Final Moss Recovery Report: Ten years after harvest

Hebo District, Siuslaw National Forest

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Abstract. Recovery of epiphyte biomass and species composition following commercial moss harvest remains slow. In annual monitoring since 1995, percent cover was estimated for all epiphyte species present on the 85 vine maple (*Acer circinatum*) stems harvested in 1994. Ten years after harvest, total average percent cover has increased to 50% (std 10%) across the remaining 6 sites, although mat depth rarely exceeds 1.5 cm. Biomass subsampling indicates that on average 56% of the originally harvested mass as re-grown, but the variation is substantial. Species were both gained and lost from 1995 through 2004 and species richness is higher now than before harvest for all sites. Trends in species composition, however, suggest that this is a temporary condition that will dissipate as the mats grow and *Isothecium* and *Antitrichia* take over more completely. Assuming constant growth rates, it will be another decade before these mats completely cover the stem surface, and another 20 years before they have comparable harvestable biomass to the originally harvested mats. Assuming compounding growth, these sites could again be harvestable in about five more years. The average required rotation period appears to be 15-20 years in the mossiest areas of the Hebo District.

Overview

In the decade since the initiation of this project, the demand for commercial moss has stabilized at a level above what the Hebo District has been able to provide. Permits sell out early in the year, intensive harvest continues on neighboring lands, and poaching is still rampant. Don Harrison, our moss Steward, reports that many of the societal aspects of harvest have radically changed in this time as well. Few of the local old-timers are left. Their practices of harvesting on a part-time basis, rotating areas over periods of 10-15 years, and harvesting in patches has been replaced by migrant crews whose short-term approach includes completely stripping bunches of trees and shrubs when they find a mossy patch, without regard for resource sustainability.

Fortunately, the results from this project will be more akin to modern strip mining practices than to the patchy harvest of yesteryear. In August of 1994, harvestable epiphytes were completely removed from an entire one-meter long segment on 85 live *Acer circinatum* (vine maple) stems across nine sites on the Hebo District. An initial estimate of recovery rates on Hebo was attempted in 1994 by assuming that moss mats could not be older than their substrate. Thus, epiphytes growing on a 20-year old shrub stem were assumed to have accumulated their mass in no more than 20 years. In this way, we estimated an accumulation rate of 5 g/m/yr for stems <15 years old, and 2.6 g/m/yr for stems from 15 to 35 years in age (Peck & McCune 1998), resulting in estimated rotation periods of 15-25 years. Because the underlying assumption was questionable due to the possibility of disturbance, it was necessary to experimentally validate these rates.

This report briefly summarizes the methodology that was employed and what has been observed at each re-measurement. From years one to five following harvest, percent cover was estimated for all species of epiphyte on each of the remaining stems at each remaining site and some destructive biomass sampling was done. The sites were again revisited in 2004, at year 10, and this report includes those data, as well some final recommendations on necessary rotation periods for the mossiest areas of the Hebo District.

Methods

In 1994, stems were harvested in nine sites in the Hebo District, Siuslaw National Forest (45°2' - 45° 13' N, 123° 5' - 123° 55' W; Peck 1996). All sites are ~1.5 ha in area, below 415 meters in elevation, have mixed conifer-hardwood canopies, and are believed to belong to the 150 year old post-fire cohort, with most dominant trees in the 80-110 year range. Bryophytes on a total of eighty-five individual stems of *Acer circinatum*, the dominant shrub harboring harvestable epiphytes at these sites, were harvested (stripped clean) from one-meter segments and these stems permanently tagged in August, 1994. Stems were selected using the point-centered quarter method (Cottam et al. 1953), with an unequal number of stems among the nine sites due to the patchy distribution of *A. circinatum* (See Peck & McCune 1998 for sampling details).

The one-meter long segment of each stem was randomly chosen between the ground and 2 m in vertical height. The diameter of the stem was taken at the midpoint of these segments. The segments were stripped of all visible epiphytes and permanently tagged. All easily removed epiphytes were taken to the laboratory for identification, to determine what epiphytes are most "harvestable," and their relative abundance in each sample was estimated (after McCune 1990). The remaining, appressed epiphytes were rubbed off each stem, but not identified (the original focus of the study was on harvestable epiphytes only; appressed species are not commercially harvestable). Nomenclature follows Anderson et al. (1990) for mosses, Stotler & Crandall-Stotler (1977) for hepatics, Esslinger & Egan (1995) for lichens, and Hitchcock & Cronquist (1973) for vascular plants.

In July, 1995 each stem was re-examined to determine the percent cover of each species in the one-meter segment harvested in 1994. Cover was estimated separately for the upper and lower surfaces of all stems. Pendant material was measured separately by estimating the percent cover of the surface that would be covered if the pendant material were to be appressed to the surface. A record was kept of whether or not the remaining epiphytes on the stem encroached into the stripped segment over time. These procedures were repeated in July, 1996, at which time one of the nine sites (site 8) was also re-harvested. The epiphytes from the 10 stems at this site were harvested, oven dried at 60° C for 24 hours, and weighed to obtain biomass estimates. These procedures were repeated in July 1997, at which time another site (5) was re-harvested, in July 1998, at which time another site (14) and several stems from an additional site were re-harvested, again in August 1999, and again in August 2004, at which time two other sites (2, 15) were re-harvested as well as two stems from each of the remaining sites. As of August 2004, 4 sites remained, with a total of 35 live stems. J. Peck performed cover estimates every year, with the help of various field assistants (such as Tom Rambo, pictured here with J. Peck).

Species richness is defined as the number of species found in a given sample and was calculated for each site and for all sites combined for each year. Mean alpha diversity is the average number of species *per* segment for a given site (stem-level) or the average number of species *per* site for a given project (site-level). Percent cover is the percent of the surface area of the one-meter long stem segments (of varying diameter) covered by epiphytes. Average cover is calculated across stems for each site and across all sites combined for each year. The rate of increase in percent cover from year to year is calculated as the total increase in cover divided by time. The average rate thus far is estimated as the increase in cover from 1994-2004 divided by ten years.

Cumulative distribution frequency (CDF) graphs were chosen to graphically display the status of species richness, cover, and growth rates for each year. These graphs indicate what proportion of the total population (e.g., 85 stems for 1994) had certain values of species richness, cover, or growth rates (with 90th percentile confidence intervals). The 50th percentile on each graph is marked to show the median value for each graph. CDF's are useful because they show a) all available samples, b) the relative position of each sample within the population, and c) the maximum potential for that population.

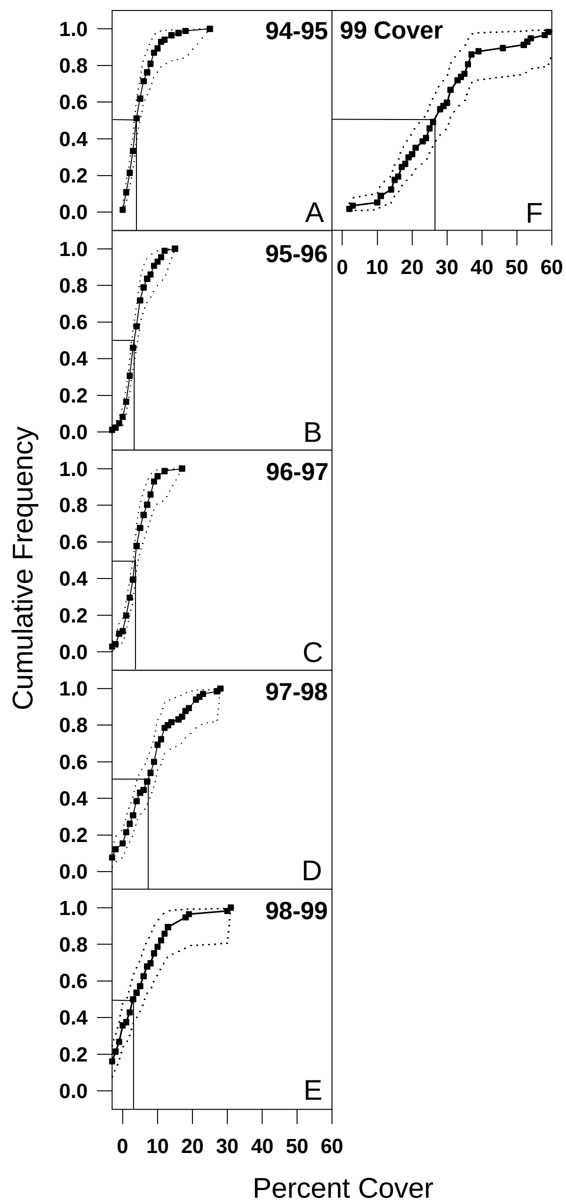
I used paired t-tests (SAS 1996) to evaluate change in species richness and cover from year to year and to evaluate the difference between the upper and lower surface of each stem in any given year. Differences in composition were determined using multi-response permutation procedures (MRPP, McCune & Mefford 1999). MRPP is a nonparametric test used here to evaluate differences among groups, on the basis of frequency and abundance of species. Indicator species analysis (Dufrêne & Legendre 1997) was used to determine which species are responsible for these differences in composition by assigning indicator values (IV's) based on the relative frequency and abundance of species in each group of interest. Large, significant IV's are assigned to species that are most abundant and frequent in a particular group. Species with significant IV's 15 points greater for a given group than any other group are considered here to be ecologically more frequent and abundant in that group.

Results

Recovery 1994-1995

From 1994, when the stems were bare, to 1995, 18 species colonized or recolonized some of the 85 stems (Table 1). There were roughly 0.4 (95% confidence interval = 0.01 - 0.8) fewer species in 1995 than 1994 ($p = 0.04$) (Table 2). During that time, average percent cover increased from 0% to 5.5% (s.d. 4.1). Species composition also differed from pre-harvest (1994) to one year post-harvest (1995) ($p = 0.001$). The upper and lower surfaces of the stem segments differed in species composition ($p = 0.004$). The upper surfaces had 1.8% (0.8 - 2.9) higher cover and 0.4 (0.1 - 0.7) more species than the lower surfaces ($p < 0.01$). On average, more than 70% of species had returned by 1995, and almost 100% of the original species richness. For fifty percent of the stems, the accumulation rate for percent cover from 1994-1995 was less than or equal to 3.9%/yr (3.3 - 4.9) (Figure 1a). Fifty percent of the sampled stems had 3.1 (2.6 - 3.6) or fewer species in 1995 (Figure 2a).

Figure 1
Accumulation Rates

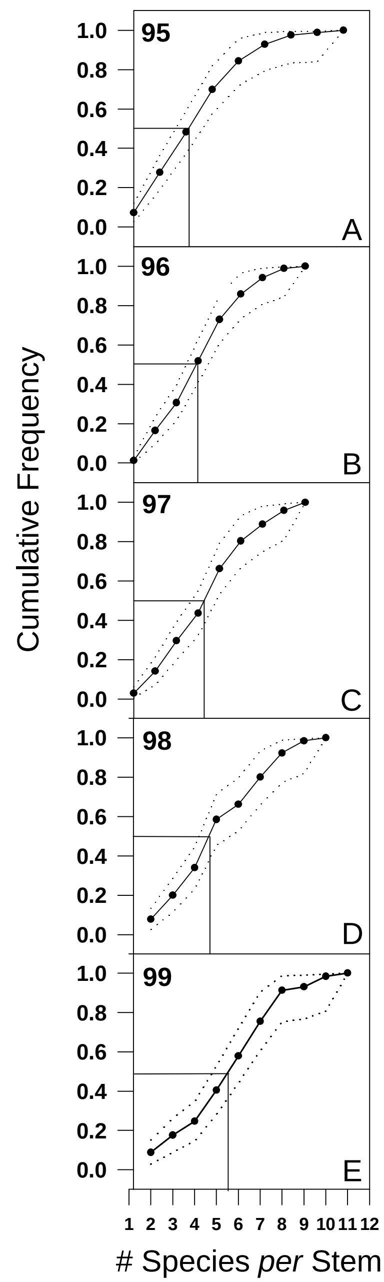


Recovery 1995-1996

From 1995 to 1996, 2 new species colonized or recolonized some of the remaining 83 stems (Table 1). There were roughly 0.7 (95% confidence interval = 0.4 - 1.0) more species in 1996 than 1995 ($p < 0.001$) (Table 2). During that time, average percent cover increased to 9.6% (s.d. 5.2), with 4.2% (3.4 - 4.9) higher cover per stem than in 1995 ($p < 0.01$). Species composition differed from pre-harvest (1994) to two years post-harvest (1996) ($p < 0.001$) and from one year post-harvest (1995) to two years post-harvest (1996) ($p < 0.005$). The upper and lower surfaces of the stem segments still differed in species composition in 1995 ($p < 0.001$). The upper surfaces had 2.1% (0.8 - 3.3) higher cover than the lower surfaces ($p = 0.001$), but species richness was no longer significantly different ($p = 0.07$). On average, nearly

80% of species had returned by 1995, and over 100% of the original species richness. For fifty percent of the stems, the accumulation rate for cover from 1995-1996 was less than or equal to 3.4%/yr (2.6 - 4.2) (Figure 1b). This rate was on average 1.3% (0.1 - 2.5) slower than the 1994-1995 rate ($p = 0.03$). Fifty percent of the sampled stems had 3.9 (3.4 - 4.4) or fewer species in 1996 (Figure 2b).

Figure 2
Mean Alpha Diversity



Recovery 1996-1997

From 1996 to 1997, 2 new species colonized or recolonized some of the remaining 71 stems (Table 1). There was no difference in species richness between 1996 and 1997 ($p = 0.6$) (Table 2). During that time, average percent cover increased to 14.4% (s.d. 8.5), with 4.3% (3.4 - 5.1) higher cover per stem than in 1996 ($p < 0.001$). Species composition continued to differ from pre-harvest (1994) to three years post-harvest (1997) ($p < 0.001$) but was only barely different from two years post-harvest (1996) to three years post-harvest (1997) ($p < 0.06$). The upper and lower surfaces of the stem segments still differed in species composition in 1995 ($p < 0.001$). The upper surfaces had 5.4% (2.7 - 8.1) higher cover than the lower surfaces ($p = 0.0001$), but species richness was again not significantly different ($p = 0.4$). On average, nearly 88% of species had returned by 1997, and nearly 120% of the original species richness. For fifty percent of the stems, the accumulation rate for cover from 1996-1997 was less than or equal to 3.6%/yr (2.9 - 4.5) (Figure 1c). This rate was not significantly different from the 1995-1996 rate ($p = 1.0$). Fifty percent of the sampled stems had 4.3 (3.7 - 4.8) or fewer species in 1997 (Figure 2c).

Recovery 1997-1998

From 1997 to 1998, 3 new species colonized or recolonized some of the remaining 66 stems (Table 1). Species richness was higher in 1998 than 1997 ($p < 0.001$) (Table 2). During that time, average percent cover increased to 24.4% (s.d. 12.4), with 7.9% (6.0% - 9.9%) higher cover per stem than in 1997 ($p < 0.001$). Species composition continued to differ from pre-harvest (1994) to four years post-harvest (1998) ($p < 0.001$) but was not different from three years post-harvest (1997) to four years post-harvest (1998) ($p = 1.0$). The upper and lower surfaces of the stem segments still differed in species composition in 1998 ($p < 0.03$), with *Isothecium myosuroides* more common and abundant on upper surfaces while *Neckera douglasii* was more so on lower surfaces ($p<0.01$). The upper surfaces had 7.0% (4.3 - 9.7%) higher cover than the lower surfaces ($p < 0.001$), but species richness was again not significantly different ($p = 0.6$). On average, 88% of species had returned by 1998, and over 120% of the original species richness. For fifty percent of the stems, the accumulation rate for cover from 1997-1998 was less than or equal to 7.2%/yr (4.0 - 9.4) (Figure 1d), substantially higher than in previous years. Fifty percent of the sampled stems had 4.7 (4.2 - 5.5) or fewer species in 1998 (Figure 2d).

Recovery 1998-1999

From 1998 to 1999, no new species colonized the remaining 57 stems (Table 1). Species richness was unchanged between 1998 and 1999 ($p = 0.16$) (Table 2). During that time, however, average percent cover increased to 28% (s.d. 15.4), with 4.9% (s.d. 8.5%) higher cover *per* stem than in 1997 (p = 0.02). Species composition continued to differ from pre-harvest (1994) to five years post-harvest (1999) (p < 0.001) but continues to be unchanged from year to year since 1997 (p = 1.0). The upper and lower surfaces of the stem segments still differed in species composition in 1999 (p < 0.001), with *Frullania*, *Isothecium myosuroides,* and *Ulota* more common and abundant on upper surfaces while *Neckera douglasii, Metzgeria,* and *Radula* were more so on lower surfaces (p<0.05). The upper surfaces had 8% (0 - 20%) higher cover than the lower surfaces (p < 0.006), but species richness was again not significantly different (p = 0.7). On average, 82% of species had returned by 1999, a slight decrease from 1998, but nearly 130% of the original species richness. For fifty percent of the stems, the accumulation rate for cover from 1998-1999 was less than or equal to 3.0%/yr (1.0 - 6.0) (Figure 1e), substantially lower than in the previous year. Fifty percent of the sampled stems had 5.5 (4.8 - 6.3) or fewer species in 1999 (Figure 2e).

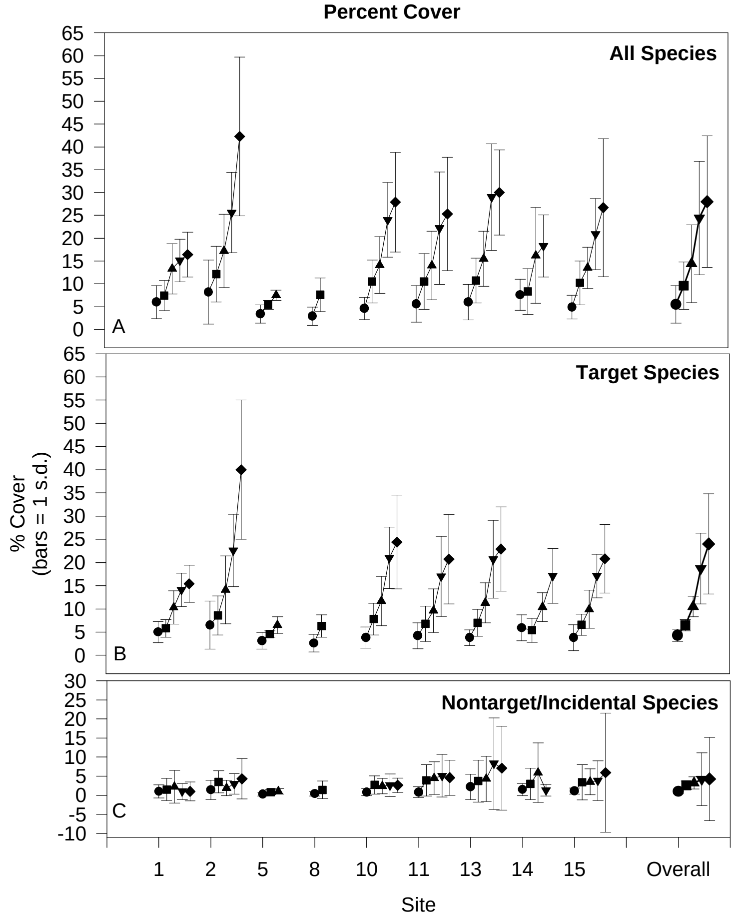
Recovery 1999-2004

From 1999 to 2004, two new species colonized the remaining 48 stems (Table 1). Overall species richness increased by an average 1.6 species (std 1.8) between 1999 and 2004 (p <0.001) (Table 2). During that same time average percent cover increased to 51% (s.d. 8.5), with 22.8% (s.d. 14.6%) higher cover *per* stem than in 1999 (p < 0.0001). Species composition was only suggestively modified over the five years since 1999 (p = 0.065; p=0.045 when rank transformed), in part due to high variation in species composition of stems within years (A=0.005, 0.011). The upper and lower surfaces of the stem segments remain highly significantly different in species composition in 2004 (p < 0.0001), with *Isothecium* and *Ulota* more common and abundant on upper surfaces while *Cladonia*, *Neckera,* and *Radula* were more so on lower surfaces (p<0.05). The upper surfaces had increased by 23.7% (std 29) more than the lower surfaces (p < 0.0001), but species richness was again not significantly different (p = 0.8). For fifty percent of the stems, the accumulation rate for cover from 1999-2004 was less than or equal to 1.6%/yr (0.8 - 3.0) (Figure 1f). Fifty percent of the sampled stems had 8 (4 - 15) or fewer species in 2004 (Figure 2f).

Figure 3

Trends in Post-Harvest Recovery:

Percent Cover

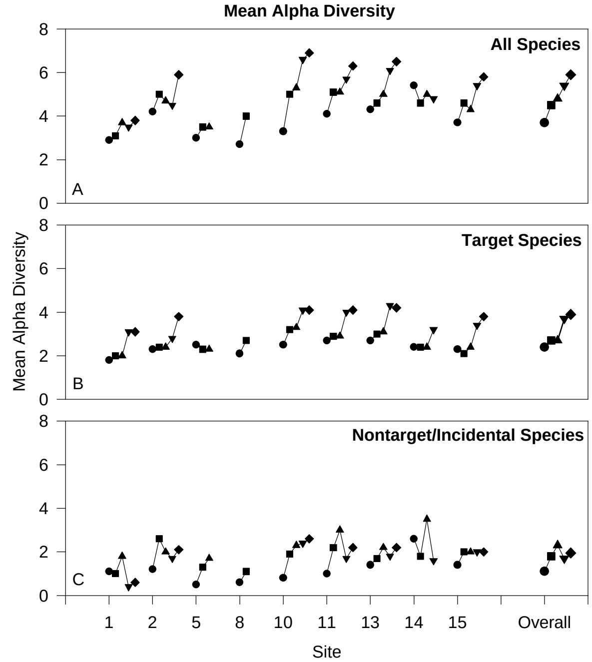


Recovery 1994-2004

Ten years following harvest, fifty percent of all stems had a cover of 67.3% (57 – 74%) or less (Figure 1f). The overall average accumulation over that period was 51% (s.d. 18.5) (Figure 3a), with a consistent average annual rate of 5% (s.d. 5%). Most of the increase in cover has been due to the growth of target species (see Peck 1997)(Figure 3b), with nontarget and incidental species making only a marginal, if variable, contribution

(Figure 3c). After a decade of recovery, the upper surfaces of stems had 30.1% (std 26.7) more cover than the lower surfaces ($p<0.001$), while species richness did not differ among the tops and bottoms of stems ($p=0.64$). In addition, with only a few exceptions, the average number of species per stem increased at each site over the past decade (Figure 4a), finally averaging 7.5 species per stem (std 3.1) after a decade of recovery. This increase was due initially to the increase in the number of target species (Figure 4b), but nontarget and incidental species have continued to increase with time (Figure 4c). The number of species changes trended downward for the first five years, but most sites saw a dramatic increase in species turnover over the next five year period. Most species eventually showed up at every site. On average, only 88% of species had returned by 2004, but 145% of the original species richness. Species composition continued to differ from pre-harvest (1994) to ten years post-harvest (2004) ($p < 0.001$), despite a continued lack of similarity in species composition among stems within years (A=0.02). This difference was primarily due to a greater frequency and abundance of *Rhizomnium* ($p=0.08$) and *Neckera* ($p=0.08$) in 1994 and a greater frequency and abundance of *Cladonia*, *Claopodium*, *Isothecium*, *Metzgeria*, *Radula*, and *Ulota* (all $p<0.05$) in 2004.

Figure 4
Trends in Post-Harvest Recovery:
Mean Alpha Diversity



Biomass Regrowth

Two years after harvest, 10 stems at Site 8 were re-harvested and the biomass of their epiphytes estimated. This site had relatively high species richness (12 pre-harvest, 8 in 1995, 12 in 1996) but low cover (2.9% in 1995, 7.6% in 1996). In 1996, these stems averaged 1.2 (s.d. 0.8) grams of dry-weight moss. The regrowth rate at this site averaged 0.6 g/m/yr.

Three years after harvest, 4 stems at Site 5 were re-harvested and the biomass of their epiphytes estimated. This site had relatively low species richness (7 pre-harvest, 5 in 1995, 6 in 1996, 6 in 1997) and low cover (3.4% in 1995, 5.4% in 1996, 7.5% in 1997). In 1997, these stems averaged 0.70 (s.d. 0.4) grams of dry-weight moss. The regrowth rate at this site averaged 0.2 g/m/yr.

Four years after harvest, five stems at Site 14 were re-harvested and the biomass of their epiphytes estimated. This site had relatively low species richness (6 pre-harvest and 9 in 1998) but relatively high cover (7.6% in 1995 and 20.9% in 1998). In 1998, these stems averaged 2.8 (s.d. 2.0) grams of dry-weight moss. The regrowth rate at this site averaged 0.7 g/m/yr**.** In addition, three stems from site 10 were re-harvested after adjacent areas were illegally harvested by moss poachers. In 1998, these stems averaged 3.2 (s.d. 2.2) grams of dry-weight moss, with an average growth rate of 0.8 g/m/yr.

Ten years after harvest, four stems at Site 2 were re-harvested and the biomass of their epiphytes estimated. Two stems each were re-harvested from sites 1, 10, 11, 13, and 15 to obtain biomass growth estimates. In 2004, these 14 stems averaged 29.8 (s.d. 22.6) grams of dry-weight moss, with an average absolute growth rate of 3.0 (s.d. 2.3) g/m/yr. The average mat depth of 3 mm (s.d. 2) remained notably lower than at the time of initial harvest in 1994 (estimated to be 3 cm). On average, these stems had recovered 56% (s.d. 43) of their original biomass over the past decade and would take, on average, about 28 (s.d. 19) years to reaccumulate that mass assuming a constant growth rate. However, solving for a compound growth rate assuming an initial weight of 0.6 g (averaged from the first three years of growth data) at year 1, the average rate of increase across all samples over the course of the study was 34%, rendering a rotation time of 14 years (95^{th} percentile confidence interval from 20% (24 years) to 49% (10 years)).

Discussion

Abundance

The recovery of moss following harvest is highly variable from site to site and stem to stem. Those seeking justification for optimistic regrowth estimates will be gratified to see that some stems have already topped 90% cover (9%), 8 mm in depth (4%), and sport some (albeit very small) harvestable quantities of moss (8%; defined in this case simply as mats loose enough to remove from the host stem). While these values demonstrate that it is possible for some mats to grow relatively rapidly, the growth rate of the fastest growing individuals is of less interest than the average reaccumulation in the population as a whole, which is highly variable. On the one hand, the slowest growing site averaged 3.7% cover increase per year, which would translate into 100% cover by year 27 (21-35). On the other hand, the fastest growing site averaged 7.3% cover increase per year, which would require only 18 years (16-20) to regain 100% cover. The average rate of 5% increase in cover per year would predict mats to reach 100% cover in 21 (18-29) years.

The method of harvest appears to affect the rate of increase in cover as well. Stems with adjacent patches of residual moss gained significant cover as a result of this moss encroaching into the harvested stem segment. Thirty-one percent of all stems in 1996, 70% by 1997, and 95% by 1998, and 98% by 1999, and all by 2004 showed signs of recruitment in the form of re-established litterfall or encroachment from epiphyte mats adjacent to the stripped segment. Further, relatively few patches of moss appeared in the central portions of the stripped segment, suggesting that regrowth from protenema or spores may be a minor factor in long-term epiphyte mat accumulation. This does not bode well for the modern practice of strip harvesting.

Cover, however, is not a very good indicator of harvestable volume. First, not all 1-m stem segments will ever reach 100% cover. Not all of the originally harvested mats covered the entirety of the 1-m stem segment. Second, mats do not grow laterally first and then radially; mat depth starts increasing on previously covered segments even before other segments become covered. Third, even stems with 100% cover will have 0% harvestable volume if the moss has rhizoids embedded in the host bark (i.e., the mat is too shallow for the rhizoids to attach to one another).

Although mat depth provides some indication of volume regrowth, few data are available. Depth was measured in 2004, but not beforehand because it was too shallow, precluding rate estimates. However, average mat depth was estimated at 1 mm or less in 1999 and measurements averaged 3 mm in 2004. Assuming that the rate of depth growth thus doubles every five years, the original mat depth of ~3 cm would be reached in another 15 years (thus a total of 25 years). Again, on the one hand the slowest sites averaged 1.3 mm and may reach original mat depth in 30 years, while the fastest averaged 4.8 mm/year and could get there in under 20 years, assuming constant rates of growth.

Perhaps the second best indication of harvestability comes from direct estimates of moss mat volume. The slowest growing sites averaged 5.7 cubic inches in volume per stem in 2004, while the fastest averaged 17.2 in^3. The total volume of moss in 2004 averaged 11 in^3. The minimum volume out of 70 typical harvestable mats near these sites was 48 in^3 (see Appendix), suggesting that none of the regrown mats have regained a desirable harvest volume. Based on the regression equations in the Appendix, the average moss volume of 11 in^3 translates into approximately 0.023 lbs of dry-weight biomass (~10.4 g). Given that the average weight of the original mats harvested in 1994 was 0.102 lbs (46 g), volume estimates would suggest that less than ¼ of the original weight had regrown in the past decade across all of the harvested stems. Only two of the re-harvested stems in 2004 had “harvestable” mats (and then less than 2 mats each).

If harvestable inventories are to be estimated by weight, however, biomass regrowth estimates are needed. The small samples in the early years of this study indicated that biomass regrew at a rate of less than 1 g/m/yr, which would have required nearly 90 years for the original mat mass to reaccumulate. Since, on average, half the biomass has returned to the re-harvested stems in only a decade, biomass growth that begins very slowly must rapidly increases after the first five years. Ten-year regrowth rates suggest only 15 years will be needed to reaccumulate the original biomass, a figure that perfectly matches the predictions of moss steward Don Harrison.

However, it appears that the biomass that has re-grown is spread out relatively evenly on the stem segment, such that although total biomass is equal to or even higher than the original biomass, the mats are more shallow. Since mats do not become harvestable until they are deep enough for the rhizoids to embed in epiphytic soil rather than the bark of the host, it may take longer for mats to become reharvestable than it does to reaccumulate the original biomass. The four stems that had some harvestable moss averaged 6.8 mm in depth; none were less than 5.5 mm deep. The minimum depth of harvestable mats near these sites was 2.5 cm (see Appendix).

The slow growth of mat thickness has implications for invertebrate habitat and potential hydrological and nutrient cycling functions. It is likely that many invertebrates require thick mats, such that stems with high cover but low mat thickness may be poor habitat for invertebrate communities. Many bryologists also believe that as moss mats grow, they reach a critical threshold above which they are able to retain sufficient moisture to avoid desiccation between rainfall events. This water retention capacity may have implications for the forest as a whole on two fronts. First, large, wet moss mats do not burn and thus may contribute to the long natural fire cycles of these coastal forests. Second, by retaining and then gradually releasing rainfall/stemflow/throughflow, large volume moss mats may reduce the incidence of flooding during heavy precipitation events and may reduce vascular transpiration between rainfall events. With fewer and fewer large mats around, these ecosystem functions would be reduced.

Diversity & Epiphyte Community Development

Rare species were never a concern at these sites, or for most harvestable epiphytes on vine maple, presumably due to three factors. First, moderately sized moss mats are dominated by a handful of common species. High diversity appears to be found either with relatively young mats, where disturbance has created new substrate for colonization, or with extremely old mats, which have developed sufficient epiphytic soil and overall volume to retain water and create log-like habitat. Second, the young mats are thin and, still lacking a thick enough layer of epiphytic soil into which the rhizoids can grow, attach instead to the host bark. Both low volume and difficulty in removing them from the host substrate render these mats generally unharvestable. Third, due to the long and extensive history of commercial moss harvest on the Hebo district, most areas have primarily small or moderately sized mats (i.e., the large ones are long gone).

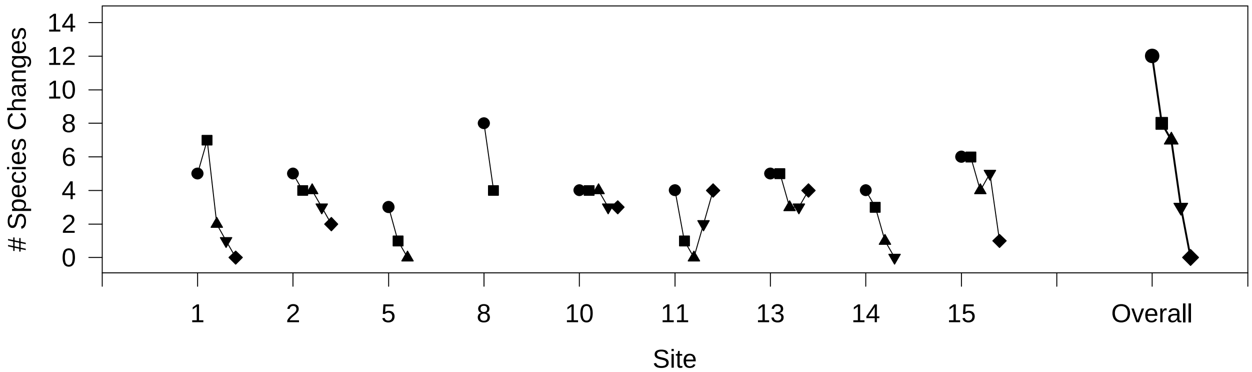
The Hebo regrowth data demonstrate these factors. We now know that the original harvestable mats were almost definitely moderately sized *second growth* moss (according to Don Harrison, who had historically harvested in the area of these sites), with species richness values two-thirds to one-half of the potential maximum diversity of a harvestable epiphytic bryophyte mat (personal observation). Although diversity decreased following harvest, it increased rapidly and had surpassed original species richness by year two when the mats were very small and cover very low. Even a decade later, species richness continues to climb as each stem now has segments of both bare substrate and ever-thickening mat available for colonization. The large size of the harvested area, a meter in length, provides several niches with its habitat heterogeneity, including plenty of elbow room for appressed species not generally considered harvestable (and not included in the original sampling). This high diversity will likely last until cover reaches 100%.

In the meantime, the mats demonstrate extremely variable species composition, which seems to change from year to year, likely as a result of the dispersal limitations of bryophytes. Those species that can get there during this window of opportunity are able to establish and grow; populations too far away for spores or propagules to travel or not established in adjacent areas are simply out of luck. Overall turnover has declined (Fig. 5) and species richness and alpha diversity have become increasingly stabilized, as demonstrated by the linearization of the cumulative frequency distribution for the latter (Fig. 2). Trends in species composition indicate that the distribution of biomass among species has already begun the inevitable march toward *Isothecium* dominance, which characterized the original mats. As this species gradually takes over most

Figure 5

Trends in Post-Harvest Recovery:

Species Turnover



growing space, diversity will decline to the level observed in the original mats. If allowed to develop undisturbed for several decades longer, diversity could increase again as moisture-loving species take advantage of the water-retaining capacity of large volume mats with thick layers of epiphytic soil. Alternatively, *Antitrichia* could establish on top of the *Isothecium* mats and, once this highly competitive moss takes over, drive out most other species. Odds are, however, that these mats will be harvested again long before this takes place.

Interestingly, even after a decade most sites still lack 1-2 species found in the original mats. These remaining species include primarily the vascular plants and lichens and several moisture-loving bryophytes, which may only establish after the mats have reached a certain size. Vascular plants, in particular, would not be expected to grow epiphytically except on a substantial moss mat with an adequate epiphytic soil and moisture-holding capacity. Several delicate hepatics (*Lophocolea, Metzgeria*) are now in greater abundance. I believe this is because these appressed species are out-competed as the mat develops; larger species shade them, intercept stemflow, and overgrow these smaller taxa.

A potentially interesting development is the pattern of reaccumulation on the tops vs. the bottoms of stems. With *Isothecium* dominating the tops of stems already, and *Neckera* colonizing the bottoms, earlier theories that *Isothecium* directly out-competed *Neckera* on the tops are weakening. Plenty of surface area remains on the tops of these stems to be colonized by *Neckera*, yet it occurs more on the bottoms. This habitat differentiation may be related to the relative abilities of the species to take advantage of water at the drip line (where *Neckera* is often found) rather than direct competition. Since this was first observed (year 5), these *Neckera* colonies have expanded and begun to grow into other portions of the stem segment.

In the 6 sites re-measured for the full 10 years, only 5 (11%) stems died, most likely as a result of having been tagged with large nails that split the stem. Five other stems were buried under falling trees, and four were harvested by poachers. Thus losses to natural disturbances were less than 20% over the course of the decade. In all cases, disturbance not only removed the epiphyte mats from the host, but eliminated the host as a potential substrate for future mats (as dead stems deteriorate, they take the moss with them to the ground, preventing the development of large, old mats). Little evidence was seen supporting the hypothesis that the patchy nature of epiphyte mats is a consequence of the patchy nature of natural disturbance. In other words, the patchy distribution of mats on an alder bole is probably not due to mats on some portions of the bole having been wiped off by a falling branch, etc., but probably more related to mat establishment dynamics. Patchy distribution on understory shrub stems is most likely due to mat establishment dynamics and in large part an artifact of patchy historic moss harvest.

Conclusions

Although the remaining 35 stems may someday be remeasured, it appears that sufficient data exist at this time to make two defensible management conclusions for commercial moss harvest.

1. Minimum rotation periods for even the mossiest areas of the Hebo Ranger District are 15-20 years. Given that much of the district was heavily harvested prior to the initiation of annually rotating moss harvest areas, and that the five year interval between rotations is insufficient for regrowth, it is likely that in order to find adequate quantities of moss harvesters are already resorting to illegal harvest practices (riparian areas, tree climbing, log moss) and this trend will continue. Harvest areas should be put on 5-year rotations to ensure adequate resource inventory.
2. Moss harvest should be prohibited in Late Successional Reserves. Even after a decade, "late successional" moss species have not returned to harvested stems. The development of large volume moss mats is part and parcel of the old-growth condition and ecosystem function toward which these areas are to be managed. Small-scale harvest would probably not significantly degrade these functions, but with the widespread tendency toward permit violations, harvesters could not be reasonably expected to follow the strict guidelines that would be necessary in LSR.

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Table 1. Taxa found in harvestable epiphyte mats (1994) and on post-harvest stems (1995-2004). Values are average proportion of total abundance. Species in bold are Target species (cf Peck 1996).

M = Moss, H = Hepatic, L = Lichen, V = Vascular plant		Pre-Harvest	Post-Harvest					
		1994	1995	1996	1997	1998	1999	2004
		(n=85)	(n=85)	(n=83)	(n=71)	(n=66)	(n=57)	(n=48)
Antitrichia curtipendula	M	0.6	0.5	0.3	0.4	0.6	1.0	0.5
Cladonia	L	0.1	0.2	<0.1	0.2	<0.1	0.1	0.2
Claopodium crispifolium	M	1.4	4.9	3.8	3.9	4.1	4.2	4.0
Dendroalsia abietina	M	0.0	0.1	0.0	0.1	<0.1	0.0	<0.1
Dicranum	M	0.3	0.1	<0.1	0.0	0.1	0.1	0.1
Eurhynchium	M	3.3	2.6	3.6	3.8	5.1	6.2	4.5
Frullania	H	3.0	4.5	7.5	6.4	7.3	5.9	4.1
Homalothecium fulgescens	M	0.0	0.1	0.2	0.6	0.2	1.4	0.4
Homalothecium nutallii	M	0.5	0.0	0.8	0.3	0.7	0.7	0.8
Hypnum circinale	M	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Hypnum subimponens	M	<0.1	0.0	0.0	0.0	0.1	0.2	0.1
Isothecium myosuroides	M	54.5	52.6	46.8	57.0	55.5	56.7	63.5
Leucolepis acanthoneuron	M	0.0	0.0	0.0	0.0	0.0	0.0	<0.1
Lophocolea heterophylla	L	0.0	0.0	0.0	0.0	0.0	0.0	<0.1
Metaneckera menziesii	M	0.1	0.0	0.1	0.0	0.2	0.0	0.0
Metzgeria conjugata	H	0.1	3.1	4.1	3.1	2.6	1.9	1.3
Neckera douglasii	M	28.1	22.1	23.1	15.2	15.8	14.3	15.6
Orthotrichum	M	1.0	1.2	0.5	0.7	0.6	0.5	0.2
Parmelia sulcata	L	0.0	0.0	0.1	0.0	0.0	0.0	<0.1
Peltigera collina	L	<0.1	0.0	0.0	0.0	<0.1	<0.1	<0.1
Polypodium glycyrrhiza	V	0.1	0.1	0.0	0.0	0.0	0.0	<0.1
Porella	H	5.5	4.7	3.4	2.6	2.4	2.2	1.0
Radula	H	0.0	2.6	4.0	2.9	2.8	2.6	1.8
Rhizomnium glabrescens	M	0.1	0.0	0.0	0.0	0.2	0.3	0.1
Rhytidiadelphus loreus	M	1.2	0.5	0.6	1.1	0.9	0.9	1.4
Sticta limbata	L	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
Ulota	M	<0.1	0.0	0.7	0.8	0.8	0.8	0.2
Usnea	L	0.0	0.1	0.0	0.0	0.0	0.0	0.0

Table 2. Site averages for 1994 and 1995-2004. SpR = species richness. Mean alpha is the average number of species per sample. # taxa gained/lost is from year-to-year or *2004 back to 1994.

	Site	**1**	**2**	**5**	**8**	**10**	**11**	**13**	**14**	**15**
	# stems in 1994	10	9	4	10	11	15	14	5	7
	Stand age	100	110	80	70	80	80	80	65	85
	Elevation (m)	365	120	250	200	245	180	170	410	210
	% Conifer BA	100	51	58	65	72	75	23	94	24
1994	SpR	6	8	7	12	13	12	13	6	11
	Mean alpha	2	3	5	4	5	5	6	4	4
	SpR	7	9	5	8	11	10	14	10	9
1995	Mean alpha	3	4	3	3	3	4	4	5	4
	% Cover	6.0	8.2	3.4	2.9	4.6	5.6	6.0	7.6	4.9
	(standard deviation)	(3.6)	(7.0)	(2.0)	(2.0)	(2.4)	(4.0)	(3.9)	(3.4)	(2.6)
	% original species	67	75	67	50	66	75	85	100	64
	% original SpR	117	113	83	80	92	83	108	167	82
	# taxa gained	3	3	2	5	3	3	2	0	4
	# taxa lost	2	2	1	3	1	1	3	4	2
	SpR	7	11	6	12	13	11	13	9	11
1996	Mean alpha	3	5	4	4	5	5	5	5	5
	% Cover	7.4	12.1	5.4	7.6	10.5	10.6	10.7	8.3	10.2
	(sd)	(3.3)	(6.1)	(1.0)	(3.7)	(4.7)	(6.1)	(4.9)	(5.0)	(4.8)
	% original species	83	100	67	70	67	75	85	100	64
	% original SpR	117	138	100	120	100	92	100	150	100
	# taxa gained	3	3	1	4	3	1	2	1	4
	# taxa lost	4	1	0	0	1	0	3	2	2
	SpR	7	13	6	-	14	11	14	9	11
1997	Mean alpha	4	5	4	-	5	5	5	5	4
	% Cover	13.3	17.2	7.5	-	14.1	14.0	15.5	16.2	13.5
	(sd)	(5.5)	(8.0)	(1.1)		(6.2)	(7.5)	(6.0)	(10.5)	(4.5)
	% original species	66	87	66	-	75	83	85	100	82
	% original SpR	116	163	86	-	108	92	100	150	92
	# taxa gained	1	3	0	-	3	0	2	0	2
	# taxa lost	1	1	0	-	1	0	1	0	2
	SpR	7	9	-	-	17	13	16	9	13
1998	Mean alpha	4	5	-	-	7	6	6	5	5
	% Cover	15.1	25.6	-	-	24.0	22.2	29.0	18.3	20.9
	(sd)	(4.7)	(8.8)			(8.2)	(12.3)	(11.7)	(6.8)	(7.8)
	% original species	83	75	-	-	92	83	85	100	100
	% original SpR	116	113	-	-	131	108	123	150	118
	# taxa gained	1	0	-	-	3	2	2	0	5
	# taxa lost	0	3	-	-	0	0	1	0	0
	SpR	7	13	-	-	16	14	17	-	14
1999	Mean alpha	3	5	-	-	6	5	5	-	5
	% Cover	16.4	42.3	-	-	27.9	25.3	30.0	-	26.7
	(sd)	(5.6)	(20.5)			(11.7)	(13.1)	(12.8)		(14.9)
	% original species	83	75	-	-	77	83	85	-	91
	% original SpR	116	163	-	-	123	117	131	-	127
	# taxa gained	0	2	-	-	0	3	2	-	1
	# taxa lost	0	3	-	-	3	1	2	-	0
	SpR	9	14	-	-	18	18	20	-	13
2004	Mean alpha	4.6	6.4	-	-	8.1	7.5	9.0	-	6.3
	% Cover	37.1	48.3	-	-	60.7	41.3	62.0	-	49.6
	(sd)	(7.7)	(15.3)			(18.1)	(18.1)	(9.9)		(9.1)
	% original species	83	100	-	-	85	92	93	-	73
	% original SpR	133	175	-	-	138	150	154	-	118
	# taxa gained*	4	6	-	-	8	7	8	-	5
	# taxa lost*	1	0	-	-	2	1	1	-	3

Appendix. Quantifying the mat volume-biomass ratio.

One method of non-destructive quantity sampling for harvestable epiphytes has been the estimation of harvestable volumes, either in specific volume units (in^3) or as numbers of “harvestable mats” of supposed fixed volume (typically 12x6x1” or 12x6x2”). However, the relationship between volume and biomass has never been determined (Figure A). A small project was initiated on the Hebo Ranger District in August 2004 to fill this need.

Figure A. A mat is not a mat. These two mats are about the same length and were harvested off shrub stems of about the same diameter, but their total volume is greatly different. The mat on the left is composed almost entirely of the large-volume species *Antitrichia*, whereas the mat on the right is composed of a mixture of species dominated by *Isothecium*. We do not know, however, if these mats also vary in age.

Methods

Seventy moss mats were harvested from vine maple shrubs within an “unharvested” area of Stewardship Area 1. The shrubs did not appear to have been harvested in the past decade, and probably not for at least 15 years. Mats were collected from about a half meter above the ground and up as high as we could reach while climbing on the vine maple host (but below the height restrictions for commercial moss harvest). Mats were collected if they could be quickly and easily removed from the host stem; they were generally not the smallest mats available, as the abundance in this area led us to high-grade rather than strip the area. Mats were removed from approximately 10 shrub clumps, totaling roughly 40 individual stems. Don Harrison, the moss Steward, indicated that these were very good quality moss. Mats were composed of primarily *Antitrichia* and *Isothecium* along with very small quantities of a dozen other species.

Mats were transported in loosely packed plastic bags to the work area, where they were moistened with ground water to allow them to “refluff” for half a day following compression during transport. Mats were then measured for their total volume (length x width x depth)(Figure B), species composition, and the number of 12x6x2” harvestable mats. After completely air drying, mats were compressed and packaged for shipping back to the lab, where they were oven dried in paper bags at 60°C for 24 hours and weighed to determine air-dry biomass.

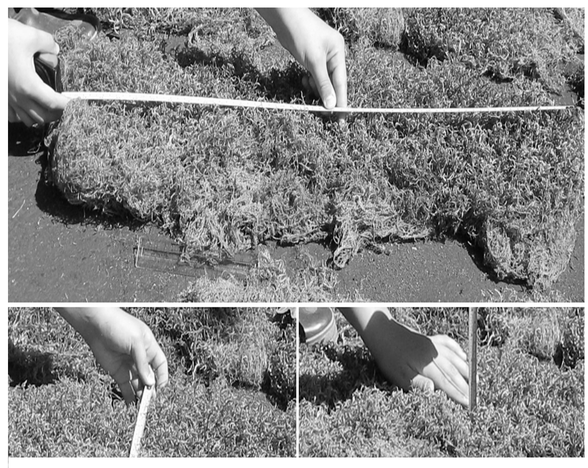


Figure B. Mats were measured for length, width, and depth, averaging multiple values for unevenly-shaped mats. Species composition was determined and the number of harvestable mats, using the 12x6x2” standard mat volume, was estimated.

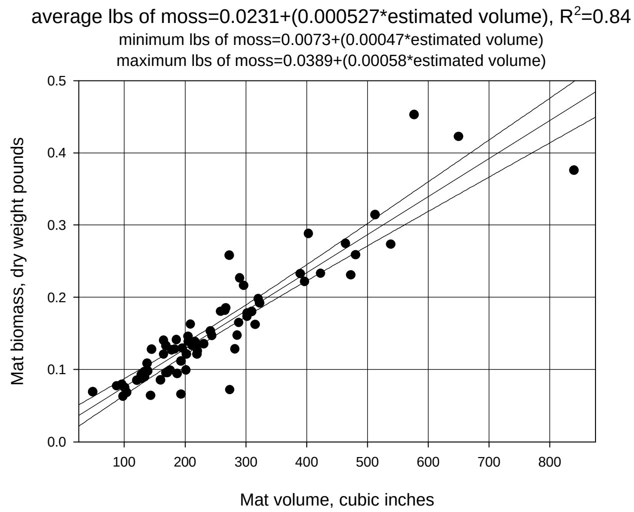
Results

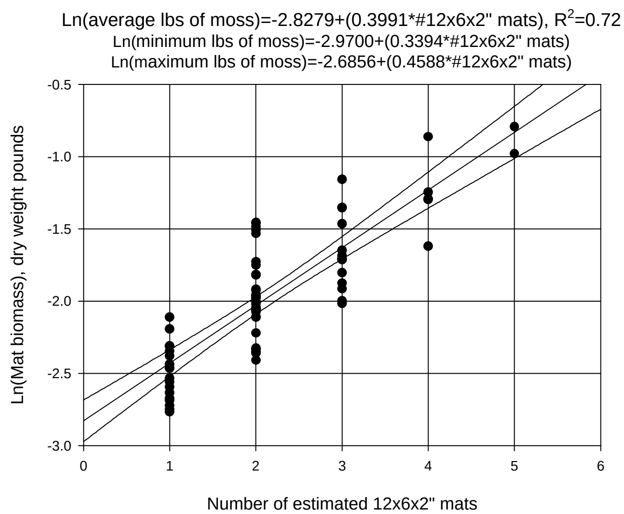
The average mat was 18 in (std 6.4) long, 10 in (std 2.4) wide, and a mere 1 in (std 0.4) deep. The average measured volume was 255 in^3 (std 143) and was estimated to be composed of 2 (std 1) harvestable mats. While the total measured volume of all 70 mats was 17,854 in^3, if volume had been estimated by multiplying standard mat volume (12x6x2”) by the total number of estimated mats (152), the resulting 21,888 in^3 would have overestimated harvestable volume by 23%. The volume of fully 68% of mats was overestimated using this thumb estimate. The average overestimate was 58 in^3 *per* mat (std 93). Based on these data, a correction factor of 0.81 will be used to downward adjust J. Peck's stand-level harvestable mat estimates for the Stewardship Areas project that were based on the 12x6x2" standard mat volume.

Given that the smallest mats harvested were slightly less than 100 in^3 in volume, and fully 20% of the harvested mats were less than 144 in^3 (the total volume of a 12x6x2" mat), it appears that the standard mat volume of 12x6x2" does not accurately reflect the minimum volume of a harvestable moss mat. During the early stages of the Stewardship Area project, a minimum volume of 12x6x1" was used, but was later adjusted upward on the basis of conversations with commercial harvesters. However, observational evidence suggesting that the operational practice of harvest involves smaller mats than they at first admit is confirmed by these findings. Thus the lower standard mat volume of 72 in^3 more accurately reflects minimum harvestable volumes and will be used in future field estimates of harvestable volume.

These 70 mats weighed 71 g (std 37 g) on average. The average weight *per* unit volume was 0.29 g/in^3 (std 0.07). The average 12x6x2" harvestable mat weighed 34 g (std 9 g). While the total mass of all 70 mats was 5 kg, had the biomass of mats been estimated by multiplying the estimated volume of harvestable mats (21888) by the average weight per unit volume from this project (g/in^3), biomass would have been overestimated by 29%.

Simple linear regressions of mat biomass on actual measured mat volume provides models that can be used to predict the mass of mats of known volume (Figure C). In the case of the models for the number of mats, back-transforming (i.e., taking e to the power of the solution to these equations) will result in the median value for biomass rather than the mean. For instance, using the bottom graph, the median weight of a volume of moss equivalent to five standard 12x6x2" harvestable mats would be approximately 0.50 lbs at 15% moisture content (95th percentile confidence interval from 0.32-0.78 lbs).





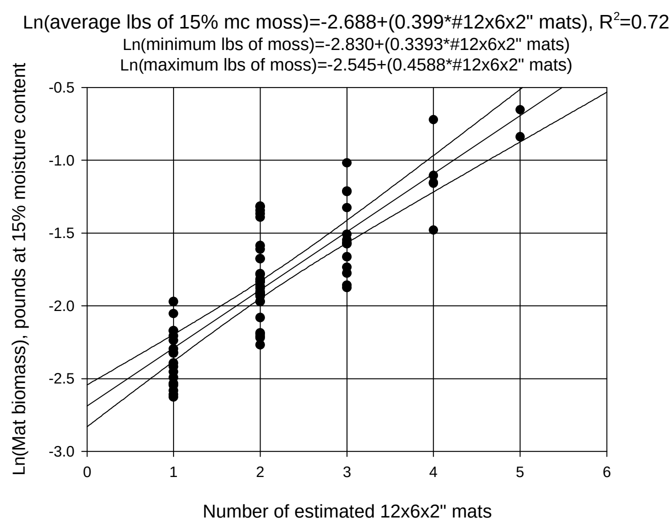


Figure C. Regression equations for predicting moss mat biomass from estimated mat volume or the estimated number of 12x6x2" mats.

Stand-level estimates, however, would require stand-level calibration.