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Vegetative and Edaphic Responses in a Northern Mixed Conifer Forest Three Decades after Harvest and Fire: Implications for Managing Regeneration and Carbon and Nitrogen Pools

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Abstract: Research Highlights: This experiment compares a range of combinations of harvest, prescribed fire, and wildfire. Leveraging a 30-year-old forest management-driven experiment, we explored the recovery of woody species composition, regeneration of the charismatic forest tree species *Larix occidentalis* Nutt., and vegetation and soil carbon (C) and nitrogen (N) pools. **Background and Objectives:** Initiated in 1967, this experiment intended to explore combinations of habitat type phases and prescribed fire severity toward supporting regeneration of *L. occidentalis*. At onset of the experiment, a wildfire affected a portion of the 60 research plots, allowing for additional study. Our objective was to better understand silvicultural practices to support *L. occidentalis* regeneration and to better understand the subsequent impacts of silvicultural practices on C and N pools within the vegetation and soil. **Materials and Methods:** We categorized disturbance severity based on loss of forest floor depth; 11 categories were defined, including controls for the two habitat type phases involved. We collected abundance, biomass, and C and N concentrations for the herbaceous layer, shrubs, and trees using nested quadrats and 6 to 10 experimental units per disturbance category plot. Moreover, we systematically sampled woody residue from transects, and forest floor, soil wood, and mineral soil with a systematic grid of 16 soil cores per disturbance category plot. **Results:** We found that (1) disturbance severity affected shrub species richness, diversity, and evenness within habitat type phases; (2) *L. occidentalis* regenerates when fire is part of the disturbance; (3) N-fixing shrub species were more diverse in the hotter, drier plots; (4) recovery levels of C and N pools within the soil had surpassed or were closer to pre-disturbance levels than pools within the vegetation. **Conclusions:** We confirm that *L. occidentalis* regeneration and a diverse suite of understory shrub species can be supported by harvest and prescribed fire, particularly in southern and western aspects. We also conclude that these methods can regenerate *L. occidentalis* in cooler, moister sites, which may be important as this species' climate niche shifts with climate change.

Keywords: carbon pools; even-aged management; harvesting; *Larix occidentalis*; nitrogen pools; prescribed fire; regeneration; soil; wildfire

1. Introduction

Forest ecosystems are dynamic, driven by disturbance that occurs commonly rather than rarely, and that encompasses a range of spatial, temporal, and severity combinations [1]. The structure, composition, and spatial arrangement of many forested ecosystems, from tropical to boreal, is a

function of disturbance by wildfire [2]. In the mountainous regions of the western United States (USA), the dynamic composition of forested landscapes is a result of ubiquitous wildfire disturbances interacting with insects, diseases, and weather [3,4]. The resulting myriad of fire characteristics yields an immense range of disturbance patterns across the landscape [5]. These patterns increase forest heterogeneity, which in turn promotes biodiversity and subsequently contributes to forest resilience [6,7].

On one hand, modern silvicultural techniques, such as thinning, harvesting, and prescribed fire, can mimic natural disturbances and implementing these techniques can allow land managers to effectively control species composition, structure, spatial arrangement, and forest function to meet management objectives [8,9]. On the other hand, exclusion of natural disturbances (e.g., wildfire suppression), which in the case of fire has predominated the landscape in the western USA [10], can alter species composition and stand structure. Lacking implementation of other management activities, these altered conditions can lead to more extreme severities of insect infestation and wildfire [11] and are expected to be exacerbated by changes in climate [12]. Thus, returning fire to fire-adapted landscapes is a major focus of forest restoration [9,13].

Returning fire to the landscape is exemplified in the mixed-conifer forests of the northern Rocky Mountains of the western USA, where *Larix occidentalis* Nutt. is an ecologically and commercially key early seral species occurring after high-severity fires [14–16]. Historically, these fires occurred frequently in higher elevation *Abies lasiocarpa* (Hook.) Nutt. forest types [17]. Despite observations that more severe fires led to exposed mineral soil and regeneration of valuable *L. occidentalis*, northern Rocky Mountain forests have been protected from natural fire cycles for decades, resulting in slow or absent regeneration of the species [18]. Recognizing a loss of *L. occidentalis* across the landscape, prescribed fire has been a major management tool to facilitate its regeneration, particularly after harvest activities [18].

Although the pathways of forest succession after harvest and prescribed fire treatments have been studied, e.g., [19], limited information is available on how specific combinations of harvesting and fire, either prescribed or wild, affect carbon (C) and nitrogen (N) storage and cycling. Repeated harvest and prescribed fire can significantly alter succession and reduce nutrient storage and recovery time in other forest types, even for several decades. Conversion of old-growth stands to plantations decreases the total stored C in the ecosystem, and recovery to pre-harvest levels can be slow (>200 years) in the coniferous forests of the Pacific Northwest and northern Rocky Mountains USA, depending on how much organic matter (OM) is removed and how much soil disturbance occurs during harvesting [20,21]. In a mixed deciduous temperate forest, stands harvested and burned twice in a 60-year period stored approximately 45% less C annually than stands receiving the same treatments only once [22]. Even whole-tree harvesting for biomass production may have only minor long-term effects on mineral soil C stocks if forest floor (inclusive of all O horizons) is left undisturbed [21,23].

Of the studies conducted on temperate coniferous forests, Bisbing et al. [24] evaluated total C storage and found that old-growth *L. occidentalis* forests in North America stored 3 times more than second-growth stands, similar to other forests in the Pacific Northwest USA [20,25]. The amount of C storage varied, however, depending on the ecosystem components. For example, mineral soil C was not different among the two stand types, but the forest floor of the old-growth stand had nearly 5 times more C compared to the second-growth stand. Harvesting caused a dramatic reduction of the overall ecosystem C levels, with little recovery after 3 to 5 decades. Their results suggest that for water-limited forests where C recovery times following harvest are long, stored C can be maintained via the increased retention of large live trees, snags, and woody debris. Optimum C sequestration is dependent on rotation length, the amount of material harvested, and the amount of slash burning [26].

Increased biomass removal may have undesirable impacts on soil and site productivity, biodiversity, and atmospheric systems [27]. The impacts and effects of intensive harvest removals have been addressed [28], but it is concerning that intensive biomass removals coupled with prescribed fire may deplete nutrient reserves, particularly N [29]. As a powerful and instantaneous modifier of the

environment, fire can have a profound effect on both short- and long-term nutrient cycles [30,31]. Loss of N after fire can limit site productivity. Nitrogen is one nutrient that is easily lost due to combustion of organic matter [32–34]. It follows that reducing the surface organic horizon depth and mineral soil organic matter levels can alter N availability, cycling, and belowground biodiversity [35]. Soil OM loss may be the chief factor in ecosystem productivity decline after severe disturbance [36,37]. In many cases, most site nutrients (including C) are contained in the forest floor and surface mineral soil [29,38,39]. Organic matter on the soil surface and in the mineral soil increases aeration, cation exchange capacity [40], and soil aggregation [41]; buffers pH changes [35]; and provides food and habitat for soil meso- and micro-fauna [42]. Therefore, quantifying changes in C and N is essential to understanding the long-term effects of disturbances and management practices on ecosystem recovery and function [43]. Knowing how harvest and fire treatments translate to C and N cycling and storage in northern Rocky Mountain forests will provide information for land managers to make informed decisions. This is especially true for managing *L. occidentalis* forests where changes in climate are expected to alter their adaptation properties and subsequent distribution [44].

As noted earlier, prescribed fire conditions for optimal regeneration of *L. occidentalis* have been a major management concern in the northern Rocky Mountain region for decades. In 1967, a large-area (240 ha) study was initiated by the United States Department of Agriculture, Forest Service to evaluate the effect of prescribed burning at various times of the year on the establishment and growth of *L. occidentalis* following clearcut harvesting. During the summer of 1967, however, a wildfire burned through some experimental plots that had already experienced prescribed fire and through some plots awaiting treatment. Consequently, the effects of wildfire were incorporated into the study plan and subsequent measurements [19,45]. This management-driven “Miller Creek Study” yielded seminal science on fire behavior, smoke management, silviculture (including regeneration), post-fire plant succession, small mammal populations, soil properties, watersheds, and their interactions, as summarized in [46,47]. Therefore, our study objective was to leverage this robust study and measure changes in plant communities (species composition and biomass) and soils (C and N pools) in selected plots after 30 years in different habitat type phases in combination with harvesting and fire.

We tested three hypotheses and their corollaries. Our first hypothesis was that increasing levels of disturbance severity would increase species richness, diversity, and evenness. The first corollary was that the increases would be more apparent in mesic sites than in xeric sites, as identified by habitat type phase. The second corollary was that disturbance severity would influence the presence and abundance of N-fixing plant species and their influence on soil N pools. Our second hypothesis was that *L. occidentalis* would regenerate more prevalently in more severely disturbed sites. The corollary was that initial conducive site conditions following disturbance would support immediate and longer-term recruitment. The third hypothesis was that disturbance severity strongly affects long-term recovery of C and N pools. This hypothesis had three corollaries: (1) above- and belowground C pools, but not N pools, increase as fire severity decreases; (2) above- and belowground N pools increase with increasing fire severity; and (3) recovery of C and N pools in the forest floor will be different from those in the mineral soil.

2. Materials and Methods

2.1. Site Location and Original Characteristics

Our study site is located in the Miller Creek and Martin Creek drainages in the Miller Creek Demonstration Forest (between latitudes 48.5 and 48.558333 and longitudes -114.643056 and -114.730278) in the Flathead National Forest near Olney in northwestern Montana, USA (Figure 1). Elevations range from 1280 to 1524 m. Soils are loamy-skeletal, isotic Andic Haplocryalfs of the Sherlock series consisting of very deep, well-drained soils formed in glacial till with a mantle of volcanic ash [48]. The horizons include an unincorporated surface organic layer (2.5 to 7.6 cm thick), above a silt loam of single-grain structure (1.3 to 2.5 cm thick), above a gravelly loam (30 cm thick), and finally above a very

stony loam that extends to depths ≥ 1.8 m [46]. Topography is gentle, with slopes ranging from 9 to 35%, with an average of 24% [45]. The original forest cover types were defined as *L. occidentalis* (Western Larch #212) and *Picea engelmannii* Parry ex Engelm.–*Abies lasiocarpa* (Engelmann Spruce–Subalpine Fir #206) [49]. Because the site has a relatively uniform, cool, moist environment with 640 mm of annual precipitation (65% as snowfall), the *Abies lasiocarpa*/*Clintonia uniflora* (Menzies ex Schult. & Schult. f.) Kunth habitat type predominates [50]. Within this habitat type, a *Menziesia ferruginea* Sm. (MEFE) phase occurs on the moister north- and east-facing slopes, whereas a *Xerophyllum tenax* (Pursh) Nutt. (XETE) phase occurs on the drier south- and west-facing slopes.

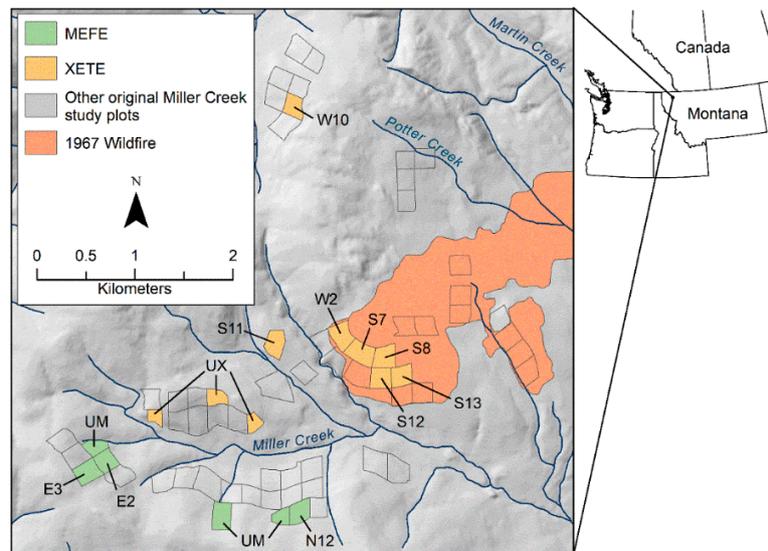


Figure 1. During 1967, a study was established in northwestern Montana, in the northwestern portion of the USA, with 15 original 4.05-ha plots on each of four cardinal aspects (60 plots total), with the intention to examine the effects of combinations of harvesting and prescribed fire on conifer regeneration, particularly *L. occidentalis*. The 1967 wildfire burned or re-burned some of the original plots. In 1996, we selected proximate stands of undisturbed forest in the *Menziesia ferruginea* (MEFE) and *Xerophyllum tenax* (XETE) phases within the *Abies lasiocarpa*/*Clintonia uniflora* habitat type and relocated 9 of the original study plots with various combinations of habitat type phase, anthropogenic activity (undisturbed or harvested stands with or without prescribed fire), and a stochastic event (wildfire) to obtain 11 distinct disturbance categories. See Table 1 for plot identifications and descriptions. Adapted from [46] (p. 6) and [51] (p. 6).

Table 1. Designations and descriptions of original Miller Creek Demonstration Forest sites in northwestern Montana, USA, including the timing of harvest and fire events, forest floor levels immediately before and after disturbance(s), and numbers of experimental units and soil cores per resulting disturbance category.

Phase ^a and Disturbances	Original Designation		1967–1968 Disturbance(s)					1996 Measurements		
			Clearcut Harvest and Slashed (1967) ^{b,c}	Prescribed Fire ^b	Wildfire (1967) ^{b,c,d}	Forest Floor ^e		Water Loss from Cans ^d	Experimental Units	Soil Cores
						Pre-burn	Post-burn			
						–(Mg ha ⁻¹)–	(g)	(n)	(n)	
<i>Menziesia ferruginea</i>										
Harvest (H)	East 2	E2	Oct	No	No	103.0	103.0	-	10	16
H + Prescribed Fire (P)	East 3	E3	October–November	7 August 1968	No	94.9	40.4	940	10	16
HP	North 12	N12	February–March	3 August 1967	No	26.7	2.3	1062	10	16
Control (C)	UM ^f	UM	No	No	No	-	-	-	30	48
<i>Xerophyllum tenax</i>										
H	South 11	S11	Yes	No	No	51.5	51.5	-	6	16
HP	West 10	W10	September–October	16 July 1968	No	46.9	22.2	519	10	16
H + Wildfire (W)	South 7	S7	May	No	23 August	47.2	13.2	1382 ^j	10	16
HPW	South 8	S8	April–May	8 August 1967	23 August	44.3	7.1 ^h	784 ^k	10	16
HW	West 2	W2	March–May	No	23 August	48.3	1.2	1473 ^j	10	16
W	South 12/13	S12/13	No	No	23 August	46.6	<0.5 ⁱ	-	12	32
C	UX ^g	UX	No	No	No	-	-	-	30	48

^a Phase within *Abies lasiocarpa*/*Clintonia uniflora* habitat type [50]; ^b [45]; ^c [51]; ^d [18]. See methods [45,52]. Original water mass = 3 kg. ^e DeByle’s unpublished data, unless otherwise noted. ^f Undisturbed forest adjoining East 2, North 8, and North 12. ^g Undisturbed forest adjoining West 1, South 1, and South 9. ^h The prescribed fire reduced forest floor by 58% (DeByle’s unpublished data) and the wildfire further reduced it to a total of 84% [53]. ⁱ Forest floor reductions were “about 100%” [53] and “100%” [19] (p. 67, Table 1, Wildfire). ^j Stands burned 23 August 1967 [18] and are listed in [45] (p. 45) under “burned by prescription”. ^k Water loss value for the prescribed fire (see footnote d above). We assume that these units had been prepared (i.e., filled water cans installed) for prescribed burning but burned in the wildfire, and thus the wildfire was classified as the prescribed fire [45]. Given the fire danger (buildup index = 239, classed as “extreme” by the National Fire Danger Rating System [54] and [45] (p. 48, Appendix D: Weather Summaries)) and the unfavorable wind conditions (see the Thursday, 24 August 1967, front page account titled “Fire Erupted Tuesday Afternoon” in *The Daily Inter Lake* (Kalispell, Montana) newspaper), prescribed fire would likely have been avoided. ^k Water loss value for the prescribed fire (see footnote d above).

2.2. Original Study Design

During 1966 and 1967, fifteen 4.05 ha plots were established on each of the four cardinal aspects (60 plots total) to examine the effects of combinations of harvesting and prescribed fire on conifer regeneration, especially for *L. occidentalis* (Figure 1). The original stands, composed mainly of 200- to 250-year-old *L. occidentalis* (26%), *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Mayr) Franco (31%), and *Picea engelmannii* (31%) trees in nearly equal volumes, averaged $143 \text{ m}^3 \text{ ha}^{-1}$ [45]. These stands reflected little to no post-European-settlement disturbance and were either left undisturbed or clearcut. Clearcutting was done by hand; the trees were directionally felled, limbs were removed, and logs were cut to length. Logs were dragged to landings using a stationary tractor-mounted, two-winch cable logging system along designated “skid trails” that were at least 200 m apart. Logging residue was spread evenly across each plot by the hand crew in combination with felling of unmerchantable trees, so that fuel loads would be as uniform as possible [45]. Two levels of prescribed fire (yes or no) were employed during different seasons to achieve various fire severities [45]. The average post-harvest fuel loads were 234 Mg ha^{-1} , with about 88% being coarse debris $>10 \text{ cm}$ in diameter [55]. To create a mostly uphill-leading prescribed fire, ignition began in the late afternoon or early evening at the upper edge of a plot, then downslope along the sides, and finally across the bottom [45]. A wildfire on 23 August 1967 burned or re-burned many of the plots, creating a mosaic of unplanned and anthropogenic impacts across the watershed.

2.3. Field Sampling

In both habitat type phases and proximate the original study plots, we identified stands of undisturbed forest. Using combinations of habitat type phases (MEFE or XETE) and anthropogenic (undisturbed or harvested stands with or without prescribed fire) and stochastic (wildfire) history, we defined 11 distinct disturbance categories. Each category was defined by relative fire severity, which was based on loss of forest floor measured immediately pre- and post-disturbance (1967 or 1968) rather than on water loss using water can analogs (Table 1; [52]) because forest floor data were more complete. Each original 1967 study plot represented a single disturbance category, except for South 12 and South 13, which we combined into a single disturbance category (South 12/13). Within each disturbance category, we systematically placed 6 to 30 experimental units to measure a variety of vegetative metrics and at least 16 soil cores in a systematic grid (Table 1). Between the initial harvest and fire events (1967–1968) and our measurements (1996–1998), some of the disturbance categories had portions treated with other silvicultural practices (i.e., tree planting, thinning [56]); we avoided these treated portions.

2.3.1. Vegetation

Aboveground

Each experimental unit was a nested quadrat [57]. Within the largest quadrat ($15 \text{ m} \times 15 \text{ m}$) we situated a $4 \text{ m} \times 4 \text{ m}$ quadrat on the downslope corner (northeast for the northern aspect, southeast for the eastern aspect, southwest for the southern aspect, and northwest for the western aspect). Similarly, a $1 \text{ m} \times 1 \text{ m}$ quadrat was placed on the downslope corner of the $4 \text{ m} \times 4 \text{ m}$ quadrat, with a second $1 \text{ m} \times 1 \text{ m}$ quadrat established in the diagonally opposite corner of the $15 \text{ m} \times 15 \text{ m}$ quadrat (Figure 2).

Within each $15 \text{ m} \times 15 \text{ m}$ quadrat, we measured trees (basal diameter $> 5 \text{ cm}$) by species (Table 2) at diameter breast height (DBH; 137 cm above ground level). Standing dead trees were measured and identified to species. Within each $4 \text{ m} \times 4 \text{ m}$ quadrat, we measured basal diameters of tree seedlings ($<5 \text{ cm}$ basal diameter; hereafter “seedlings”); dead seedlings were not identified to species. We also measured shrubs $\geq 50 \text{ cm}$ in height by species (see Table 2 for shrub and tree nomenclature) 2 cm above ground level at seven intervals: ≤ 0.5 , 0.51–1.0, 1.01–1.5, 1.51–2.0, 2.01–3.0, 3.01–5.0, and >5.0 [58]. Dead shrubs were measured but not identified. We removed a branch ($\geq 5 \text{ cm}$ in length) from the upper crown of each seedling and shrub (including dead) for further analysis. In each $1 \text{ m} \times 1 \text{ m}$

quadrat, all aboveground vegetation was harvested (except lichens and moss, shrubs taller than 50 cm), hereafter named “herbaceous” vegetation.

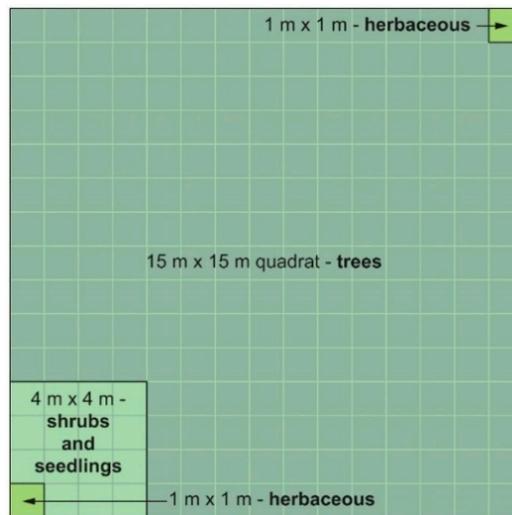


Figure 2. Schematic of the quadrat placement within each experimental unit. Each disturbance category was sampled with 6 to 10 experimental units; undisturbed forest contained 30 units.

Table 2. Cumulative accounting of species of trees and shrubs observed within 11 disturbance categories in the Miller Creek Demonstration Forest in northwestern Montana, USA. Nitrogen-fixing species are shown in bold.

Form	Genus, Species, and Authority ^z
Tree/seedling	<i>Abies lasiocarpa</i> (Hook.) Nutt. <i>Larix occidentalis</i> Nutt. <i>Picea engelmannii</i> Parry ex Engelm. <i>Pinus contorta</i> Douglas ex Loudon <i>Pinus monticola</i> Douglas ex D. Don <i>Populus tremuloides</i> Michx. <i>Populus trichocarpa</i> (Torr. & A. Gray ex Hook.) Brayshaw <i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>glauca</i> (Mayr) Franco <i>Taxus brevifolia</i> Nutt.
Shrub	
Low ^y	<i>Berberis repens</i> L. <i>Cornus canadensis</i> L. <i>Paxistima myrsinites</i> (Pursh) Raf. <i>Ribes lacustre</i> (Pers.) Poir. <i>Rosa gymnocarpa</i> Nutt. <i>Rubus parviflorus</i> Nutt. <i>Spiraea betulifolia</i> Pall. <i>Symphoricarpos albus</i> (L.) S.F. Blake <i>Vaccinium membranaceum</i> Douglas ex Torr.
Medium ^y	<i>Ceanothus velutinus</i> Douglas ex Hook. <i>Lonicera utahensis</i> S. Watson <i>Juniperus communis</i> L. <i>Menziesia ferruginea</i> Sm. <i>Shepherdia canadensis</i> (L.) Nutt.
High ^y	<i>Acer glabrum</i> Torr. <i>Alnus viridis</i> (Chaix) DC. ssp. <i>sinuata</i> (Regel) A. Löve & D. Löve <i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M. Roem. <i>Salix scouleriana</i> Barratt ex Hook.
Dead	—

^z Nomenclature [59]. ^y Stature classification [58].

For each species of seedling and shrub, branch samples were composited by experimental units; samples from half the units formed one sample and samples from the remaining units forming the second sample. Samples were further composited by the basal diameters (≤ 2 or > 2 cm) of the original plants. Finally, we segregated branch samples into foliage and wood. Therefore, the maximum sample number for any given species within a disturbance category was eight (2 experimental unit composites \times 2 basal diameter categories \times 2 tissue types). Within each experimental unit, we composited the herbaceous material from both 1 m \times 1 m quadrats.

Belowground

We estimated the coarse root biomass using Equation (1):

$$\text{Biomass}_{\text{root}} = 0.26 \cdot \text{Biomass}_{\text{aboveground}} \quad (1)$$

where the constant 0.26 is the root-to-shoot ratio of temperate tree species [60]. Fine root biomass was the average oven-dry weight of material collected in each forest floor and mineral soil core multiplied by the number of cores (area basis) per hectare (see Section 2.3.3).

2.3.2. Woody Residue

To estimate the amount of sound and rotten woody residue ≥ 0.6 cm in diameter (woody residue; WR) on the soil surface, we used wood classification categories [61] and two randomly placed 10.7 m linear transects within each experimental unit. Woody debris < 0.6 cm in diameter (1-h fuel) was sampled as part of the forest floor (see next section). Random samples of WR (across diameter classes) were collected for C and N analyses. We corrected transect biomass using an average of the appropriate specific gravity values and to estimate volume on a per hectare basis [61].

2.3.3. Soil

Within each disturbance plot we collected surface organic horizons and mineral soil from a grid of at least 16 systematically located points (Table 1). At each point, surface organic horizon samples (inclusive of the O_i , O_e , and O_a horizons) were removed from within a 10 cm diameter circle and the depths were recorded. Surface organic horizons included all dead organic matter in the O horizons and any woody debris < 0.6 cm in diameter. Surface mineral soil (0–30 cm) samples were obtained with a large (10 cm diameter \times 30 cm depth) corer [62] that allowed us to gather representative soil samples, including large coarse fragments [63]. A total of 160 surface organic horizons and mineral soil samples were taken from the original study plots ($n = 10$ plots \times 16 cores), and 96 were taken from adjacent undisturbed control stands ($n = 2$ habitat type phases \times 3 stands \times 16 cores). Soil wood and fine roots found within the mineral soil were collected for processing. Soil wood is highly decomposed woody residue of decay class 5 [64] that is covered by the forest floor material or within the mineral soil and not measured in woody residue transects [35].

2.4. Laboratory Analysis

2.4.1. Vegetation

Tree and seedling biomass levels per hectare were estimated using the Fire and Fuels Extension (FFE) [65] of the Forest Vegetation Simulator (FVS) [66] with the Northern Idaho/Inland Empire geographic variant [67]. Dead seedlings were analyzed as “other softwoods.” We assumed that snags had branches. Aboveground biomass (g) for shrub components (total and foliage) within each experimental unit was approximated with Brown’s [58] regression components and Equations (2) and (3):

$$\text{Biomass}_{\text{total}} = \sum_{i=1}^n (e^{[a_{ii} + b_{ii}(\ln D)]}) \quad (2)$$

$$\text{Biomass}_{\text{foliage}} = \sum_{i=1}^n (e^{[a_{if} + b_{if}(\ln D)]}) \quad (3)$$

where i is the shrub species, D is the basal diameter (cm), and the regression parameters a and b stand for the total (t) and foliage (f) biomass. We used Brown's [58] diameter class midpoints 0.34, 0.40, and 0.44 for low, medium, and high shrub groups (Table 2), respectively, in the <0.5 class; 0.75, 1.25, 1.75, and 2.5 for the 0.51-1.0, 1.01-1.5, 1.51-2.0, and 2.01-3.0 classes; 3.62 for the 3.01-5.0 class; and the actual diameters when $D > 5.0$. For shrubs not specified by Brown [58], we used *Ribes* spp. for *Ribes lacustre*, *Rosa* spp. for *Rosa gymnocarpa*, *Salix* spp. for *Salix scouleriana*, and *Berberis repens* for *Cornus canadensis* because of their similar growth statures. The parameters for "combined species" of the low shrub stature class were used for *Paxistima myrsinites* (Table 2). We estimated stem biomass (including branches) with Equation (4), and assumed that $\text{Biomass}_{\text{stem}}$ was the best estimate for dead shrub biomass. For dead shrubs, we used the average of the regression parameters for all shrub species:

$$\text{Biomass}_{\text{stem}} = \text{Biomass}_{\text{total}} - \text{Biomass}_{\text{foliage}} \quad (4)$$

All tree, shrub, herbaceous, woody residue, and fine root samples were oven-dried at 60 °C to a constant weight, then a sub-sample was finely ground with an 8000D Mixer/Mill (Spex SamplePrep, Metuchen, NJ, USA) and analyzed on a LECO TruSpec CN analyzer (Leco Corp., St. Joseph, MI, USA) to attain total C and total N concentrations. Estimates of biomass ha⁻¹ were multiplied by C and N concentrations to calculate pool sizes.

2.4.2. Species Diversity

We explored species diversity and evenness using Shannon diversity functions [68]. Equation (5) describes species diversity and Equation (6) describes evenness; that is, the equitable distribution of individuals within the plot among species:

$$H' = \sum_{i=1}^S (p_i \ln p_i) \quad (5)$$

$$J' = \frac{H'}{\ln S} \quad (6)$$

where H' is the diversity index, p_i is the proportion of the entire population made up of species i , S is the total number of species within an experimental unit (i.e., richness), and J' is the evenness index.

2.4.3. Soil

All forest floor and soil wood samples were removed from the mineral soil and dried at 60 °C. Forest floor and soil wood samples were then processed and analyzed as described above for vegetation. Mineral soil samples were dried to a constant weight at 105 °C, weighed, finely ground to pass a 0.04 mm mesh, and analyzed for C and N concentrations (described above).

The dry mass levels of forest floor, soil wood, and mineral soil in each core were extrapolated to a per hectare basis. Mineral soil C, N, and organic matter contents were corrected for coarse rock fragment contents and re-extrapolated to a per hectare basis using fine fraction bulk density [63,69]. We did not analyze the coarse rock fragments (>2 mm), which have been found to contain appreciable amounts of C and N in some soils [70,71]. The total and fine bulk densities and gravimetric and volumetric rock contents were calculated following Page-Dumroese et al. [63].

2.5. Statistical Analysis

For biomass, C and N concentrations, and C and N contents of pool components (e.g., aboveground shrub biomass, coarse roots, mineral soil), pairwise comparisons ($\alpha = 0.1$) of disturbance categories were computed using the R language [72] and multcomp library [73] after adjustment for family-wise

error rate using the Tukey–Kramer method [74]. We prepared a principal coordinates analysis (PCoA) using the Bray–Curtis dissimilarity method to visualize similarities in shrub communities across the disturbance categories [75,76]. Because shrub diversity (H') and species evenness (J') within each disturbance category are responses from the same set of variables, we used MANOVA to first test for differences between habitat type phases, and secondly for differences within each habitat type phase among disturbance categories. The resulting p -values for Pillai's trace revealed no significant difference between habitat type phases ($p = 0.3568$). Thus, we used separate ANOVAs to assess whether more of the variability seen in the preceding MANOVA was due to H' or to J' . Because data failed the univariate normality test, we separated means using the Kruskal–Wallis method [77]. For tissue N concentrations, we first explored whether any data could be pooled by calculating a mean for each species \times tissue type (wood or foliage) \times stem basal diameter (<2 or >2 cm) combination and then comparing weighted means among plant types using equal variance t -tests, but found that N concentration was usually highly significant ($p < 0.0001$) across metrics, so that no pooling combinations of tree, shrub, or N-fixing species could be justified. We then used equal variance t -tests to compare tissue N concentrations across stem basal diameters and ANOVA to compare concentrations within tissues for seedling, shrub, and N-fixing shrub species, separating means with Tukey's Honestly Significant Difference test when appropriate.

3. Results

3.1. Disturbances

3.1.1. MEFE

For this cooler, moister phase, disturbance was only a result of harvesting and prescribed fire. All three disturbance plots were harvested, but East 3 and North 12 also experienced prescribed fire. As shown in Table 1, 42% of the forest floor persisted in East 3 after the prescribed fire in August 1968, while only 9% remained in North 12, as this area was burned with a hotter fire in August 1967.

3.1.2. XETE

Disturbance on the warmer, drier XETE phase was a function of harvesting and prescribed fire, but with the additional impact of wildfire. Immediately after harvest, five of the six XETE plots burned with combinations of prescribed fire and wildfire; the disturbance level increased with fire severity, as measured by the loss of forest floor (Table 1). The lowest disturbance was to the harvest-only South 11 plot. West 10 and South 8 were harvested and burned with a low severity prescribed fire that removed 16% and 68% of their forest floors, respectively. Fifteen days after the prescribed fire, South 8 was re-burned by wildfire, further reducing its forest floor to 16% of the original level. South 7 and West 2 were harvested, but before they could be treated with prescribed fire, were burned by wildfire that removed 72% and 98% of their forest floors, respectively. South 12 and 13 were not harvested but were burned in the wildfire that resulted in almost total loss of the forest floor.

3.2. Vegetation

3.2.1. Herbaceous and Shrubs

Across the experimental landscape, we observed 18 species of shrubs (Table 2); the nine most common "species" (including dead stems as a species) in terms of relative abundance were *Alnus viridis* ssp. *sinuata*, "dead" material, and *Vaccinium membranaceum* (15% each); *M. ferruginea* (11%); *P. myrsinites* (9%); *S. scouleriana* (8%); and *Ceanothus velutinus*, *Shepherdia canadensis*, and *Spiraea betulifolia* (7% each); these accounted for 93% of all stems ha^{-1} and 96% of the total biomass (Supplementary Materials Table S1). Three species were uncommon, recorded in low numbers (<125 stems ha^{-1}), and only for single disturbance categories: *C. canadensis*, *B. repens*, and *Juniperus communis*. The remaining seven species (*Acer glabrum*, *Amelanchier alnifolia*, *Lonicera utahensis*, *R. lacustre*, *R. gymnocarpa*, *Rubus parviflorus*,

and *Symphoricarpos albus*) occurred more frequently (present on 5 to 7 categories) but contributed < 1% each to the total number of plants observed across all 11 disturbance categories (Table S1). Neither shrub H' nor J' were significantly affected by habitat type phase ($p = 0.3568$), with less variability observed in H' ($p = 0.7316$) than in J' ($p = 0.4819$) (Figure 3).

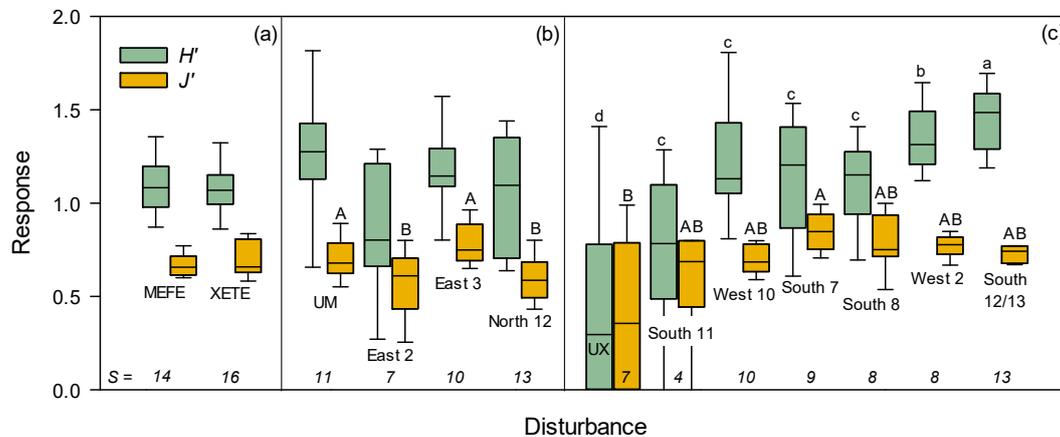


Figure 3. Species richness (S) and box plots for Shannon functions of species diversity (H') and evenness (J') for the 11 disturbance categories (see Table 1 for descriptions) on the Miller Creek Demonstration Forest 30 years after the disturbances: (a) no significant differences were observed between the *Menziesia ferruginea* (MEFE) and *Xerophyllum tenax* (XETE) phases within the *Abies lasiocarpa*/*Clintonia uniflora* habitat type ($p = 0.3568$), and H' was less variable ($p = 0.7316$) than J' ($p = 0.4819$); (b) responses within the MEFE disturbance categories were significant ($p = 0.0027$); H' was less variable ($p = 0.0339$) than J' ($p = 0.0048$); (c) responses within the XETE disturbance categories were significant ($p < 0.0001$); H' was less variable ($p < 0.0001$) than J' ($p = 0.0001$). Within panels b and c, x-axis values progress from undisturbed forest (left) to the highest severity disturbance (right). Larger values of H' indicate increasing levels of biodiversity as a function of abundance, whereas larger values of J' reflect more consistent abundance across species observed in each disturbance category. Vertical boxes represent approximately 50% of the observations, lines extending from each box are the upper and lower 25% of the distribution, and the solid horizontal line in the center of each box is the median value. Different lowercase (H') and uppercase (J') letters within habitat type phases and panels indicate significant differences (Kruskal-Wallis).

Although relative abundance and relative biomass across most species usually followed the same trend (i.e., more relative abundance generated more relative biomass), this did not consistently translate for low stature shrubs (listed in Table 2). For example, on the wildfire-only plot (South 12/13), *S. betulifolia* accounted for 21% of all stems ha^{-1} (Table S1) (13,646 stems ha^{-1} ; Table 3) but < 1% of the biomass (Table S1). Often, many low-stature shrubs produced less biomass relative to a few high stature shrubs, e.g., *V. membranaceum* accounted for 47% of all stems ha^{-1} and 21% of the biomass on the harvested and prescribed fire plot East 3, whereas *A. v. sinuata* accounted for 3% of all stems ha^{-1} but 40% of the biomass. In addition, the high relative abundance of low stature shrubs on the undisturbed plots was often dwarfed in terms of relative biomass by standing dead material, e.g., *V. membranaceum* accounted for 41% of all stems ha^{-1} and 11% of the biomass on the MEFE phase, whereas the “dead” category accounted for 7% of all stems ha^{-1} but 34% of the biomass (Table S1).

MEFE

After 30 years, disturbance had no significant effect on Shannon species diversity (H'), despite a trend of more species richness with increasing disturbance (Figure 3) and varied species composition among MEFE plots (Figure 4). On the harvest-only plot East 2, being mainly *V. membranaceum*, *M. ferruginea*, and *A. v. sinuata* (Figure 5 and Table S1), species evenness (J') was lower than on the harvested East 3 that had prescribed fire. The occurrence of fire on East 3 (and the 57% loss of forest floor) shifted the shrub community composition (Figure 4) and increased S to 10 (Figure 3), although abundance and biomass were reduced for *V. membranaceum* and *M. ferruginea* and increased for N-fixing *A. v. sinuata* (Figure 5 and Table S1). The combination of harvest with a more severe prescribed fire on North 12 (91% loss of forest floor) further increased species richness ($S = 13$), but because *V. membranaceum* and *M. ferruginea* were nearly eliminated and *A. v. sinuata* and *S. scouleriana* predominated (nearly 90% of the biomass; Figure 5 and Table S1), J' was significantly lower than when harvested and burned by prescription in East 3 and the undisturbed plots (UM). The total shrub biomass values significantly increased with fire severity, with the lowest value observed in the harvest-only plot East 2 (no loss of forest floor) with 5.2 (2.3 standard deviation) Mg ha^{-1} , then in the harvested and burned by prescription East 3 (57% of forest floor consumed) with 8.6 (4.4) Mg ha^{-1} , while the greatest values occurred in the harvested and burned by prescription North 12 (91% of forest floor consumed) with 19.3 (8.4) Mg ha^{-1} (Table S4). The relative biomass of the “dead” material was low across the disturbed plots ($\leq 6\%$) compared to the undisturbed plots (UM; 34%) The amount of herbaceous material was low across all MEFE plots (Table 4).

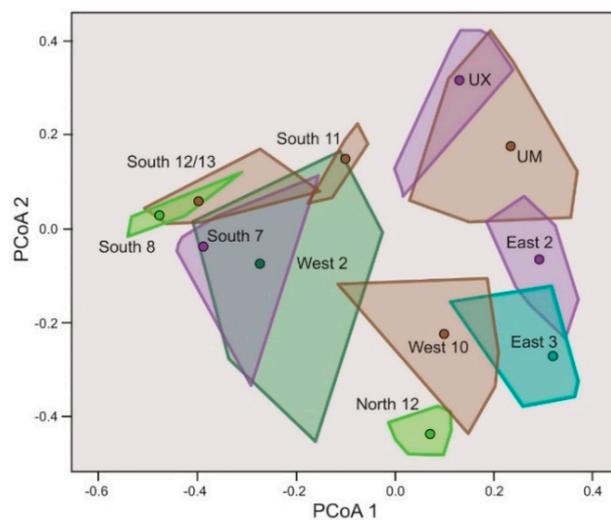


Figure 4. Shrub composition (species and abundance) ordination based on Bray-Curtis dissimilarities. Polygons delineate the range of data for the 11 disturbance categories in the Miller Creek Demonstration Forest (see Table 1 for descriptions).

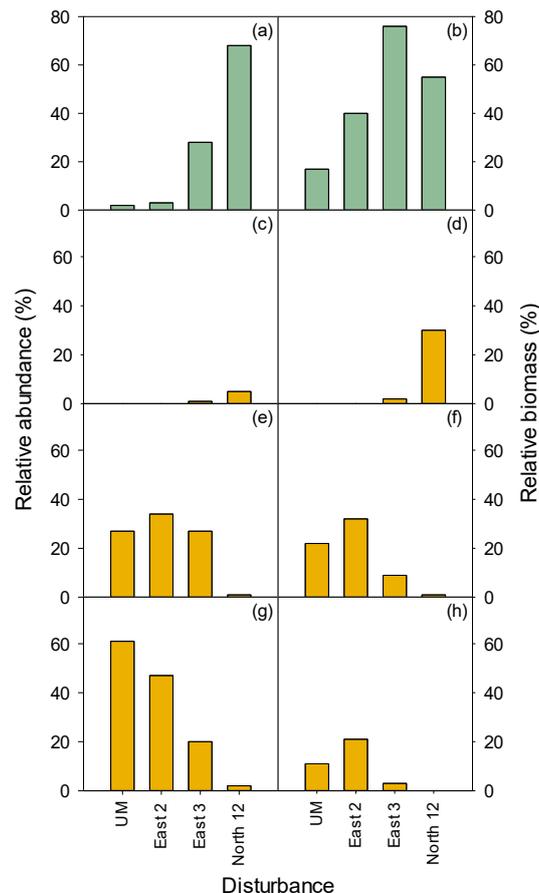


Figure 5. The *Menziesia ferruginea* (MEFE) habitat type phase 30 years after disturbance and the relative abundances (%) for shrubs of high stature (a) *Alnus viridis* ssp. *sinuata* and (c) *Salix scouleriana*; medium stature (e) *Menziesia ferruginea*; and low stature (g) *Vaccinium membranaceum*, and their respective relative biomass values (%), (b,d,f,h). Note: N-fixing shrubs in green; x-axis values progress from undisturbed forest (left) to the highest severity disturbance (right); see Table 1 for disturbance category descriptions.

XETE

Without fire, the herbaceous biomass was 2- to 5-fold greater than when fire occurred (Table 4). For shrubs, harvesting alone stimulated shrub development compared to the control; the amount of shrub stems ha^{-1} increased from 1584 in the undisturbed plots (UX) to 28,750 in the harvest-only South 11 plot (Table S1), while aboveground shrub biomass significantly increased from 0.1 (0.3) to 2.6 (2.4) Mg ha^{-1} (Table S4). Moreover, H' increased by almost 2-fold and J' increased by 50% (Figure 3). Fire further stimulated shrub occurrence; relative abundance and relative biomass each increased from about 30% to 2.5-fold compared to the harvest-only South 11 (Table S1), while aboveground shrub biomass in non-harvested South 12/13, the most severely disturbed plot with 100% of the forest floor consumed by wildfire, was significantly different from harvest-only South 11 (7.2 (6.0) vs. 2.6 (2.4) Mg ha^{-1}) (Table S4). *Salix scouleriana*, absent on undisturbed plots (UX) and harvest-only South 11, became abundant on southern aspects after fire, but its total abundance decreased with increasing fire severity (Figure 6 and Table 3, and Table S1). Although the principle component analysis indicated that XEFE plots (with the exception of West 10, which was harvested and had prescribed fire) were quite similar in terms of composition (Figure 4), only four species were detected (*A. alnifolia*, *S. canadensis*, *S. betulifolia*, and *V. membranaceum*) after harvest alone (South 11) compared to 8 to 13 species on the burned plots. The H' and J' functions both increased with the addition of fire, with maximum H' occurring in plots with the most severe disturbance (i.e., 100% loss of forest floor by wildfire in South 12/13) (Figure 3).

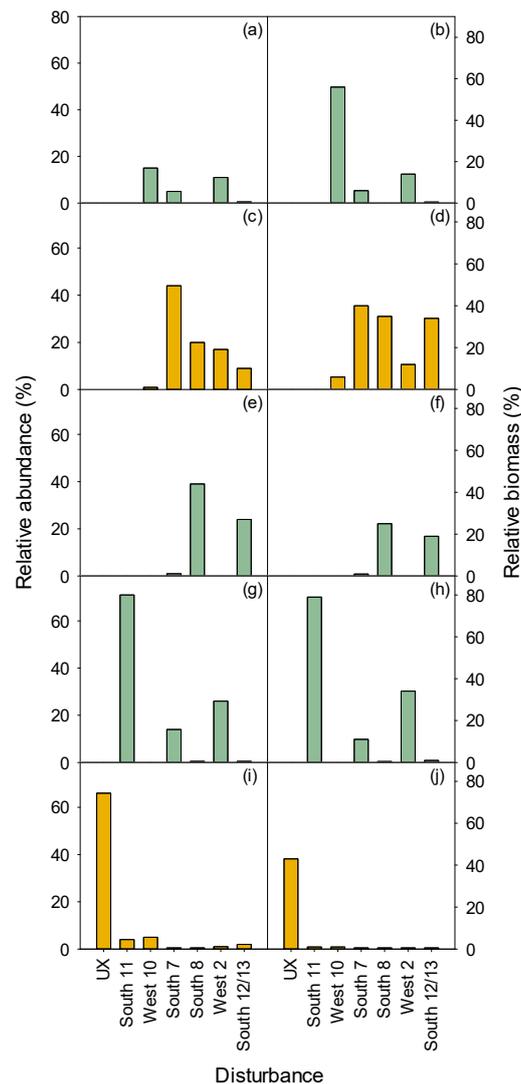


Figure 6. The *Xerophyllum tenax* (XETE) habitat type phase 30 years after disturbance and the relative abundances (%) for shrubs of high stature (a) *Alnus viridis* ssp. *sinuata* and (c) *Salix scouleriana*; medium stature (e) *Ceanothus velutinus* and (g) *Shepherdia canadensis*; and low stature (i) *Vaccinium membranaceum*, along with their respective relative biomass (%) values (b,d,f,h,j). Note: N-fixing shrubs are shown in green; x-axis values progress from undisturbed forest (left) to the highest severity disturbance (right); see Table 1 for disturbance category descriptions.

While the N-fixing *A. v. sinuata* had appreciable aboveground relative biomass in the MEFE plots, ranging from 17% in the undisturbed plots to 76% in the harvested and burned by prescription East 3 plot, it only had considerable aboveground biomass on the western aspects of the XETE area, where it contributed 14% in West 2 (harvested and wildfire) and 56% in West 10 (harvested and prescribed fire) (Figure 6 and Table S1). Instead, *C. velutinus* was the primary N-fixing species in South 8 (harvested, prescribed fire, and reburn by wildfire) and South 12/13 (wildfire), having relative aboveground biomass values of 25% and 19%, respectively (Figure 6 and Table S1), while *S. canadensis* filled that niche in plots that were either harvested and burned by prescription (South 7, 11%), harvest-only (South 11, 79%), or were harvested and burned by wildfire (West 2, 34%) (Figure 6 and Table S1). In contrast to the disturbed MEFE plots, between 16 and 45% of the relative biomass across all XETE plots, including the undisturbed plots (UX), were associated with dead shrubs (Table S1).

Table 4. Thirty-year post-treatment measures of total biomass and carbon and nitrogen pools for the two phases (*Menziesia ferruginea*, MEFE; *Xerophyllum tenax*, XETE) of the *Abies lasiocarpa*/*Clintonia uniflora* habitat type [50] and the subsequent 11 disturbance categories at the Miller Creek Demonstration Forest, Montana, USA (see Table 1 for descriptions). For treatments: H = harvested; P = prescribed fire; W = wildfire; C = control.

MEFE	Biomass (Mg ha ⁻¹)				Carbon (Mg ha ⁻¹)				Nitrogen (kg ha ⁻¹)												
	E2	E3	N12	UM	E2	E3	N12	UM	E2	E3	N12	UM									
Treatment	H	HP	HP	C	H	HP	HP	C	H	HP	HP	C									
Vegetation																					
Trees	23	26	4	227	11	13	2	110	111	160	24	992									
Seedlings	<1	4	3	1	<1	2	1	<1	3	33	30	9									
Shrubs	5	9	19	1	2	4	9	5	43	68	137	6									
Herbaceous	1	1	1	<1	<1	<1	<1	<1	12	9	10	4									
Roots																					
Coarse	6	7	1	59	3	3	<1	29	28	42	6	258									
Fine	58	96	52	226	21	30	15	84	376	654	230	807									
Total	94	142	80	514	38	52	28	228	573	966	437	2076									
Woody Residue	4	4	4	19	2	2	2	9	14	12	14	62									
Soil																					
Forest floor	189	180	116	139	102	98	42	74	4738	3797	1519	2277									
Soil wood	58	23	34	69	32	10	26	38	579	418	804	959									
Mineral soil	218	198	183	155	67	44	37	40	2513	1577	1323	1487									
Total	465	401	333	363	201	152	105	152	7830	5792	3646	4723									
Total pool	563	547	418	896	241	206	135	389	8417	6770	4083	6861									
XETE	S11	W10	S7	S8	W2	S12/13	UX	S11	W10	S7	S8	W2	S12/13	UX	S11	W10	S7	S8	W2	S12/13	UX
Treatment	H	HP	HW	HPW	HW	W	C	H	HP	HW	HPW	HW	W	C	H	HP	HW	HPW	HW	W	C
Vegetation																					
Trees	12	33	38	28	49	46	185	6	16	18	14	24	22	89	76	146	223	188	309	256	917
Seedlings	0	1	1	1	1	<1	2	0	1	1	<1	<1	<1	1	0	9	11	6	7	3	11
Shrubs	3	4	4	5	5	7	<1	1	2	2	2	2	3	<1	40	33	25	42	47	55	<1
Herbaceous	5	2	2	2	1	1	1	2	1	1	1	<1	1	1	36	14	18	15	7	11	13
Roots																					
Coarse	3	8	10	7	5	12	48	2	4	5	4	6	6	23	20	38	58	49	80	67	238
Fine	49	45	105	41	138	102	148	15	14	30	14	41	32	61	211	201	466	193	743	560	474
Total	72	94	84	84	206	168	384	26	38	57	35	74	64	176	387	441	801	491	1193	952	1654
Woody Residue	4	4	1	5	4	9	13	2	2	<1	2	2	4	6	12	10	3	11	10	23	39
Soil																					
Forest floor	89	51	33	55	34	45	131	57	28	17	34	29	29	70	1794	936	514	1386	936	884	2010
Soil wood	5	59	0	5	0	8	17	4	37	0	2	0	5	11	138	664	0	122	0	142	258
Mineral soil	122	131	150	125	227	118	118	34	29	36	32	46	29	26	1485	1382	1469	1361	2068	1279	1109
Total	217	241	184	186	261	171	266	95	94	53	68	75	63	107	3417	2982	1983	2869	3004	2305	3377
Total pool	292	339	344	274	471	348	664	123	134	110	150	151	131	289	3813	3434	2787	3371	4207	3208	5070

3.2.2. Seedlings and Trees

Seven tree species were present across all experimental plots as seedlings (Table 3). In terms of relative abundance, *A. lasiocarpa* was most abundant (30%), followed by *P. engelmannii* (19%) and *P. menziesii* (14%); these three species were observed in 10 of 11 disturbance categories (Table S2). *Larix occidentalis* was observed in 54% of the plots and accounted for 12% of all seedlings. *Populus trichocarpa* was found in 45% of the plots and comprised 10% of the seedlings observed. For relative biomass, *A. lasiocarpa* contributed the most (33%), followed by *P. menziesii* (20%), *L. occidentalis* (17%), *P. engelmannii* (15), and *P. trichocarpa* (8%). Although *Taxus brevifolia* accounted for 6% of the seedlings observed, its contribution to biomass was < 0.1% (Table S2).

Eight species were present as trees (Table 3). The two *Populus* species, *tremuloides* and *trichocarpa*, were each observed in four plots, while *T. brevifolia* was observed in just one. The other five species (*A. lasiocarpa*, *L. occidentalis*, *P. engelmannii*, *Pinus contorta*, *P. menziesii*) were seen in nearly all plots, had relative abundance values of 13% to 25%, and accounted for 94% of all trees and 99% of the tree biomass observed (Table S3).

MEFE

Increasing levels of fire severity promoted the occurrence of more tree seedlings (Table 3 and Table S2). On the harvest-only East 2 plot, *A. lasiocarpa*, *P. engelmannii*, and *P. menziesii* dominated in terms of relative abundance (Figure 7 and Table S2) and stems ha^{-1} (Table 3), but *A. lasiocarpa* and *P. menziesii* accounted for almost all seedling biomass (Figure 7 and Table S2). The addition of a low-severity prescribed fire increased the relative abundance and biomass of *P. engelmannii* and decreased that of *P. menziesii* in East 3 (harvest and prescribed fire, 58% loss of forest floor), whereas the most severe fire (North 12; harvest and prescribed fire, 91% loss) resulted in a plot dominated by *A. lasiocarpa* (Figure 7).

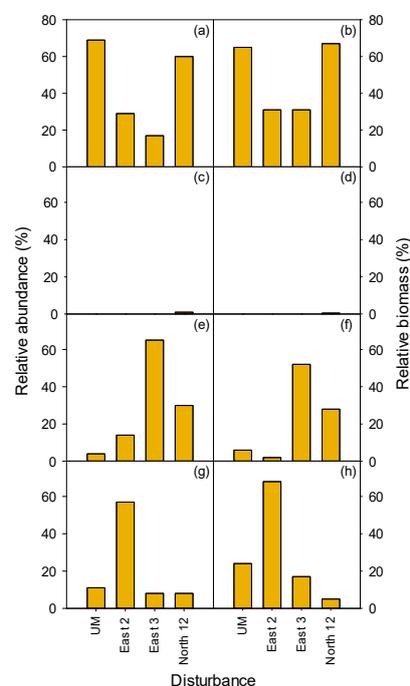


Figure 7. The *Menziesia ferruginea* (MEFE) habitat type phase 30 years after disturbance and the relative abundance values (%) for seedlings of (a) *Abies lasiocarpa*, (c) *Larix occidentalis*, (e) *Picea engelmannii*, and (g) *Pseudotsuga menziesii* var. *glauca*, along with their respective relative biomass values (%) (b,d,f,h). Note: x-axis values progress from undisturbed forest (left) to the highest severity disturbance (right); see Table 1 for disturbance category descriptions.

In contrast to shrub biomass, tree biomass decreased with increasing disturbance severity (Table 4). In the low-disturbance, harvest-only plot East 2, the same species that dominated as seedlings in terms of composition also dominated as trees, but most of the tree biomass was associated with *A. lasiocarpa* (Figure 8 and Table S3). The increasing disturbance severity from East 2 to East 3 to North 12 had mixed effects on *L. occidentalis*, while its relative abundance increased from 2% to 28% and its relative biomass grew from 4% to 75% (Figure 8 and Table S3); the most trees ha⁻¹ were observed in East 3, where the forest floor was reduced about 57% by prescribed fire (Table 3). The fine root biomass was highest in East 3, which experienced a moderate disturbance level.

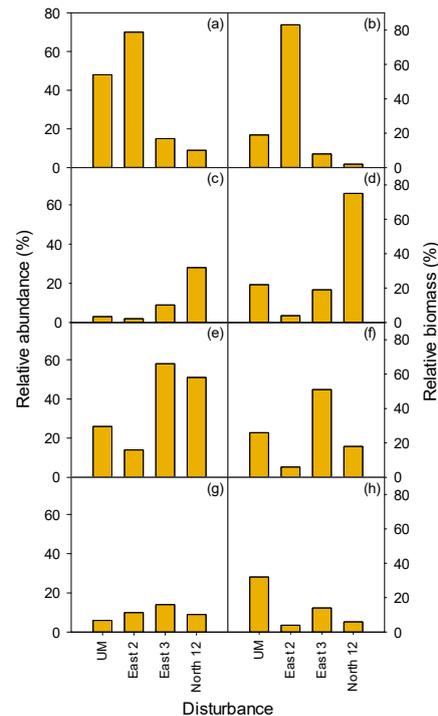


Figure 8. The *Menziesia ferruginea* (MEFE) habitat type phase 30 years after disturbance and the relative abundance values (%) for trees of (a) *Abies lasiocarpa*, (c) *Larix occidentalis*, (e) *Picea engelmannii*, and (g) *Pseudotsuga menziesii* var. *glauca*, along with their respective relative biomass values (%) (b,d,f,h). Note: x-axis values progress from undisturbed forest (left) to the highest severity disturbance (right); see Table 1 for disturbance category descriptions.

XETE

Absence of fire eliminated the occurrence of any seedlings 30 years after harvest in South 11 (Table 3). As the fire severity increased, the dominant seedling species in terms of relative abundance ranged from *A. lasiocarpa* (West 10; harvest and prescribed fire, 53% loss of forest floor) to *P. contorta* (South 7; harvest and wildfire, 72% loss) to *P. tremuloides* (South 8, harvest, prescribed fire, and wildfire, 84% loss), with *L. occidentalis* being most abundant in the sites with the highest fire severity (West 2, harvest and wildfire, 98% loss; South 12/13, wildfire, 100% loss) (Figure 9 and Table S3).

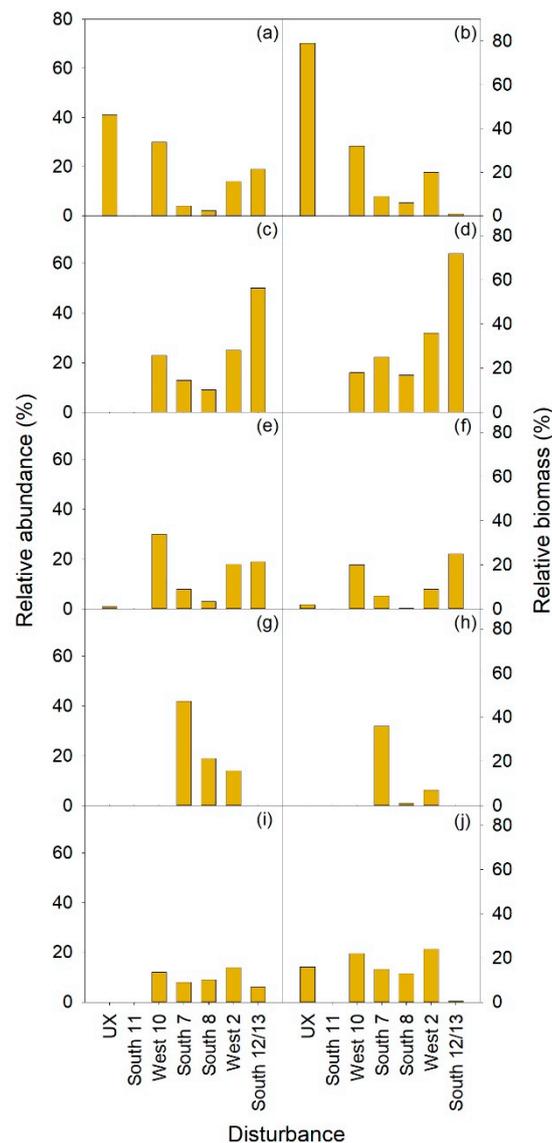


Figure 9. The *Xerophyllum tenax* (XETE) habitat type phase 30 years after disturbance and the relative abundance values (%) for seedlings of (a) *Abies lasiocarpa*, (c) *Larix occidentalis*, (e) *Picea engelmannii*, (g) *Pinus contorta*, and (i) *Pseudotsuga menziesii* var. *glauca*, along with their respective relative biomass values (%) (b,d,f,h,j). Note: x-axis values progress from undisturbed forest (left) to the highest severity disturbance (right); see Table 1 for disturbance category descriptions.

Regarding the aboveground relative biomass of trees, *A. lasiocarpa* was dominant in the harvest-only plot South 11, whereas any occurrence of fire stimulated regeneration of *L. occidentalis* (Figure 10, Table 3 and Table S3). As was the case for MEFE, the highest numbers of *L. occidentalis* seedlings and trees ha^{-1} were observed in the plot with the lowest fire severity (i.e., West 10, harvest and prescribed fire, 53% loss of forest floor), where the number was 3 times that of any other disturbance category (Figure 10 and Table 3).

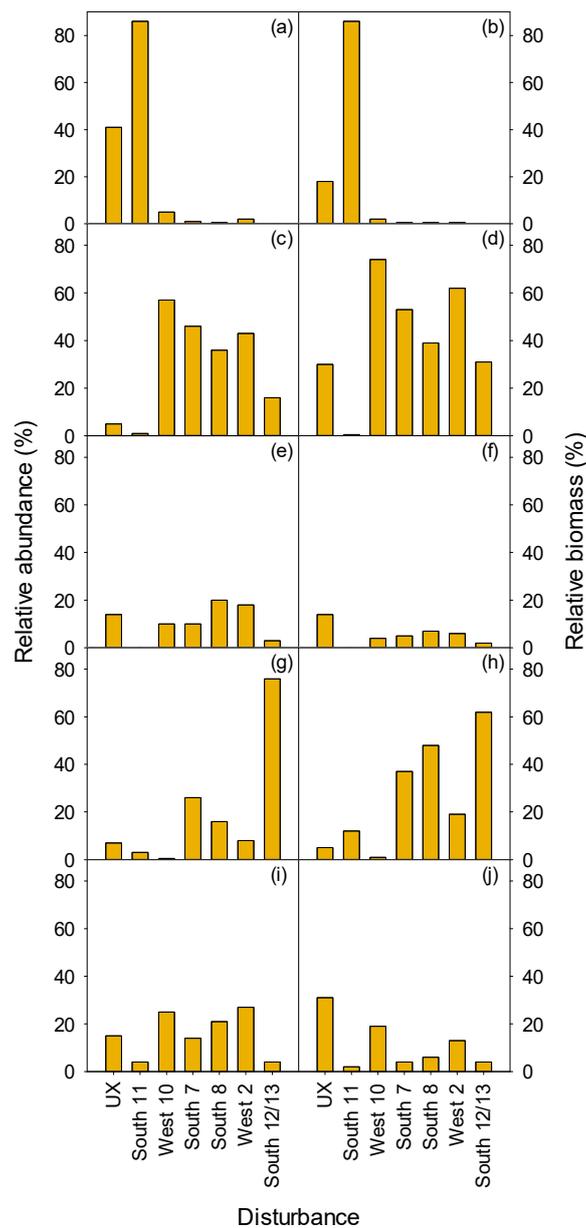


Figure 10. The *Xerophyllum tenax* (XETE) habitat type phase 30 years after disturbance and the relative abundance values (%) for trees of (a) *Abies lasiocarpa*, (c) *Larix occidentalis*, (e) *Picea engelmannii*, (g) *Pinus contorta*, and (i) *Pseudotsuga menziesii* var. *glauca*, long with their respective relative biomass values (%) (b,d,f,h,j). Note: x-axis values progress from undisturbed forest (left) to the highest severity disturbance (right); see Table 1 for disturbance category descriptions.

3.2.3. Total Vegetation

The three disturbed MEF plots averaged just 20% of the total vegetation biomass found in the undisturbed, 225-year-old stands (UM; Table 4). In contrast, the six disturbed XETE plots averaged about 34% of the total vegetation biomass of the average found for the undisturbed plots (UX). The biomass in the least disturbed harvest-only South 11 plot was just 19% of the UX value, whereas the two plots with the most disturbance (West 2, harvest and wildfire; South 12/13, wildfire) had almost 50% of the biomass value, 28% of the total vegetation C pool value, and 43% of the total vegetation N pool value found for UX (Table 4).

Although we segregated aboveground plant tissues by species and into four categories (wood or foliage from plants with basal diameters < 2 cm or > 2 cm), we found that overall basal diameter was

not significant when sampling foliage or wood (branches) from tree seedlings. Basal diameter was, however, significant for shrubs (excluding N-fixing species; Table 5); N concentrations for wood and foliage ranged from 0.38 to 0.80 and 1.16 to 2.45, respectively, and we noted significant differences among species (Table S5). As with tree species, basal diameter was not significant for overall N concentrations for the wood or foliage of N-fixing shrub species ($p = 0.9161$ and 0.6327 , respectively), but we observed differences among species (Table 6). In particular, the wood of *S. canadensis* had a significantly higher N concentration, whereas *C. velutinus* had the lowest foliage N concentration.

Table 5. Thirty-year post-treatment measures (means) of nitrogen (N) concentration (%) in the wood (branches) and foliage of tree seedlings and shrubs (excluding N-fixing species) observed in the Miller Creek Demonstration Forest, Montana, USA. Sample numbers shown in parentheses. Values for individual species shown in Table S5.

Basal Diameter		Nitrogen Concentration (%)	
		Seedlings	Shrubs
<2 cm	Wood	0.43 (67)	0.56 (163)
>2 cm	Wood	0.45 (69)	0.48 (34)
		<i>p</i> -value	0.0015
<2 cm	Foliage	1.37 (72)	1.86 (169)
>2 cm	Foliage	1.32 (65)	2.01 (37)
		<i>p</i> -value	0.0703

Table 6. Thirty-year post-treatment measures (means) pooled across basal diameter classes of nitrogen (N) concentration values (%) in the wood (branches) and foliage of the three N-fixing shrubs observed in the Miller Creek Demonstration Forest, Montana, USA. Sample numbers shown in parentheses. Different letters for each tissue type indicate a significant difference among species.

Species	Nitrogen Concentration (%)	
	Wood	Foliage
<i>Alnus viridis</i> ssp. <i>sinuata</i>	0.78 (25) a	2.60 (26) y
<i>Ceanothus velutinus</i>	0.92 (19) a	1.97 (19) x
<i>Shepherdia canadensis</i>	1.49 (23) b	2.45 (24) y
<i>p</i> -value	<0.0001	<0.0001

3.3. Woody Residue and Soil

Regardless of habitat type phase and disturbance, the amount of woody residue was similar and low ($1\text{--}9 \text{ Mg ha}^{-1}$), at about 25% of the undisturbed MEFE (UM) and XETE (UX) plots (Table 4 and Table S4). Across the landscape, the forest floor levels decreased with increasing amounts of disturbance at the onset of the study. Despite this, in the moister MEFE sites the amount of forest floor exceeded the levels found in undisturbed plots (UM), whereas in XETE sites the levels were about one-third of the undisturbed plots (UX); overall, forest floor levels had recovered to about 80% of the undisturbed plots (UM and UX). Soil wood provided the smallest contribution to soil biomass (Table 4), the levels of which were about 60% of those in undisturbed plots (UM and UX). Mineral soil biomass values were about 25% higher in MEFE plots than XETE plots, but regardless of disturbance or habitat type phase, the values usually increased (up to 40%) compared to the undisturbed plots. Overall, the soil biomass levels were about the same in disturbed plots compared to undisturbed plots.

3.3.1. MEFE

Surface coarse woody residues and mineral soil biomass values were less affected by disturbance than the forest floor and soil wood categories were. Woody residue biomass values were similar for all disturbance treatments and were 21% of the values in undisturbed plots (UM) (Table 4). Forest floor

levels were significantly lower in the harvested North 12 plot (116 (2) Mg ha⁻¹), which had 91% of its forest floor removed by prescribed fire, compared with either of the other two plots that were harvested and burned by prescription (East 2 and East 3), which averaged 185 Mg ha⁻¹ and showed significantly higher values than undisturbed plots (139 (60) Mg ha⁻¹) after 30 years (Table S4). Soil wood values ranged from 23 to 69 Mg ha⁻¹ (Table S4). Overall, total soil biomass levels (inclusive of forest floor, soil wood, and mineral soil) in the least disturbed plots (East 2 and East 3, harvested and prescribed fire with > 42% of the forest floor remaining) exceeded those measured on the undisturbed plots (UM). North 12, which experienced the most disturbance (harvest and prescribed fire, 91% loss of forest floor), had 88% of the total profile biomass of UM (Table 4 and Table S4).

3.3.2. XETE

Woody residue biomass in South 12/13, the uncut plot consumed by wildfire, was 2- to 6-fold higher than the other disturbed plots, but the level was still lower than in the undisturbed plots (UX) (Table 4). Despite soil wood in West 10 (harvest and prescribed fire) being 3 times higher than in UX, and despite some XETE plots having no soil wood, we found no significant differences among plots (Table S4). Unlike in the MEFÉ plots, the mineral soil biomass values were similar among the disturbed and undisturbed plots (Table 4).

3.4. C and N Pools

The total vegetation biomass across the disturbed plots was about 25% of that for the undisturbed plots, whereas the soil biomass level was similar to that for undisturbed plots (Table 4). The overall biomass (vegetation + soil) for disturbed plots was about 55% of that for the undisturbed plots. Carbon generally followed this same pattern. The total N in the vegetation was low, at about 37% of that in undisturbed forest plots, regardless of the habitat type phase. The total soil N exceeded the values in the undisturbed plots by 22% (MEFÉ) and 8-fold (XETE).

3.4.1. MEFÉ

Aboveground biomass (plus roots) had 83% less C and 32% less N on average in the disturbed plots than in undisturbed plots (Table 4). For total soil, disturbed plots averaged nearly the same C pool as undisturbed plots (UM). Soil samples in plots that experienced harvest and prescribed fire where > 42% of the forest floor remained (East 2 and East 3) had about 120% of the total N pool values as those found in UM plots. Soil total C and N pools in the most disturbed plot (North 12; harvested and prescribed fire, 91% loss of forest floor), however, were only about two-thirds those of UM after 30 years, with less than half of the N as in the other two MEFÉ plots (Table 4). For total pools (vegetation plus soil), the two plots with the lowest relative disturbance levels (East 2 and East 3) averaged about 58% and 111% of the C and N pools, respectively, of the undisturbed plots (UM), whereas when most (91%) of the forest floor was removed by prescribed fire (North 12), the total C and N pools were slower to recover and reached only 35% and 60% of the levels of the undisturbed plots (Table 4). As expected, the greatest coarse woody residue C and N pools were located in undisturbed plots (UM). In all MEFÉ phase plots, the dominant C and N pools were found in the soil.

3.4.2. XETE

After 30 years, total C and N pools (vegetation plus soil) of the disturbed plots were about 44% and 69%, respectively, of the undisturbed plots (UX) (Table 4). Total soil N increased with the increasing relative biomass of N-fixing plants (Figure 11). Overall, the mineral and organic portions of the soil in these six disturbed plots averaged about 70% of the total soil C pool and about 80% of the total soil N pool values as those found in UX (Table 4). Compared to UX, the total C pool in the most disturbed plot (South S12/13, 100% of forest floor consumed by wildfire) was about 59% of the UX value, whereas for the plots with the least disturbance (South 11, harvest-only; West 10, harvest and burned by prescription; >53% of forest floor remained) the values were about 84% of the UX value.

In addition, the total N in the vegetation plus soil in the UX was 32% greater than the disturbed plots, with most located in the soil pool. The total C and N pools were generally lower in XETE plots as compared to MEFE plots.

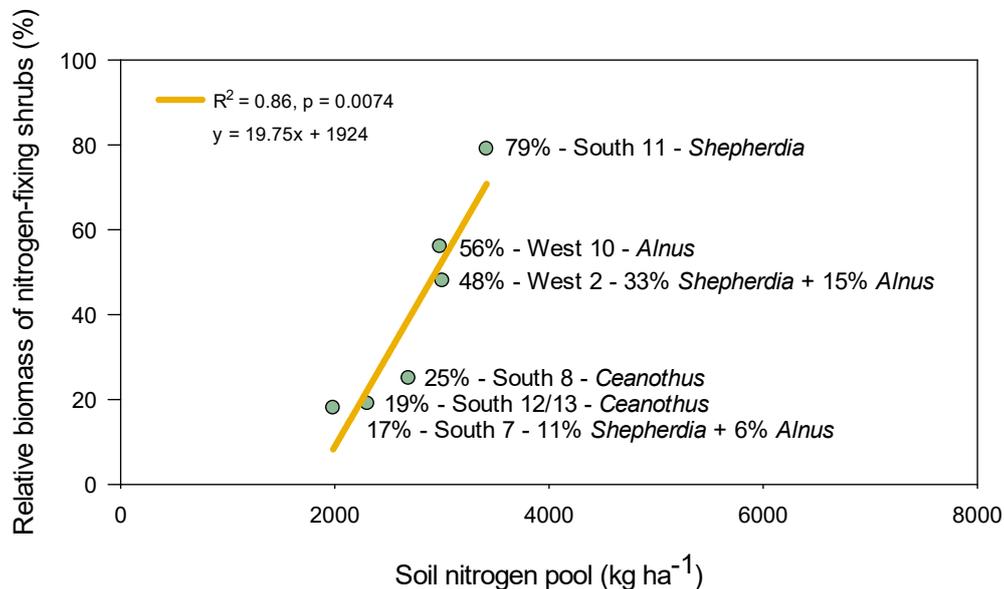


Figure 11. The relationship between the relative biomass of nitrogen-fixing shrubs (*Alnus viridis* ssp. *sinuata*, *Ceanothus velutinus*, and *Shepherdia canadensis*) and the soil nitrogen pool for 30-year-old disturbances in the *Xerophyllum tenax* (XETE) habitat type phase within the *Abies lasiocarpa*/*Clintonia uniflora* habitat type. See Table 1 for disturbance category descriptions.

4. Discussion

4.1. Shrub Regeneration

In forest sites, shrubs have a key role in supporting forest function by providing wildlife habitats, cycling nutrients, and adding to overall forest biodiversity [78–80]. After disturbances that remove the tree overstory, the shrub cover can expand rapidly due to increased access to light, water, and nutrients, and because shrubs regenerate promptly by sprouting from the root collar, from rhizomes, or from the germination of seeds from the seed bank [81–84]. After disturbances in the northern Rocky Mountains, shrubs reach their maximum potential in about 10–30 years [85–87]. In a nearby study site in northwestern Montana with similar species to those in our study, the shrub community after biomass removal was persisting at pre-harvest levels 38 years later [88]. Our measurements from five out of six disturbed XETE plots 30 years after disturbance revealed that the relative abundance of dead shrubs was high (>18%), and that in plots with the greatest disturbance levels (i.e., West 2, harvest and wildfire; South 12/13, wildfire; >98% loss of forest floor) the relative abundance of dead shrubs surpassed the relative abundance of any individual live species. This decline of shrubs, which can occur rapidly [87], is likely the result of canopy closure [85,89], marking entry into the stem exclusion phase of forest stand development [90]. We did not, however, see a similar amount of mortality in the more mesic MEFE sites, which also had comparatively higher biomass production. These results contrast with Alldredge et al. [87]; their productivity models, which were developed using data obtained from a range of silvicultural methods, suggest higher rates of productivity for southern aspects than for northern aspects and a faster decline of shrubs on northern aspects.

In the undisturbed MEFE plots (UM), the overall number of shrub species was high (11); the most prevalent shrub species were *M. ferruginea* and *V. membranaceum*. While both species can regenerate from root crowns, *M. ferruginea* also reproduces from seeds [91], whereas *V. membranaceum* also reproduces from rhizomes [92]. Although harvesting had little influence on their relative abundance

(East 2) or overall species biodiversity, their relative abundance and relative biomass levels were reduced by the increasing levels of fire severity that removed the forest floor, likely destroying the seed bank and rhizomes. In contrast, *A. v. sinuata*, an actinorhizal N-fixing species found in moist sites, increased in relative abundance as fire severity increased. This species is an aggressive colonizer after fire because of its ability to sprout from the root crown and its prolific production of wind-borne seeds [93]. Reproduction through wind-borne seeds is characteristic of large, woody, actinorhizal N-fixing plants, which leads to them being more evenly distributed across the landscape and favoring earlier development in succession [94].

In the drier XETE sites, any level of disturbance reduced *V. membranaceum*, the most abundant shrub in the undisturbed plots. Removal of the overstory in South 11 and harvest and fire in the other XETE plots nearly eliminated this shade-tolerant, rhizomatous, late seral species. Disturbance did, however, result in four species (*S. scouleriana*, *A. v. sinuata*, *S. canadensis*, and *C. velutinus*) that were not observed in undisturbed plots (UX) becoming abundant, three of which are actinorhizal N-fixers. We did not observe *S. scouleriana* in any of the undisturbed plots (UX or UM), in agreement with other observations [87]. Thus, even though *S. scouleriana* can sprout from the root crown [95], its high relative abundance in the disturbed XETE plots suggests that its small, fluffy, airborne seeds are its prominent method of early successional colonization [81]. As in some MEF plots, *A. v. sinuata* was a robust colonizer, but only on the western aspect; the southern aspect was likely too dry [93]. *Shepherdia canadensis* can regenerate by sprouting from the root crown and via its seeds [96]. Its high relative abundance in South 11, where harvest was the sole disturbance, could be a function of existing plants able to grow more vigorously without the overstory competition for resources [84], likely because this species is more prevalent in later successional stages, and as we observed can be present in old-growth stands [97]. Its presence may also be a result of the off-site transfer of seeds onto the disturbed forest floor [96]. Because seed scarification is often used to stimulate germination [98], it is likely that seeds persist in the seed bank. However, the abundance of *S. canadensis* in sites with frequent fire (<50 year intervals [99]) suggests a shorter longevity in the seed bank than *C. velutinus*, for which some evidence suggests can persist for 200 + years [100].

Ceanothus velutinus presents its greatest potential on southern aspects [101], where in the first three years after severe fire it can account for 40% of the relative abundance [102], and within seven years can bring site N concentrations (i.e., soil, litter, and biomass) to pre-burn levels [103]. While these four species were absent in the undisturbed XETE plots (UX), they became prevalent post-disturbance, leading to an overall increase in shrub diversity compared to the UX plots. In the harvest-only plot South 11, the resurgence of *S. canadensis* with 71% relative abundance yielded the lowest within-plot species diversity (H') and evenness (J') in the study. It is noteworthy that any disturbance on the southern aspects resulted in robust development of an N-fixing shrub species, and unlike a previous study [104], we observed mixtures of N-fixing shrub species in some plots.

We observed a strong relationship between the relative abundance of the actinorhizal N-fixing shrubs (*A. v. sinuata*, *C. velutinus*, and *S. canadensis*) and the amount of N in the total soil pool. While Newland and Deluca [104] found that potentially mineralizable N (PMN) and the ratio of PMN to total N were greater in non-burned stands than burned stands when sampling herbaceous and woody N-fixing species in western Montana, they found no correlation between PMN and N-fixer abundance (i.e., cover or frequency). In developing floodplain soils in Alaska, *S. canadensis* contributed about 50% of the total N accretion obtained from inception through to 300 years later, with maximum accretion occurring when this shrub dominated the community [105]. Reported N-fixation rates for *S. canadensis* and *C. velutinus* vary widely, likely the result of differing shrub densities, community dynamics, measuring techniques, and other variables [106–109]. Nonetheless, recent studies have demonstrated that where productivity is limited by N availability, non-N-fixing plants respond positively to increased soil N generated by N-fixing plants [110,111], although changes to soil biota [111], increased soil organic matter levels [110], subsequent slow release of chemically bound organic N [112], and service as nurse plants for other species' establishment and growth [97,113] may also be important.

4.2. *Larix occidentalis* Regeneration

Natural regeneration of *L. occidentalis* is negatively correlated with the amount and diversity of understory species [114]. A primary objective of the original 1967 treatments was to elucidate silvicultural practices to encourage natural regeneration of *L. occidentalis*, with the general finding that although germination occurred in a variety of seedbed types, seedling survival was limited to mineral soil seedbeds [18,115]. This is not surprising, given its high level of shade and drought intolerance [116]. On *L. occidentalis* sites, fire can reduce forest floor and microsite heterogeneity (i.e., increases levels of bare mineral soil) and competing vegetation [117], which would reduce competition for light and water. In East 2 and South 11, where the only disturbance was harvest, little regeneration of *L. occidentalis* was apparent, likely because of the lack of mineral soil substrate and the high abundance of shrubs. The addition of any level of fire stimulated the regeneration of *L. occidentalis*. On the harvested East 3 plot, which experienced low-severity fire, *L. occidentalis* regenerated. The relative abundance of biomass for *L. occidentalis* compared to other tree species was similar to the levels found in undisturbed MEFE plots. The likely rapid recovery of other vegetation in East 3 probably decreased the number of suitable microsites for *L. occidentalis* seed germination and persistence, as revealed by a subsequent lack of seedlings 30 years later. Harvested plot North 12 experienced a hotter fire, as evidenced by the greater loss of forest floor; although colonization by the high-stature shrubs *A. v. sinuata* and *S. scouleriana* greatly reduced the number of *L. occidentalis* trees ha⁻¹, the rapid juvenile growth of this species [118] did allow some trees to out compete the shrubs, leading to its high relative biomass.

In the hotter, drier XETE plots, where fire-induced changes to the forest floor may have persisted longer, more *L. occidentalis* seedlings were observed compared to MEFE plots, especially in South 12/13, which experienced a complete loss of forest floor in the 1967 stand-replacing wildfire. While all levels of disturbance in XETE plots fostered *L. occidentalis* regeneration, we noted a trend of decreasing *L. occidentalis* relative abundance and relative biomass with increasing fire severity, however the actual numbers of trees ha⁻¹ were quite variable. Undoubtedly other factors may be involved, including disturbance plot hysteresis. For example, in South 13, *P. contorta* was a component of the original stand (7%) [51], and its serotinous cones likely contributed to the dominance of this species in this disturbance category.

The ability of *L. occidentalis* to readily regenerate when presented with early seral stand conditions as the result of fire has allowed this species to respond favorably to short-term changes in climate [119]. The continuing shift toward a hotter and drier climate, which facilitates more frequent and intense fires, has benefitted seedling recruitment, indicating that climatic factors are apparently less important to regeneration than those associated with overstory competition [119].

4.3. Soil Responses and C and N Pools

Low-temperature surface fires alter forest ecosystems; surface combustion reduces the levels of WR, forest floor, soil wood, and understory vegetation, and thereby releases nutrients, which in turn increase nutrient availability. As fires increase in severity, the result is more oxidation of OM within the mineral soil, volatilization of nutrients, and reduced nutrient availability, which may persist for a few years or have a longer term impact [120]. This is evident in our moister MEFE plots; the harvested East 3 plot, which experienced lower severity prescribed fire, had a soil N pool similar to the undisturbed plots (UM); whereas harvested North 12, which experienced higher severity prescribed fire, did not. Similarly, while the overall vegetation C pool in disturbed MEFE plots averaged only 17% of that in UM, the soil C pools were equal to or exceeded those of UM plots, except under the highest disturbance level in North 12. In the drier XETE plots, the soil C values were greater in the undisturbed plots, but N values were generally lower.

In the MEFE plots, the proportion of biomass in the WR, surface organic horizons, and soil wood were greater in disturbed plots than in the undisturbed plots (UM), but the distribution of these substrates was different. For example, WR levels were almost 5 times greater in UM plots and 3 times greater in undisturbed XETE plots than in the disturbed plots. Across both MEFE and XETE plots,

the total WR biomass was less than half that of undisturbed plots, with the greatest residue levels occurring in the uncut plot burned by wildfire (South 12/13). Woody residue amounts are a function of forest type, site type, time since disturbance, type of disturbance, and decomposition [121–123]; therefore, in the same climate, plots with the greatest severity of disturbance, whether from harvest or fire, will have less WR. The woody residue, forest floor, and soil wood account for 44–84% of C in several mid-successional stands across the western USA [29]. Similarly, the C pools in disturbed plots represented 88% and 48% of the C pools in MEFE and XETE plots, respectively, as compared to the undisturbed plots for either habitat type phase. The forest floor and soil wood levels in the moister MEFE plots had nearly recovered from burning.

The recovery of the forest floor and soil wood is important for overall site productivity [35], because of the physical (i.e., water-holding capacity), chemical (i.e., nutrient cycling), and biological (i.e., non-symbiotic N-fixation [124]) functions they support. Therefore, even though we saw reductions in WR, forest floor, and soil wood levels relative to undisturbed MEFE plots, the C and N pools we observed 30 years after harvesting and prescribed fire in the MEFE plots suggest that these activities were not detrimental to stand productivity. Our results are similar to those in a moist, east-facing *L. occidentalis* forest in western Montana [21]. After three decades, however, the XETE disturbed plots showed less recovery than the moister MEFE plots. In particular, most of the soil wood was removed in all XETE plots (except West 10) after harvesting and fire. Soil wood and forest floor material are critical for supporting ectomycorrhizal activity, maintaining soil moisture through the summer drought, and facilitating seedling survival and understory development [125].

In the western USA, N is a limiting nutrient in soils [126], with N pools typically being much larger in the mineral soil than surface organic layers [29]. We did not, however, observe this pattern in our MEFE or XETE plots, where more N was located in the forest floor than in the mineral soil samples to a 30 cm depth. This means that soil N pools are at-risk if another fire occurs, the result of which could compromise stand recovery.

It is important to recognize how stands accumulate C and N after disturbance, as this has implications for climate change. Increased fire frequency in Canada has converted boreal forests to a net source for C [127]. Unless high-severity fires predominate, woody residues are resistant to burning, meaning this pool would be a resilient source of ecosystem C. Further, in wetter ecosystems, such as our MEFE plots, the forest floor would likely recover before the next disturbance. In the drier XETE habitat type phase, the C and N soil pools in harvest-only South 11 were close to initial levels within the forest floor, however if wildfire occurs this pool will be vulnerable.

4.4. Management Implications

When this experiment was initiated in the late 1960s, the management focus for federal forests in the USA was extraction of timber, and *L. occidentalis*, with its desirable growth characteristics, was seen as an important species [128]. As noted, however [129], traditional forest management techniques often target a specific outcome that can lead to unforeseen negative consequences. Often, the result is more homogeneity among stands across the landscape [129], associated with loss of biodiversity, and subsequently resilience, which is necessary to retain as a vital pillar of climate change adaptation in forests [130]. Despite the use in western Montana of prescribed fire following clearcut harvesting, which are silvicultural techniques that emulate stand-replacing wildfire, researchers suggest that silvicultural practices may have caused a fundamental loss of N-fixing species across the landscape, with possible repercussions in terms of long-term nutrient cycling and forest productivity [104].

As concluded in [129], silvicultural techniques that retain patterns and processes of natural disturbances can be successful, however the fundamental differences between practiced silviculture techniques and natural disturbances mean that full ecosystem benefits may not be provided. Of course, the natural disturbance being emulated and the realization of benefits are both social constructs often lacking consensus [8,131].

Nonetheless, the novelty of our experiment was the opportunity to compare a range of silviculture techniques (e.g., harvest and prescribed fire) in combination with a naturally occurring, stand-replacing wildfire. Our results suggest that harvest plus prescribed fire is a viable method for maintaining *L. occidentalis* as part of a mixed conifer forest, and can also support diverse understory shrub species, especially N-fixing species. While we observed composition shifts with varied disturbance levels, the homogenous overall increase in shrub biodiversity, abundance, and biomass after fire suggests attainment of a heterogenous landscape [83]. In this experiment, many of the soil metrics we measured were approaching, or had already surpassed, those of the undisturbed forest. In contrast, the vegetation total biomass and C levels were a fraction of those observed in the undisturbed forest. Given the wood volume of the undisturbed forest this is not surprising, and gives support to others who concluded that achieving pre-disturbance C pools requires mature trees [20,24,26,132].

Although the recovery trajectory of disturbed forests can vary in the northern Rocky Mountains, “the eventual outcome is relatively consistent”, which is a “dominant conifer overstory with an understory of shade-tolerant shrubs and herbs” [81] (p. 357). Our results appear to concur with that conclusion, and confirm that *L. occidentalis* regeneration can be supported by harvest and prescribed fire in mixed conifer forests, particularly on southern and western aspects. As the climate niche for *L. occidentalis* continues to retract within its current range and regeneration shifts to the cool, dry subset of the sites now occupied by this species [119], land managers may need to place additional focus on eastern and northern aspects. Our results show that *L. occidentalis* can be regenerated with harvest and prescribed fire in these cooler, moister sites as well, although additional treatment(s) may be necessary to control competition that would otherwise prevent this seral, shade-intolerant species from establishing its renowned place in western USA landscapes and from fulfilling desired ecosystem functions.

5. Conclusions

Our study evaluated the 30-year responses of vegetation and soil to 11 disturbances of varying severity, which occurred within the context of a large-area (240 ha) study initiated in 1967. Although the original objective of this management-driven study was to evaluate the effects of prescribed burning at various times of the year on the establishment and growth of *L. occidentalis* following clearcut harvesting, a 1967 wildfire within the study site allowed the effects of wildfire to be incorporated. Thus, we leveraged this experiment to measure changes in plant communities (species composition and biomass) and soils (C and N pools) in different habitat type phases in combination with harvesting and fire.

Our first hypothesis and its corollaries were that increasing levels of disturbance severity would increase species richness, diversity, and evenness more in mesic sites than in xeric sites, as identified by habitat type phase, and that disturbance severity would influence the presence and abundance of N-fixing plant species and their influence on soil N pools. Our results provided mixed support. While disturbance severity in the cooler, moister habitat type phase had no effect on species diversity, it did increase diversity in the hotter, drier habitat type phase, whereas species evenness showed the opposite pattern. In the cooler, moister sites, extremes of disturbance severity skewed the individual abundance of shrub species, whereas abundance was more even in the hotter, drier sites. Overall, species diversity and evenness across all disturbance severities and habitat type phases were similar. Regardless of disturbance type (i.e., harvest, prescribed fire, or wildfire), the abundance of N-fixing shrubs increased and a positive effect of their relative abundance on the soil N pool was noted.

We hypothesized that *L. occidentalis* would regenerate prevalently in more severely disturbed sites and that these conducive site conditions would further support longer term recruitment. Indeed, regardless of the habitat type phase, harvesting without fire resulted in few *L. occidentalis* trees and no seedlings 30 years hence, whereas any severity of fire (58 to 100% losses of forest floor) promoted the density, relative abundance, and relative biomass of *L. occidentalis*. In the hotter, drier sites, seedling recruitment continued through the first 30 years, whereas seedling recruitment in the cooler, moister

sites was only observed with the greatest fire severity (91% loss of the forest floor). Thus, the trend of greater *L. occidentalis* regeneration in cooler, drier sites in response to climate change may require land managers to consider higher severity prescribed burns on northern and eastern aspects to promote *L. occidentalis* regeneration.

We accept our final hypothesis and its corollaries, which stated that long-term C and N pool recovery depends on disturbance severity, but in different ways. Less severe disturbance favors above- and belowground C pool development, whereas N pools increase with increasing disturbance severity. The recovery of soil C is linked to vegetation regeneration, and additional fires in this forest type may not allow for complete re-accumulation of C in above- and belowground pools. Nitrogen pools after harvesting resulted in greater N for all horizons, except soil wood. We note that although prescribed fire can increase aboveground N pools, high burn severity reduced it in the moister plots and increased it in the drier plots. Because conifer forest soil N limits productivity, the size of the N pool after disturbance and the speed of recovery will also affect future aboveground vegetative re-growth. Finally, we note that in many plots, mineral soil pools were near or above the undisturbed levels after 30 years, but these pools are located in forest floor horizons vulnerable to fire.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/11/10/1040/s1>. Supplementary tables provide 30-year post-treatment measures of relative abundance (% of total) and relative biomass (% of total) for shrubs (Table S1), seedlings (Table S2), and trees (Table S3); and the means (plus standard deviations) of biomass and N in the vegetation, woody residue, and soil (Table S4) for the 11 disturbance categories. Table S5: Nitrogen concentrations in wood and foliage of trees and shrubs.

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Data Availability: Data are available at the USDA Forest Service Research Data Archive [133].

References

1. Turner, M.G. Disturbance and landscape dynamics in a changing world. *Ecology* **2010**, *91*, 2833–2849. [[CrossRef](#)] [[PubMed](#)]
2. Myers, R.L. *Living with Fire-Sustaining Ecosystems & Livelihoods through Integrated Fire Management*; The Nature Conservancy: Tallahassee, FL, USA, 2006; 36p.
3. Bassman, J.H.; Johnson, J.D.; Fins, L.; Dobrowolski, J.P. Rocky Mountain ecosystems: Diversity, complexity and interactions. *Tree Physiol.* **2003**, *23*, 1081–1089. [[CrossRef](#)] [[PubMed](#)]
4. Long, J.N. Diversity, complexity and interactions: An overview of Rocky Mountain forest ecosystems. *Tree Physiol.* **2003**, *23*, 1091–1099. [[CrossRef](#)]
5. Agee, J.K. The landscape ecology of western forest fire regimes. *Northwest Sci.* **1998**, *72*, 24–34.
6. Fischer, J.; Lindenmayer, D.B.; Manning, A.D. Biodiversity, ecosystem function, and resilience: Ten guiding principles for commodity production landscapes. *Front. Ecol. Environ.* **2006**, *4*, 80–86. [[CrossRef](#)]
7. Thompson, I.; Mackey, B.; McNulty, S.; Mosseler, A. Forest Resilience, Biodiversity, and Climate Change. In *A Synthesis of the Biodiversity/Resilience/Stability Relationship in Forest Ecosystems*; Technical Series 43; Secretariat of the Convention on Biological Diversity: Montreal, QC, Canada, 2009; 67p.

8. Long, J.N. Emulating natural disturbance regimes as a basis for forest management: A North American view. *For. Ecol. Manag.* **2009**, *257*, 1868–1873. [[CrossRef](#)]
9. Stanturf, J.A.; Palik, B.J.; Dumroese, R.K. Contemporary forest restoration: A review emphasizing function. *For. Ecol. Manag.* **2014**, *331*, 292–323. [[CrossRef](#)]
10. Keane, R.E.; Agee, J.K.; Fulé, P.; Keeley, J.E.; Key, C.; Kitchen, S.G.; Miller, R.F.; Schulte, L.A. Ecological effects of large fires on US landscapes: Benefit or catastrophe? *Int. J. Wildland Fire* **2008**, *17*, 696–712. [[CrossRef](#)]
11. Williams, J. Exploring the onset of high-impact mega-fires through a forest land management prism. *For. Ecol. Manag.* **2013**, *294*, 4–10. [[CrossRef](#)]
12. Stanturf, J.A.; Palik, B.J.; Williams, M.I.; Dumroese, R.K.; Madsen, P. Forest restoration paradigms. *J. Sustain. For.* **2014**, *33*, S161–S194. [[CrossRef](#)]
13. Keeley, J.E.; Aplet, G.H.; Christensen, N.L.; Conard, S.C.; Johnson, E.A.; Omi, P.N.; Peterson, D.L.; Swetnam, T.W. *Ecological Foundations for Fire Management in North American Forest and Shrubland Ecosystems*; General Technical Report PNW-GTR-779; USDA Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2009; 92p. Available online: <https://www.fs.usda.gov/treearch/pubs/32483> (accessed on 11 August 2020).
14. Agee, J.K. *Fire and Weather Disturbances in Terrestrial Ecosystems of the Eastern Cascades*; General Technical Report PNW-GTR-320; USDA Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 1994; 52p. [[CrossRef](#)]
15. Arno, S.F.; Fischer, W.C. *Larix occidentalis—Fire Ecology and Fire Management*. In *Ecology and Management of Larix Forests: A Look Ahead*; General Technical Report, GTR-INT-319; Schmidt, W.C., McDonald, K.J., Compilers; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1995; pp. 130–135.
16. Schmidt, W.C.; Shearer, R.C. *Larix occidentalis: A Pioneer of The North American West*. In *Ecology and Management of Larix Forests: A Look Ahead*; General Technical Report, GTR-INT-319; Schmidt, W.C., McDonald, K.J., Compilers; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1995; pp. 33–37.
17. Camp, A.; Oliver, C.; Hessburg, P.; Everett, R. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *For. Ecol. Manag.* **1997**, *95*, 63–77. [[CrossRef](#)]
18. Shearer, R.C. *Seedbed Characteristics in Western Larch Forests after Prescribed Burning*; Research Paper INT-167; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1975; 26p.
19. Shearer, R.C.; Stickney, P.F. Natural Revegetation of Burned and Unburned Clearcuts in Western Larch Forests of Northwest Montana. In *Fire and the Environment: Ecological and Cultural Perspectives*; General Technical Report, SE-69; Nodvin, S.C., Waldrop, T.A., Eds.; USDA Forest Service, Southeastern Forest Experiment Station: Asheville, NC, USA, 1991; pp. 66–74. [[CrossRef](#)]
20. Harmon, M.E.; Ferrell, W.K.; Franklin, J.F. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* **1990**, *247*, 699–702. [[CrossRef](#)] [[PubMed](#)]
21. Jang, W.; Page-Dumroese, D.S.; Keyes, C.R. Long-term soil changes from forest harvesting and residue management in the Northern Rocky Mountains. *Soil Sci. Soc. Am. J.* **2016**, *80*, 727–741. [[CrossRef](#)]
22. Gough, C.M.; Vogel, C.S.; Harrold, K.H.; George, K.; Curtis, P.S. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. *Glob. Chang. Boil.* **2007**, *13*, 1935–1949. [[CrossRef](#)]
23. Powers, R.F.; Scott, D.A.; Sanchez, F.G.; Voldseth, R.A.; Page-Dumroese, D.; Elioff, J.D.; Stone, D.M. The North American long-term soil productivity experiment: Findings from the first decade of research. *For. Ecol. Manag.* **2005**, *220*, 31–50. [[CrossRef](#)]
24. Bisbing, S.M.; Alaback, P.B.; DeLuca, T.H. Carbon storage in old-growth and second growth fire-dependent western larch (*Larix occidentalis* Nutt.) forests of the Inland Northwest, USA. *For. Ecol. Manag.* **2010**, *259*, 1041–1049. [[CrossRef](#)]
25. Spies, T.A.; Franklin, J.F.; Thomas, T.B. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* **1988**, *69*, 1689–1702. [[CrossRef](#)]
26. Harmon, M.E.; Marks, B. Effects of silvicultural practices on carbon stores in Douglas-fir—western hemlock forests in the Pacific Northwest, USA: Results from a simulation model. *Can. J. For. Res.* **2002**, *32*, 863–877. [[CrossRef](#)]
27. Lattimore, B.; Smith, C.T.; Titus, B.D.; Stupak, I.; Egnell, G. Environmental factors in woodfuel production: Opportunities, risks, and criteria and indicators for sustainable practices. *Biomass Bioenergy* **2009**, *33*, 1321–1342. [[CrossRef](#)]

28. Thiffault, E.; Hannam, K.D.; Paré, D.; Titus, B.D.; Hazlett, P.W.; Maynard, D.G.; Brais, S. Effects of forest biomass harvesting on soil productivity in boreal and temperate forests—A review. *Environ. Rev.* **2011**, *19*, 278–309. [[CrossRef](#)]
29. Page-Dumroese, D.S.; Jurgensen, M.F. Soil carbon and nitrogen pools in mid- to late-successional forest stands of the northwestern United States: Potential impact of fire. *Can. J. For. Res.* **2006**, *36*, 2270–2284. [[CrossRef](#)]
30. McNabb, D.H.; Cromack, K., Jr. Effects of prescribed fire on nutrients and soil productivity. In *Natural and Prescribed Fire in Pacific Northwest Forests*; Walstad, J.D., Radosevich, S.R., Sandberg, D.V., Eds.; Oregon State University Press: Corvallis, OR, USA, 1990; pp. 125–142.
31. Grogan, P.; Bruns, T.D.; Chapin, F.S. III. Fire effects on ecosystem nitrogen cycling in a California bishop pine forest. *Oecologia* **2000**, *122*, 537–544. Available online: <https://www.jstor.org/stable/4222577> (accessed on 11 August 2020). [[PubMed](#)]
32. DeBano, L.F.; Eberlein, G.E.; Dunn, P.H. Effects of burning on chaparral soils: I. Soil nitrogen. *Soil Sci. Soc. Am. J.* **1979**, *43*, 504–509. [[CrossRef](#)]
33. Raison, R.J.; Khanna, P.K.; Woods, P.V. Mechanisms of element transfer to the atmosphere during vegetation fires. *Can. J. For. Res.* **1985**, *15*, 132–140. [[CrossRef](#)]
34. Gillon, D.; Rapp, M. Nutrient losses during a winter low-intensity prescribed fire in a Mediterranean forest. *Plant Soil* **1989**, *120*, 69–77. [[CrossRef](#)]
35. Jurgensen, M.F.; Harvey, A.E.; Graham, R.T.; Page-Dumroese, D.S.; Tonn, J.T.; Larsen, M.J.; Jain, T.B. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. *For. Sci.* **1997**, *43*, 234–251. [[CrossRef](#)]
36. Powers, R.F.; Alban, D.H.; Miller, R.E.; Tiarks, A.E.; Wells, C.G.; Avers, P.E.; Cline, R.G.; Fitzgerald, R.D.; Loftus, N.S., Jr. Sustaining Site Productivity in North America Forests: Problems and Prospects. In *Sustained Productivity of Forest Soils, Proceedings of the Seventh North American Forest Soils Conference, University of British Columbia, Vancouver, British Columbia, Canada, August 1998*; Gessel, S.P., Lacate, D.S., Weetman, G.F., Powers, R.F., Eds.; Forestry Publications, Faculty of Forestry, University of British Columbia: Vancouver, BC, Canada, 1990; pp. 49–79.
37. Burger, J.A.; Mitchem, D.O.; Scott, D.A. Field Assessment of Mine Site Quality for Establishing Hardwoods in the Appalachians. In *Proceedings: American Society of Mining and Reclamation 19th Annual National Conference and International Affiliation of Land Reclamation 6th International Conference, Lexington, KY, USA, 9–13 June 2002*; Barnhisel, R., Collins, M., Eds.; American Society of Mining and Reclamation: Lexington, KY, USA, 2002; pp. 226–240.
38. Sanchez, F.G.; Tiarks, A.E.; Kranabetter, J.M.; Page-Dumroese, D.S.; Powers, R.F.; Sanborn, P.T.; Chapman, W.K. Effects of organic matter removal and soil compaction on fifth-year mineral soil carbon and nitrogen contents for sites across the United States and Canada. *Can. J. For. Res.* **2006**, *36*, 565–576. [[CrossRef](#)]
39. Clarke, N.; Gundersen, P.; Jönsson-Belyazid, U.; Kjonaas, O.J.; Persson, T.; Sigurdsson, B.D.; Stupak, I.; Vesterdal, L. Influence of different tree-harvesting intensities on forest soil carbon stocks in boreal and northern temperate forest ecosystems. *For. Ecol. Manag.* **2015**, *351*, 9–19. [[CrossRef](#)]
40. Shepherd, M.; Harrison, R.; Webb, J. Managing soil organic matter—implications for soil structure on organic farms. *Soil Use Manag.* **2002**, *18*, 284–292. [[CrossRef](#)]
41. Jastrow, J. Soil aggregate formation and the accrual of particulate and mineral-associated organic matter. *Soil Boil. Biochem.* **1996**, *28*, 665–676. [[CrossRef](#)]
42. Harvey, A.E.; Larsen, M.J.; Jurgensen, M.F. Ecology of Ectomycorrhizae in a Northern Rocky Mountain Forest. In *Environmental Consequences of Timber Harvesting in Rocky Mountain Coniferous Forests*; General Technical Report GTR-INT-90; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1980; pp. 189–208.
43. Walker, B.H.; Steffen, W.L. The Nature of Global Change. In *The Terrestrial Biosphere and Global Change*; Walker, B.H., Steffen, W.L., Canadell, J., Ingram, J., Eds.; Cambridge University Press: Cambridge, UK, 1999; pp. 1–18.
44. Rehfeldt, G.E.; Jaquish, B.C. Ecological impacts and management strategies for western larch in the face of climate-change. *Mitig. Adapt. Strat. Glob. Chang.* **2010**, *15*, 283–306. [[CrossRef](#)]

45. Beaufait, W.R.; Hardy, C.E.; Fischer, W.C. *Broadcast Burning in Larch-Fir Clearcuts: The Miller Creek-Newman Ridge Study*; Research Paper INT-175; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1977; 53p.
46. DeByle, N.V. *Clearcutting and Fire in the Larch/Douglas-fir Forests of Western Montana—A Multifaceted Research Summary*; General Technical Report INT-99; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1981; 73p.
47. Shearer, R.C.; Stickney, P.F.; VanDenburg, J.H.; Wirt, S.E. A Long-Term Management and Research Partnership Facilitates Ecosystem Management Opportunities in a Montana Western Larch Forest. In *Silviculture: From the Cradle of Forestry to Ecosystem Management: Proceedings of the National Silviculture Workshop*; General Technical Report, SE-88; Foley, L.H., Compiler; USDA Forest Service, Southeastern Forest Experiment Station: Asheville, NC, USA, 1994; pp. 194–200. [[CrossRef](#)]
48. Soil Survey Staff, USDA Natural Resources Conservation Service. Official Soil Series Descriptions. Available online: <https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/> (accessed on 13 July 2020).
49. Eyre, F.H. (Ed.) *Forest Cover Types of the United States and Canada*; Society of American Foresters: Bethesda, MD, USA, 1980; 148p.
50. Pfister, R.D.; Kovalchik, B.; Arne, S.; Presby, R. *Forest Habitat Types of Montana*; General Technical Report INT-34; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1977; 174p. Available online: <https://www.fs.usda.gov/treearch/pubs/41077> (accessed on 11 August 2020).
51. Stickney, P.F.; Campbell, R.B., Jr. *Data Base for Early Postfire Succession in Northern Rocky Mountain Forests*; General Technical Report RMRS-GTR-61CD; USDA Forest Service, Rocky Mountain Research Station: Ogden, UT, USA, 2000. [[CrossRef](#)]
52. Beaufait, W.R. An integrating device for evaluating prescribed fire. *For. Sci.* **1966**, *12*, 27–29. [[CrossRef](#)]
53. Latham, P.A.; Shearer, R.C.; O'Hara, K.L. *Miller Creek Demonstration Forest—A Forest Born of Fire: A Field Guide*; General Technical Report RMRS-GTR-7; USDA Forest Service, Rocky Mountain Research Station: Ogden, UT, USA, 1998; 68p. [[CrossRef](#)]
54. U. S. Department of Agriculture. *National Fire-danger Rating Handbook*; Handbook 5109.1; USDA Forest Service: Washington, DC, USA, 1964.
55. DeByle, N.V. Broadcast burning of logging residues and the water repellency of soils. *Northwest Sci.* **1973**, *47*, 77–87.
56. Shearer, R.C.; Schmidt, J.A.; Stickney, P.F. *Development of Natural and Planted Conifer Regeneration and Forest Succession of Young Stands Following Clearcutting and Burning Treatments, within the Western Larch Forest Cover Type, Miller Creek Demonstration Forest, Tally Lake Ranger District, Flathead National Forest*; Study Plan INT-4151-021; USDA Forest Service, Intermountain Research Station: Missoula, MT, USA, 1991.
57. Bonham, C.D. *Measurements for Terrestrial Vegetation*; John Wiley & Sons Inc.: New York, NY, USA, 1989; 338p.
58. Brown, J.K. Estimating shrub biomass from basal stem diameters. *Can. J. For. Res.* **1976**, *6*, 153–158. [[CrossRef](#)]
59. Integrated Taxonomic Information System (ITIS) Online Database. Available online: <https://www.itis.gov> (accessed on 13 July 2020).
60. Cairns, M.A.; Brown, S.; Helmer, E.H.; Baumgardner, G.A. Root biomass allocation in the world's upland forests. *Oecologia* **1997**, *111*, 1–11. [[CrossRef](#)]
61. Brown, J.K. *Handbook for Inventorying Downed Woody Material*; General Technical Report INT-GTR-16; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1974; 24p.
62. Jurgensen, M.F.; Larsen, M.J.; Harvey, A.E. *A Soil Sampler for Steep, Rocky Slopes*; Research Note INT-RN-217; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1977; 5p.
63. Page-Dumroese, D.S.; Brown, R.E.; Jurgensen, M.F.; Mroz, G.D. Comparison of methods for determining bulk densities of rocky forest soils. *Soil Sci. Soc. Am. J.* **1999**, *63*, 379–383. [[CrossRef](#)]
64. Triska, F.J.; Cromack, K., Jr. The Role of Woody Debris in Forests and Streams. In *Forests: Fresh Perspectives from Ecosystem Analysis*; Waring, R.H., Ed.; Oregon State University Press: Corvallis, OR, USA, 1979; pp. 171–190.
65. Reinhardt, E.D.; Crookston, N.L. (Eds.) *The Fire and Fuels Extension to the Forest Vegetation Simulator*; General Technical Report RMRS-GTR-116; USDA Forest Service, Rocky Mountain Research Station: Ogden, UT, USA, 2003; 209p. [[CrossRef](#)]

66. Dixon, G.E. (Compiler) *Essential FVS: A User's Guide to the Forest Vegetation Simulator*; Internal Report (12 August 2011 revision); USDA Forest Service, Forest Management Service Center: Fort Collins, CO, USA, 2002; 244p. Available online: <https://www.fs.fed.us/fmsc/fvs/documents/userguides.shtml> (accessed on 5 April 2017).
67. Keyser, C.E. (Compiler) *Northern Idaho/Inland Empire (NI/IE) Variants Overview—Forest Vegetation Simulator*; Internal Report (4 October 2011 revision); USDA Forest Service, Forest Management Service Center: Fort Collins, CO, USA, 2008; 49p. Available online: <https://www.fs.fed.us/fmsc/fvs/documents/userguides.shtml> (accessed on 5 April 2017).
68. Shannon, C.E. A mathematical theory of communication. *Bell Syst. Tech. J.* **1948**, *27*, 379–423.
69. Cromack, K., Jr.; Miller, R.E.; Anderson, H.W.; Helgerson, O.T.; Smith, R.B. Soil carbon and nutrients in a coastal Oregon Douglas-fir plantation with red alder. *Soil Sci. Soc. Am. J.* **1999**, *63*, 232–239. [[CrossRef](#)]
70. Harrison, R.B.; Adams, A.B.; Licata, C.; Flaming, B.; Wagoner, G.L.; Carpenter, P.; Vance, E.D. Quantifying deep-soil and coarse-soil fractions. *Soil Sci. Soc. Am. J.* **2003**, *67*, 1602–1606. [[CrossRef](#)]
71. Whitney, N.; Zabowski, D. Total soil nitrogen in the coarse fraction and at depth. *Soil Sci. Soc. Am. J.* **2004**, *68*, 612–619. [[CrossRef](#)]
72. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria. Available online: <https://www.R-project.org/> (accessed on 3 January 2020).
73. Hothorn, T.; Bretz, F.; Westfall, P. Simultaneous inference in general parametric models. *Biom. J.* **2008**, *50*, 346–363. [[CrossRef](#)] [[PubMed](#)]
74. Kramer, C.Y. Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics* **1956**, *12*, 307–310. [[CrossRef](#)]
75. Bray, J.R.; Curtis, J.T. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* **1957**, *27*, 325–349. [[CrossRef](#)]
76. McCune, B.; Grace, J.B. *Analysis of Ecological Communities*; MjM Software Design: Gleneden Beach, OR, USA, 2002.
77. Kruskal, W.H.; Wallis, W.A. Use of ranks in one-criterion variance analysis. *J. Am. Stat. Assoc.* **1952**, *47*, 583–621. [[CrossRef](#)]
78. Erickson, H.E.; Soto, P.; Johnson, D.W.; Roath, B.; Hunsaker, C. Effects of vegetation patches on soil nutrient pools and fluxes within a mixed-conifer forest. *For. Sci.* **2005**, *51*, 211–220. [[CrossRef](#)]
79. Bormann, B.T.; Darbyshire, R.L.; Homann, P.S.; Morrisette, B.A.; Little, S.N. Managing early succession for biodiversity and long-term productivity of conifer forests in southwestern Oregon. *For. Ecol. Manag.* **2015**, *340*, 114–125. [[CrossRef](#)]
80. Schrempp, T.V.; Rachlow, J.L.; Johnson, T.R.; Shipley, L.A.; Long, R.A.; Aycrigg, J.L.; Hurley, M.A. Linking forest management to moose population trends: The role of the nutritional landscape. *PLoS ONE* **2019**, *14*, e0219128. [[CrossRef](#)]
81. Lyon, L.J.; Stickney, P.F. Early Vegetal Succession Following Large Northern Rocky Mountain Wildfires. In *Proceedings of the Montana Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium*; 14. Tall Timbers Research Station: Tallahassee, FL, USA, 1976; pp. 355–375.
82. Lentile, L.B.; Morgan, P.; Hudak, A.T.; Bobbitt, M.J.; Lewis, S.A.; Smith, A.M.S.; Robichaud, P.R. Post-fire burn severity and vegetation response following eight large wildfires across the western United States. *Fire Ecol.* **2007**, *3*, 91–108. [[CrossRef](#)]
83. Crotteau, J.S.; Varner, J.M.; Ritchie, M.W. Post-fire regeneration across a fire severity gradient in the southern Cascades. *For. Ecol. Manag.* **2013**, *287*, 103–112. [[CrossRef](#)]
84. Chase, C.W.; Kimsey, M.J.; Shaw, T.M.; Coleman, M.D. The response of light, water, and nutrient availability to pre-commercial thinning in dry inland Douglas-fir forests. *For. Ecol. Manag.* **2016**, *363*, 98–109. [[CrossRef](#)]
85. Mueggler, W.F. Ecology of seral shrub communities in the cedar-hemlock zone of Northern Idaho. *Ecol. Monogr.* **1965**, *35*, 165–185. [[CrossRef](#)]
86. Irwin, L.L.; Peek, J.M. Shrub production and biomass trends following five logging treatments within the cedar-hemlock zone of northern Idaho. *For. Sci.* **1979**, *25*, 415–426. [[CrossRef](#)]
87. Alldredge, M.W.; Peek, J.M.; Wall, W.A. Shrub community development and annual productivity trends over a 100-year period on an industrial forest of Northern Idaho. *For. Ecol. Manag.* **2001**, *152*, 259–273. [[CrossRef](#)]
88. Jang, W.; Keyes, C.R.; Page-Dumroese, D.S. Recovery and diversity of the forest shrub community 38 years after biomass harvesting in the northern Rocky Mountains. *Biomass Bioenergy* **2016**, *92*, 88–97. [[CrossRef](#)]

89. Alaback, P.B. Dynamics of understory biomass in Sitka spruce—western hemlock forests of Southeast Alaska. *Ecology* **1982**, *63*, 1932–1948. [[CrossRef](#)]
90. Oliver, C.D. Forest development in North America following major disturbances. *For. Ecol. Manag.* **1980**, *3*, 153–168. [[CrossRef](#)]
91. Habeck, R.J. *Menziesia ferruginea*. In *Fire Effects Information System*; USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory: Missoula, MT, USA, 1992. Available online: <https://www.fs.fed.us/database/feis/plants/shrub/menfer/all.html> (accessed on 16 July 2020).
92. Simonin, K.A. *Vaccinium membranaceum*. In *Fire Effects Information System*; USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory: Missoula, MT, USA, 2000. Available online: <https://www.fs.fed.us/database/feis/plants/shrub/vacmem/all.html> (accessed on 16 July 2020).
93. Uchytel, R.J. *Alnus viridis* subsp. *sinuata*. In *Fire Effects Information System*; USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory: Missoula, MT, USA, 1989. Available online: <https://www.fs.fed.us/database/feis/plants/shrub/alnvirs/all.html> (accessed on 15 July 2020).
94. Wilcots, M.; Taylor, B.; Kuprewicz, E.K.; Menge, D.N.L. Small traits with big consequences: How seed traits of nitrogen-fixing plants might influence ecosystem nutrient cycling. *Oikos* **2019**, *128*, 668–679. [[CrossRef](#)]
95. Anderson, M.D. *Salix scouleriana*. In *Fire Effects Information System*; USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory: Missoula, MT, USA, 2001. Available online: <https://www.fs.fed.us/database/feis/plants/tree/salsco/all.html> (accessed on 15 July 2020).
96. Walkup, C.J. *Shepherdia canadensis*. In *Fire Effects Information System*; USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory: Missoula, MT, USA, 1991. Available online: <https://www.fs.fed.us/database/feis/plants/shrub/shecan/all.html> (accessed on 15 July 2020).
97. Walls, L.; Zamora, B.A. Nitrogen-fixing Nodule Characterization and Morphology of Four Species in the Northern Intermountain Region. In *Shrubland Ecosystem Genetics and Biodiversity: Proceedings*; Proceedings, RMRS-P-21; McArthur, E.D., Fairbanks, D.J., Eds.; USDA Forest Service, Rocky Mountain Research Station: Ogden, UT, USA, 2001; pp. 295–301. Available online: <https://www.fs.usda.gov/treearch/pubs/44600> (accessed on 15 July 2020).
98. Rosner, L.S.; Harrington, J.T. Optimizing acid scarification and stratification combinations for russet buffaloberry seeds. *Native Plants, J.* **2003**, *4*, 81–86. [[CrossRef](#)]
99. Johnstone, J.F. Response of boreal plant communities to variations in previous fire-free interval. *Int. J. Wildland Fire* **2006**, *15*, 497–508. [[CrossRef](#)]
100. Gratkowski, H.J. Seeds of *Ceanothus velutinus* var. *laevigatus* T. & G. Ph.D. Dissertation, Oregon State University, Corvallis, OR, USA, 1962; 122p.
101. Noste, N.V.; Bushey, C.L. *Fire Response of Shrubs of Dry Forest Habitat Types in Montana and Idaho*; General Technical Report INT-239; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1987; 22p.
102. Stickney, P.F. *Data Base for Post-Fire Succession, First 6 to 9 Years, in Montana Larch-Fir Forests*; General Technical Report INT-62; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1980; 133p.
103. Youngberg, C.T.; Wollum, A.G., II. Nitrogen accretion in developing *Ceanothus velutinus* stands. *Soil Sci. Soc. Am. J.* **1976**, *40*, 109–112. [[CrossRef](#)]
104. Newland, J.A.; DeLuca, T.H. Influence of fire on native nitrogen-fixing plants and soil nitrogen status in ponderosa pine—Douglas-fir forests in western Montana. *Can. J. For. Res.* **2000**, *30*, 274–282. [[CrossRef](#)]
105. Rhoades, C.; Binkley, D.; Oskarsson, H.; Stottlemeyer, R. Soil nitrogen accretion along a floodplain terrace chronosequence in northwest Alaska: Influence of the nitrogen-fixing shrub *Shepherdia canadensis*. *Écoscience* **2008**, *15*, 223–230. [[CrossRef](#)]
106. Zavitkovski, J.; Newton, M. Ecological importance of snowbrush *Ceanothus velutinus* in the Oregon Cascades. *Ecology* **1968**, *49*, 1134–1145. [[CrossRef](#)]
107. Hendrickson, O.Q.; Burgess, D. Nitrogen-fixing plants in a cut-over lodgepole pine stand of southern British Columbia. *Can. J. For. Res.* **1989**, *19*, 936–939. [[CrossRef](#)]
108. Busse, M.D. Suitability and use of the ¹⁵N-isotope dilution method to estimate nitrogen fixation by actinorhizal shrubs. *For. Ecol. Manag.* **2000**, *136*, 85–95. [[CrossRef](#)]
109. Yelenik, S.; Perakis, S.; Hibbs, D. Regional constraints to biological nitrogen fixation in post-fire forest communities. *Ecology* **2013**, *94*, 739–750. [[CrossRef](#)]

110. Freund, S.M.; Soper, F.; Poulson, S.R.; Selmanns, P.C.; Sullivan, B.W. Actinorhizal species influence plant and soil nitrogen status of semiarid shrub-dominated ecosystems in the western Great Basin, USA. *J. Arid. Environ.* **2018**, *157*, 48–56. [\[CrossRef\]](#)
111. Png, G.K.; Lambers, H.; Kardol, P.; Turner, B.L.; Wardle, D.A.; Laliberté, E. Biotic and abiotic plant–soil feedback depends on nitrogen-acquisition strategy and shifts during long-term ecosystem development. *J. Ecol.* **2019**, *107*, 142–153. [\[CrossRef\]](#)
112. Hibbs, D.E.; Cromack, K., Jr. Actinorhizal Plants in Pacific Northwest Forests. In *The Biology of Frankia and Actinorhizal Plants*; Schwintzer, C.R., Tjepkema, J.D., Eds.; Academic Press: San Diego, CA, USA, 1990; pp. 343–363.
113. Walker, L.R. Nitrogen fixers and species replacements in primary succession. In *Primary Succession on Land*; Miles, J., Walton, W.H.D., Eds.; Blackwell Scientific Publications: Oxford, UK, 1993; pp. 249–272.
114. Shen, C.; Nelson, A.S. Natural conifer regeneration patterns in temperate forests across the Inland Northwest, USA. *Ann. For. Sci.* **2018**, *75*, 54. [\[CrossRef\]](#)
115. Artley, D.K.; Shearer, R.C.; Steele, R.W. *Effects of Burning Moist Fuels on Seedbed Preparation in Cutover Western Larch Forests*; Research Paper INT-211; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1978; 16p.
116. Niinemets, Ü.; Valladares, F. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* **2006**, *76*, 521–547. [\[CrossRef\]](#)
117. Oswald, B.P.; Neuenschwander, L.F. Microsite variability and safe site description for western larch germination and establishment. *Bull. Torrey Bot. Club* **1993**, *120*, 148–156. [\[CrossRef\]](#)
118. Schmidt, W.C. *Seedbed Treatments Influence Seedling Development in Western Larch Forests*; Research Note INT-93; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1969; 7p.
119. Steed, J.E.; Goeking, S.A. Western Larch Regeneration Responds More Strongly to Site and Indirect Climate Factors than to Direct Climate Factors. *Forest* **2020**, *11*, 482. [\[CrossRef\]](#)
120. Neary, D.G.; Klopatek, C.C.; DeBano, L.F.; Ffolliott, P.F. Fire effects on belowground sustainability: A review and synthesis. *For. Ecol. Manag.* **1999**, *122*, 51–71. [\[CrossRef\]](#)
121. Harmon, M.E.; Hua, C. Coarse Woody Debris Dynamics in Two Old-Growth Ecosystems. *Bioscience* **1991**, *41*, 604–610. [\[CrossRef\]](#)
122. Tinker, D.B.; Knight, D.H. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems* **2000**, *3*, 472–483. [\[CrossRef\]](#)
123. Wirth, C.; Schulze, E.-D.; Lühker, B.; Grigoriev, S.; Siry, M.; Hades, G.; Ziegler, W.; Backor, M.; Bauer, G.; Vygodskaya, N. Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant. Soil* **2002**, *242*, 41–63. [\[CrossRef\]](#)
124. Tonn, J.R.; Jurgensen, M.F.; Graham, R.T.; Harvey, A.E. Nitrogen-fixing Processes in Western Larch Ecosystems. In *Ecology and Management of Larix Forests: A Look Ahead*; General Technical Report, GTR-INT-319; Schmidt, W.C., McDonald, K.J., Eds.; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1995; p. 327333.
125. Harvey, A.E.; Larsen, M.J.; Jurgensen, M.F. Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitat types. *For. Sci.* **1979**, *25*, 350–358. [\[CrossRef\]](#)
126. Binkley, D. Connecting soils with forest productivity. In *Proceedings: Management and Productivity of Western-Montane Forest Soils*; General Technical Report, INT-GTR-280; Harvey, A.E., Neuenschwander, L.F., Compilers; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1991; pp. 66–69. [\[CrossRef\]](#)
127. Kurz, W.A.; Apps, M.J. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol. Appl.* **1999**, *9*, 526–547. [\[CrossRef\]](#)
128. Keegan, C.E., III.; Blatner, K.A.; Wichman, D.P. Use and Value of Western Larch as a Commercial Timber Species. In *Ecology and Management of Larix Forests: A Look Ahead*; General Technical Report GTR-INT-319; Schmidt, W.C., McDonald, K.J., Compilers; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1995; pp. 155–157.
129. Drever, C.R.; Peterson, G.; Messier, C.; Bergeron, Y.; Flannigan, M. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* **2006**, *36*, 2285–2299. [\[CrossRef\]](#)
130. Millar, C.I.; Stephenson, N.L.; Stephens, S.L. Climate change and forests of the future: Managing in the face of uncertainty. *Ecol. Appl.* **2007**, *17*, 2145–2151. [\[CrossRef\]](#)

131. Klenk, N.; Bull, G.; Cohen, D. What is the “END” (emulation of natural disturbance) in forest ecosystem management? An open question. *Can. J. Forest Res.* **2008**, *38*, 2159–2168. [[CrossRef](#)]
132. Johnson, D.; Murphy, J.D.; Walker, R.F.; Glass, D.W.; Miller, W.W. Wildfire effects on forest carbon and nutrient budgets. *Ecol. Eng.* **2007**, *31*, 183–192. [[CrossRef](#)]
133. Dumroese, R.K.; Jurgensen, M.F.; Page-Dumroese, D.S. *Soil and Vegetation Responses to 1967-1968 Disturbances on the Miller Creek Demonstration Forest: Thirty Year Data*; USDA Forest Service Research Data Archive: Fort Collins, CO, USA, 2020. [[CrossRef](#)]



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