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Estimating epiphytic macrolichen biomass from topography, stand structure and lichen community data

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Abstract.
Question/Location: We modelled lichen epiphyte biomass in relation to topography, stand structure, and lichen community composition in the central Cascades of western Oregon.
Methods: Sampling was stratified by stand structure. Epiphyte biomass was estimated based on lichen litter for three functional groups: cyanolichens, forage lichens, and matrix lichens. Regression models for estimating lichen biomass ($\log_{10}$ kg.ha^{-1}) were developed based on three pools of predictors, each pool demanding different levels of effort to obtain the data. First, we created models from topographic predictors that are easily extracted from GIS data. We then developed models based on both topographic and stand-structure variables. Finally, we developed models using topography, stand structure, and lichen community data.
Results/Conclusions: Lichen biomass changed with elevation, cyanolichen biomass highest at low elevations (470-950 m) and forage lichen biomass highest at higher elevations (950-1470 m). Lichen biomass was lowest in even-aged young stands and highest in mature stands with remnant trees and in old-growth. Stands with remnant trees had more lichen biomass than even-aged stands.

Models with the greatest explanatory power were: cyanolichen biomass predicted as a function of elevation, stand age index, the sum of *Lobaria oregana* and *L. pulmonaria* abundance, and cyanolichen species richness (R^2 = 0.85); forage lichen biomass predicted as a function of stand age index and, *Alectoria sarmentosa* abundance (R^2 = 0.55); and matrix lichen biomass predicted as a function of stand age index and matrix lichen abundance (R^2 = 0.58). These models are useful tools for understanding and predicting the distribution of epiphytic macrolichen biomass at a landscape scale.

Keywords: Cyanolichen; Ecosystem function; Forest canopy; Forest management; Landscape; Predictive model.

Nomenclature: McCune & Geiser (1997).

Abbreviations: AI = age index; OG = old growth; PNW = Pacific Northwest.

Introduction

Epiphytic macrolichens are important components of forest ecosystems. Lichens contribute to forest biodiversity (Lesica et al. 1991; Dettki & Esseen 1998; Kuusinen & Siitonen 1998; Pharo et al. 1999) and are used for forage by some animals. The genera *Alectoria* and *Bryoria* are important food sources for deer (Stevenson 1978; Stevenson & Rochelle 1984), woodland caribou (Edwards et al. 1960; Rominger & Oldemeyer 1989; Servheen & Lyon 1989), and flying squirrels (Maser et al. 1985, 1986; Rosentreter et al. 1997; Zabel & Waters 1997). Lichens provide nesting material for birds (Hagar 2004) and flying squirrels (Hayward & Rosentreter 1994) and are used for habitat by many invertebrates (Pettersson et al. 1995). Lichens may also play important roles in productivity and nutrient cycling of forest ecosystems (Pike 1978; Boucher & Nash 1990; Knops et al. 1991; Esseen et al. 1996). Lichens with cyanobacteria as a photobiont (cyanolichens), such as *Lobaria oregana*, fix atmospheric nitrogen and are especially important to nutrient cycles of Pacific Northwest forest ecosystems (Pike 1978; Denison 1979; Antoine 2004). In addition, lichen epiphytes are useful indicators of forest health because they are sensitive to forest management practices and they serve as indicators of air quality (Richardson 1989; McCune 2000).

Epiphytic lichen biomass of temperate forests slowly increases with stand age, typically reaching high levels in mature and old-growth forests (McCune 1993; Neitlich 1993) and in stands that are more structurally complex (McCune et al. 1997a; Clement & Shaw 1999; Pipp et al. 2001). In the Pacific Northwest (PNW), cyanolichens are major components of lichen biomass in old-growth forests at low elevations (ca. 1000 kg.ha^{-1} dry weight, McCune 1993; Pike et al. 1977; Neitlich 1993), comprising 60-80% of the total lichen biomass in such stands (Pike et al. 1977; Neitlich 1993; McCune 1994; Sillett 1995). Cyanolichen biomass in the PNW conifer

forests is dominated primarily by *Lobaria oregana* (Pike et al. 1977; McCune 1993; Neitlich 1993). *Lobaria oregana* is considered old-growth associated, but is also capable of growing well in young stands (Sillett & McCune 1998; Sillett et al. 2000a, b). Cyanolichens are nearly absent in young, regenerating conifer forests and when present, they are in very low abundance (Neitlich 1993; Sillett & Neitlich 1996; Berryman 2002). Recent studies suggest that some cyanolichens, such as *Lobaria oregana*, are dispersal-limited (Sillett et al. 2000a, b) and as a result, are well established in old-growth forests simply because they had more time to get there.

Lichen diversity and abundance may be maintained by preserving existing populations and suitable habitat in the landscape and by managing to promote dispersal of lichen propagules among forest stands, especially to young even-aged forests where lichen diversity and biomass are low (Neitlich 1993; Neitlich & McCune 1997; Dettki & Esseen 1998; Peterson & McCune 2001). Various management practices, such as retaining old remnant trees during harvest, may benefit the survival and propagation of lichen communities in managed landscapes. Canopy structure is enhanced with increased remnant tree retention, and is positively related to cyanolichen biomass (Peck & McCune 1997; Sillett & Goslin 1999) and overall lichen biomass (Pipp et al. 2001). Other forest structural features such as hardwood patches and snags may also enhance forest lichen diversity and biomass (Sillett & Neitlich 1996; Rosso 2000; Pipp et al. 2001). We must better understand the relationships between epiphytic lichen communities and lichen biomass to manage for both at the landscape scale.

In this paper, we evaluate patterns in epiphytic macrolichen biomass by functional group as they relate to topography, stand age, remnant tree retention, and lichen communities in the Blue River watershed of western Oregon. We use these relationships to develop regression models for estimating epiphytic macrolichen biomass by functional group in forest stands.

Sampling epiphytic macrolichen biomass in forests is slow and tedious. We developed models for estimating epiphytic macrolichen biomass that will facilitate large-scale studies of lichen biomass. It is important to understand the distribution of lichen biomass in the forest landscape, because contributions of lichens, such as nitrogen fixation and provision of forage, are likely proportional to their biomass (Pike 1978).

The models provide a method for estimating stand-level biomass for three lichen functional groups (cyanolichens or 'nitrogen-fixers', forage lichens, and matrix lichens or other 'green-algal' lichens). Regression models were developed based on three pools of predictors, each pool demanding different levels of time and effort to obtain the predictor variables: those based only on topographic variables that can be derived from GIS data; those based on topographic variables and stand structure; and those models that were developed from topographic variables, stand structure, and lichen community data. Models based on stand structural variables and lichen community data presumably provide better estimates of biomass, but require visiting the stands for data collection.

Methods

Study area

We studied forests that were, for the most part, in the Blue River watershed of the Central Cascades Adaptive Management Area in the Willamette National Forest, Oregon, USA (see Berryman 2002 for site details). The Adaptive Management Area is currently managed under the experimental Blue River Landscape Plan in which management is based, in part, on historical fire regimes (Cissel et al. 1999). The Blue River watershed consists of 23 900 ha of mainly conifer forest on steep terrain ranging from 317-1639 m a.s.l. The watershed receives an average annual precipitation of 2200 mm (ranging from 550 to 3610 mm). The winters are cold and wet with a mean temperature of 2 °C (ranging from –1.5 to 7.3 °C) in January, and the summers are warm and dry with a mean temperature in July of 19 °C (ranging from 15 to 22 °C). The northern part of the watershed consists of a narrow band of high elevation forests (> 950 m) dominated by *Abies amabilis* (Pacific silver fir) and *Abies procera* (Noble fir) – hereafter, '*Abies* series' (Logan et al. 1987). Most of the watershed is forest at lower elevations (< 950 m) dominated by *Pseudotsuga menziesii* (Douglas fir) and *Tsuga heterophylla* (Western hemlock) – hereafter, '*Tsuga* series' (Logan et al. 1987).

Sample design

This study was part of an extensive lichen community study implemented in the Blue River watershed (Berryman 2002). Lichen communities and biomass were sampled in forest stands using a stratified random design based on the following attributes:

1. Two plant series (*Tsuga* and *Abies*);
2. Four age classes (the younger tree cohort; young < 20 a, pole 21-80 a, mature 81-200 a; and old growth > 200 a);
3. Four classes of remnant tree retention based on the percent canopy cover of remnant trees that survived from the previous stand following a disturbance that

initiated tree regeneration: 0 = 0-7.5%; 15 = 7.5-22.5%; 30 = 22.5-37.0%; 50 = 37.0-62.0%. Remnant trees included the older live trees that remained following the most recent timber harvest or that survived a forest fire. The characteristics of remnant trees (i.e. size, crown structure) varied among stands because remnants from a timber harvest were often smaller and younger than those remnants surviving forest fires. Old-growth stands were not stratified by remnant classes. Only 0% and 15% classes were sampled in the *Abies* series, since future management strategies will prescribe only these retention levels in the *Abies* series (Cissel et al. 1999).

Each combination of the three attributes defines a 'stand type'. While we sought to sample lichen communities in three stands for each stand type, many combinations of these strata were not present in the landscape and thus, were not sampled.

Stand types were located using aerial photos, then verified on the ground. The age class was estimated for the stand, or, if the age class was difficult to determine, we cored representative trees. We used total percent canopy cover of remnant trees as a surrogate for total percent remnant tree retention. Canopy cover of each remnant tree was estimated from tree diameter at breast height (DBH) and crown width (J. Mayo unpubl. data).

Lichen communities

The Forest Health Monitoring (FHM) lichen community method (McCune et al. 1997b) was used for the permanent installation and sampling of the lichen community plots. Each of the 117 stands was sampled for lichen community data using one FHM plot (Berryman 2002). The FHM plot center was randomly located within the stand. The FHM method is a time-constrained ocular survey of epiphytic macrolichens that occur on woody plants (including tall shrubs) in a 0.4 ha circular plot (34.7 m radius). The survey includes all epiphytic macrolichens that occur in the forest litter and on boles and branches that were within reach, excluding the lower 0.5 m of tree boles and shrubs. Species abundance was recorded in five coarse abundance classes (modified from McCune et al. 1997b) as follows: 0 = absent; 1 = rare (< three individuals per plot); 2 = uncommon (four to ten individuals per plot); 3 = common (> ten, but < 40 individuals per plot); 4 = very common (> 40 individuals per plot, but less than half of available substrate covered by the species); and 5 = abundant (present on more than half of the available substrate).

Litter plots

We estimated epiphytic lichen biomass from lichen litter fall on the forest floor. We converted our estimates of lichen litter biomass to epiphytic lichen biomass using a 100 : 1 relationship between epiphyte biomass and litter biomass ($R^2 = 0.89$) collected in late summer in forests of the western Cascades (McCune 1994). Epiphytic lichen biomass includes all epiphytic lichens growing on boles and branches of trees and tall shrubs. Collecting lichen litter in late summer (late August through October) avoids the large and variable amounts of litter that can occur in winter months due to large storm events (Stevenson & Rochelle 1984; Esseen 1985). Late summer litter does not represent annual litter fall because lichen litter in the forests of the western Cascades is eaten and decomposes rapidly (McCune & Daly 1994). However, such samples can be used to estimate epiphytic lichen biomass at the stand level (Neitlich 1993; McCune 1994; Peck & McCune 1997; Sillett & Goslin 1999). Annual variation in litter fall is one source of error in such estimates. Hence, this method should be based on samples collected during one late-summer period and is best used for estimating large relative differences in epiphytic lichen biomass among stands over a large area (McCune 1994).

Lichen litter was collected in a minimum of one stand per stand type. Of the 117 stands in which we collected lichen community data, we sampled 63 stands for lichen litter biomass. The 63 stands were chosen to include the full range of stand types included in the 117 stands. In each stand, epiphytic macrolichen litter was sampled in 2 m radius circular plots ('litter plots'). Depending on the stand age and complexity of canopy structure, 10 to 15 litter plots were sampled for each stand (McCune 1994). Stands with obviously low lichen biomass (e.g. even-aged young stands, < 20 a) were sampled with ten litter plots. Old growth (> 200 a), mature stands (81-200 a), and most stands with remnants were sampled with 15 litter plots.

Litter plots were placed along three transects per stand at randomly selected intervals, but constrained to 12-30 m between plots (two transects if sampling only ten litter plots). Transects were established parallel to the contour, intersecting the FHM plot center for the first transect. The other two transects were parallel to the first, separated by 12 m. This achieved interspersion throughout the stand. Some litter plots were placed outside of the FHM plot boundaries, though still within the stand. Five litter plots were sampled per transect.

Sampling lichen litter biomass

Epiphytic macrolichens were divided into three functional groups based on their roles in the forest ecosystem (McCune 1993). These groups include 'cyanolichens', which consist of all nitrogen-fixing lichens with cyanobacteria present as either the primary or secondary photobiont; the major contributors to this group included primarily *Lobaria oregana* and to a lesser degree *L. pulmonaria*. 'Forage lichens' consist of all pendulous fruticose lichens. These are used for forage by wildlife, primarily the genera *Usnea, Alectoria,* and *Bryoria*. 'Matrix lichens' account for all remaining green-algal macrolichens, primarily foliose in growth form, most commonly *Platismatia* and *Hypogymnia*.

We modified McCune's (1994) litter-pickup method for estimating stand-level lichen biomass to expedite sampling across many stands at the landscape scale. The 'reference method' was developed based on visual biomass estimates of thalli to sample lichen litter from the forest floor more rapidly, while maintaining a similar level of accuracy to that obtained with the litter-pickup method. The visual estimates of lichen biomass were made using reference lichen samples for calibration. This method was adapted from Rosso et al. (2000) and Campbell et al. (1999), in which they visually estimated biomass of lichens and bryophytes in the forest canopy using air-dried reference samples for calibration. The reference method is also a modification of the abundance classes (defined by grams of lichen) used by Stevenson et al. (1998) to estimate arboreal forage lichen biomass. We modified these approaches to visually estimate lichen litter biomass by functional group on the forest floor.

We estimated lichen litter biomass during the late summers of 1997-1999; each of the 63 stands was sampled once for lichen litter. Within each plot, oven-dried samples from each functional group (0.1, 1.0, 5.0, 10.0 g) were used as references for calibrating estimates of lichen litter biomass in the field. To assess reliability of the method, estimates from the reference method were calibrated against true litter-pickup masses for one litter plot in each of 16 different stands. Two field collectors calibrated their biomass estimates from the lichen litter plot to true lichen masses (16 litter plots per field collector). The 'picked-up' specimens were air-dried, then oven-dried at 60 °C for 24 h, and then weighed to the nearest milligram in the lab. Daily calibrations were also made between estimates of biomass for individual clumps of lichen litter and true lichen masses for each functional group. These calibrations allowed field collectors to gauge the accuracy of their litter estimates. We also calibrated litter estimates between field collectors to improve precision of the estimates.

Analysis

The biomass of lichen litter for each functional group was averaged for each stand and then converted to epiphytic lichen biomass using the 100 : 1 ratio of epiphyte biomass to litter biomass (McCune 1994). The average epiphytic macrolichen biomass values were log-transformed: $\log_{10}(x + 1)$; where x was an estimate of oven-dried epiphyte biomass, $kg.ha^{-1}$, based on lichen litter estimates, to reduce skewness in the analyses and for model development because epiphyte biomass values ranged across one to five orders of magnitude. All results are reported as biomass of epiphytic macrolichens (oven-dried; $\log_{10} kg.ha^{-1}$).

Patterns of lichen biomass in the landscape

Non-metric multidimensional scaling (NMS; Kruskal 1964; Mather 1976) was used to ordinate forest stands in lichen species space (N = 117, of which 63 were sampled for lichen biomass), using lichen abundances from the community surveys. Ordination allows us to relate patterns in lichen biomass to gradients in lichen community composition and to environmental gradients (see community results in Berryman 2002). The ordination was rotated to maximize the correlation of canopy biomass for each lichen functional group with one axis. This required a separate rotation for each group, resulting in three different rotations of the one ordination. Stand scores from the rotated ordinations form the basis for estimating lichen biomass from lichen community composition.

We compared total lichen biomass and lichen biomass for each functional group among stand types for the 63 stands in which biomass was sampled. Comparisons of lichen biomass in relation to all stand types were made separately for the two plant series using one-way analysis of variance in SPSS version 8.0 (Anon. 1998). Stand types with fewer than two stands were omitted from the analysis.

Predictive models for estimating biomass

We developed predictive regression models using SPSS version 8.0 (Anon. 1998) and HyperNiche version 1.0 (McCune & Mefford 2004) for estimating epiphytic macrolichen biomass for each functional group. Models were developed in three stages, each stage demanding more field data. The dependent variable in these models was epiphytic macrolichen biomass (oven-dried; $\log_{10} kg.ha^{-1}$) by functional group. Models were developed based on the 63 stands in which lichen biomass was gathered.

First, we developed models from topographic

variables that can be derived from a digital elevation model in GIS (the topographic variables we used, however, were collected on site). Second, we developed models based on both topography and stand structure. Obtaining the stand structure variables requires a site visit or access to previously collected data on tree ages and remnant tree retention. The third level in our model building included variables based on topography, stand structure, and lichen communities. These models can be used only at sites where lichen community data have been collected. In the third level, all classes of variables were not always represented in the best models. Although meaningful interaction terms were considered, none contributed significantly ($p \geq 0.05$) to the models.

Topographic predictors included: elevation, slope, potential incident radiation, heat load index, and topographic position (Table 1). Stand structure predictors included average total basal area of live and dead trees ($m^2.ha^{-1}$) and the age index (Table 1). Stand types were not used as predictors in the regression models because stand types are categorical and in some cases only one or two stands were sampled per stand type. The age index integrates the many stand types into a single continuous variable, representing what we conceive as a single biological phenomenon: the influence of old trees on lichen communities and biomass.

The age index is a combination of 'age credits' for the stand age class and the retention of remnant trees, expressed as a percentage of old growth. In the field, stands were assigned to age classes based on age estimates. We used the median age of the younger cohort and of old growth to assign age credits to a stand (Table 2). The median age was calculated as a percentage of the median age for old growth (i.e. 300 a). The median age for old growth was an *a priori* estimate based on an estimate of the median age of old-growth forests in the Blue River watershed. This percentage represented the base age credits for each age class. If remnants were present, the percent canopy cover class by remnants (15, 30, or 50%) was added to the base credits. Values for the raw age index ranged between three and 100, where three represented even-aged young stands and 100 represented old growth (Table 2). The age index was $\log_{10}$-transformed to improve linearity in the models (hereafter the log-transformed age index will be referred to as 'age index' or 'AI').

The lichen community predictors included: species richness of each lichen functional group by stand, sum of abundance classes for all observed species in each lichen functional group by stand, stand scores from the NMS ordination rotated for each functional group, and the abundance classes for selected individual species within a lichen functional group (usually the dominant species; Table 1). There were three stand scores from the ordination, one for the rotation of each lichen functional group.

Table 1. Topography, stand structure, and lichen community descriptors considered as predictors (independent variables) in regression models estimating epiphytic macrolichen biomass for functional groups. The table shows the range or minimum and maximum values for each predictor across all 63 stands in which lichen biomass was collected.

Symbol	Description			
Topography predictors			Min.	Max.
E	elevation (m)		469	1469
PDIR	potential direct incident radiation ($MJ.cm^{-2}.a^{-1}$) (McCune & Keon 2002)		0.28	1.04
HLI	heat load (McCune & Keon 2002)		0.39	1.04
SLP	slope (degrees)		0.9	36.0
Stand structure predictors			Min.	Max.
BA	total basal area of live and dead trees from prism measurements ($m^2.ha^{-1}$)		4	129
AI	$\log_{10}$ (age index) of trees in a stand (see Table 2)		0.48	2
Lichen community predictors		Functional Group	Min.	Max.
L	sum of abundance classes for *Lobaria oregana* and *L. pulmonaria* by stand	Cyano	0	8
AL	abundance class for *Alectoria sarmentosa* in each stand	Forage	0	5
S	NMS ordination scores for stands in lichen species space from the axis most strongly correlated with biomass of the lichen functional group	Cyano	–1.29	0.78
		Forage	–0.87	0.54
		Matrix	–1.27	0.61
R	species richness of lichens in each functional group by stand	Cyano	0	12
		Forage	2	10
		Matrix	10	26
A	sum of abundance classes for all lichens in each functional group by stand	Cyano	0	34
		Forage	4	32
		Matrix	20	78

Table 2. Definition of the age index, where the median age of a stand is calculated as a percentage of the median age of old growth (300 a assumed for all old growth, see Text). Raw age index = ((median age/median age of old growth)*100) + % remnants. AI represents $\log_{10}$(raw age index).

Stand type	Median age	Raw age index	AI
Young, < 20 a, no remnants	10	3	0.48
Young, < 20 a, 15% remnants	10	18	1.26
Young, < 20 a, 30% remnants	10	33	1.52
Young, < 20 a, 50% remnants	10	53	1.72
Pole, 21-80 a, no remnants	50	17	1.23
Pole, 21-80 a, 15% remnants	50	32	1.51
Pole, 21-80 a, 30% remnants	50	47	1.67
Pole, 21-80 a, 50% remnants	50	67	1.83
Mature, 81-200 a, no remnants	140	47	1.67
Mature, 81-200 a, 15% remnants	140	62	1.79
Mature, 81-200 a, 30% remnants	140	77	1.89
Mature, 81-200 a, 50% remnants	140	97	1.99
Old growth, > 200 a	300	100	2.00

Models based on lichen community data included abundance codes for the lichen species that dominated a given functional group. For example, in PNW forests where cyanolichens are present, the majority of cyanolichen biomass consists of *Lobaria oregana* and *L. pulmonaria*. Therefore, abundances of *L. oregana* and *L. pulmonaria* were predictors that were considered when building the regression models for estimating cyanolichen biomass. Similarly, *Alectoria sarmentosa* is the predominant forage lichen in the Blue River watershed. Therefore, abundance of *A. sarmentosa* was considered as a predictor when making models for forage lichen biomass.

Because patterns in lichen biomass differed among functional groups, predictive models for estimating lichen biomass were determined separately for each group using each of the three classes of predictors described in the steps above. We calculated the standard deviation of the unstandardized residuals for each non-linear and linear regression model (not calculated for the non-parametric multiplicative regression models). The standard deviation of the biomass estimate was reported for each model using a 95% confidence interval.

Scatterplots of cyanolichen biomass and the predictors revealed that both non-linear (three-parameter sigmoid) and linear terms were needed in the models. We combined these by first using non-linear regressions, obtaining the residuals from those regressions, and then using stepwise-linear regression of the residuals against the remaining predictors. The total coefficient of determination was combined for both models:

$$\text{Overall } R^2 = R_Y^2 + (1 - R_Y^2) * R_Z^2 \quad (1)$$

where R_Y^2 is the coefficient of determination from the non-linear model based on topography and forest structure, and R_Z^2 is the coefficient of determination from the stepwise-linear model used to predict the residuals from the non-linear regression. The form of the non-linear equation was:

$$B = \frac{a x_1}{1 + \left(\frac{x_2}{b} \right)^c} \quad (2)$$

where B is biomass, x_1 is age index, x_2 is elevation, b is a fitted parameter controlling the steepness of the elevation response, and c is a fitted parameter controlling the elevation of the inflexion point of the biomass response. The lower asymptote is fixed at zero biomass. The upper asymptote (maximum biomass at a given elevation) is controlled by the parameter a.

Stepwise-linear regression was used to develop predictive models for forage lichen biomass. Initial models from these regressions had many statistically significant parameters ($p \geq 0.05$), but their inclusion in the models explained very little additional variation. Consequently, for the sake of parsimony, we included a term in a model if it resulted in a minimum increase of the coefficient of determination (adjusted R^2) by 0.05.

Scatterplots demonstrated a need for a more complex non-linear model for matrix lichens, so we used non-parametric multiplicative regression (NPMR implemented in HyperNiche version 1.0; McCune & Mefford 2004). NPMR uses a local multiplicative smoothing function with leave-one-out cross-validation to estimate the response variable. We used a Gaussian weighting function with a local mean estimator in a forward stepwise regression of biomass against the predictors, then expressed fit as a cross-validated R^2 (or xR^2).

The xR^2 differs from the traditional R^2 because each data point is excluded from the basis for the estimate of the response at that point. Consequently, with a weak model, the residual sum of squares can exceed the total sum of squares and thus xR^2 becomes negative. Rather than fitting coefficients in a fixed equation, NPMR fits 'tolerances', the standard deviations used in the Gaussian smoothers.

Results

Patterns of lichen biomass in the landscape

Elevation gradient

Elevation was the strongest environmental gradient describing patterns in lichen communities and biomass in the Blue River watershed (Fig. 1; see Berryman 2002 for community results). Overall, lichen biomass was related to patterns in lichen communities (correlations of lichen biomass with ordination scores from axis one: cyanolichens, $R^2 = 0.65$; forage lichens, $R^2 = 0.33$, matrix lichens, $R^2 = 0.40$). The elevation gradient was related to the vascular plant series, where most stands at higher elevations were in the *Abies* series and low elevation stands were in the *Tsuga* series. Epiphytic cyanolichens were nearly absent from high elevation *Abies* stands, dropping off at approximately 900-1000 m (Fig. 1). Biomass of forage lichens increased slightly with elevation (Fig. 1), reaching the highest biomass in high elevation old-growth stands (median biomass in *Abies* OG, 1443 kg.ha^{-1}). Forage lichens in higher elevation stands were typically present in large, dense clumps, covering over 50% of the boles and branches in the stand. Matrix lichen biomass did not change with elevation (Fig. 1).

Stand types

Total epiphytic macrolichen biomass across all functional groups differed among stand types in both the *Tsuga* (from a one-way ANOVA; $F = 10.47, p < 0.001$) and *Abies* series ($F = 7.17, p = 0.001$; Table 3). Cyanolichen biomass differed among stand types in the *Tsuga* series ($F = 6.03, p < 0.001$; Fig. 2). In contrast, there was very little cyanolichen biomass in the *Abies* forests and when present; it did not seem related to stand types. Forage lichen biomass differed among stand types in both the *Tsuga* ($F = 7.88, p < 0.01$) and *Abies* series ($F = 5.21, p = 0.01$), as did matrix lichen biomass (*Tsuga*, $F = 5.55, p < 0.001$; and *Abies*, $F = 10.88, p = < 0.001$; Fig. 2).

Stand age

Differences in total epiphytic macrolichen biomass were related to stand age in both plant series (Table 3). Total lichen biomass differed across all even-aged stands and old growth in the *Abies* series. However, in the *Tsuga* series, total lichen biomass did not differ between even-aged young and pole stands, but biomass was greatest in even-aged mature stands and in old growth. In both plant series, lichen biomass was lowest in even-aged young stands (Table 3). Total lichen biomass was similar in even-aged mature and old-growth stands in both plant series (Table 3). Total macrolichen biomass in even-aged mature stands of the *Abies* series was

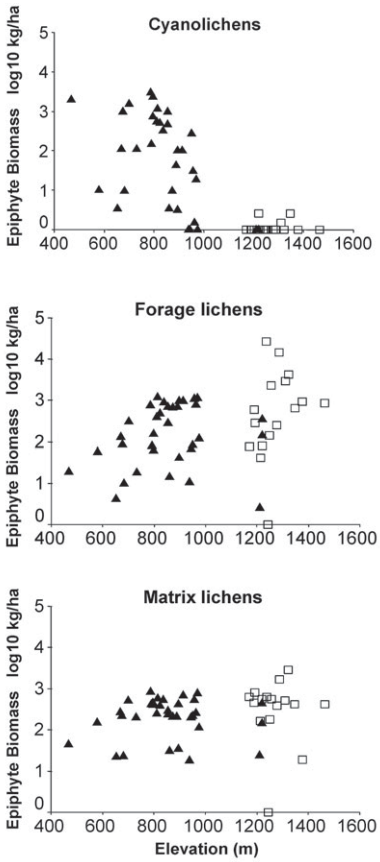

Fig. 1. Estimated biomass (oven-dried; $\log_{10}$ kg.ha^{-1}) of epiphytic macrolichens by functional group in stands versus elevation (m). Symbols code plant series: solid triangles = *Tsuga* series; open squares = *Abies* series. Biomass values are shown for all stands with the exception of even-aged young stands (< 20 a); in general these stands have very little or zero lichen biomass.

Table 3. Total epiphytic lichen biomass estimates (oven-dried, $\log_{10}$ kg.ha^{-1}) of each functional group by stand type and plant series. Stand types are: Y0 = even-aged young (< 20 a); Y15 = young with 15% remnants; Y50 = young with 50% remnants; P0 = even-aged pole (21-80 a); P15 = pole with 15% remnants; P30 = pole with 30% remnants;, M0 = even-aged mature (81-200 a); M15 = mature with 15% remnants; M30 = mature with 30% remnants; OG = old growth (> 200 a).

Stand type		*N*	Median	Min.	Max.
Tsuga	Y0	3	0.82	0.41	2.08
	Y15	6	2.70	2.37	3.05
	Y50	2	2.68	2.34	3.02
	P0	8	1.64	1.41	3.13
	P30	3	2.99	2.90	3.15
	M0	9	3.22	2.71	3.44
	M30	2	3.38	3.30	3.47
	OG	4	3.28	3.10	3.67
Abies	Y0	7	0.70	0	2.25
	Y15	3	3.05	2.85	3.54
	P0	3	2.98	0	3.11
	M0	5	2.81	2.50	3.85
	OG	5	3.03	2.31	4.44

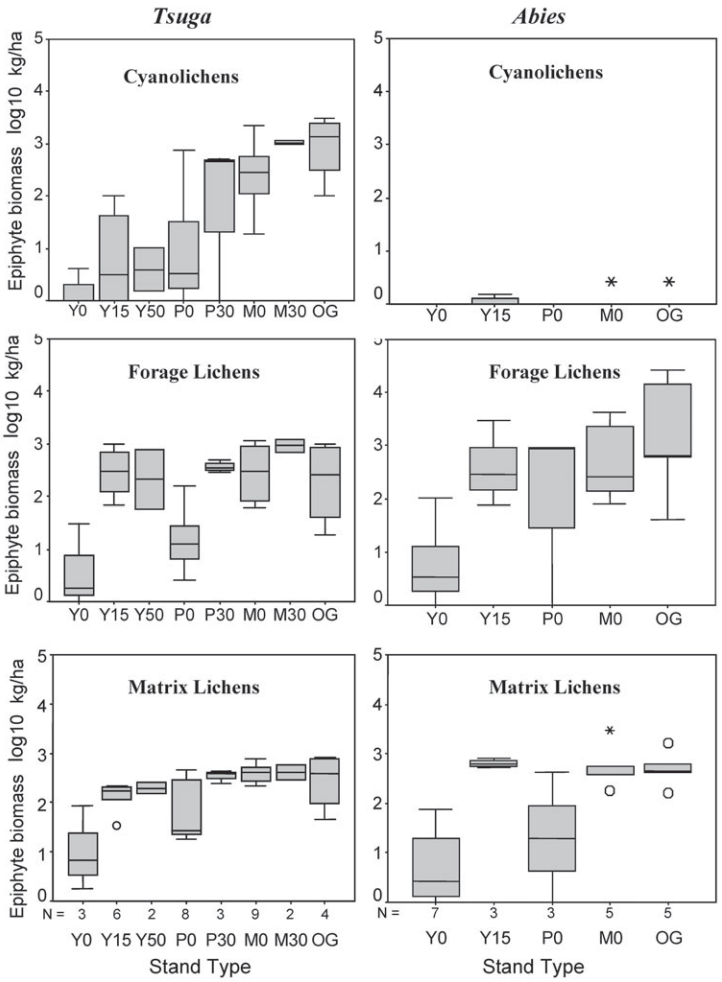

Fig. 2. Distribution of estimated epiphytic macrolichen biomass (oven-dried; $\log_{10}$ kg.ha^{-1}) by functional groups in even-aged stands and stands with remnants in both the *Tsuga* and *Abies* series. Stand type abbreviations are described in Table 3. 50% of the data falls within the interquartile range of the box, with the top of the box representing the 75th percentile and the bottom the 25th percentile. The horizontal line in the box represents the sample median. The whiskers on either end of the box represent the range of values that fell within 1.5 box lengths; these are extreme values that were not considered outliers. Circles indicate moderate outliers (1.5 to 3 box lengths from either end of the box) and asterisks indicate extreme outliers (> 3 box lengths from either end). Stand types with $N < 2$ are not shown.

lower than in even-aged pole stands (median biomass 630 kg.ha^{-1}). Biomass was very high in some even-aged mature stands and old-growth stands in the *Abies* series, most of this being forage lichens (primarily *Alectoria sarmentosa*). However, the median total biomass for old growth was slightly higher in the *Tsuga* series (1905 kg.ha^{-1}) than in the *Abies* series (1070 kg.ha^{-1}; Table 3).

In the *Tsuga* series, cyanolichen biomass was highest in older stands (Fig. 2). Cyanolichens were absent from most young stands (< 20 a; median biomass 0 kg.ha^{-1}), while the highest levels of cyanolichen biomass were in old-growth stands (ranging from 99 to 3089 kg.ha^{-1}; median 1377 kg.ha^{-1}). Four old-growth stands were sampled for lichen biomass in the *Tsuga* series, three of which were sampled between 450 and 800 m elevation, these stands had cyanolichen biomass ≥ 1000 kg.ha^{-1}. The fourth old-growth stand was sampled at 916 m and had much lower cyanolichen biomass (99 kg.ha^{-1}) than the other stands at relatively lower elevations. Cyanolichen biomass was positively correlated with cyanolichen species richness ($R^2 = 0.72$) and with richness of all macrolichens ($R^2 = 0.32$) in the *Tsuga* series, suggesting that older stands host both abundant and diverse lichen communities. In contrast, only eight of the 50 stands sampled for lichen communities in the *Abies* series supported cyanolichens and when present, they were always in low abundance.

In even-aged stands of the *Tsuga* series, forage lichen biomass increased with stand age and leveled off in mature and old-growth stands. Similarly, forage lichen biomass in the *Abies* series increased with age, but was greatest in old-growth stands, in some stands reaching very high levels which were mostly likely overestimates (e.g. 26 915 kg.ha^{-1} of forage lichen biomass in one old-growth stand; Fig. 2). Forage lichen biomass was not correlated with forage lichen species richness ($R^2 = 0.01$) or with species richness of all macrolichens ($R^2 = 0.07$). *Alectoria sarmentosa* was the leading contributor to forage biomass in the Blue River watershed, while other forage species such as *Bryoria* and *Usnea* were only minor contributors. Forage lichen biomass in even-aged pole stands was greater in the *Abies* series (median 286 kg.ha^{-1}) than in the *Tsuga* series (median 11.0 kg.ha^{-1}).

The matrix lichen functional group includes many ubiquitous lichen species that are considered early colonizers (e.g. the genera *Hypogymnia* and *Platismatia*). These genera are often abundant across stands of various ages. Matrix lichen biomass in even-aged stands generally increased with stand age, but leveled off in mature and old-growth stands for both plant series (reaching 500-600 kg.ha^{-1}; Fig. 2). Matrix lichen biomass was positively correlated with matrix lichen species richness (R^2 = 0.30) and with species richness of all macrolichens (R^2 = 0.25).

Remnant tree retention

In both plant series, the presence of remnant trees in young and pole stands was related to increased lichen biomass from similar even-aged stands, however, this was not true for mature stands in the *Tsuga* series (Table 3; Fig. 2). Pole and mature stands with remnants were few (N < 2 per stand type) in the *Abies* series and were not included in these analyses.

In the *Tsuga* series, stands with remnants had more cyanolichen biomass than even-aged stands. In young stands (< 20 a) with 15% retention cyanolichen biomass reached 100 kg.ha^{-1}, while cyanolichen biomass only reached 10 kg.ha^{-1} in young stands with 50% retention (Fig. 2). Cyanolichen biomass was greater by two orders of magnitude in pole stands (21-80 a) with remnants as compared to even-aged pole stands in the *Tsuga* series (Fig. 2). In the *Tsuga* series, cyanolichen biomass in mature stands with remnants (median ca. 1000 kg.ha^{-1}) was similar to that of even-aged mature stands and old growth.

In both plant series, stands with remnant retention had greater forage and matrix lichen biomass than in similar even-aged stands (Fig. 2). This pattern was most dramatic in very young stands (< 20 a) with remnants (Fig. 2). In the *Tsuga* series, differences in forage and matrix lichen biomass between even-aged mature stands and mature stands with remnants were less dramatic than for cyanolichens (Fig. 2).

Predictive models for estimating lichen biomass

Estimating cyanolichen biomass

Elevation was the strongest topographic predictor for estimating cyanolichen biomass. We used a non-linear regression model for this relationship because cyanolichen biomass followed a sigmoid pattern with elevation (Table 4). A predictive model for estimating cyanolichen biomass based solely on elevation will overestimate biomass in young forests at low elevations. To account for this, the non-linear model included both elevation and AI (i.e., the logarithm of the age index, Table 2) as predictors (Table 4). The model based on AI and elevation had substantial predictive power for cyanolichen biomass (R^2 = 0.81).

Table 4. Predictive equations from non-linear, stepwise-linear, and non-parametric multiplicative regression for estimating epiphytic macrolichen biomass ('B'; oven-dried, $\log_{10}$ kg.ha^{-1}) of functional groups using topographic, stand structure, and lichen community predictors (see Table 1 for detailed descriptions of predictors). Best models from non-linear and stepwise-linear regression are shown with a 95% confidence interval for the estimates (CI). R^2 is reported for the linear regression models and adjusted R^2 is reported for non-linear regression models, while xR^2 is reported for the non-parametric multiplicative regression models.

Predictors	Equation	CI	
Cyanolichens			
Topography			
E	B = 2.30 / (1 + (E/924.95)$^{23.36}$)	±1.48	R^2 = 0.64
Topography and stand structure			
AI, E	B = (1.50*AI) / (1 + (E/937.75)$^{26.99}$)	±1.07	R^2 = 0.81
Topography, stand structure, and lichen community			
AI, E	B = (1.50*AI) / (1 + (E/937.75)$^{26.99}$)	±1.07	R^2 = 0.81
and			
L, R	Residuals = –0.15 + 0.17 L – 0.10 R	±0.95	R^2 = 0.20 Overall R^2 = 0.85
Forage lichens			
Topography and stand structure			
AI, E	B = –1.38 + 1.55 AI + 0.001 E	±1.53	Adj. R^2 = 0.47
Stand structure and lichen community			
AI, AL	B = –1.26 + 1.26 AI + 0.44 AL	±1.14	Adj. R^2 = 0.55
Matrix lichens			
Topography and stand structure			
AI, BA	Tolerances: AI = 0.23, BA = 18.7		xR^2 = 0.55
Average neighborhood size = 10.8			
Stand structure and lichen community			
HLI, AI, A	Tolerances: HLI = 0.13, AI = 0.23, A = 3.3		xR^2 = 0.73
Average neighborhood size = 3.9			

Epiphytic cyanolichen biomass was related to lichen community composition in the ordination (R^2 = 0.65). However, the ordination scores explained very little beyond that explained by elevation and AI in the predictive models for cyanolichen biomass. Other community variables such as the sum of abundance for *Lobaria oregana* and *L. pulmonaria* and cyanolichen species richness were better predictors for explaining the additional variation in the model. The regression model for predicting cyanolichen biomass from topography, stand structure, and lichen community variables was based on two regression models. The first model was the non-linear regression in which the AI and elevation were the best predictors of cyanolichen biomass (Table 4). The remaining predictors (including all lichen community predictors) were used in a stepwise-linear regression to predict the unexplained residuals from the non-linear model. The residuals from the non-linear model were best predicted by the sum of abundance classes for *Lobaria oregana* and *L. pulmonaria* and by cyanolichen species richness, explaining additional variation in cyanolichen biomass (Table 4). The total variation explained by the combination of these two models was 85% (Table 4).

Estimating forage lichen biomass

We found no strong predictive models for estimating forage biomass based on only topographic variables (maximum adjusted R^2 = 0.19). However, forage lichen biomass can be predicted from AI and elevation (Table 4). The regression model including community predictors was based on AI and the abundance of *Alectoria sarmentosa*. In this model, no topographic variables were significant (at $p \leq 0.05$) predictors. Most forage lichen biomass was composed of *A. sarmentosa,* especially in the higher elevation stands. Unlike cyanolichens, forage lichen biomass was not as highly correlated with lichen community composition (R^2 = 0.33).

Estimating matrix lichen biomass

Topographic variables were poor predictors for matrix lichen biomass and are not reported (xR^2 = 0.03 for three predictors). AI and basal area were the best predictors for matrix biomass when using only topographic and stand structure predictors (Table 4). The model based on all available predictors included the heat load index, AI and the sum of abundance classes for all matrix lichens found in a stand (Table 4). Matrix lichens were present and abundant in most stands in the Blue River watershed. Matrix lichen biomass was correlated with lichen community composition in the ordination (R^2 = 0.40), however the ordination scores explained little variation beyond other variables.

Discussion

Patterns of lichen biomass in the landscape

Epiphytic macrolichen biomass of all functional groups generally increased with stand age and with the presence of remnant trees (particularly in younger stands). Lichen biomass in young even-aged stands was low (< 10 kg.ha^{-1}) in both plant series. Cyanolichen biomass in even-aged young stands was often zero or extremely low (< 10 kg.ha^{-1}) in both plant series. In the *Tsuga* series, highest cyanolichen biomass (median ca. 1000 kg.ha^{-1}) was found in mature stands with remnants and in old growth (OG: ranged from 99 to 3089 kg.ha^{-1}). The presence of remnant trees in stands was related to increased cyanolichen biomass across all age classes. Our lichen biomass estimates are roughly consistent with and greatly supplement the few estimates available from other studies in the PNW forests (Pike et al. 1972, 1977; Rhoades 1981; Neitlich 1993; McCune 1993; McCune et al. 1997a; Pipp et al. 2001).

Forage lichen biomass in the *Tsuga* series was highest in stands with remnants in mature and old-growth stands. In the *Abies* series, forage lichen biomass was highest in young stands with 15% retention of remnants and in old growth. High-elevation *Abies* forests are important habitat for forage lichens, where they are the dominant epiphytes. These forests contain few cyanolichens and bryophytes, and consequently, there may be more available substrate for forage lichens to colonize. *Alectoria sarmentosa* is the major contributor of forage lichen biomass in the Blue River watershed, consistent with previous findings (Neitlich 1993; Peck & McCune 1997) and is considered old-growth-associated in forests of this region (Neitlich & McCune 1997; Peterson & McCune 2001). This lichen may be dispersal-limited, especially in young dense stands in which wind-dispersed fragments may have difficulty reaching and colonizing appropriate substrates (Neitlich 1993; Dettki 1998; Dettki et al. 2000).

Our estimates of forage lichen biomass are much higher than previously documented estimates for forage lichens (Peck & McCune 1997) or for combined green-algal lichens (Rhoades 1995). Caution must be used in applying our high biomass estimates for forage lichens. These values are based on the ratio of 100 : 1 lichen epiphyte biomass to lichen litter biomass, which was developed by McCune (1994) in *Pseudotsuga-Tsuga heterophylla* forests at lower elevations. The ratios may not be appropriate for estimating biomass of epiphytic lichens from litter fall in the higher elevation *Abies* forests. Low and high elevation forests may differ in litter decomposition rates, duration of snow burial, in litter fall rates, and abundance of litter herbivores.

Many matrix lichens are early colonizers, such that

biomass of this group is generally considered to plateau in younger stands, usually around ca. 100 a (Neitlich 1993; McCune 1993). Biomass for this group persisted throughout mature and old-growth stands with and without remnants in the Blue River watershed (*Tsuga* series: 43-841 kg.ha^{-1}; *Abies* series: 161-2883 kg.ha^{-1}). In both plant series, the median matrix lichen biomass was slightly higher in even-aged mature than in old-growth stands (matrix lichen biomass for *Tsuga* series: even-aged mature = median 415 kg.ha^{-1}, OG = median 384 kg.ha^{-1}; matrix lichen biomass for *Abies* series: even-aged mature = 549 kg.ha^{-1}, OG = median 445 kg.ha^{-1}). The presence of remnants in young stands was related to greater levels of matrix lichen biomass. However, remnant presence in mature stands appeared to have little influence on stand biomass of matrix lichens since matrix biomass seems to level out at this point in stand development.

Other studies have shown that lichen biomass increases with stand age, and that in many cases accumulation of epiphytes in a forest is slow (Neitlich 1993; McCune 1993; Esseen et al. 1996; Pipp et al. 2001). The slow accumulation of some species may not be attributable to unsuitable habitat in younger forests, but may depend more on time and dispersal. The dispersal-limitation hypothesis is supported by a recent lichen transplant and sowing study that shows *Lobaria oregana*, considered an old-growth-associate, is capable of growing in very young stands if propagules are introduced (Sillett et al. 2000a, b). However, not all old-growth associated lichens are dispersal-limited; some species appear to require specific microhabitat in old growth (Tibell 1992; Rosso et al. 2000).

Increased forest continuity through maintenance of patches of late-successional habitat throughout the landscape and retention of remnant trees may promote lichen dispersal across a landscape. Lichen biomass increases with the presence of old remnant trees in a stand, however, the contribution of remnant trees to lichen biomass is most pronounced in young stands (< 80 a). Remnant trees apparently serve as refugia for epiphytes during disturbances (e.g., through timber harvests), shed lichen propagules onto younger trees, moderate the microclimate, and create a more complex microhabitat with variable canopy structure, which seems to enhance lichen diversity and biomass (Berryman 2002; Pipp et al. 2001; Sillett & Goslin 1999; Peck & McCune 1997). Not only the number of remnants, but also the quality (i.e., age, size, and wind firmness) of the remnant trees may also be a factor influencing lichen abundance. For example, younger remnant trees likely host lower lichen abundance than older remnants. The quality of remnants left after harvest may be important to long-term lichen abundance, but needs further study.

Predictive models for estimating lichen biomass

Lichen communities are related to lichen biomass in the Blue River watershed. However, lichen community ordination scores were not selected as the best predictors for lichen biomass because they explained less variation than other predictors. Models including lichen community predictors had slightly more predictive power than models that included only topography and stand structure predictors (Fig. 3). Lichen community data are not always available and such data collection requires field personnel who are trained in lichen identification. Predictive models for estimating epiphytic lichen biomass based on topography and stand structure may have a broader application because they eliminate the step of surveying the lichens, requiring less effort to obtain data for the models.

The model for estimating cyanolichen biomass from elevation, age index, cyanolichen species richness, and the abundance codes for *Lobaria oregana* and *L. pulmonaria* had the strongest predictive power overall ($R^2 = 0.85$). However, the model based on elevation and age index may be more effective for estimating cyanolichen biomass since lichen community data are not required and the predictive power is still strong ($R^2 = 0.81$). Models estimating forage and matrix lichen biomass had less predictive power than models for cyanolichens (Fig. 3). However, the most effective and parsimonious models for estimating forage and matrix lichens were those including topography and stand structure variables.

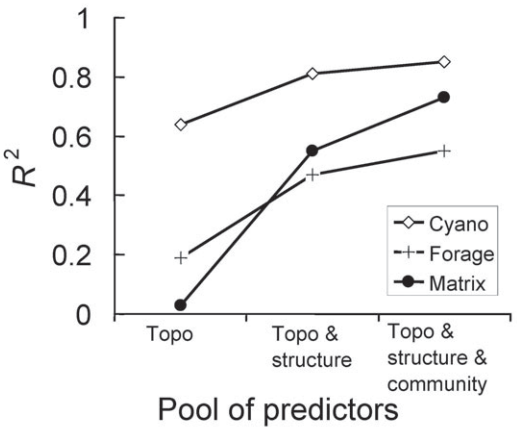

Fig. 3. Predictive power (R^2) of the regression models based on three pools of variables for estimating biomass of lichen functional groups.

Management implications

Biomass models provide a useful tool for describing and understanding the distribution of epiphytic macrolichen abundance at landscape scales. Biomass estimates are important for understanding lichen function at a landscape level. Furthermore, models for estimating lichen biomass can be used to assess probable consequences of alternative management strategies (Cissel et al. 1999) by forecasting future biomass distribution in the landscape based on changes in forest structure (Dettki & Esseen 2003; Berryman 2002). Considering impacts of forest management on lichen biomass allows managers to assess possible impacts that management strategies may have on future lichen communities (Dettki & Esseen 2003) and their contributions to ecosystem functions and properties.

Currently, the Northwest Forest Plan (NWFP) calls for stands in the upland matrix designation of PNW federal forests to be harvested on 80-year rotations leaving 15% green tree retention (USDA & USDI 1994). In the Blue River watershed, young stands with 15% remnants had fairly high levels of lichen biomass (*Tsuga* series, median 500 $kg.ha^{-1}$; *Abies* series, median 962 $kg.ha^{-1}$), due to abundant matrix and forage lichens. However, cyanolichen biomass was consistently low in young stands with 15% remnants (median 3 $kg.ha^{-1}$ in the *Tsuga* series and was nearly absent in the *Abies* series). Leaving remnants during timber harvest may enhance lichen biomass in young regenerating stands. Our study supports the importance of maintaining structural features like old remnant trees and mature and old-growth stands to maintain abundant lichens and encourage lichen dispersal in a fragmented landscape.

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