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Research paper

Recovery and diversity of the forest shrub community 38 years after biomass harvesting in the northern Rocky Mountains

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ABSTRACT

We investigated the long-term impact of biomass utilization on shrub recovery, species composition, and biodiversity 38 years after harvesting at Coram Experimental Forest in northwestern Montana. Three levels of biomass removal intensity (high, medium, and low) treatments combined with prescribed burning treatment were nested within three regeneration harvest treatments (shelterwood, group selection, and clearcut). Four shrub biomass surveys (pre-treatment, 2, 10, and 38 years after treatment) were conducted. Shrub biomass for all treatment units 38 years after treatment exceeded the pre-treatment level, and biomass utilization intensity did not affect shrub recovery (ratio of dry biomass at time *t* to pre-treatment biomass). Species composition changed immediately after harvesting (2 years); however, the species composition of treated units did not differ from the untreated control 38 years after harvesting. Biodiversity indices (Shannon's and Pielou's indices) also decreased immediately following harvesting, but recovered 10 years after harvesting. The responses of diversity indices over time differed among biomass utilization levels with the high-utilization level and unburned treatment producing the most even and diverse species assemblages 38 years after harvesting. Our results indicate the shrub community is quite resilient to biomass harvesting in this forest type.

1. Introduction

Forest understory vegetation (e.g., herbs, shrubs, tree seedlings, and saplings) plays an important role in temperate forest ecosystems, providing wildlife habitat and food resources, sustaining site productivity, and underlying biodiversity [1–4]. For example, huckleberries are well known as the most important food source of grizzly bear (*Arctos ursus)* in Montana [5]. In addition, shrubs and understory herbs serve critical functions in nutrient cycling [1,6,7]. Abundance of understory vegetation is a critical factor in determining tree growth, especially in early stand development stages [8]. From a biodiversity perspective, understory vegetation comprises a large portion of plant diversity in forest ecosystems [9–11]. Thus, considerable efforts have been devoted to understanding impacts of forest management on understory vegetation structure and composition [4].

Increasing volatile fossil fuel costs and concerns about climate change have raised public interest in utilizing forest biomass as a renewable alternative energy feedstock. As a result, more intensified biomass harvesting trials beyond whole-tree harvesting are being conducted in North America (e.g., [12–14]). However, logging activity for increased woody biomass utilization inevitably involves a greater magnitude of soil disturbance and nutrient export [15]. Furthermore, logging activity may result in understory vegetation mortality and an altered microclimate [16]. Therefore, increased woody biomass utilization can also impact understory vegetation dynamics and consequently alter forest ecosystem functions.

However, knowledge gaps exist regarding the long-term impacts of biomass utilization on understory vegetation. The majority of such studies have focused on overstory vegetation or belowground layers, and several on-going studies are not mature enough to yield long-term assessments of increased biomass harvesting in North America (e.g., Long-Term Soil Productivity research network [17]). Long-term studies – spanning decades rather than years – acquire an exceptional importance in evaluating the biomass harvesting impacts, because long-term assessment provides a critical asset for understanding complex changes in forest ecosystem function and structure. Knowledge gaps in the northern Rocky Mountain forest are especially great; mill closures in the pulp and

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panel sectors has degraded the industrial infrastructure for intensive biomass harvesting, and has thereby limited opportunities to evaluate harvested sites and compare them to other forms of forest management (including prescribed fire).

In 1974, an interdisciplinary research project was conducted at the USDA Forest Service, Rocky Mountain Research Station's Coram Experimental Forest in Montana to evaluate the ecological consequences of intensified biomass harvesting [18]. About four decades later, this historical research project can now provide clues to the long-term impact of biomass harvesting on understory vegetation. The objective of this study was to identify whether biomass utilization intensity alters understory shrub dynamics. For this, we investigated the temporal changes of shrub recovery (ratio of dry biomass at time t to pre-treatment biomass), species composition, and diversity over time (pre-harvest, 2, 10, and 38 years after harvest) at four different levels of biomass utilization intensity.

2. Methods

2.1. Study site

The study was conducted at Coram Experimental Forest (CEF), on the Flathead National Forest in northwestern Montana. The experimental units were established on an east-facing slope in Upper Abbot Creek Basin (48°25′ N, 113°59′ W), ranging in elevation from 1195 to 1615 m asl, and from 30% to 80% slope. Soils originated from impure limestone, containing approximately 40–80% rock-fragment [19], and classified as loamy-skeletal, isotic Andic Haplocryalfs [20]. Average annual temperature ranges from 2 °C to 7 °C [21], and average annual precipitation is 1076 mm, mainly in the form of snow from late fall to early spring [22]. The climate of CEF is a modified Pacific maritime type [23].

The study was implemented in mature stands (>200 years without any harvesting history) of the Western Larch cover type (Society of American Foresters Cover Type 212 [24]). The pre-harvest overstory consisted of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western larch (*Larix occidentalis* Nutt.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and western white pine (*Pinus monticola* Dougl.) [25,26].

The understory vegetation of the study site is typified by queencup beadlily (*Clintonia uniflora* (Menzies ex Schult. & Schult. f.) Kunth), wild sarsaparilla (*Aralia nudicaulis* L.), and bunchberry dogwood (*Cornus canadensis* L.) [27], including prostrate shrubs such as twinflower (*Linnaea borealis* L.) and Oregon boxleaf (*Paxistima myrsinites* (Pursh) Raf.) [27,28]. Heartleaf arnica (*Arnica cordifolia* Hook.) and beargrass (*Xerophyllum tenax* (Pursh) Nutt.) are the characteristic perennial herbs. The forest is subject to various disturbances including fire, insect, and wind-throw [27]. The fire regime of the study site can be classified as mixed-severity with 90–130 years of (stand-replacing) fire-free interval [29], indicating that structurally and compositionally complex forests have been constructed by fires of various severities [27].

2.2. Experimental design

The experiment was conducted with a split-plot design, in which sub-plot treatments were nested within a whole-plot (Fig. 1). Three kinds of regeneration harvest treatment (shelterwood, group selection, and clearcut) plus an uncut control were implemented at the whole-plot level. The treatments were replicated twice, one per elevation block (lower block at 1195 m to 1390 m, and upper block at 1341 m to 1615 m). The average pre-harvest volume of aboveground woody material was 512 m^3 ha^{-1}.

Thus, the regeneration harvest units consisted of:

1. Two shelterwood units (14.2 and 8.9 ha in size): Based on merchantable volume, approximately half of the standing timber was harvested. The retained trees were primarily old-growth larch or Douglas-fir, and those overstory trees were left uncut. Thirty six percent of total woody biomass was removed.
2. Two clearcut units (5.7 and 6.9 ha): All standing timber was cut, 84% of total woody materials were removed.
3. Two group selection units, each unit contains eight cutting gaps (0.1–0.6 ha, 0.3 ha on average): All standing timber was cut within gap, 70% of total woody materials were removed.

At the sub-plot (hereafter, "biomass utilization treatment") levels, three levels of biomass utilization intensity (high, medium, and low) combined with post-harvest burning treatment (burn and unburned) were randomly assigned. The original experimental design was not able to adopt a full-factorial design, because the low biomass utilization level resulted in too large fuel load for the unburned treatment, whereas the high biomass utilization left too little fuels for burning. As a result, M_U (medium/unburned), H_U (high/unburned), L_B (low/burned), and M_B (medium/burned) were implemented as the biomass utilization treatments (see Table 1 for experimental design details).

In 1974, trees were hand-felled and removed via a running skyline yarder to minimize soil disturbance. Subsequent broadcast burning was applied in the fall of 1975. However, due to cool and wet weather condition, the burning treatment was not implemented in lower shelterwood unit [30,31]. Thus, an additional biomass utilization treatment (i.e., low/unburned) occurred in the lower shelterwood unit, but was excluded from this study's data analysis to remain consistent and avoid analytical problems during model construction.

There was no subsequent entry or disturbance, thus the study sites have been conserved intact. Thirty years after harvesting, the regeneration biomass reached 56.1, 34.5, and 19.7 Mg ha^{-1} for the clearcut, group selection, and shelterwood, respectively [32]. The biomass of residual trees in the shelterwood was 116.5 Mg ha^{-1}, and in the control was 194.6 Mg ha^{-1} [33].

2.3. Data collection and analysis

In the shelterwood, clearcut, and control units, ten permanent sample points were systematically located in 5 × 2 (row × column) grids within each sub-plot (i.e., biomass utilization treatment sub-plots), at 30.5 m spacing. In the group selection units, five permanent points were installed in each cutting gap (8 gaps per replicate) at various distances, depending on the size of gaps. Therefore, a total of 40 permanent points were assigned in each of the 3 regeneration harvest units per replicate, for a total of 280 points.

Measured crown volumes or root-collar diameters were used to compute shrub biomass. In 1973, 1976, and 1984, shrub crowns were measured for each species using a nested quadrat system. Shrub volume was assumed as a cylindroid; thus, two diameters of the ellipse (projected area of crown) and height were measured. In 2012, a nested circular sampling system was utilized. Instead of measuring shrub crown volume, root-collar diameter for every stem was measured via digital caliper because the diameter often shows better prediction for shrub biomass [34,35]. Data were collected from four permanent points (3rd, 4th, 7th, and 8th) out of ten points. Plot sizes and measured shrub size classes are described in Table 2. This methodological choice and its potential effects on the interpretation of results are discussed in the next section.

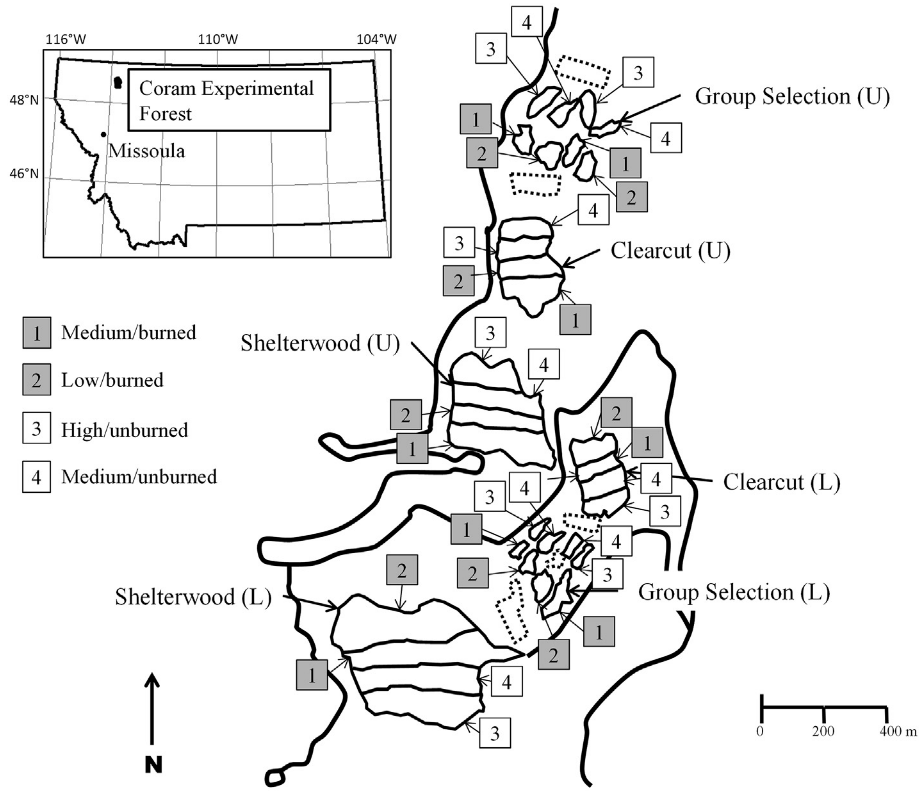

Fig. 1. Study site and the experimental units. The upper (U) and lower (L) replicates were indicated by letters following regeneration harvest. Numbers inside boxes represent biomass utilization treatments (sub-plot treatment). Dotted lines represent the uncut controls.

Table 1
Biomass utilization treatments within regeneration harvest units.

Utilization treatment	Utilization intensity	Burning treatment	Cut trees[a]	Max. Size of retained woody materials[b]	Removed woody material volume (%)
Medium-unburned (M_U)	Medium	Unburned	>17.8 cm dbh	7.6 cm × 2.4 m	62.9
High-unburned (H_U)	High	Unburned	All trees	2.5 cm × 2.4 m	72.3
Low-burned[c] (L_B)	Low	Burned	All trees	14.0 cm × 2.4 m	54.2
Medium-burned (M_B)	Medium	Burned	All trees	7.6 cm × 2.4 m	65.6

[a] Except designated overstory shelterwood trees.
[b] Live and dead down logs (small-end diameter × length); for dead down logs, they were removed if sound enough to yard.
[c] 1974 Forest Service standards.

Table 2
Plot sizes for vegetation sampling and shrub sizes measured.

Plot type	Measurement year	Plot size	Sampled tree size
Quadrat	1973, 1976, 1984	5.0 m × 5.0 m	≥2.5 m height
		3.0 m × 3.0 m	≥1.5 m and <2.5 m height
		1.5 m × 1.5 m	≥0.5 m and <1.5 m height
Circular	2012	0.80 m (radius)	<1.0 m height
		1.78 m (radius)	≥1.0 m height

We used regression equations to convert shrub volume to dry biomass; the equations were previously derived through destructive sampling performed in the vicinity of the cutting units in 1974 (Table 3; W. Schmidt, unpublished data). Brown's [36] shrub biomass equations were employed for the 2012 measurement, converting root-collar diameter to shrub biomass.

Shrub recovery was computed on a per-plot basis as the ratio of observed shrub (dry) biomass in the measurement year to the pre-treatment (1973) value. Due to violation of assumption for variance homogeneity of residuals, shrub recovery was transformed by natural log. Because the experimental design is a split-plot design, and the variables were measured repeatedly, we constructed a mixed-effects model specified as:

$$y_{ijklm} = \mu + \alpha_i + B_k + \varepsilon_{(1)ik} + \beta_j + \varepsilon_{(2)ijk} + \gamma_l + \varepsilon_{(3)ijkl} + \varepsilon_{ijklm} \tag{1}$$

where y_{ijklm} = log-transformed shrub recovery (log %), μ = grand mean of shrub recovery, α_i = effect of regeneration harvest type i (whole-plot effect), B_k = kth block effect (random effect), β_j = jth biomass utilization treatment effect (sub-plot effect), γ_l = lth measurement year effect, and $\varepsilon_{(1)ik}$, $\varepsilon_{(2)ijk}$, $\varepsilon_{(3)ijkl}$, and ε_{ijklm} are the whole-plot, sub-plot, and (repeated) subject error terms, and the variation among sampling plots in a subplot of a measuring year, respectively. Interaction terms between fixed effects (measurement year × biomass utilization treatment) also were tested.

Non-metric Multidimensional Scaling (NMS) was used to investigate species composition (based on biomass) and its shifts over time. NMS is one of the ordination methods most widely used in plant ecology [37]; it reduces dimensionality of the original data, facilitating the display of multivariate data points. The Bray-Curtis

Table 3
Regression coefficients to predict total live shrub biomass from volume (W. Schmidt, unpublished data). Standard errors for the coefficients were not available.

Species	Species code	Coefficient[a]	R^2
Acer glabrum	ACGL	0.1590	0.91
Alnus viridis ssp. *sinuata*	ALVI	0.1775	0.93
Amelanchier alnifolia	AMAL	0.1403	0.96
Lonicera utahensis	LOUT	0.2702	0.83
Berberis repens	BERE	0.1715	0.68
Menziesia ferruginea	MEFE	0.2292	0.87
Pachistima myrsinites	PAMY	0.4579	0.88
Physocarpus malvaceus	PHMA	0.1477	0.93
Ribes lacustre	RILA	0.1331	0.96
Ribes viscossissimum	RIVI	0.1824	0.87
Rosa gymnocarpa	ROGY	0.0564	0.93
Rubus parviflorus	RUPA	0.0450	0.92
Salix scouleriana	SASC	0.1479	0.95
Shepherdia canadensis	SHCA	0.3265	0.95
Sorbus scopulina	SOSC	0.1156	0.98
Spirea betulifolia	SPBE	0.1266	0.91
Symphoricarpos albus	SYAL	0.1117	0.95
Vaccinium membranaceum	VAME	0.2532	0.92
Vaccinium myrtillus	VAMY	0.4292	0.91

[a] $\boldsymbol{y} = \beta_1 \cdot \boldsymbol{x}$; where $\boldsymbol{y}$ = shrub biomass (g), and $\boldsymbol{x}$ = shrub volume (m^3).

distance was used for distance matrix construction, and the distances to control for each measurement year were tested. The analysis was conducted through the *vegan* package [38] in R [39].

Species diversity and evenness were evaluated with Shannon's species diversity index (H'; [40]) and Pielou's evenness index (J'; [41]):

$$H' = -\sum p_i \ln p_i \quad (2)$$

$$J' = H'/\ln S \quad (3)$$

where p_i is the relative abundance of *i*th species within a plot, and S is total number of species in a plot. These indices were compared to those indices of the untreated control using equation (1). Shannon's index provides an important quantitative indication measuring species diversity in a community rather than simple count of species number (i.e., species richness), because it can take species richness and evenness (how equally species are distributed) into account simultaneously. All statistical analyses were conducted via R. The *nlme* package [42] was used to fit the mixed effects models, and *multcomp* [43] was used for testing the linear contrasts among the biomass utilization treatments at each measurement period.

3. Results

A total of 19 shrub species was recorded from 1973 to 2012 (Table 3). The major species are Rocky Mountain maple (*Acer glabrum* Torr.; ACGL), Saskatoon serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.; AMAL), Sitka alder (*Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) Á. Löve & D. Löve; ALVI), mallow ninebark (*Physocarpus malvaceus* (Greene) Kuntze; PHMA), dwarf rose (*Rosa gymnocarpa* Nutt.; ROGY), huckleberry (*Vaccinium membranaceum* Douglas ex Torr.; VAME, *Vaccinium myrtilloides* Michx.; VAMY), and white spirea (*Spiraea betulifolia* Pall.; SPBE). ACGL occupied 41% of total shrub biomass; 72% of total biomass was composed of five shrub species (i.e., ACGL, AMAL, ALVI, PHMA, and ROGY).

Understory vegetation recovery of the study site is summarized in Fig. 2. Mean shrub biomass in 1973 (pre-treatment) and in 2012 were 4.7 Mg ha^{-1} (SE: 0.4) and 7.0 Mg ha^{-1} (SE: 0.9), respectively, indicating that after 38 years the shrub biomass exceeded the pre-treatment biomass and increased by about 50% during that time. Although the overgrowth might be partially attributed to the change of sampling scheme in 2012, the ANOVA table for log-transformed shrub recovery (biomass ratio to measures in 1973; log %) indicates no effect of biomass utilization treatment on these values ($p = 0.1665$, Table 4). Increased accuracy of 2012's sampling method seems to compensate for the sampling size reduction in terms of sampling error, thus the increased variance in 2012 attributes likely to the increased mean biomass in 2012, which is a natural phenomenon. The regeneration harvest factor was non-significant ($p = 0.3292$), whereas measurement year was highly significant (as anticipated) ($p < 0.0001$).

The NMS biplot for shrub species composition illustrates the species composition and changes over time at the study site (Fig. 3a). The pre-treatment communities were clustered on the upper-left region of NMS plane. After harvesting and post-harvesting treatments (in 1976), all treated shrub communities shifted to lower regions. In 1984, the shrub communities returned to the pre-treatment conditions. The unburned units (including the control units) are located on the center of NMS plane, whereas the burned units moved to the right region of the plane in 2012. The confidence regions of mean NMS scores for all treatments overlapped (Fig. 3b), thus, we conclude that the species composition of all treatments is not materially different than the untreated control in 2012. Temporal changes in treatment dissimilarity (i.e., Bray-Curtis distance; here, dissimilarity to control) exhibited an immediate peak of dissimilarity after harvesting; thereafter, there was a general convergence to the pre-harvesting states (Fig. 4).

Temporal change in species composition over all treatments sheds additional light on the movement of the NMS coordinates (Fig. 5). Two years after harvesting, the relative abundance (ratio of a species' biomass to total shrub biomass) of AMAL decreased considerably (31%). The relative abundance of ACGL (3%) and VAME (3%) also decreased slightly. On the other hand, the relative abundance of SPBE (13%), ROGY (9%), PHMA (6%), and thimbleberry (*Rubus parviflorus* Nutt.; RUPA) (6%) increased prominently two years after harvesting. Ten years after harvesting (1984), the species composition seemed to have recovered to the pre-harvesting status (Fig. 3a and Fig. 5). Thirty eight years after harvesting (2012), the species composition was similar to 10 years after harvesting, except for Oregon boxleaf (PAMY), which showed a 12% increase in relative abundance from 10 to 28 years after harvesting.

Shannon's diversity index exhibited an immediate post-treatment effect (Table 5). The mean pre-treatment Shannon index was 0.41 (including control, SE: 0.03); after harvesting (in 1976), the Shannon index dropped to 0.33 (SE: 0.03). In 1984, the Shannon index increased to 0.88 (SE: 0.03), and maintained a similar level until 2012 (mean: 0.90, SE: 0.05). The relative Shannon's index (ratio to the index of untreated control) followed the same pattern (Fig. 6a). The ANOVA table for relative Shannon's index indicated that regeneration harvest was not a significant factor (Table 4). On the other hand, biomass utilization level, measurement year, and their interaction were all highly significant ($p < 0.0001$, $p = 0.04$, and $p < 0.0001$, respectively).

The pre-treatment evenness index was 0.37 (including control, SE: 0.02) on average. Even after harvesting, the evenness index remained similar (0.36, SE: 0.03). The index increased in 1984 (0.57, SE: 0.01) and slightly decreased in 2012 (0.48, SE: 0.02). However, the temporal pattern of the relative evenness index showed a close similarity to the relative Shannon's index. The relative evenness index also decreased immediately after harvesting treatment, and recovered in 1984 (Fig. 6b). ANOVA results for the relative evenness indices in 2012 were consistent with those for the relative Shannon index by the utilization treatments. The test result indicated that biomass utilization level, measurement year, and interaction were significant ($p < 0.0001$, $p = 0.38$, and $p = 0.0002$, respectively;

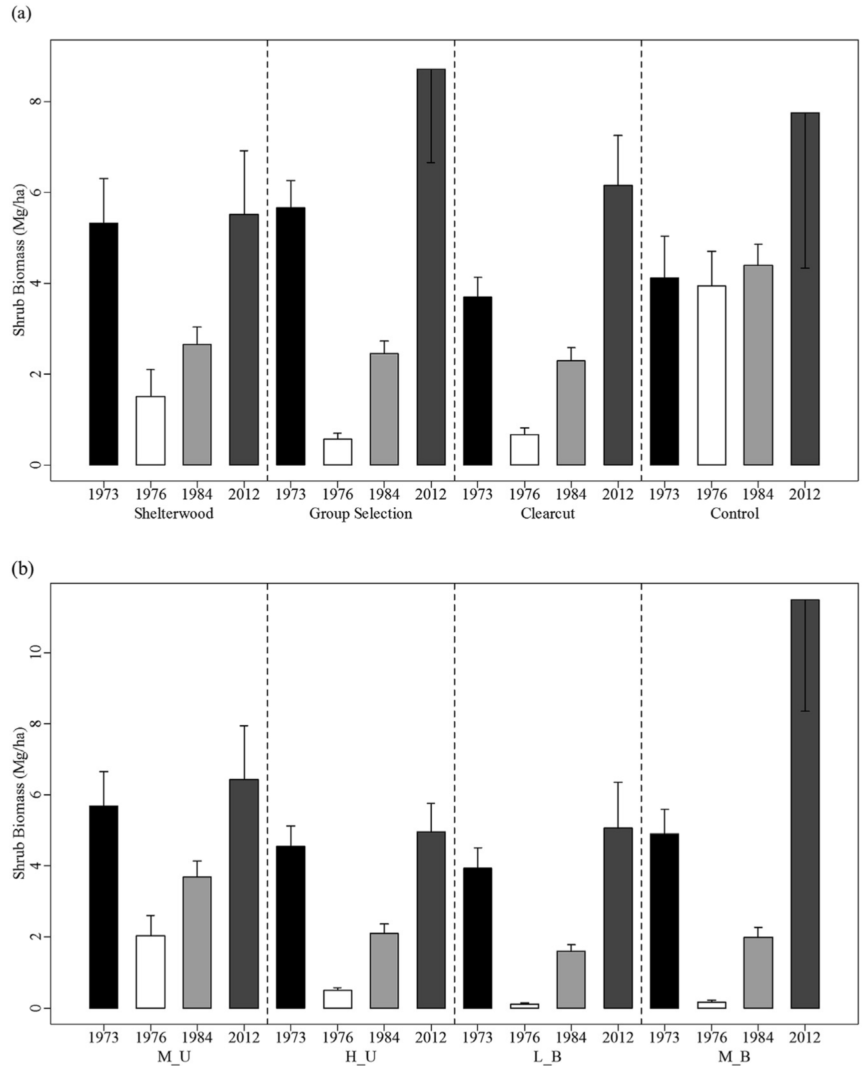

Fig. 2. Shrub biomass recovery according to (a) regeneration harvest and (b) biomass utilization treatment. Error bars stand for standard errors. Abbreviations for the biomass utilization treatments are described in the text and Table 1.

Table 4
Summary of test results for shrub biomass recovery (based on the 1973 measurements), dissimilarity index (Bray-Curtis distance to control), and relative Shannon and Evenness index (based on the untreated control measurement of each year).

Source of variance	df	F Value	P-value
Shrub biomass recovery (log %)			
Measurement year	2	67.130	<0.0001
Regeneration harvest	2	2.037	0.3292
Biomass utilization	3	1.960	0.1665
Dissimilarity Index (Bray-Curtis Distance)			
Measurement year	3	53.083	<0.0001
Regeneration harvest	3	0.790	0.5588
Biomass utilization	4	5.280	0.0016
Measurement year × Biomass utilization	12	1.903	0.0496
Relative Shannon Index			
Measurement year	3	116.565	<0.0001
Regeneration harvest	3	0.862	0.4614
Biomass utilization	4	2.520	0.0416
Measurement year × Biomass utilization	12	6.813	<0.0001
Relative Evenness Index			
Measurement year	3	25.034	<0.0001
Regeneration harvest	3	0.812	0.4884
Biomass utilization	4	1.053	0.3801
Measurement year × Biomass utilization	12	3.182	0.0002

Table 4), and the regeneration harvest treatment was not significant ($p = 0.48$).

Linear contrasts among the utilization treatments for relative diversity indices showed differences from the untreated control in 1973 (Table 6). Except for the M_B utilization treatment, all treatment units had lower species diversity than the control. After two years, burning treatments resulted in a decrease in Shannon index ($p < 0.01$ for L_B, and $p < 0.001$ for M_B, respectively), whereas unburned units exhibited an increase, bringing it to the level of the control. Ten years after harvesting, the Shannon's indices of these burning treatments were recovered to the level of the control. The M_U treatment showed an increase in relative Shannon's index 10 years after harvesting ($p < 0.01$). Thirty eight years after harvesting, the Shannon's index of the H_U treatment was significantly greater than the controls ($p < 0.01$). On the other hand, the relative evenness index tended not to respond to the harvesting and post-harvesting treatment as much as Shannon index. Only the M_U treatment 2 years after harvesting showed significantly lower evenness compared to the control ($p < 0.01$), and the evenness index of the M_U treatment after 10 years harvesting was greater than the control ($p = 0.02$).

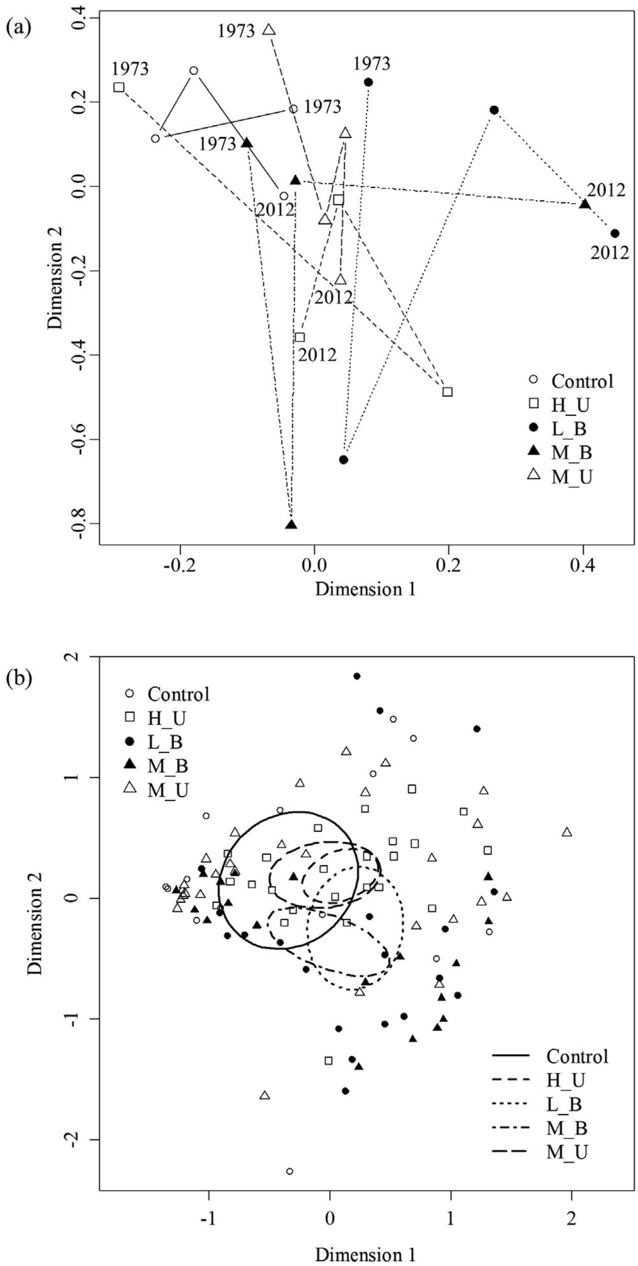

Fig. 3. Biplot of NMS ordination for shrub species drawn by (a) the means of all measurements (1973–2012), and (b) the individual plots of 2012 measurement with 95% confidence regions (ellipses). In Fig. 2a, two unlabeled data points between 1973 and 2012 points represent 1976 and 1984 measurements, respectively. Abbreviations for the biomass utilization treatments are described in the text and Table 1.

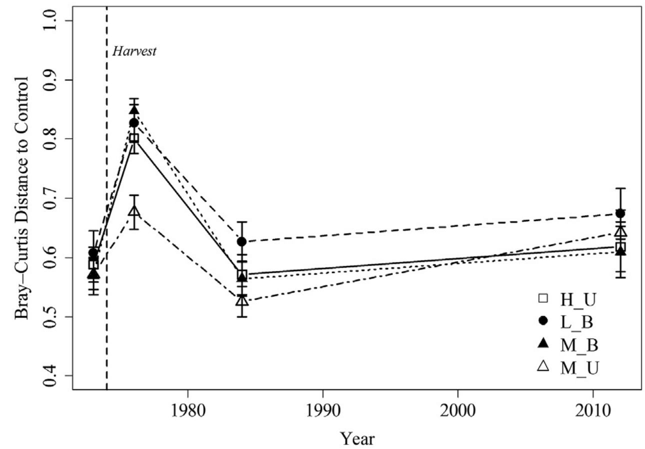

Fig. 4. Dissimilarity indices (Bray-Curtis distance) between the treatments and control for shrub species composition before harvesting (1973) and 2, 10, and 38 years after treatment. Error bars stand for standard errors. Refer to Table 3 for abbreviations.

4. Discussion

4.1. Shrub recovery

In our study, about 50% of total shrub biomass recovered to the pre-harvest levels within 10 years after harvesting. This shrub recovery rate of the study site seems comparable to findings from nearby forests. In a northern Idaho forest, shrub cover was recovered to over half of the pre-harvest level in less than seven years [44]. Lentile et al. [45] found that approximately 15% shrub cover was recovered one-year after a low-severity fire in a northwest Montana forest. It is noteworthy that differences in shrub recovery among the biomass utilization treatments at our study site that were observed at year 4 ([31]) had disappeared by year 10, and remained negligible through year 28. In that early study, Schmidt [31] theorized that the initial responses of the shrub layer were more affected by the biomass utilization treatments than the regeneration harvests. It seems obvious that physical impacts of machinery and prescribed burning plays a more critical role on short-term shrub layer responses than changes in overstory cover (i.e., regeneration harvest). However, that initial impact diminished over time and was undetectable decades following harvest. That is likely because the more intensively disturbed understory grew more rapidly due to abundant growing space and available resources. Thereafter, the effect of treatments on understory vegetation was depressed according to stand development [10]. This result is consistent with those reported by southern United States' Long-Term Soil Productivity Study, which exhibited little impact on understory plant composition 15 years after intensive biomass removal [46].

Thirty eight years after harvesting, the shrub biomass levels exceeded the pre-harvest levels. The positive effect of harvesting on shrub biomass is not surprising because of the increased resource availability (e.g., light, water, nutrient) resulting from canopy disturbance [47–49]. However, as stand development proceeds to the stem exclusion stage [50], we expect that shrub cover will decline and eventually approach control levels. Various studies conducted in nearby northern Rocky Mountain forests maintained that shrub layer biomass production reaches a maximum 10–30 years after the conclusion of harvesting and post-harvesting treatments (e.g., [44,51,52]. Thus, shrub development at this study site may have already reached its maximum level.

We found insufficient evidence for differences in understory recovery among biomass utilization treatments, adding to mounting evidence that there have been no adverse long-term impacts of intensified biomass extraction on productivity (biomass production in a given time) at this study site [32,33]. If intensive biomass utilization treatment had a negative long-term impact on site productivity, then we would have expected a reduction in overstory tree growth, and a concomitant gain in the availability of light, moisture, and nutrients for understory vegetation. Observations of the negative relationship between canopy cover and shrub cover are numerous (e.g., [47,53,54]; but see Ref. [55]). Thus, as site productivity decreases, understory cover will generally increase [10,49]. In a related study, we found that biomass

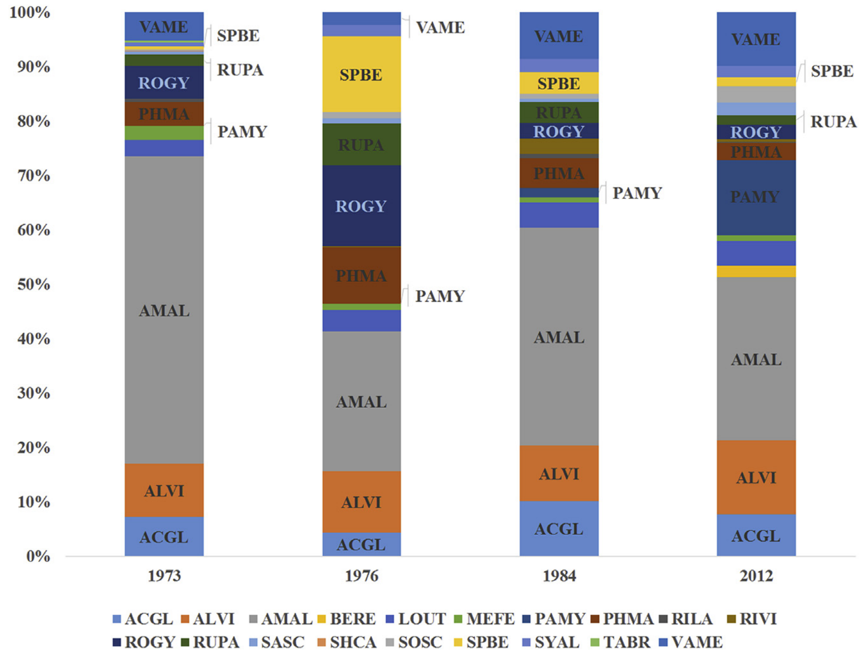

Fig. 5. Relative abundance (species biomass/total shrub biomass; pooled across all treatments) of shrub species before harvesting (1973) and 2, 10, and 38 years afterward. Vertical axis represents mass fraction of each species, and abbreviations for species are provided in Table 3.

Table 5
Mean biodiversity indices (and standard errors) of shrub species pre-(1973) and post-regeneration harvest and biomass utilization treatments.

Treatment	Shannon Index				Evenness Index			
	1973	1976	1984	2012	1973	1976	1984	2012
Regeneration harvest								
Shelterwood	0.31 (0.05)	0.33 (0.05)	0.88 (0.05)	0.95 (0.09)	0.28 (0.04)	0.36 (0.05)	0.57 (0.03)	0.50 (0.05)
Group Selection	0.51 (0.05)	0.32 (0.04)	0.90 (0.04)	0.88 (0.09)	0.44 (0.04)	0.33 (0.04)	0.59 (0.02)	0.48 (0.05)
Clearcut	0.42 (0.04)	0.36 (0.05)	0.86 (0.04)	0.87 (0.07)	0.38 (0.04)	0.39 (0.06)	0.54 (0.02)	0.54 (0.03)
Biomass utilization[a]								
M_U	0.37 (0.05)	0.39 (0.05)	0.86 (0.05)	0.80 (0.10)	0.33 (0.04)	0.38 (0.04)	0.54 (0.03)	0.42 (0.05)
H_U	0.38 (0.05)	0.40 (0.05)	0.91 (0.04)	1.23 (0.08)	0.36 (0.05)	0.41 (0.05)	0.58 (0.02)	0.61 (0.04)
L_B	0.36 (0.05)	0.23 (0.06)	0.76 (0.05)	0.87 (0.08)	0.36 (0.05)	0.31 (0.08)	0.55 (0.03)	0.50 (0.04)
M_B	0.59 (0.06)	0.20 (0.05)	1.00 (0.06)	0.67 (0.09)	0.48 (0.04)	0.26 (0.07)	0.61 (0.03)	0.37 (0.05)
Control	0.55 (0.06)	0.54 (0.05)	0.78 (0.06)	0.70 (0.14)	0.45 (0.05)	0.47 (0.04)	0.51 (0.04)	0.41 (0.08)

[a] M_U: medium/unburned, H_U: high/unburned, L_B: low/burned, M_B: medium/burned (refer to Table 1).

production among biomass utilization treatments did not differ [32,33].

4.2. Shrub species composition

The NMS biplot and temporal change in dissimilarity indices demonstrated drastic changes in species composition after harvesting and burning treatments. Among all treatments, community shift in the M_U treatment was least. Understory vegetation was specifically protected in the M_U treatment [31], so this result is both unsurprising and is a validation of the effectiveness of that prescription in meeting the understory protection goal. Despite initial changes in species composition, the shrub community was restored to pre-treatment condition 10–38 years after harvesting in each treatment, thus the eventual species composition of the shrub layer seems unaffected by biomass utilization. This outcome agrees with the finding of Jenkins and Parker [56], who investigated the impacts of regeneration harvestings (clearcut, group selection and single-tree selection) on understory vegetation composition in central hardwood forests in Indiana. Although there were small differences in understory vegetation cover, seven to twenty seven years after harvesting, the effect of regeneration harvest was not severe enough to cause any fundamental shifts of species composition. In northern hardwood forests of Michigan, understory vegetation composition recovered to the pre-harvest status within 50 years after harvest [57]. In that study, there were drastic changes in understory vegetation species composition and diversity immediately after harvesting (4–5 years), but the effects of regeneration harvest on the understory vegetation dissipated after 50 years. In Wisconsin hardwood forests, neither spring nor summer flora of ground-layer were significantly different among regeneration harvest treatments four decades after harvesting [58]. Furthermore, in a related study, we observed no differences among the four treatments in aboveground biomass production and belowground soil organic matter, and C and N contents [33].

Changes to shrub community composition immediately after harvesting is the cumulative result of each species' individual response to harvesting operations (Fig. 5). AMAL proved to be the most responsive to harvesting. Decades earlier, the reduction of AMAL was significantly more pronounced in the understory protected treatment (M_U) relative to the other biomass utilization treatments [31]. In contrast to AMAL, other large shrubs (such as

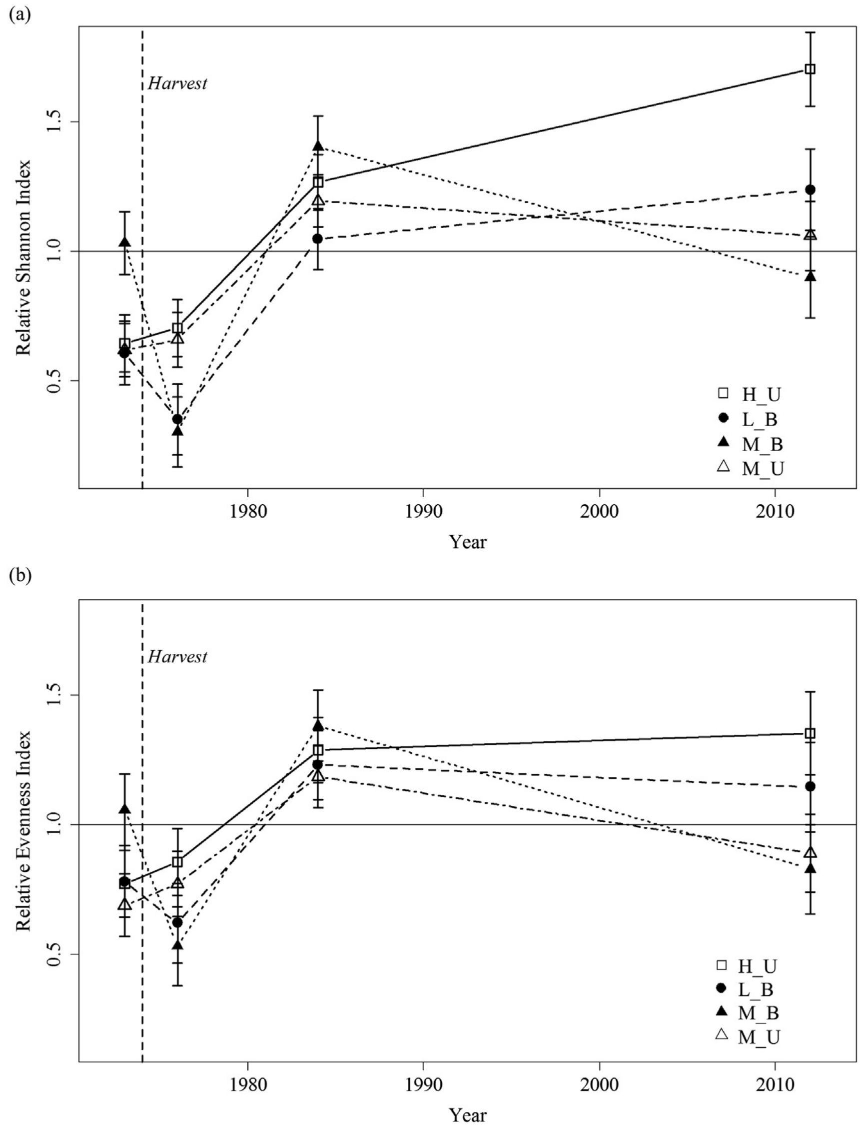

Fig. 6. Relative (a) Shannon's indices and (b) evenness indices (with standard errors) according to each biomass utilization treatment. Abbreviations for the biomass utilization treatments are described in the text and Table 1.

Table 6
Linear contrasts between treatments for relative Shannon's indices and evenness indices.

Linear hypothesis[a]	1973 (pre-treatment)		1976		1984		2012	
	Contrast (SE)	p-value[b]	Contrast (SE)	p-value	Contrast (SE)	p-value	Contrast (SE)	p-value
Relative Shannon Index								
H_U[c] − 1 = 0	−0.36 (0.11)	0.01*	−0.32 (0.14)	0.29	0.24 (0.15)	0.64	0.68 (0.17)	<0.01**
L_B − 1 = 0	−0.39 (0.12)	0.02*	−0.61 (0.17)	<0.01**	0.08 (0.16)	1.00	0.27 (0.19)	0.80
M_B − 1 = 0	0.03 (0.12)	1.00	−1.12 (0.18)	<0.001***	−0.02 (0.17)	1.00	−0.52 (0.20)	0.09
M_U − 1 = 0	−0.38 (0.10)	<0.01**	0.07 (0.15)	1.00	0.61 (0.15)	<0.01**	0.47 (0.18)	0.09
Relative Evenness Index								
H_U − 1 = 0	−0.23 (0.13)	0.51	−0.23 (0.17)	0.82	0.20 (0.16)	0.88	0.27 (0.19)	0.78
L_B − 1 = 0	−0.22 (0.14)	0.67	−0.39 (0.19)	0.34	0.22 (0.18)	0.88	0.14 (0.21)	1.00
M_B − 1 = 0	0.06 (0.13)	1.00	−0.74 (0.19)	<0.01**	0.10 (0.19)	1.00	−0.45 (0.21)	0.31
M_U − 1 = 0	−0.31 (0.12)	0.11	0.14 (0.17)	0.99	0.55 (0.17)	0.02*	0.26 (0.19)	0.84

[a] The contrasts tested the difference of the indices between the biomass utilization level and the control.
[b] Significant codes: 0 < *** < 0.001 < ** < 0.01 <* < 0.05.
[c] H_U: high/unburned, L_B: low/burned, M_B: medium/burned, M_U: medium/unburned (refer to Table 1).

ACGL and ALVI) showed little reduction in relative abundance. We suppose that this is likely due to their relatively higher resistance to machinery damage and vigorous resprouting after harvesting.

Some increases in relative abundance after harvesting are notable. Some species, including ROGY, SPBE, and PHMA, showed immediate increases in their relative abundance 2 years after harvesting. Those species are disturbance-tolerant, early-successional species known to benefit from harvesting [28]. However, their relative abundance decreased with additional years after harvesting. After 10 years, the relative abundance of these pioneer species had returned to pre-harvesting levels. Only the relative abundance of PAMY, which is a late-successional species, significantly increased 38 years after harvesting. A similar observation was reported in northern Idaho, where PAMY cover decreased initially after harvest (year 7), but by 25 years after harvest, it flourished to five times more than the untreated control [44]. This transition illustrates the incrase in shade-tolerant species as the canopy closes and subsequent moisture condition become more favorable [28,59].

4.3. Shrub species biodiversity

As the scope of silviculture has expanded to include restoring and sustaining ecosystem functions and services, species diversity has become one metric to judge a successful silvicultural treatment [58,60,61]. The appropriate application of silvicultural treatments has been shown to be capable of enhancing tree species diversity (e.g., [62–65]). However, the responses of understory diversity to forest management activity show substantial variation not only spatially, but also temporally [61]. Thus, spatial variation and temporal change should be considered when trying to predict the impacts of forest management on understory diversity.

The relationship between disturbance intensity and biodiversity has been frequently addressed by “the intermediate disturbance” hypothesis [66,67]. That hypothesis states that the highest biodiversity levels are maintained at an intermediate disturbance intensity, because that intensity of disturbance can preserve the species that are relatively less competitive at the extreme levels (low and high) of disturbance intensities. Empirical trials using various thinning intensities have corroborated this hypothesis. For example, a study in spruce-hemlock forests of the coastal Oregon showed that a heavy thinning operation decreased understory vegetation diversity, whereas the diversity often increased at the moderate thinning intensity [2]. In this study, we observed that the high biomass utilization level (H_U) exhibited the highest shrub diversity 38 years after harvesting. We speculate that the high utilization treatment prevented a single large sprouting shrub species (i.e., ACGL) from dominating the understory layer and thereby allowed a greater diversity of species to become established. Since the yarder-based logging system minimized understory disturbance, we contend that the high biomass utilization level of this study falls on the intermediate range of disturbances.

In addition, we observed the lowest ACGL relative abundance and the highest ALVI relative abundance in the L_B treatment. Although this finding did not result in a statistically significant difference in biodiversity, the L_B treatment exhibited the second highest shrub diversity as measured by the Shannon index. This observation indicated that ALVI benefitted by the broadcast burning treatment. On the other hand, the relative abundance of ALVI decreased in the M_B treatment, whereas the relative abundance of ACGL increased. These trends suggest that biomass utilization intensity and burning treatment interact with each other. However, due to our unbalanced experimental design, statistical testing for the interaction with separation (i.e., utilization intensity $\times$ burning treatment) was impossible in this study. The results of this study can provide a clue for tailoring understory responses to biomass harvesting and burning treatment in this region. However, a better understanding is still needed of the impacts of ground-based biomass harvesting methods and their interaction with burning treatments on understory vegetation.

5. Conclusion

Total shrub biomass 38 years after biomass harvesting was greater than that of the control. The recovery of the shrub layer did not differ among biomass utilization intensities. There was a considerable change of species composition immediately after harvesting, but species composition seemed to recover about four decades after harvesting. We speculate the burning effects outrank the cutting effects, because the high-utilization but unburned treatment produced the highest species diversity. Overall, the study provides evidence of high resilience of the shrub community to biomass harvesting in this region.

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