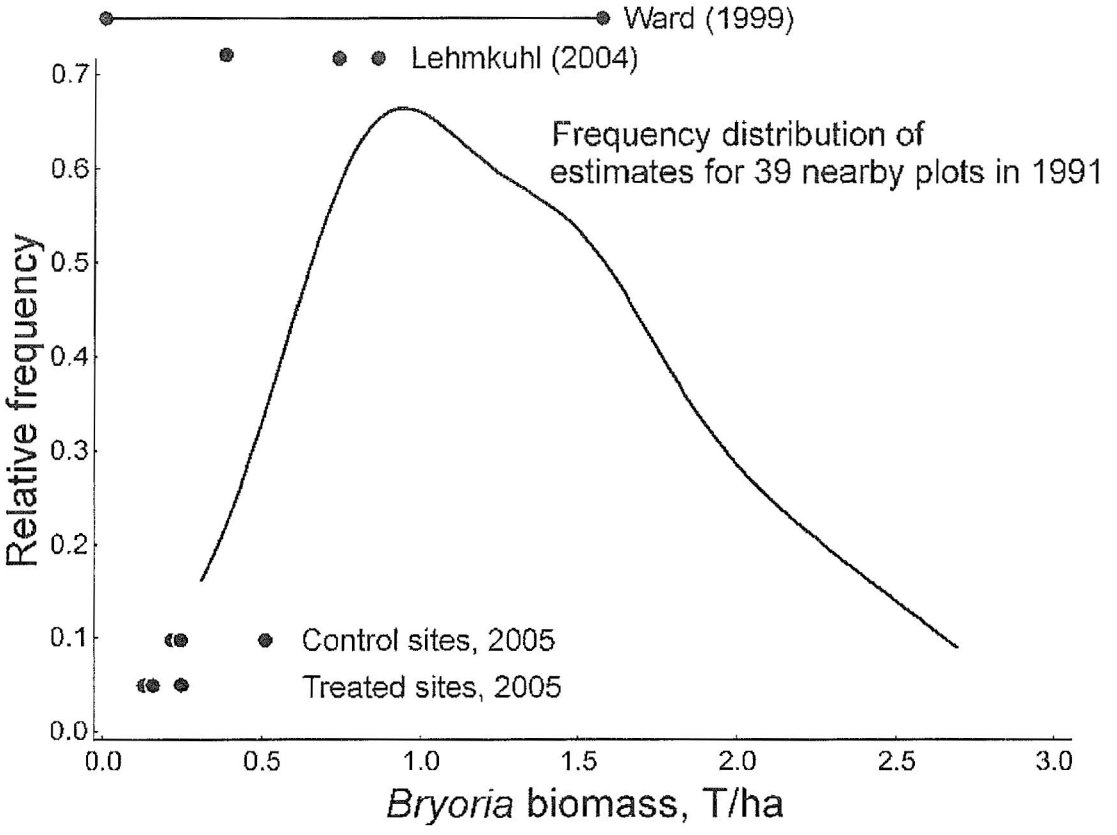

Figure 7. *Bryoria* biomass (metric T/ha) in treated and control sites compared to a frequency distribution of estimates based on stand structure in 39, 0.9 ha plots measured for trees in 1991. The 1991 data were collected early in the mortality process, so that they represent relatively intact forests, though with numerous dead trees. Estimates from three similar forests from Lehmkuhl (2004) in central Washington and a range of stands sampled by Ward (1999) in western Montana are superimposed for comparison.

this difference (Table 2), the test had very low power owing to the small number of replicates. Likewise, *Bryoria* biomass did differ considerably among sites within treatments (Table 2). This heterogeneity probably arises from a combination of pre-existing natural differences in stand structure among paddocks, differences in treatment intensity across stands, and varied density of tree regeneration.

We expect that pre-disturbance biomass in experimental plots was comparable to that of nearby intact stands. Using the 1991 historical dataset for Syrup Creek, biomass estimates for individual 0.9 ha plots ranged from 310-2688 kg/ha, with most values falling between 500 and 2000 kg/ha (median = 1168 kg/ha, mean = 1302 kg/ha), This median is about five times larger than in the disease-ridden plots. *Current Bryoria* biomass in experimental plots is thus clearly much lower than the potential biomass for forests of this type (Fig. 7).

Studies in similar forests from other areas provide additional benchmarks for assessing biomass potential (Fig. 7). Lehmkuhl (2004) used McCune's (1994) litterfall pickup method to

estimate *Bryoria* biomass from three contrasting stands in eastern Washington Cascades. These included an open pine stand (342 kg/ha), a young mixed-species stand (mainly *Abies grandis* and *Pseudotsuga;* 751kg/ha; perhaps most similar to our study area), and a mature mixed-species stand (855 kg/ha; Fig. 7). Ward (1999) also used the litterfall pickup method (McCune 1994) to estimate *Bryoria* biomass in a variety of forests in west-central Montana. Stands were mostly dominated by second-growth *Pseudotsuga* over 60 years old, with varying amounts of *Larix occidentalis, Abies lasiocarpa, Abies grandis, Pinus contorta, Pinus ponderosa,* and *Picea engelmannii.* Standing *Bryoria* crop ranged from 7-1558 kg/ha. *Larix* abundance and canopy cover were two key factors promoting high *Bryoria* biomass. Typical *Bryoria* biomass values for stands with moderate *Larix,* about 50-60% canopy cover, were about 400-500 kg/ha. Again, these values are much higher than in our diseased stands.

Based on historical plot data and both benchmarks, we conclude that the biomass of *Bryoria* in intact, mature forests in Starkey Experimental Forest should be about 0.5 - 2.0 T/ha (Fig. 7). This means that insects and disease caused a loss of about 50-80% of starting *Bryoria* biomass, and fuel reduction treatments removed roughly another 10%. How long it will take for the biomass to recover is unknown, but we assume that *Bryoria* recovery will keep pace with structural recovery of the canopy.

Old, large, live trees supported the greatest lichen biomass. Therefore, processes that kill trees (e.g., insects and disease) will decrease biomass of forage lichens, as would processes that promote small-diameter and young forests, such as overstocking or short-rotation lengths.

Even though small, young trees individually supported very low *Bryoria* biomass (Figs. 3-4), their combined contribution to standing biomass will soon be appreciable in some paddocks due to high regeneration density.

Table 2. Analysis of variance comparing *Bryoria* biomass in treated (fuels reduction) and untreated sites. Biomass was expressed as $\log_{10}$(kg/ha). Paddocks are nested within sites. The treatment was tested by comparison to the variance among sites. Differences among sites within treatments were tested by comparison to the variance among paddocks within sites.

Source	SS	df	MS	*F*	*p*
Treatment	1.053	1	1.053	4.10	0.113
Site	1.027	4	0.257	3.47	0.016
Paddock	3.109	42	0.074		

The *Bryoria* on the small trees can be considered "advance regeneration" of epiphytes. Advance regeneration of trees refers to tree seedlings already established on a site before the overstory trees are harvested or otherwise removed. Thus, advance regeneration of epiphytes is the biomass established on seedlings and saplings before the canopy was removed. Both kinds of advance regeneration will normally speed recovery.

Bryoria as forage

We apply the annual turnover rate of Stevenson (10.5-16.1%;1979) to median *Bryoria* biomass from Syrup Creek to estimate that 123-188 kg/ha/yr of *Bryoria* forage would be available to deer and elk in the litterfall of mature, intact stands of Starkey Experimental Forest. With the currently depleted canopy, we estimate that less than 10 kg-ha^{-1}-yr^{-1} of *Bruoria* is available for animal consumption at ground level. Most of the paddocks are now being subjected to elk and cow grazing trials although we do not anticipate that the canopy pool of *Bryoria* will be much impacted. An exception is biomass on the younger cohort of trees, much of which lies within the browse line. We have noted that this *Bryoria* is rapidly consumed soon after ungulates are introduced (A. Hardman, pers. obs.).

Given the palatability of *Bryoria* to ungulates and its importance in their winter diets (Rochelle 1980; Jenks and Leslie 1988, 1989; Gray and Servello 1995, Ward 1999, Ward and Marcum 2005), maintenance of high *Bryoria* biomass in western forests should enhance ungulate habitat. The recovery rate of *Bryoria* after major disturbance is limited by the quantity of both remnant lichen biomass and remnant standing trees. To hasten recovery, we recommend that fuel reduction treatments retain as many of the *Bryoria-laden* trees as possible. When treating areas with decimated canopies, retention of larger trees in the advance regeneration should promote recovery of *Bryoria.*

The forage lichen *Bryoria* is a large, yet underappreciated, wildlife resource. Our understanding of the roles and dynamics of *Bryoria* in the ecosystem is limited by the extremely sparse information on critical rates in population dynamics of *Bryoria:* population growth, litterfall, herbivory, and the factors that influence these rates. These critical rates are the weights of the arrows in Figure 5, the fluxes in biomass *of Bryoria.* Population growth rates need to be addressed by both short-term observations and long-term monitoring, herbivory by exclosure studies, and litterfall by repeated litterfall pickup or litterfall traps. In particular, the exclosures at Starkey Experimental Forest provide an opportunity to study population growth and herbivory of *Bryoria.* These key processes control how *Bryoria* will respond to the dynamic forest landscape, a landscape set in motion by fires, insects and disease, climate change, and stand development.

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