## ---------- NOTICE ----------

The chapters contained herein will be published as separate papers in peer-reviewed journals. However, they will be revised based upon comments from my thesis committee and other reviewers. While the overall conclusions will remain the same, certain specifics may differ between the thesis and the published papers. Information contained within the published papers will supersede information contained within the thesis. If results presented in the published papers differ from those in the thesis, those from the papers should be used, as they have been subjected to additional peer review.

I expect the papers to be published according to the following schedule:

| | **Status** | **Journal** | **Anticipated publication date** |
|---|---|---|---|
| Chapter 2 | in prep. | *Conservation Biology* | late 2002/early 2003 |
| Chapter 3 | in press | *The Bryologist* | early 2002 |
| Chapter 4 | in press | *The Lichenologist* | early 2002 |

Sincerely,

Dylan Keon

18 October 2001
E-mail: keon@nacse.org

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**AN ABSTRACT OF THE THESIS OF**

Dylan B. Keon for the degree of Master of Science in Botany and Plant Pathology presented on May 1, 2001. Title: Factors Limiting the Distribution of the Sensitive Lichen *Usnea longissima* in the Oregon Coast Range: Habitat or Dispersal?

Abstract approved: _____

Patricia S. Muir

The sensitive lichen *Usnea longissima* Ach., formerly a fairly common circumboreal species, has been extirpated from much of its range (e.g., Eastern Europe). Although the U.S. Pacific Northwest (PNW) remains a relative stronghold for the species, *U. longissima* faces increasing pressure in the region from habitat loss, air pollution, and commercial harvesting. *Usnea longissima* has a patchy distribution at both stand and landscape levels in the PNW, which may result from a lack of suitable habitat, dispersal limitations, or both. Although the species has been researched extensively in Scandinavia, no studies have examined its habitat associations or dispersal dynamics in the PNW. I used two approaches to assess the relative importance of habitat versus dispersal limitations as influences on the current distribution of *U. longissima* in the Oregon Coast Range. First, I collected environmental data from sites where *U. longissima* was present (n=75) and absent (n=75) to determine habitat associations for the species. In addition to identifying the variables that best predict habitat occupied by *U. longissima*, analysis of the data also yielded a statistical model that I combined with raster-based GIS modeling to assess the availability of apparently suitable habitat for the species across the study area. Second,

I placed 360 transplants among 12 sites in 4 habitats within the study area, and measured their growth (change in biomass) after one year. Habitats were determined from analysis of the environmental data described above, and represented a range of apparent suitability for the species, from sites of unlikely suitability where it did not occur (i.e., clear cuts on south-facing slopes), through highly suitable sites where the species was abundant (i.e., old stands on north-facing slopes). Statistical analysis of the environmental data from sites of presence and absence produced a model incorporating four of the environmental variables, in which the most significant variable (stand age) was positively associated with *U. longissima* presence. The spatial analysis results suggest that apparently suitable habitat is not limiting at the landscape level. Additionally, the transplants grew well across all habitats, and gained the most weight in sites predicted to be the least suitable habitat. Overall, the results suggest that dispersal may play a more important role than habitat in limiting the distribution of *U. longissima* within the study area, although the potential influence of habitat on establishment of the species should be assessed to lend certainty to this suggestion. Retention of remnant trees containing *U. longissima* will enhance its dispersal within regenerating stands, and preservation of intact stands harboring the species will increase its chances of spreading to uncolonized stands and persisting across the landscape.

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# Factors Limiting the Distribution of the Sensitive Lichen *Usnea longissima* in the Oregon Coast Range: Habitat or Dispersal?

by

Dylan B. Keon

A THESIS

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APPROVED:

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Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Dylan B. Keon, Author

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Factors Limiting the Distribution of the Sensitive Lichen *Usnea longissima* in the Oregon Coast Range: Habitat or Dispersal?

# Chapter 1

# Introduction

This research investigated factors that affect the current distribution of *Usnea longissima* Ach. (Fig. 1.1) across a section of the Oregon Coast Range. Specifically, I examined whether dispersal limitations or a lack of suitable habitat appear to play a greater role in limiting the distribution of *U. longissima* within the study area.

The epiphytic lichen *Usnea longissima* was once a fairly common, nearly circumboreal species (Ahlner 1948, Ahti 1977); however, its abundance has declined significantly throughout its global range, particularly in Scandinavia and Eastern Europe (Esseen et al. 1981, Pišút 1993, Tønsberg et al. 1996, Thor 1999). Habitat loss due to timber harvesting is the most significant factor that has contributed to the demise of the species in these countries, although air pollution is also an important factor (Esseen et al. 1981, Trass and Randlane 1987, Kuusinen et al. 1990, Olsen and Gauslaa 1991). Although the species faces similar threats in North America, due to certain forestry practices, air pollution, and commercial harvesting, the northern Pacific coast of North America remains a relative stronghold for *U. longissima*, where its range extends from Northern California to Alaska (Noble 1982). In Oregon, *U. longissima* occurs throughout the Coast and western Cascade mountain ranges (McCune and Geiser 1997). In most of the U.S. Pacific Northwest (PNW), including our study area, *U. longissima* is currently listed as a Survey and Manage, Category F species under the

**Figure 1.1** *Usnea longissima* hanging from *Alnus rubra* Bong. (red alder) branches above a creek in the Oregon Coast Range.

Northwest Forest Plan (USDA and USDI 2000, 2001). This classification requires that land managers conduct strategic surveys to determine whether *U. longissima* meets basic Survey and Manage criteria. Known *U. longissima* populations receive no protection under this classification.

Some epiphytic macrolichens are thought to have limited dispersal abilities, which result in their dependence upon old-growth forests (e.g., Dettki et al. 2000, Sillett et al. 2000). While *Usnea longissima* is thought to be dispersal-limited (e.g., Esseen 1985, McCune and Geiser 1997), relatively little is known about its habitat associations and dispersal limitations in the PNW, making it difficult to formulate specific recommendations regarding its management. I used two approaches to explore the probable roles of habitat availability versus dispersal limitations in influencing the distribution of *U. longissima* within the study area.

The second chapter presents results from a study of *Usnea longissima* habitat conditions at sites where the species occurs, and availability of apparently suitable habitat across the landscape. I collected environmental data from sites of *U. longissima* presence (n=75) and absence (n=75), and used discriminant analysis to compare habitat conditions in the two types of sites and indicate which environmental variables were most important in distinguishing between them. I obtained digital grids covering the study area, from which I derived grids representing the significant environmental variables, and used raster-based GIS analysis to model the availability of habitat across the study area.

The third chapter describes results from a transplant experiment. I placed 360 *Usnea longissima* transplants among 12 sites in 4 habitats of varying predicted

suitability within the study area, and measured their growth (change in biomass) after one year. Habitat suitability was determined from analysis of an initial set of the environmental data collected from sites of *U. longissima* presence and absence. Comparison of *U. longissima* growth rates among the varying habitats allowed inference as to whether the distribution of the species appears to be constrained by a lack of suitable habitat; if all transplants grew well in all habitats, I could infer that the species is probably more limited by dispersal than by lack of suitable habitat.

In chapter 4, I describe a fertile population of *Usnea longissima* that I discovered in the study area, and discuss how the species' reproductive methods affect its dispersal. This is the first published account of fertile *U. longissima* specimens in North America, although apotheciate specimens have been described in other continents (Krempelhuber 1853, Harmand 1905).

While the results of this project cannot be extrapolated beyond the Oregon Coast Range study area, they do provide useful information about the factors that appear to influence the distribution of *Usnea longissima* within the study area. These results may be useful as a starting point for further investigation of the species in other areas of the PNW, and should provide land managers with information they can use when planning strategic surveys for this species, and when determining the appropriate status for the species under the Northwest Forest Plan.

Chapter 2

# Modeling Habitat for the Sensitive Lichen *Usnea longissima*: a Multivariate GIS-based Approach

Dylan B. Keon and Patricia S. Muir

For submission to *Conservation Biology*,
Society for Conservation Biology

## ABSTRACT

It is challenging to predict the occurrence of uncommon species in fragmented, highly managed landscapes, particularly when it is unclear whether a species' distribution is limited by dispersal, lack of suitable habitat, or both. The sensitive lichen *Usnea longissima* Ach. has a patchy distribution across the highly managed Oregon Coast Range, and reasons for its current distribution are unclear. To assess the relative importance of habitat and dispersal limitations in influencing the current distribution of *U. longissima*, we used discriminant analysis to identify the environmental variables most important in predicting habitat occupied by the species, based on its present distribution. An independent data set from the same study area was used to cross-validate the model, which had modest predictive power. We combined the resulting discriminant function with grids representing each variable in a GIS to model the availability of apparently suitable habitat across the study area. The resulting spatially explicit model suggests that apparently suitable habitat covers 11.5% (79,275 ha) of the study area. These results, combined with results from an accompanying transplant study, which examined growth rates of the species in a variety of habitats, lead us to conclude that the distribution of *U. longissima* in the study area is more strongly limited by dispersal than by lack of habitat. This study informs land managers in the Pacific Northwest about factors influencing the distribution of *U. longissima* in the Oregon Coast Range. It also provides a general modeling approach that can improve efficiency of landscape-level surveys for sensitive species by identifying areas of probable occurrence, and may help land managers refine survey and management requirements

for other species listed under the Northwest Forest Plan, for which causes of old-growth association are unknown.

## INTRODUCTION

Predicting habitat for a species at the landscape scale can significantly aid land managers and researchers; reliable predictive models can make field surveys more efficient by indicating suitable habitat and helping to find previously unknown occurrences of a species. However, managed, heterogeneous landscapes present complex challenges to the development of predictive models of species occurrence. Forest structure and composition often vary greatly at all scales across managed landscapes (Harris 1984). For example, forests in the U.S. Pacific Northwest (PNW) have become highly fragmented by intensive timber harvesting on both private and public land (Harris 1984, Ripple 1994, Spies et al. 1994). Species dependent upon older forests in the PNW may be increasingly threatened as available habitat shrinks and local populations become isolated (Harris 1984, USDA and USDI 2000).

Modeling habitat at the landscape scale requires an understanding of the environmental factors that contribute to a species' pattern of distribution. Factors contributing to these patterns can be examined through traditional, ground-based field studies, as well as through analysis of remotely sensed and GIS-based data. Researchers have used numerous multivariate, spatially explicit approaches to model habitat across broad scales. For instance, Pereira and Itami (1991) combined results from logistic multiple regression with GIS-based data to model habitat for the Mt. Graham red squirrel; Clark et al. (1993) modeled female black bear habitat in a GIS

based upon results from discriminant analysis and calculation of Mahalanobis distances; Knick and Dyer (1997) calculated Mahalanobis distances in a GIS to predict habitat for black-tailed jackrabbits; and others have used similar methods (e.g., Mlandenoff et al. 1995, Rushton et al. 1997, Dettmers and Bart 1999). These methods have been used most frequently to predict habitat for wildlife species, although similar methods have been used to predict habitat for sensitive plant species (Sperduto and Congalton 1996) and exotic plant species (Buchan and Padilla 2000). Few studies have modeled occurrence or habitat for lichens. Peterson et al. (2000) described a non-parametric method for modeling occurrence of poorly understood species at the landscape scale, using calicioids (pin lichens) as an example. Dettki and Rännar (2000) described a spatially explicit raster-based model designed to predict lichen biomass at the landscape scale, using *Bryoria* spp. as an example.

*Usnea longissima* Ach. is a pendant, epiphytic lichen that was once a fairly common, nearly circumboreal species (Ahlner 1948, Ahti 1977). During the last century, its abundance has declined significantly throughout its range, particularly in Scandinavian and Eastern European forests (Esseen et al. 1981, Pišút 1993, Tønsberg et al. 1996, Thor 1999). The northern Pacific coast of North America remains a relative stronghold for the species, where its range extends from Northern California to Alaska (Noble 1982). In Oregon, *U. longissima* occurs throughout the Coast and western Cascade mountain ranges (McCune and Geiser 1997). In most PNW forests west of the Cascades crest, including our study area, it is currently listed as a Survey and Manage, Category F species under the Northwest Forest Plan (USDA and USDI 2000, 2001). This plan was developed to balance, within the range of the Northern Spotted Owl:

1) management of habitat for late-successional and old-growth forest-related species, in a manner that provides for the species' long-term health, with 2) a sustainable level of timber harvest. The Survey and Manage, Category F classification requires that land managers conduct strategic surveys to determine whether *U. longissima* meets basic Survey and Manage criteria under the Northwest Forest Plan. Known *U. longissima* populations receive no protection under this classification. Relatively little is known about the habitat associations and dispersal limitations of *U. longissima* in the PNW, making it difficult to conduct efficient surveys or formulate specific recommendations regarding its management.

*Usnea longissima* has a limited, patchy distribution at both stand and landscape levels within the Oregon Coast Range. It is not clear whether this distribution has resulted from inherent dispersal limitations, lack of suitable habitat, or both. Dispersal limitations are most likely important, since the species reproduces primarily through fragmentation of relatively large pieces of thalli, which generally do not travel > 5 m from their source (Esseen et al. 1981, Esseen 1985). In the PNW, sexual reproduction is extremely rare, and small asexual propagules (soredia) are rare (Noble 1982, McCune and Geiser 1997, Keon *in review*). Although *U. longissima* dispersal has been examined in Scandinavia (Esseen 1985, Gauslaa 1997), we know little about its dispersal dynamics in the PNW, and dispersal of lichens is poorly understood, in general. However, recent studies have revealed that dispersal limitations may be important for some epiphytic lichens. Several studies found that dispersal limitations contribute to the slow accumulation of epiphytic lichens in young forests (e.g., Peck and McCune 1997, Sillett and McCune 1998, Dettki et al. 2000). Sillett et al. (2000)

concluded that the dispersal-limited epiphytic lichen *Lobaria oregana* (Tuck.) Müll. Arg. is dependent upon old-growth forests in the Oregon Cascades as sources of inoculum, and suggested that *U. longissima* has a similar dependency. Esseen (1985) indicated that *U. longissima* disperses primarily by relatively large thallus fragments and, consequently, is most often dispersed within the source tree.

Although forest management practices in the PNW have changed significantly in the past decade (Swanson and Franklin 1991, Franklin et al. 1997, USDA and USDI 2000), the Oregon Coast Range landscape retains the legacy of past management practices and is dominated by relatively young, managed forests. Young stands often have different species composition and lower abundance of epiphytic lichens than old-growth stands (e.g., McCune 1993, Esseen et al. 1996, Dettki and Esseen 1998, Peterson 2000, Rosso 2000). Habitat loss due to timber harvesting is the main reason for the severe decline of *Usnea longissima* in Scandinavia over the past several decades (Esseen et al. 1981, Tønsberg et al. 1996), and the same pattern of decline may be repeating in the PNW, also due to habitat loss (Harris 1984, Bennett 1995, Rosentreter 1995). Clearing forests may have destroyed much of the suitable habitat for *U. longissima* in the PNW; however, its habitat associations are not well known and, thus, the availability of suitable habitat in the region is uncertain (Keon 2001, Keon and Muir *in review*). While no studies have explicitly quantified suitable habitat for *U. longissima*, older stands and cooler/wetter sites (i.e., north-facing aspects, high relative humidity, etc.) appear to be associated with *U. longissima* occurrence in Sweden (Esseen et al. 1981) and Norway (Tønsberg et al. 1996).

Air pollution has contributed to the demise of *Usnea longissima* in Eastern Europe and Scandinavia (Esseen et al. 1981, Trass and Randlane 1987, Kuusinen et al. 1990, Olsen and Gauslaa 1991), and may have influenced its distribution in the PNW, where the species is considered to be sensitive to air pollution (McCune and Geiser 1997). However, air quality in the Oregon Coast Range and much of the west Cascade mountain range is probably not poor enough to harm *U. longissima*; its distribution in western Oregon is more likely influenced by habitat or dispersal limitations.

The primary goals of this study were to determine, for forests within the Oregon Coast Range study area: (1) whether habitat at sites where *Usnea longissima* occurs significantly differs from habitat at sites lacking it, (2) which variables appear to be most influential in predicting habitat occupied by the species, based on its present distribution, and (3) the distribution and quantity of apparently suitable habitat across the study area. Additionally, our goal was to provide useful information to land managers who must make decisions regarding the status of *U. longissima* in PNW forests. The results from this study, combined with results from an accompanying study that examined growth of *U. longissima* transplants in four habitats within the Oregon Coast Range (Keon and Muir *in review*), allowed us to assess the relative influences of dispersal and habitat on the distribution of *U. longissima* within the study area.

## METHODS

### Experimental design and sampling

We collected environmental data from 75 sites where *Usnea longissima* was present and 75 sites where it was absent (Table 2.1, Fig. 2.1). Study sites were located

**Table 2.1** Environmental data collected from *Usnea longissima* and CVS sites of presence and absence (4 outliers removed; see *Statistical analyses and model construction—Data Adjustment* and *Discussion*).

| | *U. longissima* sites of presence (n=72) | | | *U. longissima* sites of absence (n=74) | | | CVS sites of presence (n=6) | | | CVS sites of absence (n=44) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site characteristic | Mean | Range | SE | Mean | Range | SE | Mean | Range | SE | Mean | Range | SE |
| Elevation (m) | 255.3 | 30-685 | 18.9 | 255.1 | 25-685 | 17.9 | 233.7 | 152-427 | 52.6 | 252.9 | 30-488 | 17.0 |
| Radiation[1] | 168.6 | 81-234 | 3.9 | 182.1 | 110-229 | 3.0 | 171.7 | 141-192 | 8.4 | 169.1 | 103-232 | 5.1 |
| Topographic position[2] | 2.8 | 1-5 | 0.18 | 3.0 | 1-5 | 0.15 | 2.7 | 1-2,4 | 0.61 | 2.9 | 1-5 | 0.16 |
| Horiz. dist to water (m) | 136.0 | 1-450 | 15.2 | 166.6 | 5-480 | 15.3 | 114.7 | 8-220 | 35.7 | 129.9 | 5-270 | 11.6 |
| Vert. dist to water (m) | 45.7 | 1-180 | 5.7 | 52.0 | 1-250 | 5.9 | 46.0 | 1-100 | 17.3 | 49.6 | 2-120 | 5.3 |
| Precipitation (cm/yr) | 200.4 | 123-366 | 5.0 | 200.7 | 123-349 | 4.8 | 188.8 | 160-203 | 6.8 | 238.6 | 183-305 | 5.4 |
| Stand age[3] | 2.9 | 1-4 | 0.09 | 2.1 | 1-4 | 0.08 | 3.0 | 1-4 | 0.52 | 2.4 | 1-4 | 0.16 |
| Conifer BA ($m^2$/ha) | 16.7 | 0-73 | 2.0 | 22.3 | 0-55 | 1.9 | 36.8 | 0-82 | 12.4 | 38.3 | 0-107 | 3.6 |
| Hardwood BA ($m^2$/ha) | 13.5 | 0-59 | 1.7 | 9.7 | 0-59 | 1.4 | 5.7 | 0-18 | 2.7 | 7.7 | 0-29 | 1.1 |

[1]Potential annual solar radiation ($kcal \cdot cm^{-2} \cdot yr^{-1}$). Incorporates slope, aspect, and latitude (see *Experimental design and sampling*).
[2]Topographic position: 1 = bottomland, 2 = lower slope, 3 = mid-slope, 4 = upper slope, 5 = ridge.
[3]Stand age: 1 = 0-30 yr, 2 = 31-70 yr, 3 = 71-120 yr, 4 = 121+ yr.

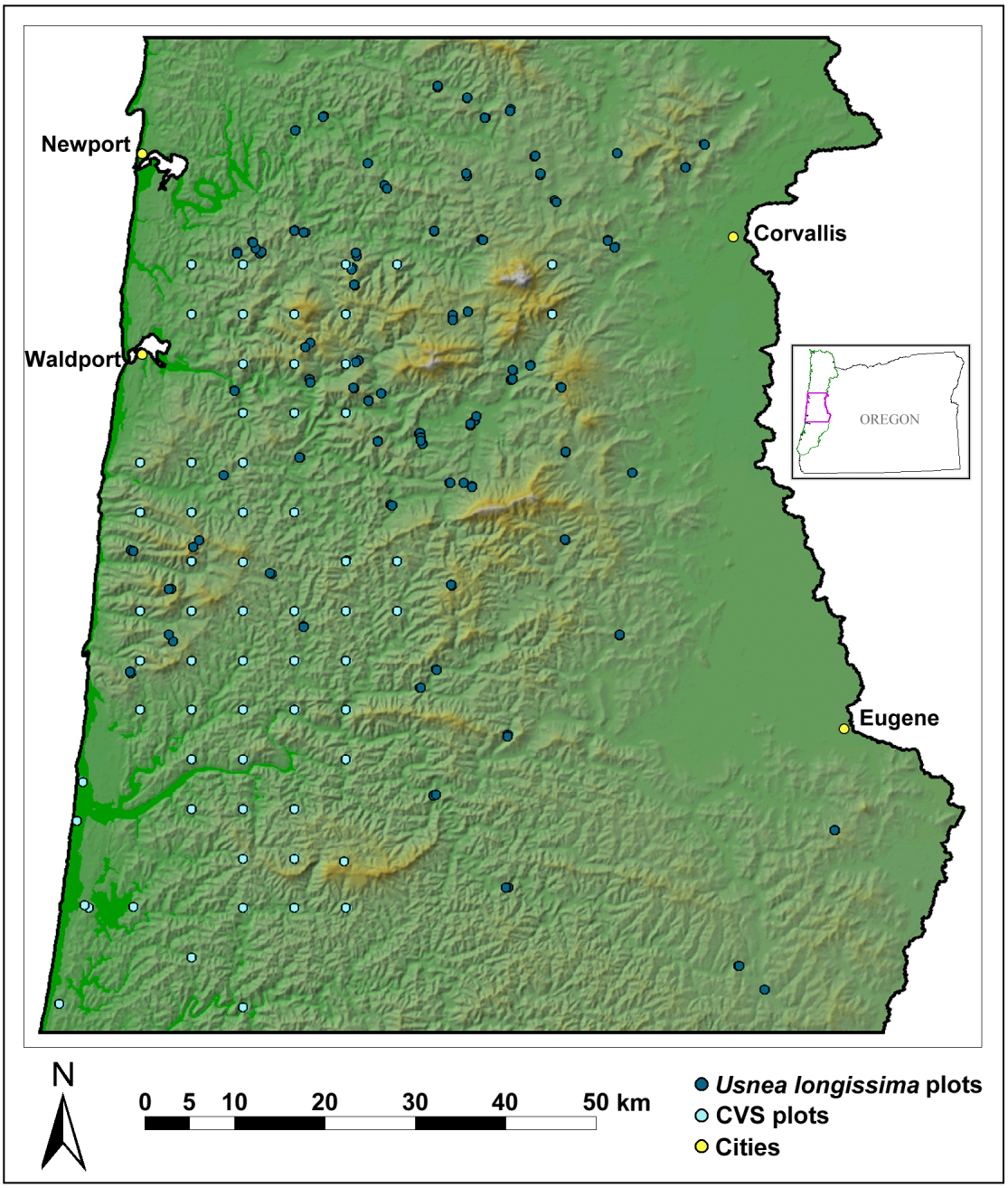


**Figure 2.1** Location of *Usnea longissima* and CVS plots across the study area.

in an 8500 $km^2$ Oregon Coast Range study area (Fig 2.2; 43°45'N to 44°45'N, 122°58'W to the Pacific coast [westernmost land point 124°12'W]). Within the study area, summers are warm and dry with very little precipitation. Winters are cool and wet with frequent fog sweeping across the landscape. Average annual rainfall in the study area ranges from approximately 100 cm to over 400 cm (Daly et al. 1994). Elevations within the study area range from 0 m to 1215 m. Most study sites were established within the *Tsuga heterophylla* (Raf.) Sarg. (Western hemlock) Zone of the Coast Range, although a small subset fell within the *Picea sitchensis* (Bong.) Carr. (Sitka spruce) Zone (Franklin and Dyrness 1973). Many sites were dominated by *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir), although late-successional forests occasionally had co-dominant *P. menziesii* and *T. heterophylla*.

We selected sites of presence with no preconceived bias, primarily based upon U.S. Forest Service (USFS) and Bureau of Land Management (BLM) databases, the collection data of other researchers, and herbarium records. Additional sites of presence were selected at random while traveling arbitrarily selected roads and trails within the study area. Sites of absence were selected by traveling along a random bearing after collecting data from each site of presence. Each site of absence was ≥ 50 m from any population of *Usnea longissima*. This sampling strategy allowed for detection of small-scale differences in habitat characteristics between sites of presence and absence, while controlling for large-scale variation. Although most sites of absence were within 100 m of sites of presence, 9% of sites of absence were located > 500 m from sites of presence in order to avoid nearby *U. longissima* populations. Each site of presence was centered on a randomly selected tree that contained *U. longissima* in its crown (hereafter, the

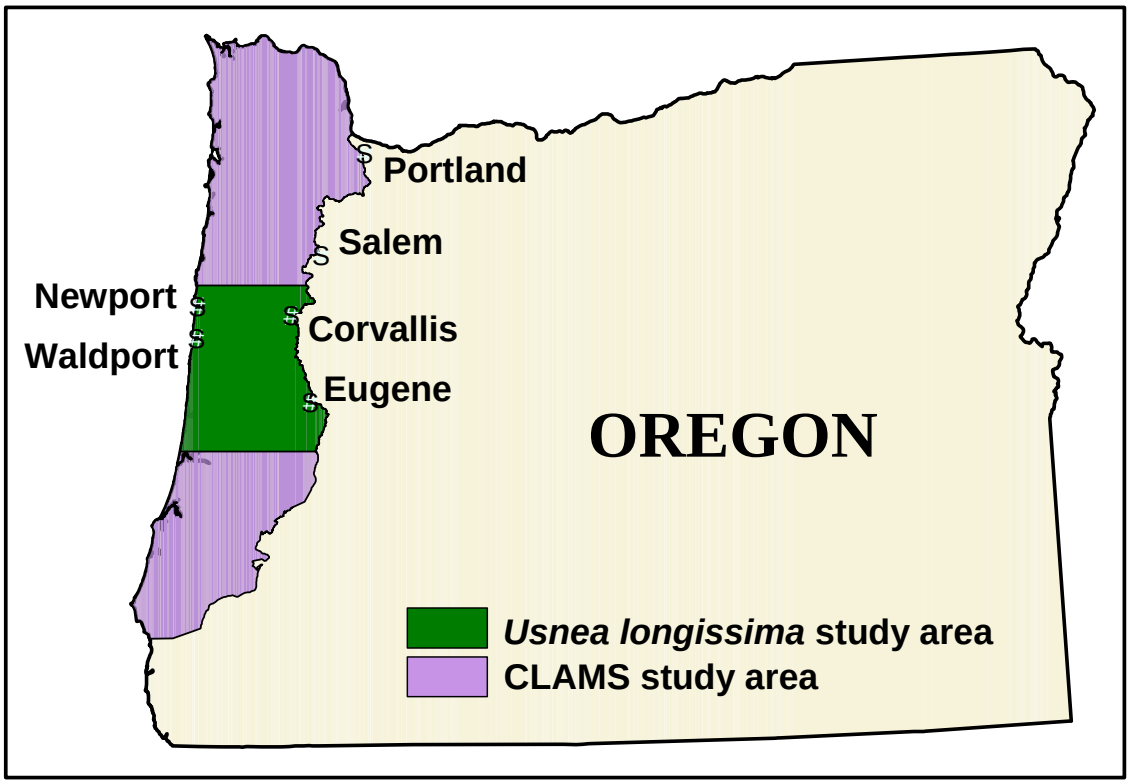


**Figure 2.2** *Usnea longissima* and CLAMS study areas.

"host tree"), while sites of absence were centered at the endpoint of each random bearing and distance traveled. Each circular study site was defined by the variable radius plot method using basal area prisms; thus, the area of each site was directly proportional to tree sizes. Plots generally included 6-8 trees, based on the use of English BAF 10 or 20 diopter prisms, depending upon tree bole sizes.

We collected data for several abiotic site characteristics, including site coordinates (latitude/longitude), slope (%), elevation (m), aspect (ºE of true N), topographic position (categorical variable), annual precipitation (cm/yr), and horizontal and vertical distance to water (m). Slope, aspect, and latitude were combined to estimate potential annual solar radiation ($cal \cdot cm^{-2} \cdot yr^{-1}$) for each site. To calculate these values, we performed a non-linear regression to predict long-standing potential annual solar radiation values calculated by Buffo et al. (1972) for three fixed latitudes (40˚N, 50˚N, 60˚N), using slope, aspect, and latitude. The equation that we derived ($R^2 = 0.97$) allowed us to calculate site-specific potential annual solar radiation values, given slope, aspect, and latitude (B. McCune and D. B. Keon *unpublished manuscript* 2000):

```
Radiation =  (55173.2916*(sin((-0.02303*slope)+1.441))) +
              237751.7391 + (-2366.9444*latitude) +
             (-1851.3025*((cos(0.01745*aspect))*slope))
```

Categories for topographic position were: 1 = bottomland, 2 = lower slope, 3 = mid-slope, 4 = upper slope, and 5 = ridge. Site coordinates were determined with a GPS unit and checked against 1:24,000 scale U.S. Geological Survey (USGS) topographic maps in the field, then compared in a GIS to 1:24,000 scale Digital Raster Graphics (DRGs; scanned, georeferenced USGS topographic maps), and 1 m digital orthophotoquads, when available. Elevation was also derived from 1:24,000 scale DRGs. Horizontal and

vertical distances to water (nearest perennial water source) were derived in a GIS from a 1:24,000 scale digital stream layer, which was developed using a 4 ha threshold by personnel from the Coastal Landscape Analysis and Modeling Study (CLAMS) group at Oregon State University (see Spies et al. *in press*). Estimates of average annual precipitation were obtained for each site by using the ArcInfo GRID module (ESRI 2000) to extract precipitation values from a grid developed through the Precipitation-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994).

We also collected biotic data from the sites, including stand age (yr), and basal area of conifers and hardwoods (BA; $m^2$/ha). Basal area values measured with English BAF 10 or 20 prisms were converted from $ft^2$/acre to $m^2$/ha. For sites where *Usnea longissima* was present, we recorded the host tree species and diameter at breast height (DBH; cm), and *U. longissima* abundance in the host tree and in a 50 m radius circle around the host tree ("local abundance"). Stand ages were determined through increment coring of the host tree and adjacent trees, and sites were then assigned to classes: 1 = 0-30 yr, 2 = 31-70 yr, 3 = 71-120 yr, and 4 = 121+ yr. We estimated abundance of *U. longissima* in the host tree crown using a variation of the 6-class dwarf mistletoe rating system (Hawksworth 1977). The crown was divided into thirds, and each third was given a rating of 0 (*U. longissima* absent), 1 (*U. longissima* present on ≤ half the branches), or 2 (*U. longissima* present on > half the branches). Scores from each third were tallied to give a final rating of 0-6 per host tree. Local abundance of *U. longissima* was estimated as a categorical variable: 1 = on 1-20% of suitable substrates (i.e., trees or shrubs), 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, and 5 = 81-100%. We also collected a voucher specimen of *U. longissima* from each site of presence.

We assembled an independent data set (n=50 plots) for validating the ability of our habitat model to predict presence or absence of *Usnea longissima*. Environmental data collected within the study area were obtained from the USFS Current Vegetation Survey (CVS) (Max et al. 1996, USDA 2001). We used CVS data that were sampled along a systematic 5.5 km grid on National Forest land in the PNW during the mid-1990s. In all, 63 CVS plots were sampled within our study area; however, 13 plots did not have complete data sets, so we excluded them. Data on *U. longissima* presence and absence from the CVS plots were obtained from the USFS Pacific Northwest Air Resource Program on the Siuslaw National Forest (L. Geiser *unpublished data* 2000). We adjusted the CVS environmental data (the "validation data set") to match the environmental data collected from our sites of *U. longissima* presence and absence (the "calibration data set") (e.g., BA data were converted from $ft^2$/acre to $m^2$/ha, topographic position data were converted to our categorical scale, etc.).

## Statistical analyses and model construction

### *Data adjustment*

The environmental data matrix contained nine raw variables for each site (Table 2.1). We separated the data into three groups prior to calculation of summary statistics: 1) sites of *Usnea longissima* presence (calibration data set; n=75); 2) sites of its absence (calibration data set; n=75); and 3) CVS sites (validation data set; n=50). Then we assessed the calibration data from sites of presence and absence separately for normality and univariate or multivariate outliers, although we applied transformations uniformly to both. We excluded the validation data from assessments of normality and outliers,

since they represented an independent set to be used strictly for cross-validation of the discriminant function derived from the calibration data. However, we also applied all adjustments made to the calibration data to the validation data, so that the data sets were comparable. We performed all transformations and analyses using SPSS (SPSS 1998) and PC-ORD (McCune and Mefford 1999).

We used the SPSS Descriptives and Split Plot functions to summarize the raw data. Vertical distance to water and hardwood BA were highly skewed (> 1.0) in both of the calibration data sets, conifer BA was highly skewed in the calibration data from sites of presence, and elevation was highly skewed in the calibration data from sites of absence. Univariate outliers (cases with very large standardized scores [$z > 3.29$, $p < 0.001$, two-tailed test], following Tabachnick and Fidell's [1996] method of data screening) were detected in each of these four highly-skewed variables, and also in the annual precipitation variable. We $\log_{10}$-transformed variables containing univariate outliers to reduce their potential effect on analyses. Prior to transformation, we added a constant (value = 1) to each of the BA variables, to eliminate values of 0 and enable their $\log_{10}$ transformation. Following transformation, all variables had skewness < 1.0 in both data sets. However, four univariate outliers remained in the data set (plots 26A [in log(elevation)], 28A [in log(conifer BA)], 69A [in radiation], 26B [in log(elevation)]). We retained all univariate outliers in the data set during the search for multivariate outliers. The data set containing raw and transformed variables was used in all subsequent examinations of the data.

Discriminant analysis is highly sensitive to outliers and departures from multivariate normality. To identify multivariate outliers, we performed a multiple

regression in SPSS with a dummy variable (integers incrementing from 1, starting with the calibration data from sites of presence) as the dependent variable, and the nine environmental variables as independent variables. As an initial check, we created a scatterplot of the residuals against the Mahalanobis distance of each variable. A large Mahalanobis distance identifies a sample unit as having extreme values on one or more of the independent variables. To confirm the visual scatterplot estimation, we evaluated Mahalanobis distances as $\chi^2$ with 9 *df*, using the criterion of Mahalanobis distance at $p < 0.001$ to identify multivariate outliers (after Tabachnick and Fidell 1996). Any plots with Mahalanobis distance > $\chi^2(9) = 27.877$ were considered multivariate outliers. One multivariate outlier was present (plot 26A, Mahalanobis distance = 33.30). We removed plot 26A and the univariate outlier plots 28A, 69A, and 26B from the data set, primarily because their influence on the analysis was obscuring the patterns present in the remaining 147 plots. The univariate and multivariate outliers were removed simultaneously, following the search for multivariate outliers. Plot 28A consisted of a single *Quercus garryana* Dougl. (Garry oak) tree in the center of an agricultural field, and was not representative of the majority of *Usnea longissima* habitat. Plots 26A and 26B were located on extremely steep local slopes (> 90%) near sea level (5 m elevation), and plot 69A was also located on an extremely steep slope (110%).

To screen for collinearity, we calculated a correlation matrix for the raw and transformed environmental variables from both groups. While no variables had correlation > 0.90 (a cutoff often used to indicate potential problems with collinearity [e.g., Hair et al. 1998, Tabachnick and Fidell 1996]), topographic position and vertical distance to water were fairly strongly correlated ($r = 0.87$). We decided to retain both

variables in the analysis, since each contained important information and their correlation was < 0.90. To screen for multicollinearity, we applied Box's M test to both groups to examine the equality of the group covariance matrices. Box's M test, which is sensitive to departures from multivariate normality, did not indicate problems with heterogeneity between the covariance matrices ($F[45, 68015] = 1.07$, $p = 0.34$). Additionally, we performed a linear regression on each group to examine variance proportions associated with each variable, after standardization, for each root (Tabachnick and Fidell 1996). To do this, we examined collinearity diagnostics produced by the COLLIN subcommand in SPSS, using criteria for multicollinearity of a conditioning index (CI) > 30 and at least two variance proportions (VP) > 0.50. No variables met these criteria, although in each group, topographic position and vertical distance to water had VPs > 0.50 associated with the root that had the highest CI. These tests confirmed that the data met the assumptions of multivariate normality and posed no threat to multivariate analysis.

We then merged the calibration presence and absence data sets. The resulting merged matrix (log[elevation], potential annual solar radiation, topographic position, horizontal distance to water, log[vertical distance to water], stand age, log[annual precipitation], log[conifer BA], log[hardwood BA]) had satisfactory summary statistics (average column skewness = -0.20, average column kurtosis = -0.54). However, the matrix produced a high coefficient of variation (299%) among the column totals. To reduce this variation, and to give all variables equal weight across their different scales of measurement, we used PC-ORD to relativize the columns by their standard deviates. Hereafter, this data set is referred to as the "adjusted data set." To ensure compatibility

between data sets, we applied the same transformations and relativization to the validation data set, relativizing the data to the means and standard deviates of the calibration data set.

To assess whether sites of presence were reasonably independent of sites of absence, or whether they should be treated as pairs, we examined scatterplots of pairs of individual variables (e.g., conifer BA at sites of presence versus conifer BA at sites of absence). Wide scatter in points, coupled with low correlation coefficients, would suggest reasonable independence between pairs for a given variable, while a more linear array of points would suggest that pair members were not independent.

*Analyses*

We performed a Multiple Response Permutation Procedure (MRPP) analysis on the calibration data set in PC-ORD, which tested the hypothesis of no difference in habitat between sites of *Usnea longissima* presence and absence. MRPP is a non-parametric procedure that tests for multivariate differences between predefined groups (Mielke 1984, Zimmerman et al. 1985). We performed the MRPP analysis using the Euclidean distance measure, with the standard n/sum(n) group weighting, and *U. longissima* presence/absence was the grouping variable. We used both blocked (McCune and Mefford 1999) and nonblocked MRPP, with the comparison of results from the two approaches serving as another check on the independence of sites of presence from sites of absence.

To determine which environmental variables were the strongest predictors of *Usnea longissima* presence, we used discriminant analysis on the adjusted data set (SPSS DISCRIMINANT procedure). All independent variables were entered directly

instead of using a stepwise variable selection. Prior probabilities of occurrence were calculated from the full validation data set for which *U. longissima* presence/absence data were available (n=63). These data provide the best available representation of the probability of *U. longissima* presence in our study area. *Usnea longissima* was present at 7 of the 63 CVS plots (11.1%); thus, we assigned prior probabilities of p = 0.111 for presence and p = 0.889 for absence. Presence/absence was the grouping variable, and the discriminant function was derived based on the calibration data set consisting of 72 plots of presence and 74 plots of absence. To cross-validate the results, we applied the resulting discriminant function to the validation data set that contained complete environmental data for each plot (n=50 plots; 6 presence, 44 absence). This tested the ability of the discriminant function to classify the CVS plots according to *U. longissima* presence or absence.

Additionally, we calculated a matrix of correlation coefficients (Pearson's *r*) to identify significant relationships at sites of *Usnea longissima* presence (n=72) between stand age and local abundance of the species, and between stand age and abundance of the species within the host tree crown.

GIS analysis and spatial modeling

*Approach*

We used raster-based spatial modeling techniques (e.g., Berry 1995, Johnston 1998) to produce a final map (grid) of apparent *Usnea longissima* habitat suitability. Each variable in the final discriminant function equation was represented by a discrete grid in the spatial model. We produced a final grid of apparent habitat suitability by entering each grid as a variable in the discriminant function equation, using the unstandardized discriminant function coefficients to weight each variable. (We refer to "apparently suitable habitat" or "habitat predicted to be suitable" because we recognize that sites where *U. longissima* does not occur may, in fact, be able to support the species, but lack it due to dispersal limitations or other factors. Our predictions of apparent habitat suitability were based solely on the empirical data collected from sites where *U. longissima* was present and absent.) The assignment of variable weightings in spatial modeling is often based upon literature review (e.g., Tucker et al. 1997) or assumptions (e.g., Gabler et al. 2000). Our approach is more robust, since the predictor weightings were determined through statistical analysis of data collected from randomly selected sites of *U. longissima* presence and absence. Fig. 2.3 displays a flow chart of the spatial modeling process.

*Digital data description and adjustment*

Digital base grids used in the GIS analysis were obtained from the CLAMS group. We clipped each grid to match our study area extent, and adjusted or modified

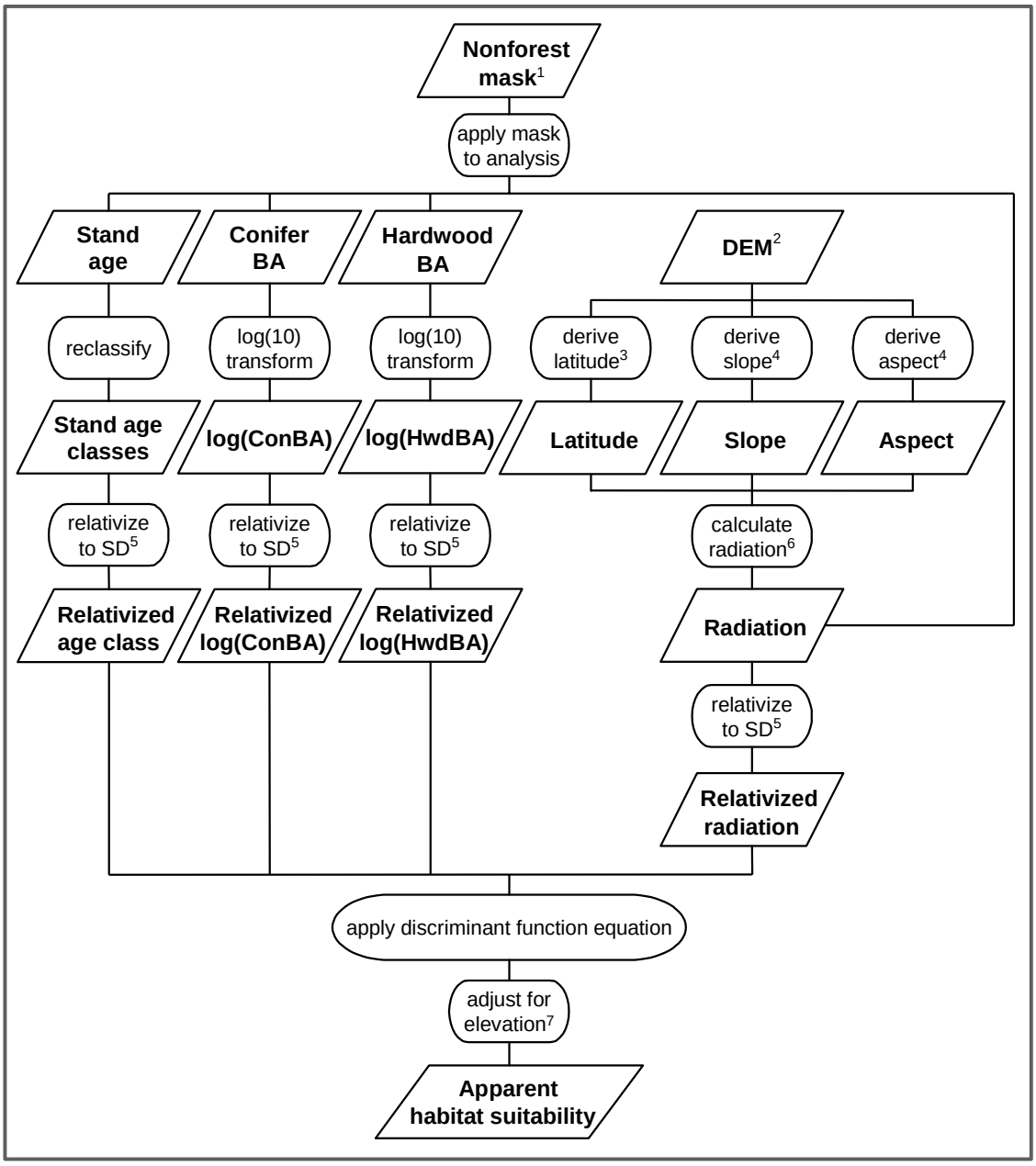


**Figure 2.3** Flow chart of the spatial modeling process. Each trapezoid represents a digital grid in the GIS. Prior to analysis, all grids were clipped to the study area extent.

*Notes*: [1]Represented nonforest areas such as roads, water bodies, agricultural fields.
[2]USGS Digital Elevation Model.
[3]Contained appropriate latitude values in each cell; the DEM was used as a base.
[4]Slope and aspect grids were derived from the DEM, using standard ArcInfo algorithms.
[5]Grids were relativized by their standard deviations.
[6]See Experimental design and sampling for radiation calculations.
[7]Areas > 915 m elevation were masked in the final grid.

the grids to match the variables that were included in the final discriminant function equation, as described below. We used the ArcInfo GRID module and ArcView GIS software with the Spatial Analyst extension (ESRI 2000) to perform all grid reclassification and analysis. We performed all grid analyses at 25 m resolution.

We derived grids representing slope and aspect from several USGS digital elevation model grids (DEMs) that were mosaicked and confined to the study area using a masking grid. An additional grid was produced that contained latitude values at the center of each grid cell, using the study area DEM as a base grid. The slope, aspect, and latitude grids were combined in the potential annual solar radiation equation (described above; see *Experimental design and sampling*) to calculate a grid that contained estimated potential annual solar radiation values in each cell (Fig. 2.4). We obtained grids representing stand age, conifer BA, and hardwood BA from the CLAMS group (Fig. 2.4, Fig. 2.5). These grids were derived through a combination of field-based vegetation measurements, mapped environmental data, and 1988 and 1996 Landsat Thematic Mapper (TM) satellite imagery. The raw TM imagery was processed through a series of steps, including normalization of adjacent and overlapping TM bands between the 1988 and 1996 imagery; transformation into Tasselled Cap indices (brightness, greenness, wetness); and median-filtering to reduce fine-scale heterogeneity, yet maintain vegetation boundaries in the landscape. Direct gradient analysis and nearest-neighbor imputation were used to ascribe stand age and basal area attributes (as well as other ground attributes of vegetation) to each grid cell (Ohmann and Gregory *in review*).

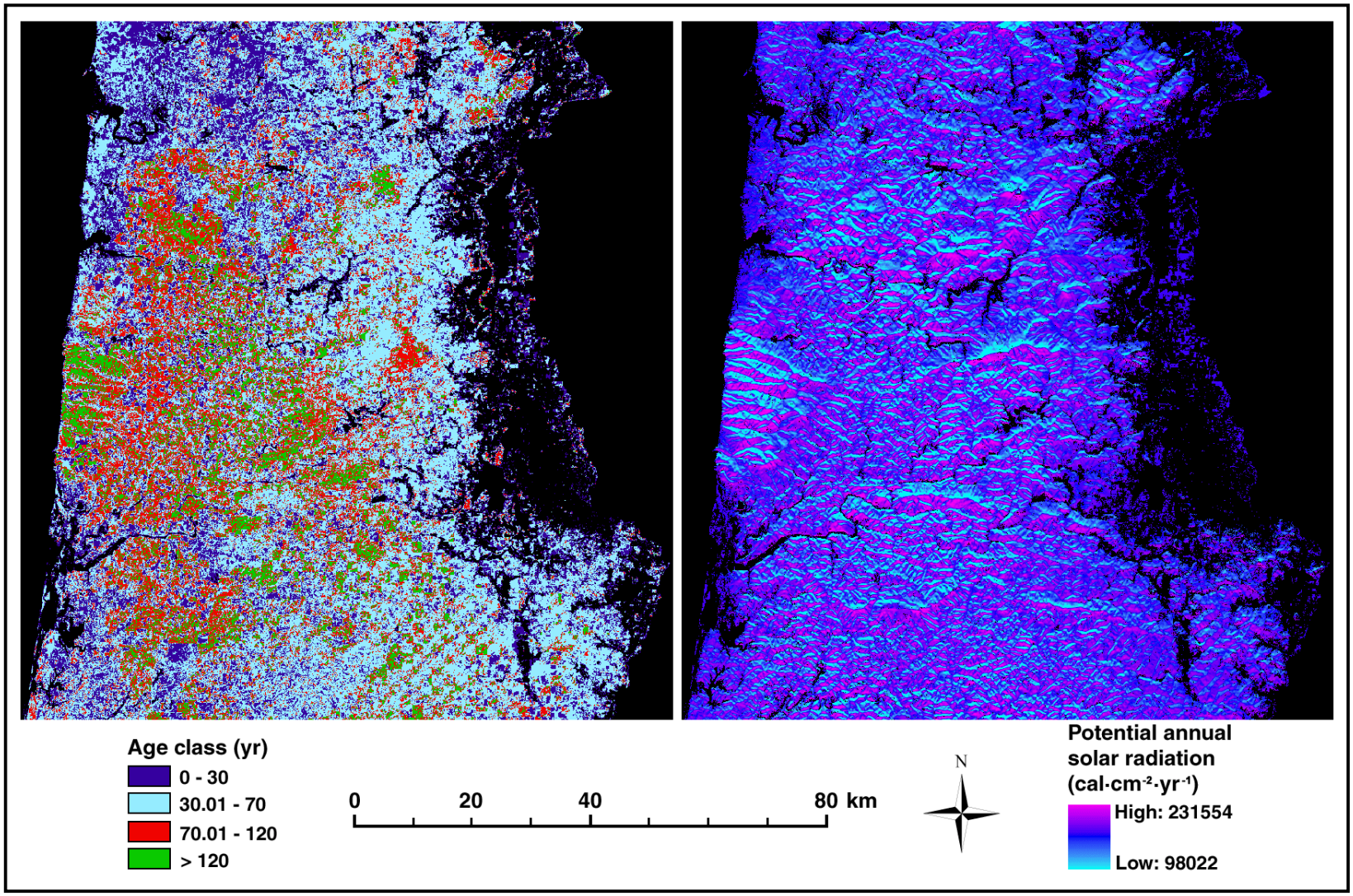


**Figure 2.4** Grids representing stand age class and potential annual solar radiation.

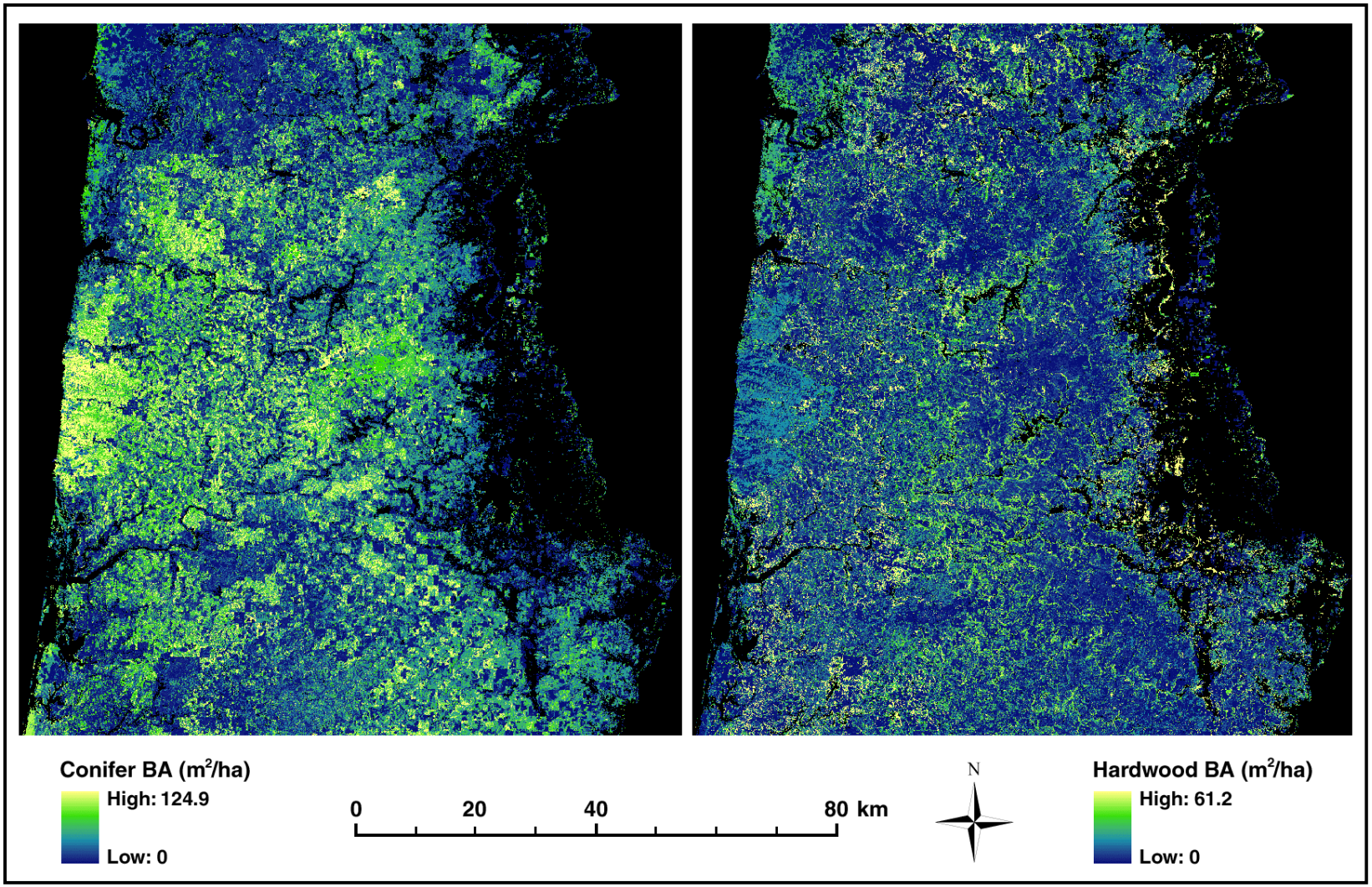


**Figure 2.5** Grids representing conifer basal area and hardwood basal area.

Forest age and basal area grids produced through the Gradient Nearest Neighbor method (Ohmann and Gregory *in review*), and used here, predicted stand attributes extremely well at the regional scale, and moderately to poorly at finer scales. Consequently, the researchers caution against using the data for local management decisions. Although there may be multiple sources of error associated with the stand age and BA grids at fine scales (e.g., due to limitations of TM imagery in forest vegetation mapping, errors in mapped explanatory variables, georegistration errors, etc.), these represent the best data available for the Oregon Coast Range, and were found to be similar in accuracy to other TM-based studies in western Oregon forests (Ohmann and Gregory *in review*).

We reclassified the stand age grid into the four categories described in *Experimental design and sampling*. To assess correspondence between our field-based age determinations and the CLAMS stand age grid, we overlayed the *Usnea longissima* study site locations with the reclassified stand age grid in the GIS. All study site age classes matched the appropriate age classes on the reclassified stand age grid. The basal area and radiation grids required adjustment (i.e., transformation and relativization, corresponding to the discriminant analysis), but not reclassification (Fig. 2.3). Nonforest areas, such as water bodies, urban areas, agricultural fields, etc., were excluded from the spatial analysis through the use of a masking grid. The nonforest mask is described in Bettinger et al. (2000). We masked areas ≥ 915 m (3000’) elevation in the final grid, since the upper elevation tolerance for *U. longissima* is thought to be approximately 3000’ in the Coast Range (McCune 1999, personal

communication), and no sites of occurrence in the calibration and validation data sets were higher than this elevation.

Although transforming variables such as local abundance and stand age to categories generalizes the information they contain, it may also result in more accurate analysis than that which would result from analysis of the raw data. For instance, in deriving forest age and structure attributes from TM imagery and other data sources, Cohen et al. (1995) demonstrated that young, mature, and old-growth classes could be estimated and mapped with moderately high accuracies in the Oregon Coast Range, with no confusion between old-growth and young stands. However, their research also indicated that acceptable classification accuracies were unlikely with finer subdivisions.

## RESULTS

### Statistical analyses

Habitat conditions at sites of *Usnea longissima* presence differed significantly from habitat conditions at sites of absence (MRPP; $p < 0.0001$, $T = -9.16$). However, the chance-corrected within-group agreement statistic was fairly small ($A = 0.024$; $A = 0$ when heterogeneity within groups equals expectation by chance, $A = 1$ when all items are identical within groups). A somewhat larger effect size occurred when pairs of presence and absence sites were treated as blocks in the calibration set (blocked MRPP; $p < 0.0001$, $T = -24.86$, $A = 0.11$). Scatterplots of individual variables from calibration sites of presence versus calibration sites of absence indicated that precipitation had a strongly significant correlation ($r = 0.49$; $p \leq 0.05$ for $r \geq |0.23|$). Vertical distance to

water and topographic position both had weakly significant correlations ($r = 0.26$ and $r = 0.24$, respectively). All other variables had $r \leq |0.20|$.

The discriminant function, based upon 72 sites of *Usnea longissima* presence and 74 sites of absence, had significant predictive power ($p < 0.001$, Wilks' $\lambda = 0.530$, $\chi^2 = 88.60$ with 9 *df*), and correctly classified *U. longissima* presence or absence for 69.9% of the plots from the calibration data set (Table 2.2). Standardized coefficients from the discriminant analysis with presence/absence as the grouping variable indicated that stand age was the most influential variable contributing to development of the discriminant function (Table 2.3). Means for stand age, potential annual solar radiation, log(conifer BA), and log(hardwood BA) differed significantly ($p \leq 0.06$) between sites of presence and absence in the calibration data set (Table 2.4; see Table 2.1 for means). Sites of presence tended to occur in older stands, and had lower potential annual solar radiation, lower conifer BA, and slightly higher hardwood BA values than sites of absence. These four variables also had the strongest correlations with the standardized discriminant function (Table 2.5).

The discriminant analysis produced the following discriminant function equation, using the unstandardized coefficients (**note**: this equation is specific to our study area and should not be applied to other regions):

```
Y = 0.003 + 1.362(stand age) – 0.202(potential annual
    radiation) – 0.625(log[conifer BA]) –
    0.032(log[hardwood BA])
```

Cross-validation of the model, using the validation (CVS) data set, resulted in correct prediction of *Usnea longissima* presence or absence for 84.0% of the CVS plots (Table 2.2).

**Table 2.2** Classification results from discriminant analysis of the calibration data. The CVS data were used to cross-validate the classification.

| | | | Predicted group membership | | |
|---|---|---|---|---|---|
| | | Group | Presence | Absence | Total |
| Calibration data set [a] | Count | Presence | 29 | 43 | 72 |
| | | Absence | 1 | 73 | 74 |
| | % | Presence | 40.3 | 59.7 | 100.0 |
| | | Absence | 1.4 | 98.6 | 100.0 |
| Validation (CVS) data set [b] | Count | Presence | 3 | 3 | 6 |
| | | Absence | 5 | 39 | 44 |
| | % | Presence | 50.0 | 50.0 | 100.0 |
| | | Absence | 11.4 | 88.6 | 100.0 |

[a]69.9% of *Usnea longissima* plots correctly classified.
[b]84.0% of CVS plots correctly classified.

**Table 2.3** Standardized discriminant function coefficients from analysis of the calibration data.

| | Coefficient |
|---|---|
| Stand age class | 1.151 |
| log(Vertical distance to water) | -1.002 |
| log(Conifer BA) | -0.616 |
| Horizontal distance to water | 0.499 |
| Topographic position | 0.294 |
| Potential annual solar radiaton | -0.198 |
| log(Elevation) | 0.173 |
| log(Precipitation) | -0.075 |
| log(Hardwood BA) | -0.032 |

**Table 2.4** Tests of equality of group means from discriminant analysis of the calibration data ($df$ = 1, 145). See Table 2.1 for group means.

| | Wilks' $\lambda$ | $F$ | $p$ |
|---|---|---|---|
| Stand age class | 0.706 | 59.892 | < 0.001 |
| Potential annual solar radiaton | 0.957 | 6.541 | 0.012 |
| log(Conifer BA) | 0.967 | 4.955 | 0.028 |
| log(Hardwood BA) | 0.976 | 3.553 | 0.061 |
| log(Vertical distance to water) | 0.984 | 2.344 | 0.128 |
| Horizontal distance to water | 0.986 | 2.002 | 0.159 |
| Topographic position | 0.996 | 0.520 | 0.472 |
| log(Elevation) | 0.999 | 0.073 | 0.788 |
| log(Precipitation) | 1.000 | 0.005 | 0.946 |

**Table 2.5** Pooled within-group correlations between each variable and the standardized discriminant function. The variables are ordered by absolute size of their correlation within the function.

| | Correlation |
|---|---|
| Stand age class | 0.685 |
| Potential annual solar radiaton | -0.226 |
| log(Conifer BA) | -0.197 |
| log(Hardwood BA) | 0.167 |
| log(Vertical distance to water) | -0.135 |
| Horizontal distance to water | -0.125 |
| Topographic position | -0.064 |
| log(Elevation) | -0.024 |
| log(Precipitation) | -0.006 |

**Table 2.6** Correlation coefficients (Pearson's *r*) and associated *p*-values between stand age and *Usnea longissima* abundance variables measured at sites of presence (n=72).

| | Stand age class | *U. longissima* host abundance |
|---|---|---|
| *U. longissima* host abundance | $r = 0.207$<br>$p = 0.082$ | - |
| *U. longissima* area abundance | $r = 0.237$<br>$p = 0.045$ | $r = 0.616$<br>$p < 0.001$ |

Local abundance of *Usnea longissima* tended to be higher in older stands, as did abundance of *U. longissima* in the host tree, although the latter relationship was weaker (Table 2.6). We performed a separate discriminant analysis using *U. longissima* absence and the five local abundance classes (presence) as the six grouping variables, to search for relationships of local abundance with the other environmental variables. The analysis substantiated the importance of stand age, which was the most significant variable contributing to the first discriminant function ($p < 0.001$, Wilks' $\lambda = 0.393$, $\chi^2 = 129.47$ with 45 *df*), but an ordination of the first two discriminant functions, which combined explained 89.2% of the variance, was not successful at clearly separating the six abundance groups.

Although vertical distance to water was not a statistically significant predictor of *Usnea longissima* occurrence ($p = 0.128$), its standardized discriminant function coefficient (-1.002) was second in magnitude only to stand age (Table 2.3), indicating that vertical distance to water may have been an important contributor to development of the discriminant function. Likewise, horizontal distance to water did not have statistically significant predictive power ($p = 0.159$), but its standardized coefficient (0.499) was fourth in magnitude to stand age. Although vertical and horizontal distance to water had some predictive power, we excluded them from the discriminant function equation for the following reasons. (1) The *p*-values associated with each variable were relatively large ($p > 0.1$; Table 2.4), hence they did not meet our criteria for statistical significance. (2) The potential annual solar radiation equation combined slope, aspect, and latitude, capturing at least some of the relevant information about each site's moisture regime. (3)Vertical and horizontal distance to water had only the fifth and

sixth strongest correlations, respectively, with the discriminant function; lower than those of the four variables that we included in the final discriminant function equation (Table 2.5).

GIS analysis

For summaries of apparent habitat suitability and ownership, we classified the final grid into 10 equal interval classes, based on the minimum and maximum discriminant function scores present in the final grid. Hereafter, these classes are referred to as "habitat suitability classes," with class 1 indicating habitat predicted to be least suitable, and class 10 indicating habitat predicted to be most suitable, based upon present patterns of occurrence of *Usnea longissima* across the study area. This classification indicated a higher percentage of apparently less suitable habitat than apparently more suitable habitat across the study area (Fig. 2.6). Splitting the classes in half, 81.1% (557,957 ha) of the study area falls into classes 1-5, and 18.9% (129,670 ha) of the study area falls into classes 6-10. These percentage data, and those that follow, do not include areas excluded as nonforest, or areas > 915 m elevation. While clear separations in levels of apparent habitat suitability were not possible, we grouped classes 7-10 as the most suitable habitat and classes 1-4 as the least suitable habitat, leaving classes 5 and 6 as intermediate. Using that classification, 11.5% (79,275 ha) of habitat in the study area was predicted to be of the highest suitability, 67.1% (461,414 ha) was predicted to be of the lowest suitability, and 21.4% (146,938 ha) was predicted to be of intermediate suitability. To visualize the distribution of habitat across the study

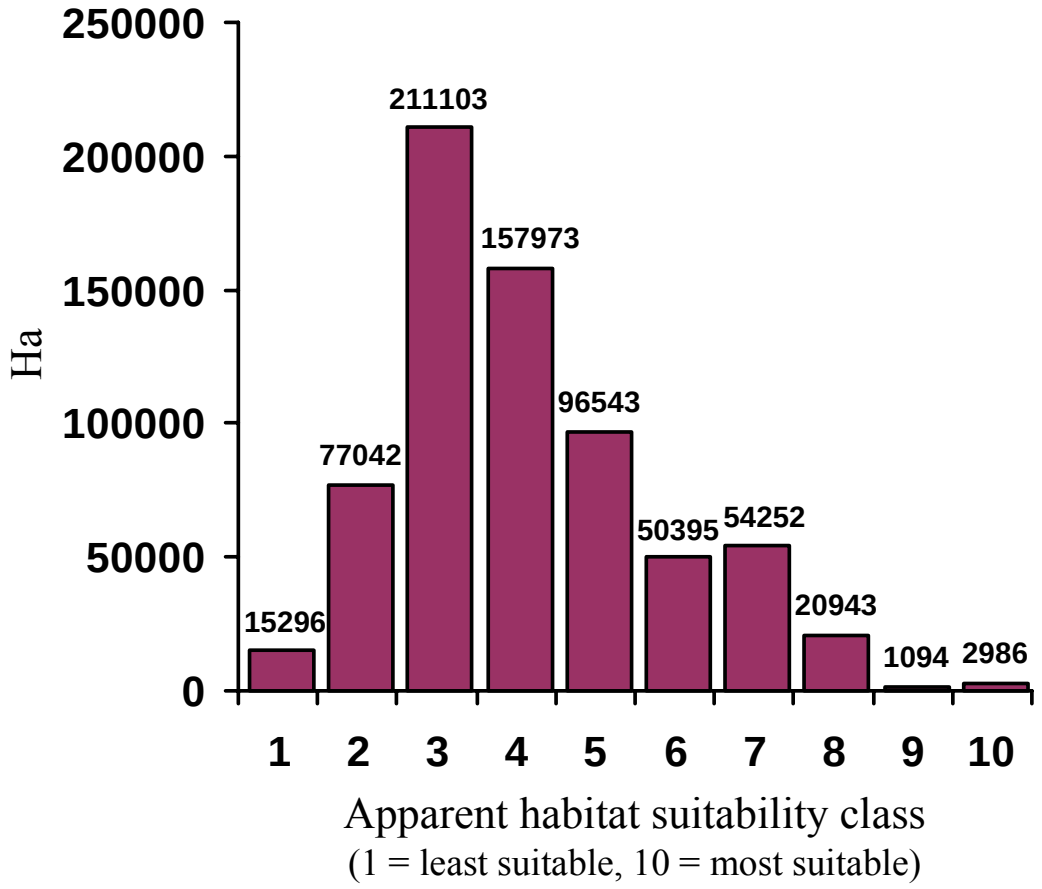


**Figure 2.6** Distribution of land within the study area, by apparent habitat suitability class.

area, we created a map by classifying the final grid into five equal interval classes (Fig. 2.7).

We also overlayed the 63 CVS plots that contained *Usnea longissima* presence/absence data on the final map of predicted habitat suitability. We calculated the average habitat suitability class value beneath each CVS point from the nearest 13 pixels (each CVS plot on the ground covered 13 pixels on the GIS grid), to determine the suitability class associated with each CVS plot. There were no differences in the distribution of habitat suitability classes between the presence and absence plots (Fig. 2.8). The distribution of CVS plots across the habitat suitability classes was nearly normal, except that none fell within the two most favorable classes (classes 9 and 10; Fig. 2.8).

Excluding areas masked as nonforest in the GIS, and areas > 915 m elevation, private industrial (PI) and private non-industrial (PNI) land occupies 56.8% of the study area (Fig. 2.9). The remaining 43.2% is owned by the BLM, USFS, State of Oregon (State), and miscellaneous (Misc) landowners, such as the U. S. Fish and Wildlife Service. Land ownership is fragmented throughout much of the study area (Fig. 2.10); however, publicly owned lands contain a higher percentage of the most suitable habitat (classes 7-10) across the study area: USFS 43.6%, BLM 31.3%, PNI 11.0%, PI 7.8%, State 5.9%, and Misc 0.4% (Fig. 2.11). Conversely, the least suitable habitat (classes 1-4) is found more frequently on privately owned lands: PI 40.4%, PNI 23.3%, USFS 16.3%, BLM 15.6%, State 3.8%, and Misc 0.6%.

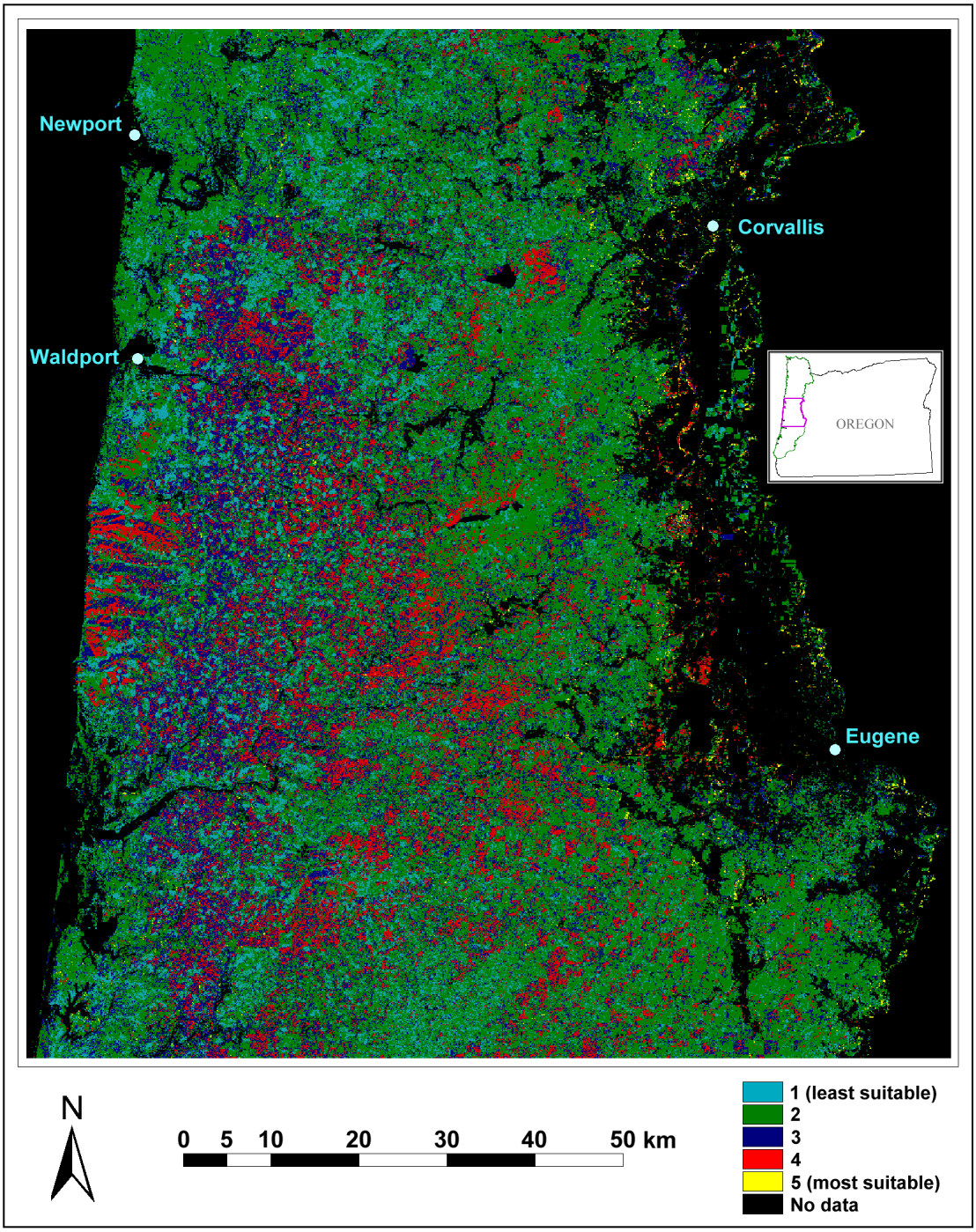


**Figure 2.7** Final map representing the range of apparent habitat suitability. "No data" values indicate either 1) areas outside the study area, or 2) nonforest areas excluded from the analysis.

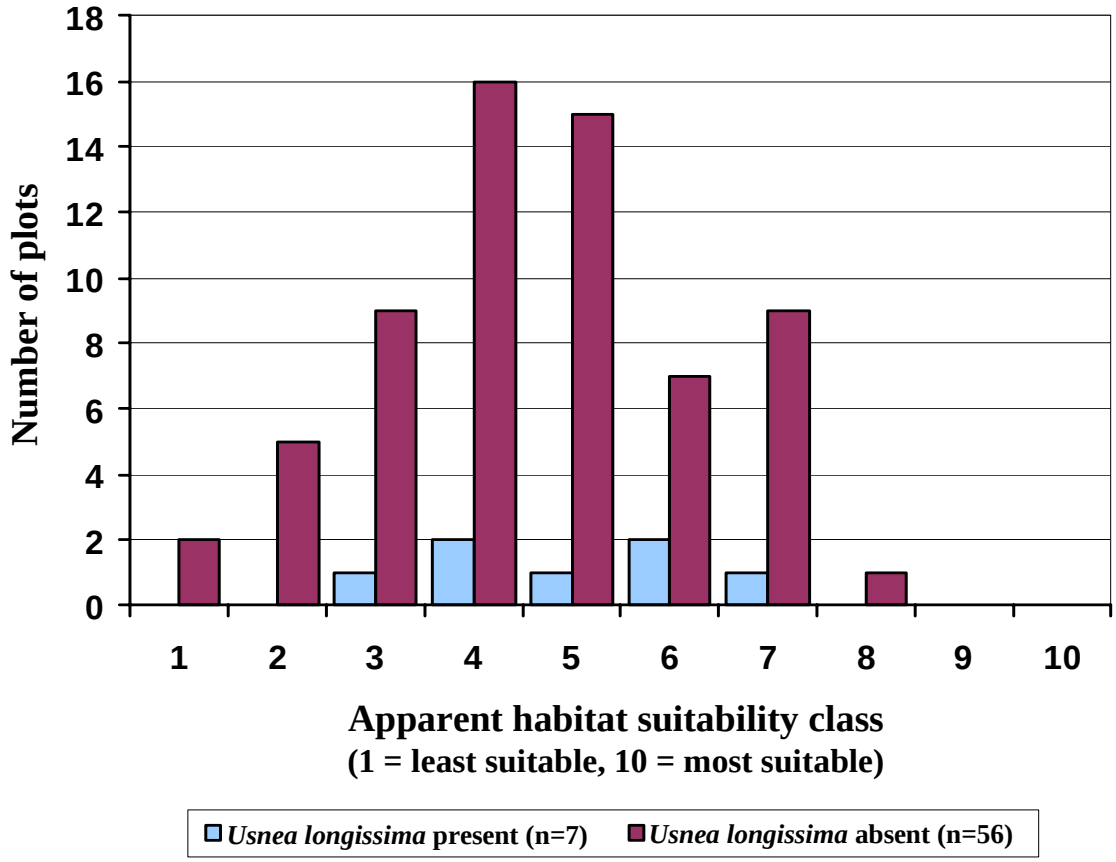


**Figure 2.8** Apparent habitat suitability classes associated with CVS plots where *Usnea longissima* presence and absence data were collected.

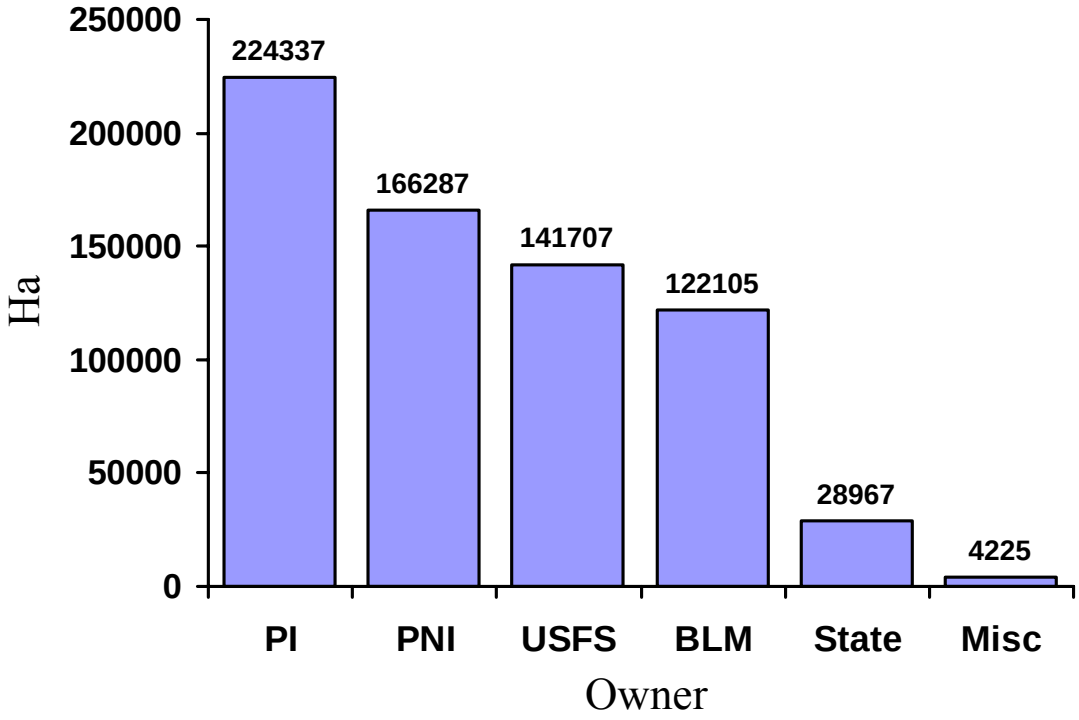


**Figure 2.9** Land ownership across the study area, excluding areas masked as nonforest in the GIS, and areas > 915 m elevation. PI = Private Industrial, USFS = USDA Forest Service, PNI = Private Non-Industrial, BLM = USDI Bureau of Land Management, State = State of Oregon, Misc = miscellaneous owners.

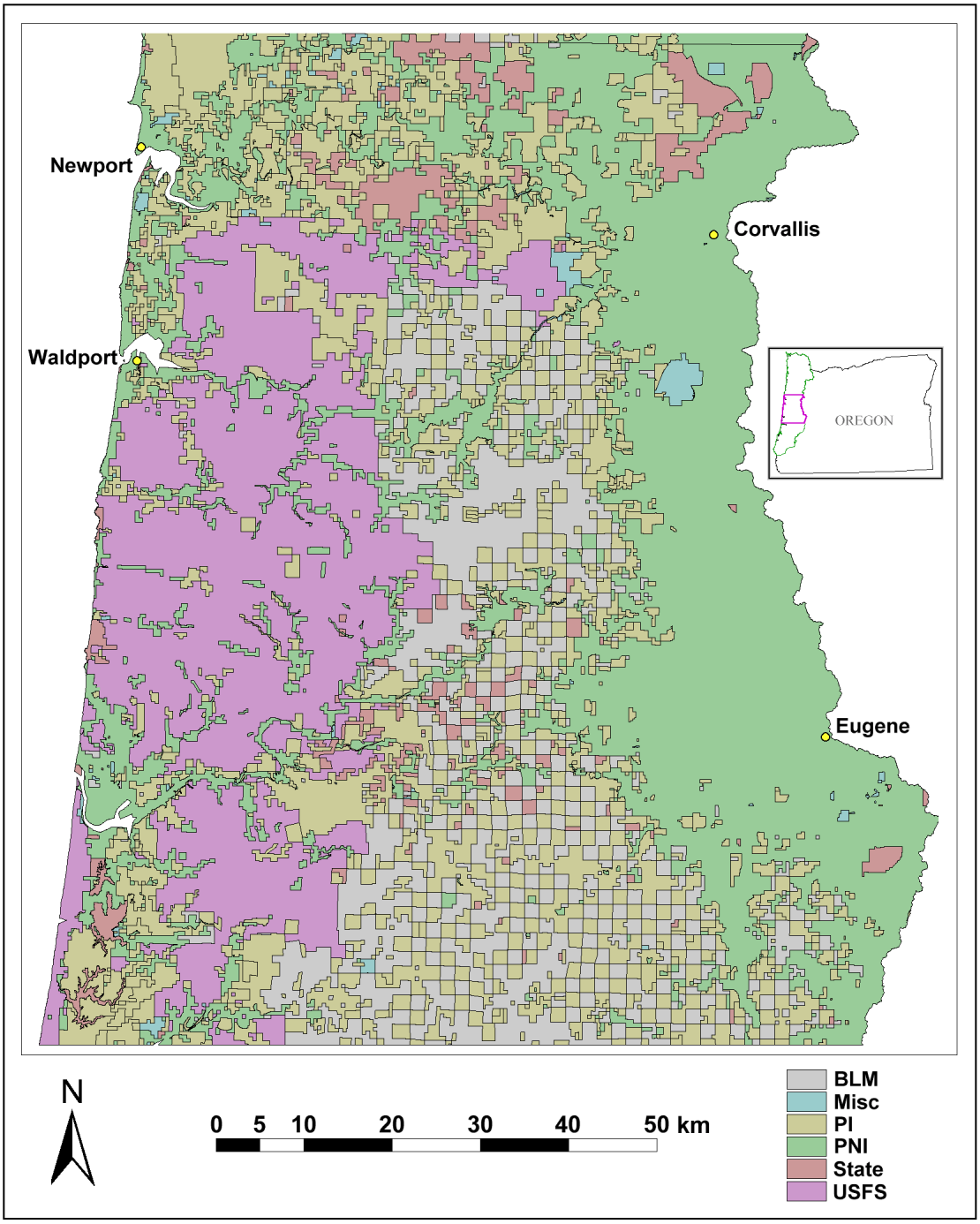


**Figure 2.10** Map of land ownership within the study area. BLM = USDI Bureau of Land Management, Misc = miscellaneous owners, PI = Private Industrial, PNI = Private Non-Industrial, State = State of Oregon, USFS = USDA Forest Service.

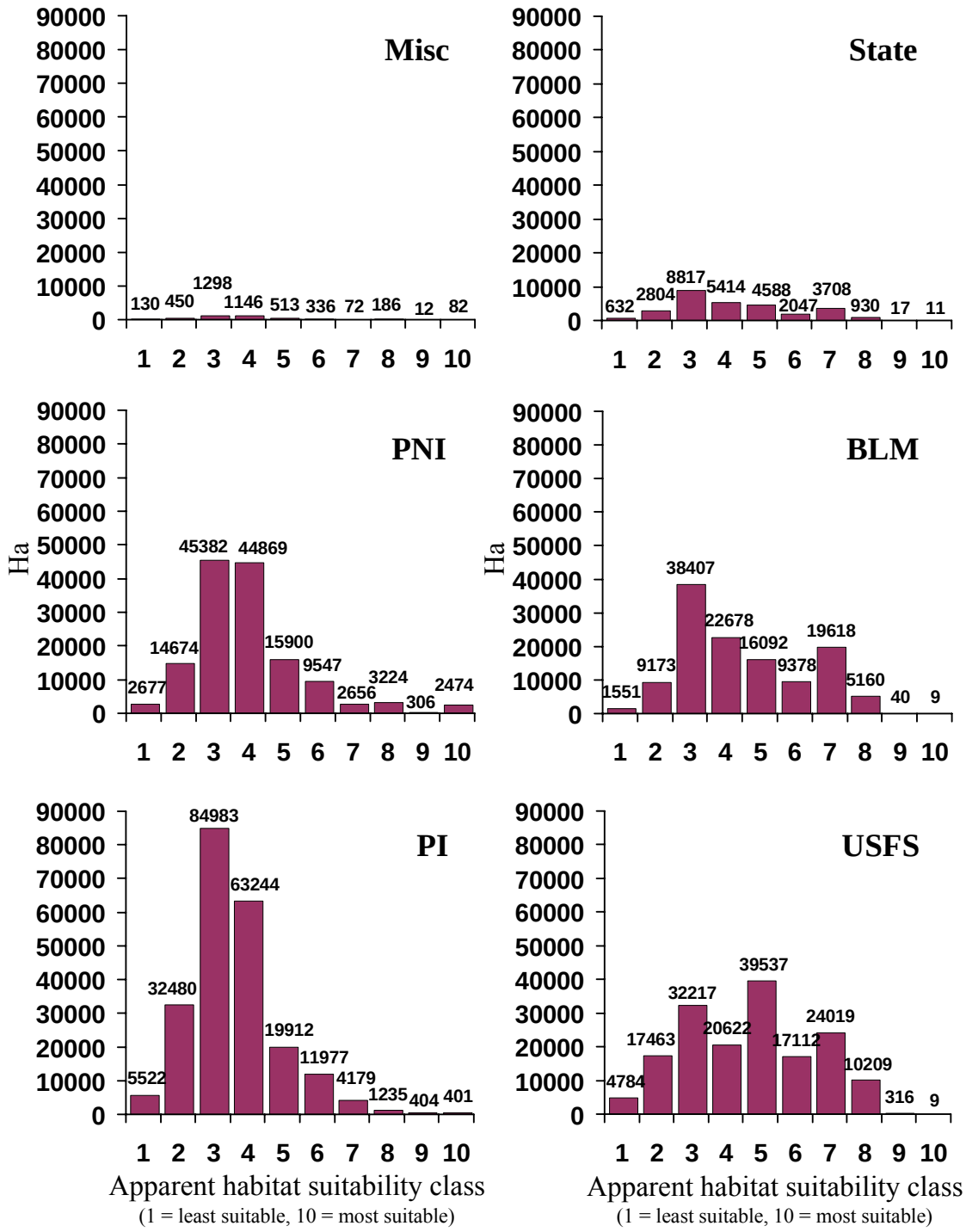


**Figure 2.11** Distribution of land among apparent habitat suitability classes, by owner, excluding areas masked as nonforest in the GIS. Misc = miscellaneous owners, State = State of Oregon, PNI = Private Non-Industrial, BLM = USDI Bureau of Land Management, PI = Private Industrial, USFS = USDA Forest Service.

# DISCUSSION

## Analysis of environmental data

### *Statistical analyses*

Although results from MRPP analyses indicated that habitat where *Usnea longissima* is present differs significantly from habitat where it is absent, results from the discriminant analysis suggest that the differences are not as clear as the *p*-values from MRPP might imply. Furthermore, the small size of the chance-corrected within-group agreement statistic (*A*; a measure of the effect size independent of the sample size) indicates that heterogeneity within groups is not very different than expected due to chance. The sample size (n=146) was large enough that MRPP could detect small differences between the observed and expected deltas (nonblocked MRPP: observed $\delta$ = 3.953, expected $\delta$ = 4.052; blocked MRPP: observed $\delta$ = 1.622, expected $\delta$ = 1.827).

While results from blocked MRPP analysis indicated a larger effect size than results from nonblocked MRPP, suggesting that the *Usnea longissima* presence and absence plots might not be completely independent of one another, the difference in effect size was not great ($A = 0.11$ from blocked MRPP versus $A = 0.024$ from nonblocked MRPP; maximum possible value is $A = 1$). Additionally, the scatterplots and associated correlation coefficients for individual variables from calibration sites of *U. longissima* presence versus absence provided strong evidence of independence between pairs of individual variables ultimately included in the final models of habitat occupancy and apparent habitat suitability. The only exceptions were precipitation and, to a lesser extent, vertical distance to water and topographic position. These variables

were similar between nearby sites of presence and absence due to their spatial proximity. However, since these variables were not included in the final models of habitat occupancy or apparent habitat suitability, we felt that lack of independence between pair members was not a problem for subsequent analyses. Thus, precipitation, vertical distance to water, and topographic position were included in the MRPP analyses, and their correlations between nearby sites of presence and absence probably contributed to the stronger effect size observed with blocked MRPP, as opposed to nonblocked MRPP.

Our finding that sites of *Usnea longissima* presence were associated with older stand ages and lower potential annual solar radiation parallels findings of Scandinavian studies. Tønsberg et al. (1996) found that, in Norway, *U. longissima* usually occurs on old trees in old-growth forests dominated by *Picea abies* (L.) Karst. They also noted that *U. longissima* frequently occurs in two habitats: 1) old *P. abies* forests on north- to east-facing slopes, and 2) forested canyons with running water. Esseen et al. (1981) found that most occurrences of *U. longissima* at their study sites in Sweden were on slopes with a northern exposure, which had higher relative humidity than sites with other exposures. The researchers translated from Gams (1961), whose description of *U. longissima* as "the most extreme fog-forest lichen of the whole Holarctic" implied a strong relationship between high humidity and presence of the species. Although *U. longissima* is often characterized as a riparian lichen in the PNW (Rosentreter 1995, McCune and Geiser 1997, USDA and USDI 2000), we frequently observed large populations of *U. longissima* in late-successional and old-growth forests on ridges and north- to east-facing slopes, often several hundred m from water. However, riparian

sites of presence were also common, and were often located in younger, mixed conifer-hardwood stands along streams and rivers. The modest but positive association that we found between sites of *U. longissima* presence and distance to water may relate to the "wetness factor" indicated by other researchers (e.g., Esseen et al. 1981) as an important component of *U. longissima* habitat. Further study is required to understand the relationship between *U. longissima* presence and site moisture.

While large, old conifers were more commonly found at sites of presence, sites of absence were often dominated by young stands of pure *Pseudotsuga menziesii*, yielding very high conifer BA values, and probably resulting in the negative relationship between log(conifer BA) and *Usnea longissima* presence (Table 2.3). This, combined with the fact that many sites of presence also contained a strong hardwood component, probably contributed to the resulting BA classification in the discriminant analysis. Although the higher mean of hardwood BA at sites of presence (Table 2.1) and its positive correlation with the discriminant function (Table 2.5) appear to contradict the negative standardized coefficient for log(hardwood BA) in the discriminant function itself (Table 2.3), that coefficient is very small (-0.03). Additional discriminant analyses, where log(hardwood BA) was retained while other significant variables were removed, resulted in a positive coefficient for log(hardwood BA) in all cases. It is likely that intercorrelations among hardwood BA, conifer BA, and stand age ($r > 0.50$ in all combinations) resulted in the slightly negative standardized coefficient for log(hardwood BA) in the final discriminant function.

The modestly successful classification of the *Usnea longissima* calibration sites as presence or absence (Table 2.2) was primarily due to correct classification of sites of

absence. Of 74 sites of absence, 73 were correctly classified; however, just 29 of the 72 sites of presence were correctly classified. These results reflect our use of prior probabilities derived from the validation data set, which weighted the probability of absence (p = 0.889) much higher than the probability of presence (p = 0.111).

*Spatial modeling*

Since stand age was weighted most heavily in the discriminant function equation, the final grid of habitat suitability is most strongly influenced by stand age. This was evidenced by a simple comparison of the grid of stand age with the final grid of habitat suitability in the GIS, particularly in locations where older stands and clear cuts are mixed together in patchwork fashion. Influences of radiation were also evident, as the most suitable habitat often appeared on north- to east-facing slopes in old stands (Fig. 2.7; see Fig.2.4 for comparisons).

It is interesting that sites of *Usnea longissima* presence in the validation (CVS) plots occurred as commonly in areas above the midpoint of the habitat suitability classes as in areas below the midpoint (Fig. 2.8). Further, many validation sites of absence occurred in areas of apparently highly suitable habitat. These results may indicate that the grid of predicted habitat suitability is not a reliable predictor of actual suitable habitat for *U. longissima*. Lack of predictive ability could result from our field data (and, thus, the discriminant function) being an inaccurate reflection of the true habitat associations of the species, although this seems unlikely given our large sample size and choice of environmental variables. Alternatively, lack of predictive power could result if the species can, in fact, grow well in a wide variety of habitats, with its occurrence influenced heavily by other factors such as site disturbance history or

dispersal limitations (see below). However, the validation sites of presence were few (n=7), and a firm determination of the model's ability to predict suitable habitat and the occurrence of *U. longissima* would, ideally, be based on a larger independent set of sites of presence for the study area. While classification of the validation data set was moderately strong, as discriminant analysis was able to correctly group 84.0% of the CVS sites as presence or absence during cross-validation of the model, this result is heavily influenced by the fact that *U. longissima* was absent from most CVS sites. Most of the successful classifications from analysis of the validation data set resulted from correct prediction of absence, influenced by the prior probabilities derived from that data set (Table 2.2).

Differences in the distribution of habitat suitability classes among land owners were striking (Fig. 2.11), although not surprising. The largest ownership category, Private Industrial (PI) (Fig. 2.9), is primarily composed of timber companies, whose land holdings include a larger proportion of young stands than the corresponding proportion found on public lands. Because stand age played a strong role in distinguishing land occupied by *Usnea longissima* and, hence, apparently suitable habitat for the species, the majority of PI land falls into habitat suitability classes that are below the midpoint of the range (< 5). Public lands tend to be more balanced across the range of suitability classes (Fig. 2.11), partially because public land in the Oregon Coast Range contains more old forest than does private land.

Dispersal vs. habitat limitations

Our results suggest that *Usnea longissima* is not limited by lack of apparently suitable habitat within the study area. Although we found just 11.5% of the available habitat to be of the apparently highest suitability, based upon analysis of the calibration data set of *U. longissima* presence and absence, that percentage represents a large area; approximately 80,000 ha. Furthermore, comparison of validation plot locations with the final grid of habitat suitability indicated that plots of *U. longissima* presence (n=7) were split nearly equally between areas of lower and higher apparent habitat suitability, suggesting that the species may not, in fact, have very narrow habitat associations.

Local abundance of *Usnea longissima* at calibration sites of presence was positively, although weakly, correlated with stand age ($p = 0.045$), which matched our general field observations that older stands tended to harbor the largest populations of the species. A similar pattern was described in Norwegian *U. longissima* populations by Tønsberg et al. (1996). Rolstad and Rolstad (1996) also reported that *U. longissima* presence was predictable in old forest stands (> 80 yr) in southeastern Norway, on northern and eastern slopes. Although Esseen et al. (1981) noted a positive correlation between *U. longissima* presence and high humidity, and that the largest populations of *U. longissima* were located in the tallest or oldest trees at their study sites in Norway, they found no correlation between *U. longissima* population size and source tree height, diameter, and age. Rolstad and Rolstad (1999) found that *U. longissima* occurred less frequently on trees 3-9 cm diameter at breast height (dbh) in south-central Norway, compared to trees ≥ 10 cm dbh. While they also noted that the species was most

abundant in their oldest stand, there was no general relationship between tree age and number of *U. longissima* thalli in stands with trees ≥ 10 cm dbh.

Our results lead us to believe that many populations of *Usnea longissima* in the PNW may be remnants of larger populations that have survived in older forests. We suggest that older stand age is positively associated with *U. longissima* presence and, to a lesser extent, with its abundance in a site, not necessarily because microclimatic characteristics of older forests provide more suitable habitat for the species, but because old stands harbor remnant populations of the species. Gauslaa et al. (1992) speculated that ancient deciduous forests in western Norway, most of which were destroyed centuries ago, formed the primary habitat for *U. longissima*, and that existing forests in the same region harbor remnant populations of the species. Additionally, Doell and Wright (2000) discussed the possibility that existing *U. longissima* populations in older Northern California forests are remnants of larger populations.

Epiphytic lichens have long been thought to accumulate slowly in forests due to inherently slow growth, or to narrow environmental tolerances, requiring time for appropriate environmental conditions to develop with stand age. However, several recent studies (Renhorn and Esseen 1995, McCune et al. 1996, Muir et al. 1997, Renhorn et al. 1997, Sillett and McCune 1998, Sillett et al. 2000, Keon and Muir *in review*) have indicated that rapid growth (> 30% annually) in several epiphytic lichen species is possible in a diversity of habitats, not just in older forests. In an accompanying transplant experiment (Keon and Muir *in review*), we found that *Usnea longissima* thalli grew well at sites across a range of habitat conditions, and actually gained the most weight in what we determined *a priori* to be the apparently least

suitable habitat (clear cuts on S- to W-facing slopes). These findings strengthen the suggestion that dispersal may play a more important role than availability of suitable habitat in defining the distribution of *U. longissima* in the Oregon Coast Range. Sillett et al. (2000) reached similar conclusions about *Lobaria oregana* in the Oregon Cascades, where the species is considered to be an old-growth associate. They found that *L. oregana* survived in clear cuts, and grew well in both young and old-growth forests, suggesting that dispersal limitations, rather than environmental requirements, have resulted in its association with old forests. It is important to note that tests of environmental conditions required for natural establishment of *U. longissima* have, to date, not been conducted. Such studies are important, and may suggest that establishment occurs in a narrower range of environmental conditions than those that support growth of transplanted thalli.

*Usnea longissima* populations found in younger stands are most likely present, in general, because of dispersal from older, taller, adjacent trees. The species appears to be strongly dispersal-limited in the PNW, since it reproduces primarily through fragmentation of relatively large pieces of thalli, which can exceed decimeters in length, and has little to no reproduction through small, easily dispersed sexual or asexual propagules (Noble 1982, McCune and Geiser 1997, Keon *in review*). While no studies have explicitly studied dispersal distances of *U. longissima* thalli, Esseen et al. (1981), who made some observations on *U. longissima* dispersal at their study sites in east-central Sweden, found that most thalli were deposited < 3 m from their source trees. Additionally, Esseen et al. (1981) and Esseen (1985) both noted that *U. longissima* fragments usually disperse either within their source tree crown, within the crown of an

adjacent tree, or fall to the understory or ground beneath the source tree. Similar patterns of dispersal have been observed in other alectorioid species; Dettki (1998) found that dispersal of the epiphytic lichens *Alectoria sarmentosa* (Ach.) Ach. and *Bryoria* spp. into a clear cut dropped sharply as distance increased from the edge of a mature *Picea abies* forest. It should be noted that Gauslaa (1997) found isidiate and sorediate specimens among *U. longissima* populations in southeast Norway, which may imply that those populations are more capable of long-distance dispersal than other populations. However, Gauslaa (1997) noted that isidia and soredia have low establishment success.

Management implications

Sources of lichen propagules must be available if epiphytic lichens are to colonize new stands or expand population sizes in currently occupied areas. The findings of Dettki et al. (2000) support the hypothesis that old-growth forests function as sources of lichen propagules, and Sillett et al. (2000) also concluded that dispersal-limited old-growth associated lichens are dependent upon populations in old-growth forests and remnant trees as sources of propagules to younger, adjacent stands. Young forests bordering old-growth stands are likely to receive more lichen propagules than young forests bordering second-growth stands (Dettki 1998). Tønsberg et al. (1996) found *Usnea longissima* on young trees only in locations where those trees bordered older stands harboring large populations of *U. longissima*. The association of *U. longissima* with older forests in our study area, and its probable dispersal limitations, suggest that old forests containing it are important as sources of propagules for other,

often younger, stands, particularly in highly fragmented landscapes such as the Oregon Coast Range.

To ensure the long-term persistence of *Usnea longissima* across the landscape, dispersal of *U. longissima* must occur both between-stands and within-stands, in both old and regenerating stands. For this to happen, trees containing *U. longissima* should be retained during logging operations, and old stands containing *U. longissima* should be preserved as refugia. Remnant trees in regenerating stands function as sources of inoculum from which epiphytic lichen propagules can disperse, and have been shown to effectively inoculate younger, adjacent trees (Peck and McCune 1997). Tønsberg et al. (1996) cited Haugmoen (1952) as concluding that *U. longissima* populations tolerated selective logging in Norway, prior to clearcutting operations that began in the 1950s, which implies that the species can tolerate disturbances and that remnant trees will supply successfully establishing propagules to regenerating stands. Results from our transplant study suggest that the species will most likely tolerate the change in environment associated with logging with green tree retention, surviving in the remnant trees and potentially growing well in the young stand (Keon and Muir *in review*), assuming that conditions are suitable for establishment of its propagules. Thus, based upon the simple "decision matrix for maintenance of old-growth associated epiphytes in managed forests" offered by Sillett et al. (2000), we can conclude that maximizing the number and dispersion of remnant trees in regenerating stands should maximize the rate of accumulation of *U. longissima* within those stands. Green-tree retention is currently required during timber harvest on most federal lands within the range of the Northern Spotted Owl in the PNW (USDA and USDI 2001). Such retention will benefit

*U. longissima* as well as other aspects of these forested ecosystems. For example, remnant trees have been shown to be important "hotspots" of lichen diversity and abundance (Neitlich and McCune 1997), and are positively associated with diversity and abundance of forest floor bryophytes (Rambo and Muir 1998).

While *Usnea longissima* can be found in a wide range of sites (Fig. 2.8), its occurrence was modestly predictable. This predictability, regardless of whether its distribution is caused by habitat associations or by stand history coupled with dispersal limitations, indicates that our methods may be useful in management of the species in the PNW. In particular, our findings may help to refine approaches to strategic surveys mandated by the Northwest Forest Plan (USDA and USDI 2000, 2001), and may ultimately aid in determination of the appropriate status of the species in the PNW. Our combination of field study, multivariate analysis of environmental factors associated with occurrence of the target species, and GIS-based habitat modeling represents a powerful set of tools for assessing availability of habitat and devising efficient field surveys, particularly for species that have relatively narrow habitat associations.

## ACKNOWLEDGMENTS

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# Chapter 3

## Growth of *Usnea longissima* Across a Variety of Habitats in the Oregon Coast Range

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## ABSTRACT

The sensitive lichen *Usnea longissima* Ach. has a limited, patchy distribution across forested landscapes in the U.S. Pacific Northwest. To gain insight into whether the current distribution within the Oregon Coast Range has resulted from a lack of suitable habitat or from dispersal limitations, we measured growth of *U. longissima* transplants placed in four habitats. We determined transplant study site locations and habitats through an accompanying study that identified significant *U. longissima* habitat characteristics, based on the present distribution of the species, and used predictive modeling to identify areas of apparently suitable habitat within the study area. We distributed transplants among 12 sites, comprised of three replicates of the four habitats, placing 90 transplants in each habitat (n=360). Growth was measured as changes in biomass and length after one year. Transplants grew in all habitats, particularly in sites where habitat was predicted to be least suitable for *U. longissima*. Transplants in those sites had mean biomass increases that were 2.7 to 4.6 times greater than those of transplants placed in the other three habitats. Increases in length were also greatest in sites where habitat was predicted to be least suitable. The fact that the transplants grew well in all habitats, and actually thrived in sites where habitat was predicted to be least suitable, indicates that dispersal limitations may play a more significant role than the availability of suitable habitat in determining the distribution of *U. longissima* in the Oregon Coast Range. These findings underscore the importance of green tree retention during timber harvests. Trees containing *U. longissima* should be retained so that they may inoculate the regenerating stand with *U. longissima* fragments. It is also

recommended that stands harboring significant populations of *U. longissima* (typically old stands) be preserved as source locations of this dispersal-limited species.

## INTRODUCTION

The epiphytic lichen *Usnea longissima* Ach. was once a fairly common, nearly circumboreal species (Ahlner 1948, Ahti 1977). During the last several decades, the species has declined significantly throughout its range, particularly in Scandinavian and Eastern European forests (Esseen et al. 1981, Pišút 1993, Thor 1999). The northern Pacific coast of North America remains a relative stronghold for the species, where its range extends from Northern California to Alaska (Noble 1982). In Oregon, *U. longissima* occurs throughout the Coastal and western Cascade mountain ranges (McCune and Geiser 1997). In most of the U.S. Pacific Northwest (PNW), including our study area, it is currently listed as a Survey and Manage, Category F species under the Northwest Forest Plan (USDA and USDI 2000, 2001). As such, land managers are required to conduct strategic surveys to determine whether *U. longissima* meets basic Survey and Manage criteria. Known *U. longissima* populations receive no protection under this classification. Relatively little is known about the habitat associations and dispersal limitations of *U. longissima* in the PNW, making it difficult for land managers to make specific recommendations regarding its management in Coast Range forests.

*Usnea longissima* has a limited and relatively patchy distribution across the Oregon Coast Range, at both stand and landscape levels. It is not clear whether the current patchy distribution has resulted from dispersal limitations inherent to the species, a lack of suitable habitat, or both factors. *Usnea longissima* reproduces

primarily through fragmentation of relatively large pieces of thalli. In the PNW, the species is non-isidiate, rarely produces soredia, and almost never produces apothecia (Noble 1982, McCune and Geiser 1997, Keon *in review*). Because of these inherent reproductive limitations, and because the majority of *U. longissima* fragments do not travel far (i.e., typically < 5 m) from their source locations (Esseen et al. 1981, Esseen 1985), the species is thought to be dispersal-limited.

Forests in the PNW have been highly fragmented by intensive timber harvesting on both private and public land (Harris 1984, Ripple 1994, Spies et al. 1994). Although forest management practices in the PNW have changed significantly in the past decade (Swanson and Franklin 1991, USDA and USDI 2000, Franklin et al. 1997), the Oregon Coast Range landscape remains a patchwork of varying forest stand structures and ages, dominated by relatively young forests. It is possible that timber harvesting has created a lack of suitable habitat for *Usnea longissima*; however, its habitat associations in the PNW are not well known and, thus, the availability of suitable habitat is uncertain. These issues only recently have been studied in the Oregon Coast Range (Keon 2001, Keon and Muir *in prep.*).

Several recent studies have examined macrolichen growth dynamics using transplant experiments (e.g., Stone 1986, Denison 1988, Boucher and Nash 1990, Sillett 1994, Muir et al. 1997, Renhorn et al. 1997). However, only two such transplant studies have measured biomass growth of *Usnea longissima* thalli (Renhorn and Esseen 1995, McCune et al. 1996). These studies were designed to assess growth rates of *U. longissima* transplants in comparison to other lichen species, and to test innovative transplant construction and placement techniques, but growth in relationship to

environment was not a focus. In contrast, the study we report here was focused on comparing growth rates of *U. longissima* transplants placed in a variety of habitat conditions in the Oregon Coast Range. Comparisons of transplant growth rates across the contrasting habitats allowed us to make inferences about the dependence of *U. longissima* growth on habitat conditions. This, in turn, allowed us to assess the probable roles of dispersal limitations versus habitat limitations in affecting the distribution of *U. longissima* within the study area.

## METHODS

Study sites

The study sites were located approximately 30 km WSW of the city of Corvallis, Oregon in a 350 $km^2$ area of the Coast Range (44°17'N to 44°29'N, 123°35'W to 123°47'W). Sites were established primarily in the Upper and Lower Alsea River watersheds (Fig. 3.1). This area is a multi-aged matrix of private land and federally-owned land managed by the US Forest Service (USFS) and Bureau of Land Management (BLM). Study sites were established primarily on land managed by the USFS and BLM, although a few sites were also established on private land.

We established all study sites within the *Tsuga heterophylla* (Raf.) Sarg. Zone of the Coast Range (Franklin and Dyrness 1973). Within the study area, nearly all forest stands are dominated by *Pseudotsuga menziesii* (Mirbel) Franco, although late-successional forests occasionally contain a mix of co-dominant *P. menziesii* and *T. heterophylla*. *Thuja plicata* Donn. and *Taxus brevifolia* Nutt. are also occasionally present in these stands. Numerous harvested areas have been replanted with

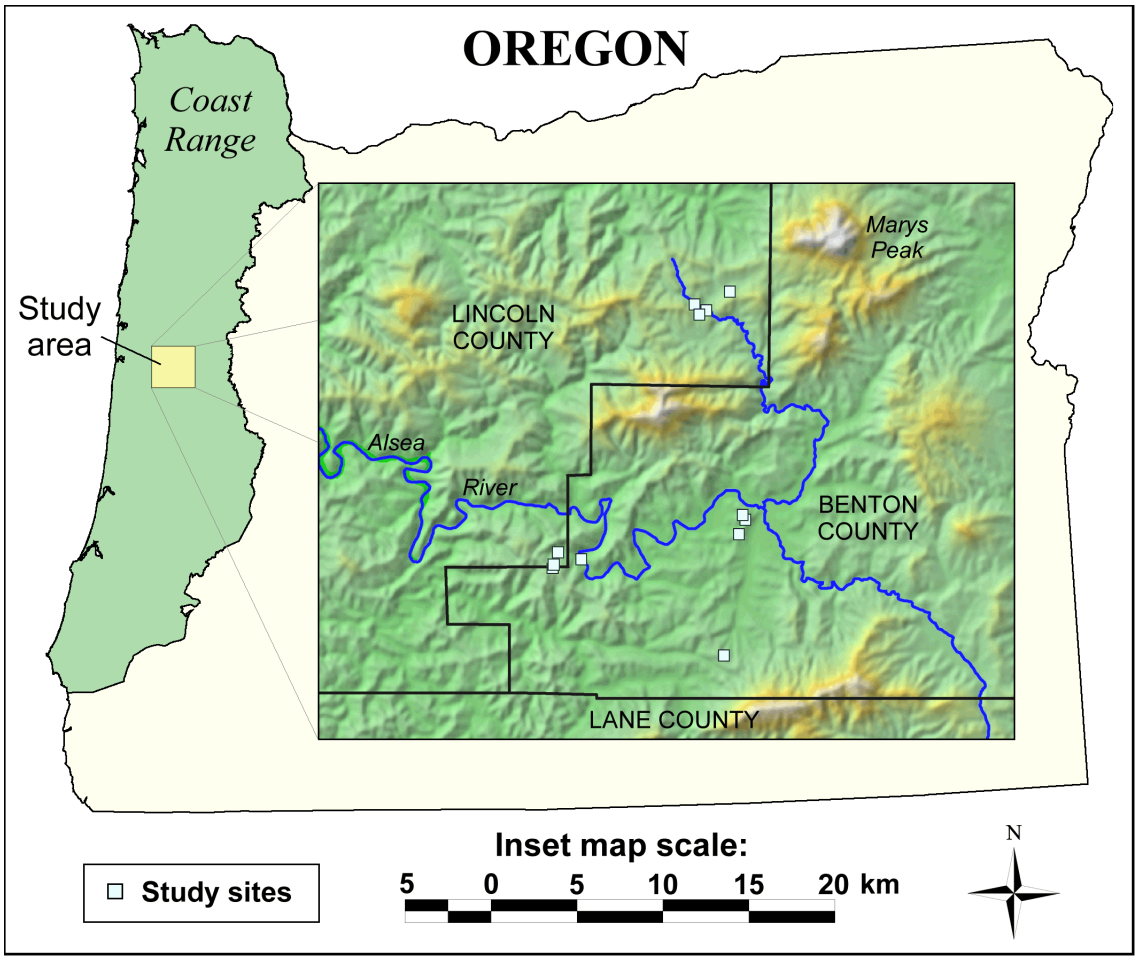


**Figure 3.1** *Usnea longissima* transplant study site locations.

*P. menziesii*. Intermediate and understory stand levels often contain one or more of the following trees and shrubs: *Acer macrophyllum* Pursh, *Acer circinatum* Pursh, *Corylus cornuta* Marsh var. *californica* (DC.) Sharp, *Alnus rubra* Bong., *Rubus spectabilis* Pursh, and *Vaccinium parvifolium* Smith.

Summers are warm and dry with virtually no precipitation. Winters are cool and wet with frequent fog sweeping across the landscape. Annual rainfall in the study area ranges from approximately 180 cm to over 400 cm (Daly et al. 1994). Elevations within the study area range from 25-750 m. Transplant study site elevations ranged from 35-590 m.

Transplant construction and placement

We collected *Usnea longissima* thalli from three distinct Coast Range source locations within the study area. Each source location supported a large population of the species and had similar habitat characteristics (i.e., stand age, aspect, distance from water). We assembled thalli into transplants in the laboratory, following the general method outlined by McCune et al. (1996). The thalli were air-dried, cut into 15.0 cm strands, and weighed to the nearest mg. The mean initial weight of the thalli was 0.244 g, standard deviation = 0.053, range 0.120 to 0.524 g. After the weights were recorded, each strand was attached to an 8 cm doubled-over nylon monofilament with a loop tied at one end, using a dab of silicone sealant (Fig. 3.2). After assembly, each transplant was weighed with its apparatus (monofilament and silicone) intact. As each transplant was assembled it was given a unique number that identified the study site, thallus source location, and individual (e.g., 3-2-142), and was attached to a releaseable,

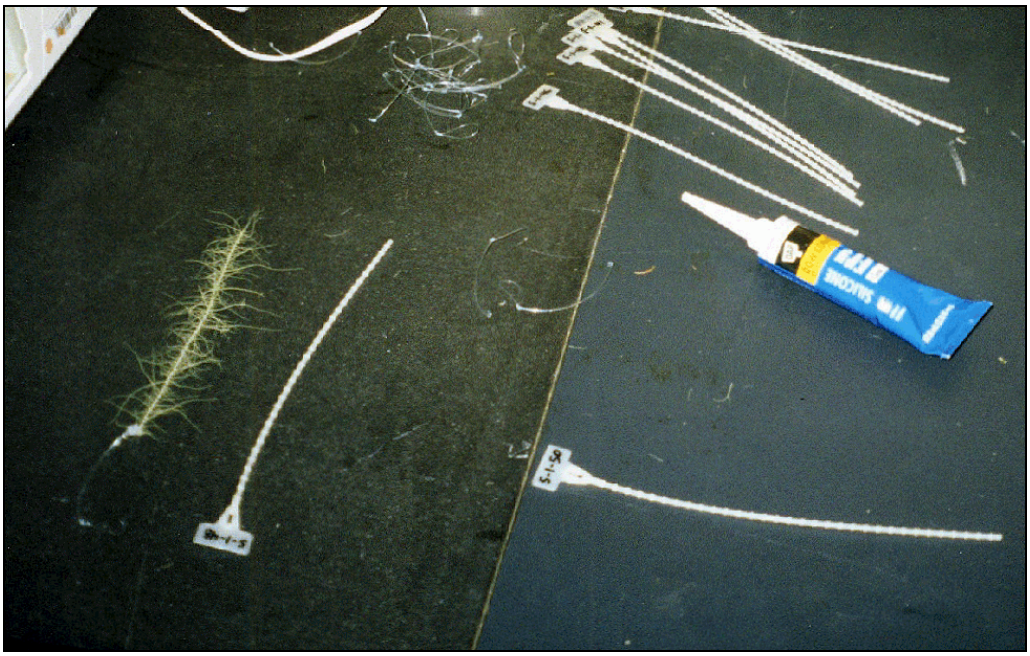

**Figure 3.2** Materials used in transplant construction. Each transplant consisted of a piece of monofilament attached to a 15 cm section of thallus with a dab of silicone sealant.

**Figure 3.3** *Usnea longissima* transplants attached to PVC crossbars with releaseable zip ties.

UV-resistant nylon zip tie (All-States, Inc., Chicago, IL) through the monofilament loop (Fig. 3.3). Identification numbers were written on tags that were built-in to the zip ties, using a permanent nylon marking pen. To correct for moisture present in the air-dried thalli, we weighed an additional set of *U. longissima* thalli from each source location using the sacrificial method (after McCune et al. 1996). Air-dry weights of sacrificial thalli were measured at the same time as the transplant thalli. Sacrificial thalli were then oven-dried at 60º C for 24 h, and the oven-dry weights measured and recorded.

Tripod racks supported the transplants at each study site. We constructed each rack from three 5 cm x 5 cm x 3 m pieces of lumber lashed together at one end with 3.2 mm nylon cord. The rack legs were spread apart at the study sites and sunk into the ground to form a stable tripod. We constructed rack crossbars from 2.5 cm inside-diameter dark gray schedule 80 PVC pipe, cut into 2 m sections. Six crossbars were attached to each tripod rack, using 3.2 mm nylon cord, to provide a surface from which the transplants could be hung (Fig. 3.4). We assumed that the pendant transplants would wrap around the crossbars in windy conditions, so, to avoid any possibility of the transplants attaching to the crossbar surface, we selected crossbars of PVC over crossbars made of wood. We chose dark gray PVC to minimize visibility, since the possibility of human disturbance was a concern.

We attached 30 transplants to each rack (five per crossbar), using releaseable zip ties (Fig. 3.4). This configuration allowed adequate spacing between transplants, so that they would not become entangled with each other or wrapped around the rack legs. To minimize any possible microclimatic effects, transplants were not enclosed within any apparatus (Renhorn and Esseen 1995). To minimize the possibility that differential

**Figure 3.4** Transplants following assembly and assignment of an indentification number and releaseable zip tie.

**Figure 3.5** Tripod rack in place at a study site. Five transplants are suspended from each of the six PVC crossbars.

growth attributable to source population vigor might be confounded with habitat effects, we placed 10 thalli from each of the three source locations on each rack.

We placed 12 racks across the study sites, one in each of three replicates of four habitats, resulting in 90 transplants per habitat (n=360 individual transplants). The four habitats were where the species was: (1) present and abundant (control), (2) present but sparse, (3) absent and habitat was predicted to be least suitable, and (4) absent but habitat was predicted to be suitable. We derived predicted suitability of habitats from habitat data collected from sites of *Usnea longissima* presence and absence during the summers of 1998 and 1999. We analyzed the habitat data using discriminant analysis to identify the variables that best distinguished sites of presence from sites of absence. These variables served as the strongest predictors of apparently suitable habitat (Keon and Muir *in prep.*). (We refer to "apparently suitable habitat" or "habitat predicted to be suitable" because we recognize that sites where *U. longissima* does not occur may, in fact, be suitable habitat, but lack the species because of dispersal limitations or other factors. Our initial assessments of habitat suitability were based simply on the empirical data from sites with and without the species.) We used results of the discriminant analysis to determine habitat characteristics of the transplant study site locations. Sites where habitat was predicted to be most suitable had the general characteristics of north- to northeast-facing slopes and older stand ages (> 120 yr). Sites where habitat was predicted to be least suitable had the general characteristics of south- to southwest-facing slopes in clear cuts or very young stands (< 10 yr) (Table 3.1).

**Table 3.1** Summary of environmental site characteristics, by habitat.

| Habitat[1] | Site no. | Elevation (m) | Slope (deg.) | Aspect (°E of N) | Topo pos.[2] | Stand age (yr) | Con BA[3] ($m^2$/ha) | Hwd BA[4] ($m^2$/ha) |
|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 215 | 39 | 95 | 4 | 220 | 155 | 18 |
| 1 | 5 | 390 | 27 | 35 | 4 | 140 | 64 | 55 |
| 1 | 9 | 370 | 30 | 40 | 3 | 150 | 110 | 0 |
| 2 | 2 | 230 | 12 | 170 | 2 | 50 | 92 | 18 |
| 2 | 6 | 250 | 21 | 25 | 3 | 90 | 110 | 5 |
| 2 | 10 | 370 | 24 | 30 | 4 | 70 | 101 | 0 |
| 3 | 3 | 35 | 27 | 260 | 3 | 3 | 0 | 0 |
| 3 | 7 | 445 | 30 | 300 | 4 | 5 | 0 | 0 |
| 3 | 11 | 500 | 12 | 310 | 5 | 0 | 0 | 0 |
| 4 | 4 | 590 | 3 | 10 | 5 | 135 | 120 | 0 |
| 4 | 8 | 165 | 21 | 30 | 2 | 120 | 64 | 27 |
| 4 | 12 | 120 | 48 | 110 | 3 | 160 | 110 | 0 |

[1]Habitat: 1 = *Usnea longissima* abundant (control); 2 = *U. longissima* sparse; 3 = predicted to be least suitable, *U. longissima* absent; 4 = predicted to be suitable, *U. longissima* absent.
[2]Topographic position: 1 = bottomland; 2 = lower slope; 3 = mid-slope; 4 = upper slope; 5 = ridge.
[3]Conifer basal area.
[4]Hardwood basal area.

We placed transplants in the study sites on 11 December 1998 and retrieved them on 12 December 1999. We collected fresh *Usnea longissima* thalli from the source locations at the time of transplant retrieval. Transplants and fresh thalli were air-dried for 24 h in the laboratory and weighed to the nearest mg. Using the sacrificial method, the fresh thalli were then oven-dried at 60ºC for 24 h and weighed to the nearest mg, to provide a correction factor for moisture present in the air-dried thalli (McCune et al. 1996). This method preserved the transplants for possible future use. Transplant thalli were also measured lengthwise along their main axis, to the nearest mm, to provide an additional measure of growth.

Data analysis

We calculated correction factors from 1998 and 1999 air-dry and oven-dry reference sample data, to correct for moisture content of the air-dried transplants. The appropriate correction factors were applied to the 1998 and 1999 air-dry transplant growth data, and growth was calculated as percent change in biomass (after McCune et al. 1996). Transplants were removed from the data set if their growth was > 2.0 standard deviations (SD) below the mean growth of all transplants (almost always the result of breakage). Transplants that simply lost biomass due to necrosis were retained in the analysis unless they met the 2.0 SD cutoff criterion. Since several studies have determined that epiphytic lichen transplants can grow quite rapidly (e.g., Renhorn and Esseen 1995, McCune et al. 1996, Muir et al. 1997, Renhorn et al. 1997), we decided to retain any transplants that experienced growth > 2.0 SD above the mean growth for all

transplants. Differences between the final measurements of transplant thalli length and the starting length of 15.0 cm were also calculated.

We used the SPSS software package for all statistical analyses (SPSS 1998). We calculated descriptive statistics, summarizing biomass and length growth data. Transplant breakage (defined as transplants that were either completely missing or whose growth was > 2.0 SD below the mean growth of all transplants) was analyzed with a chi-squared test to determine whether the number of broken versus intact thalli was independent of habitat. Because individual transplants were not independent within each site (transplants were all placed on a single rack at each site), we used a nested ANOVA design to test for differences in transplant growth among the four habitats (thalli were nested within sites within habitats). We used Satterthwaite's approximation to calculate degrees of freedom in this mixed model design, where "site" was treated as a random effect, and "habitat" was treated as a fixed effect (Satterthwaite 1946). This analysis was performed using the GLM General Factorial function within SPSS. Since an equivalent number of thalli from each *Usnea longissima* source location were placed on each rack during plot establishment, potential source material effects were controlled for in the analysis.

## RESULTS

### Attrition of thalli

There was 41% attrition of transplants due to breakage. The study began with 360 transplants, and 212 remained after one year in the study sites. In most cases of breakage (127 of 148), the thallus was completely missing, while the transplant

apparatus remained on the crossbar. The apparatus allowed identification of each missing thallus. The remainder of the thalli classified as missing (21 of 148) were removed from the data set because their growth after one year was > 2.0 SD below the mean growth of all thalli. These thalli were partially broken and most lost over half of their initial biomass due to breakage; only one of these thalli experienced a loss in biomass that was close to the 2.0 SD cutoff criterion. Although other thalli also lost weight, their loss apparently resulted from necrosis as opposed to breakage. All thalli that lost weight simply due to necrosis were ultimately retained in the analysis since none of them had growth rates > 2.0 SD below the mean growth of all thalli. (Hereafter, thalli that weren't missing or otherwise eliminated from the data set are referred to as "surviving transplants.")

Transplant breakage was not independent of habitat ($p < 0.001$, $\chi^2 = 68.42$ with 6 *df*). Breakage was much more common in relatively open sites where habitat was predicted to be least suitable (60% of transplants were missing from these recently clear cut sites). Transplant racks in the other three habitats were located in forest understories, and transplants in these sites suffered 30%-39% attrition (Table 3.2).

Overall growth rates

Mean transplant growth (percent change in biomass per year) differed among the four habitats, and among sites within each habitat (Table 3.3; ANOVA: $p = 0.006$). Although positive in all habitats, mean growth was substantially higher in sites where habitat conditions were predicted to be least suitable for *Usnea longissima.* Mean biomass growth in these sites was 2.7 to 4.6 times greater than in sites located in the

**Table 3.2** Summary of growth results by habitat and transplant source location. Growth values represent percent change in biomass or length over one yr for surviving thalli. Values within the "Surviving transplants" column exclude both missing individuals and individuals whose biomass growth was > 2.0 SD below the mean growth of all transplants.

| Category | Surviving transplants | Survivors with positive growth | Change in biomass (%) | | | Change in length (cm) | | |
|---|---|---|---|---|---|---|---|---|
| | | | Mean ± SE | Min-max | 75th percentile | Mean ± SE | Min-max | 75th percentile |
| Habitat[1] | | | | | | | | |
| 1 | 55/90 (61.1%) | 53/55 (96.4%) | 5.62 ± 0.48 | -1.95 – 11.88 | 8.18 | 3.5 ± 0.23 | 0.5 – 9.2 | 4.6 |
| 2 | 58/90 (64.4%) | 57/58 (98.3%) | 8.85 ± 0.70 | -5.35 – 23.94 | 11.62 | 4.4 ± 0.27 | 0.7 – 9.5 | 5.4 |
| 3 | 36/90 (40.0%) | 36/36 (100%) | 23.66 ± 1.68 | 0.91 – 39.50 | 31.40 | 9.1 ± 0.73 | 0.2 – 18.4 | 12.3 |
| 4 | 63/90 (70.0%) | 45/63 (71.4%) | 5.12 ± 0.78 | -4.09 – 16.20 | 11.04 | 3.5 ± 0.27 | 0.7 – 10.8 | 4.5 |
| Source | | | | | | | | |
| A | 65/120 (54.2%) | 57/65 (87.7%) | 11.66 ± 1.24 | -4.10 – 39.50 | 13.68 | 6.0 ± 0.46 | 1.0 – 18.4 | 7.6 |
| B | 60/120 (50.0%) | 56/60 (93.3%) | 7.53 ± 0.97 | -5.35 – 34.82 | 10.64 | 3.8 ± 0.32 | 0.5 – 14.7 | 5.0 |
| C | 87/120 (72.5%) | 78/87 (89.6%) | 9.05 ± 0.99 | -4.09 – 36.84 | 11.10 | 4.2 ± 0.33 | 0.2 – 13.5 | 4.9 |
| Overall | 212/360 (58.9%) | 191/360 (53.1%) | 9.42 ± 0.63 | -5.35 – 39.50 | 12.12 | 4.7 ± 0.22 | 0.2 – 18.4 | 5.7 |

[1]Habitat: 1 = *U. longissima* abundant (control); 2 = *U. longissima* sparse; 3 = predicted to be least suitable, *U. longissima* absent; 4 = predicted to be suitable, *U. longissima* absent.

**Table 3.3** Test of differences in transplant growth rates (as change in biomass) among habitats, using nested analysis of variance (ANOVA).

| ***Source*** | ***df*** | **SS** | **MS** | ***F*** | ***p*** |
|---|---|---|---|---|---|
| ***Between habitats*** | | | | | |
| Habitat | 3 | 6302.4 | 2100.8 | 8.756 | 0.006 |
| Error (sites within habitat)[1] | 8.127 | 1950.0 | 239.93 | | |
| ***Within habitats*** | | | | | |
| Sites within habitat | 8 | 2026.8 | 253.34 | 8.113 | < 0.001 |
| Error (transplants within sites) | 200 | 6245.8 | 31.229 | | |

[1]*Between habitats* Error degrees of freedom were calculated using Satterthwaite's approximation.

other three habitats (Table 3.2, Fig. 3.5). Excluding outliers, biomass growth of the surviving transplants ranged from -5.4% to 39.5% after one yr. Overall, 90.0% (191 of 212) of the surviving transplants increased in weight while 10.0% decreased (Table 3.2).

No surviving transplants lost weight in sites where habitat was predicted to be least suitable, 1.7% lost weight in control sites, and 3.6% lost weight in sites with some *Usnea longissima* present (Table 3.2). The greatest weight loss occurred in sites where habitat was predicted to be suitable but no *U. longissima* was present, where 28.6% of the transplants lost weight. Transplants located in these sites typically lost only 1-2% of their initial biomass, although a few outliers lost 7-9% of their initial biomass and were removed, since their biomass loss was > 2.0 SD below the mean growth of all thalli.

Changes in length provided a striking visual comparison of growth (Fig. 3.6). Although not as accurate a measure of growth as change in biomass, the length data provided additional evidence that transplants located in sites where habitat was predicted to be least suitable (clear cuts) experienced much higher rates of growth than transplants in the other three habitats. Transplants located in clear cuts had a mean increase in length that was 2.1-2.6 times greater than means for transplants in the other three habitats (Table 3.2). One particular transplant, located in a clear cut, more than doubled in length, adding 18.4 cm to the original 15.0 cm thallus. Among the surviving transplants, 11.3% (24) elongated primarily through growth of a side branch, and the remaining 88.7% (188) grew primarily along their main axes, elongating through intercalary growth.

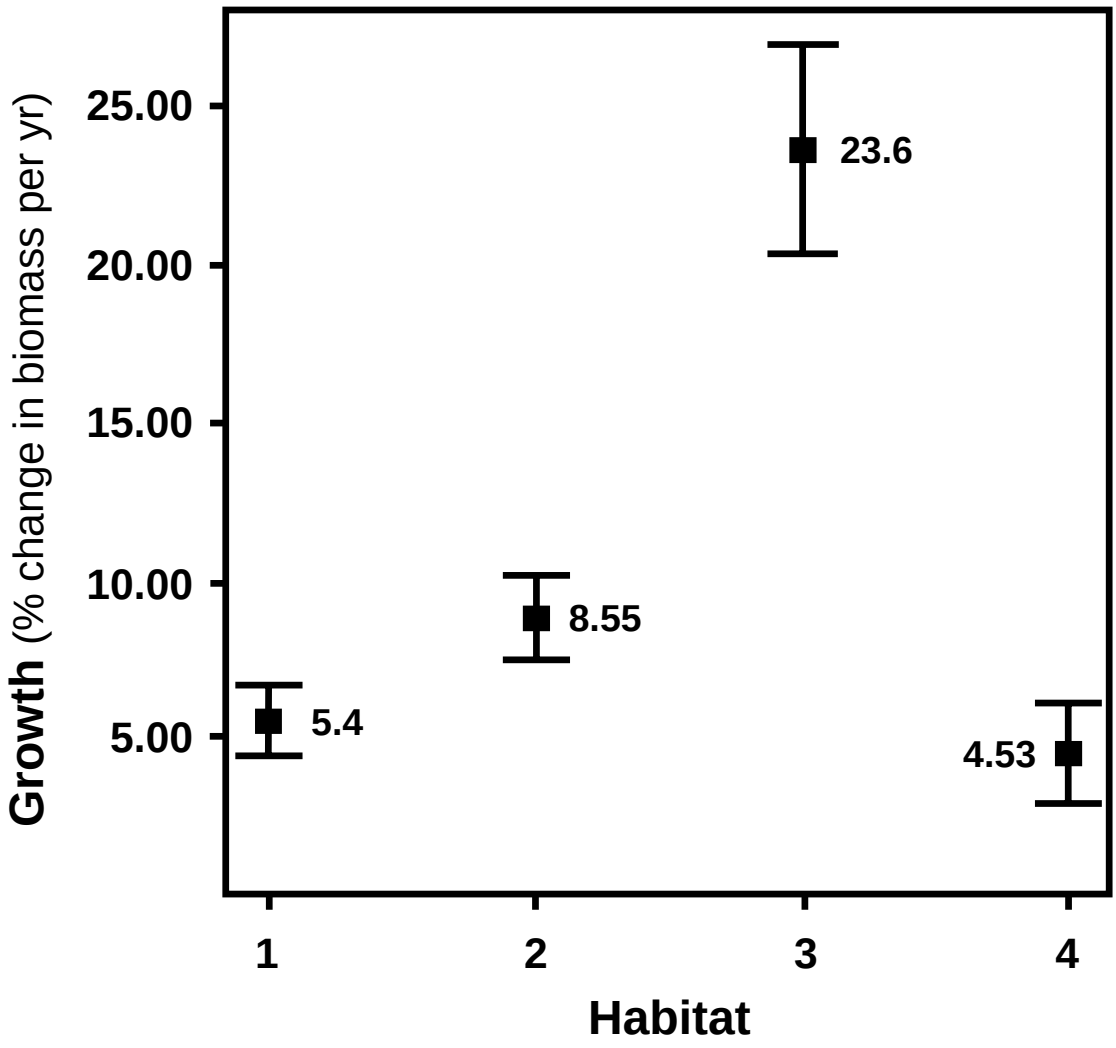


**Figure 3.6** Mean growth (percent change in biomass per year) of *Usnea longissima* transplants, by habitat. Error bars indicate ± 2.0 standard errors. Habitat: 1 = *U. longissima* present and abundant (control), 2 = some *U. longissima* present, 3 = predicted to be least suitable and no *U. longissima* present, 4 = predicted to be suitable but no *U. longissima* present.

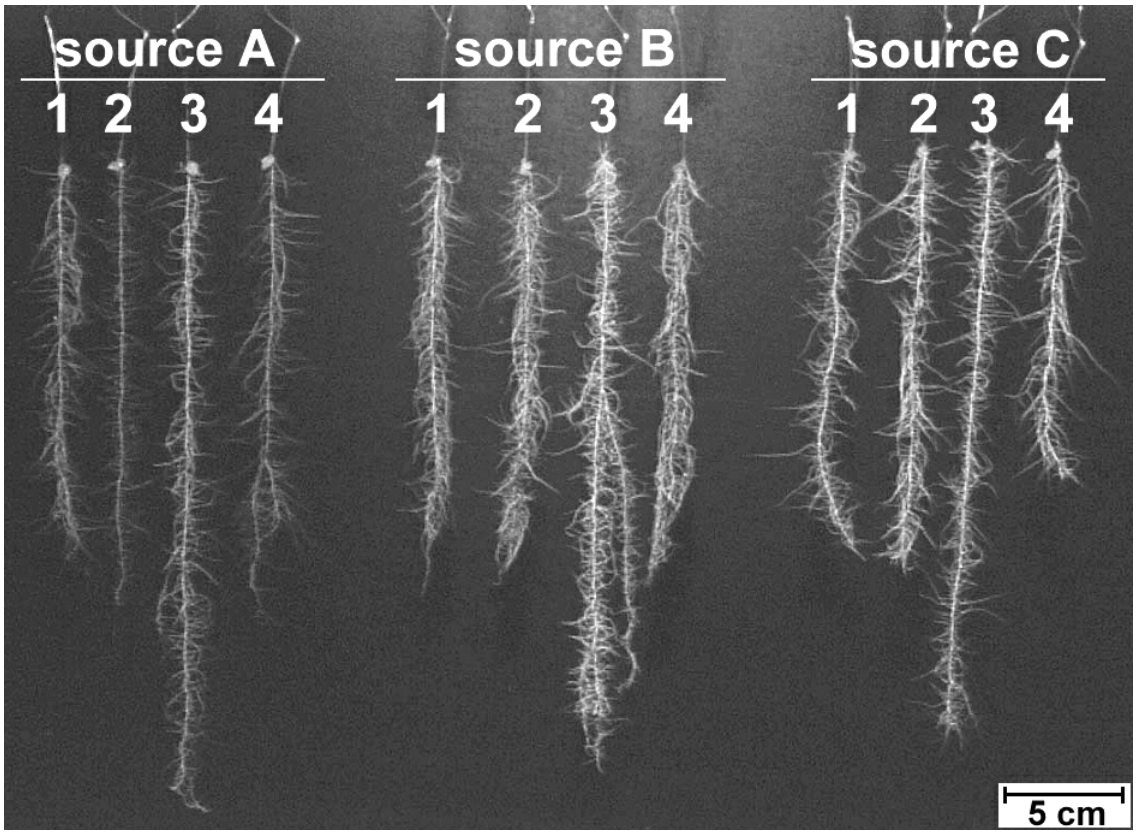


**Figure 3.7** *Usnea longissima* transplant length after one year. One representative transplant from each rack is displayed. The transplants are grouped by source material location, and three replicates from each of the four habitats are displayed. Habitat: 1 = *U. longissima* abundant (control); 2 = *U. longissima* sparse; 3 = predicted to be least suitable, *U. longissima* absent; 4 = predicted to be suitable, *U. longissima* absent.

Surviving transplants that were assembled from source location A material grew more rapidly (in both length and biomass) than transplants assembled from other source location material (Table 3.2). However, survivorship of source location A transplants was not greater than that of transplants assembled from other source location material.

## DISCUSSION

Growth dynamics by habitat

Some transplant breakage was expected due to the pendant nature of the transplants, and the results of prior transplant experiments (e.g., McCune et al. 1996, Muir et al. 1997). We began with a large number of transplants (n=360) to mitigate expected attrition. However, we did not anticipate the amount of breakage that occurred in sites where habitat was predicted to be least suitable. Since these sites were located in clearcuts and very young stands (< 10 yr), the greater amount of breakage in this site type probably resulted from increased exposure to wind. Transplants in the other three habitats were located in relatively protected forest understories. It is also possible that some breakage in all four habitats resulted from herbivory. Certain ungulates, small mammals, and birds utilize fragments of *Usnea* spp. in the PNW for food or nesting material (Cowan 1936, Sharnoff 1994). However, as broken transplants were often found on the ground beneath the racks, we suspect that most transplant breakage was caused by wind or other exposure to the elements (e.g., ice buildup, falling branches, heavy rain).

Overall, our results were comparable to those of Renhorn and Esseen (1995), whose *Usnea longissima* transplants had a mean annual biomass increase of 9.2%

(minimum 2.9%, maximum 18.0%), and also to those of McCune et al. (1996), who found mean annual biomass increases of 6%-30% in *U. longissima* transplants placed in various habitats in western Oregon. The more rapid growth experienced by transplants assembled from source location A material suggests that it was important to use transplant material from a variety of source locations, and certainly important to avoid confounding source location with habitat. It is not clear whether the different growth rates among material collected from the three source locations resulted from genetic differences or environmental conditioning.

We expected the transplants to grow fastest in control sites (where habitat was predicted to be suitable, and *Usnea longissima* was abundant), and most slowly in sites where habitat was predicted to be least suitable (clear cuts and very young stands on SW-facing slopes). However, in contrast with expectation, transplants in the young, open stands grew much faster than those in the other site types, and probably benefitted from increased exposure to light. This hypothesis is consistent with Gauslaa et al. (1998), who stated that the position of *U. longissima* thalli on *Picea abies* (L.) Karst. branches in E. Norway, along with the higher frequency of *U. longissima* in stands with living branches at ground level, suggests a high requirement for light. Similarly, Gauslaa and Solhaug (1996) found that *U. longissima* thalli in Norway tolerated more intense light than other old forest lichens, such as *Lobaria pulmonaria* (L.) Hoffm. However, greater exposure to light may not benefit all epiphytic macrolichens, and a given species may respond differently to light under different conditions. For example, while Gauslaa and Solhaug (1996) found that *L. pulmonaria* was less tolerant of high light intensities in the laboratory, Renhorn et al. (1997) concluded that faster growth in

*L. pulmonaria* transplants near a forest edge, compared to the forest interior, resulted from the higher amount of light received near the forest edge. In another example, Sillett (1994) transplanted two cyanobacterial lichen species (*Lobaria oregana* (Tuck.) Müll. Arg. and *Pseudocyphellaria rainierensis* Imshaug) from the interior of an old-growth forest in the Oregon Cascades to its edge, and found a reduction in growth in both species in the edge environment. However, other transplant studies suggest that *L. oregana* grows more rapidly in open than in closed-canopy sites (Muir et al., unpublished data). Although *U. longissima* transplants in our study experienced much higher growth in open sites than in closed-canopy sites, they also suffered significantly higher attrition in open sites (Table 3.2). Conditions that give lichens increased exposure to radiation may also result in increases in physical damage (Esseen and Renhorn 1998).

We do not know why such a relatively large percentage of surviving transplants lost weight in sites where habitat was predicted to be suitable but no *Usnea longissima* was present. While mean growth of transplants in this habitat was positive (5.12%), it was lower here than in the other three habitats. Slower growth was concentrated in one site, where mean growth was -1.32%; mean growth at the other two sites in this habitat was 8.68% and 9.08%. Site characteristics at all sites within this habitat were very similar to site characteristics in control sites, where *U. longissima* was abundant (Table 3.1). It may be that one or more unmeasured environmental variables caused transplants to lose weight in the site where mean growth was -1.32%. The differences among sites in mean growth are not attributable to differences in transplant source populations, as the design balanced source material across sites within habitats.

Dispersal limitations

*Usnea longissima* thalli are prone to fragmentation since they rarely possess holdfasts and often develop weak spots along main axes where they are draped across branches (Esseen 1985, Gauslaa 1997). The long, relatively unbranched thalli contain abundant, fine fibrils that are particularly well-suited for gripping and becoming entangled among small twigs and conifer needles, especially when the thalli are wet. These characteristics allow *U. longissima* fragments to attach easily when they are dispersed to a new substrate. However, since *U. longissima* disperses primarily through fragmentation of relatively large pieces of thalli (Esseen et al. 1981, Esseen 1985), it is presumed to be generally ineffective at long distance dispersal. *Usnea longissima* thalli in the PNW and British Columbia are non-isidiate and rarely produce soredia or apothecia (Noble 1982, McCune and Geiser 1997, Keon *in review*), further limiting the species' dispersal potential. Because of these limitations, *U. longissima* is considered to be dispersal limited at both stand and landscape levels across the PNW (McCune and Geiser 1997, Sillett et al. 2000). *Usnea longissima* often produces abundant soredia and isidia in Sweden and Norway; therefore, dispersal may not be a limiting factor in those locations (Gauslaa 1997, Gauslaa et al. 1998).

Some alectorioid lichens produce large fragments that disperse shorter distances than smaller propagules (e.g., soredia, isidia) produced by other species (Esseen et al. 1996). *Usnea longissima* fragments are often quite large; fragments collected by Esseen et al. (1981) were typically 10-40 cm long, and Esseen (1985) found that 95.6% of 2597 fragments collected over a 3-year period in Sweden were > 2 cm long. These fragments usually disperse either within their source tree crown, or within the crown of

an adjacent tree, or fall to the understory or ground (Esseen et al. 1981, Esseen 1985). While Esseen et al. (1981) observed that most *U. longissima* thalli at study sites in eastern central Sweden were deposited less than 3 m from their source trees, no published studies have been designed to specifically examine dispersal distances of *U. longissima* fragments. However, such studies have been conducted with other alectorioid species. Dettki (1998) found that 94% of 2214 *Alectoria sarmentosa* (Ach.) Ach. and *Bryoria* spp. fragments were dispersed less than 100 m from their source locations. Fragments of these two alectorioid species are typically smaller than *U. longissima* fragments, and are therefore able to disperse across greater distances (Esseen 1985).

Several studies have determined that *Usnea longissima* occurs more frequently, and is more abundant, in relatively undisturbed sites that possess one or more of these habitat characteristics: north- to east-facing slopes, older stand age, and higher relative humidity or annual rainfall (Esseen et al. 1981, Tønsberg et al. 1996, Halonen 1997, Rolstad and Rolstad 1999, Keon 2001, Keon and Muir *in prep.*). These observations may lead one to assume that habitat characteristics are most important in determining where *U. longissima* will occur. However, our results indicate that dispersal may play a more important role than availability of suitable habitat in limiting the distribution of *U. longissima* in the Oregon Coast Range, as the species grew relatively well over a wide range of habitat conditions. Indeed, transplants placed in sites where habitat characteristics were predicted to be least suitable for the species (based on empirical observations of current occurrence; see Methods) had much higher mean increases in biomass and length than transplants placed in the other habitats. Clearly, *U. longissima*

can grow well in a diversity of habitats, even in clear cuts on SW-facing slopes in the Oregon Coast Range. Dispersal limitations have also been determined to be the most likely cause of the sensitivity of other alectorioid species to timber harvesting (Esseen et al. 1996, Dettki 1998).

In light of these results, and the fact that *Usnea longissima* does seem to occur more frequently in relatively old, moist stands on cool aspects, it is likely that many populations are remnants that have persisted over time. Other researchers (e.g., Gauslaa et al. 1992, Tønsberg et al. 1996, Doell and Wright 2000) have also discussed this possibility. Older forests are most often relatively undisturbed, and can act as refugia that allow the dispersal-limited species to establish substantial populations over time.

Management implications

Dettki's (1998) results implied that young forests bordering old-growth stands containing alectorioid lichens would most likely experience a greater influx of dispersed fragments and higher colonization rates than young forests bordering lichen-poor second growth forests. Indeed, Tønsberg et al. (1996) found *Usnea longissima* on young trees only in locations where those trees bordered older stands harboring large populations of *U. longissima*. We expect the same dynamic to occur in highly fragmented PNW forests, where old growth stands harboring significant populations of *U. longissima* often border much younger stands. Our results also directly support Dettki's (1998) statement that colonization of second-growth forests by alectorioid lichen fragments is likely to be more dependent upon the position of the stand in relation to lichen-rich older stands than on the specific biotic and abiotic habitat

characteristics of the younger stand. *Usnea longissima* appears to grow well in very young stands, provided it is able to disperse to them.

Decades of forest management in the Oregon Coast Range have resulted in a patchwork of harvested and intact stands, creating large areas of young forests that are often far from potential sources of *Usnea longissima*. Since dispersal appears to be the main factor limiting the distribution of *U. longissima*, and its largest populations tend to occur in older stands within the Oregon Coast Range (Keon and Muir *in prep.*), it is important that older stands harboring the species be preserved to provide source populations of the species. These source populations are important for both within-stand and between-stand dispersal. When *U. longissima* fragments are dispersed from the crowns of trees in older stands, they often depart the source tree at a height of 30 m or more, increasing their chances of dispersal to a greater distance. As these older stands are harvested, sources of propagules are depleted, and the chance of establishment of new populations is reduced.

The long-term persistence of *Usnea longissima* across the landscape will also be enhanced if dispersal from within clear cuts and regenerating stands is possible, in addition to dispersal from intact, older stands. For this reason, green tree retention during timber harvests is particularly important, as remnant trees containing *U. longissima* can distribute propagules across the regenerating stand. Remnant trees (both conifers and hardwoods) function as sources of inoculum, from which epiphytic lichen propagules can disperse (Peck and McCune 1997). Additionally, remnant trees function as important “hotspots” of lichen diversity and abundance (Neitlich and McCune 1997, Rambo and Muir 1998). Green-tree retention is currently required during timber

harvest on federal lands within the range of the Northern Spotted Owl in the PNW (USDA and USDI 2001). Such retention will benefit *U. longissima* as well as other aspects of these forested ecosystems.

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# Chapter 4

## Fertile *Usnea longissima* in the Oregon Coast Range

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## ABSTRACT

Apothecia from *Usnea longissima* thalli collected in the Oregon Coast Range are described. Fertile *U. longissima* specimens seldom have been observed and rarely are documented in the literature. A brief history of accounts in the literature is given, and possible reasons for the infrequent occurrence of apothecia are discussed. This is the first published account of fertile *U. longissima* specimens in the U.S. Pacific Northwest.

## INTRODUCTION

The epiphytic lichen *Usnea longissima* was once a fairly common, nearly circumboreal species (Ahlner 1948, Ahti 1977). During the last several decades the species has declined significantly throughout its range, particularly in Scandinavian and Eastern European forests (Esseen 1981, Pišút 1993, Thor 1999). The northern Pacific coast of North America remains a relative stronghold for the species, where its range extends from Northern California to Alaska (McCune and Geiser 1997). *Usnea longissima* occurs throughout the Coastal and western Cascade mountain ranges of Oregon.

## HISTORY OF *Usnea longissima* APOTHECIA

Accounts of fertile *Usnea longissima* are quite rare in the literature. Tuckerman (1848) noted that he possessed a fertile specimen from the Cape of Good Hope, Africa. Krempelhuber (1853) documented fertile specimens collected in Bavaria, and noted that

apothecia were previously known only from Tuckerman's (1848) mention of the Cape of Good Hope specimen. Another account of fertile *U. longissima* was made by Harmand (1905), who described specimens collected near Gerardmer, France in 1903. Harmand mentioned that apothecia were almost never observed on *U. longissima*, even though the species had been collected from several continents. In his *Usnea* monograph, Motyka (1936-1938) noted that apothecia were extremely rare on *U. longissima*, observed only in *U. longissima* var. *sinica*, from China. I recently observed apothecia on several *U. longissima* herbarium specimens from PC. Apotheciate herbarium specimens also exist in BM (B. McCune, personal communication, June 2000). All specimens were collected during the 19$^{th}$ and early 20$^{th}$ centuries, but many lack more detailed collection information.

*Selected specimens examined*.—CHINA. WESTERN CHINA. *Wilson 5419* (BM). YUNNAN. Yentzehay, *Delavay 1582* (PC); Likiang, *Delavay 2340* (PC). INDIA. *Jacquemont 763* (PC); near Sinla *Watt 9672* (BM). BAVARIA. Between Enterrottach and Vallep, near Tegernsee *Arnold 1685a*, *1685b* (BM). BHUTAN. *Gould 1037* (BM). INDONESIA. JAVA. *Teysmann 2* (PC).

Although *Usnea longissima* apothecia have been described in the North American literature, I found no published accounts of fertile specimens in North America. In his 1848 description, Tuckerman stated that *U. longissima* specimens from the United States and Europe were infertile. Later, Tuckerman (1882) commented that apothecia were known from Bavarian specimens (possibly referring to Krempelhuber (1853)), but made no mention of fertile U.S. specimens. Howe (1910) noted that apothecia were "practically unknown" from North American specimens. Fink (1910)

copied his description of *U. longissima* apothecia from Arnold's European Exsiccati, noting that Minnesota specimens were "uniformly sterile." It is possible that Fink observed fertile specimens in the United States at some point, since he later (1935) gave a different description of *U. longissima* apothecia and noted that fertile specimens were "very rare" in the U.S. Herre (1910) also may have observed fertile specimens, as he provided a brief description of *U. longissima* apothecia in his California description. Neither author provided further information about fertile specimens. Other authors have also noted the rarity of fertile *U. longissima* in North America (e.g., Schneider 1898, Hale 1979, Hale and Cole 1988, McCune and Goward 1995).

In the Pacific Northwest, Howard (1950) noted that fertile *Usnea longissima* had not been seen in Washington State. Noble (1982) stated that apothecia had not been observed on coastal British Columbia specimens, and deferred to Fink's (1935) description. More recently, McCune and Geiser (1997) noted that apothecia had not been seen on *U. longissima* in the Pacific Northwest. Halonen et al. (1998) reported that apotheciate specimens were rarely found in British Columbia. One apotheciate specimen is reported to exist at UBC, collected from the Queen Charlotte Islands in 1966 (P. Halonen, personal communication, May 2000). Apothecia have not been observed on *U. longissima* in northern California (Doell and Wright 2000).

## DESCRIPTION OF FERTILE SPECIMENS

I collected several fertile *Usnea longissima* thalli in a mature (ca.100 yr old) Douglas fir (*Pseudotsuga menziesii*) stand in the Oregon Coast Range, located on the border of Lincoln and Benton counties, about 13 km WSW of the town of Alsea

(44°21'N, 123°45'W). Fertile specimens were collected in January 1999, February 2000, and May 2000 (herbarium specimens deposited in OSC). The stand is along a ridge at an elevation of 390 m, with a northeast-facing aspect, and is open to the northeast. Average annual precipitation is approximately 230 cm (Daly et al. 1994), and the area is frequently blanketed in fog during the winter months. The *U. longissima* population is quite large—nearly all overstory trees within the 5 ha stand contain abundant thalli within their crowns, and thalli are also abundant on understory shrubs and trees. Fertile specimens were collected from branches of understory shrubs and trees (*Acer circinatum*, *Rubus spectabilis*, and *Alnus rubra*), and were found only in one small (75 $m^2$) area of the stand. Of the thalli examined in the understory of this area, 5% possessed abundant apothecia (one 50 cm long strand possessed over 40 apothecia), 15% possessed a smaller number of apothecia, and the remainder were sterile. This was the only population in which fertile material was observed, out of 75 populations visited in an 8500 $km^2$ area of the Oregon Coast Range.

Apothecia were 1-3 (5) mm across, terminal on the ends of side branches, with numerous fibrils extending from the thalline exciple (Fig. 4.1). Fibrils were typically as long as or longer than the apothecia-bearing side branches and often twisted into a single, loose strand on the younger apothecia. As in other *Usnea* species, younger apothecia were cup-shaped while older apothecia consisted of a flat disk with a thinner margin. Older apothecia typically possessed fewer fibrils along the margin. Disks were light brown or tan, often with a mottled appearance due to small deposits of a dark brown granular material on the disk surface. Numerous cross sections of apothecia were examined and, although many asci were observed, few contained spores. Asci

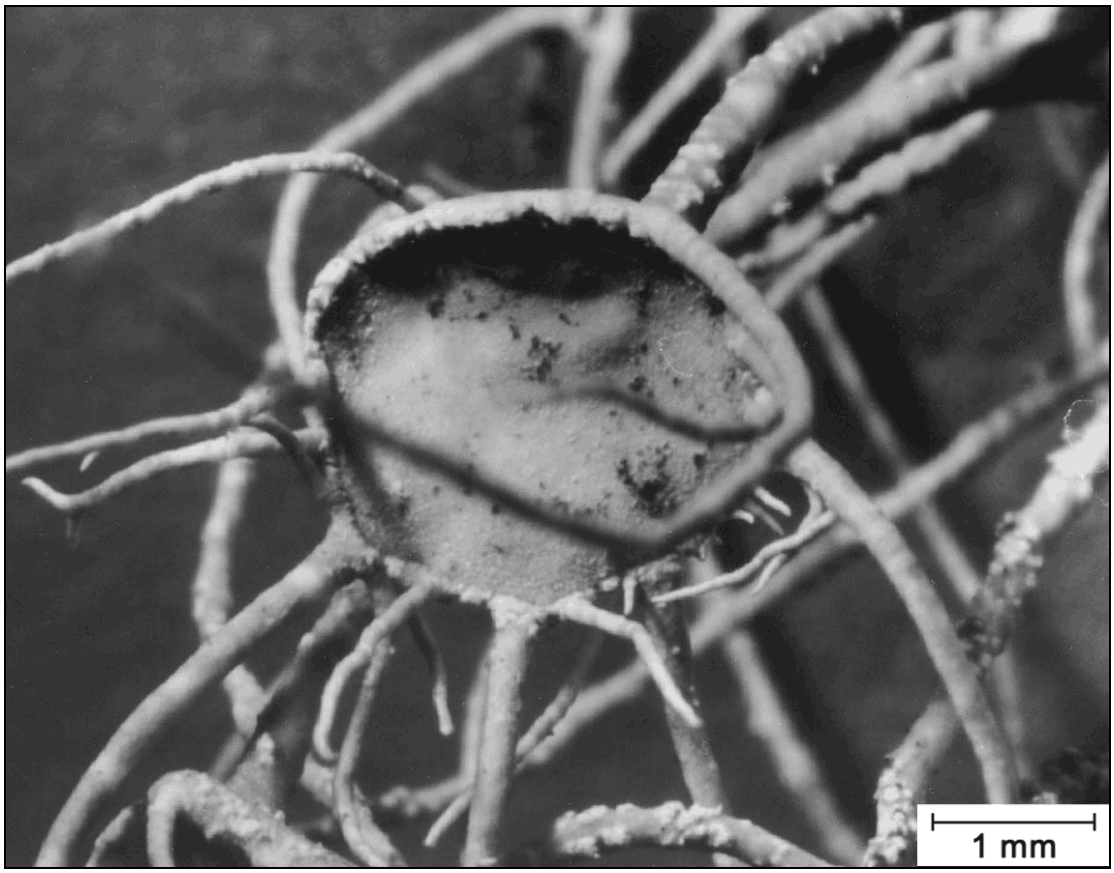


**Figure 4.1** Mature apothecium with brown granular material on disk surface.

were cylindrico-clavate, paraphyses were simple and abundant. Spores were 7-9 x 4-5 µm, oblong-ellipsoid, non-septate, hyaline, and eight per ascus.

## DISCUSSION

Reasons for the infrequent occurrence of apothecia in *Usnea longissima* are not clear. One possible explanation is that the species produces apothecia in response to stressful environmental conditions. For example, apparently sterile thalli collected near Cascadia State Park in Oregon (44°24'N, 122°29'W) produced apothecia following relocation to a partially wooded backyard in relatively arid Boise, Idaho (R. Rosentreter, personal communication, May 2000). However, the Coast Range site where fertile thalli exist appears to be excellent *U. longissima* habitat.

Other possibilities include genetic differences between fertile and sterile individuals or between fertile and sterile populations. For example, heterothallism may be lacking from most populations (i.e., most populations may consist of only one mating type), preventing the formation of apothecia. An occasional mutation or other event may yield a second mating type, making sexual reproduction possible. It is also possible that fertile individuals are simply remnants of older, more diverse *Usnea longissima* populations.

It would be interesting to assess genetic variability within the fertile Oregon Coast Range *Usnea longissima* population to determine whether the fertile and sterile thalli possess different genotypes. Researchers studying *Lobaria pulmonaria* in Switzerland found that the highest genetic variability occurred in populations where both fertile and sterile thalli were present (Zoller et al. 1999). Since populations

containing higher genetic variability are generally considered more likely to persist and evolve, the researchers assigned a higher conservation priority to populations that contained both fertile and sterile thalli. *Lobaria pulmonaria* populations in Switzerland have been decimated by factors similar to those currently threatening *U. longissima* in the Pacific Northwest (primarily air pollution and habitat loss due to forestry practices).

The paucity of fertile *Usnea longissima* populations contributes to dispersal limitations inherent within the species. Long-distance dispersal mechanisms are practically non-existent in *U. longissima*, which reproduces primarily through fragmentation of relatively large pieces of thalli, is non-isidiate, and rarely produces soredia (Noble 1982, McCune and Geiser 1997). Dispersal limitations may be more important than habitat availability in determining the distribution of *U. longissima* in the Oregon Coast Range (Keon 2001, Keon and Muir *in prep.*). As a result, populations containing fertile thalli may play a more important role in dispersal of the species than populations containing only sterile thalli. An understanding of the factors governing production of apothecia in *U. longissima* (i.e., genetic vs. environmental) may allow identification of populations in greatest need of protection, and may help land managers refine conservation priorities for the species in the U.S. Pacific Northwest.

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# Chapter 5

# Conclusions

*Usnea longissima* Ach. may be limited more by dispersal than by lack of suitable habitat in our Coast Range study area. The habitat modeling study results indicate that *U. longissima* presence tends to be associated with older stand age and cooler, often moister, sites. However, testing of the model on the independent CVS data set indicates that the species may not, in fact, be limited by narrow habitat associations, as sites of presence occurred as commonly in areas predicted to be less suitable habitat as in areas predicted to be more suitable (although no occurrences were in areas predicted to be least suitable). Other studies that examined habitat specificity of epiphytic macrolichens (e.g., Sillet et al. 2000) also have concluded that availability of suitable habitat often does not significantly limit their distribution, since many habitats appear to be suitable. Further, areas predicted to be relatively suitable cover a sizeable percentage of the landscape in the study area, also suggesting that the fairly sparse distribution of the species does not result from lack of habitat. Finally, results from the transplant experiment also suggest that dispersal may play a more important role than availability of suitable habitat in limiting the distribution of *U. longissima* in the Oregon Coast Range, as the species grew relatively well over a wide range of habitat conditions. In fact, *U. longissima* transplants had the highest growth in sites that were predicted to be the least suitable habitat.

It has been suggested previously that *Usnea longissima* may be strongly dispersal-limited in the Pacific Northwest (PNW), since it reproduces primarily through

fragmentation of relatively large pieces of thalli, and shows little evidence of long-distance dispersal mechanisms (Noble 1982, McCune and Geiser 1997). My results strengthen this suggestion. It is likely that many populations of *U. longissima* in the PNW consist of remnants of larger populations that have survived in older forests, or remnant trees. Thus, rather than interpreting the positive association of older stand age with *U. longissima* presence and higher abundance at the site level as resulting from more favorable environmental conditions for the species in older forests (e.g., favorable microclimate), I believe the association exists because older stands harbor remnant populations of *U. longissima*, which can increase over time. *Usnea longissima* populations in younger stands are most likely there, in general, because of dispersal from older, taller, adjacent trees.

If *Usnea longissima* is to persist and spread to new areas, attention must be paid to protecting extant populations and to providing a source of propagules to uncolonized stands. To this end, it is recommended that: (1) remnant trees containing *U. longissima* should be retained during logging operations, and (2) old stands containing *U. longissima* should be preserved. Both will serve as refugia, and as sources of inoculum of the species. The transplant study suggests that *U. longissima* will survive and grow well in remnant trees left after logging with green tree retention. Older stands containing *U. longissima*, in addition to providing sources of inoculum, are more likely to preserve important population-level characteristics than are isolated remnant trees.

Further investigation into the dispersal mechanisms of *Usnea longissima* in the PNW (i.e., the frequency of occurrence of sorediate specimens, or distances traveled by fragments dispersed from forest edges into clear cuts) may provide more information

about the extent to which the species is actually limited by dispersal. It is possible that populations containing fertile thalli, while apparently uncommon, may play a more important role in dispersal of the species than populations containing only sterile thalli. While just one fertile *U. longissima* population was discovered during this study, others may exist. Further study is likely to provide us with a better understanding of the species' population dynamics.

The modeling techniques used here were effective for assessing the suitability and availability of *Usnea longissima* habitat across the study area, and I believe that these methods may be useful in management of the species in the PNW. In particular, this study may help to refine: (1) approaches to strategic surveys mandated by the Northwest Forest Plan (USDA and USDI 2000, 2001), and (2) the appropriate status of *U. longissima* in the PNW. Additionally, these methods may be particularly successful for other species that have relatively narrow habitat associations, with results facilitating effective field surveys and management actions.

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