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Managing early succession for biodiversity and long-term productivity of conifer forests in southwestern Oregon



Bernard T. Bormann^{a,*}, Robyn L. Darbyshire^b, Peter S. Homann^c, Brett A. Morrisette^d, Susan N. Little^{e,1}

^aUSDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, United States

^bUSDA Forest Service, Pacific Northwest Regional Office, 1220 SW 3rd Ave, Portland, OR, United States

^cDept. of Environmental Sciences, Huxley College of the Environment, Western Washington Univ., Bellingham, WA 98225, United States

^dDept. of Forest Ecosystems and Society, Oregon State Univ., Corvallis, OR 97331, United States

^eUSDA Forest Service, Pacific Northwest Research Station, Portland, OR, United States

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ABSTRACT

Early-successional stages have been truncated and altered in many western U.S. forest landscapes by planting conifers, controlling competing vegetation, suppressing fire, and focusing on maintaining late-seral species and undisturbed riparian zones. Declining area of early-successional stages may be reducing resilience and sustainability on landscapes that experience elevated disturbance related to future climate changes. In this study, two post-harvest early-successional treatments were compared to each other and to two mature-forest treatments using 20 years of evidence from replicated 7-ha experimental units in a southwestern Oregon forest dominated by Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco). One early-successional treatment (Douglas-fir plantation) planted Douglas-fir and was followed by a brushing to reduce hardwood competition to move quickly to the conifer stem-exclusion stage; the other (Early-seral plantation) favored natural sprouting and regeneration of hardwood shrubs and trees and planted scattered knobcone pines (*Pinus attenuata* Lemmon) and Douglas-fir. Plant diversity in the Early-seral plantation was 56% (year 2) and 26% (year 6) higher than in the Douglas-fir plantation. Both early-successional treatments far exceeded plant diversity in Unaltered and Thinned mature stands. Fifteen years of growth of shrubs and hardwood trees in the Early-seral plantation was remarkable, resulting in total aboveground biomass increment (18 Mg ha⁻¹ yr⁻¹) double that of the Douglas-fir plantations. Important process effects related to primary productivity were noted: losses of soil organic matter from the B horizon in young Douglas-fir, and, after wildfire, increases in N₂-fixing plant cover in Early-seral plantation. The burl-sprouting and deep rooting of many hardwoods also created opportunities for nutrient retention and release from primary minerals as well as deep-profile water supply. Recognizing the importance of intentionally managing for shrubs and hardwood trees is particularly relevant at this site, because stand reconstruction and historical records indicate these species, along with knobcone pine, dominated the site for 40 years before the current mature Douglas-fir forest started gaining dominance. In contrast, the prolific natural regeneration of Douglas-fir after recent harvest and wildfire suggests that what comes back “naturally” in modern times will not allow this history to be repeated.

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Abbreviations: dbh, diameter at breast height; DSLR, digital single-lens reflex; FEMAT, forest ecosystem management assessment team (assessment that the Northwest Forest Plan was based); LTEP, long-term ecosystem productivity; NFMA, National Forest Management Act of 1976; O&C, Oregon and California Revested Lands Act of 1937; USDA, United States Department of Agriculture.

* Corresponding author.

E-mail addresses: bbormann@fs.fed.us (B.T. Bormann), rdarbyshire@fs.fed.us (R.L. Darbyshire), Peter.Homann@wwu.edu (P.S. Homann), brett.morrisette@oregonstate.edu (B.A. Morrisette), myrtleconn@earthlink.net (S.N. Little).

¹ Present address: Retired, Portland, OR, United States.

1. Introduction

A broad debate is underway about how important early-successional stages are to a landscape, for maintaining or increasing forest sustainability and resilience to disturbance. Adequate representation of all seral stages across a forested landscape is thought to underpin resilience and sustainability by assuring that natural processes are maintained through time and space (Pickett and White, 1985). Reasoned concern about depleted late-successional stands may have overshadowed a growing scarcity of early-seral stages

in Europe (Angelstam, 1998), New England (DeGraaf et al., 2003; King and Schlossberg, 2014), and the Pacific Northwest (Noss et al., 2006; Swanson et al., 2011; Campbell and Donato, 2014). A wide range of factors, including intensive plantation management on private lands, fire suppression and exclusion, and old-growth and riparian habitat objectives on public lands, are inadvertently leading to a scarcity of early-seral conditions in the Pacific Northwest (Kennedy and Spies, 2004). We use long-term experimental evidence from the Long-Term Ecosystem Productivity study to better understand early succession in the Pacific Northwest, and to link empirical evidence to the general but difficult-to-quantify goals of forest sustainability and resilience.

Slowly evolving scientific concepts of early succession have shaped the policy context for early-succession management. The National Forest Management Act (NFMA, 1976), responding to “cut and run” practices, required that conifers be reestablished after forest harvesting, and mandated a detailed and expensive accounting system to assure this objective was met. At that time, this concept was aligned with strong conifer production goals on public and private lands in the western states. Later, scientists concerned with disappearing late-successional stages began to study succession, but mostly in older forests. Time-series graphs showing disturbance, usually fire, followed by conifer regeneration and conifer-dominated sequence of stand structures ending with old-growth are common (e.g., Franklin and Spies, 1991). Other species were absent from studies and diagrams, and deviations from this simple sequence were in effect considered rare. As knowledge of the stochastic nature of disturbances emerged, the linear model was replaced by processes that could create many diverse pathways (Botkin, 1990; O’Hara et al., 1996). Following changes in land-management objectives catalyzed by the Northern Spotted Owl (*Strix occidentalis caurina*) injunction, however, the late-seral, conifer-centric paradigm continues on federal lands today. The Northwest Forest Plan was based on conservation biology concerns about an adequate distribution of seral stages, with a clear focus on the lack of old growth (FEMAT, 1993). Young, intensively managed Douglas-fir (*Pseudotsuga menziesii* Bong.) plantations were considered as a sufficient form of early succession. The Plan recognized “legacies” of old-growth stands that carry into early succession, by mandating minimum standards of leave trees, snags, and down wood, but not other early-seral conditions, such as biodiversity of herbs, shrubs, and hardwood species, and their function in maintaining early-seral foodchains and soil as a basis for plant productivity. The role of non-conifer vegetation in early succession started gaining attention when wildlife biologists began to realize that many species dependent on early succession were declining regardless of the abundance of young conifer plantations. This linking of early-seral stages with habitat needs has propelled the issue into policy discussions. The current debate (O & C Act, 2013) includes the need for legacies and large openings, but also suggests that the resulting vegetation should not be further managed, allowing natural processes to unfold.

Scientific knowledge about the effects of early stages of succession in managed coniferous forests in the Pacific Northwest depends largely on studies of conifer plantations with and without vegetation control (e.g., Gratkowski, 1961; Roberts et al., 2005; Rose et al., 2006; Newton and Cole, 2008; Maguire et al., 2009). After planting and tending strategies became very effective at speeding conifer canopy closure at the expense of early-seral species, concerns arose over biodiversity (Bunnell et al., 1999; Koivula et al., 1999; Hanley, 2005). The threat extends beyond plant diversity because the low stature, diversity, and reproductive strategies of many early-seral plants drive energy flows into secondary production, supporting more herbivores, granivores, nectarivores, frugivores, and omnivores than conifers. For example, Hagar (2007) identifies several reptiles and amphibians and many birds and

mammals closely associated with food supply and cover provided by early-seral species in Pacific Northwest forests. One of these species, the dusky-footed wood rat (*Neotoma fuscipes*), is even critical to the survival of the threatened Northern Spotted Owl (Franklin et al., 2000a), though the owl is usually associated with late-successional conditions. Similar dependencies are seen in Europe (Enoksson et al., 1995) and the eastern U.S. (DeGraaf et al., 2003; King and Schlossberg, 2014) as well.

Primary and post-disturbance succession chronosequences and mesocosm mass-balance studies are the primary sources of information on the effects of succession on processes controlling long-term soil productivity. For example, N_2 -fixers and some hardwoods increase soil organic matter and nutrient availability (e.g., Binkley, 1983; Batterman et al., 2013); pines (*P. resinosa* and *rigida*) can increase weathering release from primary minerals (Bormann et al., 1998; Balogh-Brunstad et al., 2008); and late-successional species such as mature spruce (*Picea* sp.) and hemlock (*Tsuga* sp.) are linked to declining rooting depth and nutrient immobilization in podzolic horizons (Bormann et al., 1995). More recently, management-oriented experiments have been implemented in the Pacific Northwest and SE Alaska that vary overstory conifer retention patterns and then examine effects on naturally regenerating species (e.g., Hanley, 2005; Wilson et al., 2009; Cole et al., 2010; Halpern et al., 2011; Burton et al., 2013). These studies are almost exclusively focused on biodiversity at stand scales and have not included an ecosystem analysis about effects on biomass distribution, energy flow, or soil nutrients and organic matter.

Here we seek to address gaps in knowledge about ecosystem functioning in early-successional Pacific Northwest forests. Our specific objectives are to: (i) quantify biodiversity and ecosystem properties and processes resulting from two early-successional management practices that establish and control vegetation composition differently; (ii) compare the early-successional management practices to mature stands, both thinned and unaltered; (iii) assess the consequences of interactions of these management strategies with unanticipated wildfire; and (iv) consider historical changes in early-successional pathways. To meet these objectives, we evaluate the 20-year vegetation and soil record of a large-scale forest-manipulation experiment in southwest Oregon, USA, and contrast modern managed-stand succession to historical responses demonstrated by local stand reconstruction and a review of historic documents. The two early-successional strategies, along with thinning and no-action, are four clear alternatives facing decision makers on fire-prone federal forest lands. Our study will inform both the design and choices among these alternatives to help meet management objectives at the landscape scale.

2. Materials and methods

2.1. Study site

The study has 5 distributed experimental blocks on the Rogue River – Siskiyou National Forest about 25 km southeast of Gold Beach, Oregon at 750–900 m elevation (Fig. 1). Soils in blocks B1 and Bb are derived primarily from schist-phyllite, in B2 from metamorphosed sandstone, and in B3 and Ba from mixed sandstone and schist-phyllite. Climate records (1971 to 2000) report average temperatures of 4 °C in January and 18 °C in July, and annual precipitation of 190 cm with only 10 cm during June to September (PRISM, 2012).

The pre-study forest developed following an 1881 fire (Little et al., 1995). In 1992, live-tree density ranged from 900 to 1300 trees ha^{-1} , and basal area from 40 to 80 $m^2 ha^{-1}$ (Table 1). The forest was dominated by Douglas-fir (68–86% of the total trees ha^{-1}), but also had a diversity of mid-story hardwoods including

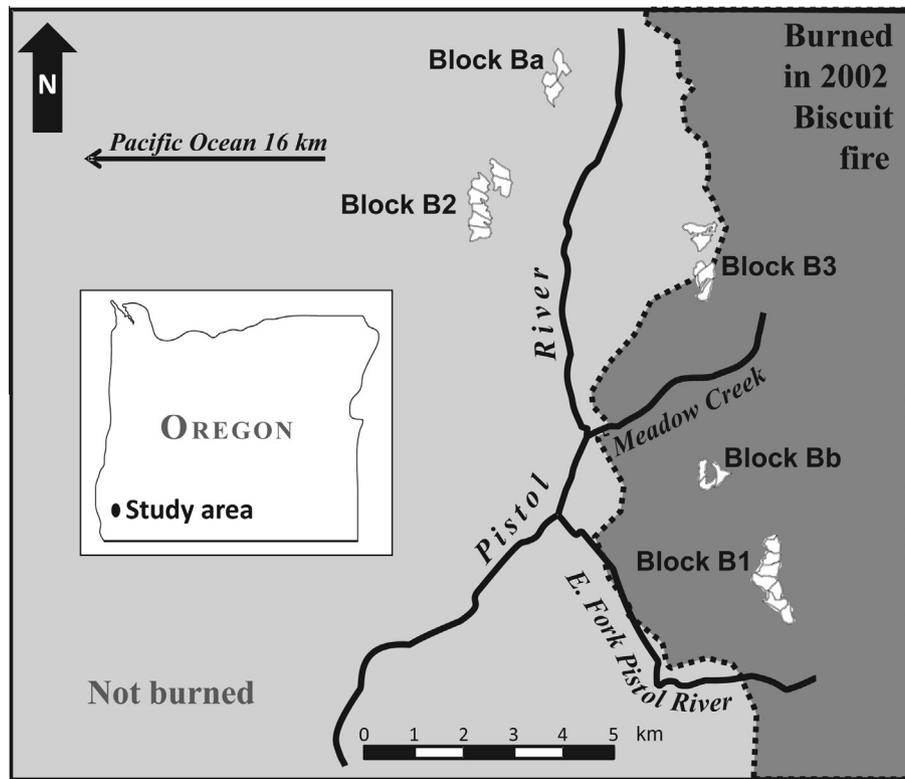


Fig. 1. Distribution of Siskiyou LTEP site experimental blocks.

Table 1
Pre-treatment (1992–1995) variability among experimental units within blocks for live trees (>3.5 cm dbh) at the Siskiyou–Rogue River long-term ecosystem productivity study, Oregon. Values are means \pm 95% confidence intervals, based on 7 experimental units in each of blocks B1, B2, and B3 and 3 experimental units in each of Ba and Bb.

Block	Tanoak	Other hardwoods	Douglas-fir	Knobcone pine	Other conifers	Total
<i>Trees ha⁻¹</i>						
B1	112 \pm 95	90 \pm 79	1233 \pm 409	48 \pm 52	8 \pm 15	1491 \pm 651
B2	274 \pm 125	98 \pm 99	644 \pm 127	None	None	1016 \pm 350
B3	87 \pm 101	139 \pm 149	1089 \pm 481	22 \pm 29	12 \pm 23	1349 \pm 783
Ba	26 \pm 38	260 \pm 205	616 \pm 118	None	None	902 \pm 361
Bb	541 \pm 253	15 \pm 42	523 \pm 207	70 \pm 49	None	1148 \pm 550
<i>Basal area (m² ha⁻¹)</i>						
B1	0.8 \pm 0.7	1.0 \pm 0.5	66.6 \pm 2.7	2.2 \pm 0.8	0.2 \pm 0.2	70.9 \pm 1.8
B2	2.0 \pm 1.4	1.9 \pm 1.0	75.1 \pm 7.1	None	None	79.1 \pm 8.2
B3	0.7 \pm 0.4	1.6 \pm 0.7	61.1 \pm 4.8	1.1 \pm 0.3	0.1 \pm 0.1	64.7 \pm 4.6
Ba	0.1 \pm 0.1	2.3 \pm 1.5	35.3 \pm 1.7	None	None	37.7 \pm 0.6
Bb	6.7 \pm 1.5	0.3 \pm 0.5	34.8 \pm 8.8	4.8 \pm 2.4	None	46.5 \pm 8.1
<i>Quadratic mean dbh (cm)</i>						
B1	7.2 \pm 1.5	9.9 \pm 3.5	28.0 \pm 4.0	28.3 \pm 8.1	16.1 \pm 0.0	
B2	9.1 \pm 3.3	12.2 \pm 3.9	38.3 \pm 4.0	None	None	
B3	14.1 \pm 6.5	12.1 \pm 5.0	29.5 \pm 5.8	27.4 \pm 7.3	13.4 \pm 0.0	
Ba	5.3 \pm 3.1	9.8 \pm 3.4	31.9 \pm 2.7	None	None	
Bb	12.0 \pm 3.4	14.4 \pm 2.4	30.6 \pm 8.0	30.7 \pm 9.5	None	

tanoak (*Liriodendron densifloros*, now *Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh); madrone (*Arbutus menziesii* Pursh); and giant chinquapin (*Chrysolepis chrysophylla* (Dougl. ex Hook.) Hjelmq. var. *chrysophylla*) (Table 1). Several other conifers may occur, including knobcone pine and rarely, sugar pine (*Pinus lambertiana* Douglas). Douglas-fir also provided 95% of the basal area, except for one block (Bb) where they were 46% of trees and 75% of basal area.

2.2. The experimental design

In 1992, National Forest personnel analyzed their lands for potential 50-ha blocks of mature Douglas-fir stands southeast of

Gold Beach, OR with the criteria: (a) soils and stands appeared consistent within a patch, and (b) management was feasible and allowable in these stands to implement an experiment. Three blocks (B1–B3) were selected for the main LTEP experiment; two more blocks (Ba, Bb) were added in 1995 with the same criteria to explore prescribed fire effects (Fig. 1). Treatments were randomly assigned within blocks. This effort created two experiments, a main LTEP experiment with 21 and an auxiliary prescribed-burning experiment with 6 experimental units (Table 1). Blocks varied in parent material and elevation, but appeared to have reasonable within-block similarity. Each 7-ha experimental unit has a central 1.5-ha measurement area. In 1997, four operational treatments were applied: Douglas-fir and Early-seral plantations (two differ-

ent early succession pathways) and Unaltered and Thinned mature forest (Table 2). Except for Unaltered, experimental units also received either low or high woody debris treatments. Low woody debris treatment removed all harvested trees and easily accessible pre-existing down wood. High woody debris treatment left 30–40 harvested trees ha⁻¹ on the ground in Early-seral and Douglas-fir plantations or 10–15 harvested trees ha⁻¹ in Thinned mature treatment. Two units that were subsequently treated with prescribed fire are not included in this analysis, reducing this comparison to 25 experimental units.

On July 12, 2002, the Biscuit Complex wildfire was sparked by multiple lightning strikes about 50 km east of the study site, and it burned out of control for 3 months. The wildfire, and backburns set to control it, burned two study blocks and a portion of a third (Fig. 1). Where the wildfire entered, all of the Early-seral and Douglas-fir plantations and Thinned treatments burned at high intensity (about 700 °C on average as measured by the melting of gridpoint aluminum tags), while the Unaltered plots burned at lower intensity (Bormann et al., 2008). The wildfire disrupted the initial experimental design, but eight treatment–burn combinations resulted: Unaltered, 2 unburned and 3 burned units; Thinned, 5 unburned and 3 burned units; Early-seral plantation, 2 unburned and 4 burned units; Douglas-fir plantation, 4 unburned and 2 burned units (Table 2).

2.3. Measurement protocols

2.3.1. Experimental measures

Between 1992 and 2011, the experimental units have been repeatedly measured for overstory, understory, coarse woody debris, fine woody debris, and soil properties. All measures are tied to a marked 25-m grid system array in a 4 by 4 or 5 by 3 matrix within the central 1.5-ha measurement area. Five tree plots (18 by 18 m) were tracked in each 1.5-ha measurement area since 1992. Standard measurements on all live trees (dbh > 3.5 cm) were: species, dbh, and treetop and base of live-crown heights. We also measured sapwood thickness and counted rings in sapwood on all trees >20 cm dbh. A subsample of live trees was cored for breast-height age. We determined biomass of mature Douglas-fir trees by applying locally derived equations of biomass versus dbh (Nay and Bormann, 2014). We also developed a biomass-increment equation that used sapwood and live-crown length as predictor variables, in addition to dbh (Bormann et al., in preparation). We calculated hardwood biomass using equations developed in and for the general area (Snell and Little, 1983). Equations for large knobcone pine were not available, so we substituted the Nay and Bormann (2014) equation for these relatively few individual trees.

Understory species canopy cover and height were measured in 15 or 16 plots per experimental unit. In 2010, we developed a protocol for estimating understory biomass ha⁻¹ based on photos of

fixed plots that were subsequently harvested to determine dry weight. We photographed 28 subjectively located quadrats, placed in the buffer areas of the treatments, covering the range of biomass, species, and mature-tree cover to be encountered on experimental units. We marked quadrats using a 3-D frame: 3 by 3-m (horizontal) and 1.5 m (vertical) made of polyvinyl chloride pipe. We leveled the frames and draped 3 sides with tarps before taking photos from several angles with a Nikon D70 DSLR, with a 18- to 200-mm lens set to 18 mm. We then collected all vegetation in the volume extending vertically above the 3 by 3-m area and dried it to a constant mass at 70 °C. Observers at each corner of the 15 or 16 vegetation plots estimated biomass based on the 28 photo plots; observations were averaged to obtain a biomass estimate. Variation between individual estimates had a standard error of <12% of the mean. We estimated an average annual change in biomass between 2003 and 2010 estimates. Because the photo system had not yet been developed in 2003, we derived estimates by multiplying 2010 biomass by a cover ratio (2003:2010) from each plot. We know this approach underestimates annual understory above-ground net primary production because changes in standing crop from 2003 to 2010 do not take into account branches and leaves that dropped to the forest floor during this period.

For young conifer saplings, not yet large enough to be classified as trees (3.5 cm dbh minimum), we used the Means et al. (1994) equations to estimate biomass. We applied tree biomass equations (Helgerson et al., 1988) to young Douglas-fir saplings. We developed a new equation for young knobcone pines (supplementary material). We derived annual biomass increment for 2010 by calculating biomass in 2010 and subtracting a biomass estimate for 2009. This 2009 estimate was based on a dbh derived for that year using ring increments.

Using methods reported in detail in Bormann et al. (2008), soil was sampled in each experimental unit in 1992 or 1995 and in 2003 to a depth of 30 cm in the mineral soil and in 2011 to a depth of 6 cm in the mineral soil. For this assessment, we determined organic matter concentration of the O horizon by loss-on-ignition; and estimated organic matter of the mineral soil layers as 1.89 times the total C concentration, measured on a Thermo NC 1112 analyzer. Using those concentrations, sample masses and cross-sectional sampler areas, we calculated organic matter mass in Mg ha⁻¹ for the O and B horizons. A fixed mass of fine (<4 mm) ashed soil defined the horizons (Bormann et al. 2008), with the O and A horizons encompassing the upper 300 Mg ha⁻¹ ash and the B horizon the subsequent 600 Mg ha⁻¹. These equate to a pre-treatment soil depth of about 6.8–20 cm for the B horizon.

Our soil respirometer incorporates an infra-red gas analyzer (LiCor Inc. LI-820) and an 8300 cm³ soil respiration chamber with internal fan. We left in place large 346-cm² collars to accommodate as much micro spatial variation as feasible and for repeated measures. We placed an array of 3 collars 2 m apart around each grid

Table 2

Operational treatments from the main and auxiliary LTEP experiments used in this analysis as implemented in 1997 on similar mature stands (Table 1) where about half were later burned in a wildfire in 2002 on the Siskiyou LTEP study, Rogue River–Siskiyou National Forest, Oregon.

Operational treatment	Treatment description	Total units	Units burned
Early-seral plantation	Create a 7-ha opening, removing logs by helicopter in 1997. Scattered knobcone pine and Douglas-fir were planted among plentiful shrub and hardwood regeneration. High-wood: 3; Low-wood: 3 units	6	4
Douglas-fir plantation	Create a 7-ha opening, removing logs by helicopter in 1997. Planted with Douglas-fir, followed by manual brushing of competing shrubs and hardwoods in 1999. High-wood: 3; Low-wood: 3 units	6	2
Unaltered	Unaltered mature stands, dominated by 80- to 110-yr-old Douglas-fir, with some knobcone pine and secondary story of tanoak (Table 1)	5	3
Thinned	Thin from below in 7 ha of mature forest, removing logs by helicopter in 1997. Averaged 240 remaining live stems ha ⁻¹ and total live basal area 23 m ² ha ⁻¹ . High-wood: 3; Low-wood: 5 units	8	3
Total experimental units		25	12

point and sampled monthly during the field season. The mean coefficient of variation of collar measurements was 0.67 (Nay and D'Amore, 2009). Logistics limited sampling to 4 units total in burned and unburned Unaltered and Early-seral plantation units.

2.3.2. Stand development

To contrast with our managed early-succession Douglas-fir and Early-seral treatments, we examined the historical development of the mature Douglas-fir stands used in the study. First, we felled the two live trees closest to the corners of the B1, B2, and B3 block measurement plots (41 trees total) and cut them into segments. We split the segments lengthwise to reveal the entire pith; chisels were required in a few places. Overwintering terminal-bud positions were identified as a darker narrow section of the pith. Errors associated with terminals that had broken off were avoided by cross-checking terminal numbers with ring counts. The narrow piths of branches that gained the terminal position after breakage were obvious as well. Stump piths to ground level were exposed on 80% of the split trees. In 2011, we measured height and diameter growth on young conifers in the 3 by 3 m understory plots. We measured the height of each terminal, working from the top down to the point where whorls were no longer interpretable, and the diameter at 10 cm above the ground. We also obtained the raw core data used in Little et al. (1995; Dave L. Peterson, USDA Forest Service, Pacific Wildland Fire Science Lab, Seattle, WA). These cores were taken in the tree plots from blocks B1, B2, and B3. The largest Douglas-fir free of stem defects was cored in each of the tree plots in each experimental unit (84 trees total). Two cores were taken from each tree; only accurately cross-dated cores were included in the analyses (Little et al., 1995). To cross check our reconstruction, we also examined the Government Land Office survey records for the general area, recorded by Rufous S. Moore in 1891 (based on Moore, 1851; <http://www.glorerecords.blm.gov>).

2.4. Statistical protocols

The wildfire disrupted the original experimental designs by burning two and a half of the five experimental blocks (Fig. 1). We were able to proceed with an analysis by combining experimental units from the main and auxiliary experiments, and by not examining woody debris treatments separately (Table 2). Woody debris treatments were not examined further because our previous analysis indicated fire-induced soil C losses did not differ between high and low woody debris treatments (Homann et al., 2011). Rather than attempt an after-the-fact statistical model, we chose a more descriptive and graphical approach to learn from the most obvious effects exposed by these unique data, and accept that we are more in the hypothesis development than testing mode at this time. For each variable and sampling time, we present the mean and simple 95% confidence interval for each of the four operational treatments. We interpret intervals with little overlap as providing conservative evidence for difference at a particular sampling time.

3. Results

3.1. Early-successional responses in managed stands and after wildfire

3.1.1. Species changes

In the absence of wildfire, Early-seral plantation treatments, applied in 1997, increased post-disturbance understory plant diversity of herbs, shrubs, fire-adapted pines, and young hardwoods by 56 (year 2) and 26 (year 6) percent compared to Douglas-fir plantations (Fig. 2). Compared to Unaltered treatments, the Early-seral treatment increased plant diversity by 53 (year 2) and

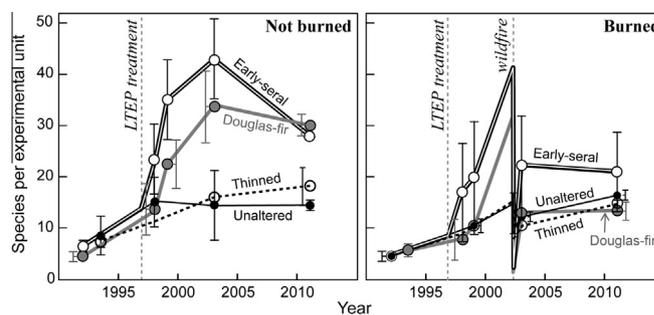


Fig. 2. Changes in species counts: harvested plantations increased species, but increases were largely reversed by wildfire. Lines were shaped to fit data points and obvious changes associated with treatment and fire to assist interpretation. Confidence intervals were derived from the simple population of experimental-unit values for this graphical analysis.

207 (year 6) percent and Douglas-fir by 47 (year 2) and 136 (year 6) percent. Increases in Early-seral and Douglas-fir diversity relative to Unaltered are smaller by about 20% than increases relative to initial condition because of background changes from 1992 to 1997 in Unaltered stands, mainly owing to openings created by the mortality of older knobcone pines. As compared to early succession changes in Early-seral and Douglas-fir treatments, species response to thinning was small and delayed until 2010.

Plant diversity responses interacted strongly with wildfire (Fig. 2), demonstrating the need to recognize uncertainty and diversity in succession patterns in these stochastic systems. Wildfire with widespread near-soil temperatures over 700 °C (Bormann et al., 2008) appeared initially to have killed nearly all plants, but remarkably, sprouting from heavily charred burls was common. Seeds and spores from ruderals arrived quickly; however, wildfire eliminated many species gained in the Early-seral and Douglas-fir treatments. Although total species numbers did not change much in Unaltered and Thinned, new species were observed that offset the loss of others. After wildfire, the number of species in Early-seral was still higher than Unaltered stands. Full species lists and changes are in [supplementary files – Table S1](#).

3.1.2. Cover responses

The understory cover in Early-seral and Douglas-fir plantation treatments increased rapidly compared to the Unaltered and Thinned, especially for shrub cover (Fig. 3). Shrubs, including hardwood trees >3.5 cm dbh, became dominant after treatment and, in most cases, again after wildfire (Fig. 3). The notable exception was where extensive bracken fern (*Pteridium aquilinum* (L.) Kuhn) replaced shrubs after young Douglas-fir plantations burned. The most common large shrubs were tanoak, giant chinquapin, Pacific rhododendron (*Rhododendron macrophyllum* D. Don ex G. Don), canyon live oak (*Quercus chrysolepis* Liebm.), and madrone. Some of these shrubs persisted in low numbers before treatment and then responded positively to openings. We separated out low-stature shrubs for analysis, called Salal+ (mainly salal (*Gaultheria shallon* Pursh) but also 3 species of Oregon grape (*Mahonia* spp.)), because they are especially deep-shade-resistant. The Salal + group responded less convincingly with an initial post-treatment cover decline, followed by later increases. Beargrass (*Xerophyllum tenax* (Pursh) Nutt) achieved modest cover later in the Douglas-fir treatment, most likely in response to control of woody shrubs. All other remaining species groups combined (Others) made up less than 10% of the cover; groups included ruderals, parasitic (achlorophyllous) plants, bracken and other ferns, N₂-fixing legumes, grasses and sedges, and other herbs (Table S1).

Response of cover to wildfire was antecedently linked to conditions set up by experimental treatments. In Early-seral plantations,

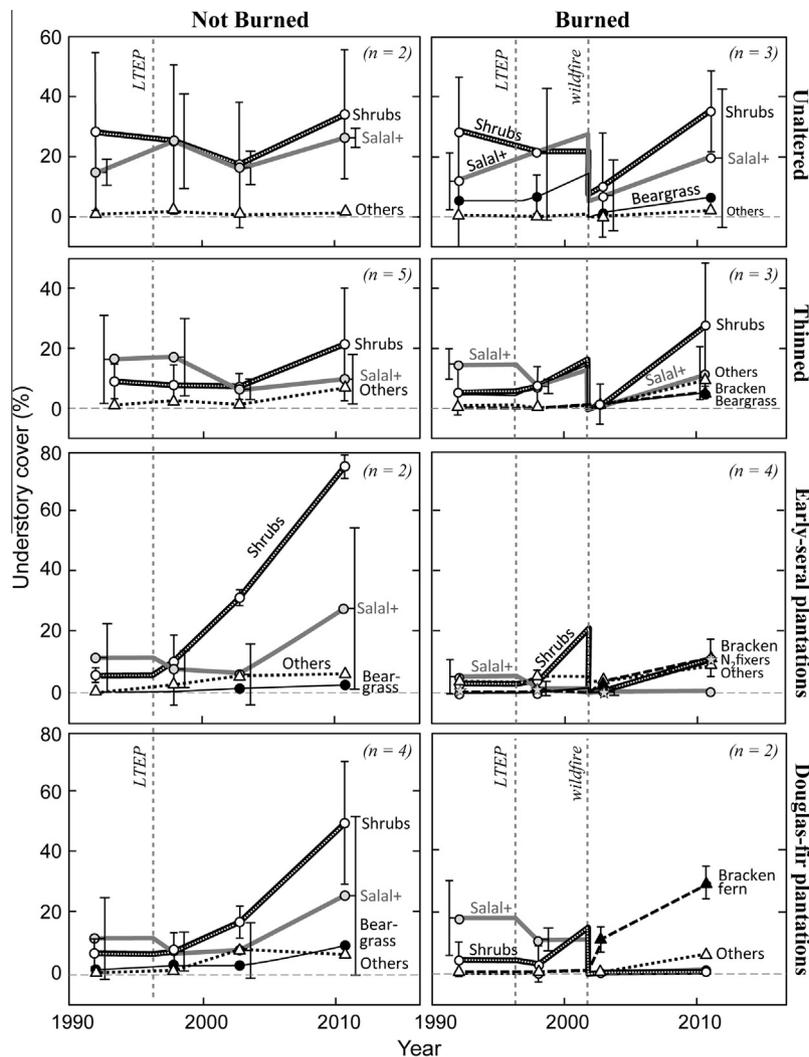


Fig. 3. Changes in cover of major groups of understory plants before and after experimental treatments and wildfire. Lines were shaped to fit data points and obvious changes associated with treatment and fire to assist interpretation.

cover of larger shrubs returned more slowly after fire than before, while large shrubs were nearly eliminated from Douglas-fir plantations and replaced by bracken fern. The only notable cover of known N_2 -fixing species (10% legumes) was achieved in Early-seral plantations after fire. Legumes achieved just 1.5% and 2.8% cover in wildfire-burned Unaltered and Thinned, and only 0.1% in burned Douglas-fir plantations. Otherwise, N_2 -fixers had 0 to 1% cover in all unburned units except the Early seral, where it was 1.4% before fire. Bracken fern had a major post-fire response equaling shrub cover in the Early-seral units, but this was less than half of what was observed in the burned Douglas-fir units. Shrub cover increased rapidly in the burned Unaltered and Thinned units to levels greater than observed in unburned stands. These large and varied responses illustrate the complexity of disturbances of different types and intensities and their interactions through time.

3.1.3. Ecosystem biomass and detritus pools

Following the 1881 fire and about 110 years of growth, the pre-treatment conditions had a combined average aboveground biomass of live-vegetation and snags of $469 \pm 87 \text{ Mg ha}^{-1}$ (mean \pm 95% CI; Fig. 4). Through harvest, treatments in 1997 reduced the initial biomass pool of live trees aboveground ($438 \pm 72 \text{ Mg ha}^{-1}$) to zero in Early-seral and Douglas-fir plantations. Post-treatment tree biomass increases are evident in the

unburned Unaltered and Thinned stands, at $4.1 \pm 1.6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. Aboveground understory biomass starts small ($27 \pm 6 \text{ Mg ha}^{-1}$; 6% of trees) but responds most in Early-seral plantations, achieving $186 \pm 6 \text{ Mg ha}^{-1}$ (42% of pre-treatment tree biomass) in just 14 years after harvest. Early-seral and Douglas-fir plantation treatments did not leave any snags, however, and the low snag biomass in the Unaltered and Thinned treatments ($31 \pm 15 \text{ Mg ha}^{-1}$) declined rapidly except after wildfire mortality when snags more than tripled to $86 \pm 34 \text{ Mg ha}^{-1}$.

Changes in biomass of large down wood (surface logs >10 cm diameter) differ among treatments and are affected by fire (Homann et al., 2014), but these patterns are obscured by combining high- and low-wood experimental units. Background change in the Unaltered treatments, however, was quite small ($<10 \text{ Mg ha}^{-1}$) through the entire experimental period compared to the other treatments, except with wildfire. Total large down wood remained below 8% of aboveground biomass. The fine woody debris (1–10 cm diameter) pools were up to 2 times larger than large down wood pools before and after treatment, and declined at about the same rate from 2003 to 2010 (Fig. 4). Fine wood increased 6- to 10-fold after harvest, but then declined at a rate of about $2.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. Elevated fine wood in all experimental units was directly linked to fire intensity (Homann et al., 2011) and tree mortality (Raymond and Peterson, 2005), and was fully consumed

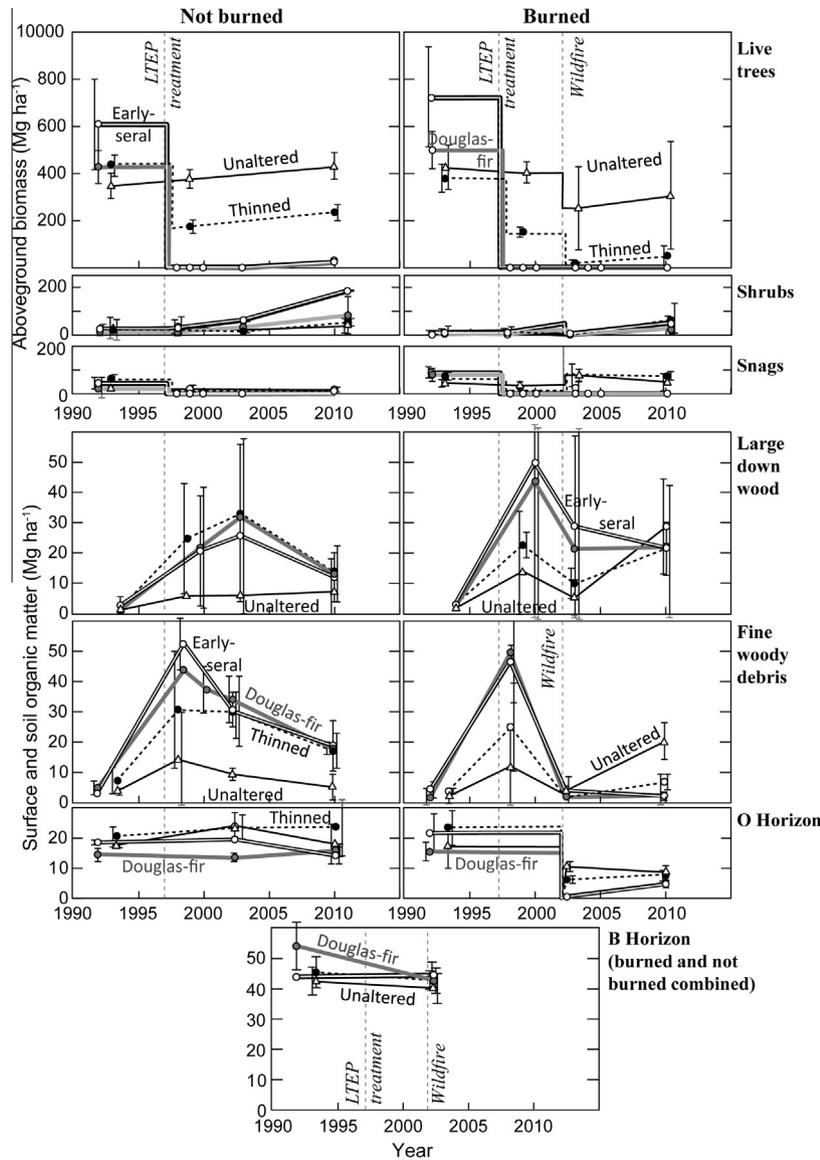


Fig. 4. Changes in aboveground biomass (top 3) and surface and soil horizon organic matter (bottom 4) in unburned and burned experimental units with 95% confidence intervals based on groups of similar experimental units. Lines were shaped to fit data points and obvious changes associated with treatment and fire to assist interpretation. Note change in y-axis scale from aboveground to surface and soils.

in most burned units. The variability of fine wood in the Unaltered treatments is large over time, based on branch and litter detritus and episodic tree mortality and snag fall. The O-horizon organic matter is controlled by leaf and fine wood inputs as well as decomposition losses. The unburned Douglas-fir O-horizon pool was initially lower than others (12 Mg ha^{-1}), likely related to needle retention, but then caught up to Early-seral and Unaltered (17 Mg ha^{-1}). The O-horizon was essentially entirely lost in the wildfire, but began rebuilding quickly in Unaltered and Thinned treatments with a large input from needle drop from heat-killed mature trees. Even so, 9 years after fire, the O horizon returned to less than half of its pre-fire mass. The B horizon was not affected by wildfire, so results were combined across all units. The only significant B-horizon change was a decline in organic matter in the Douglas-fir plantations, presumably related to root distribution and the need for nutrients to sustain rapid growth.

3.1.4. Annual biomass increment and soil respiration

As measured in 2010, the unburned Early-seral plantations had the highest annual growth increment ($18 \pm 3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) out

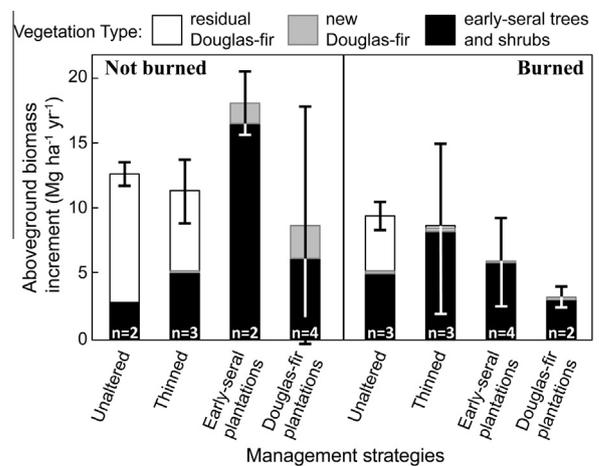


Fig. 5. Aboveground biomass annual increment in 2010 (a major portion of annualized net primary production) with 95% confidence intervals.

producing both 110 year-old Unaltered ($13 \pm 2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and Douglas-fir plantations ($9 \pm 11 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; Fig. 5). The rapid growth of the early-seral species of shrubs, young hardwoods, and knobcone pines is primarily responsible. Within the burned units, the Douglas-fir plantations increment ($3 \pm 1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) is less than half the Unaltered and Thinned and early-seral treatments ($6 \pm 3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Wildfire reduced biomass increment in Unaltered treatment, but changes in other treatments are unclear at this point because of age differences since disturbance (13 years since harvest for unburned and 9 years since wildfire for burned) and large estimate uncertainties. Cumulative annual soil respiration—because it includes belowground biotic metabolism in roots and heterotrophs including energy-expensive processes such as N_2 fixation and biological weathering—stands as a surrogate for relative belowground biomass allocation. In our limited sampling, 13 years after harvesting all trees, soil respiration in an unburned Early-seral plantation was 12% higher than the Unaltered control. As might be expected, high aboveground biomass increment is matched with high belowground biotic activity. In corresponding units burned by wildfire, respiration rates are only about half of unburned units reflecting losses of decomposable fine woody debris and organic matter in the O and B horizons (Fig. 4).

3.2. Historical changes in early-successional trajectories

From about 1950 to 2002, natural and managed succession and fire exclusion in coastal southwest Oregon led to a predominance of young and mature Douglas-fir stands, with some hardwood stands in patches on hotter drier, south-facing slopes. Based on land-survey records, forest composition in 1891 was remarkably different, with fir-dominated, closed stands on only 4% of the landscape, while large open shrublands with “scattered” conifers covered over 70% (Table 3). Fire-scar analysis of the area indicates a major fire in 1881 without a reburn (Little et al., 1995). Notations on “recently burned” conifers, size of knobcone pines, and preponderance of “brush” along lines in the land survey taken in 1891, 10 years after the fire, supports the no-re-burn conclusion. The extent that the 1891 GLO benchmark represents hundreds of years before this point is uncertain. An Indian war had been fought along the Rogue River in the 1850s (UO Archives, 2014). The records indicate a small number of settlers in nearby townships, mostly along streams. Little mining had been attempted in the area at that time. Regardless, the abundant shrubs and lack of mature Douglas-fir stands in 1891 suggests a strong history of fire for decades if not centuries before this. Whether the 1881 fire was ignited by settlers, Indians, or lightning is not known.

Past growth of living trees found on our site in 1990 also reveals a low density of Douglas-fir regeneration initially after the 1881 fire. Analysis of 127 trees (and many stumps) found no live Douglas-fir, surviving to 1990, that could have been present in the first

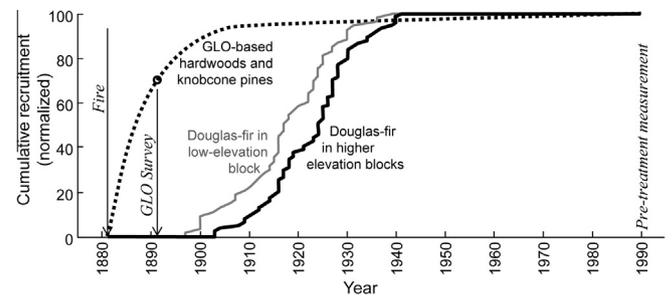


Fig. 6. Douglas-fir recruitment following an 1881 fire as indicated by reconstruction of year of origin on trees selected randomly and as part of an on-site fire history study (Little et al., 1995), and supported by GLO records surrounding the study area 10-years after the fire. Hardwood and pine regeneration are inferred from GLO data.

15–20 years after 1891 fire (Fig. 6). We observed some geographic variation, with Douglas-fir recruitment delayed longer on the higher, compared to lower, elevation blocks. The block difference of 5–10 years persisted until full recruitment was achieved. After about 1915, Douglas-fir invaded what had been stands of hardwoods and knobcone pines, gaining height dominance by about 1930. Taken together, the historical evidence supports a sequence of temporal dominance: (a) about 40 years of stands similar to our Early-seral plantation; (b) a 50-year transition to dominant mature Douglas-fir, and (c) a 20-year decline in hardwoods and pines to achieve pre-treatment conditions in 1990 (Table 1).

Modern, post-disturbance Douglas-fir establishment following harvest and wildfire ($1500\text{--}8000 \text{ trees ha}^{-1}$; Fig. 7) does not have much if any lag, contrasting sharply with the historical record (Fig. 6). Wildfire disturbance in 2002 resulted in seedling density of $2000\text{--}7000 \text{ trees ha}^{-1}$ in year 9, while harvest disturbance resulted in seedling density of only $1500\text{--}2000 \text{ trees ha}^{-1}$ in 14 years. Although there was a wide range of seedling sizes, and many small seedlings would be expected to perish, that no seedlings on the burned units would survive to become mature trees seems unlikely.

4. Discussion

4.1. Effects of management strategies

In theory, management strategies vary in the degree and mechanisms by which they alter total energy capture, biomass pool stability and quantity, and processes controlling energy flow into above and belowground pools (Fig. 8). How variation in the biomass pool quality and quantity, driven by different species mixtures, alters foodchains and other aspects of plant and animal habitat has been broadly studied. Effects on total production and direct investments

Table 3

Stand types along 1891 survey lines (left) and witness tree composition and average witness-tree dbh (right) for township boundaries surrounding the LTEP site, based on Government Land Office (GLO) survey records (see Table S2 and Figs. S1–S6 in online supplementary file for an example of original data).

Boundary line stand type in 1891	Proportion (%)	Witness-tree class in 1891	Proportion (%)	dbh (cm)
Open forest	71	No trees present	21	
Scattering with brush	44	Small trees ^a	25	5
Brush	19	Large conifers	44	58
Glades	3	Douglas-fir	28	63
Young pines	2	Knobcone pine	7	38
Recently burned	3	Cedar	9	58
Closed forest	29	Large hardwoods	10	43
Fir alone	4	Tanoak	3	56
Fir-hardwood mix	17	Madrone	2	31
Hardwood mix	8	Others	5	38

^a Conifer or hardwood trees <15 cm dbh.

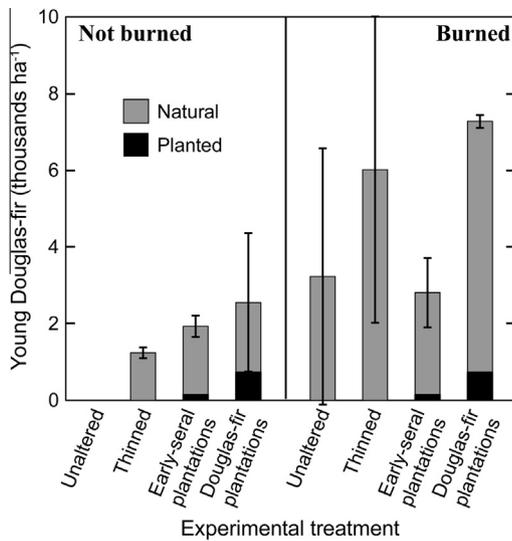


Fig. 7. Density of planted and naturally regenerated young Douglas-fir trees and seedlings 14 years after disturbance (not burned), and 9 years after wildfire (burned), assuming no mortality of seedlings planted at known spacings.

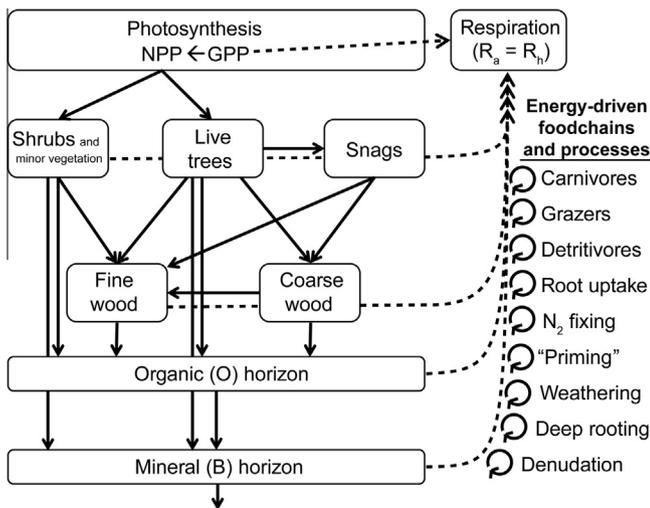


Fig. 8. Conceptualized energy flow through biomass pools, and return to the atmosphere through autotrophic (R_a) and heterotrophic (R_h) respiration, driving food chains and ecosystem processes.

by certain early-seral species in key ecosystem processes like N_2 fixation, deep rooting, weathering, and release of nutrients from recalcitrant organic matter are less obvious. Our evidence demonstrates that management strategies variably affect process investments.

In 2010, 13 years after disturbance, aboveground biomass annual increment was clearly highest in the Early-seral plantations. Shrubs and young hardwoods are able to more rapidly produce a complete leaf cover, capturing more light than young Douglas-fir plantations where shrubs were cut back. Shrubs and young hardwoods often grow more horizontally than vertically, as compared to the upward growth of Douglas-fir. Some shrubs do this because they produce flowers in terminal buds. Basal lignotubers (burls) in many species of shrubs and hardwoods are a special case where adventitious or dormant buds and starch are stored below the soil surface, where they are better protected from fire and other disturbances. Burl-bearing plants can take immediate advantage of openings even if the plant top was killed, because many roots survive the disturbance (Harrington et al., 1984), which may also decrease nutrient losses after wildfire.

The major effects of shrubs and hardwoods are consistent with the role of understory in energy flow as described by Varie (1980). Early-seral species have a competitive advantage on highly disturbed lands, which often comes from their ability to obtain resources in ecosystems where organic-matter-linked nutrients are scarce. The jump in N_2 -fixing legume cover (Fig. 3) in Early-seral plantations suggests increased N_2 fixation. Another adaptation may be deeper rooting, enhancing plant access to water and weatherable minerals in rocky soils. The principal shrubs and hardwoods in our system have been shown to root to more than 4 m, compared to Douglas-fir which is largely confined to the B horizon on similar parent material (Zwieniecki and Newton, 1994). Root penetration into the finest cracks (Zwieniecki and Newton, 1995) affects water uptake (Zwieniecki and Newton, 1996) and most likely weathering as well. The rapid growth of pines, planted knobcone in our case, may also reflect deep rooting and weathering (Balogh-Brunstad et al., 2008). Our study is too young, however, to provide convincing evidence whether relative increases in soil organic matter, water-holding capacity, nitrogen, and other nutrients mediated by early-seral species will facilitate longer-term conifer growth, as suggested by Weigand et al. (1993) and Busse et al. (1996), or hinder it (Harrington and Tappeiner, 2009). Results support our contention that truncating processes that increase soil fertility and organic matter by preventing disturbance or by repeatedly shunting growth into late-seral conifers will result in losses of productivity over the long term.

4.2. Wildfire-management interactions

Management strategies clearly interacted with wildfire. Across all treatments, the main effect of wildfire was to open or reopen stands and start new successional pathways that differed from unburned pathway in many ways. Wildfire effects on biomass pools were mediated by wildfire consumption of fine and coarse wood pools and variable tree mortality. High fine wood fueled more intense fire and mortality (Raymond and Peterson, 2005; Bormann et al., 2008; Homann et al., 2011, 2014), so Early-seral, Douglas-fir, and Thinned stands burned hotter than Unaltered. The partial mortality in Unaltered after fire put fine wood on an increasing trajectory. The magnitude and frequency of changes in fine wood suggests that periods of intense fire risk are transitory. Effects of intense fire on long-term soil productivity cannot yet be clearly determined in this study.

4.3. The historical context of early succession

The long-term historical context is critical to interpreting the data to inform modern management choices. Responses to openings are temporally specific to the history that created the pre-treatment conditions including the type or degree of disturbance that created the opening, seed dispersal from surrounding areas, and post-disturbance weather. Our historical reconstruction of tree growth on the experimental sites bears this out. The historic slow, extended Douglas-fir regeneration pattern appears to reflect old-growth reconstruction studies (Tappeiner et al., 1997; Poage et al., 2009) that demonstrated initial low Douglas-fir densities and high age variability in modern, older Douglas-fir stands. Faster Douglas-fir regeneration has been reported in some stands further north, in the mid-Cascades (Winter et al., 2002). We see a strong temporal disconnect between historical and modern natural regeneration of Douglas-fir in the early-succession treatments, with and without fire. Modern natural regeneration following study treatments and after the wildfire was abundant (Fig. 7) and this is consistent with a survey of recent fire responses in the Klamath region (Shatford et al., 2007) and from Forest Service post-harvest experience in the area (R. Darbyshire, pers. comm.). This disconnect

might be explained by: (1) more abundant and frequent, perhaps Indian-set, fires that kept Douglas-fir seed supply low for a prolonged time before 1881; (2) a more prominent historical role of short-lived knobcone pine, that upon mortality, may have provided openings for Douglas-fir 20–30 years after the fire; (3) later fire exclusion and clearcut harvests at a smaller scale (about 15 ha) that increased seed supply; or (4) post-1881 patches without surviving Douglas-fir that were much larger than in 2002. Indigenous Americans, at least up to first contact in 1774, were known to widely use fire in this region and to favor hardwoods such as tan-oak as a food source (Anderson, 2005). The influence may have been so large that we need to think of many historical wildfires as intentional fires instead. Loss of this type of fire may result in more of a conversion of forest types, from glades and shrublands to forest, rather than a change in proportion of different stages. Regardless of cause, it is essential to recognize the difference in Douglas-fir regeneration patterns between the late 1880s and late 1990s. Factors controlling the species composition of early-successional stands are changing all the time including climate, human influences, and seed supply. Choosing to define early succession as “what comes back” and avoiding any management of species during early succession, as described by Wilson et al. (2009) and Halpern et al. (2011), runs the risk of altering key long-term diversity and processes in ways that might not be compatible with people’s concepts of sustainability and resilience, or for that matter the continued high production of conifer saw timber, especially in fire-prone areas.

Within this historical context, treatments achieved substantially different outcomes in terms of plant diversity and ecosystem properties and processes. The number of understory plant species increased sharply in both the Early-seral and young Douglas-fir treatments, and then began to decline as trees started dominating sites (Fig. 2), suggesting a strong relationship between openness and diversity, consistent with Hanley (2005) and Wilson et al. (2009). Early-seral plantation dominance (percent cover) moved quickly to shrubs and a wide array of other species. Douglas-fir plantations with some shrub control had a similar response except that the low-stature shrubs, salal and Oregon grape and beargrass, increased relative to larger shrub cover (Fig. 2). Consistent with many other studies of early-seral openings (Hanley, 2005; Wilson et al., 2009; Cole et al., 2010; Halpern et al., 2011; Burton et al., 2013), the Early-seral treatment increased both major and minor species. The young Douglas-fir treatment had about half of Early-seral diversity.

5. Conclusions

Of the two early-successional plantation treatments, Early-seral had higher understory species diversity, stability of B-horizon organic matter, and especially aboveground biomass increment relative to Douglas-fir; but small or no differences in fine wood and O horizon mass. Beyond treatment-induced aboveground biomass changes in the early successional treatments relative to mature stands, differences were limited to understory diversity and cover and fine wood. Wildfire interrupted early-succession patterns differently by treatment, reducing diversity more in Douglas-fir than Early-seral plantations and increasing certain species (bracken fern in Douglas-fir and N_2 -fixers in Early-seral plantations). Successional patterns clearly have also changed over the last century at this site, where initially Douglas-fir gained dominance only after 40 years of hardwood shrubs and knobcone pine and now Douglas-fir is abundant from the start. These conclusions suggest that existing early succession concepts can be better integrated before being elevated into policy debates: (1) “early succession” can be defined by more than just species diversity,

specifically to also consider key properties and processes that control what the forest ecosystem can produce over the long term; (2) planning for early-successional management needs can include surveys of longer-term historical influences; and (3) that accepting whatever species come back after opening up the forest may not be sufficient to meet management goals. Revisiting the ecology research of the mid-1900s that focused on processes of energy flow through foodchains, nutrient cycling, and forest productivity may be beneficial.

Biodiversity and ecosystem processes weave together over a spatial array of experimental treatments and over both decadal and century-long post-disturbance development periods in complex ways. The value in integrating across space and time is to examine how effects of management actions intervene in ongoing dynamic development processes, where the effects of actions may depend on what the action was and when and where it was made. Here, we also see that timing of disturbance can be more important than the type of disturbance (wildfire or complete or partial harvest). Specifically, modern successional pattern trajectories differ from historical patterns here—where increased seed supply, planting, and tending has given Douglas-fir great advantage at the expense of early-seral shrubs, hardwoods, and pines. What’s viewed as natural regeneration today cannot be viewed as natural, i.e. independent of modern human effects, because it appears to reflect fire suppression, increased Douglas-fir seed supply, and reduced early-seral seed and lignotuber abundance. Consequences reflected in changing soil conditions also portend future growth responses. Managers need to better understand this complex context to develop strategies that account for past processes, by considering active management for early-seral compositions across landscapes to meet societal goals including biodiversity, ecological resilience, and long-term productivity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.12.016>.

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