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CONSEQUENCES OF BIOMASS HARVESTING ON FOREST CONDITION AND
PRODUCTIVITY IN THE NORTHERN ROCKY MOUNTAINS

By

Woongsoon Jang

B.S., Seoul National University, Seoul, Korea, 2006
M.S., Seoul National University, Seoul, Korea, 2008

Dissertation

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for the degree of

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in Forestry

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Approved by:

Sandy Ross, Dean
The Graduate School

Dr. Christopher R. Keyes, Chair
Department of Forest Management

Dr. David L.R. Affleck
Department of Forest Management

Dr. Ragan M. Callaway
Division of Biological Sciences

Dr. John M. Goodburn
Department of Forest Management

Dr. Deborah S. Page-Dumroese
USDA Forest Service
Rocky Mountain Research Station
Consequences of Biomass Harvesting on Forest Condition and Productivity in the Northern Rocky Mountains

Chair: Dr. Christopher R. Keyes

Emerging public interests to utilize forest woody biomass as an alternative feedstock accompanies a concern about potential nutrient depletion by increased woody biomass extraction. This study was conducted to investigate the long-term impact of intensive biomass utilization on site productivity and forest condition in the northern Rockies. The 1974 Forest Residues Utilization Research and Development Program site at Coram Experimental Forest of western Montana were revisited, and responses from individual tree to ecosystem level were measured. The experiment was designed to address the effect of biomass utilization intensity (high, medium and low) combined with prescribed broadcast burning treatment following conventional regeneration cuttings (i.e. shelterwood, group selection, and clearcut).

Planted trees showed no differences in height, dbh, and volume growth, as well as the individual’s physiological traits such as mean leaf area, growth efficiency, and foliar C and N concentration. At the stand level, metrics including basal area, density, and quadratic mean diameter for regenerated trees production were affected by regeneration cutting treatment. However, the biomass utilization intensity was not a significant factor for the regenerated tree biomass production. Initial impacts of biomass harvesting on understory shrub vegetation were significant, but the shrub vegetation rapidly recovered within 10 years after harvesting, and shrub biomass, species composition and diversity 38 year after harvesting were unaffected by biomass utilization intensity. Analysis at the ecosystem level, encompassing the mineral soil layer to the overstory tree layer, yielded a consistent result, concluding that there is no evidence for the adverse long-term impact of intensive biomass utilization on site productivity.
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CHAPTER 1

INTRODUCTION

WOODY BIOMASS AS AN ALTERNATIVE FEEDSTOCK

In the United States, recent federal policies such as the Energy Policy Act of 2005 and the Energy Independence and Security Act (EISA) of 2007 reflect a growing national sentiment that forests represent one key to resolving climate and energy concerns. Public concerns over both climate change and increased energy costs seem to have fed a growing interest in using forest biomass as an alternative energy feedstock to support biofuel-based energy production, displacing fossil fuels and reducing the production of greenhouse gases that contribute to climate change (Perlack et al. 2005; Guo et al. 2007; Janowiak and Webster 2010). National policies endorsing biomass energy are likely to impact the way that public (and to some extent, private) forests are managed. This potentially influential new forest management objective brings with it concerns over the capacity of western forests to yield biomass feedstocks with undue consequences to their condition and productive capacities.

Forestry paradigms in the western United States have evolved greatly over the past century, with management activities expanding from an initial focus on timber production to a greater focus on promoting forest stand health, resilience, and wildfire resistance. Yet, a feature common to each of these objectives has been the application of silvicultural treatments resulting in biomass removal (Patton-Mallory 2008; Reinhardt et al. 2010). However, biomass energy harvests could – and likely would – result in biomass removal at levels that have not been seen previously under past forest management paradigms.

Although the development of a bioenergy infrastructure in the West is still at a tentative stage (with many economic and engineering elements also currently under investigation), it seems inevitable that
future demands on forests to yield biomass feedstocks will increase. There are many advantages to using forest biomass as an energy feedstock, including: 1) reducing greenhouse gas emissions, 2) sustaining rural communities and economies through expanded economic opportunities, 3) reduction of energy costs, 4) reducing emissions from forest waste burning treatments, 5) mitigating dependency on foreign energy feedstock imports, and 6) local utilization and recycling of waste materials (Farr and Atkins 2010). Federal policies will likely spur the expansion of biomass energy harvest methods to contribute to those outcomes. For example, the EISA calls for biofuel production to be increased five times within the next 15 years, and that 60% of biofuel should be derived from cellulosic feedstocks.

How will biomass energy yields be expanded? In their discussion of this subject, Janowiak and Webster (2010) theorized that forestland management activities will respond to meet growing future demands in three general ways. First, a biofuel demand will spur an expansion of harvesting activities to include forest stands that are currently unmanaged or passively-managed (underused due to their low-market values). Second, on forests already receiving some form of active management, biomass harvest intensity will be increased through increased residue removal. And third, a greater acreage of forest stands will be established and managed more intensively to produce crops over shorter rotations. Among those alternatives, the second response is most likely to be realized immediately due to its feasibility.

Terminology for this growing field is still evolving, with traditional terms and concepts adapted fit to this new management objective, and with new terms developed where necessary. Federal regulation [48 C.F.R. § 1437.7203; http://www.gpo.gov/fdsys/pkg/CFR-2005-title48-vol5/pdf/CFR-2005-title48-vol5-part1437-subpart1437-72.pdf] defines woody biomass as “the trees and woody plants, including limbs, tops, needless, leaves, and other woody parts, grown in a forest, woodland, or rangeland environment, that are the by-products of management, restoration and/or hazardous fuel reduction treatment.” A related term, forest residues, refers to the accumulation of the living or dead organic matter caused by both anthropogenic and natural processes (Pierce 2003). Thus, residues encompass all biomass remaining after cutting, such as slash and cull trees, as well as snags and coarse woody debris (Barger 1981; Benson and
Schlieter 1981). Recently, the term “energy wood” has been used from residue’s end-user point of view (Benjamin et al. 2010; Breidis et al. 2011; Berger et al. 2013). In this study, the terms “woody biomass,” “forest residues,” and “energy wood” are used interchangeably.

Concerns exist regarding potential negative effects of repeated intensive biomass removals on critical ecosystem functions (sensu de Groot et al. 2002). Providing an alternative energy source must be balanced against maintaining ecosystem functions and services. National policies – such as the National Forest Management Act of 1976 in the U.S., and the National Standard for Sustainable Forest Management in Canada –, and organizations such as Sustainable Forest Initiative specify this principle distinctly (Page-Dumroese et al. 2010). Thus, the long-term effect of biomass removal on a forest ecosystem and its productivity should be a primary consideration among forest managers.

What might be the salient impacts of increased levels of residue harvests on forest properties and functions? It is well known that forest residues play an important role in forests, since they form one of primary structural features of forest ecosystem with crucial ecological functions (Harmon et al. 2004). Many studies have addressed the importance of residues for various ecological functions, such as providing soil organic matter, influencing nutrient cycling and hydrology, and supplying wildlife habitat (Reijnders 2006; Patton-Mallory 2008).

Although the importance of biomass to forest ecosystem functions is known, current understanding of the long-term effects of depleting this resource through biomass removal remains limited. Many studies (e.g. nutrient budget analysis, modeling approach) on this topic have yielded uncertainty thus far (Mann et al. 1988; Egnell and Valinger 2003), since biotic and abiotic factors change and interact intricately after harvest. Instead, studies have demonstrated the necessity of long-term field experiments (Egnell and Leijon 1999; Egnell and Valinger 2003). The majority of studies have consisted of short-term (4 yrs - 16 yrs after treatment; but see Pierce 2003) assessments of response to experimental biomass utilization. Long-term assessment is critical in order to thoroughly understand complex changes in ecosystem function and structure (Likens 2004), but conducting and maintaining such experiments is often
infeasible, expensive, and impractically time- and resource-consuming (Reinhardt et al. 2010). The subject is tangentially addressed by several long-term research networks – such as the North American Long-Term Soil Productivity (LTSP; for detail see Powers 2006; Page-Dumroese et al. 2006) and Long Term Ecological Research (LTER) networks. Although LTER conducts research of ecological issues including impacts of forest management, and the LTSP investigates the long-term impact of extensive woody biomass extraction and soil compaction on soil productivity, the studies specifically focusing on biomass harvesting are insufficient, or are too young to permit the drawing of long-term inferences.

1974 FOREST RESIDUES UTILIZATION RESEARCH AND DEVELOPMENT PROGRAM

A unique opportunity exists in the northern Rocky Mountains for better understanding the impacts of forest biomass harvesting on forest condition and productivity. At the USDA Forest Service’s Coram Experimental Forest, a comprehensive and multidisciplinary research effort, the Forest Residues Utilization Research and Development Program, was established in 1974. Then as now, societal concerns over the availability of fossil fuels (the first “oil shock”; Klass 2004) led to a greater societal focus on alternative fuel sources, including woody biomass. Concurrently, concerns had been growing worldwide over the increasingly documented undesirable impacts of human activities on natural systems (Benson and Schlieter 1980b). These factors provided the impetus a long-term study of biomass harvest level effects at Coram Experimental Forest. From the forest manager’s point of view, two societal management objectives were emerging with potentially conflicting needs: 1) to meet energy demands and improve the recovery and utilization of wood resources with minimal residues, and 2) to address environmental concerns and reduce the unfavorable esthetic and environmental consequences of management activities (Barger 1980; 1981).

The Forest Residues Utilization Research and Development Program sought to address these concerns. Managed by researchers at the USDA Forest Service’s Intermountain and Range Experiment
Station (now Rocky Mountain Research Station), the program was initiated to investigate timber harvesting alternatives and pursue the improved intensity and environmental compatibility of timber utilization. This interdisciplinary program included the cooperative efforts of researchers from diverse fields, such as engineering, wood science, meteorology, microbiology, silviculture, mycology, fire management, hydrology, wildlife habitat, and economics.

The regeneration harvests of three common silvicultural systems (shelterwood, clearcut, and group selection) were performed, and four utilization treatments ranging from conventional sawlog utilization to near complete utilization were applied to each harvest. Generally, the harvests and post-harvest treatments were designed to represent best operational practices used by forest managers, to the fullest extent possible. A running skyline yarder, still a novel harvesting technique, was used to yard logs with minimal damage to residual trees and understory vegetation. Researchers determined that to dispose of excess slash, prescribed fire would be necessary at the least efficient utilization levels that produced the greatest quantities of debris; thus, prescribed broadcast burning treatment was applied to two of the four utilization treatments.

The results provided some valuable information for similar forests as well as for general coniferous forests (Shearer and Kempf 1999), but the study’s value has not been fully exploited. Since its establishment in 1974, results of the research program have been reported through various symposia (e.g. USDA Forest Service 1980; USDA Forest Service 1981) and publications (for detail, see Shearer and Kempf 1999). However, the publications and reports spawned by the program contain only short-term responses or interim results, and the long-term impacts of biomass utilization level and harvest on ecosystems remain unclear.

Today, this experimental installation has remained as a legacy of a historical research project, providing some advantages to document the long-term effects of biomass utilization on productivity and regeneration dynamics. First, it has been nearly 40 years since treatments were put in place, so the site now allows a proper opportunity to explore the long-term impacts of biomass utilization and harvest on
forest ecosystems of the northern Rocky Mountains. In addition, Coram Experimental Forest’s conditions suitably represent upland mixed conifer forests that are common to the Northern Rocky Mountains (Shearer and Kempf 1999), thus the potential value of research findings generated by this site is great. Moreover, there are no operational constraints to utilizing this research area, facilitating various research activities. Finally, every block and treatment unit is easily accessed via a well-maintained forest road, and the integrity of treatment units remains largely intact.

STUDY SITE

This study was conducted in the Upper Abbot Creek Basin (48°25’N, 113°59’W) of Coram Experimental Forest in northwestern Montana. Coram Experimental Forest was established in 1933, and comprises 3,019 ha of the Hungry Horse Ranger District of the Flathead National Forest. It is located 20 kilometers east of Columbia Falls, and 9 kilometers south of Glacier National Park. The elevation of Coram Experimental Forest ranges from 1,195 to 1,615 m (Shearer and Schmidt 1999). Slopes range from 30 to 80%.

The climate of Coram Experimental Forest is classified as a modified Pacific maritime type (Adams et al. 2008). The annual precipitation is 890-1,270 mm, averaging 1,076 mm (Farnes et al. 1995). Most precipitation occurs in the form of snow during November - March. The mean annual temperature is 2 °C to 7 °C (Hungerford and Schlieter 1984); the mean temperature of May through August and the mean winter temperatures is about 16 °C , and –7 °C, respectively (Adams et al. 2008). The length of growing season near Abbot Creek is 81 days, whereas it is about twice as long on a nearby east-facing slope.

Precambrian sedimentary rock, glacial till, and thin surface volcanic ash are the main components of soils on Coram Experimental Forest. The mixture of these soil components created the rich, loamy soils in this area. Coram Experimental Forest soils are classified into 6 categories, and the soils of the study area can be grouped into the loamy-skeletal soils on materials weathered from impure limestone and argillite (i.e., type I; for detail, see Klages et al. 1976).
Coram Experimental Forest exhibits a various mixture of coniferous species (Shearer and Kempf 1999). The majority of the forest is composed of the western larch (*Larix occidentalis*) cover type (Society of American Foresters Cover Type 212, Eyre 1980) in association with Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), and spruce (*Picea engelmannii* and *P. glauca*). Sometimes sporadic western hemlock, (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) are included. Paper birch (*Betula papyrifera*), black cottonwood (*Populus trichocarpa*), and quaking aspen (*P. tremuloides*) are the main broadleaf tree species. The major shrub species include twinflower (*Linnaea borealis*), ninebark (*Physocarpus malvaceus*), shiny-leaf spiraea (*Spiraea betulifolia*), kinnikinnick (*Arctostaphylos uva-ursi*), Sitka alder (*Alnus sinuate*), Scouler’s willow (*Salix scouleriana*), and huckleberry (*Vaccinium globulare*) (Shearer and Kempf 1999).

Intensive habitat mapping from the 1960s to 1970s enabled the classification of Coram Experimental Forest into three forest series (Shearer and Kempf 1999): subalpine fir/clintonia (ABLA/CLUN), Douglas-fir/ninebark (PSME/PHMA), and western hemlock/clintonia (TSHE/CLUN, Pfister et al. 1977). The dominant habitat type of the study site is the subalpine fir/clintonia (ABLA/CLUN) habitat type.

Several regulations have contributed to the fact that Coram Experimental Forest has suitable conditions for research activities. The southeast quarter of Coram Experimental Forest was designated as Coram Natural Area (later, designated as Coram Research Natural Area) in 1938. Only minimal recreation activities are allowed in this area. In 1976, the entire experimental forest was designated as a biosphere reserve in company with Glacier National Park by the United Nations Educational, Scientific and Cultural Organization (UNESCO). Coram Experimental Forest, as a manipulated biosphere reserve, has been managed to provide a field research site especially for understanding the effects of alternative forest management practices. In addition, since Coram Experimental Forest is located inside the primary conservation area for grizzly bear recovery (U.S. Fish and Wildlife Service 2013), most roads are gated and the motorized access is strictly limited. As a result, Coram Experimental Forest has been well protected as research site, and the treatments on the study site remain relatively intact.
MEASURING FOREST PRODUCTIVITY

The assessment of site productivity is important to value a forest site, to assess its present condition, and to predict future yield (Reinhardt 1982). Forest site productivity can be defined as the rate of biomass production in a unit area by any kind of organisms (Helms 1998). In forestry practice, the definition, measurement, and expression of site productivity have varied according to objectives and professional background (Ford 1983). Until recently, the focus on productivity in forestry was predominantly on timber production (e.g. Ford-Robertson 1971). As public interest in forestland management has expanded from timber production to other objectives that include biomass production, additional perspectives—such as biodiversity or forest services—can also be included in definitions of forest site productivity. Just as the range of site productivity definitions vary, a commensurate variety of indicators and methodologies to evaluate forest site productivity have been suggested. This section will classify the various approaches to measuring forest productivity, and introduce useful allometric characteristics to assess individual tree productivity used in this project.

Classification of productivity indicators

Classification of productivity indicators can employ the dichotomy between phytocentric and geocentric methods by their standpoints (Leary 1985; Vanclay 1992). Under the phytocentric (plant-based) view, site productivity can be explained by plant property, whereas the geocentric (earth-based) view attempts to explain the site productivity through environmental factors such as soil and climate. In addition, each category can be subdivided into direct or indirect indicators, according to how closely the indicator is related to actual production (Skovsgaard and Vanclay 2008). Since indirect methods are usually more feasible, convenient, and cost-effective, they are generally preferable to direct methods in practice.
Indirect geocentric approaches for site productivity assessment can also be classified into two: assaying the physical site property, and vegetative characterizations. The physical site property approach utilizes environmental variables such as climate, topography, and soil, instead of relying on direct crop property measurement. However, this approach involves and inherent comparison with direct crop properties, and it has substantial uncertainty (Vanclay 1992). In contrast, the vegetative characteristics approach is to measure indicative vegetative variables, such as habitat type (e.g. Pfister et al. 1977) or indicator plants (e.g. Webb et al. 1971). This approach is based on the principle that vegetation reflects, and serves as the expression of, all environmental components that are important to plant production (Daubenmire 1976).

The direct geocentric approach is to use environmental factors to determine plant production. The requisites for production such as available water, nutrient, and solar radiation are the major factors of interest. Knowledge derived from this approach can be applied to process-based growth and yield models (e.g. FOREST-BGC (Running and Coughlan 1988)). One advantage of such a modeling approach is that it enables the projection of changes in site productivity that might follow changes in climate.

In forestry practice, the indirect phytocentric approach to site productivity measurement is the most common method (Vanclay 1992). This approach is to measure crop property such as stand height, age, and diameter for evaluation of a site’s productivity. Site index is the most commonly used and representative measurement of the indirect phytocentric approach; it evaluates the site’s productivity with the empirical information of stand height and age. Site index was developed under the assumptions that dominant tree height growth can be a good indicator of the site’s ability to produce wood, and that the height growth of dominant trees is independent of stand density.

But there have been some skeptics of productivity assessment through site index (Huang and Titus 1993; Skovsgaard and Vanclay 2008). They pointed out that the relationship between the site index and volume production is not always constant. Substantial variation was found depending on stand densities,
thinning regimes, and regions (Skovsgaard and Vanclay 2008). In addition, sampling of (co-) dominant trees for site index estimation should be restricted in older, even-aged, undisturbed, and well-stocked stand (Carmean and Lenthall 1989; Huang and Titus 1993). Yet, despite these limits, site index is still used most widely due to its convenience, straightforwardness, and abundant supporting research data.

Literally, the direct phytocentric approach refers to direct measurement of plant biomass. Undoubtedly, this method is most meaningful to forestry, since it measures actually realized (wood) volume. Thus, direct volume measures such as maximum mean annual volume increment can be more useful indicators than other indices (Skovsgaard and Vanclay 2008). However, it often requires destructive methods with excessive resource costs. In addition, using correlation, the volume can be driven from other measurements such as height of the stand. Thus, many modeling efforts to estimate the amount of biomass using easy-to-measure variables have been made. As a result, estimation of the amount of biomass of a plant is possible using diameter or height, and not only for the major commercial timber species, but even for understory vegetation as well (e.g. Brown 1976; Alaback 1986).

The boundary of each of these classes is not clear-cut, and many indicators might not be cleanly classified according to these criteria. Moreover, it is apparent that one approach is not always superior to others. The suitability of methods depends upon the purpose and scale (Skovsgaard and Vanclay 2008).

**Growth efficiency**

Wood production is a major concern for the commercial forestry. Wood production is determined by three factors: (1) amount of acquired resources by trees, (2) efficiency of converting resources into biomass, and (3) the allocation of biomass to the stem (Ex and Smith 2014). Wood production efficiency has often been described as the volume increment per unit leaf area and time, since leaf area represents the amount of resources that an individual tree can acquire, and the periodic volume increment
incorporates the resources conversion efficiency and biomass allocation (Waring 1983). Therefore, the indicator of wood (volume) production per unit leaf area and time (hereafter referred to as growth efficiency) can be a good measure of productivity.

Because directly measuring amount of foliage is exceedingly time-consuming work, various efforts to find a close correlation with relatively easy-to-measure indicators have been made (Waring 1983). After the fundamental discovery that the amount of leaf area in a tree can be estimated by its cross-sectional sapwood area (Grier and Waring 1974; Dean et al. 1988), cross-sectional sapwood area has been used most frequently to estimate the amount of foliage. This relationship is based on the “pipe model theory” (Shinozaki et al. 1964a, b), in which the tree stem is viewed analogous to a pipe system, suggesting that the area of water-transporting xylem cells should be correlated with the amount of foliage. Combined with observed tree growth, this allometry has been used widely to assess tree vigor (Waring et al. 1980), growing space efficiency (Waring 1983; O’Hara 1988; Smith and Long 1989; O’Hara 1996), and disease and insect susceptibility and impacts (e.g., Waring and Pitman 1985; Maguire and Kanaskie 2002).

However, it has been revealed that the leaf area-sapwood area ratio has considerable variation. From lodgepole pine data from Utah, Dean et al. (1988) found that ignoring stand-to-stand variation could result in a bias in estimates of leaf area, pointing out the variation could be caused by differences in stand structure. Effects of stand structure characteristics such as stand age, density, and site productivity on the leaf area-sapwood area ratio can be found in some other studies (e.g. Bancalari et al. 1987; Long and Smith 1988). In a western Montana in subalpine forest, Callaway et al. (2000) found that the ratio can be affected by the seral stage. Moreover, climate can also change the leaf area/sapwood area ratio (Callaway et al. 1994; Mencuccini and Grace 1995).

**OBJECTIVES AND HYPOTHESES: OVERVIEW OF CHAPTERS**
The primary objective of this study is to identify the effects of biomass harvest levels (varying utilization standards combined with post-harvest prescribed burning treatment), when coupled with each of three common silvicultural systems (regeneration harvest methods), on northern Rocky Mountain forest vegetation and productivity. Before investigating the impacts biomass harvesting on site (forest) productivity, a literature review was conducted on the impacts of intensive biomass removal, with focus on soil productivity (Chapter 2). The primary study spans scales varying from the individual tree (Chapter 3, and 4) to stand (Chapter 5), including understory vegetation (Chapter 6). Additionally, this study evaluates the best model for the estimation of bark thickness for Douglas-fir trees (Chapter 7).

I will investigate the following research questions and hypotheses:

1. Does biomass utilization treatment impact the response of planted trees? (Chapter 3)

Since artificial regeneration can cancel out the variance in natural regeneration growth rate, it allows for more accurate empirical analysis of biomass harvest effects on site productivity. In addition, if there were any adverse impacts of biomass utilization on natural regeneration (such as removing advanced regeneration, or limiting new seedling establishment), artificial regeneration by planting can be a reliable means to offset those effects by assuring the occupancy of desirable species and promoting seedling establishment and growth. Therefore, seedlings of Douglas-fir that were planted from 1976 to 1979 within the biomass utilization treatment units were utilized to investigate the impact of intensive biomass harvesting on site productivity. The hypotheses to be examined are:

**Hypothesis 1A**: If intensive biomass utilization impacts the site productivity negatively, then planted trees will exhibit reduced height, dbh, and volume growth by increased biomass utilization levels.

**Hypothesis 1B**: If intensive biomass utilization has a negative impact on the planted trees, then total leaf area, basal area increment, and growth efficiency of planted trees will differ by biomass utilization levels.
**Hypothesis 1C:** If the reduced individual tree growth is caused by available nutrients, then the nitrogen concentration (i.e., C and N concentration) on foliage of planted trees will be different by biomass utilization levels.

2. Does natural regeneration respond to regeneration cuttings and biomass utilization treatments? (Chapter 4)

Regeneration can be affected not only by biomass utilization treatments but also by regeneration cuttings, or both. In addition, retained overstory trees in shelterwoods could limit regeneration establishment and growth. The experimental installation in the study site resembles some variations of variable-retention harvesting such as aggregated retention (group selection) and dispersed retention (shelterwood with reserves). Furthermore, biomass utilization treatments can be regarded as a post-harvest understory treatment. Therefore, this study can provide an analogy to variable-retention harvesting, and can inform about the impact of overstory retention and following understory vegetation treatment of on regeneration. For this, I will test the hypotheses:

**Hypothesis 2A:** If retained overstory trees exert negative impacts on regeneration, then the individual growth and vigor of natural regeneration in shelterwood should be the lowest among the regeneration cuttings.

**Hypothesis 2B:** If the post-harvest understory treatments (i.e., biomass utilization treatments) influenced the shrub biomass recovery, and shrub biomass affected the responses of natural regeneration, then the understory protected treatment should yield the lowest regeneration.

**Hypothesis 2C:** If the growth of retained trees compensated for reduced growth in natural regeneration, then we should observe a negative relationship between regeneration and retained tree growth.
3. Do biomass utilization treatments impact vegetation composition and structure? (Chapter 5)

Possible reduction in overall stand biomass due to biomass harvesting is one concern, but changes to species composition and stand structure are possible as well. Biomass removal from the forest seems to influence vegetation composition and structure in conjunction with harvesting system and silvicultural practices. Some evidences have shown that increasing species diversity could increase productivity (e.g. Tilman et al. 1996, Mulder et al. 2001). However, there is still debate over the relationship between diversity and productivity (Long and Shaw 2010). Thus, the study site can provide an opportunity to examine the following hypotheses:

*Hypothesis 3A*: If the responses to biomass harvesting vary by species, then the species composition of the tree and shrub community will differ among biomass utilization treatments.

*Hypothesis 3B*: If biomass utilization levels affect the shrub biodiversity differently, then the maximum biodiversity of shrub community will be observed at the biomass utilization treatment associated with an intermediate level of disturbance.

4. Do biomass utilization treatments impact biomass production at the stand- or ecosystem-level? (Chapter 6)

Many scientists have pointed out that intensive biomass utilization raises the risk of decreasing forest productivity. Our knowledge of long-term effects of biomass harvesting on site productivity is still insufficient. I will test the following hypotheses:

*Hypothesis 4A*: If there is a negative relation between biomass utilization level and stand production, then the total above-ground biomass of the stand will be maximum at the lowest level of biomass utilization.
Hypothesis 4B: If the magnitudes of intensive biomass utilization impacts on vegetation production vary with stand vegetation strata (shrub, seedling, sapling and pole size-tree, and residual tree layer), then the response of each stratum will differ by biomass utilization treatments.

Hypothesis 4C: If there is an interaction between biomass utilization level and regeneration harvest method (silvicultural system), then the magnitude of effect on production will differ by regeneration harvest method.

REFERENCES


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CHAPTER 2

IMPACT OF BIOMASS HARVESTING FOREST SOIL PRODUCTIVITY IN THE NORTHERN ROCKY MOUNTAINS

ABSTRACT

Biomass harvesting extracts an increased amount of organic matter from forest ecosystems over conventional harvesting. Since organic matter plays a critical role in forest productivity, concerns of potential negative long-term impacts of biomass harvesting on forest productivity (i.e., changing nutrient/water cycling, aggravating soil properties, and compaction) have emerged. There is abundant prediction of long-term impacts of intensive biomass removal on forest productivity. However, the empirical knowledge and comprehensive understanding, especially on western forests, are limited thus far. Therefore, we utilize the available findings to evaluate potential impacts of increased biomass extraction on western forests. We compare biomass harvesting with natural disturbance regimes or conventional harvesting systems in terms of organic matter redistribution in order to evaluate the possible consequences of biomass harvesting on forest productivity. We review the role of organic matter on forest productivity and compare the organic matter redistribution or removal through biomass harvesting and natural disturbances or conventional harvesting to assess potential impacts. The summarized findings are: (1) the long-term impacts of intensive biomass harvesting will be mitigated by protection of the belowground organic matter; (2) biomass harvesting could result in the accelerated leaching of nutrients; (3) immediate understory vegetation recovery can minimize potential negative impacts. And some forest sites and conventional silvicultural treatments should be used with caution and prior consideration were indicated.
INTRODUCTION

Timber harvesting involves the redistribution and exportation of forest biomass (i.e., organic matter). Due to emerging attention on using forest biomass as an alternative energy source, it is likely that the quantity and variety of forest biomass removal will increase (Janowiak and Webster 2010). Forest residues that had previously been considered non-merchantable, such as tops, branches, slash, cull, snags, course wood debris, stumps, and bark, are now being harvested for use (Benson and Schlieter 1980a; Barger 1981; Berger et al. 2013). Although intensive (whole-tree) harvesting has been conducted for decades in many temperate and boreal forests across the world (Thiffault et al. 2011), most western U.S. operations and infrastructure have not been operating at that level. However, many of these western U.S. forests will likely be managed more intensively in the future, thereby increasing the level of biomass utilization.

As interest in biomass harvesting increases so do resulting ecological concerns. The diverse concerns for ecosystem functions include: wildlife habitat, water quality, biodiversity, air, and forest productivity. Among these, the primary concern for foresters and silviculturists is the potential negative impact on forest productivity. Therefore, the key question in this study is whether increased biomass removal causes undesirable long-term consequences to forest stand and soil productivity.

Productivity (forest/site) can be defined as: “The relative capacity of an area to sustain a supply of goods or services in the long run” (Society of American Foresters 1998), and “The capacity of a forest to produce specific products (i.e., biomass, lumber) over time as influenced by the interaction of vegetative manipulation and abiotic factors (i.e., soil, climate, physiography)” (Soil Science Society of America 2008). Therefore, forest productivity is the integration of all environmental factors encompassing soil productivity, climate, topography, geology, vegetation, and the history of natural disturbances and anthropogenic interventions (Morris and Miller 1994; Grigal 2000). These interrelated factors can affect
one another directly and indirectly, making the prediction of potential impacts on forest productivity complex. Biomass harvesting has few long-term impacts on those environmental factors, except soil productivity. Changes in soil nutrient cycling, compaction, and water holding are critical determinants of future forest productivity, which is why many biomass harvesting studies have placed the emphasis on alteration of soil productivity (Thiffault et al. 2011). Later, we discuss the potential negative effects of biomass harvesting on soil productivity as well as ways to mitigate those effects.

Among forest scientists and land managers in North America, a fundamental change in forest management philosophy has occurred in recent decades. Emulating natural disturbance regimes has become a primary strategy to ensure resilient forest ecosystems (Drever et al. 2006; Franklin et al. 2007; Berger et al. 2013). This strategy maintains that natural disturbances and processes should be the foundation of silviculture (Attiwill 1994; Rogers 1996; Seymour and Hunter 1999; Seymour et al. 2002; Franklin et al. 2007), and resource managers should use harvest methods that maintain complex structure, composition, and function of forest ecosystems (Long et al. 2004) within their historical range and variability (sensu Keane et al. 2009). A key assumption of this paradigm is that the indigenous vegetation community has evolved within a full range of environmental conditions; therefore, maintaining the ecosystem within this range is the best method to prevent undesirable consequences (Seymour and Hunter 1999). Ecological concerns can assessed by asking if the ecological consequences (impact) of biomass harvesting on forest productivity exceed the range of consequences created by natural disturbances.

As previously noted, biomass harvesting increases organic matter removal and results in a different configuration of the remaining organic matter within a forest. Therefore, comparing the amount of transferred organic matter through biomass harvesting to natural disturbances can provide a basis for predicting possible impacts to forest productivity. The objectives of this report are to: (1) review the role of the various organic matter types in forest productivity; (2) compare changes in organic matter resulting
from natural disturbances and from biomass harvesting regimes; and (3) discuss the potential effects of biomass harvesting on forest productivity.

ROLE OF ORGANIC MATTER IN FOREST PRODUCTIVITY

Classification and distribution of organic matter in the forest ecosystem

Forest biomass refers to any organic matter, including living and non-living material. Roughly, carbon (C) pools in forest ecosystems can be grouped as: living (above and belowground) organisms, coarse woody debris (standing and fallen), forest floor (litter, duff, and humus, combined), and mineral soil. However, classification of organic matter pools often depends on the research objective. Moreover, the focus of a study may include only a subset of total C pools (Page-Dumroese et al. 2006).

The simplest classification of organic matter pools is living and non-living. In this case, live biomass commonly refers to aboveground vegetation, including roots. Non-living biomass, also called detritus (e.g., Schlesinger 1977) or necromass (e.g., Palace et al. 2007), represents non-living organic material from the canopy layer (i.e., snags), including the mineral soil to bedrock. Similarly, organic matter pools can be classified according to strata in the aboveground or belowground pool (e.g., Attiwill and Adams 1993). Living roots are pooled with aboveground biomass. Beyond these simple classification schemes, classification of forest detritus (non-living organic matter above the mineral soil layer) versus organic material in the mineral soil layer (e.g., Wang et al. 2003) can be further separated into coarse or fine woody debris, litter fall, humus, duff, or soil wood (e.g., Jurgensen et al. 1997; Rice et al. 2004).

Site organic matter is commonly expressed as C stock, since C is a major element of organic matter. C stock is defined as the amount of carbon in a pool, representing a system or reservoir’s capacity to accumulate or release C (Forest Resources Assessment Programme 2004). For example, live biomass comprises 42% of total C stock of forest ecosystems in global scale (Pan et al. 2013; Table 2-1).
However, in boreal forests, only about 20% of total biomass is comprised of living biomass. C stock distributions are different for different biomes, but, generally, the most abundant organic matter pools are located in the soil (Goodale et al. 2002; Rumpel and Kögel-Knabner 2011; Schmidt et al. 2011).

Organic matter in woody residues, the forest floor, and mineral soil are essential for maintaining ecosystem function by supporting soil C cycling and sequestration, nitrogen (N) availability, gas exchange, water availability, and biological diversity (Jurgensen et al. 1997). Loss of organic matter resulting from stand disturbance can drastically change long-term soil productivity (Grigal and Vance 2000; Page-Dumroese and Jurgensen 2006). For example, undisturbed subalpine fir/queen's cup (Abies lasiocarpa (Hook.) Nutt./Clintonia uniflora (Menzies ex Schult. & Schult. f.) Kunth) stands in Montana and Idaho can have different total amounts of organic matter in and on the soil (Montana total organic matter pool 431 Mg/ha; Idaho total organic matter pool 593 Mg/ha; Page-Dumroese and Jurgensen 2006). However, in Montana 40% of the organic matter pool was on the soil surface, whereas in Idaho 27% of the organic matter pool was in the soil. The distribution of organic matter in and on the soil depends on various factors, such as soil type and texture, stand age, species composition, geographic region, and stand history. However, the majority of soil organic matter (SOM; in this paper, refers non-living organic matter in understory collectively) is concentrated in the organic layer near the forest surface (Jurgensen et al. 1997). In the mineral soil layer, a large amount of SOM is distributed at a shallow depth (Harvey et al. 1994). Between 39 and 70% of total organic matter in the top 1 m of soil is concentrated in the first 30 cm (Batjes 1996). More than 90% of total root biomass of temperate coniferous forest is concentrated in the top 1 m of soil, and other forest types have even shallower root distribution (e.g., 83% of root biomass is concentrated within only the top 30 cm in boreal forests) (Jackson et al. 1996). It is now known that considerable amounts of organic matter are allocated in deeper soil layers, the importance of which is emphasized in specific regions, but there is very little work on its distribution (Rumpel and Kögel-Knabner 2011). Understanding the distribution of organic matter within a given stand is crucial for determining the impacts of harvesting for saw timber or bioenergy, prescribed fire, or wildfire.
Living organic matter

Living organic matter (i.e., vegetation) plays an essential role in nutrient and energy cycling (Figure 2-1) and, therefore, in productivity of forest ecosystems. Nutrients enter forest ecosystem as the forms of rain and dust and by biological fixation (nutrient conversion to available form by living organisms) and exit in stream water (drainage) and gaseous form (e.g., volatilization by fire). Vegetation captures (“uptake” in Figure 2-1) the inorganic nutrients, holds and synthesizes organic matter (“internal redistribution”), and redistributes (“return”) organic matter through litter fall and leaching (Attiwill and Adams 1993, Farve and Napper 2009). In other words, vegetation consumes available (but mobile) nutrients, transforms the nutrients into stationary forms, and releases the formed nutrients simultaneously.

In addition to nutrient and energy cycle, forest vegetation is a core component to determining forest productivity. As shown in Figure 2-1, living organic matter can produce non-living organic matter such as litter, dead branches, and cones. Litter from vegetation is a primary source of SOM (Lorenz and Lal 2005) that is utilized and decomposed (decomposition) by various organisms. Annual production of litter fall in Sitka spruce (*Picea sitchensis* (Bong.) Carrière) was calculated as 3.151 Mg/ha in Scotland and Northern England, indicated that the annual litter fall production was equivalent to approximately 11% of total accumulated organic matter contents in the forest floor (Miller et al. 1996).

Mortality of fine roots can provide essential resources to soil microbes. Decaying fine roots are regarded as more important input to soil layer than surface residues (Powers et al. 2005). Annual SOM derived from fine roots was estimated at about 4.1 Mg/ha on mixed hardwood forest in Massachusetts (McClougherty et al. 1982). Annual fine root production was measured as 3.76 Mg/ha on multiple stands in Wisconsin and Massachusetts (Aber et al. 1985). Aber et al. (1985) reported that turnover rate of fine roots ranged from 48 to 82% (1.8 to 3.1 Mg/ha/yr).
On the other hand, living vegetation can influence understory productivity through modifying microclimate. First, solar radiation can be regulated by upper-layer vegetation. The amount of available light for photosynthesis generally decreases closer to the forest floor (Wright et al. 2006). According to the Beer-Lambert Law, the amount of photosynthetically available radiation in the understory decreases exponentially as the leaf area aboveground increases (e.g., Pierce and Running 1988). Only 0.5 to 5% of the full solar radiation can reach the understory in many closed forests (Chazdon and Pearcy 1991). Since diminished light availability limits growth and, therefore, determines species composition in the understory (Montgomery and Chazdon 2002; Neufeld and Young 2003), the amount of vegetation in the canopy layer also affects forest productivity. In addition, attenuated solar energy reaching the understory helps regulate soil temperature. Since soil temperature is involved in various belowground processes such as root growth, decomposition, and N mineralization (Waring and Running 2007), change of soil temperature can affect soil productivity significantly. In the inland Pacific Northwest, Jurgensen et al. (1992) found a general trend that removing the overstory increased the temperature of the soil layer. In the northern Rocky Mountains, Hungerford and Babbitt (1987) suggested that understory vegetation removal can increase the ground surface temperature up to 6.1 °C (11.0 °F) in some months. If soil respiration is measured to quantify the belowground processes, a temperature increase of 10 °C (18 °F) can result in 3.4 to 5.6 times increase in soil respiration in mixed hardwood forests of the northeastern United States (Davidson et al. 1998).

Aboveground vegetation can affect the soil moisture content. Aboveground vegetation biomass influences soil water content directly through two kinds of hydrological processes: evapotranspiration and interception of rainfall. In the northern Rocky Mountain region, about 30 to 40% of total annual precipitation is lost through evapotranspiration (Running et al. 1989). Vegetation can intercept from 5 to 26% of total annual precipitation (Helvey and Patric 1965; Waring and Running 2007). Therefore, aboveground vegetation determines the amount of water in soil layer that plants can utilize. Since soil
moisture is utilized not only by plants but also by diverse soil microorganisms pertaining to nutrient cycling (Harvey et al. 1980b), soil water content can also be an influential factor for forest productivity.

*Non-living organic matter*

Non-living organic matter occupies the majority of total organic matter in most biomes (Table 2-1). These materials are distributed among the course woody debris, forest floor, soil wood (woody residue in the forest floor), and mineral soil layers (Table 2-2). In western-montane forest, non-living organic matter was averaged at 26%, 9%, 10%, and 55%, respectively (Page-Dumroese et al. 1990). SOM content is closely bound to soil productivity unless an environmental factor (e.g., extremely low temperature and drought) limits microbial activity. In general, organic matter depth reflects forest productivity (Jurgensen et al. 1997); the deeper the organic matter, the more productive the site. This highlights the importance of belowground processes and the amount of soil organic matter for soil productivity. The majority of nutrients in organic matter exist in forms that cannot be rapidly utilized by plants. Therefore, organic materials must be disassembled (i.e., decomposition) and transformed (i.e., mineralization) into inorganic forms by belowground processes. SOM is involved deeply in these processes and can influence forest productivity indirectly, but crucially, through altering physical, chemical, and biological properties of soil (Grigal 2000; Hatten and Zabowski 2009).

*Physical properties*

*Soil water retention*

Organic matter can enhance the soil water condition in various ways. First, organic matter on the soil surface can lower soil temperature and increase soil moisture retention to prevent evaporative loss.
(Powers et al. 2005). In addition, large amounts of moisture may be captured by detritus, especially fallen and decaying coarse wood. Page-Dumroese et al. (1990) reported that more than five times more available water was stored in woody residue than in mineral soil in a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand in northern Idaho. Abundant soil water is crucial for seedling survival, establishment, and growth and is essential on sites that experience a summer drought (Padilla and Pugnaire 2007). In addition, as climate changes, SOM may provide available water to keep trees healthy longer in times of drought (Allen et al. 2010).

### Soil structure

SOM can also increase porosity, thereby decreasing bulk density, improving soil structure, and enhancing soil water holding capacity (Shepherd et al. 2002). SOM is a major binding agent, cementing individual soil particles together into more stable soil aggregates (Jastrow 1996). Aggregates alter pore size distribution and can enhance water infiltration into the soil. Increased porosity improves soil gas exchange, which is required for respiration (Bronick and Lal 2005). Moreover, porosity enhances root expansion through providing soft space that is easily penetrated by roots.

### Chemical properties

#### Nutrients

Plants require various essential nutrients to grow. Some elements can be absorbed from atmosphere through stomata (e.g., C, hydrogen, and oxygen), but the majority of other essential nutrients must be acquired from the soil layer through the root system. Non-living organic matter consists of these essential elements primarily since it is made up of matter that was once alive. Thus, the amount of organic matter
reflects the quantity and quality of essential nutrients in soil. The majority of available nutrients are concentrated in the soil organic layer. In Idaho batholith, the soil organic layer contained 88% of total potassium (K), calcium (Ca), magnesium (Mg), N, phosphorous (P) (Megahan 1990). In Minnesota, the forest floor and mineral soil layers contained 4 to 20 times more N, Ca, and Mg than aboveground vegetation (Alban et al. 1978).

**Cation exchange capacity (CEC)**

CEC refers to the ability of soil particles to hold and exchange metallic nutrients such as Ca, Mg, and K. Many essential nutrients are only supplied from soil, existing as a form of cations to be utilized by plants. However, due to their electrical characteristics, the cations may easily be leached by water. Since SOM is charged negatively, it can hold these base cations. Therefore, soils with high CEC (clay particles are also charged negatively; DeByle 1980) have many sites to capture nutrients for the vegetation, preventing cations from leaving the ecosystem. For this reason, soil CEC can be a barometer to evaluate soil productivity.

**Buffering of soil pH change**

The availability of soil nutrients is affected by soil acidity. For example, P is highly sensitive to soil pH; it converts easily into its less available form both in alkaline and acidic conditions. In addition, nitrification rate can be affected by soil pH. In acidic soil, nitrification proceeds slowly (De Boer and Kowalchuk 2001). Since it is the process that the unavailable N convert to available from to plants, the slower nitrification rate can limit plant growth. Other micronutrients, such as manganese, iron, and copper, tend to be less available as soil pH increases, in general.
Soil acidity can also impact the soil microbial activities. Nicol et al. (2008) found that the abundance and diversity of nitrifying bacteria differs according to soil pH, which indicates that nitrification might change in accordance with soil pH gradient. In general, the richness of soil bacteria is highest in neutral soils and decreases as the soil becomes more acidic (Fierer and Jackson 2006). Similarly, mycorrhizal abundance and nutrient uptake ability are also affected by soil acidity. Erland and Söderström (1990) found that the number of mycorrhizal root tips of Scots pine (Pinus sylvestris L.) seedlings was maximized around pH 5 and decreased with decreasing pH (increased acidity). Chalot et al. (1995) reported that nutrient (amino acid) uptake through ectomycorrhizae was optimized around pH 4. Therefore, rapid change of soil acidity might cause soil microbial activity to shrink.

However, abundant SOM can ameliorate the potential adverse impacts of sudden changes in soil pH. Here, CEC plays a key role as a buffer. Soil acidity is determined by the concentration of hydrogen ion (H+) in the soil. As a cation, the hydrogen ion competes with other cations. If soil acidity increases (i.e., higher hydrogen ion concentration), more hydrogen ions occupy the exchangeable sites, thereby increasing the leaching risk of base cations. Therefore, soils with higher CEC can have more resistance to the sudden changes of soil acidity.

**Biological properties**

SOM provides food and habitat resources to various soil mesofauna (soil invertebrates) and microfauna (e.g., bacteria and fungus). They are the backbones of decomposition and mineralization processes, breaking down and converting organic matter to forms that plants can use. The nutrients are then re-absorbed by roots and recycled by vegetation. Thus, soil organism activity positively impacts forest productivity through the creation of soil porosity, allowing air and water movement. Also, some soil microbes secrete chemical compounds to alter and stabilize soil structure (Tan et al. 1978; Tisdall and
Oades 1979). The predation (grazing) of these soil microbes has been found to release considerable amounts of available nutrients to plants (Molina and Amaranth 1990).

Soil microbe activity is determined entirely by the amount of organic matter in the soil layer (Harvey et al. 1980a). Nitrogen-fixing soil microbes require decaying wood as a major energy resource (Jurgensen et al. 1980). Since N is generally known as a major limiting nutrient of soil productivity (Binkley 1991; Vitousek and Howarth 1991), there is a strong positive relationship between the amount of SOM and forest productivity. Jurgensen et al. (1980) found this to be true when comparing forest productivity and the amount of fixed N in western larch (Larix occidentalis Nutt.) forest of Montana.

Additionally, organic matter in mineral soil performs a crucial function to support ectomycorrhizae. Ectomycorrhizae are the fungus-fine root-associated structure that helps determine tree performance (Kropp and Langlois 1990) of most commercial coniferous species in northwestern U.S. forests (Wiensczyk et al. 2002). Ectomycorrhizae enhance conifer water and nutrient uptake through a symbiotic relationship that supplies the fungus with carbohydrates. Therefore, the abundance and diversity of ectomycorrhizae are closely related to soil productivity (Perry et al. 1987). In northern Rocky Mountain forests, Harvey et al. (1980b) reported that more than 60% of total ectomycorrhizae were distributed in soil wood and humus. And in other parts of the world, the highest concentrations of mycorrhizal activity are found in organic layer and mineral soils close to the surface (Neary et al. 1999). Thus, the distribution and abundance of SOM determine the mycorrhizae abundance and, in turn, affect soil productivity.

**ORGANIC MATTER REDISTRIBUTION FOLLOWING NATURAL DISTURBANCES AND BIOMASS HARVESTING**

There are very few data in the western United States on the distribution of organic material on and in the soil. This information is critical to gauge the impacts of bioenergy harvesting on the stand (Page-
Dumroese and Jurgensen 2006; Page-Dumroese et al. 2010). We stress the importance of maintaining organic detritus because it is important for ecological function of mammals and birds (Maser and Trappe 1984) as well as plants (Harmon and Franklin 1989). Logs store nutrients and water (Sollins et al. 1987) and provide for humus formation (McFee and Stone 1966). And forest detritus is an important nutrient cycling pool (Franklin and Waring 1980). However, there are few links that show the importance of organic matter pools to tree (or other vegetation) growth. For example, the North American Long-Term Soil Productivity (LTSP) study found no effect following removal of large quantities of organic matter from a loblolly pine (Pinus taeda L.) stand after 10 years, even though organic matter removal would be expected to lower N mineralization rates and hinder tree growth (Sanchez et al. 2006). Further, in a meta-analysis of several LTSP study sites, forest floor removal had no overall significant effect on seedling diameter, except in ponderosa pine (Pinus ponderosa Lawson & C. Lawson) ecosystems (Fleming et al. 2006). The authors attributed growth difference to warm-humid conditions and rapid growth demands for available soil nutrients. Organic matter removal may promote early season growth by increasing soil temperatures, but it may suppress summer growth by reducing soil water content (Fleming et al. 2006).

Land management paradigms have shifted from standard silvicultural practices (e.g., clearcut, selection harvests, and shelterwoods) to emulating natural disturbances. With this shift in ecosystem management philosophies, the view of natural disturbance has changed. Now, forest scientists emphasize the complementary function of natural disturbances to ecosystem (Rogers 1996). Further, many forest scientists assert that silviculture should be founded in the ecosystem processes (Seymour et al. 2002). As a result, scientists are endeavoring to understand and integrate diverse ecosystem processes, including natural disturbance, into silvicultural knowledge and skills (e.g., Seymour and Hunter 1999; Noss et al. 2006; Franklin et al. 2007; Berger et al. 2013).

Disturbance can be defined as a discrete event causing a change in an ecosystem's structure, composition, or physical environment (Pickett and White 1985). Forest response to disturbance is
dynamic (McClugherty et al. 1982; Oliver and Larson 1996) and can be described by agent (e.g., fire, disease, and insects), frequency (interval), size, magnitude (intensity and severity), predictability, and synergism (Pickett and White 1985). The primary disturbance agents in northern Rocky Mountain forests are: fire, insects/pests, wind, and debris avalanches. These disturbances can be considered mechanisms for redistributing organic matter from one pool to another and/or exporting organic matter out of the ecosystem. For example, fuel combustion by fire results in the loss of organic materials, whereas tree mortality by bark beetles transfers organic matter from the living to non-living pool.

In this section, we discuss the characteristics of biomass harvesting in western forests, particularly the Inland Northwest forest ecosystems. We compared the ecological consequences of biomass harvesting with those of natural disturbance agents and highlight changes in the organic matter pools.

**Biomass harvesting in western forests**

Thus far in the northern Rocky Mountain Region, only merchantable stems (e.g., pole timber: 12.7-22.6 cm diameter, saw timber: larger than pole size; Simmons et al. 2014) are extracted, and residues (non-merchantable material) are piled-and-burned or broadcast-burned (Figure 2-2). More intensive biomass harvesting can be roughly classified into two methods: whole-tree and complete-tree harvesting (*sensu* Hakkila and Parikka 2002). Non-merchantable tops and crowns are harvested in whole-tree harvesting. Complete-tree harvesting is more intensive and extracts both stumps and roots (e.g., Walmsley and Godbold 2010). Whole-tree harvesting has been studied in northern Europe and northeastern America for decades. Recently, foresters from those regions are investigating the feasibility of complete-tree harvesting for bioenergy (Benjamin et al. 2010; Berger et al. 2013). However, because complete-tree harvesting requires additional operations and processes, further economic feasibility assessments are needed. In addition, impacts on societal values for more intensive harvesting should be
investigated. Biomass harvesting in the northern Rocky Mountains is more likely be whole-tree harvesting rather than complete-tree.

Whole-tree harvesting has a substantial impact on live vegetation (Berger et al. 2013). Usually, every tree over a certain diameter size class is cut and a significant proportion of the (living) organic matter is permanently removed from forest. According to Smith et al. (1986), about 90% of the total above-stump biomass was harvested in a red spruce (Picea rubens Sarg.)-balsam fir (Abies balsamea (L.) Mill.) forest in Maine. The residual stumps and roots transfer from the living organic matter pool to the detritus pool. If the root:shoot ratio for biomass is 0.26 (Cairns et al. 1997), then 26% of total removed biomass transfers to SOM pool. Changes in coarse and fine woody debris pools are minimal. Mortality of smaller sized trees and understory vegetation can occur during operation but the impact may be negligible. Forest floor displacement can also occur during harvest operations, leaving the mineral soil exposed to erosion, rainfall impact, and localized nutrient removals (Ballard 2000). In addition, slash piling and burning of logged areas can remove a significant portion of N over the affected area (Hickling 1997).

Natural disturbance agents in northwestern forests

Wildfire

Fire is a primary disturbance agent, not only in northern Rocky Mountains but also in most forest regions throughout the world. Wildfires alter various ecosystem components, including vegetation, soil, water, and air. Wildfire also changes the distribution of organic matter pools in many ecosystems (Page-Dumroese and Jurgensen 2006). Fire consumes organic matter through combustion (Hatten and Zabowski 2009). Depending on the fire’s severity, organic matter is distillated, charred, or completely oxidized (Neary et al. 1999; Certini 2005). Substantial organic matter consumption begins around 220°C (428 °F),
and beyond this the consumption increases rapidly. At this temperature, many nutrients (e.g., N and P) are volatilized or transformed into unavailable forms (Giovannini et al. 1990; Neary et al. 1999).

During fire, organic C in live vegetation and SOM is converted to C mono/dioxide and methane, which are immediately released into the atmosphere (Czimczik et al. 2005). C loss during a wildfire in Alaska was calculated to be as much as 20.1 Mg C/ha (French et al. 2002). In the Canadian boreal forest, the average amount of direct C lost during a fire was estimated to be 13 Mg C/ha (Amiro et al. 2001). On a global scale, van der Werf et al. (2010) calculated that in the United States, approximately 6.3 Mg C/ha was consumed during wildfire. A small fraction (0.7-8%; Czimczik et al. 2005) of C is converted into charred organic C (black C) which highly resists decomposition in many ecosystems (DeLuca and Aplet 2008). Nevertheless, in many fire-prone ecosystems, black C accounts for a considerable proportion of the total soil C pool (Schmidt et al. 1999).

Fire affects living plant tissue in several ways. Low intensity fire (e.g., surface fire) sweeps understory vegetation, resulting in dead forb, grass, and shrub layers and the loss of some forest floor material. High intensity fire (e.g., crown fire) damages overstory crown and bole and can kill the tree. The threshold temperature for killing plant roots is 48°C (118°F; DeBano et al. 1998), but disruptions in the biological function of soil begin at 40 to 70°C (104 to 158°F). Microbial mortality occurs between temperatures of 50 and 121°C (122 to 250°F; Neary et al. 1999).

Consequences of wildfire regime and biomass harvesting are summarized in Table 2-3. Wildfire results in the loss of organic matter, the magnitude of which depends on the fire intensity. In the aspect of tree mortality, biomass harvesting seems to have a similar impact to the stand-replacement fire regime. Even though trees are killed by wildfire, a considerable amount of organic matter remains on-site. For example, only 15% of aboveground biomass in coastal Douglas-fir was consumed in a wildfire, despite complete mortality of the trees (Fahnestock and Agee 1983; Agee 1996). Van der Werf et al. (2010) estimated 60% of the total biomass of killed trees remains on site after combustion. Abundant coarse
woody debris is produced as snags begin to fall to the ground (Oliver and Larson 1996; Tappeiner et al. 2007). According to Berger et al. (2013), fire produces the 18-31 Mg/ha of coarse deadwood biomass. In contrast, biomass harvesting provides little coarse wood debris except through the remaining stumps and any snags left as wildlife trees.

The dissimilarity between biomass harvesting and fire regimes is apparent in what remains in the understory and belowground layers. Even low severity fires kill most understory vegetation (Oliver and Larson 1996), whereas biomass harvesting results in minor changes to understory biomass and diversity. In addition, wildfire burning on the soil surface removes the forest floor. Loss of organic matter within the mineral soil is the most critical impact to belowground processes (Neary et al. 1999). About 75% of total surface organic materials (e.g., forest floor, twigs, leaves, and coarse wood) are depleted after fire in U.S. forests (van der Werf et al. 2010). Approximately 38% of the understory vegetation and 23% of the forest floor remained in a ponderosa pine forest after a moderate to severe wildfire in Arizona (Campbell et al. 1977). Furthermore, heat that transfers into the mineral soil can disrupt soil microfauna and fine root biomass (Agee 1996). However, biomass harvesting usually results in additional branches and twigs on the soil surface from falling the trees and can also result in only small patches of exposed mineral soil. Such differences affect water balance and chemistry, stream flow, and sedimentation differently (Long 2009). The temporal redistribution pattern of organic matter is also worth considering. The rotation age of ponderosa pine (biomass harvesting) can be calculated as 40 to 160 years based simply on culmination of mean annual increment (Tappeiner et al. 2007). It appears that the rotation age is comparable to interval of the mixed severity fire regime (Table 2-3). However, fire-return intervals of natural ponderosa pine are known to be less than 20 years (Weaver 1959; Agee 1996), which is more similar to the low severity fire regime. This means there is conflict between the ecological interval to maintain a ponderosa pine stand and the rotation cycle to yield timber. Presumably, these discords can be found in many different species and will probably cause a transition of species composition, resulting in different biomass productions, even from the same site.
Similarity between fire regimes and other silvicultural treatments can be found in terms of structural change after disturbance. Stand-replacement fire regimes resemble even-aged silvicultural systems (e.g., clearcut, shelterwood, and seed tree harvesting) in terms of stand initiation and consequent single cohort generation. From this standpoint, biomass harvesting might be comparable to the stand-replacement fire regime. Correspondingly, mixed severity fire regimes can be linked to uneven-aged silvicultural systems such as group or single tree selection harvest methods. These silvicultural systems can create patches and mimic species-specific mortality. Lastly, various fuel reduction treatments such as prescribed burning, thinning, or releasing treatments (in understory) can emulate low severity fire regime in terms of intensive understory removal. In particular, prescribed fire has been used to mimic this natural disturbance regime (Long 2009).

*Insect/Pest Attack*

The extent of damage from insect/pest attack varies depending on the condition of insect/pathogen, host, and environment. Insect or pathogens may cause immediate mortality or temporary weakness such as defoliation or stunted growth. Even when damage to one tree is initially limited, it can later be killed by successive attacks (e.g., Långström and Hellqvist 1993). Moreover, infected stands are more likely to be disturbed by other agents (e.g., windthrow and wildfire). Understanding these complex interactions and consequences is quite challenging. The following discussion focuses mainly on fatal insect/pest disturbance agents for simplicity.

The insect/pest attack disturbance regime can be grouped into two classes by its severity: stand-replacing and gap-scale (Table 2-4). The most distinctive characteristic of insect/pest attack is the host specificity. Therefore, the severity of stand-replacement by insect/pest can occur only on the pure or close to pure stand. The representative example of stand-replacing insect/pest disturbance is recent mountain
pine beetle (Dendroctonus ponderosae Hopkins) outbreak in North America. During the last decade, more than 10 Mha of pine stands were severely damaged in western United State and British Columbia (Meddens et al. 2012).

The insect/pest attack regime is distinctly different from fire. Insect/pest attack scarcely causes direct leakage of organic matter. Due to its host specificity, mortality rates vary by species. Host specificity also results in erratic patch patterns, increasing complexity of the landscape. Unless the disturbance agent kills the seedlings of its host, mortality of understory is negligible. Insect/pest attack generates a pulse of fine woody debris input due to the loss of foliage (a common symptom of weakened by trees). In addition, a dead tree becomes an element of snags or coarse woody debris. These can be interpreted as organic matter transfers from living vegetation to the SOM pool.

As shown in Table 2-4, gap-scale insect/pest outbreak does not seem to be similar to biomass harvesting. Like the mixed severity fire regime, gap-scale insect/pest attack seems to be close to single or group selection system. In terms of understory impact, insect/pest attack is more similar to silvicultural systems than to the fire disturbance regime. For stand-replacing insect/pest attack, only high overstory mortality can be considered a similarity; all other aspects demonstrate distinct differences from biomass harvesting. Even though the outbreak occurs in a pure and homogeneous stand with highly aggressive manner, the complexity generated after disturbance would be higher than that of biomass harvesting. These points are the same as with the other silvicultural systems.

*Wind*

Wind might be the most primary disturbance agent in many forest types. It encompasses not only the disturbances driven by strong wind events, but also various gap-forming disturbances (unless the mortality was caused by direct impact of other major agents). In a wide sense, mortalities of weakened
trees by senescence, insect/disease, fire, competition, herbivory, and other environmental stresses can be included in the wind disturbance regime. This implies that wind disturbance interacts frequently with other agents and often plays the role of “secondary” disturbance (Franklin et al. 2007; Sibold et al. 2007). These small-scale disturbances play a pivotal role in forming and maintaining the forest stand structure, especially in forests where stand-replacing disturbances are scarce (Lertzman et al. 1996).

Severity of wind disturbance can vary from the magnitude of single tree mortality to stand-replacement (e.g., hurricane, typhoon, and tornado). However, stand-replacing wind events are rare in the northern Rocky Mountain region, so we primarily discuss the gap-scale wind disturbance agent here.

Winds can cause mortality by either uprooting or breaking the stem. Neither case results in direct organic matter loss. Uprooting can damage understory vegetation, expose the mineral soil layer, and bring subsurface rocks close to the surface, but the affected area is localized and restricted to the extent that nearby soil horizons and understory vegetation can remain intact (Franklin et al. 2007). Emergent and senescent trees are usually most vulnerable to winds. Fallen and broken trees simultaneously increase the coarse woody debris organic matter pool and decrease the living organic matter pool. Since gap-scale wind disturbance produces relatively small sized patches in general, spatial heterogeneity of the stand can increase (<200 m²; White et al. 1985).

There are not many similarities between wind disturbances and biomass harvesting. Common traits exist only in terms of intact understory and soil layer. Rather, uneven-aged management (single tree or group selection) appears to have more similarities to the gap-scale wind disturbance regime. However, single tree selection cannot emulate wind disturbance perfectly since, in most cases, it cannot generate coarse woody debris and localized soil perturbation (Franklin et al. 2007).

*Debris Avalanche*
Disturbance related to soil erosion processes is one of the major disturbance agents in the northern Rocky Mountain region. The term “debris avalanches” refers to rapid soil mass-water (plus vegetation) movement from hillslopes, such as landslides, avalanches, and debris flows (Swanson and Swanson 1976). Although these disturbance agents may play a pivotal function in a specific area (e.g., determination of timberline by avalanche), very few studies pertain to the impacts of these disturbances on ecosystem function (Attiwill 1994).

Similar to biomass harvesting, debris avalanches remove a sizable amount of living organic matter and generate high mortality regardless of canopy strata. Since almost all aboveground material (and even some mineral soil close to the surface) is swept out to a lower place, generation of coarse woody debris is impossible.

Regardless of these similarities, debris avalanches are different from biomass harvesting in that they result in damages to the understory, forest floor, and mineral soil that are quite detrimental. These damages substantially hinder regeneration and understory vegetation recovery, leading to reduced productivity (Grigal 2000). Given the nature of avalanches, these disturbance agents are quite dissimilar to the other silvicultural treatments.

**Comparing impacts of biomass harvesting and natural disturbance agents on forest productivity**

If nutrient losses can be compensated by influx in the soil nutrients pool, then the impact of a natural disturbance on productivity can be determined by its influence on the SOM pool (Tables 2-3 and 2-4). Following natural disturbances, the amount of newly produced coarse woody debris and the magnitude of perturbation on understory vegetation can affect productivity as well. In this manner, we can predict and compare the potential impact of natural disturbances on productivity.
As previously mentioned, debris avalanches produce the most devastating results from natural disturbance. They remove not only aboveground vegetation but also transfer most of the forest floor and a sizable depth of topsoil, thereby having a highly detrimental effect on forest productivity. Moreover, since debris-avalanches are more likely to occur on productive sites (e.g., soil-water accumulated zone), the magnitude of negative impacts might be greater than on lower productivity sites. In conifer forests of British Columbia, a landslide site had a 70% reduction of wood volume production compared to adjacent harvested stands in first 60 years (Smith et al. 1986). Megahan (1990) argued that the impacts in the northern Rocky Mountain region are likely similar to those in British Columbia.

Fire can also adversely impact forest productivity. Potential hazardous impacts include: interruption of litter fall from the overstory, consumption of organic pool in the forest floor and soil layer, disruption of belowground biota, and increased leaching due to lack of aboveground vegetation. However, fire can also create several beneficial conditions to promote vegetation production. These impacts, whether detrimental or beneficial, are directly related to and determined by the extent, duration, and severity of the fire.

Winds and insect/pest attack seem to result in similar consequences to forest productivity (Table 2-4). For both disturbance agents, little organic matter is lost; dead overstory trees stay on-site as either snags or fallen logs, and detrimental impacts on understory and belowground layers are rare.

In summary, biomass harvesting appears to have a stronger negative impact on productivity than insect/pest attack and winds but less severe impacts than fire since biomass harvesting can conserve the understory vegetation, forest floor, and soil layer. Therefore, the presumable rank of detrimental impacts among the disturbance agents can be seen as: debris avalanches>fire>biomass harvesting>winds ≈ insect/pest attack. However, note that the adverse consequences depend on the intensity of disturbances, and other conditions can substantially ameliorate or aggravate the negative impacts.
BIOMASS HARVESTING AND FOREST PRODUCTIVITY: KEY FINDINGS

Impact of biomass exportation

Nutrient removals during timber harvesting can be substantial, especially where whole-tree harvesting is practiced (Ballard 2000). Most western forests are considered to be N deficient (Binkley 1991), so removal of a large proportion of N (or other nutrients) during harvesting may be a cause for concern (Weetman and Webber 1972; Foster and Morrison 1976). Additionally, the change in other macronutrients, such as P (e.g., Yanai 1998) and K (e.g., Goulding and Stevens 1988), after increased biomass removal has been noted. Leaves, branches, and tops are the major forms of additionally harvested biomass. The concern is these parts contain much higher concentration of nutrients than boles. Generally, plants allocate the highest concentration of nutrients into foliage and branches and the lowest concentration into the stem (Table 2-5; Farve and Napper 2009). This has been reported in various studies from mixed hardwood forests in Wisconsin (Pastor and Bockheim 1984) and New Hampshire (Whittaker et al. 1979), to Douglas-fir in British Columbia (Pang et al. 1987). Therefore, biomass harvesting would remove a much larger amount of nutrients than conventional (bole-only) harvesting. Alban et al. (1978) asserted that the whole-tree harvesting removes 2 to 11 times more nutrients than conventional harvesting in northeastern forests. In upland mixed oak forest of Tennessee and coniferous forest in Maine, whole-tree harvest resulted in about three times more nutrient removal than sawlog harvesting (Johnson et al. 1982; Smith et al. 1986). Mälkönen (1976) found consistent results for N, P, K, and Ca in northern Europe.

Calcium is known to be the nutrient most vulnerable to whole-tree harvesting throughout the United States (Boyle et al. 1973; Johnson 1982; Federer et al. 1989). This is because the amount of Ca in the soil pool is often relatively low, and, in contrast, the accumulation of Ca in aboveground vegetation for several species (e.g., aspen (Populus spp.), sugar maple (Acer saccharum Marshall), and white spruce
(Picea glauca (Moench) Voss)) is significant. Various studies have indicated that Ca is the nutrient most likely to be lost even though it seldom limits plant growth in natural condition (Farve and Napper 2009).

The key question in determining whether biomass harvesting would deplete nutrients in the long term is whether the amount of nutrient influx through precipitation and fixation can balance the nutrient requirement for vegetation growth. Annual accumulation of nutrients in vegetation shows similar magnitudes with nutrient influx through precipitation in general temperature forests (Alban et al. 1978). In the northern Rocky Mountain region, Stark (1980) estimated that the amount of nutrients removed by biomass harvesting did not exceed the amount that could be recovered within the next rotation (70-100 years) of Douglas-fir stands. Generally, much larger amounts of nutrients exist in the mineral soil and forest floor pools (Alban et al. 1978; Farve and Napper 2009). Therefore, the additional amount of nutrients removed by biomass harvesting is only a small portion of the total ecosystem pool. If the forest floor and mineral soil layer is conserved, then vegetation growth does not seem to be immediately delayed.

Impact of living organic matter removal

Canopy opening as a result of harvesting alters the microclimate of the understory. Increased solar radiation will increase soil temperature. Decreased transpiration and rainfall interception through aboveground vegetation removal can increase soil moisture contents. Consequently, decomposition and mineralization processes will be accelerated. Unless the increased available nutrients are taken up and stored immediately by vegetation, the majority of these extra nutrients will be leached. Therefore, prompt recovery of vegetation after harvesting is critical to prevent leaching. If aboveground vegetation is removed, then influx of fresh litter from the overstory will be interrupted temporarily. As the decomposition rate is accelerated, the duff layer depth decreases more rapidly. In the soil mineral layer,
fine root turnover will be temporarily interrupted as well. However, pulse of non-living organic matter (roots) input will occur immediately after harvesting. Again, rapid aboveground re-vegetation is most critical; otherwise, the total belowground organic matter pool will decrease.

**Impact on soil physical properties**

One of the most critical adverse impacts of harvesting operations on soil productivity is compaction caused by the traffic of heavy machinery (Janowiak and Webster 2010; Page-Dumroese et al. 2010). We can easily predict that more intensive harvesting will exacerbate soil compaction. Compaction increases soil bulk density, hampering air movement and water permeability (Thibodeau et al. 2000). In compacted soil, soil fauna activity and fine root development can be restricted (Kozlowski 1999). Moreover, as previously mentioned, since the majority of fine root distribution and microbial activity are concentrated within the shallow range of topsoil, the negative impact of compaction on forest productivity is substantial (Page-Dumroese et al. 2010).

Although diverse factors can affect the susceptibility of soil to compaction (Page-Dumroese et al. 2010), soil texture is a primary determinant (Powers et al. 2005). Soil with high clay (<0.002 mm) fraction is more susceptible to compaction. In addition, SOM can play an important role in ameliorating the compaction susceptibility since it can improve the soil structure, aeration, permeability, and activity of soil organisms. Therefore, harvesting should be conducted with consideration of compaction susceptibility, and sufficient amounts of organic matter must be retained to maintain soil productivity. In mixed conifer stands of British Columbia, Hope (2007) found that soil compaction was recovered in 10 years. Initial differences in soil bulk density caused by harvesting operation disappeared, and planted lodgepole pine (*Pinus contorta* Douglas ex Loudon) and hybrid spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry) seedling growth was no different after 10 years. The author hypothesized the
amelioration of soil compaction is related to the amount of SOM contributed by abundant fine roots. A similar result was observed in the lodgepole pine forest of British Columbia (Simard et al. 2003).

**Impact on soil chemical properties**

If increased decomposition rate and interruption of litter provision decrease the organic pool in the soil layer, they may also influence soil chemical properties. First of all, soil CEC might decrease. Nutrient leaching occurs more easily in soil with low CEC since soil particles do not possess enough sites to hold cations. In addition, whole-tree harvesting can increase the C:N ratio (Olsson et al. 1996), making the immobilization of N more dominant (Farve and Napper 2009) and resulting in delayed aboveground vegetation recovery. The longer the delay, the more nutrients are lost.

Timber harvesting can alter soil acidity in a way that affects soil productivity. Soil pH generally increases after harvest (Jurgensen et al. 1997), explained by: (1) transformation of humus, (2) release of cations during decomposition of organic matter, and (3) utilization of hydrogen ions during the mineralization process (Nykvist and Rosén 1985). In general, soil microbes prefer alkaline conditions (Jurgensen et al. 1997). However, intensive biomass harvesting can render a soil environment that is relatively more acidic than with conventional harvesting. Soil with low CEC will acidify more easily and, consequently, lose base cations (i.e., leaching). Furthermore, formation of soil aggregate structure can be hindered in acidic soil. Therefore, maintaining the soil organic pool by keeping SOM in the forest floor and mineral soil intact and aiding quick aboveground re-vegetation are essential for maintaining forest productivity.

**Impact on soil biological properties**
Decreases in the SOM pool also affect the biological property of the forest. The abundance and activity of soil organisms would likely be limited in cases of deficient food and habitat resources. Bengtsson et al. (1997) found that intensive harvesting decreased the abundance of soil arthropods in a Scots pine stand in Sweden 15 to 18 years after harvesting. Since soil fauna can contribute significantly to N mineralization (Anderson et al. 1983; Verhoef and Brussaard 1990), the decrease of soil mesofauna might result in decreased productivity. Among those soil organisms, ectomycorrhizae deserve emphasis due to both their important role in productivity and their specific life cycle. Without a host, ectomycorrhizae can hardly survive more than 3 years (Wienczyk et al. 2002). Repeated intensive biomass harvesting might negatively impact ectomycorrhizal abundance (Mahmood et al. 1999).

Therefore, ensuring advanced regeneration is critical to protect the ectomycorrhizae community. Otherwise, artificial regeneration should be considered.

**Climate change and biomass harvesting**

Running (2009) expected future climate change in the northern Rocky Mountain region to be manifest in longer growing seasons owing to increased temperatures, less snow, more rain, and longer summer drought. Elevated CO₂ levels are expected to increase photosynthetic rates. In this scenario, nutrient cycling processes such as mineralization and nitrification would be stimulated by increased temperatures. At a glance, forest productivity in the northern Rocky Mountains is projected to increase. However, increased summer drought would limit forest productivity. Whether biomass harvesting would adversely affect forest productivity under changing climate depends on if retained soil and organic matter provide ample nutrients and water to vegetation.

If Running’s prediction is realized, intensive biomass harvesting may constrain forest productivity. Increased vegetation production would, in turn, demand increased amounts of nutrients. Retained organic
matter in the forest floor and soil layers would enhance beneficial soil properties such as water holding capacity during summer drought. Thus, if biomass harvesting damages soil properties or decreases the soil nutrient pool, climate change will exacerbate the negative impacts on forest productivity.

**DISCUSSION**

In Johnson and Curtis’ (2001) meta-analysis, they noted that whole-tree harvesting decreases soil C and N by 6%, whereas conventional sawlog harvesting increases both C and N by 18%. N reductions during harvesting may need to be offset by fertilization treatments (Himes et al. 2014). Current empirical experiments have reported no loss of soil C with increasing biomass removal intensity (e.g., Powers et al. 2005; Nave et al. 2010; Thiffault et al. 2011). Also, Olsson et al. (1996) found no difference in soil C according to the biomass removal intensity in Scots pine and Norway spruce (*Picea abies* (L.) Karst.) stands in Sweden 15 years after harvesting.

In European experiments, differences in stand production between whole-tree harvesting and conventional harvesting are more commonly detected. In a Sitka spruce plantation in England, Walmsley et al. (2009) observed a 10% reduction in dbh increment after whole-tree harvesting. Proe et al. (1996) found 32% tree volume reduction of planted Sitka spruce seedling 14 years after harvesting in England. In Scandinavia, Egnell and Leijon (1999) and Egnell and Valinger (2003) observed a consistent reduction of Norway spruce and Scots pine tree growth after whole-tree harvesting. In addition, Jacobson et al. (2000) found a significant difference in tree volume growth in pine and spruce stands 10 years after harvesting. However, North American study results often do not follow those of the European studies. The LTSP research network did not show any significant impacts of intensive biomass removal on vegetation production after 10 years (Powers et al. 2005). In addition, a western larch forest in western Montana showed results consistent with LTSP 38 years after intensive biomass harvesting (Jang et al. 2013).
Responses of intensive harvesting likely differ by site and species. For example, some loblolly pine stands showed a different response (i.e., consistent volume growth reduction) than other stands in LTSP studies (Powers et al. 2005). Likewise, Scots pine stands were less consistent than Norway spruce stands in European studies (Egnell and Leijon 1999). In that sense, the difference of Johnson and Curtis’ (2001) analysis might be driven not by the harvesting intensity but by the species (i.e., conifer versus hardwood).

There are still numerous gaps in our understanding of intensive biomass utilization for bioenergy production and nutrient cycling, changes in stand productivity, and soil quality. In addition, how a changing climate will interact with biomass harvesting, thereby influencing SOM decomposition rate, is also controversial. Climate change can impact both input and output sources of SOM pools. Specifically, it may increase primary production of vegetation which would increase input to SOM pools and increase the decomposition rate of belowground organic matter, resulting in simultaneously increased output of the SOM pool. Thus, if the contribution of increase in primary production to SOM pools exceeds the increase in output of organic matter through elevated decomposition rate, then climate change would not result in adverse consequences on forest productivity or vice versa. However, there remains controversy regarding the potential impact of climate change on the SOM cycle (Davidson and Janssens 2006). We must endeavor to fill these knowledge gaps to prevent undesirable consequences of biomass harvesting on our ecosystems.

**MANAGEMENT IMPLICATIONS**

Several research efforts to predict long-term impacts of intensive biomass removal on forest productivity have been made. However, the empirical knowledge and comprehensive understanding, especially on western forests, are limited thus far. Therefore, we utilize the available findings to evaluate potential impacts of increased biomass extraction on western forest, summarized as:
1. In general, the long-term impacts of intensive biomass harvesting for bioenergy production will likely cause few impacts on within-stand nutrient cycling if the forest floor and mineral soil are protected (Page-Dumroese et al. 2010). Considerable amounts of nutrients were stored in the belowground layer, and inputs through precipitation or dry deposition support the nutrient requirement by nest rotation.

2. Nevertheless, there is a risk of substantial leakage of nutrients out of ecosystems. Excess nutrients from the addition of needles, leaves, and branches would likely be leached through the mineral soil profile unless rapid re-vegetation occurred (Boyle et al. 1973). Increased leaching can result in one or more nutrient deficiencies, and subsequent seedling or shrub growth can be stunted (“nutrient shock”; sensu Stark 1980).

3. Fortunately, favorable conditions created after harvesting can usually accelerate immediate understory vegetation recovery. In a clearcut western larch stand in Montana, 37% of pre-harvest shrub volume recovered within 4 years after harvesting. Remarkably, in the understory protected treatment, 62% of pre-harvest shrub volume recovered during the same period (Schmidt 1980). Such a rapid re-vegetation of understory has been reported to play an important role in maintaining the forest productivity in the early stand developmental stage (e.g., Turner and Long 1975).

4. It must be noted that these general conclusions are not necessarily applicable to every forest and site condition; some forest sites likely require further attention. For example, low productivity, dry sites usually have larger soil organic pools but also have less nutrient inputs through precipitation and dry deposition (Jurgensen et al. 1997; Page-Dumroese and Jurgensen 2006). Moreover, if precipitation occurs when plants are not growing, the risk of nutrient leaching increases (Alban et al. 1978). Conversely, wetter and warmer sites with higher productivity by higher decomposition rate tend to have a shallower organic layer. Reductions in the forest floor layer occur rapidly if harvesting accelerates decomposition
rates. On these sites, it is critical to retain the forest floor during harvest operations and to recruit the organic horizon parent material (woody residue). For example, Jurgensen et al. (1997) argued that larger amounts of woody residue should be retained on moist sites (22-36 Mg/ha) as opposed to dry sites (10 Mg/ha). In addition, forest soils that are not resilient to ground-based harvest systems, are relatively infertile, are compaction prone, have a short fire return interval, have insufficient regeneration sources and understory vegetation, or have species that demand high soil nutrient concentrations should be harvested with care (Page-Dumroese et al. 2010).

5. Several conventional silvicultural treatments should be reconsidered in biomass-harvested sites. For successful regeneration, site preparation treatments such as prescribed burning and scalping are often required for some species (e.g., western larch and longleaf pine (Pinus palustris Mill.)). Since these treatments remove the forest floor, their adverse consequences should be considered before harvest operations begin. Fuel reduction treatments such as repeated thinnings can result in insufficient nutrient cycling for healthy and productive forests (Page-Dumroese et al. 2010).

REFERENCES


Smith, R.B., P. Commandeur, and M.W. Ryan. 1986. Soils, vegetation, and forest growth on landslides and surrounding logged and old-growth areas on the Queen Charlotte Islands.


Table 2-1. Distribution of carbon stock (Mg C/ha) by biome in 2007 (from Pan et al. 2013).

<table>
<thead>
<tr>
<th></th>
<th>Boreal</th>
<th>Temperate</th>
<th>Tropical intact</th>
<th>Tropical regrowth</th>
<th>Global</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live biomass</td>
<td>47.5</td>
<td>60.7</td>
<td>163.9</td>
<td>60.8</td>
<td>94.2</td>
</tr>
<tr>
<td>Non-living biomass</td>
<td>191.7</td>
<td>94.0</td>
<td>118.6</td>
<td>78.6</td>
<td>129.4</td>
</tr>
<tr>
<td>Total</td>
<td>239.2</td>
<td>154.7</td>
<td>282.5</td>
<td>139.4</td>
<td>223.6</td>
</tr>
</tbody>
</table>
Table 2-2. The distribution of non-living organic matter (Mg/ha) in western-montane forests (from Page-Dumroese et al. 1990).

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Residue</th>
<th>Forest floor</th>
<th>Soil wood</th>
<th>Mineral soil</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cedar/hemlock (Montana)</td>
<td>84</td>
<td>50</td>
<td>51</td>
<td>145</td>
<td>330</td>
</tr>
<tr>
<td>Cedar/hemlock (Idaho)</td>
<td>154</td>
<td>23</td>
<td>48</td>
<td>201</td>
<td>426</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>146</td>
<td>36</td>
<td>36</td>
<td>153</td>
<td>371</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>45</td>
<td>26</td>
<td>26</td>
<td>133</td>
<td>230</td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>20</td>
<td>7</td>
<td>2</td>
<td>160</td>
<td>189</td>
</tr>
<tr>
<td>Average (%)</td>
<td>26</td>
<td>9</td>
<td>10</td>
<td>55</td>
<td>100</td>
</tr>
</tbody>
</table>
Table 2-3. Impacts of fire and biomass harvesting on organic matter and stand structure, as well as comparison with silvicultural treatments.

<table>
<thead>
<tr>
<th></th>
<th>Fire Stand replacement</th>
<th>Fire Mixed severity</th>
<th>Fire Low severity</th>
<th>Biomass harvesting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Organic matter extraction</td>
<td>High</td>
<td>Moderate</td>
<td>Low</td>
<td>Very high</td>
</tr>
<tr>
<td>Overstory tree mortality</td>
<td>Most</td>
<td>Selective</td>
<td>None</td>
<td>Most</td>
</tr>
<tr>
<td>Understory mortality</td>
<td>High</td>
<td>High</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>CWD production(a)</td>
<td>High</td>
<td>Moderate</td>
<td>Rare</td>
<td>Low</td>
</tr>
<tr>
<td>Impact on SOM(b)</td>
<td>High (–)</td>
<td>High (–)</td>
<td>High (–)</td>
<td>Moderate (+)</td>
</tr>
<tr>
<td>Heterogeneity creation</td>
<td>Low</td>
<td>High</td>
<td>Moderate</td>
<td>Low</td>
</tr>
<tr>
<td>Interval (years)(c)</td>
<td>100-400</td>
<td>30-100</td>
<td>5-30</td>
<td>40-160(d)</td>
</tr>
<tr>
<td>Similarity to biomass</td>
<td>Moderate</td>
<td>Low</td>
<td>Rare</td>
<td>-</td>
</tr>
<tr>
<td>harvesting</td>
<td>Even-aged management</td>
<td>Uneven-aged</td>
<td>Fuel reduction</td>
<td>-</td>
</tr>
<tr>
<td>treatments</td>
<td>management</td>
<td>management</td>
<td>treatment</td>
<td></td>
</tr>
</tbody>
</table>

\(a\) Snags and fallen CWD; CWD = coarse woody debris
\(b\) Both organic layer and soil layer were lumped together; SOM = soil organic matter
\(c\) Arno et al. 2000
\(d\) Rotation cycle of ponderosa pine (source: Tappeiner et al. 2007)
\(e\) Agee 1998
Table 2-4. Impacts of beetle attack, windthrow, debris avalanche flowon organic matters and stand structure, as well as comparison to silvicultural treatments. CWD = coarse woody debris and SOM = soil organic matter.

<table>
<thead>
<tr>
<th>Insect/pest attack</th>
<th>Stand-replacing</th>
<th>Gap-scale</th>
<th>Windthrow&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Debris avalanche&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Organic matter extraction</td>
<td>Rare</td>
<td>Rare</td>
<td>Rare</td>
<td>Very High</td>
</tr>
<tr>
<td>Overstory tree mortality</td>
<td>Selective/high</td>
<td>Selective/ moderate</td>
<td>Selective/low</td>
<td>Most</td>
</tr>
<tr>
<td>Understory mortality</td>
<td>Rare</td>
<td>Rare</td>
<td>Rare</td>
<td>High</td>
</tr>
<tr>
<td>CWD production</td>
<td>High</td>
<td>Moderate</td>
<td>Moderate</td>
<td>None</td>
</tr>
<tr>
<td>Impact on SOM</td>
<td>High (+)</td>
<td>Rare (+)</td>
<td>Rare (+)</td>
<td>High (−)</td>
</tr>
<tr>
<td>Heterogeneity creation</td>
<td>Low&lt;sup&gt;c&lt;/sup&gt;</td>
<td>High</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Interval (years)</td>
<td>40-100&lt;sup&gt;d&lt;/sup&gt;</td>
<td>24-46&lt;sup&gt;e&lt;/sup&gt;</td>
<td>100&lt;sup&gt;f&lt;/sup&gt;</td>
<td>2-25&lt;sup&gt;g&lt;/sup&gt;</td>
</tr>
<tr>
<td>Similarity to biomass harvesting</td>
<td>Moderate</td>
<td>Low</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Similarity to other silvicultural treatments</td>
<td>Even-aged management</td>
<td>Uneven-aged management</td>
<td>Uneven-aged management</td>
<td>Biomass harvesting</td>
</tr>
</tbody>
</table>

<sup>a</sup> Gap-scale disturbances were considered
<sup>b</sup> Swanson and Swanson 1976
<sup>c</sup> In case of aggressive epidemic in homogenous stand
<sup>d</sup> Spruce bark beetle (Zhang et al. 1999)
<sup>e</sup> 2-year-cycle budworm (Wong et al. 2003)
<sup>f</sup> White et al. 1985
<sup>g</sup> Debris flows (Parrett et al. 2004)
Table 2-5. Nutrient distribution in aboveground tree components of 34-year-old Douglas-fir (from Pang et al. 1987; Farve and Napper 2009).

<table>
<thead>
<tr>
<th>Tree component</th>
<th>Nutrient concentration (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
</tr>
<tr>
<td>Current foliage</td>
<td>29</td>
</tr>
<tr>
<td>Old foliage</td>
<td>26</td>
</tr>
<tr>
<td>Current twigs</td>
<td>21</td>
</tr>
<tr>
<td>Branches</td>
<td>10</td>
</tr>
<tr>
<td>Bark</td>
<td>7</td>
</tr>
<tr>
<td>Dead branches</td>
<td>6</td>
</tr>
<tr>
<td>Wood</td>
<td>2</td>
</tr>
</tbody>
</table>
Figure Captions

Figure 2-1. Schematic illustration of general nutrient cycle in forest ecosystems (modified from Attwill and Adams 1993).

Figure 2-2. Biomass components of a tree (redrawn from Hakkila and Parikka 2002).
Figure 2-1.
Figure 2-2.
CHAPTER 3

DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII* MIRB. FRANCO)
SEEDLING RESPONSE TO INTENSIFIED FOREST BIOMASS
EXTRACTION IN THE NORTHERN ROCKY MOUNTAINS

ABSTRACT

To investigate the long-term impacts of biomass harvesting on site productivity, we remeasured the 1974 Forest Residues Utilization Research and Development Program at Coram Experimental Forest in western Montana. Four levels of biomass utilization intensity were assigned within three regeneration cuttings (clearcut, shelterwood, and group selection). From 1976-79, 2-0 bare root seedlings of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) were planted in 3 different biomass utilization treatments in western larch (*Larix occidentalis* Nutt.) stands that were clearcut in 1974. In 2013, tree height, dbh, foliar N and C concentrations were measured. From cross-sectional sapwood area, leaf area was estimated and tree-level growth efficiency (5-year-basal area increment (cm$^2$) / total leaf area (m$^2$)) was calculated. Previous measurements from 1980, 1992, 1987, and 2001 were used for dbh and height growth analyses. At this site, none of the response variables were affected by biomass utilization levels. Only seedling planting year contributed significantly to affect tree mean height, dbh, volume, basal area increment, and total leaf area. These results indicate that there was no apparent effect of biomass extraction level on site productivity, for the range of biomass harvest levels performed.
INTRODUCTION

Forest biomass harvesting for bioenergy, which involves extracting increased amounts of biomass from a site that is above the level of extraction typically associated with conventional timber harvesting, is emerging as a source of alternative energy feedstocks, due mainly to the increasing cost of fossil fuels and public concerns over climate change. Conventional harvesting produces a considerable amount of woody biomass residues. Those are usually left on the ground, broadcast burned, or piled and burned to reduce wildfire hazard. Intensive utilization of those woody biomass residues is not a wholly new concept. Whole-tree harvesting has been practiced since circa the 1970s in North American forests. Moreover, further intensive harvesting methods (e.g., energy-wood harvesting; Benjamin et al. 2010) have been investigated in the forests of northern Europe and the northeastern United States. It seems apparent that future timber harvesting in northern Rocky Mountain forests will utilize greater levels of biomass than contemporary harvests, but the effects of such harvests on productivity in this region are poorly understood.

Increased biomass removal can lead to losses of nutrients from forest ecosystems. Branches, twigs, and foliage have higher nutrient concentrations than stemwood and their removal may cause excessive declines in site productivity (Pastor and Bockheim 1984, Pang et al. 1987). Studies of whole-tree harvesting have consistently indicated significantly greater nutrient loss than conventional harvesting methods (Alban et al. 1978, Mann et al. 1988, Roberts et al. 2005, Farve and Napper 2009). Several simulation efforts and nutrient budget analyses have warned of the site productivity impacts of nutrient depletion by intensive biomass utilization (e.g., Weetman and Webber 1972, White 1974, Kimmins 1977). Additionally, abrupt elimination of aboveground vegetation exacerbates the temporal loss of soluble nutrients through soil leaching (e.g., Likens et al. 1970). Thus, the concern that increased biomass extraction could adversely impact site productivity is reasonable.
Biomass harvesting for bioenergy can also influence a site’s nutrient flux indirectly by altering other environmental factors. Increased biomass removal can affect the understory microclimate by altering solar radiation, soil temperature, and soil moisture. In addition, soil properties can be altered by intensive biomass utilization. For example, Nykvist and Rosén (1985) and Staaf and Olsson (1991) found that the increased biomass utilization can exacerbate soil acidification. By modifying organic matter dynamics, these environmental alterations can affect soil biota, consequently modifying nutrient cycling and availability (Jurgensen et al. 1997, Egnell and Leijon 1999). Such complex effects of intensive biomass utilization make it difficult to predict the protracted impacts of biomass harvesting on site productivity, underlining the necessity of long-term field experiments.

Several experimental efforts have sought to determine the consequences of intensive biomass utilization on site productivity in recent years. These have focused on the growth of regenerating stands following intensified biomass harvesting, as indicators of site productivity impacts. In the United Kingdom, Proe et al. (1996) reported that whole-tree harvesting led to a 13% volume reduction of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) plantation seedlings compared to conventional harvesting after 12 years. In another Sitka spruce stand in North Wales, whole-tree harvesting caused an approximately 10% reduction in dbh (diameter at breast height) 23 years after seedling planting (Walmsley et al. 2009). In Sweden, increased biomass utilization resulted in a 17% basal area reduction for Scots pine (*Pinus sylvestris* L.) seedlings after 24 years (Egnell and Valinger 2003) and negative impacts on growth of Norway spruce (*Picea abies* (L.) Karst.) seedlings after 15 years (Egnell and Leijon 1999). Jacobson et al. (2000) observed reduced tree volume growth in Scots pine and Norway spruce stands (5 and 6 %, respectively) from a series of experimental sites across Scandinavian countries 10 years after thinning with whole-tree removal. Conversely, the North American Long-Term Soil Productivity (LTSP) study yielded somewhat different results from those of northern European forests. Ten years after biomass removal treatment, Powers et al. (2005) and Ponder Jr. et al. (2012) failed to find a consistent consequence of intensive biomass utilization on tree responses. Thus, tree responses to increased biomass
removal appear to vary depending on regional factors such as vegetation, soil properties, and disturbance/harvest regimes.

The equivocal impacts of biomass removal emphasize the necessity for experimental efforts to evaluate site-specific long-term impacts on productivity. An opportunity to evaluate the long-term impacts of intensive biomass extraction on site productivity in the northern Rocky Mountains exists at western Montana’s Coram Experimental Forest. In 1974, timber harvesting was conducted with three levels of biomass utilization in a western larch forest (*Larix occidentalis* Nutt.). For four consecutive years thereafter (1976 to 1979), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings were planted within each biomass utilization treatment. This experimental trial enables an isolation of the long-term effects of biomass harvesting on site productivity by holding constant or randomizing other factors that can affect seedling growth, such as genetic traits, microsite, spacing, time of initiation, and competition. The objective of this study was to investigate the long-term impact of intensified biomass utilization on individual tree growth. To achieve this objective, we compared tree responses such as height, diameter, and volume growth, tree vigor, and foliar nutrient concentrations among three biomass utilization levels.

**METHODS**

**Study site**

This study was conducted at Coram Experimental Forest (CEF), on the Flathead National Forest in northwestern Montana, located about 9 km south of Glacier National Park. The elevation of the study site ranges from 1,195 to 1,615 m, with 30-80% slopes. Soils have approximately 40-80% rock-fragment content, are underlain with glacial till (Klages et al. 1976), and are classified as loamy-skeletal, isotic Andic Haplocryalfs (Soil Survey Staff 2009). The climate of CEF is classified as a modified Pacific
maritime type (Adams et al. 2008). Average annual precipitation is 1,076 mm, primarily occurring in the form of snow from November to March (Farnes et al. 1995). Mean annual temperature is reported as 2 °C to 7 °C (Hungerford and Schlieter 1984).

The biomass utilization experiment was implemented in mature stands of the Western Larch cover type (Society of American Foresters Cover Type 212; Eyre 1980) on the Upper Abbot Creek Basin (48°25′ N, 113°59′ W) of the CEF. Major tree species of the study site are: western larch, Douglas-fir, subalpine fir (Abies lasiocarpa (Hook.) Nutt.), Engelmann spruce (Picea engelmannii Parry ex Engelm.), and paper birch (Betula papyrifera Marshall). The study site is relatively moist and productive, predominantly classified as the subalpine fir/queencup beadelily (Clintonia uniflora (Menzies ex Schult. & Schult. f.) Kunth) (ABLA/CLUN) habitat type (Pfister et al. 1977; Shearer and Kempf 1999). Understory woody vegetation consists of twinflower (Linnaea borealis L.), ninebark (Physocarpus malvaceus (Greene) Kuntze), shiny-leaf spiraea (Spiraea betulifolia Pall.), kinnikinnick (Arctostaphylos uva-ursi (L.) Spreng.), Sitka alder (Alnus viridis (Chaix) DC. ssp. sinuata (Regel) Á. Löve & D. Löve), Scouler’s willow (Salix scouleriana Barratt ex Hook.), and huckleberry (Vaccinium globulare Douglas ex Torr.) (Shearer and Kempf 1999), and includes seedlings of shade-tolerant conifers such as subalpine fir and Engelmann spruce (Shearer and Schmidt 1999).

**Experimental design**

In 1974, experimentally controlled clearcuts were performed at two sites (high and low elevation). Within each of these sites, three residues utilization treatments were designated that combined utilization level with prescribed burning (high-unburn, low-burn, and medium-burn; Table 3-1). Harvested trees were removed via a skyline yarding system. For four consecutive years afterward (1976-79), a row of 25 seedlings of Douglas-fir was planted, at 1.8 m spacing. The seedlings were two-year-old bare root stock.
Circa 2000s, due to tree growth and overlapping crowns, alternating trees were removed to maintain the growth of residual seedlings.

**Data collection and analysis**

Measurements of dbh and height were conducted in 1980, 1987, 1992, 2001, and 2013. Dbh was measured by diameter tape at 1.37 m height, and height was measured by using a height pole or laser clinometer. Individual tree volumes were computed with a volume equation using the dbh and height measurements (Wykoff et al. 1982). In 2013, tree cores and foliage samples were taken from five trees in each treatment, replicate, and planting year (n=118). Five trees in each row (2nd, 4th, 6th, 8th, and 10th trees) were systematically selected. Two tree cores were taken perpendicular to each other at breast height; bark thickness was measured by caliper to nearest 0.1 mm and sapwood boundary was marked.

In the lab, recent five-year radial growth and sapwood length from core samples were measured by digital caliper to the nearest 0.01 mm. Foliage samples were oven-dried at 60°C to constant mass, and ground to pass a 0.04-mm mesh. Subsamples of 0.3 grams per sample were analyzed on a LECO TruSpec CN analyzer (Leco Corp., St. Joseph, Michigan USA) for total C and N concentrations.

Growth efficiency (GE) is commonly used to compare tree vigor, or efficiency of leaf area utilization (growing space efficiency; *sensu* O’Hara 1988). Growth efficiency can be expressed in stem wood production (volume or weight) per unit leaf surface area in general (Waring 1983). However, basal area increment has sometimes been substituted for stem wood production (e.g., Waring et al. 1980, O’Hara 1988, Fajardo et al. 2007). For this study, the estimation of periodic stem wood production would have required additional previous measurement of tree heights and bark thicknesses, which were not available. Thus, basal area increment was used rather than stem wood production.
Using the equation provided by Gower et al. (1987), leaf area was calculated from cross-sectional sapwood area as:

\[ Y = 10^{-0.226 + 0.849 \log_{10}(X)} \]

where, \( Y \) is leaf area (m\(^2\)), and \( X \) is sapwood area at breast height (cm\(^2\)). Growth efficiency was calculated per tree as: 5-year-basal area increment (cm\(^2\)) / total leaf area (m\(^2\)).

Since the experimental design at CEF was regarded as a split-plot design, linear mixed-effects models were used to analyze growth efficiency, 12-year basal area increment, tree height, and foliar C and N concentrations. The biomass utilization treatment was considered the whole-plot, and planting year was treated as the sub-plot. The plots were blocked by elevation, which was treated as a random effect. The model was constructed as:

\[ y_{ijkl} = \mu + \alpha_i + B_k + \epsilon_{(1)ik} + \beta_j + (\alpha\beta)_{ij} + \epsilon_{(2)ijk} + \epsilon_{ijkl} \]  

(1)

where \( y_{ijkl} \) = response variable, \( \mu \) = grand mean, \( \alpha_i \) = effect of biomass utilization treatment (whole-plot effect), \( B_k \) = \( k^{th} \) block effect (random effect), \( \beta_j \) = effect of planting year (sub-plot effect), \( (\alpha\beta)_{ij} \) = the interaction between biomass utilization treatment and planting year, and \( \epsilon_{(1)ik} \), \( \epsilon_{(2)ijk} \), and \( \epsilon_{ijkl} \) are the whole-plot error, sub-plot error, and the variation among trees in a subplot, respectively.

The approaches to handling repeated measures can be largely classified as 1) adjusted univariate split-plot analysis, 2) multivariate analysis, and 3) profile analysis (Quinn and Keough 2002). In this study, we estimated the coefficients of response curves (\textit{sensu} Meredith and Stehman 1991) for repeated measures of height and dbh, which can be regarded as a type of profile analysis. Since the experimental design (split-plot) of this study was intrinsically complex, adjusted univariate or multivariate approaches...
required additional assumptions. On the other hand, analysis of coefficients can provide straightforward inferences given our objectives. We followed the approach of Meredith and Stehman (1991); orthogonal polynomial coefficients summarized the response curves (such as linear and quadratic), and were compared among other factors, avoiding the problems of serial correlation. The assumption of variance heterogeneity was diagnosed by residual plot.

Adopting this approach, orthogonal polynomial coefficients for each individual seedling were calculated. Since the measurement years were spaced unequally, the mean ($Z$), linear ($B$), and quadratic ($Q$) contrasts of seedling height were calculated via R as:

\[
Z_{ijk} = \frac{(y_{ijk1980} + y_{ijk1992} + y_{ijk2001} + y_{ijk2013})}{4} \quad (2)
\]

\[
B_{ijk} = (-0.682y_{ijk1980} - 0.186y_{ijk1992} + 0.186y_{ijk2001} + 0.682y_{ijk2013}) \quad (3)
\]

\[
Q_{ijk} = (0.5y_{ijk1980} - 0.5y_{ijk1992} - 0.5y_{ijk2001} + 0.5y_{ijk2013}) \quad (4)
\]

These variables were used as the coefficients, and were fitted into equation (1). Dbh and volume measures were also analyzed in the same manner, but only the last 3 measures were used since the majority number of seedlings had no dbh records until 1987.

The statistical significance of interaction terms were determined with $F$-tests (0.05 $\alpha$-level). If the interaction term was not significant, then the reduced model was chosen. All analyses were conducted via R (R Development Core Team 2008). The package of nlme (Pinheiro et al. 2014) was used to fit the mixed effects models.
RESULTS

The mean height and dbh of planted Douglas-fir trees measured in 2013 were 8.59 m (SE: 0.15 m) and 13.5 cm (SE: 0.3 cm), respectively (Table 3-2). The average individual tree volume was 0.068 m$^3$ (SE: 0.003 m$^3$). Planted trees grew an average of 42.6 cm$^2$ (SE: 2.1 cm$^2$) in basal area during the recent 5 year period. Leaf area was estimated to be 31.7 m$^2$ (SE: 1.4 m$^2$) per tree. From 5-year basal area increment and estimated leaf area, the average growth efficiency was calculated as 1.32 cm$^2$/m$^2$ (SE: 0.03 cm$^2$/m$^2$). Foliar C and N concentrations were 50.0 % (SE: 0.07 %) and 0.79 % (0.01 %). The treatment-level means of each metric are presented in Table 3-2, Figure 3-1, and Figure 3-2.

Foliar N and C concentrations were unaffected by biomass utilization treatment and planting year (Figure 3-1, Table 3-3). Tables 3-4, 3-5, and 3-6 show the results of analyses for repeated measures of height, dbh, and volume. None of the interaction terms for biomass utilization treatment by planting year were significant. Reduced models indicated that biomass utilization treatment had no effects on growth curve elements (i.e., mean, slope, and curvature) of height, dbh, and volume. Even these measures in 2013 were also unaffected by biomass utilization treatment ($p = 0.72, 0.69, 0.90$ for height, dbh, and volume, respectively). Rather, the effect of planting year on these metrics of Douglas-fir trees was significant. There are decreasing trends of tree height, dbh, and volume as trees were planted later, but only trees planted in 1978 and 1979 showed statistically significant size reductions.

Similar to the analyses of tree height, dbh, and volume measures, biomass utilization treatment had no effect on any of the tested productivity metrics. The interaction terms between biomass utilization treatment and planting year were consistently non-significant for leaf area, 5-year basal area increments, and growth efficiency (Table 3-3). From reduced models, only 5-year basal area increment and leaf area were affected by planting year. Growth efficiency was affected neither by biomass utilization treatment nor by planting year.
DISCUSSION

Biomass production

The majority of previous studies have reported growth reduction of planted seedlings associated with intensive biomass harvesting and have commonly attributed this to limited nutrient availability. For example, Proe and Dutch (1994) measured a reduction of Sitka spruce seedling growth in whole-tree harvesting treatments 10 years after harvesting in the United Kingdom. They suggested that woody residues reduction increased understory competition and decreased nutrient availability. In Sweden, whole-tree harvesting resulted in the reduction of growth for Norway spruce seedlings 10-15 years after planting (Egnell and Leijon 1999); nitrogen availability was suspected as the reason. Nyland et al. (1979) found that the removal of litter caused the reduction of height growth of Norway spruce 9 years after clearcutting and planting in New York. Foliar N and P concentration represented the nutrients deficiency of those spruce seedlings.

The magnitude of negative impacts of biomass harvesting may change with time and stand developmental stages (Ares et al. 2007). In Sweden, a basal area reduction of Scots pine only became detectable 12 years after whole-tree harvesting (Egnell and Valiger 2003). Such a time lag has been observed at several studies from young stands such as Sitka spruce (Proe et al. 1996) and Norway spruce (Jacobson et al. 2000). However, the planted Douglas-fir at our study site were mature (> 34 years) enough to begin canopy closure associated with the stem exclusion stage. In this stage, nutrient demand is at its peak (Cannell 1989, Ponder Jr. et al. 2012; c.f. Oliver and Larson 1996) and if there are any adverse effects of the utilization treatments on site productivity, the cumulative negative impact on tree growth should have been prominent. Since we observed no clear evidence of nutrient deficiency even after the onset of this developmental stage, our results indicate there is no long-term deterioration of site productivity from biomass harvesting at this site.
One reason for our failure to identify any differences in seedling growth may be that the study site is relatively productive, like the LTSP sites in North America (Powers et al 2005, Ponder Jr. et al. 2012). On nutrient rich sites, a slight reduction in nutrient availability does not always lead to seedling growth reduction (*sensu* Sikström 2004). At our site, Stark (1980) had previously anticipated that the amount of nutrients lost through these different utilization treatments for biomass harvesting would not exceed vegetation demand during stand establishment. The forest floor and mineral soil pools in the study site retain large concentrations of nutrient even after intensive biomass extraction (Harvey et al. 1979).

Secondly, the use of a skyline yarder system for this study’s harvest operations minimized soil disturbance, loss of the forest floor, and soil compaction which are the factors typically thought to adversely impact forest productivity. The indications are that intensive biomass harvesting in this moist, western larch forest type will likely cause no adverse long-term impacts on site productivity (Powers et al. 2005, Page-Dumroese et al. 2010).

**Nutrient concentrations and physiological traits**

Foliar N concentration is an important indicator for assessing the general nutrient condition of a site after biomass harvesting (see Thiffault et al. 2011). Nitrogen is a major limiting factor of tree growth in coniferous stands (Binkley 1991, Vitousek and Howarth 1991, Jurgensen et al. 1997, Himes et al. 2014), and observed growth reduction after intensified biomass utilization is suggested to result from the reduction of N availability (Proe and Dutch 1994, Jacobson et al. 2000, Harrington et al. 2013). Foliar nutrients analyses provide an important tool to evaluate soil nutrient availability (Thiffault et al. 2011). Often, foliar N concentrations correlate with various nitrogen cycling processes such as mineralization and nitrification, representing the quality and quantity of available N of belowground (Pan et al. 2004).
Our results support the hypothesis that increased nutrients loss by biomass harvesting in northern Rocky Mountains was not severe enough to reduce nutrient pools, even at high (removal of all woody biomass down to a 2.5 cm top) utilization levels. Empirical studies suggest that increased biomass extraction does not necessarily reduce N availability. In Pacific coastal forests of Washington, a study of biomass removal showed no difference in the N concentration of Douglas-fir seedlings 5 years after planting (Ares et al. 2007). Thiffault et al. (2006) failed to find any apparent differences of foliar N for three conifer species (black spruce, jack pine, and balsam fir) between whole-tree and stem-only harvesting 15-20 years after clearcutting in the boreal forests of Canada. Even when effects on N concentrations are observed, they appear to be temporary. For example, Olsson et al. (2000) found differences of initial (about 8 years) foliar N concentration for Norway spruce and Scots pine in Sweden; the differences were eliminated in next 8 years.

Foliar C concentration was not affected by biomass utilization treatment. Foliar C concentration measured in this study includes both structural carbohydrates to produce photosynthates and non-structural carbohydrates required for growth. Although the distinction between the two carbohydrates is not available in this study, foliar carbon concentration can represent the ability of trees to produce and use carbohydrate (Oren et al. 1988). If the growth of Douglas-fir trees in our site had been limited by nutrient depletion through biomass harvesting, then the foliar carbon concentration should have been lower in the greatest utilization level (such as the high/unburn treatment unit).

The leaf area of individual trees can reflect the nutrient condition of a site. In this study, biomass utilization treatment levels did not produce difference in either leaf area or basal area increment, suggesting a lack of biomass utilization level effect on nutrient condition. New foliage production is affected by nutrient availability (Gower et al. 1992), and an abundance of plant growth nutrients could increase retention of older foliage (Cannell 1989). Fertilization experiments have demonstrated that leaf area responds strongly to nutrient condition. In North Carolina, Albaugh et al. (1998) found that
maintaining the “optimum nutrient condition” through continuous fertilization increased the leaf area of 8-yr-old loblolly pines (*Pinus taeda* L.) by 61%. Similar results were observed in Australia by Linder (1987), where the leaf area of Monterey pine (*Pinus radiata* D. Don) seedlings was highest in the fertilized treatment 12 years after plantation.

Likewise, if there is any obvious difference of nutrient condition among biomass utilization treatments, basal area increment should be influenced by these treatments. Theoretically, stem wood production has a lower carbon allocation priority than foliar production (Waring and Schlesinger 1985, Colbert et al. 1990, Oliver and Larson 1996); if an individual tree produces insufficient photosynthate, then its basal area increment should respond more sensitively. Although lateral growth of stems is affected by tree size, the outcome of our study seems to be free from a tree size effect on basal area increment, since there was no difference of tree size among biomass utilization treatments. Therefore, we can conclude that nutrient deficiency was not enough to reduce lateral stem growth of Douglas-fir trees.

Several empirical studies testing fertilization impacts have reported that nutrient availability increased GE. (e.g., Linder 1987, Will et al. 2002, Albaugh et al. 2004). Samuelson et al. (2001) and Albaugh et al. (2004) suggested that the GE responded more significantly to nutrient availability than water availability for loblolly pine. However, GE is also determined by leaf area which can be also affected by nutrient condition. Moreover, leaf area and basal area increment are influenced by tree size (Will et al. 2002). Therefore, GE can show very complex responses depending on various conditions. Despite these complexities, we observed a consistent outcome: no differences in leaf area, tree size, nor basal area increment, and consequently, no difference in GE among biomass utilization treatments.

Mason et al. (2012) classified nursery seedling establishment after planting into two phases: the root-soil contact establishment and the free-to-grow phase. Our results suggest that seedlings planted in later years were delayed in reaching the second phase because of intensified understory competition, which resulted in lower height, diameter and volume growth trajectories than for the trees planted earlier. Our
model indicated that there was a significant effect of planting year, which showed reduced height, dbh, and volume accumulation for planted Douglas-fir trees. The decreasing trends of seedling growth rates can be explained by the rapid understory recovery after harvesting. Understory shrub volume at this site recovered to 14 and 37 percent of the preharvest level within two (1976) and four (1978) years after harvesting, respectively (Schmidt 1980). Therefore, it is apparent that the later-planted trees suffered from more intensive competition by understory vegetation. To avoid this outcome, immediate replanting before understory vegetation recovery or the use of vegetation control seems critical.

Delay in seedling diameter, height, and volume growth does not necessarily imply a reduction in site productivity. Egnell and Leijon (1999) wondered whether the observed reduction of stand growth is temporary or permanent. That is, whether intensive biomass utilization caused a reduction in growth potential is critical to our understanding of site impacts. In the present study, planting year proved to have non-significant effects on linear (slope) and quadratic (curvature) contrasts for height and volume growth curves; results were consistent regardless of biomass utilization level (Table 3-4, 3-5, and 3-6). Thus, we conclude that increased understory competition due to late planting led not to the reduction of growth potential of seedlings, but to a temporal retardation of seedlings in reaching the rapid growth rate stage.

There are still knowledge gaps in the consequence of biomass harvesting. Since this study tested only three kinds of biomass harvesting scenarios, other forms of biomass harvesting (e.g., stump removal) could yield different outcomes. In contrast with skyline yarder system used in this study, ground-based logging system can cause a detrimental consequence on soil productivity through compaction or soil displacement (Page-Dumroese et al. 2010). The impacts of biomass harvesting on site productivity may also differ from post-harvesting treatment such as fuel treatment and slash disposal. Results will likely be different on sites with varying site quality, other nutrient (e.g., K, P, and Ca) limitations, climate, soil properties, vegetation, and disturbance regimes. Therefore, localized and multidisciplinary long-term
experimental efforts are essential to fill knowledge gaps, and to avoid negative impacts of intensive biomass utilization.

We conclude that intensive biomass utilization for bioenergy production had no long-term impact on site productivity of our northern Rocky Mountains study site. Foliar C and N concentrations were not significantly influenced by any of the treatments, implying biomass harvesting is unlikely to cause the adverse long-term impacts on site productivity in moist, western larch forests. Additionally, none of the growth variables were significantly affected by biomass utilization treatments. Rather, only planting year was significant in determining tree mean height, dbh, basal area increment, and total leaf area. However, the delay owing to late-planting does not seem to alter the growth trajectory curve of the seedlings. This study shows the great value of long-term studies of biomass harvesting and productivity.

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REFERENCES


Table 3-1. Design of the utilization treatments within harvesting units (from Benson and Schlieter 1980; Shearer and Schmidt 1999; Shearer and Kempf 1999).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Max. size of retained woody materials(^1)</th>
<th>Post-harvest treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>High-unburn (H_U)</td>
<td>2.5 cm × 2.4 m</td>
<td>Slashed/unburned</td>
</tr>
<tr>
<td>Low-burn (L_B)(^2)</td>
<td>14.0 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
<tr>
<td>Medium-burn (M_B)</td>
<td>7.6 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
</tbody>
</table>

\(^1\)Live and dead, standing and down logs (small-end diameter × length); for dead down logs, they were removed if 1/3 sound.

\(^2\)Followed the United States Forest Service standards in 1974.
Table 3-2. Mean (standard error) of foliar N and C concentrations, tree height, dbh, and volume, leaf area, 5-year basal area increment (5-yr BA Inc), and growth efficiency (GE) for planted Douglas-fir trees (1976-1979), 39 years after harvesting at Coram Experimental Forest.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Foliar N (% )</th>
<th>Foliar C (%)</th>
<th>Height (m)</th>
<th>Dbh (cm)</th>
<th>Volume (m$^3$)</th>
<th>Leaf Area (m$^2$)</th>
<th>5-yr BA Inc (cm$^2$)</th>
<th>GE (cm$^2$/m$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>High-unburn (H_U)</td>
<td>0.84 (0.02)</td>
<td>50.1 (0.13)</td>
<td>7.40 (0.34)</td>
<td>11.8 (0.6)</td>
<td>0.055 (0.006)</td>
<td>27.2 (2.4)</td>
<td>35.4 (3.4)</td>
<td>1.31 (0.05)</td>
</tr>
<tr>
<td>Low-burn (L_B)</td>
<td>0.77 (0.01)</td>
<td>50.2 (0.12)</td>
<td>9.23 (0.22)</td>
<td>14.0 (0.4)</td>
<td>0.073 (0.005)</td>
<td>34.3 (2.1)</td>
<td>49.8 (3.9)</td>
<td>1.39 (0.04)</td>
</tr>
<tr>
<td>Medium-burn (M_B)</td>
<td>0.74 (0.02)</td>
<td>49.7 (0.11)</td>
<td>9.00 (0.20)</td>
<td>14.3 (0.4)</td>
<td>0.073 (0.004)</td>
<td>33.3 (2.3)</td>
<td>42.3 (3.3)</td>
<td>1.25 (0.04)</td>
</tr>
<tr>
<td>Overall treatments</td>
<td>0.79 (0.01)</td>
<td>50.0 (0.07)</td>
<td>8.59 (0.15)</td>
<td>13.5 (0.3)</td>
<td>0.068 (0.003)</td>
<td>31.7 (1.4)</td>
<td>42.6 (2.1)</td>
<td>1.32 (0.03)</td>
</tr>
</tbody>
</table>
Table 3-3. Test statistics for the foliar N and C concentrations, leaf area, 5-year basal area increment, and growth efficiency of planted Douglas-fir trees at Coram Experimental Forest.

<table>
<thead>
<tr>
<th>Response variable / Variance source</th>
<th>df</th>
<th>Error df</th>
<th>Model with interaction</th>
<th>df</th>
<th>Error df</th>
<th>Model without interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foliar N concentration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>2.988 0.251</td>
<td>2</td>
<td>2</td>
<td>2.782 0.264</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>2.456 0.130</td>
<td>15</td>
<td>2</td>
<td>2.828 0.074</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>0.709 0.651</td>
<td>15</td>
<td>2</td>
<td>0.709 0.651</td>
</tr>
<tr>
<td>Foliar C concentration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.631 0.613</td>
<td>2</td>
<td>2</td>
<td>0.627 0.615</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>0.670 0.576</td>
<td>15</td>
<td>2</td>
<td>1.041 0.403</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>0.190 0.972</td>
<td>15</td>
<td>2</td>
<td>0.190 0.972</td>
</tr>
<tr>
<td>Leaf area</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.018 0.614</td>
<td>2</td>
<td>2</td>
<td>0.629 0.614</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>8.688 0.005**</td>
<td>15</td>
<td>2</td>
<td>7.605 0.003**</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>1.777 0.210</td>
<td>15</td>
<td>2</td>
<td>1.777 0.210</td>
</tr>
<tr>
<td>5-year basal area increment</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>1.946 0.339</td>
<td>2</td>
<td>2</td>
<td>1.986 0.335</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>5.713 0.018*</td>
<td>15</td>
<td>2</td>
<td>5.477 0.010*</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>1.420 0.305</td>
<td>15</td>
<td>2</td>
<td>1.357 0.423</td>
</tr>
<tr>
<td>Growth efficiency</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>1.484 0.403</td>
<td>2</td>
<td>2</td>
<td>1.357 0.423</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>0.240 0.866</td>
<td>15</td>
<td>2</td>
<td>0.241 0.867</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>0.932 0.517</td>
<td>15</td>
<td>2</td>
<td>0.932 0.517</td>
</tr>
</tbody>
</table>

Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05.
Table 3-4. Analysis of variance table for repeated measures of planted Douglas-fir tree height.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Model with interaction</th>
<th>Model without interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Error df</td>
<td>F value</td>
</tr>
<tr>
<td>Whole-unit analysis (Z)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1</td>
<td>237</td>
<td>22.741</td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.817</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>11.301</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>0.786</td>
</tr>
<tr>
<td>Analysis of repeated measure factor</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Linear (B) contrast</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1</td>
<td>237</td>
<td>64.642</td>
</tr>
<tr>
<td>Contrast × biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.262</td>
</tr>
<tr>
<td>Contrast × planting year</td>
<td>3</td>
<td>9</td>
<td>2.523</td>
</tr>
<tr>
<td>Contrast × treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>1.095</td>
</tr>
<tr>
<td>Quadratic (Q) contrast</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1</td>
<td>237</td>
<td>0.158</td>
</tr>
<tr>
<td>Contrast × biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.201</td>
</tr>
<tr>
<td>Contrast × planting year</td>
<td>3</td>
<td>9</td>
<td>1.498</td>
</tr>
<tr>
<td>Contrast × treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>0.638</td>
</tr>
</tbody>
</table>

Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05.
Table 3-5. Analysis of variance table for repeated measures of planted Douglas-fir tree diameter at breast height.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Model with interaction</th>
<th></th>
<th>Model without interaction</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>df</td>
<td>Error df</td>
<td>F value</td>
<td>p-value</td>
</tr>
<tr>
<td>Whole-unit analysis (Z)</td>
<td></td>
<td>df</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1</td>
<td>237</td>
<td>237</td>
<td>29.378</td>
<td>&lt;0.0001***</td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>0.087</td>
<td>0.920</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>9</td>
<td>6.401</td>
<td>0.016*</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>9</td>
<td>0.582</td>
<td>0.737</td>
</tr>
</tbody>
</table>

Analysis of repeated measure factor

Linear (B) contrast

| Mean                                        | 1  | 237| 237      | 45.800   | <0.0001*** | 237| 237      | 57.821  | <0.0001*** |
| Contrast × biomass utilization treatment     | 2  | 2  | 2        | 0.035   | 0.966   | 2  | 2        | 0.042   | 0.960   |
| Contrast × planting year                     | 3  | 9  | 9        | 5.872   | 0.020*  | 15 | 15       | 5.960   | 0.008** |
| Contrast × treatment × planting year         | 6  | 9  | 9        | 0.849   | 0.567   | 15 | 15       | 0.966   | 0.097   |

Quadratic (Q) contrast

| Mean                                        | 1  | 237| 237      | 51.156   | <0.0001*** | 237| 237      | 61.428  | <0.0001*** |
| Contrast × biomass utilization treatment     | 2  | 2  | 2        | 0.032   | 0.969   | 2  | 2        | 0.039   | 0.963   |
| Contrast × planting year                     | 3  | 9  | 9        | 2.970   | 0.097   | 15 | 15       | 2.762   | 0.081   |
| Contrast × treatment × planting year         | 6  | 9  | 9        | 1.310   | 0.352   | 15 | 15       | 0.737   | 0.016*  |

Significance codes:  0 < *** < 0.001 < ** < 0.01 < * < 0.05.
Table 3-6. Analysis of variance table for repeated measures of planted Douglas-fir tree volume.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>df</th>
<th>F value</th>
<th>p-value</th>
<th>df</th>
<th>F value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole-unit analysis (Z)</td>
<td>1</td>
<td>237</td>
<td>125.964</td>
<td>&lt;0.001***</td>
<td>237</td>
<td>146.742</td>
<td>&lt;0.0001***</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.358</td>
<td>0.736</td>
<td>2</td>
<td>0.440</td>
<td>0.695</td>
</tr>
<tr>
<td>Planting year</td>
<td>3</td>
<td>9</td>
<td>10.688</td>
<td>0.004**</td>
<td>15</td>
<td>11.223</td>
<td>0.001***</td>
</tr>
<tr>
<td>Treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>0.802</td>
<td>0.595</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Analysis of repeated measure factor

Linear (B) contrast

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>df</th>
<th>F value</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>1</td>
<td>237</td>
<td>154.377</td>
<td>&lt;0.0001***</td>
<td>237</td>
<td>170.265</td>
<td>&lt;0.0001***</td>
</tr>
<tr>
<td>Contrast × biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.017</td>
<td>0.983</td>
<td>2</td>
<td>0.018</td>
<td>0.982</td>
</tr>
<tr>
<td>Contrast × planting year</td>
<td>3</td>
<td>9</td>
<td>3.130</td>
<td>0.088</td>
<td>15</td>
<td>2.220</td>
<td>0.131</td>
</tr>
<tr>
<td>Contrast × treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>2.092</td>
<td>0.165</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Quadratic (Q) contrast

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>df</th>
<th>F value</th>
<th>p-value</th>
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</thead>
<tbody>
<tr>
<td>Mean</td>
<td>1</td>
<td>237</td>
<td>56.435</td>
<td>&lt;0.0001***</td>
<td>237</td>
<td>61.101</td>
<td>&lt;0.0001***</td>
</tr>
<tr>
<td>Contrast × biomass utilization treatment</td>
<td>2</td>
<td>2</td>
<td>0.775</td>
<td>0.563</td>
<td>2</td>
<td>0.821</td>
<td>0.549</td>
</tr>
<tr>
<td>Contrast × planting year</td>
<td>3</td>
<td>9</td>
<td>1.072</td>
<td>0.414</td>
<td>15</td>
<td>1.079</td>
<td>0.390</td>
</tr>
<tr>
<td>Contrast × treatment × planting year</td>
<td>6</td>
<td>9</td>
<td>0.832</td>
<td>0.577</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significance codes:  0 < *** < 0.001< ** < 0.01 < * < 0.05.
Figure Captions

Figure 3-1. Foliar (a) nitrogen and (b) carbon concentrations of planted Douglas-fir seedlings at Coram Experimental Forest 39 years after harvest. The descriptions of treatment codes are listed in Table 3-1.

Figure 3-2. Douglas-fir tree responses to the biomass utilization treatments 39 years after harvest; (a) leaf area, (b) five-year basal area increment, and (c) growth efficiency. Treatment codes are described in Table 3-1.
Figure 3-1.
Figure 3-2.
CHAPTER 4

LONG-TERM TREE RESPONSES TO REGENERATION CUTTING AND UNDERSTORY TREATMENT IN THE NORTHERN ROCKIES: AN ANALOGY TO VARIABLE-RETENTION HARVESTING

ABSTRACT

Responses of regeneration and retained trees to classical regeneration cuttings (clearcut, group selection, and shelterwood with reserves) can be analyzed to analogously predict the consequences of variable-retention harvesting (VRH). A historical research site in the northern Rocky Mountains was re-measured to evaluate the potential long-term effects of VRH. Thirty eight years after harvest (in 2012), responses of the regenerated and retained trees to regeneration cuttings combined with post-harvest understory treatments (understory protected, understory removed, and understory broadcast-burned) were evaluated. Compared to the overstory-free condition of the clearcut, shelterwood and group selection overstory influences reduced the basal area of regeneration by 69% and 50% (p=0.032), respectively. In addition, the shelterwood reserves reduced regenerated tree growth efficiency by 0.79 cm$^2$ m$^{-2}$ (p=0.005), and recent 5-year basal area increment by 67.8 cm$^2$ (p<0.001). Post-harvest understory treatments (i.e. burning) increased the regeneration density, but decreased tree size. As a result, these treatment effects on regeneration basal area zeroed out. Although a negative correlation in basal area increment between retained trees and regenerated trees was detected at individual tree levels, we failed to observe any correlations at the stand level due to different stand densities. In spite of the considerable regeneration growth reduction in shelterwood, advance regeneration can play an important role in alleviating the negative impacts of retained overstory trees on the growth of the new cohort.
INTRODUCTION

Conservation of biodiversity is increasingly emphasized in contemporary silviculture, and has become a fundamental element for ecological sustainable forest management (Seymour and Hunter Jr. 1999, Lindenmayer and Franklin 2002, Carey 2003). Since structural heterogeneity plays a critical role in forest biodiversity and other ecosystem functions, creating and promoting complex structure has become a major goal in silvicultural prescriptions (Bunnell et al. 1999, Mitchell and Beese 2002). Natural disturbances generate structural and compositional complexity (Drever et al. 2006); forest scientists recognize that even stand-replacing natural disturbances create higher structural variability than conventional timber harvesting (Mitchell and Beese 2002, Palik et al. 2014). Mimicking natural disturbance processes has risen in prominence as a silvicultural implementation goal (Seymour and Hunter Jr. 1999). Strategies such as variable-retention harvesting (e.g., Franklin et al. 1997), green tree retention (e.g., Rose and Muir 1997), irregular shelterwood (e.g., Raymond et al. 2009), and multi-aged management (e.g., O’Hara 2014) have been developed (or re-evaluated) and promoted in response to this goal.

Variable-retention harvesting (VRH) refers to a cutting method that maintains live trees as the structural elements for prescribed ecological objectives (Franklin et al. 1997, Helms 1998). Retained structures provide refugia for surviving species, contribute to reestablishment of stand structure, and help connect separate habitats (Franklin et al. 1997). Since VRH can theoretically utilize a wide range of retention levels, VRH is often advocated to meet management objectives related to maintenance, enhancement, or restoration of structural complexity (Franklin et al. 1997, Palik et al. 2014). Defining the specific number, species, sizes and spatial distribution of retained trees become fundamental issues in the silvicultural prescription development (Franklin et al. 1997, Franklin et al. 2007).

Because it represents a significant departure from traditional silvicultural systems, many questions have been posed regarding the impacts of VRH on subsequent stand dynamics (Maguire et al. 2006). One
criticism of VRH is that the retained overstory structure (primarily live trees) can potentially limit the establishment and growth of regeneration (Palik et al. 2014). A number of studies have argued that retained canopy trees reduce the new cohort’s growth through the competition for limited resources (e.g., Birch and Johnson 1992, Long and Roberts 1992, Rose and Muir 1997, Acker et al. 1998, Elfving and Jakobsson 2006, Temesgen et al. 2006). However, new cohort responses should differ depending on overstory tree spatial distribution (Coates 2000). Considering flexible attribute of VRH, it may be possible to ameliorate reduced regeneration growth by manipulating overstory retention or understory vegetation control to reduce competition (Palik et al. 2014). Unfortunately, too little is known about retention level effects, spatial pattern effects, post-harvest vegetation treatment effects (and their interactions) to provide sufficient information for VRH prescription decision making (Zenner et al. 1998, Maguire et al. 2006).

Exploring the long-term impact of VRH on site productivity can be conducted via several approaches including chronosequence, retrospective, simulation approaches, and empirical experiment. Among those approaches, the use of empirical trials can provide significant advantages: 1) complete control of treatments, 2) control of errors, 3) definitive conclusion within a range of the experimental design, and 4) ability of quantifying uncertainty (Powers et al. 1994). Thus, long-term empirical assessment has been strongly stressed from the various fields of ecosystem-oriented science (e.g., Likens 2004, Powers 2006, Puettmann et al. 2008). However, conducting and maintaining such long-term experimental trials is often expensive, and is time- and resource-consuming (Reinhardt et al. 2010). Furthermore, the infrastructure for addressing the impact of VRH is insufficient, especially in northern Rocky Mountain forests.

Relying solely on newly established experiments which require long post-treatment response periods may not be necessary. Under certain circumstances, we can infer the legacy of several silvicultural trials to VRH indirectly. For example, a shelterwood with reserves is structurally similar to a dispersed overstory VRH (Maguire et al. 2006). Group selection gaps are comparable to the openings created by
aggregated overstory VRH. Conventional silvicultural systems may not have been applied originally with recognition of the multiple ecological functions that structural retention achieves (Franklin et al. 2007) or to achieve that objective, but they can closely resemble structural conditions created by VRH, and can therefore enables us to make conjectures about consequences of VRH.

Northwestern Montana’s Coram Experimental Forest provides an opportunity to address the impacts of overstory conditions similar to VRH but created by conventional harvesting strategies. In the mid-1970s, Coram Experimental Forest was the site of a multidisciplinary research effort to understand the ecological consequences of increased biomass utilization levels under three different regeneration cuttings (clearcut, group selection, and shelterwood) in mature forests of the northern Rocky Mountains (Barger 1980). This research site has been conserved without any additional cutting, providing an opportunity to compare the consequences of clearcut, group selection, and shelterwood with reserves, approximately four decades after harvesting. Because the group selection and shelterwood systems were never followed by subsequent cutting, this one-time harvest simulates (in addition to the clearcut) aggregated and dispersed retention cuttings. These treatments serve as VRH analogues that can provide useful information about the long-term effects of tree retention on understory dynamics.

Here, we investigated the stand- and individual tree-level long-term responses of regeneration cuttings. For this, we tested the following hypotheses:

1. Since the overstory tree retention level is highest in the shelterwood, the growth and vigor of natural regeneration in the shelterwood should be the lowest among the regeneration cuttings.

2. If the post-harvest understory treatments positively influenced the shrub biomass production (recovery), then, in turn, shrub biomass should negatively affect the responses of natural regeneration. Thus, the understory protected treatment should result in the lowest yield of regeneration.
3. In the shelterwood, growth of retained trees compensate for reduced growth in natural regeneration.

This study can provide insight to regeneration and retained tree responses to VRH and post-harvest understory treatments. The authors anticipate the results of this study can be analogously utilized to evaluate the responses for open gaps in aggregated retention (via group selection responses) and for dispersed retention (via shelterwood responses), and contrasted with the open control (clearcut).

METHODS

Study area

This study was conducted in western larch (*Larix occidentalis* Nutt.) forests at Coram Experimental Forest (CEF). The CEF is located in northwest Montana, about 9 km south of the Glacier National Park. The study plots were established on east slopes in Upper Abbot Creek Basin (48°25′ N, 113°59′ W). The elevation and slope of the study area range from 1,195 to 1,615 m, and from 30% to 80%, respectively. Soils of the CEF consist of Precambrian sedimentary rock, glacial till, and thin surface volcanic ash, classified into the loamy-skeletal soils on materials weathered from impure limestone and argillite (Klages et al. 1976).

The climate of the study area is modified Pacific maritime type (Adams et al. 2008). The annual precipitation ranges from 890 to 1,270 mm (mean: 1,076 mm; Farnes et al. 1995). The majority of precipitation occurs as a form of snow during winter. The mean annual temperature ranges from 2 °C to 7 °C (Hungerford and Schlieter 1984), mean temperatures in summer and winter temperatures are 6 °C, and –7 °C, approximately (Adams et al. 2008). The length of growing season near Abbot Creek is 81 days.
The forest cover type of the study area is the western larch cover type (Society of American Foresters Cover Type 212, Eyre 1980). Western larch, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western hemlock, (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don) are mixed with several broadleaf tree species such as paper birch (*Betula papyrifera* Marshall), black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa* (Torr. & A. Gray ex Hook.) Brayshaw), and quaking aspen (*Populus tremuloides* Michx.). Major shrub species of the study area include Rocky Mountain maple (*Acer glabrum* Torr.), Saskatoon serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.), Sitka alder (*Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) Á. Löve & D. Löve), mallow ninebark (*Physocarpus malvaceus* (Greene) Kuntze), dwarf rose (*Rosa gymnocarpa* Nutt.), huckleberry (*Vaccinium membranaceum* Douglas ex Torr., *Vaccinium myrtilloides* Michx.), and white spirea (*Spiraea betulifolia* Pall.). The dominant habitat type is the subalpine fir/queencup (*Clintonia uniflora* (Menzies ex Schult. & Schult. f.) Kunth) (ABLA/CLUN) habitat type (Pfister et al. 1977).

**Experimental design**

The basic experimental design of this study was the split-plot design, with three regeneration cutting treatments (whole-plots; shelterwood, group selection, and clearcut) and three post-harvest understory treatments (sub-plots). The post-harvest understory treatments are understory protected (U_P), understory removed (U_R), and understory broadcast burned (U_B). Post-harvest treatment prescription details are described in Table 4-1. The entire experimental units were replicated twice according to elevation: 1,195 m - 1,390 m for the lower block, and 1,341 m - 1,615 m for the upper block.

Trees were harvested in the fall of 1974, and were extracted via a running skyline yarder. Across the lower and upper blocks, respectively, shelterwood units were 14.2 to 8.9 ha in size; clearcut units were 5.7 to 6.9 ha in size. For the group selection, eight cutting gaps were harvested. The average cut size in
group selection units was 0.3 ha, ranging from 0.1 to 0.4 ha. In the shelterwood, 36.0% of overstory trees (based on volume) were retained, whereas 0.7% of overstory tree volume was retained in group selection openings and clearcut units on average (Table 4-2). Subsequent broadcasting burning treatment was applied in September 1975. However, cool and wet weather conditions prevented the lower shelterwood unit from being burned (Artley et al. 1978, Schmidt 1980).

In the shelterwood and clearcut, ten permanent sample points were systematically established in 5×2 grids within each sub-plot (i.e., post-harvest understory treatment sub-plots), at 30.5 m spacing. In the group selection units, five permanent points were located in each cutting gap at various distances, according to the sizes of gaps. Therefore, a total of 40 permanent points were installed in each regeneration cutting unit per replicate.

Data collection

To test the hypotheses, stand-level responses including regenerated tree basal area (BA), density, and quadratic mean diameter (QMD) and individual tree-level responses such as recent 5-year BA increment, and growth efficiency (GE) were assessed. For the second hypothesis, the evaluation of shrub biomass was added. For hypothesis 3, tree response variables for retained trees in shelterwood unit, including the initial 5-year BA increment and 38-year BA increment, were measured.

For the evaluation of stand-level responses (BA, density, and QMD), tree dbh was recorded in a nested circular plot system in 2012. Centering the permanent sample point, trees larger than 25 cm dbh were measured in a 12.62 m (1/20th ha) radius plot. Trees less than 25 cm and 10 cm dbh were measured in 5.64 m (1/100th ha) and 2.52 m (1/500th ha), respectively. Only trees taller than breast height (1.37 m) were measured.
To assess the individual-level responses, naturally regenerated trees were also sampled based on permanent sampling points. The closest one or two naturally regenerated dominant Douglas-fir trees (mean: 15.0 cm, range: 6.5 - 32.8 cm diameter at breast height [1.37 m]; dbh) from permanent sampling points were selected. A total of 150 regenerated Douglas-fir trees were selected. Dbh of sample trees was measured in 2012. Two perpendicular tree cores at breast height and foliage samples were taken from each sample tree. For retained trees in shelterwood units, 20 Douglas-fir trees from each understory treatment sub-plot were selected in 2013, avoiding the trees near the treatment edge. Dbh was measured, and two core samples were taken perpendicularly at breast height.

Bark thickness, recent 5-year tree ring growth, and sapwood length were measured from tree cores by digital calipers to nearest 0.01 mm. From the measurements, recent 5-year basal area (BA) increment, cross-sectional sapwood area were calculated. For retained tree samples, 5-year basal area increment after harvesting (i.e., BA increment from 1974-1979; hereafter, initial 5-year BA increment) was also estimated.

Growth efficiency was used to estimate tree vigor. It represents production of stem volume per unit leaf area, thus, it is generally expressed the ratio of a periodic volume growth to total surface leaf area (Waring 1983). Basal area increment is a common replacement for stem volume growth in GE (e.g., Waring et al. 1980, O’Hara 1988, Fajardo et al. 2007). In this study, the GE was expressed as the ratio of 5-year basal area increment to total leaf area (unit: cm² m⁻²). Total leaf area was estimated from cross-sectional sapwood area (Gower et al. 1987), according to the log-linear relationship between the cross-sectional sapwood area of stem and total amount of foliage (Shinozaki et al. 1964).

Shrub biomass was estimated from measurements of canopy cover or root collar diameter. In 1976 (2 years after harvesting), and 1984, shrub canopy cover was measured from every permanent point using a nested quadrat plot system. Shrubs taller than 2.5 m, taller than 1.5 m and shorter than 2.5 m, and shorter than 1.5 m were measured from 25 m², 9 m², and 2.25 m²-square-plots, respectively. We assumed shrub
crowns were cylindroids, thus, we measured height and two diameters of the ellipse. In 2012, another nested circular sampling system was applied for shrub measurement. Root-collar diameter of each woody shrub species was measured by caliper. The data were collected from four (3rd, 4th, 7th, and 8th) out of ten permanent points. Shrubs taller than 1.0 m height were sampled using 1.78 m radius plots; shorter shrubs were sampled using 0.80 m radius plots. Shrub biomass in 1976 (“two-year shrub biomass”) and biomass increment during 1976 to 1984 (year 2-10; “eight-year shrub biomass increment”) were calculated through equations converting canopy volume to biomass (in situ regression derived in 1974 via destructive sampling; W. Schmidt, unpublished data). Shrub biomass in 2012 was calculated using Brown’s (1976) biomass equations for northern Rocky Mountain shrub species.

Data analysis

Since the experimental design of this study was a split-plot design, a mixed-effects model was used. The basic model form is as:

\[
y_{ijk} = \mu + \alpha_i + B_k + \epsilon_{(1)ik} + \beta_j + \alpha_i\beta_j + \epsilon_{(2)ijk} + \epsilon_{ijk1}
\]

where \(y_{ijk}\) = response variable, \(\mu\) = grand mean, \(\alpha_i\) = effect of regeneration cutting (whole-plot effect), \(B_k\) = block effect (random effect), \(\beta_j\) = effect of post-harvest understory treatment (sub-plot effect), \(\alpha_i\beta_j\) = interaction between whole-plot and sub-plot effects, and \(\epsilon_{(1)ik}\), \(\epsilon_{(2)ijk}\), and \(\epsilon_{ijk1}\) are the whole-plot error, sub-plot error, and the variation among sampling plots in a subplot, respectively. For the retained trees in shelterwood units, a simpler model was constructed since there is no regeneration cutting effect. If a significant treatment effect was detected, then linear contrasts among regeneration cuttings (clearcut vs. shelterwood, clearcut vs. group selection, and group selection vs. shelterwood) and understory treatments...
were tested. To assess the understory treatment effects, the understory removal and understory burning treatments were compared against the understory protected treatment (i.e., U_P vs. U_R and U_P vs. U_B).

To test hypothesis 1, regenerated tree basal area (BA), density, and quadratic mean diameter (QMD), as well as individual tree recent 5-year BA increment and growth efficiency (GE), were tested as the response variables. Individual tree dbh was added into the model as a linear covariate to account for the size-effect when BA increment and GE were tested. For the second hypothesis, Pearson’s correlation tests were conducted between shrub biomass and those tree response variables at the plot level. For hypothesis 3, tree response variables for retained trees in the shelterwood unit, including the initial 5-year BA increment and 38-year BA increment, were compared among the post-harvest treatments. These variables were also compared with regenerated trees using correlation tests.

All analyses were conducted via R (R Development Core Team 2008). The package nlme (Pinheiro et al. 2014) was used to fit mixed effects models. Linear contrasts among regeneration cuttings and post-harvest treatments were investigated via the multcomp (Hothorn et al. 2014) package.

RESULTS

Regeneration tree responses to regeneration cuttings

Regeneration BA was significantly different by regeneration cutting treatment in 2012 (p=0.032), but was not affected by retained tree density (p=0.317; Table 4-3, Table 4-4, and Figure 4-1). There was strong evidence that regeneration cutting and post-harvest treatment interaction terms were the significant factors affecting regenerated tree QMD (p<0.001) and 5-year BA increment (p=0.048) in 2012. Regeneration growth efficiency (GE; Douglas-fir) differed by regeneration cutting treatment (p=0.053, p=0.043 from the model without interaction term).
The shelterwood with reserves reduced regeneration BA and GE by 11.81 m² ha⁻¹ (SE: 1.42 m² ha⁻¹; p<0.001) and 0.79 cm² m⁻² (SE: 0.14 cm² m⁻²; p<0.001) compared to the clearcut. A difference in regeneration QMD was detected only in the U_R treatment, where the shelterwood decreased the QMD by 6.44 cm (SE: 1.39 cm; p<0.001) versus the clearcut. On the other hand, differences in 5-year BA increment between the shelterwood and clearcut were observed in the U_B and U_P treatments. In the U_B treatment, shelterwood reduced 5-year BA increment by 67.8 cm² (SE: 19.9 cm²; p=0.005) and by 44.0 cm² (SE: 12.2 cm²; p=0.002) in the U_P treatment.

Similar to the comparison between clearcut and shelterwood, regeneration BA and GE showed similar patterns in a contrast between group selection and shelterwood. We found a trend for shelterwood reducing the regeneration BA by 3.50 m² ha⁻¹ (SE: 1.42 m² ha⁻¹; p=0.064) less than group selection, and there was strong evidence that the shelterwood decreased the regeneration GE by 0.67 cm² m⁻² (SE: 0.14 cm² m⁻²; p<0.001) versus the group selection. Moreover, the 5-year BA increment of regenerated Douglas-fir was reduced in the shelterwood U_B treatment by 72.5 cm² (SE: 20.0 cm²; p=0.002) versus the group selection. In contrast, the shelterwood U_P treatment produced a regeneration QMD that was higher than group selection by 3.2 cm (SE: 1.1 cm; p=0.033).

Between clearcut and group selection, only regeneration BA differed. Regeneration BA in the group selection was 8.31 m² ha⁻¹ (SE: 1.39 m² ha⁻¹; p<0.001) less than in the clearcut, showing that seedlings in the group selection gaps were indeed affected by retained trees although they were spatially segregated from them. All other contrasts were not statistically significant.

**Regeneration responses to post-harvest treatment and shrub layer**

Regeneration density and QMD were influenced by the post-harvest treatment (p=0.001, p<0.0001, respectively; Table 4-4 and Figure 4-1), whereas regeneration BA (p=0.198) and GE (p=0.104; p=0.111 from the model without interaction term) were not affected. Although an interaction term between
regeneration cutting and post-harvest treatment for recent 5-year BA increment was significant, we did not detect any significant differences in the tested contrasts.

Differences among the post-harvest treatments were primarily observed in the contrast between the U_P and the U_B treatments. The U_B treatment increased tree density by 2710 trees ha\(^{-1}\) (SE: 834 trees ha\(^{-1}\); p=0.004) relative to the U_P treatment across the regeneration cuttings. In contrast, the QMDs of U_B treatment in clearcut, group selection, and shelterwood units were 6.6 cm (SE: 1.7 cm; p<0.001), 6.2 cm (SE: 1.7 cm; p=0.001), and 11.3 cm (SE: 1.7 cm; p<0.001) less than in the U_P treatment, respectively. A difference of post-harvest effects between the U_P treatment and the U_R treatment was only detected in QMD in the shelterwoods. The QMD in the U_R treatment was 7.9 cm (SE: 1.3, p<0.001) less than in the U_P treatment.

Shrub layer biomass for clearcut, group selection, and shelterwood 38 years after harvesting were 6.85 Mg ha\(^{-1}\) (SE: 1.43 Mg ha\(^{-1}\)), 10.40 Mg ha\(^{-1}\) (SE: 2.67 Mg ha\(^{-1}\)), and 5.37 Mg ha\(^{-1}\) (SE: 1.85 Mg ha\(^{-1}\)), respectively. Shrub biomass in 2012 was not affected by either regeneration cutting treatment (p=0.410) or post-harvest understory vegetation treatment (p=0.184). On the other hand, shrub biomass immediately after harvesting (two years after harvesting, in 1976) was 0.75 Mg ha\(^{-1}\) (SE: 0.15 Mg ha\(^{-1}\)), 0.69 Mg ha\(^{-1}\) (SE: 0.18 Mg ha\(^{-1}\)) and 1.91 Mg ha\(^{-1}\) (SE: 0.77 Mg ha\(^{-1}\)) for clearcut, group selection, and shelterwood. Shrub biomass two years after harvesting was only affected by the post-harvest treatment (p<0.001). Specifically, the U_P treatment retained approximately 2.0 times (p<0.001) the shrub biomass than the U_B treatment. However, the eight-year (years 2-10) shrub biomass increment was not affected by either regeneration cutting (p=0.205) or post-harvest treatment (p=0.580).

Regeneration BA in 2012 was not correlated with any shrub measurements including shrub biomass in 2012 (Pearson’s correlation tests at plot-level, p=0.748), nor two years after treatment (in 1976, p=0.687), nor the 8 years after that (1976-1984; p=0.939). In addition, there was no correlation between regeneration density or QMD in 2012 versus shrub biomass in 2012 (p=0.454 and p=0.257, respectively).
However, regeneration density in 2012 was negatively correlated with shrub biomass two years after harvesting ($r=-0.339; p<0.001$) and the eight-year shrub biomass increment ($r=-0.206; p=0.022$). On the other hand, regeneration QMD in 2012 was positively correlated with the two-year shrub biomass ($r=0.334; p<0.001$) and the eight-year shrub biomass increment ($r=0.257; p=0.004$).

**Retained tree responses and relationship with regenerated tree**

Thirty eight years after harvesting, the mean BA, tree density, and QMD of shelterwood retained trees were 18.64 m$^2$ ha$^{-1}$ (SE: 1.13 m$^2$ ha$^{-1}$), 122 trees ha$^{-1}$ (SE: 9 trees ha$^{-1}$), and 45.90 cm (SE: 0.96 cm; Table 4-5), respectively. Recent 5-year BA increment ($p<0.0001$), GE ($p=0.0032$), and initial 5-year BA increment ($p<0.0001$) of retained trees were affected by tree diameter, implying significant size-effects on these attributes. Diameter was positively related with both recent (coefficient: 1.38), and initial 5-year BA increment (coefficient: 2.09), whereas it was negatively related with GE (coefficient: -0.008). However, the retained overstory tree volume immediately after harvesting had no significant impact on any of those responses ($p=0.7918$ for 5-year BA increment, $p=0.4170$ for GE, and $p=0.3374$ for initial 5-year BA increment, respectively).

There was moderate evidence of a post-harvest understory treatment effect on GE ($p=0.052$) and strong evidence of its effect on the initial 5-year BA increment ($p=0.010$) for the retained Douglas-fir trees. Meanwhile, there was weak evidence for post-harvest treatment effects on the recent 5-year ($p=0.080$) and 38-year BA increment ($p=0.080$, Table 4-6). The U_P treatment increased GE by 0.15 cm$^2$ m$^{-2}$ (SE: 0.07 cm$^2$ m$^{-2}$) over the U_B treatment ($p=0.049$). However, there was no difference in the initial 5-year BA increment between the U_P and U_R treatment ($p=0.099$). Instead, the initial 5-year BA increment in the U_B treatment was 31.7 cm$^2$ ($p=0.009$) less than in the U_P treatment for the same tree size.
Although we did not find evidence of a post-harvest treatment effect on individual-tree BA increment with either retained trees (Table 4-6) or regenerated trees (Table 4-4), we found a trend of the treatment impacts between these groups (Figure 4-2). In the U_R treatment, the largest positive effect (633.6 cm², SE: 82.2 cm²) on BA increment of the retained trees accompanied the largest negative impact on regenerated trees (-755.1 cm², SE: 101.6 cm²). In contrast, the least positive effect on retained trees observed in the U_B treatment (467.6 cm², SE: 89.6 cm²), resulted in the least negative impact on regenerated tree BA increment (-296.8 cm², SE: 182.2 cm²). The U_P treatment had a moderate impact on both retained and regenerated Douglas-fir tree BA increment (581.0 cm², SE: 78.7 cm², -726.8 cm², SE: 101.6 cm², respectively).

At the stand level, the relationship between retained tree BA and regeneration BA was not statistically significant (p=0.702). Although there was only weak evidence for a difference in retained tree BA among the post-harvest treatments (p=0.089), the combined BA of overstory plus regenerated trees showed a significant difference among the post-harvest treatments (p<0.001). In 2012, total BA (retained + regenerated tree) in the U_P treatment was 10.3 m² ha⁻¹ (SE: 2.6 m² ha⁻¹) greater than in the U_R treatment, and 14.3 m² ha⁻¹ (SE: 3.6 m² ha⁻¹) greater than in the U_B treatment.

DISCUSSION

Effect of regeneration cuttings

Supporting hypothesis 1, we found the largest reduction in regeneration BA in shelterwood units. Several previous simulation studies have predicted this outcome. The Prognosis model estimated that retained trees with 86 trees ha⁻¹ reduce the total volume growth of a Douglas-fir stand by 54% in northern Idaho (Long and Robert 1992). The ORGANON model predicted that about 50 retained trees ha⁻¹ (and with 11.7 m² ha⁻¹ of BA) resulted in 25.5% less volume growth for a new cohort of Douglas-fir, 60 years after harvesting (Birch and Johnson 1992). The ZELIG model estimated that BA accumulation at 100 and
150 retained trees ha\textsuperscript{-1} was 54.7% and 56.3% less than in the no-retention tree level, 240 years after harvesting in a mixed coniferous forest of western hemlock (\textit{Tsuga heterophylla} (Raf.) Sarg.), Douglas-fir, and western redcedar (\textit{Thujaplicata} Donn ex D. Don) (Hansen et al. 1995). The TASS model predicted an 8-32\% reduction of future yield for new cohorts of pure lodgepole pine (\textit{Pinus contorta} Douglas ex Loudon) and interior spruce stands according to overstory retention levels of 2-12 m\textsuperscript{2} ha\textsuperscript{-1}, 80 years after harvesting (Temesgen et al. 2006).

Retrospective studies have also reported results consistent with our finding. A negative relationship between regeneration BA and retained tree density (0-45 trees ha\textsuperscript{-1}) was observed from the 132 stands encompassing southern Washington to central Oregon, USA (Rose and Muir 1997). In the nearby Douglas-fir dominated forests, a 47\% decrease in understory volume with 50 trees ha\textsuperscript{-1} were observed (Zenner et al. 1998). Furthermore, a subsequent study predicted that 10 m\textsuperscript{2} ha\textsuperscript{-1} of retained tree basal area would reduce new cohort MAI by 27\% (median age of 97: Acker et al. 1998). In Sweden, new cohorts (30-90 years old) in Scots pine (\textit{P. sylvestris} L.) stands exhibited a 3\% reduction in volume production at just 10 retained trees ha\textsuperscript{-1} (Elfving and Jakobsson 2006).

In this study, shelterwood reserves reduced regeneration BA by 69\% when compared to the clearcut. That amount of growth reduction would seem to be quite considerable, since it surpassed the previously observed or predicted reduction extents. However, in the coastal hemlock forest, observed shelterwood stem volumes were 36\% and 42\% of clearcut volume levels in Pacific silver fir (\textit{Abies amabilis} (Douglas ex Loudon) Douglas ex Forbes) and western hemlock, 12 years after harvesting combined with the understory vegetation control (Mitchell et al. 2007). In spite of this extensive reduction, regeneration BA in 2012 at our study site is relatively larger than predictions from other research with the corresponding retained tree levels. For example, according to Rose and Muir’s (1997) equation, our site’s regeneration BA in the shelterwood unit with 122 trees ha\textsuperscript{-1} retention level would be predicted at 2.02 m\textsuperscript{2} ha\textsuperscript{-1}. Yet, the observed regeneration BA was approximately 7.05 m\textsuperscript{2} ha\textsuperscript{-1}. 

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This implies that direct comparison of absolute values with existing literature is not appropriate since the study site’s retained tree density and BA exceeded the inferential ranges of most previous studies. The understory responses have been commonly regarded as non-linear (e.g., Birch and Johnson 1992, Rose and Muir 1997, Acker et al. 1998), thus extrapolation to heavy retention should be implemented with caution. In addition, the regeneration growth responses might differ by species composition (Temesgen et al. 2006) and site productivity (Elfving and Jakobsson 2006). Localized studies embracing wide ranges of overstory conditions, species composition, and productivity may be necessary.

One of the striking results of this study is that we found a substantial reduction of regeneration BA in the group selection treatment. Although the overstory was removed in an almost identical way as the clearcut, regeneration BA was only 50% of that in the clearcut, indicating the effect of retained trees that were beyond the immediate vicinity of seedlings. This can be attributed to the effects of gap size and regenerated tree position within the gap. In coniferous forests of British Columbia, an increasing trend in coniferous seedlings’ 5-year radial growth was observed as gap size increased (Coates 2000). In his study, Coates argued that, especially in small gaps, seedling growth is affected by the specific location within a gap; the largest seedlings were found in the middle of gaps. In our study, the cut area of group selection ranged from 0.1 to 0.4 ha. Thus, gap sizes were small enough to exert negative influences on regeneration. Furthermore, sampling was conducted in plots, which means that some outer trees within a plot were located close to the gap edge. In fact, several points were less than 12.62 m from the edge trees. Therefore, many sampled trees within a plot might have been affected by the edge trees.

Overstory retention effect on regeneration in shelterwoods seems to include not only a BA reduction but also increased mortality of regeneration. A previous regeneration study conducted at the study site revealed significantly greater numbers of established regeneration (19895 trees ha\(^{-1}\) by 1992) in the shelterwood versus the clearcut (6843 trees ha\(^{-1}\)) and group selection (7168 trees ha\(^{-1}\)), due most likely to the abundant onsite seed source and shade from overstory retained trees (Shearer and Schmidt 1999). In
addition, Urgenson et al. (2012) similarly reported that regeneration in the dispersed retention treatment was 1.5-2.5 times more abundant than in clearcuts in the Pacific Northwest coniferous forests 12 years after harvesting.

However, 20 years later (in 2012), differences in regeneration density among regeneration cuttings had reversed. Regeneration density in the shelterwood became the sparsest (2198 trees ha⁻¹). On the other hand, regeneration density in clearcut became the highest (4729 trees ha⁻¹), slightly larger than the group selection (3325 trees ha⁻¹). However, there is no statistical difference in regeneration density between the clearcut and groups selection not only in 1992 (Shearer and Schmidt 1999) but also in 2012 (p=0.568), implying the overstory effect and understory competition in group selection were not strong enough to cause a regeneration mortality difference versus the clearcut. Our finding that a significant decrease in individual GE was only observed in the shelterwood support this idea.

Effect of understory vegetation

Previous research has predicted a negative correlation between regeneration growth and understory shrub cover (e.g., Harrington 2006, Mitchell et al. 2007, Urgenson et al. 2013, Palik et al. 2014). We found a significant difference in regeneration density in 2012 by post-harvest treatment. Moreover, as expected, the post-harvest treatments also significantly influenced the 2-year after shrub biomass and 8-years (2-10 years after harvest) shrub biomass increment. Consequently, correlations between shrub biomass and its increment and regeneration density in 2012 were detected.

Differences in regeneration traits were primarily observed in the comparisons between the understory protected (U_P) treatment and the prescribed burning (U_B) treatment; the U_B treatment increased regeneration density over the U_P treatment. Shrub biomass in the U_P treatment 2-years after harvesting had already recovered to over 70% of the pre-harvesting level (Schmidt 1980), thus, regeneration was highly limited in this treatment. In contrast, the U_B treatments had low levels (<10% of pre-harvesting
level) of shrub biomass, and regeneration flourished with the increased resource availability. As a result, a negative correlation between regeneration density and shrub biomass 2 years after harvesting was observed. However, where shrub biomass recovered rapidly in the highly-disturbed treatments, regeneration was restricted more severely. Therefore, regeneration mortality in the U_B treatment increased as the shrub biomass increased. The observed negative correlation between 8-year shrub biomass increments and regeneration density supports this argument.

However, the reduction in regeneration density was compensated by greater regeneration size. Regeneration QMD consistently shows the opposite trends to regeneration density. In other words, since stands with less regeneration tend to have the larger regeneration, overall regeneration basal areas across the stands are not different. The greater QMD of regeneration can be attribute to the preservation of advance regeneration and reduced competition with other seedlings and shrub species. The preservation of advance regeneration seems to be critical particularly in the shelterwood (Figure 4-1), although the significance of the interaction term is quite moderate (p=0.099 for the regeneration BA; Table 4-4).

We did not find any significant correlation between shrub biomass in 2012 and regeneration traits (BA, density, and QMD) in 2012. This indicates the shrub layer had already recovered and stabilized, the treatment effects on the shrub layer had attenuated, and the understory shrub layer in 2012 was regulated by other factors such as pre-harvesting vegetation community, resource availability, and overstory condition.

*Retained tree vs. regenerated tree*

Although strong statistical evidence of the effect of post-harvest treatment on retained trees was only observed in initial 5-year BA increment, similar trends were suggested in the recent 5-years period and in total (38 years) BA increment (p=0.080 for both variables; Figure 4-2, Table 4-6). Figure 4-2 illustrates
the effects of post-harvesting treatment on these variables for the mean-size individual trees (i.e., 16.5 cm dbh in 2012 for regenerated trees and 28.8 cm inner bark diameter in 1974 for retained tree, respectively). The figure indicated that the burning treatment exerted a negative impact on retained trees, whereas the treatment increased regeneration BA increment. In other words, thirty eight-year BA increment for retained trees in the U_B treatment was 113.8 cm² less than in the U_P treatment, whereas the 38-years regeneration BA increment was 429.9 cm² more at the individual tree level.

Negative impacts of prescribed burning treatment on retained trees can be attributed to changes in growth conditions and physiological responses due to heat damage and proliferation of understory vegetation. Adverse impacts of burning treatment on tree growth have been well-documented, especially for mature ponderosa pine ecosystems across the Rocky Mountain regions (e.g., Sutherland et al. 1991, Swezy and Agee 1991, Landsberg 1992, Busse et al. 2000). However, several contradictory results have also been published suggesting there was positive or no burning effect on tree growth (e.g., Wyant et al. 1983, Feeney et al. 1998). In addition, any negative impacts of burning on retained tree growth might be temporary (Sala et al. 2005, but see Monleon et al. 1997). Moreover, the fire intensities of this study were mild (Artley et al. 1978, Schmidt 1980). Therefore, the negative impacts on retained trees in this study is likely not due to a physiological response to fire.

Rather, increased competition with understory vegetation seems more plausible to explain the burning effect. The effect of fire on regeneration is likely indirect, and expressed through the direct effect of fire on understory vegetation. Burning treatment released a pulse of available growing space and resources; proliferated regeneration, accompanied with rapid shrub recovery, increased the demand of resources drastically. Although overstory trees possessed an advantage of pre-occupancy for light, dominant tall sprouting shrub species such as Rocky Mountain maple and Sitka alder could be competitive, since they could preserve their root systems intact. Harrington (2006) found that in shelterwood treatments, root competition is a primary limiting factor rather than light. Therefore, flourishing understory vegetation
after burning treatment increased the competition for limited resource with overstory trees, and as a result, the BA increment of retained trees was restrained relative to the unburned treatments. Thus, we may conclude that our results support the third hypothesis that growth of retained trees compensated for reduced growth in natural regeneration at the individual tree level.

Yet, it seems that the opposite effects between retained tree and regeneration at the tree level does not necessarily result in a negative correlation at the stand level, since stand density is a critical determinant of the stand level response. Weak evidence of correlation between retained tree BA and regeneration BA demonstrated this result. We found that larger regeneration QMD in the U_B treatment was correlated with lower regeneration density. Higher regeneration density elevated the competition intensity and mortality of regeneration. Consequently, self-thinning decreased the tree density and increased the average tree size of regeneration. As a result, the overall BA of regeneration for each treatment maintained a similar level.

Advance regeneration plays an important role for BA production, especially in the shelterwood. At the stand level, retained tree BA did not differ by the post-harvest treatments. However, differences in regeneration BA were obvious, indicating the U_P treatment had the largest BA. In addition, the U_P treatment in the shelterwood had the largest regeneration QMD. Thus, we can conclude that the protected advance regeneration in the U_P treatment resulted in superior performance in the shelterwood. Furthermore, the regeneration BA difference caused a difference in overall tree BA in the shelterwood among the post-harvest treatments. In fact, regeneration BA in the shelterwood’s U_P treatment was equivalent to that of the group selection (Figure 4-1). Therefore, protection of advance regeneration can help offset growth reduction of regeneration caused by overstory retention.

**Implications for VRH**
Given the forest type and overstory and understory conditions, we expect that the results of this study can be utilized to inform VRH application in the northern Rocky Mountain region.

1. Small patch size aggregate retention, and high retained tree density in disperse retention, will limit regeneration growth.

2. High retention levels of VRH also reduce the GE and BA increment of individual regenerated trees, and the negative impacts can last over 38 years after harvesting.

3. Post-harvest vegetation control and burning treatments can influence regeneration density, but counteracting tree-size responses offset the post-harvest treatment effect on regeneration BA. Repeated vegetation control or pre-commercial thinning might be useful to increase the diameter growth of the new cohort. However, since the retained trees would also derive the benefits of released understory competition, the effectiveness of the subsequent treatment on diameter class increase is not certain.

4. At the individual level, relative increase in retained tree BA growth due to post-harvest treatments is correlated with the relative reduction of regeneration BA. However, this inverse relationship between retained tree BA growth and regeneration BA may not be manifested depending on the each cohort’s density.

5. Advance regeneration in shelterwood can play an important role in determining the aboveground vegetation growth. It can ameliorate the negative effect that overstory retention has on the growth of a new cohort.

ACKNOWLEDGEMENTS

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REFERENCES


Table 4-1. Post-harvest treatments within regeneration cutting units.

<table>
<thead>
<tr>
<th>Post-harvest Treatment</th>
<th>Abbreviation</th>
<th>Cut trees$^1$</th>
<th>Max. size of retained woody materials$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Understory protected</td>
<td>U_P</td>
<td>&gt;17.8 cm dbh</td>
<td>7.6 cm × 2.4 m</td>
</tr>
<tr>
<td>Understory removed</td>
<td>U_R</td>
<td>All trees</td>
<td>2.5 cm × 2.4 m</td>
</tr>
<tr>
<td>Understory broadcast burned</td>
<td>U_B</td>
<td>All trees</td>
<td>7.6 cm × 2.4 m</td>
</tr>
</tbody>
</table>

$^1$ Except designated overstory shelterwood trees.
$^2$ Live and dead down logs (small-end diameter × length); for dead down logs, they were removed if sound enough to yard.
Table 4-2. Pre- and post-harvest aboveground woody vegetation volumes (>7.62 cm diameter, unit: m³/ha) (Benson and Schlieter 1980). Post-harvest treatments are listed in Table 4-1. Block 1 and 2 are low and high elevation replication, respectively.

<table>
<thead>
<tr>
<th>Harvesting treatments</th>
<th>Pre-harvest Volume</th>
<th>Post-harvest Volume</th>
<th>% Retained</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Block1</td>
<td>Block2</td>
<td>Block1</td>
</tr>
<tr>
<td>Clearcut</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U_P</td>
<td>286</td>
<td>222</td>
<td>2</td>
</tr>
<tr>
<td>U_R</td>
<td>173</td>
<td>120</td>
<td>0</td>
</tr>
<tr>
<td>U_B</td>
<td>247</td>
<td>289</td>
<td>0</td>
</tr>
<tr>
<td>Group Selection</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U_P</td>
<td>325</td>
<td>466</td>
<td>11</td>
</tr>
<tr>
<td>U_R</td>
<td>231</td>
<td>320</td>
<td>0</td>
</tr>
<tr>
<td>U_B</td>
<td>432</td>
<td>269</td>
<td>0</td>
</tr>
<tr>
<td>Shelterwood</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U_P</td>
<td>239</td>
<td>271</td>
<td>113</td>
</tr>
<tr>
<td>U_R</td>
<td>284</td>
<td>212</td>
<td>21</td>
</tr>
<tr>
<td>U_B</td>
<td>395</td>
<td>303</td>
<td>117</td>
</tr>
</tbody>
</table>

1U_P: understory protected, U_R: understory removed, U_B: understory broadcast burned (refer to Table 4-1).
Table 4-3. Mean (standard error) basal area (BA), tree density, and quadratic mean diameter (QMD) of regeneration 38 years after harvesting at Coram Experimental Forest.

<table>
<thead>
<tr>
<th>Regeneration Cutting</th>
<th>Post-harvest Treatment</th>
<th>Basal Area (m² ha⁻¹)</th>
<th>Tree density (trees ha⁻¹)</th>
<th>QMD (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
</tr>
<tr>
<td>Clearcut</td>
<td>U_P¹</td>
<td>18.24</td>
<td>1.65</td>
<td>5150</td>
</tr>
<tr>
<td></td>
<td>U_R</td>
<td>19.29</td>
<td>2.19</td>
<td>3035</td>
</tr>
<tr>
<td></td>
<td>U_B</td>
<td>20.22</td>
<td>2.09</td>
<td>7089</td>
</tr>
<tr>
<td>Group Selection</td>
<td>U_P</td>
<td>11.30</td>
<td>1.33</td>
<td>3730</td>
</tr>
<tr>
<td></td>
<td>U_R</td>
<td>11.30</td>
<td>1.71</td>
<td>2795</td>
</tr>
<tr>
<td></td>
<td>U_B</td>
<td>6.60</td>
<td>1.86</td>
<td>3156</td>
</tr>
<tr>
<td>Shelterwood</td>
<td>U_P</td>
<td>9.73</td>
<td>1.19</td>
<td>1489</td>
</tr>
<tr>
<td></td>
<td>U_R</td>
<td>4.67</td>
<td>1.33</td>
<td>2635</td>
</tr>
<tr>
<td></td>
<td>U_B</td>
<td>3.54</td>
<td>1.19</td>
<td>3500</td>
</tr>
</tbody>
</table>

¹ U_P: understory protected, U_R: understory removed, U_B: understory broadcast burned (refer to Table 4-1).
Table 4-4. ANOVA for the responses of basal area, tree density and QMD of regeneration and recent 5-year basal area increment growth efficiency of regenerated Douglas-fir trees.

<table>
<thead>
<tr>
<th>Responses</th>
<th>Regeneration Cutting (R)</th>
<th>Post-harvest treatment (P)</th>
<th>Interaction (R×P)</th>
<th>DBH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F value</td>
<td>p-value¹</td>
<td>F value</td>
<td>p-value</td>
</tr>
<tr>
<td>Basal Area</td>
<td>30.21</td>
<td>0.032*</td>
<td>1.64</td>
<td>0.198</td>
</tr>
<tr>
<td>Tree density</td>
<td>2.16</td>
<td>0.317</td>
<td>6.98</td>
<td>0.001**</td>
</tr>
<tr>
<td>QMD</td>
<td>3.59</td>
<td>0.218</td>
<td>31.29</td>
<td>&lt;0.001***</td>
</tr>
<tr>
<td>5-year BA Inc.</td>
<td>8.43</td>
<td>0.106</td>
<td>1.54</td>
<td>0.220</td>
</tr>
<tr>
<td>Growth Efficiency</td>
<td>17.79</td>
<td>0.053</td>
<td>2.32</td>
<td>0.104</td>
</tr>
</tbody>
</table>

¹ Significance codes: 0 < *** < 0.001< ** < 0.01 < * < 0.05.
Table 4-5. Mean (standard error) basal area (BA), tree density, and quadratic mean diameter (QMD) of retained trees in shelterwood unit 38 years after harvesting at Coram Experimental Forest.

<table>
<thead>
<tr>
<th>Post-harvest Treatment</th>
<th>Basal Area (m² ha⁻¹)</th>
<th>Tree density (trees ha⁻¹)</th>
<th>QMD (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
</tr>
<tr>
<td>U_P¹</td>
<td>19.97</td>
<td>1.65</td>
<td>138</td>
</tr>
<tr>
<td>U_R</td>
<td>16.98</td>
<td>1.87</td>
<td>97</td>
</tr>
<tr>
<td>U_B</td>
<td>18.01</td>
<td>2.78</td>
<td>126</td>
</tr>
</tbody>
</table>

¹ U_P: understory protected, U_R: understory removed, U_B: understory broadcast burned (refer to Table 4-1).
Table 4-6. Result summary of ANOVA for the responses (recent 5-year basal area increment, growth efficiency, and initial 5-year basal area growth) of retained Douglas-fir trees in the shelterwood units.

<table>
<thead>
<tr>
<th>Responses</th>
<th>DBH(^1)</th>
<th>Retained tree volume after harvesting</th>
<th>Post-harvest treatment(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F value</td>
<td>p-value</td>
<td>F value</td>
</tr>
<tr>
<td>Initial 5-year BA Inc.</td>
<td>37.72</td>
<td>&lt;0.001***</td>
<td>0.93</td>
</tr>
<tr>
<td>Recent 5-year BA Inc.</td>
<td>21.14</td>
<td>&lt;0.001***</td>
<td>2.76</td>
</tr>
<tr>
<td>Total BA Inc.</td>
<td>12.07</td>
<td>&lt;0.001***</td>
<td>3.53</td>
</tr>
<tr>
<td>Growth Efficiency</td>
<td>10.40</td>
<td>0.002**</td>
<td>0.66</td>
</tr>
</tbody>
</table>

1 In the analysis for initial 5-year BA Inc., the inner bark diameter in 1974 was used as a covariate.
2 Statistics were calculated from the reduced models (i.e., models without the retained tree volume variable).
3 Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05.
Figure Captions

Figure 4-1. Regeneration (a) basal area, (b) tree density, and (c) quadratic mean diameter by the regeneration cuttings combined with the post-harvest treatments (38 years after harvest). The abbreviations for the post-harvest understory vegetation treatments were described in text and Table 4-1.

Figure 4-2. Post-harvest understory vegetation treatment effects on the retained tree basal area increment and regenerated Douglas-fir tree basal area in shelterwood units 38 years after harvest. Numbers in y-axis represent the predicted basal area increment for mean size trees (i.e., 16.5 cm dbh in 2012 for regenerated trees and 28.8 cm inner bark diameter in 1974 for retained tree, respectively). Abbreviations for the treatments were referred in Table 4-1.
Figure 4-2.
CHAPTER 5

LONG-TERM IMPACTS OF INTENSIVE FOREST BIOMASS UTILIZATION ON UNDERSTORY SHRUB BIOMASS RECOVERY, COMPOSITION, AND DIVERSITY IN THE NORTHERN ROCKY MOUNTAINS

ABSTRACT

We investigated the long-term impact of intensive biomass utilization on understory vegetation dynamics including shrub recovery, species composition, and biodiversity 38 years after harvesting at Coram Experimental Forest in northwestern Montana. Three levels of biomass removal intensity (high, low, and medium) combined with prescribed burning treatment were applied under three regeneration cutting treatments (shelterwood, group selection, and clearcut). Four shrub biomass surveys (pre-treatment, 2-, 10-, and 38-years after treatment) were conducted. Shrub biomass for all treatment units in 2012 exceeded the pre-treatment level, and biomass utilization intensity did not affect shrub recovery. Species composition changed drastically immediately after harvesting (1976), however, the species composition of treated units in 2012 did not differ from the control. Biodiversity indices (Shannon index and evenness index) also decreased immediately following harvesting, but recovered 10 years after harvesting. The responses of diversity indices over time differed among biomass utilization levels with the high-utilization level and unburned treatment species assemblages the most even and diverse 38 years after harvesting. Our results indicate the shrub community is quite resilient to biomass harvesting in this forest type.
INTRODUCTION

Forest understory vegetation plays an important role in temperate forest ecosystems, providing wildlife habitat and food resources, sustaining site productivity, and underlying biodiversity (Yarie 1980, Alaback and Herman 1988, Chen et al. 2004, D’Amato et al. 2009). For example, huckleberries are well known as the most important food source of grizzly bear (*Arctos ursus*) in Montana (Mace and Jonkel 1986). In addition, shrubs and understory herbs serve critical functions in nutrient cycling (MacLean and Lean 1977, Yarie 1980, Chapin 1983). Abundance of understory vegetation is a critical factor to determine tree growth, especially in early stand development stages (Turner and Long 1975). From a biodiversity perspective, understory vegetation is the lead contributor to species diversity (Halpern and Spies 1995, Thomas et al. 1999). Thus, considerable efforts have been devoted to understanding impacts of forest management on understory vegetation structure and composition (D’Amato et al. 2009).

Increasing fossil fuel costs and concerns about climate change have raised public demands for utilizing forest biomass as an alternative energy feedstock. As a result, it is expected that more intensified biomass harvesting trials beyond whole-tree harvesting will be more prevailing in North America (e.g., Benjamin et al. 2010, Breidis et al. 2011, Berger et al. 2013). However, logging activity for increased woody biomass utilization inevitably involves a greater magnitude of soil disturbance and nutrient export. Furthermore, logging activity may result in understory vegetation mortality and an altered microclimate. Therefore, increased woody biomass utilization can also impact understory vegetation dynamics and consequently alter forest ecosystem functions.

However, knowledge gaps exist regarding the long-term impacts of biomass utilization on understory vegetation. The majority of such studies have focused on overstory or belowground layers, and several on-going studies are not mature enough to yield long-term assessments of increased biomass harvesting in North America (e.g., Long-Term Soil Productivity research network; Powers et al. 2005). Knowledge
gaps in the northern Rocky Mountain forest are especially great, since the infrastructure for intensive biomass harvesting is modest and research efforts on its potential impacts are still insufficient.

In 1974, an interdisciplinary research project was conducted at Montana’s Coram Experimental Forest to evaluate the ecological consequences of intensified biomass harvesting (Barger 1980). About four decades later, this historical research forest can now provide clues to the long-term impact of biomass harvesting on understory vegetation. The objective of this study was to identify whether biomass utilization intensity alters understory vegetation dynamics and species diversity. For this, we investigated the temporal changes of shrub recovery, species composition, and diversity over time (pre-harvest, 2, 10, and 38 years after harvest) by four different levels of biomass utilization intensity.

**METHODS**

**Study site**

The study was conducted at Coram Experimental Forest (CEF), on the Flathead National Forest in northwestern Montana. The experimental units were established on an east-facing slope in Upper Abbot Creek Basin (48°25’ N, 113°59’ W), ranging in elevation from 1,195 to 1,615 m asl, and from 30% to 80% slope. Soils originated from impure limestone, containing approximately 40-80% rock-fragment (Klages et al. 1976), and classified as loamy-skeletal, isotic Andic Haplocryalfs (Soil Survey Staff 2009). Average annual temperature ranges from 2 °C to 7 °C (Hungerford and Schlieter 1984), and average annual precipitation is 1,076 mm, mainly in the form of snow from late fall to early spring (Farnes et al. 1995). The climate of CEF is a modified Pacific maritime type (Adams et al. 2008).

The study was implemented in mature stands of the Western Larch cover type (Society of American Foresters Cover Type 212; Eyre 1980). The pre-harvest overstory consisted of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western larch (*Larix occidentalis* Nutt.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western hemlock (*Tsuga*
heterophylla (Raf.) Sarg.), western redcedar (Thuja plicata Donn.), lodgepole pine (Pinus contorta Dougl. ex Loud.), and western white pine (Pinus monticola Dougl.) (Shearer 1980, Shearer and Schmidt 1999). The study sites consisted primarily of the subalpine fir/queencup (Clintonia uniflora (Menzies ex Schult. & Schult. f.) Kunth) (ABLA/CLUN) habitat type (Pfister et al. 1977).

Experimental design

The experiment has a split-plot design. Treatments included three kinds of regeneration cuttings (shelterwood, group selection, and clearcut; whole-plot) and four levels of biomass utilization treatments (sub-plot). Control units were established on both sides of the group selection units. The biomass utilization levels were nested into each regeneration cutting treatment. The treatments were replicated twice, one per elevation block (lower block at 1,195 m - 1,390 m, and upper block at 1,341 m - 1,615 m). The sizes of lower and upper clearcut and shelterwood blocks were 5.7 and 6.9 ha, 14.2 to 8.9 ha, respectively. For the group selection, eight cutting gaps were harvested. The sizes of group selection cutting gaps ranged from 0.1 to 0.6 ha. The average pre-harvest volume of woody material was 512 m³/ha. On average, 36%, 84%, and 70% of total woody materials were removed from shelterwood, group selection, and clearcut units, respectively.

The four levels of biomass utilization consisted of a combination of three biomass utilization levels (high, medium, and low) with post-harvest burning treatments (burn and unburn). As a result, M_U (medium/unburn), H_U (high/unburn), L_B (low/burn), and M_B (medium/burn) treatments were implemented for the biomass utilization treatments (see Table 5-1 for experimental design details).

Trees were harvested and removed via a running skyline yarder in 1974. Subsequent broadcast burning was applied in the fall of 1975. However, due to cool and wet weather condition, the burning treatment was not implemented in lower shelterwood unit (Artley et al. 1978; Schmidt 1980). Thus, an
additional biomass utilization treatment (i.e., low/unburn) occurred in the lower shelterwood unit, but was excluded from this study’s data analysis.

**Data collection and analysis**

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

Measured crown volumes or root-collar diameters were used to compute shrub biomass. In 1973, 1976, and 1984, shrub crowns were measured for each species using a nested quadrat system. Shrub volume was assumed as a cylindroid; thus, two diameters of the ellipse (projected area of crown) and height were measured. In 2012, a nested circular sampling system was utilized. Instead of measuring shrub crown volume, root-collar diameter was measured via digital caliper to reduce the measurement errors. Data were collected from four permanent points (3rd, 4th, 7th, and 8th) out of ten points. Plot sizes and measured shrub size classes are described in Table 5-2.

We used regression equations to convert shrub volume to biomass; the equations were previously derived through destructive sampling performed in the vicinity of the cutting units in 1974 (Table 5-3; W. Schmidt, unpublished data). Brown’s (1976) shrub biomass equations were employed for the 2012 measurement, converting root-collar diameter to shrub biomass.

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

\[ y_{ijklm} = \mu + \alpha_i + B_k + \epsilon_{(1)ik} + \beta_j + \epsilon_{(2)ijk} + \gamma_l + \epsilon_{(3)ijkl} + \epsilon_{ijklm} \] (1)

where \( y_{ijkl} \) = log-transformed shrub recovery (log %), \( \mu \) = grand mean of shrub recovery, \( \alpha_i \) = effect of harvest type \( i \) (whole-plot effect), \( B_k \) = \( k \)th block effect (random effect), \( \beta_j \) = \( j \)th biomass utilization treatment effect (sub-plot effect), \( \gamma_l \) = \( l \)th measurement year effect, and \( \epsilon_{(1)ik} \), \( \epsilon_{(2)ijk} \), \( \epsilon_{(3)ijkl} \), \( \epsilon_{ijklm} \) are the whole-plot, sub-plot, and (repeated) subject error terms, and the variation among sampling plots in a subplot of a measuring year, respectively. Interaction terms between fixed effects also were tested.

Non-metric Multidimensional Scaling (NMS) was used to investigate species composition and its shifts. NMS is one of the ordination methods most widely used in plant ecology (Austin 1985); it reduces dimensionality of the original data, facilitating the display of multivariate data points. The Bray-Curtis distance was used for distance matrix construction, and the distances to control for each measurement year were tested. The analysis was conducted through the \textit{vegan} package (Oksanen et al. 2015) in R (R Development Core Team 2008).

Species diversity and evenness were evaluated with Shannon’s species diversity index \((H' ; \text{Shannon 1948})\) and Pielou’s evenness index \((J' ; \text{Pielou 1969})\):

\[ H' = -\sum p_l \ln p_l \] (2)
\[ J' = H' / \ln S \]  

where \( p_i \) is the relative abundance of \( i^{th} \) species within a plot, and \( S \) is total number of species in a plot.

These indices were compared to those indices of the untreated control using equation (1). All statistical analyses were conducted via R. The `nlme` package (Pinheiro et al. 2014) was used to fit the mixed effects models, and `multcomp` (Hothorn et al. 2014) was used for testing the linear contrasts among the biomass utilization treatments at each measurement period.

RESULTS

A total of 19 shrub species were recorded from 1973 to 2012 (Table 5-3). The major species are Rocky Mountain maple (Acer glabrum Torr.; ACGL), Saskatoon serviceberry (Amelanchier alnifolia (Nutt.) Nutt. ex M. Roem.; AMAL), Sitka alder (Alnus viridis (Chaix) DC. ssp. sinuata (Regel) Á. Löve & D. Löve; ALVI), mallow ninebark (Physocarpus malvaceus (Greene) Kuntze; PHMA), dwarf rose (Rosa gymnocarpa Nutt.; ROGY), huckleberry (Vaccinium membranaceum Douglas ex Torr.; VAME, Vaccinium myrtilloides Michx.; VAMY), and white spirea (Spiraea betulifolia Pall.; SPBE). ACGL occupied 41% of total shrub biomass; 72% of total biomass was composed of five shrub species (i.e., ACGL, AMAL, ALVI, PHMA, and ROGY).

Understory vegetation recovery of the study site is summarized in Table 5-4 and Figure 5-1. Mean shrub biomass in 1973 (pre-treatment) and in 2012 are 4.7 Mg/ha (SE: 0.4 Mg/ha) and 7.0 Mg/ha (SE: 0.9 Mg/ha), respectively, indicating that the shrub biomass exceeds the pre-treatment level and increased by about 50% after 38 years. The ANOVA table for log-transformed shrub recovery (biomass ratio to measures in 1973; log %) indicates no effect of biomass utilization treatment on these values (p=0.167, Table 5-5). The regeneration cutting factor was non-significant (p=0.167), whereas measurement year was highly significant (as anticipated) (p<0.0001).
The biplot of NMS for shrub species composition illustrates the species composition and changes over time at the study site (Figure 5-2a). The pre-treatment communities were clustered on the upper-left region of NMS plane. After harvesting and post-harvesting treatments (in 1976), all treated shrub communities were drastically changed. In 1984, the shrub communities returned toward the pre-treatment conditions. However, there is a difference of species composition between burned and unburned treatments in 2012. The unburned units (including the control units) are located on the center of NMS plane, whereas the burned units moved to the right region of the plane. The biplot of NMS drawn by measurement in 2012 indicates the shrub composition differed slightly between burned and unburned treatments (e.g., M_B vs. H_U in Figure 5-2b). However, since the confidence regions of mean NMS scores for all treatments overlapped, we conclude that the species composition of all treatments is not different from the species composition of the untreated control in 2012.

Temporal changes in dissimilarity (i.e., Bray-Curtis distance) of treatments yielded a consistent result with NMS (Figure 5-3). ANOVA indicated the significant interaction between biomass utilization treatment and measurement year (p=0.050), however, there was no effect of regeneration cutting on difference in species composition between treatment and control (p=0.559, Table 5-5). Pre-treatment dissimilarity index to control was 0.58 (SE: 0.02) across treatments. Two years after treatment, mean dissimilarity index for treatments increased to 0.77 (SE: 0.02). The M_B treatment showed the highest dissimilarity (0.85, SE: 0.02), whereas the species composition of M_U treatment was closest to control (0.68, SE: 0.03). The difference in dissimilarity index between the M_B and M_U treatment in 1976 was significant (p<0.0001). On the other hand, in 1984, the dissimilarity indices for all treatment decreased; the L_B treatment showed the most different species composition to control (0.63, SE: 0.03). The lowest dissimilarity to control was observed in the M_U treatment, and the difference between two treatments (the L_B versus the M_U treatment) remained significant (p=0.003). In 2012, the mean dissimilarity index of all treatments was 0.64 (SE: 0.02), with the L_B and M_B treatments exhibiting the highest (0.67, SE: 0.04) and lowest (0.61, SE: 0.04) dissimilarity indices, respectively. However, there was
insignificant evidence for the differences of dissimilarity index for those two treatment by 2012 (p= 0.817).

Temporal change in species composition over all treatments sheds additional light on the movement of the NMS coordinates (Figure 5-4). Two years after harvesting, the relative abundance (ratio of a species’ biomass to total shrub biomass) of AMAL decreased considerably (31%). The relative abundance of ACGL (3%) and VAME (3%) also decreased slightly. On the other hand, the relative abundance of SPBE (13%), ROGY (9%), PHMA (6%), and thimbleberry (Rubus parviflorus Nutt.; RUPA) (6%) increased prominently two years after harvesting. Ten years after harvesting (1984), the species composition seemed to have recovered to the pre-harvesting status (Figure 5-2a and Figure 5-4). Thirty eight years after harvesting (2012), the species composition was similar to 10 years after harvesting, except for PAMY, which showed a 12% increase in relative abundance from 10 to 28 years after harvesting.

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

The pre-treatment evenness index was 0.37 (including control, SE: 0.02) on average. Even after harvesting, the evenness index remained similar (0.36, SE: 0.03). The index increased in 1984 (0.57, SE: 0.01) and slightly decreased in 2012 (0.48, SE: 0.02). However, the temporal pattern of the relative evenness index showed a close similarity to the relative Shannon’s index. The relative evenness index
also decreased immediately after harvesting treatment, and recovered in 1984 (Figure 5-5b). ANOVA results for the relative evenness indices in 2012 were consistent with those for the relative Shannon index by the utilization treatments. The test result indicated that biomass utilization level, measurement year, and interaction were significant (p<0.0001, p=0.38, and p=0.0002, respectively; Table 5-5), and the regeneration cutting treatment was not significant (p=0.48).

Linear contrasts among the utilization treatments for relative Shannon’s index and evenness index showed differences from the untreated control in 1973 (Table 5-7). Except for the M_B utilization treatment, all treatment units had lower species diversity than the control. After two years, burning treatments resulted in a decrease in species diversity (p<0.01 for L_B, and p<0.001 for M_B, respectively), whereas unburned units exhibited an increase in the Shannon index, bringing it to the level of the control. Ten years after harvesting, the Shannon’s indices of these burning treatments were recovered to the level of the control. The M_U treatment showed an increase in relative Shannon’s index 10 years after harvesting (p<0.01). Thirty eight years after harvesting, the Shannon’s index of the H_U treatment was significantly greater than the controls (p<0.01). On the other hand, the relative evenness index tended not to respond to the harvesting and post-harvesting treatment as much as Shannon index. Only the M_U treatment 2 years after harvesting showed significantly lower evenness compared to the control (p<0.01), and the evenness index of M_U treatment after 10 years harvesting was greater than the control (p=0.02).

DISCUSSION

Shrub recovery

In our study, about 50% of total shrub biomass recovered to the pre-harvest levels within 10 years after harvesting. In a northern Idaho forest, shrub cover was restored to over half of the pre-harvest level in less than seven years (Wittinger et al. 1977). Thus, shrub recovery rate of the study site seems to be
comparable to nearby forests. It is noteworthy that the differences in shrub recovery among the biomass utilization treatments at year 4 (Schmidt 1980) in our study site disappeared by year 10, and remained negligible through year 28. Schmidt theorized that the initial responses of the shrub layer were more affected by the biomass utilization treatments than the regeneration cuttings. It seems obvious that physical impacts of machinery and prescribed burning plays a more critical role on short-term shrub layer responses than changes in overstory cover (i.e., regeneration cutting). However, that initial impact vanished with time. That is likely because the more intensively disturbed understory grew more rapidly due to abundant growing space and available resources. Thereafter, the effect of treatments on understory vegetation was depressed according to overstory tree recovery (Thomas et al. 1999).

Thirty eight years after harvesting, the shrub biomass levels exceeded the pre-harvest levels. The positive effect of harvesting on shrub biomass level is not surprising because of the increased resource availability (e.g., light, water, nutrient) resulting from canopy disturbance (Klinka et al. 1996, Bailey et al. 1998, Lindh and Muir 2004). However, as stand development proceeds to the stem exclusion stage (Oliver and Larson 1996), we expect that shrub cover will decline and eventually approach control levels. Various studies conducted in nearby northern Rocky Mountain forests maintained that shrub layer biomass production reaches a maximum 10-30 years after the conclusion of harvesting and post-harvesting treatments (e.g., Mueggler 1965, Wittnger et al. 1977, Irwin and Peek 1979). Thus, shrub development at this study site may have already reached its maximum level.

We found insufficient evidence for differences in understory recovery among biomass utilization treatments, adding to mounting evidence that indicates there have been no adverse long-term impacts of intensified biomass extraction on productivity at this study site. If intensive biomass utilization treatment had a negative long-term impact on site productivity, then we would have expected a reduction in overstory tree growth, and a concomitant gain in the availability of light, moisture, and nutrients for understory vegetation. Observations of the negative relationship between canopy cover and shrub cover
are numerous (e.g., Klinka et al. 1996, Stone and Wolfe 1996, Brais et al. 2004; but see He and Barclay 2000). Thus, as site productivity decreases, understory cover will generally increase (Oliver and Larson 1996, Thomas et al. 1999). In a related study, we found that biomass production among biomass utilization treatments did not differ (W. Jang, dissertation in preparation).

**Shrub species composition**

The NMS biplot and temporal change in dissimilarity indices demonstrated drastic changes in species composition after harvesting and burning treatments. Among all treatments, community shift in the M_U treatment was least. Understory vegetation was specifically protected in the M_U treatment (Schmidt 1980), so this result is both unsurprising and is a validation of the effectiveness of that prescription in meeting the understory protection goal. Despite initial changes in species composition, the shrub community was restored to pre-treatment condition 10-38 years after harvesting in each treatment, thus the eventual species composition of the shrub layer seems unaffected by biomass utilization. This outcome agrees with the finding of Jenkins and Parker (1999), who investigated the impacts of regeneration harvestings (clearcut, group selection and single-tree selection) on understory vegetation composition in central hardwood forests in Indiana. Seven to twenty seven years after harvesting, although there were little differences in understory vegetation cover, the effect of regeneration cutting was not severe enough to cause any fundamental shifts of species composition. In northern hardwood forests of Michigan, understory vegetation composition recovered to the original status within 50 years after harvest (Metzger and Scholtz 1984). In that study, there were drastic changes in understory vegetation species composition and diversity immediately after harvesting (4-5 years), but the effects of regeneration cutting on the understory vegetation dissipated after 50 years. In Wisconsin hardwood forests, neither spring nor summer flora of ground-layer were significantly different among regeneration cutting treatments four decades after harvesting (Kern et al. 2006). Furthermore, in a related study, we
observed no difference among the four treatments in aboveground biomass production and belowground soil organic matter, and C and N contents (W. Jang, dissertation in preparation).

Changes to shrub community composition immediately after harvesting is the cumulative result of each species’ individual response to harvesting operations (Figure 5-4). AMAL proved to be the most responsive to harvesting. Decades earlier, the reduction of AMAL was significantly more pronounced in the understory protected treatment (M_U) relative to the other biomass utilization treatments (Schmidt 1980). In contrast to AMAL, other large shrubs (such as ACGL and ALVI) showed little reduction in relative abundance. We suppose that this fact is likely due to their vigorous resprouting after harvesting.

Some increases in relative abundance after harvesting are notable. Some species, including ROGY, SPBE, and PHMA, showed immediate increases in their relative abundance 2 years after harvesting. However, their relative abundance decreased with additional years after harvesting. After 10 years, the relative abundance of these pioneer species had returned to pre-harvesting levels. Only the relative abundance of PAMY, which is a late-successional species, significantly increased 38 years after harvesting. A similar observation was reported in northern Idaho, where PAMY cover decreased initially after harvest (year 7), but by 25 years after harvest, it flourished to five times more than the untreated control (Wittinger et al. 1977).

**Shrub species biodiversity**

As the scope of silviculture has expanded to include restoring and sustaining ecosystem functions and services, species diversity has become one metric to judge a successful silvicultural treatment (Seymour et al. 2002, Kern et al. 2006, Cole et al. 2008). The relevant application of silvicultural treatments has been shown capable of enhancing tree species diversity (e.g., Wang and Nyland 1993, O’Hara 1998, Kerr 1999, Battles et al. 2001). However, the responses of understory diversity to forest management activity show substantial variation not only spatially, but also temporally (Cole et al. 2008). Thus, spatial variation
and temporal change should be considered to predict the impacts of forest management on understory diversity.

The relation between disturbance intensity and biodiversity has been frequently addressed by “the intermediate disturbance” hypothesis (Connell 1978, Sousa 1979). That hypothesis states that the highest biodiversity levels are maintained at an intermediate disturbance intensity, since that intensity of disturbance can preserve the species that are relatively less competitive at the extreme levels (low and high) of disturbance intensities. Empirical trials using various thinning intensities have corroborated this hypothesis. For example, a study in spruce-hemlock forests of the coastal Oregon showed that a heavy thinning operation decreased understory vegetation diversity, whereas at the moderate thinning intensity that diversity often increased (Alaback and Herman 1986). In this study, we observed that the high biomass utilization level (H_U) exhibited the highest shrub diversity 38 years after harvesting. We speculate that the high utilization treatment prevented a single large sprouting shrub species (i.e., ACGL) from dominating the understory layer and thereby allowed a greater diversity of species to become established. Since the yarder-based logging system minimized understory disturbance, we contend that the high biomass utilization level of this study falls on the intermediate range of disturbances.

In addition, we observed the lowest ACGL relative abundance and the highest ALVI relative abundance in the L_B treatment. Although this finding did not result in a statistically significant biodiversity difference, the L_B treatment exhibited the second highest shrub diversity. This observation indicated that ALVI benefitted by the broadcast burning treatment. On the other hand, the relative abundance of ALVI decreased in the M_B treatment, whereas the relative abundance of ACGL increased. These trends may imply that biomass utilization intensity and burning treatment interact with each other. However, due to our imbalanced experimental design, statistical testing for treatment interactions was impossible in this study. A better understanding of the impacts of ground-based biomass harvesting and their interaction with burning treatments on understory vegetation is needed.
The initial response of biodiversity to the burning treatment was much stronger than to the biomass utilization level. In 1976 (2 years after harvesting), Shannon’s indices for the burned treatments were significantly less than the unburned treatments. In contrast, the unburned treatment units maintained the diversity level of the control even though their pre-harvest levels (in 1973) were quite low. However, lack of difference in the species evenness between pre- and post-harvest (in 1976) indicated that there was no species-specific response to the burning treatment. In addition, the difference between the burned and unburned treatment also disappeared within 10 years after harvesting, indicating the shrub community of this region is resilient to prescribed fire. Artley et al. (1978) had reported that the burning treatment was not severe due to the wet fuel and weather condition. Therefore, the burning treatment effect in this study might not have been intense enough to affect the dynamics of the shrub layer.

CONCLUSION

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

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REFERENCES


Table 5-1. Biomass utilization treatments within regeneration cutting units (from Benson and Schlieter 1980; Shearer and Schmidt 1999; Shearer and Kempf 1999).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Abbreviation</th>
<th>Cut trees&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Max. size of retained woody materials&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Post-harvest treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium-unburn</td>
<td>M_U</td>
<td>&gt;17.8 cm dbh</td>
<td>7.6 cm × 2.4 m</td>
<td>Understory protected/unburned</td>
</tr>
<tr>
<td>High-unburn</td>
<td>H_U</td>
<td>All trees</td>
<td>2.5 cm × 2.4 m</td>
<td>Slashed/unburned</td>
</tr>
<tr>
<td>Low-burn&lt;sup&gt;3&lt;/sup&gt;</td>
<td>L_B</td>
<td>All trees</td>
<td>14.0 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
<tr>
<td>Medium-burn</td>
<td>M_B</td>
<td>All trees</td>
<td>7.6 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
</tbody>
</table>

<sup>1</sup> Except designated overstory shelterwood trees.

<sup>2</sup> Live and dead down logs (small-end diameter × length); for dead down logs, they were removed if sound enough to yard.

<sup>3</sup> 1974 Forest Service standards.
Table 5-2. Plot sizes for vegetation sampling and shrub sizes measured.

<table>
<thead>
<tr>
<th>Plot type</th>
<th>Measurement Year</th>
<th>Plot size</th>
<th>Sampled tree size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quadrat</td>
<td>1973, 1976, 1984</td>
<td>5.0 m × 5.0 m</td>
<td>≥2.5 m height</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.0 m × 3.0 m</td>
<td>≥1.5 m and &lt;2.5 m height</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.5 m × 1.5 m</td>
<td>≥0.5 m and &lt;1.5 m height</td>
</tr>
<tr>
<td>Circular</td>
<td>2012</td>
<td>0.80 m (radius)</td>
<td>&lt;1.0 m height</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.78 m (radius)</td>
<td>≥1.0 m height</td>
</tr>
</tbody>
</table>
Table 5-3. Regression coefficients to predict total live shrub biomass from volume (W. Schmidt, unpublished data).

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

\[ y = \beta_1 \cdot x; \text{ where } y = \text{shrub biomass (g)}, \text{ and } x = \text{shrub volume (m}^3\text{)}. \]
Table 5-4. Shrub biomass and recovery. The recovery was calculated based on 1973 (pre-treatment) measurements.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Shrub biomass (Mg/ha)</th>
<th>Recovery (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regeneration cutting</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shelterwood</td>
<td>5.3 (1.0)</td>
<td>1.5 (0.6)</td>
</tr>
<tr>
<td>Group Selection</td>
<td>5.7 (0.6)</td>
<td>0.6 (1.3)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>3.7 (0.4)</td>
<td>0.7 (1.4)</td>
</tr>
<tr>
<td>Biomass utilization(^2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M_U</td>
<td>5.7 (1.0)</td>
<td>2.0 (0.6)</td>
</tr>
<tr>
<td>H_U</td>
<td>4.5 (0.6)</td>
<td>0.4 (0.1)</td>
</tr>
<tr>
<td>L_B</td>
<td>3.9 (0.5)</td>
<td>0.1 (0.0)(^3)</td>
</tr>
<tr>
<td>M_B</td>
<td>4.9 (0.7)</td>
<td>0.2 (0.0)(^3)</td>
</tr>
<tr>
<td>Control</td>
<td>4.1 (0.9)</td>
<td>3.9 (0.8)</td>
</tr>
</tbody>
</table>

\(^1\) Pre-treatment condition.

\(^2\) M_U: medium/unburn, H_U: high/unburn, L_B: low/burn, M_B: medium/burn (refer to Table 5-1).

\(^3\) Less than 0.05 Mg/ha.
Table 5-5. Summary of test results for shrub biomass recovery (based on the 1973 measurements), dissimilarity index (Bray-Curtis distance to control), and relative Shannon and Evenness index (based on the untreated control measurement of each year).

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>F value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shrub biomass recovery (log %)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Measurement year</td>
<td>2</td>
<td>67.130</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Regeneration cutting</td>
<td>2</td>
<td>2.037</td>
<td>0.3292</td>
</tr>
<tr>
<td>Biomass utilization</td>
<td>3</td>
<td>1.960</td>
<td>0.1665</td>
</tr>
<tr>
<td><strong>Dissimilarity Index (Bray-Curtis Distance)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Measurement year</td>
<td>3</td>
<td>53.083</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Regeneration cutting</td>
<td>3</td>
<td>0.790</td>
<td>0.5588</td>
</tr>
<tr>
<td>Biomass utilization</td>
<td>4</td>
<td>5.280</td>
<td>0.0016</td>
</tr>
<tr>
<td>Measurement year × Biomass utilization</td>
<td>12</td>
<td>1.903</td>
<td>0.0496</td>
</tr>
<tr>
<td><strong>Relative Shannon Index</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Measurement year</td>
<td>3</td>
<td>116.565</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Regeneration cutting</td>
<td>3</td>
<td>0.862</td>
<td>0.4614</td>
</tr>
<tr>
<td>Biomass utilization</td>
<td>4</td>
<td>2.520</td>
<td>0.0416</td>
</tr>
<tr>
<td>Measurement year × Biomass utilization</td>
<td>12</td>
<td>6.813</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Relative Evenness Index</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Measurement year</td>
<td>3</td>
<td>25.034</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Regeneration cutting</td>
<td>3</td>
<td>0.812</td>
<td>0.4884</td>
</tr>
<tr>
<td>Biomass utilization</td>
<td>4</td>
<td>1.053</td>
<td>0.3801</td>
</tr>
<tr>
<td>Measurement year × Biomass utilization</td>
<td>12</td>
<td>3.182</td>
<td>0.0002</td>
</tr>
</tbody>
</table>
### Table 5-6. Mean biodiversity indices (and standard errors) of shrub species pre- (1973) and post- regeneration cutting and biomass utilization treatments.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Shannon Index</th>
<th></th>
<th></th>
<th></th>
<th>Evenness Index</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Regeneration cutting</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shelterwood</td>
<td>0.31 (0.05)</td>
<td>0.33 (0.05)</td>
<td>0.88 (0.05)</td>
<td>0.95 (0.09)</td>
<td>0.28 (0.04)</td>
<td>0.36 (0.05)</td>
<td>0.57 (0.03)</td>
<td>0.50 (0.05)</td>
</tr>
<tr>
<td>Group Selection</td>
<td>0.51 (0.05)</td>
<td>0.32 (0.04)</td>
<td>0.90 (0.04)</td>
<td>0.88 (0.09)</td>
<td>0.44 (0.04)</td>
<td>0.33 (0.04)</td>
<td>0.59 (0.02)</td>
<td>0.48 (0.05)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>0.42 (0.04)</td>
<td>0.36 (0.05)</td>
<td>0.86 (0.04)</td>
<td>0.87 (0.07)</td>
<td>0.38 (0.04)</td>
<td>0.39 (0.06)</td>
<td>0.54 (0.02)</td>
<td>0.54 (0.03)</td>
</tr>
<tr>
<td>Biomass utilization</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M_U</td>
<td>0.37 (0.05)</td>
<td>0.39 (0.05)</td>
<td>0.86 (0.05)</td>
<td>0.80 (0.10)</td>
<td>0.33 (0.04)</td>
<td>0.38 (0.04)</td>
<td>0.54 (0.03)</td>
<td>0.42 (0.05)</td>
</tr>
<tr>
<td>H_U</td>
<td>0.38 (0.05)</td>
<td>0.40 (0.05)</td>
<td>0.91 (0.04)</td>
<td>1.23 (0.08)</td>
<td>0.36 (0.05)</td>
<td>0.41 (0.05)</td>
<td>0.58 (0.02)</td>
<td>0.61 (0.04)</td>
</tr>
<tr>
<td>L_B</td>
<td>0.36 (0.05)</td>
<td>0.23 (0.06)</td>
<td>0.76 (0.05)</td>
<td>0.87 (0.08)</td>
<td>0.36 (0.05)</td>
<td>0.31 (0.08)</td>
<td>0.55 (0.03)</td>
<td>0.50 (0.04)</td>
</tr>
<tr>
<td>M_B</td>
<td>0.59 (0.06)</td>
<td>0.20 (0.05)</td>
<td>1.00 (0.06)</td>
<td>0.67 (0.09)</td>
<td>0.48 (0.04)</td>
<td>0.26 (0.07)</td>
<td>0.61 (0.03)</td>
<td>0.37 (0.05)</td>
</tr>
<tr>
<td>Control</td>
<td>0.55 (0.06)</td>
<td>0.54 (0.05)</td>
<td>0.78 (0.06)</td>
<td>0.70 (0.14)</td>
<td>0.45 (0.05)</td>
<td>0.47 (0.04)</td>
<td>0.51 (0.04)</td>
<td>0.41 (0.08)</td>
</tr>
</tbody>
</table>

1 M_U: medium/unburn, H_U: high/unburn, L_B: low/burn, M_B: medium/burn (refer to Table 5-1).
Table 5-7. Linear contrasts between treatments for relative Shannon’s indices and evenness indices.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Contrast (SE)</td>
<td>p-value²</td>
<td>Contrast (SE)</td>
<td>p-value</td>
<td>Contrast (SE)</td>
<td>p-value</td>
<td>Contrast (SE)</td>
<td>p-value</td>
</tr>
<tr>
<td>Relative Shannon Index</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H_U – 1 = 0</td>
<td>-0.36 (0.11)</td>
<td>0.01*</td>
<td>-0.32 (0.14)</td>
<td>0.29</td>
<td>0.24 (0.15)</td>
<td>0.64</td>
<td>0.68 (0.17)</td>
<td>&lt;0.01**</td>
</tr>
<tr>
<td>L_B – 1 = 0</td>
<td>-0.39 (0.12)</td>
<td>0.02*</td>
<td>-0.61 (0.17)</td>
<td>&lt;0.01**</td>
<td>0.08 (0.16)</td>
<td>1.00</td>
<td>0.27 (0.19)</td>
<td>0.80</td>
</tr>
<tr>
<td>M_B – 1 = 0</td>
<td>0.03 (0.12)</td>
<td>1.00</td>
<td>-1.12 (0.18)</td>
<td>0.02</td>
<td>-0.02 (0.17)</td>
<td>1.00</td>
<td>-0.52 (0.20)</td>
<td>0.09</td>
</tr>
<tr>
<td>M_U – 1 = 0</td>
<td>-0.38 (0.10)</td>
<td>&lt;0.01**</td>
<td>0.07 (0.15)</td>
<td>1.00</td>
<td>0.61 (0.15)</td>
<td>&lt;0.01**</td>
<td>0.47 (0.18)</td>
<td>0.09</td>
</tr>
<tr>
<td>Relative Evenness Index</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H_U – 1 = 0</td>
<td>-0.23 (0.13)</td>
<td>0.51</td>
<td>-0.23 (0.17)</td>
<td>0.82</td>
<td>0.20 (0.16)</td>
<td>0.88</td>
<td>0.27 (0.19)</td>
<td>0.78</td>
</tr>
<tr>
<td>L_B – 1 = 0</td>
<td>-0.22 (0.14)</td>
<td>0.67</td>
<td>-0.39 (0.19)</td>
<td>0.34</td>
<td>0.22 (0.18)</td>
<td>0.88</td>
<td>0.14 (0.21)</td>
<td>1.00</td>
</tr>
<tr>
<td>M_B – 1 = 0</td>
<td>0.06 (0.13)</td>
<td>1.00</td>
<td>-0.74 (0.19)</td>
<td>0.01</td>
<td>0.10 (0.19)</td>
<td>1.00</td>
<td>-0.45 (0.21)</td>
<td>0.31</td>
</tr>
<tr>
<td>M_U – 1 = 0</td>
<td>-0.31 (0.12)</td>
<td>0.11</td>
<td>0.14 (0.17)</td>
<td>0.99</td>
<td>0.55 (0.17)</td>
<td>0.02*</td>
<td>0.26 (0.19)</td>
<td>0.84</td>
</tr>
</tbody>
</table>

¹ The contrasts tested the difference of the indices between the biomass utilization level and the control.

² Significant codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05.

³ H_U: high/unburn, L_B: low/burn, M_B: medium/burn, M_U: medium/unburn (refer to Table 5-1).
Figure Captions

Figure 5-1. Shrub biomass recovery according to (a) regeneration cutting and (b) biomass utilization treatment. Abbreviations for the biomass utilization treatments are described in the text and Table 5-1.

Figure 5-2. Biplot of NMS ordination for shrub species drawn by (a) the means of all measurements (1973 to 2012), and (b) the individual plots of 2012 measurement. In figure (5-2a), two unlabeled data points between 1973 and 2012 points represent 1976 and 1984 measurements, respectively. Table 5-1 describes the abbreviations for the biomass utilization treatments.

Figure 5-3. Dissimilarity indices (Bray-Curtis distance) between the treatments and control for shrub species composition before harvesting (1973) and 2, 10, and 38 years after treatment. Refer to Table 5-3 for abbreviations.

Figure 5-4. Relative abundance (species biomass/total shrub biomass; pooled across all treatments) of shrub species before harvesting (1973) and 2, 10, and 38 years afterward. Abbreviations for species are provided in Table 5-3.

Figure 5-5. Relative (a) Shannon’s indices and (b) evenness indices according to each biomass utilization treatment. The biomass utilization treatments abbreviations are described in Table 5-1.
Figure 5-1.
Figure 5-2.
Figure 5-3.
Figure 5-4.
Figure 5-5.
CHAPTER 6

IMPACT OF INTENSIVE BIOMASS UTILIZATION ON ABOVEGROUND FOREST BIOMASS PRODUCTION, VEGETATION COMPOSITION, AND SOIL TRAITS IN THE NORTHERN ROCKY MOUNTAINS

ABSTRACT

With increasing public demand for more intensive biomass utilization from forests, the concerns over adverse impacts on productivity by nutrient depletion are increasing. We remeasured the 1974 site of the Forest Residues Utilization Research and Development in northwestern Montana to investigate long-term impacts of intensive biomass utilization on aspects of site productivity. The historical experiment was implemented in a western larch (*Larix occidentalis* Nutt.) forest at three biomass utilization levels (high, medium, and low) combined with prescribed post-harvest burning treatments (burned and unburned) under three regeneration cuttings (clearcut, group selection, and shelterwood). Regenerated tree height and diameter at breast height, shrub root collar diameter, and soil properties (C, N, and total organic matter) of the forest floor and mineral soil layers were measured. Regenerated tree, shrub, and total aboveground biomass and total C, N, and organic matter contents of the soil layers were calculated. Results indicated that total organic matter pools at the ecosystem level were similar across regeneration cutting treatments, and there were no differences among the utilization treatments for either aboveground biomass production or soil properties 38 years after harvest. Minor differences observed among treatments seem to originate not from an alteration of nutrient pools, but from differences in regeneration dynamics and responses to burning treatment. Our results indicate that site productivity in this forest type is unaffected by these four biomass utilization levels.
INTRODUCTION

Logging residues such as slash and cull trees, as well as snags and coarse woody debris, have been considered as an important alternative energy feedstock due to increasing cost of fossil fuels and emerging public concerns over climate change. On a global scale, timber harvesting typically removes less than 66% of cut biomass from forests (Parrikka 2004). In northern Rocky Mountains forests, only about half of total aboveground woody biomass is typically extracted (Benson and Schlieter 1980). The harvesting convention for biomass utilization in the western United States seems to have remained constant over past decades (see Simmons et al. 2014), and the development of a bioenergy infrastructure is still at a tentative stage.

The advantages of using forest biomass as an alternative energy feedstock over fossil fuels have been summarized as: 1) reduction of greenhouse gas emissions, 2) improvement of sustainability for rural communities and economies through expanded economic opportunities, 3) reduction of energy costs, 4) reduction of emissions from forest waste burning treatments, 5) mitigation of dependency on foreign energy feedstock imports, and 6) local utilization and recycling of waste materials (Farr and Atkins 2010). It seems likely that federal policies will spur forest woody biomass utilization as a new energy feedstock, and some efforts have already been undertaken. The Energy Policy Act of 2005 and the Energy Independence and Security Act (EISA) of 2007 are two examples of such polocies. Forest harvesting involving a more expanded removal of woody materials – such as whole-tree harvesting or energy-wood harvesting (sensu Benjamin et al. 2010) – seems likely to occur in this region.

Increased biomass removal may possibly have undesirable impacts on soil, water, site productivity, biodiversity, and atmospheric systems (Lattimore et al. 2009). Among these impacts, the effects of intensive harvesting on site productivity have been most addressed (Thiffault et al. 2011). Of primary concern is that more intensive woody biomass removal might deplete nutrient budgets, resulting in the reduction of site productivity. However, since a majority of these studies (e.g., Ares et al. 2007, Fleming
et al. 2006, Roberts et al. 2005) addressed short-term consequences, the long-term impact on site productivity is still widely unknown. Moreover, such research in the inland Northwest forests is relatively limited. Research examining the longer-term impacts of increased biomass utilization on site productivity in this region is required.

Western forests usually require post-harvest fuel reduction treatments involving the shift of organic matter pools (Agee and Skinner 2005). Broadcast burning has provided an inexpensive and effective solution to reduce wildfire hazard. Prescribed burning treatments have been known to increase short-term site productivity through elevation of the N mineralization rate and availability of inorganic N (e.g., Covington and Sackett 1984, DeLuca and Zouhar 2000, Gundale et al. 2005, White 1986). Yet, it has also been proven that burning treatments can affect soil productivity negatively in certain forest ecosystems (e.g., Carter and Foster 2004, Monleon et al. 1997). There is still insufficient research to assess the long-term impacts of prescribed burning (in company with biomass extraction) on site productivity (Carter and Foster 2004).

Site productivity is generally defined as the capacity of a site to produce vegetative biomass. Diverse methods (e.g., site index) have been suggested to measure site productivity directly or indirectly (for details, see Skovsgaard and Vanclay 2008). Among them, measuring stand volume growth provides the most straightforward way to evaluate site productivity. However, stand volume growth can be variable, since individual tree growth can be affected by various factors such as tree age, stand developmental stage, stocking level, and management history (Powers 2006). Fortunately, these sources of variation can be minimized by controlled experiments. Moreover, an indirect alternative measurement of productivity might involve measuring soil properties, such as soil nutrients and/or physical conditions, which can provide reliable methods to evaluate stand growth potential (Powers 2006).

Coram Experimental Forest in western Montana provides a timely opportunity to investigate the long-term impacts of intensive biomass utilization on forest productivity. Here, multidisciplinary research
program was conducted in response to the energy crisis of the early 1970s. One objective of the research effort was to reduce adverse ecological consequences while maximizing the efficiency of harvests (Barger 1980). Biomass utilization treatment levels combined with burning treatments were applied following three common regeneration cuttings in a typical mixed coniferous forest of the northern Rocky Mountains. This paper assesses the impacts of those biomass utilization intensity and prescribed fire treatments on forest productivity 38 years afterwards.

METHODS

Study site

The study was conducted in the Upper Abbot Creek Basin (48°25’N, 113°59’W) of Coram Experimental Forest in northwestern Montana (Figure 6-1). Coram Experimental Forest was established in 1933, and comprises 3,019 ha of the Hungry Horse Ranger District of the Flathead National Forest. It is located 9 kilometers south of Glacier National Park. The elevation of Coram Experimental Forest ranges from 1,195 to 1,615 m (Shearer and Schmidt 1999). Slopes range from 30 to 80%.

The climate of Coram Experimental Forest is classified as a modified Pacific maritime type (Adams et al. 2008). The annual precipitation is 890-1,270 mm, averaging 1,076 mm (Farnes et al. 1995). Most precipitation occurs in the form of snow during November-March. The mean annual temperature is 2 °C to 7 °C, with summer temperature ranging from 13 °C to 17 °C, and winter temperatures typically falling below –18 °C (Hungerford and Schlieter 1984). The length of growing season is between 81 and 160 days (Adams et al. 2008).

Precambrian sedimentary rock, glacial till, and a thin surface of fine-textured volcanic ash are the main soil components of soils on Coram Experimental Forest. The mixture of these soil components created the rich-loamy soils in this area. Although soils on Coram Experimental Forest can be classified
into 6 categories, soil at our study area is classified as a loamy-skeletal isotic Andic Haplocryalf (Soil Survey Staff, 2006). Stands in Coram Experimental Forest were classified into three potential climax vegetation associations (i.e., habitat type) by Pfister et al. (1977): subalpine fir (Abies lasiocarpa (Hook.) Nutt.)/queen-cup bead lily (Clintonia uniflora (Menzies ex Schult. & Schult. f.) Kunth); (ABLA/CLUN), Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)/ninebark (Physocarpus malvaceus (Greene) Kuntze); (PSME/PHMA), and western hemlock (Tsuga heterophylla (Raf.) Sarg)/queen-cup bead lily; (TSHE/CLUN). The dominant habitat type in our study area is ABLA/CLUN (Shearer and Kempf 1999).

Coram Experimental Forest has a suitable condition for a varied mixture of coniferous species (Shearer and Kempf 1999). The majority of the forest is composed of the western larch (Larix occidentalis Nutt.) cover type (Society of American Foresters Cover Type 212, Eyre 1980), associated with Douglas-fir, subalpine fir, and spruces (Picea engelmannii Parry ex Engl. and P. glauca (Moench) Voss), plus western hemlock and western redcedar (Thuja plicata Donn ex D. Don). Paper birch (Betula papyrifera Marshall), black cottonwood (Populus balsamifera L. ssp. trichocarpa (Torr. & A. Gray ex Hook.) Brayshaw), and quaking aspen (Populus tremuloides Michx.) are the main broadleaf tree species. The major shrub species include twinflower (Linnaea borealis L.), ninebark (Physocarpus malvaceus (Greene) Kuntze), white spiraea (Spiraea betulifolia Pall.), kinnikinnick (Arctostaphylos uva-ursi (L.) Spreng.), Sitka alder (Alnus viridis (Chaix) DC. ssp. sinuata (Regel) Á. Löve & D. Löve), Scouler’s willow (Salix scouleriana Barratt ex Hook.), and huckleberry (Vaccinium myrtilloides Michx.) (Shearer and Kempf 1999). The site index (base age 50) is 15.24 to 18.28 m (Schmidt et al. 1976).

**Experimental design**

The experimental design consisted of the combination of three regeneration cuttings (shelterwood, clearcut and group selection) with four biomass utilization levels (Figure 6-1, Table 6-1). Four biomass utilization treatments are composed of three removal levels (high, medium, and low) and subsequent
burning treatments (Table 6-1): M_U (medium/unburn), H_U (high/unburn), L_B (low/burn), and M_B (medium/burn) treatments. The treatments were established in 2 replications at two different elevations (1,195 m - 1,390 m, and 1,341 m - 1,615 m).

For the clearcut (5.7 and 6.9 ha in size) and shelterwood (14.2 and 8.9 ha in size) regeneration cuttings, four biomass utilization subunits were randomly assigned to four adjacent strips stretching down slope. For the group selection cutting, eight cutting clusters averaging 0.3 ha (range 0.1 to 0.6 ha) were arranged in four rows and two columns; biomass utilization subunits were randomly allocated into cluster pairs. Logging was conducted in 1974 via a running skyline yarder to minimize soil disturbance and erosion. The average pre-harvest volume of woody material was 512 m³/ha, which is equivalent to 381.8 Mg/ha when we assume 0.7458 Mg/m³ as a mean specific gravity of green wood and bark weight for the major tree species on our study site (Miles and Smith 2009). A summary of volumes for each harvesting unit and treatment is presented in Table 6-2.

For reduction of fire hazard and seedbed preparation, the prescribed broadcast burning treatment was assigned to two of four utilization treatments. Prescribed broadcast burning was applied in 1975. However, the burning treatments were mild relative to the planned fire treatment due to cool and wet weather. Moreover, the broadcast burning could not be applied to the lower shelterwood units because the moisture contents of dead fuel and duff were above the prescription limits (Artley et al. 1978; Schmidt 1980). As a result, an extra unplanned treatment (i.e., low-unburn treatment) resulted in the lower shelterwood unit. Since this additional treatment renders the experimental design unbalanced and poses a computational problem to analyzing the interaction between regeneration cutting effect and biomass utilization effect, the treatment was excluded from the analyses.

A total of 40 permanent sampling points were established in each cutting unit. The sampling points were systematically located in an 8 × 5 grid at 30.5 m intervals. As a result, ten sampling points (in a 2 ×
5 grid) were assigned to each biomass utilization subunit. For group selection units, five sampling points were allocated within each cluster.

**Data collection and analysis**

*Vegetation biomass*

Since the pilot data collected in 2010 showed that the current tree sizes require a bigger sample size than the original sampling design, a new sampling design was developed for tree surveys. Based on nested circular plots, three concentric circular plots were established using permanent points as plot centers to measure trees that regenerated post-treatment (Table 6-3). Shelterwood units contained residual (unharvested) trees, thus a fourth (larger) plot was added to the nesting system. The plot sizes varied according to the measured tree sizes. Residual tree (larger than 25 cm dbh) were measured in a 12.6 m radius plot (1/20th ha), and pole-sized trees (larger than 10 cm but smaller than 25 cm dbh) were measured in a 5.6 m radius plot (1/100th ha). The plot size for saplings (smaller than 10 cm) was a 2.5 m radius (1/500th ha), and only the trees taller than breast height (1.37 cm) were measured.

In summer 2012, all 280 permanent points in every cutting unit were surveyed as tree plots. Species of each sample tree was recorded. Dbh and height were measured with diameter tape and laser clinometer or height pole. For shrub and seedlings, root collar diameter was measured by caliper from four sampling points (out of ten) in each subunit according to the sample size (Table 6-3). Measurements were used for the computation of biomass using published, species-specific biomass equations: Biomass equations from Standish et al. (1985) were used for ponderosa pine, white pine, and black cottonwood. Equations by Ung et al. (2008) were used for Douglas-fir, Engelmann spruce, lodgepole pine, subalpine fir, western red cedar, and western hemlock. Biomass of western larch was estimated by Gower et al. (1987). Brown (1976)’s equations were used to estimate the shrub biomass. Forbs and grasses were clipped in the 1×1 m plot from the five sampling points in each subunit, and were packaged and sent to the laboratory. For
analysis, the samples were oven-dried to constant weight at 60°C to measure dry weight. For downed woody debris, one line-intercept transect was established in a random direction from each soil sampling point, following the protocol by Brown (1974).

Soil Properties

In each clearcut and shelterwood unit, ten soil sampling points were allocated on two parallel transects in each treatment unit (five cores/transect) for a total of 40 sampling points at 30.48 m spacing. For group selection units, three soil sampling points were assigned to each cluster. At each sampling location, the forest floor (O_i, O_e, and O_a horizons combined) was collected in a 30 cm diameter hoop and its depth was recorded. Organic material <0.6 cm in diameter (i.e., 1-hr fuel) was collected. Mineral soil samples were collected using a 10 cm diameter core sampler to a depth of 30 cm (Jurgensen et al. 1977). The large size of the corer allowed us to obtain samples of the coarse-fragment components. Once the mineral soil core was collected, the sample was removed from the corer and divided into 3 sample depths (0-10, 10-20, and 20-30 cm). Each soil sample was placed in a zip-type bag and taken to the laboratory for processing. All live roots were hand-separated from the forest floor and mineral soil samples. Soil and root samples were dried at 80°C and the mineral soil was passed through a 2 mm mesh sieve to remove coarse fragments. All forest floor and mineral-soil subsamples were ground to pass a 0.04-mm mesh and were analyzed for total carbon and nitrogen with a LECO-600 analyzer (LECO Corp, St. Joseph, Mich.). Total organic matter contents were measured by weight loss after 8-h combustion at 375°C (Ball 1964). Mineral soil carbon, nitrogen, and organic matter contents were corrected for coarse-fragment content and were extrapolated to a hectare basis using the fine-fraction bulk density (Cromack et al. 1999). We did not further analyze the coarse-fragment component (>2 mm), which has been found to contain appreciable amounts of carbon and nitrogen in some soils (Harrison et al. 2003; Whitney and Zabowski 2004).

Statistical analyses
Since the experiment was treated as a split-plot design, all biomass and soil properties were analyzed via the mixed effects modeling approach. Aboveground vegetation biomass was classified into regenerated tree (trees regenerated after harvesting, excluding retained trees in shelterwood units), shrub biomass, and aboveground biomass (regenerated tree + shrub biomass). Five major species (Douglas-fir, subalpine fir, Engelmann spruce, western larch, and paper birch) were tested separately. The shrub layer was divided into three layers (tall, medium, and short) following the Brown’s (1976) classification.

Explanatory variables were regeneration cutting method, biomass utilization treatment, and interaction between these two factors (Table 6-1). Block was treated as a random effect. Since the biomass utilization treatments are compounded with burning treatment and biomass utilization levels as in an incomplete factorial manner, three linear contrasts were introduced to test the treatment effects within a regeneration cutting. That is, to test the effect of biomass utilization levels, the H_U treatment was compared with the M_U treatment, and the L_B treatment was compared with the M_B treatment, respectively. To examine the burning treatment effect, the M_U and M_B treatments were compared. For shrub biomass evaluation, the next-higher shrub layer’s biomass were tested as a covariate. All analyses were conducted through R (R Development Core Team 2008); the lme4 (Bates et al. 2014) package was used to fit the mixed effects model, and multcomp (Hothorn et al. 2014) was used for testing the linear contrasts.

RESULTS

Ecosystem biomass distribution

Mean woody biomass occurring in trees, shrubs, forbs and grasses, woody debris, forest floor, and mineral soil was 423.4 Mg/ha across all regeneration cutting units (Table 6-4; Figure 6-2). In the clearcut and group selection units, 420.0 and 430.0 Mg/ha of biomass were allocated from mineral soil layer to overstory tree layer. In the shelterwood unit, the biomass of trees retained from the previous harvest
(115.3 Mg/ha) was approximately 27% of the total ecosystem biomass (419.4 Mg/ha) and 85% of total aboveground live vegetation biomass (135.6 Mg/ha).

Thirty eight years after harvesting, the forest floor was the biggest organic matter pool. Approximately 39% (166.6 Mg/ha) of total organic matter in the ecosystem was found in the forest floor. Combined with mineral soil (70.5 Mg/ha) organic matter pools, more than 56 % of total ecosystem organic matter was distributed in belowground pools. These forest floor and mineral soil organic matter pools were approximately 3 times the biomass of aboveground vegetation, including retained trees in shelterwood units.

**Vegetation response to harvest and burn treatments**

Total aboveground biomass (including regenerated trees, shrubs, forbs, and grasses) in clearcut units was the highest 38 years after harvesting (Table 6-4, Figure 6-3a). In 2012 the mean aboveground biomass in clearcut units was 61.6 Mg/ha (SE = 5.1 Mg/ha). The mean aboveground biomass in the group selection and shelterwood units were 45.9 Mg/ha (SE = 4.4 Mg/ha) and 20.8 Mg/ha (SE = 3.6 Mg/ha), respectively. Analysis of variance (ANOVA) indicated that there were no significant differences in biomass among either regeneration cuttings or biomass utilization levels (Table 6-5). The linear contrast among biomass utilization levels and burning treatments indicated that total aboveground biomass production was not affected by these factors regardless of the regeneration cutting method (Table 6-6).

Mean height, dbh and crown ratio of regenerated trees were 4.8 m, 5.1 cm, and 64.4%, respectively. Regenerated tree biomass accounted for 84% of total aboveground biomass. Clearcut units produced the highest regeneration tree biomass (56.0 Mg/ha; SE = 3.1 Mg/ha), followed by the group selection and shelterwood at 34.5 Mg/ha (SE = 3.5 Mg/ha) and 19.7 Mg/ha (SE = 2.8 Mg/ha), respectively. Unlike total aboveground biomass, differences in regenerated tree biomass were significant among both regeneration
cuttings and biomass utilization levels (Table 6-5; P < 0.01). The M_U treatment in the shelterwood units had higher biomass production than H_U and M_B treatments (P = 0.005, and 0.01, respectively). Regenerated tree biomass in clearcut and group selection units did not differ.

Five major tree species (subalpine fir, Douglas-fir, Engelmann spruce, paper birch, and western larch) composed 96% of total regenerated tree biomass. Paper birch and western larch were relatively unaffected by the biomass utilization treatments (Table 6-6). Subalpine fir and Douglas-fir responded only to the burning treatment. Subalpine fir biomass in the burning treatments were 13.3 and 12.8 Mg/ha less than the unburned treatments in group selection (P = 0.004) and shelterwood units (P = 0.041). In contrast, the burning treatment increased Douglas-fir biomass by 16.0 Mg/ha (P = 0.036) in the clearcut unit. Engelmann spruce responded in a similar manner to subalpine fir, where broadcast burning decreased biomass production by 0.7 and 9.3 Mg/ha at the medium biomass utilization level in the clearcut and shelterwood units. In addition, the high biomass removal without broadcast burning decreased Engelmann spruce’s biomass production by 9.0 Mg/ha as compared to the medium biomass removal without broadcast burning.

Although tall shrub biomass seemed generally unaffected by biomass utilization treatments (Table 6-5), there was a significant difference between the M_B and L_B treatments in the group selection harvest units (Table 6-6). The M_B treatment in the group selection increased 13.9 Mg/ha of tall shrub biomass relative to the L_B treatment (P = 0.009), and was the major reason for a significant increase in total shrub biomass. Short shrub biomass was 1.1Mg/ha (P = 0.014) greater in the H_U treatment as compared to the M_U treatment for group selection. Short shrub biomass of the M_B treatment was 1.3 Mg/ha (P = 0.038) greater than the M_U treatment in the shelterwood unit. Tall shrub biomass production was unaffected by overstory tree biomass. Similarly, medium and short shrub biomass production was not influenced by high and medium shrub biomass, respectively.
Soil response to harvest and burn treatments

Forest floor organic matter, carbon, and nitrogen pools showed similar patterns in 2012 (Figure 6-4). The interaction terms between regeneration cutting and utilization treatment were significant for all forest floor analyses (Table 6-4). However, differences in organic matter, carbon, and nitrogen pools among biomass utilization treatments were significant only in the clearcut units (Table 6-6). Increased biomass utilization intensity (i.e., H_U vs. M_U, and M_B vs. L_B) tended to increase organic matter, carbon and nitrogen. In addition, broadcast burning increased total organic matter (143.8 Mg/ha; P = 0.046) and carbon pools (89.1 Mg/ha; P = 0.019) in the medium utilization subunits of the clearcut units.

Within the mineral soil profile (0-30 cm depth), organic matter pools were unaffected by biomass utilization treatment, or by regeneration cutting (Table 6-5). Carbon and nitrogen pools were significantly different among the biomass utilization treatments, but only between the H_U treatment and M_U treatment in clearcut units: the H_U subunits had 25.4 Mg/ha (P < 0.001) more carbon and 0.5 Mg/ha (P = 0.040) more nitrogen than the M_U treatment.

DISCUSSION

Ecosystem biomass and nutrients distribution

We had little pre-harvest tree biomass data for our study sites. However, we refer to a recent study conducted in nearby western larch forest (Bisbing et al. 2010). Biomass production can be directly converted into carbon content, thus we can compare our results with results of other ecosystem carbon distribution research. Bisbing et al. (2010) reported that the mean overstory carbon content (i.e., about 50% of wood biomass) of western larch stands 40 years after harvest was 23.83 Mg C/ha, assuming the carbon contents of wood is 50%. Excluding shelterwood units, the overall overstory carbon content of our study site 38 years after harvest was 22.64 Mg C/ha. Seemingly, the aboveground biomass production of our site does not differ from second-growth stands harvested by the conventional harvesting standard.
This level of overstory biomass is 15.7% of the overstory biomass in old-growth western larch stands of western Montana (144.23 Mg C/ha; Bisbing et al. 2010).

There are few soil impacts noted 38 years after harvest. Since these sites were skylined logged, few if any detrimental soil impacts during harvesting can be expected. When this study was initiated in 1974 there was concern that the use of broadcast burning and intensive utilization of woody material would deplete the site’s carbon, organic matter and nitrogen cycling capability (Harvey et al. 1976). After 38 years, organic matter on the soil surface was unaffected by the utilization and burning treatments. More intensive and burning treatments actually increased organic matter on the soil surface in clearcut units (Table 6-4). Due to the abundant soil surface and belowground organic matter pools, our study site had more than 1.5 times greater organic matter and carbon pools than other second growth western larch forests, and approximately 1/2 the amounts found in old-growth stands (Bisbing et al. 2010). We also found that the similar aboveground vegetation and coarse root biomass production with second-growth stands reported by Bisbing et al. (2010).

Soil carbon or organic matter pools in the forest floor and mineral soil were 133.7 Mg C/ha and 237.02 Mg OM/ha, respectively, (excluding coarse woody debris C) and are slightly higher than carbon pools found in an old-growth western larch stand (99.28 Mg C/ha; Bisbing et al. 2010). However, in a study evaluating soil pools, Page-Dumroese and Jurgensen (2006) found that in late-successional subalpine fir and western hemlock stands in northwestern Montana, forest floor and mineral soil organic matter pools ranged from 171-391 Mg/ha, while carbon pools ranged from 85-178 Mg/ha. Together, these three studies (ours, Bisbing et al. (2010), and Page-Dumroese and Jurgensen (2006)) show that there is significant variation in carbon, organic matter, and nitrogen pools depending on site and stand conditions. However, in all cases there was abundant storage or building of organic matter pools on the soil surface and in the mineral soil, which should ameliorate concerns that soil organic matter might be exhausted by intensive biomass utilization.
Thirty-eight years after harvest and site treatment (utilization and broadcast burning), a greater proportion of organic matter was in the forest floor than the mineral soil. This is similar to some late-successional stands in the Inland northwest (Page-Dumroese and Jurgensen 2006), but many mature forest types show a pattern of greater organic matter in the mineral soil than in the forest floor (e.g., Grier et al. 1981, Harmon et al. 1990, Harmon et al. 2004). For this CEF site, high organic matter contents in the forest floor are likely related to prolific understory vegetation production. Bisbing et al. (2010) reported that the understory carbon pools of adjacent old-growth and second growth western larch stands in northwestern Montana were 0.23 and 0.44 Mg C/ha, respectively; in comparison, carbon pools of the understory at our site was 3.61 Mg C/ha. We speculate that the abundant shrub vegetation contributed to increased depth of the forest floor and therefore greater organic matter pools. Thick forest floor layers are regulated by site microclimate resulting in slower or faster organic matter decomposition rates.

In many Inland Northwest stands, most of the carbon and organic matter pools are held on the soil surface (inclusive of woody residues), whereas nitrogen pools are primarily located in the mineral soil (Page-Dumroese and Jurgensen 2006). However, on our study sites, 2.8 and 1.7 Mg N/ha of nitrogen were distributed in the forest floor and the mineral soil, respectively. The nitrogen content of mineral soil at our site is approximately 70 % of the nitrogen pool of late-successional conifer forests in northwestern Montana (sensu MT1 in Page-Dumroese and Jurgensen 2006). Meanwhile, the forest floor at our site had nitrogen contents 14 times greater than those of the aforementioned conifer forests. Consistent with the soil organic matter and carbon pool, the relative abundance of nitrogen in the forest floor can also be attributed to the richness of understory vegetation.

**Vegetation response to harvest and burn treatments**

Regeneration biomass of the shelterwood units was lower than both clearcut and group selection units, presumably because competition with retained overstory trees in shelterwood units limited the
growth rate or stocking level of seedlings after harvest (e.g., Long and Roberts 1992; Oliver and Dolph 1992; Rose and Muir 1997). Similarly, the result that group selection units had lower stand biomass than clearcut units suggests that regenerated trees were affected by the residual trees around cutting cluster boundaries (Table 6-4; Figure 6-3).

Although this study was implemented with a unique set of biomass utilization levels, the results are comparable to empirical studies contrasting the consequences between whole-tree harvesting and conventional (i.e., stem-only) harvesting. In northern Europe, tree response has been shown to decline with increasing levels of biomass utilization. For example, whole-tree harvesting reduced the dbh for 23-year-old planted Sitka spruce (*Picea sitchensis* (Bong.) Carrière) seedlings by ten percent, versus stem-only harvesting in North Wales (Walmsley et al. 2009). In an earlier study, whole-tree harvesting reduced the volume of planted Sitka spruce seedlings by 32% after 12 years, relative to conventional harvesting (Proe et al. 1996). In Scandinavia, Egnell and Leijon (1999) and Jacobson et al. (2000) found consistent reductions of tree growth for Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) stands 10-15 years after whole-tree harvesting, versus stem-only harvesting.

On the other hand, the continent-scale North American Long-Term Soil Productivity (LTSP) study illustrates another consequence of intensive biomass utilization. The general conclusion of the LTSP study is that biomass extraction intensity had no impact on vegetation growth 10 years after harvesting (Powers et al. 2005). However, there was substantial variation in vegetation response to biomass utilization intensity for species, soil disturbance, and elapsed time after harvesting (e.g., Egnell and Valinger 2003; Kranabetter et al. 2006). Thus, examining the response of each species is necessary for a better understanding of the consequences of intensive biomass utilization (Kranabetter et al. 2006). At the CEF, except for the M_U treatment in shelterwood, the results indicate that there is no evidence for reduced regenerated tree growth by biomass removal intensity, irrespective of regeneration cutting.
method and burning treatment. Therefore, our findings in this cool, wet ecosystem are generally consistent with those of the LTSP study.

One of the most prominent differences observed in this study is that the M_U treatment in shelterwood cuts had the highest level of biomass production (Figure 6-3b). However, the outcome is probably not due to difference in nutrients but to the presence of advance regeneration in this treatment. Since the M_U treatment protected the understory vegetation (Table 6-1), it retained abundant advance regeneration (Table 6-2). Delay of natural regeneration on the other treatments exacerbated this difference. Shearer and Schmidt (1999) noted that the CEF had suffered from an intense western spruce budworm (Choristoneura occidentalis Freeman) outbreak around the harvest year, and Shearer (1980) reported that reproductive buds of conifers were damaged severely in 1974 by spruce budworm. Cone production was limited, so conifer regeneration was delayed for years; Shearer and Schmidt (1999) noted that the majority of regeneration (besides western larch) established after 1980. Therefore, we infer that the reason M_U treatment in the shelterwood units produce the same amount of biomass as group selection is not because of nitrogen nutrient changes associated with the harvest types, but because of the success of immediate regeneration.

The combination of regenerated tree and shrub biomass was not different among treatments. In other words, even those few differences in regenerated tree biomass were offset by the inclusion of shrub biomass. This suggests that the difference in regenerated tree biomass was caused by different vegetation dynamics rather than differences in soil nitrogen, organic matter or carbon. The fact that scatterplots relating aboveground biomass to carbon, nitrogen, and organic matter contents in the forest floor and mineral soil layers reveal no correlations, further supports this theory (Figure 6-5).

The response of each species differed across treatments, indicating that species composition is shaped by biomass utilization treatments. Differences can be primarily attributed to broadcast burning rather than the intensity of biomass extraction. Significant differences were observed between burned and unburned
treatments (Table 6-6). Species composition is the cumulative result of the response of each species to broadcast burning. Most juvenile conifers are vulnerable to fire, thus broadcast burning likely killed most advance regeneration. Subalpine fir and Engelmann spruce show relatively slower initial seedling growth than other coniferous species (i.e., western larch and Douglas-fir). Thus, the elimination of advance regeneration, in company with the hindrance of immediate regeneration by spruce budworm, may have substantially reduced the relative proportions of these species. In contrast, Douglas-fir seems to have benefited from broadcast burning through decreased competition.

Thirty-eight years after harvesting, shrub biomass exceeded its pre-harvest level. Biomass of the shrub layer prior to harvesting was 5.9 Mg/ha on average (Schmidt 1980), versus the current shrub biomass of 7.0 Mg/ha; shrub biomass recovery has exceeded that of the pre-harvest stand by 19%. It seems that recovery of understory vegetation was completed rather early. Schmidt (1980) reported that shrub biomass had recovered to 56% and 75% of the pre-harvest level within 2 and 4 years after harvest, respectively. We expect that the shrub layer likely played a more prominent role in building the forest floor organic matter pool than the regenerated trees.

Tall shrub layer biomass production at the M_B treatment in the group selection units has considerable biomass, mostly attributed to Rocky Mountain maple (*Acer glabrum* Torr.). Total shrub biomass was dominated by the disproportionately high production of maple in this treatment: maple biomass was 18.7 Mg/ha (84% of total shrub biomass, whereas maple averaged 48% of total in other treatments) and was more than 10 times greater than the biomass of maple in other treatments. Since broadcast burning conditions in 1975 were not favorable, the fire treatment was relatively benign (Artley et al. 1978). As a result, buds on stumps of mature maples likely survived the fire and sprouted prolifically, producing shoots that benefited from increased resource availability and decreased competition.
Soil response to harvest and burn treatments

Previous studies of soil responses to intensive biomass harvesting have produced conflicting results. A meta-analysis by Johnson and Curtis (2001) indicated that whole-tree harvesting tended to reduce soil carbon and nitrogen, whereas stem-only harvesting increased content of both elements. In contrast, several studies report no impact of biomass removal intensity on soil carbon or nitrogen budgets. Olsson et al. (1996) found no difference of soil carbon and nitrogen pools between whole-tree harvesting and stem-only harvesting in Swedish boreal forests 15-16 years after harvesting. Similar results were also found in the boreal forest of Canada (Thiffault et al. 2006). At the North America LTSP sites, treatments that retained an intact forest floor prevented any decline in soil carbon contents 5 to 15 years after harvesting (Kabzems and Haeussler 2005; Powers et al. 2005; Kurth et al. 2014).

Our findings are generally consistent with the results from the LTSP study. Aside from the clearcut units, none of our measured soil properties were affected by biomass utilization intensity. The Pearson’s correlation test indicated no evidence of correlation between aboveground biomass and measured soil properties (Figure 6-5), implying these soil properties were not limiting factors to aboveground biomass production. Nitrogen often limits tree growth in this region due to low nitrogen mineralization levels (DeLuca and Zoubar 2000); these results should lessen concerns that increased biomass extraction will exacerbate nitrogen limitations in this region.

It is unclear why the clearcut units exhibited differences in forest floor properties. We hypothesize that litterfall production in the clearcut units was sufficiently abundant to initiate organic matter accumulation on the forest floor, and that organic matter, carbon, and nitrogen contents in the forest floor responded to that litter production. Another interesting result in the clearcut units is that higher biomass removal treatments and broadcast burning in clearcut units produced greater carbon, nitrogen, and organic matter in the forest floor than did the lower utilization levels. Presumably, this is related to the rapid recovery rate and cumulative organic matter production of the shrub layer. Schmidt (1980) reported that
the recovery rate of the shrub layer four years after harvesting was higher in the clearcuts than other regeneration cuttings. In other words, intensive biomass removal decreased competition and increased the utilization of released nutrients, thus rapidly accelerating the understory recovery rate. Prolific understory vegetation annually produced abundant fresh litter, and resulted in elevated levels of forest floor organic matter. The fact that the pattern of each soil property (Figure 6-4) within clearcut units showed an identical pattern with those of shrub biomass in clearcut units (Figure 6-3) makes this a plausible explanation. Turner and Long (1975) emphasized the importance of understory vegetation on site productivity in the early development stage of coastal Douglas-fir stands. Shrubs annually allocate relatively more organic matter into a fresh litter source (i.e., leaves) than do overstory trees. Thus, prompt understory re-vegetation after harvesting might have a significant impact on preventing adverse consequences to site productivity after harvesting.

It is well known that organic matter in the forest floor can enhance soil productivity. This study’s evidence of abundant woody residue in the forest floor 38 years after harvest and treatment should help further abate concerns over potential deterioration of site productivity. Organic matter can increase soil moisture by regulating soil temperature and preventing evaporative loss (Powers et al. 2005). Woody debris has been shown to hold soil moisture more than 5 times than mineral soil in a Douglas-fir stand of northern Idaho (Page-Dumroese et al. 1990). Soil organic matter can also enhance the aeration of mineral soil and contribute to the formation of more stable soil aggregates by binding soil particles (Jastrow 1996). Moreover, organic matter can provide essential food and habitat to various soil biotas; therefore, soil organic matter determines soil microbe activity. Harvey et al. (1976) suggested that 95% of total active ectomycorrhizae were distributed in soil organic matter.

Differences in soil traits among the biomass utilization treatments in the forest floor did not also correspond to the differences in the mineral soil layer (Table 6-6). It seems that the majority of carbon from the forest floor was not incorporated into the mineral soil layer, but was instead released to
atmosphere as CO$_2$ (Palviainen et al. 2004; Kurth et al. 2014). This result supports the contention that the primary carbon inputs to the mineral soil pool originate not from aboveground litter fall, but from root turnover in the soil layer (Powers et al. 2005). Despite this, the importance of the forest floor organic matter should not be overlooked because of the other critical functions it performs.

**CONCLUSION**

We found that total organic matter pools at the ecosystem level were similar regardless of regeneration cuttings, and conclude that there were no negative consequences of intensive biomass utilization on forest productivity 38 years after harvesting. This study indicated that at this relatively moist and cool site, long-term negative impacts of intensive biomass utilization on site productivity are not evident across all regeneration cutting methods. Regenerated trees showed some differences among regeneration cutting methods, but any differences in aboveground growth or composition was likely caused by inherent regeneration dynamics rather than disruption of soil carbon, organic matter, or nitrogen pools. Observed minor differences in biomass production among the biomass utilization treatments were also explained by regeneration dynamics rather than alteration of nutrient pools. The species composition of regenerated trees might be affected by utilization treatments, but the burning treatment seems to be the factor of primary influence in determining species composition.

Furthermore, we observed no difference in soil pools associated with biomass utilization levels and the use of broadcast burning (albeit, burning) when the soil was cool and wet. Belowground carbon, nitrogen, and organic matter contents were not correlated with aboveground biomass, implying these soil properties were not limiting factors for vegetation growth. Soil properties of the mineral soil layer and forest floor were generally unaffected by biomass utilization levels. The few observed differences among soil properties at the forest floor followed clearcutting, and were attributed to the recovery and cumulative biomass production of the shrub layer, rather than to changes in soil properties.
These findings imply that intensified biomass removal from this forest type should not cause a decline in site productivity. Our results may not extend to other forest types, even within the northern Rocky Mountain region. Treatment effects can vary by diverse factors such as site conditions and species composition (Thiffault et al. 2011), so lesser productive, drier sites might exhibit different results. In addition, disturbance of the forest floor by other logging systems could produce different consequences. Whereas the skyline yarder technique used at our site minimized soil perturbation, intensive biomass removal through ground-based harvesting operations are more likely to adversely impact soils. Differences between our results and those from European trials might be caused by these factors. We conclude that subsequent studies comparing both more and less productive sites of various forest types, soil and climate conditions, and harvesting techniques are essential to fully understanding the relation of biomass utilization to site productivity for that range of circumstances.

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REFERENCES


Table 6-1. Design of the utilization treatments within harvesting units (from Benson and Schlieter 1980; Shearer and Schmidt 1999; Shearer and Kempf 1999).

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<thead>
<tr>
<th>Treatment Name</th>
<th>Abbreviation</th>
<th>Cut trees¹</th>
<th>Max. size of retained woody materials²</th>
<th>Post-harvest treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium-unburn</td>
<td>M_U</td>
<td>&gt;17.8 cm dbh</td>
<td>7.6 cm × 2.4 m</td>
<td>Understory protected/unburned</td>
</tr>
<tr>
<td>High-unburn</td>
<td>H_U</td>
<td>All trees</td>
<td>2.5 cm × 2.4 m</td>
<td>Slashed/unburned</td>
</tr>
<tr>
<td>Low-burn</td>
<td>L_B</td>
<td>All trees</td>
<td>14.0 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
<tr>
<td>Medium-burn</td>
<td>M_B</td>
<td>All trees</td>
<td>7.6 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
</tbody>
</table>

¹ Except designated overstory shelterwood trees.
² Live and dead down logs (small-end diameter × length); for dead down logs, they were removed if sound enough to yard.
³ 1974 Forest Service Standards.
Table 6-2. Volumes of all woody material (>7.62 cm diameter, unit: m$^3$/ha) pre- and post-harvest (Benson and Schlieter 1980). Utilization treatment levels are listed in Table 6-1. Block 1 and 2 are low and high elevation replication, respectively. Numbers in parentheses of post-harvest volume column represent retained overstory tree/sapling volumes.

<table>
<thead>
<tr>
<th>Harvest/Treatment</th>
<th>Pre-harvest Volume</th>
<th>Post-harvest Volume</th>
<th>Removed Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Block1</td>
<td>Block2</td>
<td>Block1</td>
</tr>
<tr>
<td>Shelterwood</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M_U</td>
<td>369</td>
<td>347</td>
<td>255 (113/20)</td>
</tr>
<tr>
<td>H_U</td>
<td>410</td>
<td>319</td>
<td>193 (21/0)</td>
</tr>
<tr>
<td>L_B</td>
<td>348</td>
<td>308</td>
<td>257 (112/1)</td>
</tr>
<tr>
<td>M_B</td>
<td>479</td>
<td>470</td>
<td>269 (177/2)</td>
</tr>
<tr>
<td>Group Selection</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M_U</td>
<td>694</td>
<td>715</td>
<td>92 (0/11)</td>
</tr>
<tr>
<td>H_U</td>
<td>577</td>
<td>530</td>
<td>42 (0/0)</td>
</tr>
<tr>
<td>L_B</td>
<td>492</td>
<td>1042</td>
<td>88 (0/0)</td>
</tr>
<tr>
<td>M_B</td>
<td>654</td>
<td>581</td>
<td>123 (0/0)</td>
</tr>
<tr>
<td>Clearcut</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M_U</td>
<td>483</td>
<td>450</td>
<td>71 (0/2)</td>
</tr>
<tr>
<td>H_U</td>
<td>414</td>
<td>387</td>
<td>66 (0/0)</td>
</tr>
<tr>
<td>L_B</td>
<td>469</td>
<td>564</td>
<td>167 (0/0)</td>
</tr>
<tr>
<td>M_B</td>
<td>570</td>
<td>617</td>
<td>121 (0/0)</td>
</tr>
</tbody>
</table>

$^1$M_U: medium/unburn, H_U: high/unburn, L_B: low/burn, M_B: medium/burn (refer to Table 6-1).
Table 6-3. Plot sizes and radii for vegetation measured.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Classification</th>
<th>Plot size</th>
<th>Plot radius (m)</th>
<th>Sampled tree size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trees</td>
<td>Residual trees</td>
<td>1/20&lt;sup&gt;th&lt;/sup&gt; ha</td>
<td>12.62</td>
<td>≥25 cm dbh</td>
</tr>
<tr>
<td></td>
<td>Poles</td>
<td>1/100&lt;sup&gt;th&lt;/sup&gt; ha</td>
<td>5.64</td>
<td>≥10 and &lt;25 cm dbh</td>
</tr>
<tr>
<td></td>
<td>Saplings</td>
<td>1/500&lt;sup&gt;th&lt;/sup&gt; ha</td>
<td>2.52</td>
<td>&lt;10 cm dbh and ≥ 137 cm ht</td>
</tr>
<tr>
<td>Seedling and Shrubs</td>
<td>Low shrubs</td>
<td>1/5000&lt;sup&gt;th&lt;/sup&gt; ha</td>
<td>0.80</td>
<td>&lt;100 cm ht</td>
</tr>
<tr>
<td></td>
<td>High shrubs</td>
<td>1/1000&lt;sup&gt;th&lt;/sup&gt; ha</td>
<td>1.78</td>
<td>≥100 cm ht</td>
</tr>
</tbody>
</table>
Table 6-4. Ecosystem biomass (Mg/ha) distribution of each compartment 38 years after harvesting. Values in parentheses are standard errors of the means.

<table>
<thead>
<tr>
<th>Regeneration Cutting</th>
<th>Biomass Utilization Treatment</th>
<th>Retained Tree</th>
<th>Regenerated Tree</th>
<th>Understory¹</th>
<th>Forbs and Glasses</th>
<th>Woody Debris</th>
<th>Forest Floor</th>
<th>Coarse Roots²</th>
<th>Mineral Soil</th>
<th>Total Ecosystem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clearcut</td>
<td>M_U³</td>
<td>-</td>
<td>48.1 (6.5)</td>
<td>5.1 (2.1)</td>
<td>0.2 (0.1)</td>
<td>51 (9)</td>
<td>125.9 (18.3)</td>
<td>12.5 (1.7)</td>
<td>62.4 (4.4)</td>
<td>305.2</td>
</tr>
<tr>
<td></td>
<td>H_U</td>
<td>-</td>
<td>59.3 (7.0)</td>
<td>7.1 (1.7)</td>
<td>0.2 (0.1)</td>
<td>59 (19)</td>
<td>280.6 (73.3)</td>
<td>15.4 (1.8)</td>
<td>81.6 (8.7)</td>
<td>503.2</td>
</tr>
<tr>
<td></td>
<td>L_B</td>
<td>-</td>
<td>61.1 (6.1)</td>
<td>4.7 (1.4)</td>
<td>0.5 (0.2)</td>
<td>82 (15)</td>
<td>123.5 (23.9)</td>
<td>15.9 (1.6)</td>
<td>71.2 (15.2)</td>
<td>358.9</td>
</tr>
<tr>
<td></td>
<td>M_B</td>
<td>-</td>
<td>55.6 (5.2)</td>
<td>7.8 (3.2)</td>
<td>0.1 (0.0)</td>
<td>99 (21)</td>
<td>269.9 (46.6)</td>
<td>14.5 (1.4)</td>
<td>66.7 (4.3)</td>
<td>513.6</td>
</tr>
<tr>
<td>Group Selection</td>
<td>M_U</td>
<td>-</td>
<td>32.8 (5.8)</td>
<td>7.5 (2.3)</td>
<td>0.2 (0.1)</td>
<td>213 (40)</td>
<td>191.6 (40.9)</td>
<td>10.7 (1.5)</td>
<td>58.4 (5.3)</td>
<td>514.2</td>
</tr>
<tr>
<td></td>
<td>H_U</td>
<td>-</td>
<td>35.7 (5.5)</td>
<td>4.1 (0.8)</td>
<td>0.7 (0.5)</td>
<td>86 (20)</td>
<td>137.1 (36.4)</td>
<td>9.3 (1.4)</td>
<td>71.5 (8.3)</td>
<td>344.4</td>
</tr>
<tr>
<td></td>
<td>L_B</td>
<td>-</td>
<td>37.1 (4.5)</td>
<td>4.8 (2.6)</td>
<td>0.7 (0.4)</td>
<td>183 (60)</td>
<td>186.8 (35.5)</td>
<td>9.7 (1.2)</td>
<td>78.2 (5.9)</td>
<td>500.3</td>
</tr>
<tr>
<td></td>
<td>M_B</td>
<td>-</td>
<td>32.6 (4.7)</td>
<td>18.7 (6.5)</td>
<td>0.8 (0.2)</td>
<td>70 (24)</td>
<td>159.4 (33.5)</td>
<td>8.6 (1.3)</td>
<td>72.9 (11.0)</td>
<td>363.0</td>
</tr>
<tr>
<td>Shelterwood</td>
<td>M_U</td>
<td>125.2 (11.3)</td>
<td>33.9 (5.0)</td>
<td>6.7 (3.0)</td>
<td>0.3 (0.2)</td>
<td>37 (7)</td>
<td>118.5 (20.3)</td>
<td>41.4 (3.8)</td>
<td>59.7 (5.3)</td>
<td>422.7</td>
</tr>
<tr>
<td></td>
<td>H_U</td>
<td>105.5 (11.2)</td>
<td>11.2 (3.6)</td>
<td>4.2 (1.2)</td>
<td>0.1 (0.0)</td>
<td>27 (10)</td>
<td>88.1 (16.3)</td>
<td>30.3 (3.9)</td>
<td>75.7 (9.7)</td>
<td>342.1</td>
</tr>
<tr>
<td></td>
<td>L_B</td>
<td>123.9 (13.6)</td>
<td>4.6 (2.8)</td>
<td>6.7 (3.2)</td>
<td>0.4 (0.1)</td>
<td>77 (16)</td>
<td>129.9 (36.0)</td>
<td>33.4 (3.2)</td>
<td>63.3 (4.2)</td>
<td>439.2</td>
</tr>
<tr>
<td></td>
<td>M_B</td>
<td>106.5 (16.9)</td>
<td>9.0 (2.9)</td>
<td>4.8 (1.8)</td>
<td>0.2 (0.1)</td>
<td>52 (9)</td>
<td>187.6 (25.3)</td>
<td>30.0 (2.7)</td>
<td>83.8 (19.2)</td>
<td>473.9</td>
</tr>
</tbody>
</table>

¹ Shrub and seedling biomass were combined.
² Coarse roots biomass was estimated through the equation of Carins et al. (1997). The ratio of 0.26 to overstory biomass was applied.
³ M_U: medium/unburn, H_U: high/unburn, L_B: low/burn, M_B: medium/burn (refer to Table 6-1).
Table 6-5. Results summary of ANOVA for aboveground biomass and soil properties.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Harvest (H)</th>
<th></th>
<th>Utilization (U)</th>
<th></th>
<th>H×U</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F value</td>
<td>p-value</td>
<td>F value</td>
<td>p-value</td>
<td>F value</td>
<td>p-value</td>
</tr>
<tr>
<td>Total aboveground biomass</td>
<td>7.258</td>
<td>0.121</td>
<td>0.367</td>
<td>0.777</td>
<td>1.447</td>
<td>0.208</td>
</tr>
<tr>
<td>Regenerated tree biomass</td>
<td>16.986</td>
<td>0.056</td>
<td>0.813</td>
<td>0.488</td>
<td>3.825</td>
<td>0.001**</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>2.743</td>
<td>0.267</td>
<td>20.321</td>
<td>&lt;0.0001***</td>
<td>0.774</td>
<td>0.591</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>4.661</td>
<td>0.177</td>
<td>3.191</td>
<td>0.025*</td>
<td>3.280</td>
<td>0.004**</td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td>2.593</td>
<td>0.278</td>
<td>8.517</td>
<td>&lt;0.0001***</td>
<td>2.376</td>
<td>0.030*</td>
</tr>
<tr>
<td>Paper birch</td>
<td>1.014</td>
<td>0.496</td>
<td>1.506</td>
<td>0.214</td>
<td>1.951</td>
<td>0.074</td>
</tr>
<tr>
<td>Western Larch</td>
<td>9.842</td>
<td>0.092</td>
<td>2.755</td>
<td>0.044*</td>
<td>2.095</td>
<td>0.055</td>
</tr>
<tr>
<td>Shrub biomass</td>
<td>1.186</td>
<td>0.458</td>
<td>2.592</td>
<td>0.059</td>
<td>1.524</td>
<td>0.181</td>
</tr>
<tr>
<td>High</td>
<td>0.838</td>
<td>0.544</td>
<td>2.668</td>
<td>0.054</td>
<td>1.616</td>
<td>0.154</td>
</tr>
<tr>
<td>Medium</td>
<td>0.271</td>
<td>0.787</td>
<td>1.932</td>
<td>0.131</td>
<td>1.306</td>
<td>0.265</td>
</tr>
<tr>
<td>Low</td>
<td>0.213</td>
<td>0.824</td>
<td>6.280</td>
<td>&lt;0.001***</td>
<td>1.523</td>
<td>0.182</td>
</tr>
<tr>
<td>Forest floor</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Organic matter</td>
<td>2.879</td>
<td>0.258</td>
<td>1.944</td>
<td>0.125</td>
<td>2.307</td>
<td>0.036*</td>
</tr>
<tr>
<td>Carbon contents</td>
<td>3.384</td>
<td>0.228</td>
<td>2.298</td>
<td>0.078</td>
<td>2.770</td>
<td>0.014*</td>
</tr>
<tr>
<td>Nitrogen contents</td>
<td>2.416</td>
<td>0.293</td>
<td>1.796</td>
<td>0.150</td>
<td>2.912</td>
<td>0.010*</td>
</tr>
<tr>
<td>Mineral soil (0-30cm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Organic matter</td>
<td>0.029</td>
<td>0.972</td>
<td>1.639</td>
<td>0.183</td>
<td>0.493</td>
<td>0.813</td>
</tr>
<tr>
<td>Carbon contents</td>
<td>0.332</td>
<td>0.751</td>
<td>7.247</td>
<td>&lt;0.001***</td>
<td>2.441</td>
<td>0.029*</td>
</tr>
<tr>
<td>Nitrogen contents</td>
<td>0.785</td>
<td>0.560</td>
<td>5.494</td>
<td>0.001**</td>
<td>3.143</td>
<td>0.007**</td>
</tr>
</tbody>
</table>

1 Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05.
Table 6-6. Test results of the linear contrasts for aboveground biomass and soil properties (units: Mg/ha).

<table>
<thead>
<tr>
<th>Response variables</th>
<th>H_U – M_U¹</th>
<th>M_B – L_B</th>
<th>M_B – M_U</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CC²</td>
<td>GS</td>
<td>SW</td>
</tr>
<tr>
<td>Total aboveground biomass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regenerated tree biomass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>7.976</td>
<td>0.363</td>
<td>-2.728</td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td>-4.796</td>
<td>-1.343</td>
<td>-8.992***</td>
</tr>
<tr>
<td>Paper birch</td>
<td>-2.226</td>
<td>5.254</td>
<td>-1.100</td>
</tr>
<tr>
<td>Western Larch</td>
<td>-1.196</td>
<td>0.330</td>
<td>-2.853</td>
</tr>
<tr>
<td>Medium</td>
<td>0.302</td>
<td>-0.004</td>
<td>0.238</td>
</tr>
<tr>
<td>Low</td>
<td>0.319</td>
<td>1.111*</td>
<td>0.593</td>
</tr>
<tr>
<td>Forest floor</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total organic matter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carbon contents</td>
<td>154.450*</td>
<td>-54.460</td>
<td>-35.040</td>
</tr>
<tr>
<td>Nitrogen contents</td>
<td>100.160**</td>
<td>-36.150</td>
<td>-14.110</td>
</tr>
<tr>
<td>Mineral soil (0-30cm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carbon contents</td>
<td>25.437***</td>
<td>12.466</td>
<td>15.903</td>
</tr>
<tr>
<td>Nitrogen contents</td>
<td>0.526*</td>
<td>0.416</td>
<td>0.561</td>
</tr>
</tbody>
</table>

¹ H_U: medium/unburn, H_U: high/unburn, L_B: low/burn, M_B: medium/burn (refer to Table 5-1).
² CC: clearcut, GS: group selection, SW: shelterwood harvest.
³ Significance codes (p-value): 0 < *** < 0.001 < ** < 0.01 < * < 0.05.
Figure Captions

Figure 6-1. Study site and the layout of experimental units at Coram Experimental Forest, MT.

Figure 6-2. Ecosystem biomass distribution of the experimental units 38 years after harvesting at Coram Experimental Forest, MT. Ground vegetation includes the biomass of seedlings, shrubs, forbs and grasses.

Figure 6-3. Biomass production 38 years after harvesting for (a) total aboveground, (b) regenerated trees, and (c) shrub layer. Error bar represents standard error of the mean biomass production.

Figure 6-4. Carbon, nitrogen, and organic matter (Mg/ha) in forest floor ((a), (b), and (c), respectively), and in mineral soil (0-30 cm depth) ((d), (e), and (f), respectively) 38 years after harvesting. Shaded bars represent burned treatments.

Figure 6-5. Scatter plot between aboveground biomass production and (a) carbon, (b) nitrogen, and (c) organic matter (Mg/ha) in forest floor (open circle) and mineral soil layer (closed circle). P-values for Pearson’s correlation test were presented with legends.
Figure 6-1.
Figure 6-2.
Figure 6-3.
Figure 6-4.
Figure 6-5.

(a) Carbon Contents (Mg/ha) vs. Total Aboveground Biomass (Mg/ha)
- Forest Floor (P = 0.124)
- Mineral Soil (P = 0.437)

(b) Nitrogen Contents (Mg/ha) vs. Total Aboveground Biomass (Mg/ha)
- Forest Floor (P = 0.181)
- Mineral Soil (P = 0.823)

(c) Organic Matter Contents (Mg/ha) vs. Total Aboveground Biomass (Mg/ha)
- Forest Floor (P = 0.140)
- Mineral Soil (P = 0.865)
CHAPTER 7

EVALUATION OF PREDICTIVE MODELS FOR DOUGLAS-FIR BARK THICKNESS AT BREAST HEIGHT FOLLOWING 12 BIOMASS HARVEST TREATMENTS

ABSTRACT

Foresters often require an estimation of bark thickness from a reference height (typically breast height) to accurately estimate the bark or wood volume of a tree. Various models for estimating the bark thickness of interior Douglas-fir (Pseudotsuga menziesii var. glauca) from measured dbh (diameter at breast height) were evaluated. Sample trees were from northern Rocky Mountain mixed conifer stands that had been subjected to four levels of experimental woody biomass harvesting. Among simple linear, nonlinear, and segmented linear mixed effects models, the segmented linear model performed best. A join point (where the linear equations are linked) for the segmentation was statistically detected at approximately 19.0 cm dbh. The join point seems to indicate the size at which juvenile Douglas-fir trees boost the production of bark tissue, perhaps as those trees express dominance over competing understory vegetation. Woody biomass utilization level had no impact on bark thickness, indicating that the bark:dbh relationship does not depend on biomass utilization intensity. The study results enable accurate bark thickness estimation for interior Douglas-fir in this region, and suggest several silvicultural applications for juvenile Douglas-fir stand management.
INTRODUCTION

Burgeoning interest in reclaiming forest residues as biomass energy feedstocks foretells that levels of biomass removal from forests will intensify relative to past forest practices (Janowiak and Webster 2010, Perlack et al. 2005). Forest residues consist not only of harvest-generated residues (such as logging slash, cull trees, snags, and other coarse woody debris; Barger 1981), but also the waste products of various wood industry processes, such as sawmill log de-barking. Tree bark figures prominently among forest residue materials, as it can comprise 10-20% of total log volumes (Parikka 2004). Whether bark is regarded as a sawmilling byproduct or a waste product depends upon local markets, transportation costs, and other factors.

Tree bark has long been considered as an alternative energy source (e.g., Ellis 1982, Schneider 1977), and is currently undergoing revived consideration as a pellet fuel feedstock due to the scarcity and cost of wastewood fiber as a pellet feedstock (Melin 2008), but its use has been constrained by its relatively high ash content (Lehtikangas 2001). Emerging biofuel-based energy production technologies may utilize bark as a feedstock and thereby increase its demand; others that rely on clean wood fiber will likely exact low bark tolerances in their forest biomass feedstock supplies, and require segregating bark volumes from wood volumes. In both cases, it will become increasingly important to make accurate predictions of bark volumes from tree and log measurements as biofuel energy production sciences continue to develop.

Estimations of tree bark volume have long been pursued because foresters must know merchantable log volumes, and subtracting bark volume from outside bark volume provides the most convenient calculation method (Meyer 1946). Numerous mathematical equations accounting for each species’ bark thickness have been developed over the past decades (e.g., Brickell 1970, Cochran 1976, Maguire and Hann 1990). They generally predict the bark thickness at any given tree height from bark thickness at a certain reference height (typically, diameter at breast height, or dbh; 1.4 m). Accurate prediction of whole tree bark and log volumes are predicated upon the accurate estimate of bark thickness from measured
diameter at the reference height, because error in that estimate is expressed and thereby amplified throughout the log.

In an ongoing study of biomass utilization at Montana’s Coram Experimental Forest (Jang et al. 2013), we have been quantifying forest vegetation and productivity responses to a variety of biomass harvest treatments. In that work, determining accurate estimates of forest biomass by segregated components is a primary objective, and one that requires a robust bark predictive model, particularly for Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco). Previous research has produced a variety of models to predict the bark thickness of Douglas-fir using diameter at breast height. For coastal Douglas-fir, Johnson (1955) developed a segmented linear equation for the estimation of bark thickness from dbh. Larsen and Hann (1985) formulated a nonlinear equation for bark thickness in a similar region. For interior Douglas-fir, Spada (1960), Monserud (1979), and Dolph (1981) each constructed simple linear regression models. Monserud (1979) and Dolph (1981) found different results among linear models across the regions, implying the necessity of locally-constructed equations for the best predictive performance.

During field surveys at Coram Experimental Forest, we observed an apparent difference in the ratio of bark thickness to tree size between small and large Douglas-fir trees. We theorized that the simple linear approach might be inappropriate, and that segmented linear regression analysis might yield a better predictive model for Douglas-fir in the northern Rocky Mountains. Segmented linear regression has been used to construct stem taper equations (e.g., Brooks and Jiang 2009, Maguire and Hann 1990, Max and Burkhart 1976). In contrast to more complex models, it provides a simpler method by producing different equations within different regions of the explanatory variable space (Rawlings et al. 1998). Two (or more) different linear equations are fitted simultaneously under a constraint: the “join point,” where the linear equations are linked. If it is possible to estimate the join point, then the model can be constructed as multiple linear forms with simplicity and robustness. This study considered segmented, simple linear and
nonlinear mixed effects regression to determine the best model for predicting the bark thickness of Douglas-fir from breast-height diameter (dbh) in northern Rocky Mountain forests, and to evaluate whether the relationship of bark thickness to dbh differs significantly among biomass utilization treatments and regeneration harvests.

METHODS AND MATERIALS

Study site

This study was conducted at the site of the interdisciplinary Forest Residues Utilization Research and Development Program at western Montana’s Coram Experimental Forest (Flathead National Forest). Established in 1974, a primary purpose of the research program was to evaluate the effects of varying biomass removal levels (and associated post-harvest burning treatments) for each of three common regeneration harvest methods. The present study is one aspect of an ongoing comprehensive analysis of that experiment, focused on the relatively long-term responses of vegetation and site productivity to biomass harvesting in northern Rocky Mountain forests (Jang et al. 2013).

The site is located in the experimental forest’s Upper Abbot Creek basin (48°25’N, 113°59’W), about 20 kilometers east of Columbia Falls, and 9 kilometers south of Glacier National Park. Elevation ranges from 1,195 m to 1,615 m with 30% to 80% slopes. Mean annual precipitation is 1,076 mm (range: 890-1,270 mm), occurring primarily in the form of snow (Farnes et al. 1995). Mean annual temperatures during summer and winter months are about 16°C, and -7°C, respectively (Adams et al. 2008).

The site is characterized by the western larch (Larix occidentalis Nutt.) forest cover type (Society of American Foresters Cover Type No. 212; Eyre 1980), mixed with Douglas-fir, subalpine fir (Abies lasiocarpa (Hook.) Nutt.), and Engelmann spruce (Picea engelmannii Parry ex Engelm.). At the lower elevations, broadleaf species such as paper birch (Betula papyrifera Marshall), black cottonwood
(Populus balsamifera L. ssp. trichocarpa (Torr. & A. Gray ex Hook.) Brayshaw), and quaking aspen (P. tremuloides Michx.) are also present. The subalpine fir – queen's cup (Clintonia uniflora (Menzies ex Schult. & Schult. f.) Kunth) (ABLA/CLUN) habitat type is dominant (Pfister et al. 1977, Shearer and Kempf 1999).

Experimental design

The experiment was established as a split-plot design with two replicates, three whole-plots, and four sub-plots. The three whole-plots consisted of shelterwood, group selection, and clearcut harvest units. Within each whole-plot harvest unit, four biomass utilization treatment combinations were imposed as sub-plots. Each sub-plot treatment consisted of a combination of biomass utilization level (high, medium, and low) and post-harvest prescribed burning (burned, unburned) (details in Table 7-1). Burning was prescribed for reduction of fire hazard; it was performed only at the medium and low utilization levels, because the high utilization level produced woody fuels loads that were insufficient to either warrant or permit burning. The four combinations of biomass utilization levels and post-harvesting treatments (burning treatment) were: 1) High-Unburned, 2) Medium-Unburned, 3) Medium-Burned, and 4) Low-Burned. In each of the clearcut and shelterwood harvest units, the four biomass utilization treatments were oriented longitudinally downslope and adjacent to each other. In the group selection units, eight patches were harvested, and two patches were randomly assigned to each of the four biomass utilization treatments. The experiment was replicated at two elevations (low, high).

Harvesting was conducted via skyline yarder in 1974, and prescribed burning treatment followed in 1975. In the lower shelterwood unit, burning was not achievable (fuel moisture contents exceeded the prescription limits; Artley et al. 1978), resulting in an imbalance in the experimental design and the
addition of a Low-Unburned treatment in that unit. The Low-Unburned treatment was excluded for data analyses.

Douglas-fir seedlings were planted during 1976-1979. Except for the Medium-Unburned treatment (understory protected treatment), 25 seedlings were planted at 1.8 m spacing on the middle-top area of each sub-plot during each of 4 consecutive years. Within each biomass utilization treatment (sub-plot) of the clearcut and shelterwood units, 10 permanent sampling points were installed (two columns × five rows) spaced at 30.5 m. Five permanent sampling points were located within each cut patch of the group selection harvest units.

**Data collection**

From 2012 to 2013, cores were taken with an increment borer from a total 393 trees (Table 7-2). The sampling procedure was selected according to tree layer and regeneration type. For overwood trees in the shelterwood units, 20 Douglas-fir trees in each biomass utilization treatment were selected, avoiding the edge effect of neighbor sub-plot. Among naturally regenerated trees, 1-2 damage-free crop trees were selected within a 15m radius of each historical permanent sampling point in all units. Sampling for the planted trees was conducted only in clearcut units. At each tree’s breast height (1.37 m), diameter was recorded and two core samples (at right angles) were taken. Bark thickness per core was measured through either a bark gauge inserted at the coring spot, or a digital caliper measurement of the removed core. The average of the two measurements was calculated as the bark thickness per tree.

**Data analysis**
Since the data were collected from an experiment with a split-plot design, mixed effects models were used for all model forms considered. For example, in the linear mixed effects model, dbh was treated as a covariate, regeneration harvests and biomass utilization treatment were considered fixed effects, and block (i.e., low and high elevation) was treated as a random effect. Therefore, the model was constructed as:

\[ y_{ijkl} = \beta_0 + \beta_1 x_{ijkl} + \alpha_i + B_k + \epsilon_{(1)ik} + \gamma_j + \epsilon_{(2)ijk} + \epsilon_{ijkl} \]  

where \( y_{ijkl} \) and \( x_{ijkl} \) are the bark thickness (mm) and dbh (cm) respectively of the \( l^{th} \) tree in regeneration harvest type \( i \) with biomass utilization treatment \( j \) in elevation block \( k \), \( \alpha_i \) = effect of regeneration harvest type \( i \) (whole-plot effect), \( B_k \) = \( k^{th} \) elevation effect (random effect), \( \gamma_j \) = \( j^{th} \) biomass utilization treatment effect (sub-plot effect), \( \epsilon_{(1)ik} \), \( \epsilon_{(2)ijk} \), and \( \epsilon_{ijkl} \) are the whole-plot, sub-plot error, and the variation among trees in a subplot. The \( \beta_0 \) and \( \beta_1 \) are model parameters.

Second, a segmented linear regression model (Rawlings et al. 1998) was constructed for the relationship between bark thickness and dbh. Since the join point of the two different regression lines is not known, the model has a nonlinear form. For convenience of description, letting \( \beta_0 = \) summation of the intercept and all fixed effects and \( \epsilon_i = \) summation of all error terms, then equation (1) can be simplified as:

\[ y_i = \beta_0 + \beta_1 x_i + \epsilon_i \]  

(2)
where \( y_i \) and \( x_i \) are bark thickness (mm) and dbh (cm) of the \( i^{th} \) tree, respectively.

If we assume the slope of this relationship between bark thickness and dbh changes for dbh values exceeding the value \( \theta \), equation (2) can be segmented at \( \theta \) via:

\[
y_i = \begin{cases} 
\beta_0 + \beta_1 x_i + \epsilon_i & \text{if } x_i \leq \theta \\
\gamma_0 + \gamma_1 x_i + \epsilon_i & \text{if } x_i > \theta
\end{cases}
\] (3)

where \( \theta \) = the joint point where the two segmented linear lines meet. Since the lines should meet where \( x = \theta \), we can impose a constraint of \( \beta_0 + \beta_1 \theta = \gamma_0 + \gamma_1 \theta \). Therefore, equation (3) can be rewritten as:

\[
y_i = \begin{cases} 
\beta_0 + \beta_1 x_i + \epsilon_i & \text{if } x_i \leq \theta \\
(\beta_0 + \beta_1 \theta - \gamma_1 \theta) + \gamma_1 x_i + \epsilon_i & \text{if } x_i > \theta
\end{cases}
\] (4)

Letting \( I_{x_i > \theta} = 1 \) if \( X_i > \theta \), and \( I_{x_i \leq \theta} = 0 \) if \( X_i \leq \theta \), the model can be simplified to one equation:

\[
y_i = (1 - I_{x_i \leq \theta}) (\beta_0 + \beta_1 x_i) + I_{x_i \leq \theta} [(\beta_0 + \beta_1 \theta - \gamma_1 \theta) + \gamma_1 x_i] + \epsilon_i
\] (5)

The above model is nonlinear, since products of two parameters exist (e.g., \( \beta_1 \theta \)) and since \( \theta \) appears in the support of the indicator function \( I_\theta \).
Three different mixed effects models were constructed: (1) linear mixed effects model (without segmentation; eq. 1), (2) nonlinear model (basic model form: \(y_t = \beta_0 x_t^{\beta_1} + \beta_2 + \epsilon_i;\) modified from Larsen and Hann (1985) and Garber and Maguire (2003)) with mixed effects (i.e., \(\alpha_i + B_k + \epsilon_{(1)ik} + y_j + \epsilon_{(2)ijkl}\) from eq. 1), and (3) segmented linear model (eq. 5) with mixed effects (\(\alpha_i + B_k + \epsilon_{(1)ik} + y_j + \epsilon_{(2)ijkl}\) from eq. 1). The variance of the residuals for all three models showed quadratic increases with dbh, so a weighted least squares approach was introduced to deal with the nonconstant error variance; specifically, the variance of the error term was weighted proportionally by the inverse of the squared dbh. Non-significant treatment effects (p>0.10) were eliminated from the models. The final models were compared to each other via the Akaike Information Criterion (AIC; Akaike 1974) and the Predicted Residual Sum of Squares (PRESS) statistic (Allen 1974). All statistical analyses were conducted using the \textit{nlme} package (Pinheiro et al. 2014) in R (R Development Core Team 2008).

**RESULTS**

The residual plots indicated that the weighted least squares approach effectively accounted for the variance heteroscedasticity problems for all models. Whereas dbh was a highly significant variable across all tested models (Table 7-3), the biomass utilization treatment variables did not explain the Douglas-fir bark thickness for any of the mixed effects models (p=0.93, 0.21, and 0.25 for the simple linear, nonlinear, and segmented linear mixed effects model, respectively). On the other hand, the regeneration harvests significantly affected bark thickness for both the nonlinear and segmented linear mixed effects models. The final nonlinear mixed effects model was constructed as:

\[
\hat{y} = 0.0793 \cdot x^{1.4521} + 4.6797 - 3.1178 \cdot I_1 - 2.7990 \cdot I_2
\]  

(6)
where \( x = \text{dbh (cm)}, I_1 = \begin{cases} 1 & \text{if } \text{group selection} \\ 0 & \text{otherwise} \end{cases}, \quad I_2 = \begin{cases} 1 & \text{if } \text{clearcut} \\ 0 & \text{otherwise} \end{cases} \), respectively.

The result indicated that the clearcut and group selection units showed a lower mean bark thickness (by approximately 2.8 and 3.1 mm) than the shelterwood unit (\( p<0.0001 \) and \( p=0.0513 \), respectively) (Figure 7-1a).

The join point was estimated at 19.0 cm dbh (p-value < 0.0001). Therefore, the final segmented linear mixed effects model was constructed as:

\[
\hat{y} = \begin{cases} 
4.1212 + 0.2484 \cdot x - 2.4466 \cdot I_1 - 2.1419 \cdot I_2 & \text{if } X \leq 19.0 \\
-3.2868 + 0.6379 \cdot x - 2.4466 \cdot I_1 - 2.1419 \cdot I_2 & \text{if } X > 19.0
\end{cases}
\] (7)

where \( x = \text{dbh (cm)}, I_1 = \begin{cases} 1 & \text{if } \text{group selection} \\ 0 & \text{otherwise} \end{cases}, \quad I_2 = \begin{cases} 1 & \text{if } \text{clearcut} \\ 0 & \text{otherwise} \end{cases} \).

The segmented linear model indicates that the mean bark thickness of Douglas-fir increases by about 0.25 mm for each 1-cm increment in dbh, up to 19.0 cm. Beyond that point, the mean bark thickness increases by about 0.64 mm for each 1-cm increment of dbh (illustrated by Figure 7-1b). Similar to the nonlinear model, bark thickness tends to be lower in the group selection and clearcut units than the shelterwood unit (\( p=0.0267 \) and \( p=0.0274 \), respectively).

Among the three models, the segmented linear mixed effects model exhibited the overall lowest AIC value (2056.681) (Table 7-3). On the other hand, the simple linear mixed effects model yielded the lowest PRESS statistic (6646.245), indicating the best agreement between actual and predicted bark thicknesses.
DISCUSSION

Biomass utilization level was consistently a non-significant factor, indicating that the relationship between bark and dbh does not depend on that aspect of treatment history. Many sample trees regenerated after the conclusion of the treatments, and any effects on the bark:dbh relationship should have had a full opportunity for expression. Although we detected a regeneration harvest effect in the nonlinear and segmented models, this outcome was likely attributed to the fact that the larger tree samples were mainly collected from just the shelterwood units. In other words, it seems that the significance of regeneration harvest originated not from true treatment effect but from this imbalance in sampling. We assume that any effect of treatment history upon wood and bark formation would likely manifest indirectly via its effect on site productivity; thus, the fact that no real treatment history effect was observed here indicates that either (1) the harvest and utilization treatments had no effect on site productivity, or (2) the bark:dbh relationship is one that is driven by tree level dynamics that are unaffected by site productivity.

The simple linear model showed the best prediction accuracy based on the PRESS cross-validation process (Table 7-3). However, the join point and statistical significance of the nonlinear model indicate that the ratio (slope) of bark thickness to dbh is not constant across the whole range of tree diameters (Figure 7-1), indicating that the simple linear model might be too simplistic to explain bark thickness. The model selection criterion (AIC) suggested the best model among the three was the segmented mixed effects model. In addition, the segmented model yielded a better PRESS statistic than the nonlinear model. Furthermore, if it is possible to find the physiological evidence for the join point from external subsequent studies, then a considerable amount of uncertainty can be decreased and the model fit improves, since the model takes a simple linear form. Therefore, we conclude that the simpler (albeit segmented) linear regression model provided the best result for modeling bark thickness.

Similar conclusions have been reached by other studies. Brickell (1970) investigated 10 species (including Douglas-fir) in western Montana, and recommended the simpler form for bark thickness...
prediction. The simple linear regression model’s performance has been found superior to more complex models for radiata pine (*Pinus radiata* D. Don) in Australia (Johnson and Wood 1987), white spruce (*Picea glauca* (Moench) Voss) in Alaska (Malone and Liang 2009), and lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) in central Oregon (Garber and Maguire 2003).

In their study, Garber and Maguire (2003) attributed the superior performance of the simple model to a narrow range of size classes and geographic distribution comprising their samples, and theorized that a more complex model form could be required to explain variances as the sample range increases. Yet, the question of how the bark:dbh relationship changes across geographic space remains unclear. Monserud (1979) and Dolph (1981) each found that model parameters were slightly different among regions with the same model form, implying that model application indeed has geographical limitations. Yet, other researchers (e.g., Johnson and Wood 1987, Malone and Liang 2009) maintained that their models were quite tolerant of geographic location. The narrow geographic range from which our samples were drawn prevents our addressing this issue.

Compared with other models, segmentation yielded the model (linear) with best performance for our dataset. Johnson (1955) similarly observed a diameter join point in a Douglas-fir dataset from western Oregon and Washington (25.4 cm, versus this study’s 19.0 cm), but did not describe the rationale used to determine that point. In both cases, however, the possible existence of a join point indicates that the allometric ratio between dbh and bark may not be constant. Nonconstant allometric ratios are uncommon, but have been observed for other tree components. For example, the foliage-sapwood area relationship has been shown to change by competition level in lodgepole pine (Long and Smith 1988), and by site quality in young Douglas-fir (Espinosa Bancelari et al. 1987). Reports have also shown that the biomass allocation pattern differs according to the degree of competition for several species, such as loblolly pine (*Pinus taeda* L.) (Naidu et al. 1998) and Scots pine (*Pinus sylvestris* L.) (Nilsson and Albrektson 1993).
Predicted bark volumes computed from the segmented regression model were significantly different from the volumes predicted by the nonlinear model (paired t-test; \( P<0.0001 \)). The magnitude of difference in predicted bark volume between our segmented model and a conventional nonlinear model (Maguire and Hann 1990) is illustrated in Figure 7-2 for a range of Douglas-fir tree sizes. The differences may appear modest, but they amplify to levels that are beyond trivial once adjusted up to stand scales.

To illustrate, consider a fully-stocked, even-aged, uniform stand of Douglas-fir with a quadratic mean diameter of 25.4 cm. Following the rationale of Cochran et al. (1994), a stand density index (SDI; Reineke 1933) of 939 can be assumed for the fully-stocked stand (Seidel and Cochran 1981). Using equations by Maguire and Hann (1990), the difference in the predicted bark volume estimate between the segmented linear model and the simple linear model is 0.005 m\(^3\) per 25.4-cm dbh tree (Figure 7-2, in the case of clearcut unit). At the stand level, this difference translates to 5.29 m\(^3\) ha\(^{-1}\). Assuming a bark specific gravity of 480 kg/m\(^3\) (Miles and Smith 2009), that difference results in a bark weight disparity of 2.5 metric tons per hectare. Moreover, the discrepancy in bark volume links directly to error in bolewood volume prediction, since bark thickness is used as a determinant of numerous log volume prediction equations (e.g., Cochran 1976, Kozak 1988, Maguire and Hann 1990).

**CONCLUSION**

For prediction of Rocky Mountain Douglas-fir bark thickness, dbh proved a significant variable; harvesting treatment was also significant, but we attribute this result to a weakness in the sampling design rather than actual treatment effect. Since biomass utilization level was a non-significant factor, we conclude that treatment history fails to materially affect the relative formation of wood and bark, and that the bark:dbh relationship remains constant, irrespective of treatment history. Among fitted models, a segmented linear regression model performed best, with greater prediction accuracy than a simple nonlinear model and applicability for various management objectives. The existence of a join point may be a manifestation of tree growth and vegetation dynamics, but remains a subject for further investigation.
Quantitatively identifying the segmented linear model’s join point is computationally challenging but involves a relatively straightforward model reparameterization and nonlinear fitting algorithm. Such a technique may be used to improve the bark:dbh models for other species and locations.

ACKNOWLEDGEMENTS

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REFERENCES


Table 7-6. Design of the utilization treatments within harvesting units (from Benson and Schlieter 1980, Shearer and Kempf 1999).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cut trees(^1)</th>
<th>Max. size of retained woody materials(^2)</th>
<th>Post-harvest treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium-Unburned</td>
<td>&gt;17.8 cm dbh</td>
<td>7.6 cm × 2.4 m</td>
<td>Understory protected/unburned</td>
</tr>
<tr>
<td>High-Unburned</td>
<td>All trees</td>
<td>2.5 cm × 2.4 m</td>
<td>Slashed/unburned</td>
</tr>
<tr>
<td>Low-Burned</td>
<td>All trees</td>
<td>14.0 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
<tr>
<td>Medium-Burned</td>
<td>All trees</td>
<td>7.6 cm × 2.4 m</td>
<td>Slashed/broadcast burned</td>
</tr>
</tbody>
</table>

\(^1\) Except designated overstory shelterwood trees

\(^2\) Live and dead down logs (small-end diameter × length); for dead down logs, they were removed if sound enough to yard.
Table 7-2. Description of samples.

<table>
<thead>
<tr>
<th>Regeneration cutting (Whole-plot)</th>
<th>Min. DBH (cm)</th>
<th>Mean DBH (SD) (cm)</th>
<th>Max. DBH (cm)</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shelterwood</td>
<td>7.0</td>
<td>44.1 (15.9)</td>
<td>78.5</td>
<td>167</td>
</tr>
<tr>
<td>Group selection</td>
<td>9.1</td>
<td>16.7 (5.9)</td>
<td>35.9</td>
<td>56</td>
</tr>
<tr>
<td>Clearcut</td>
<td>5.6</td>
<td>15.3 (4.9)</td>
<td>34.1</td>
<td>170</td>
</tr>
</tbody>
</table>
Table 7-3. Model parameters, their standard errors (SE), and corresponding p-values of each model. Model evaluation statistics (AIC and PRESS) for each model were represented. Symbols for each parameter are described in the text.

<table>
<thead>
<tr>
<th>Model Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>p-value</th>
<th>AIC</th>
<th>PRESS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simple linear mixed effects model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$ (intercept)</td>
<td>-0.4752</td>
<td>0.9118</td>
<td>0.6025</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_1$ (dbh)</td>
<td>0.5128</td>
<td>0.0163</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nonlinear mixed effects model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$ (coefficient of dbh)</td>
<td>0.0793</td>
<td>0.0298</td>
<td>0.0080</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_1$ (power of dbh)</td>
<td>1.4521</td>
<td>0.0910</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_2$ (intercept)</td>
<td>4.6797</td>
<td>0.7313</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_3$ (effect of group selection)</td>
<td>-3.1178</td>
<td>0.7126</td>
<td>0.0513</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_4$ (effect of clearcut)</td>
<td>-2.7990</td>
<td>0.6597</td>
<td>0.0485</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Segmented linear mixed effects model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$ (intercept when $x \leq \theta$)</td>
<td>4.1211</td>
<td>0.7169</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_1$ (slope when $x \leq \theta$)</td>
<td>0.2483</td>
<td>0.0496</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\theta$ (join point)</td>
<td>19.0212</td>
<td>1.4466</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\gamma_1$ (slope when $x &gt; \theta$)</td>
<td>0.6379</td>
<td>0.0245</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_2$ (effect of group selection)</td>
<td>-2.4466</td>
<td>0.5898</td>
<td>0.0267</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_3$ (effect of clearcut)</td>
<td>-2.1419</td>
<td>0.5232</td>
<td>0.0274</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure Captions

Figure 7-1. Bark thickness at breast height predictions of Douglas-fir from (a) nonlinear mixed effected model and (b) segmented linear mixed effects model. Solid and dashed line represent the each model’s prediction for clearcut unit and shelterwood unit, respectively. Dotted line represents the prediction through the simple linear mixed model. The prediction line for group selection was omitted since the line was undistinguishable from the line for clearcut.

Figure 7-2. Comparison of model performances according to Douglas-fir dbh size classes. Solid, dashed, and dotted lines represent the simple linear, nonlinear, and segmented linear regression model, respectively.

Figure 7-3. The prediction differences of Douglas-fir bark thickness (dbh as a predictor) by this study’s segmented linear regression model versus the nonlinear model (solid line) and the simple linear regression model (dashed line).
Figure 7-1.
Figure 7-2.

- Linear
- Nonlinear
- Segmented

PRESS Statistics

Midpoint of DBH class (cm)
Figure 7-3.

The graph shows the difference of bark volume prediction (m³/tree) against diameter at breast height (cm). Two lines are depicted: one for Nonlinear vs. Segmented and another for Linear vs. Segmented.
CHAPTER 8

SYNTHESIS AND SUMMARY

The studies in this dissertation investigated any possible negative impact of extensive biomass utilization on site productivity and understory vegetation dynamics and diversity in the northern Rocky Mountains. From Chapter 3 and 4, we found a consistent result from individual trees both for regenerated and artificially planted Douglas-fir trees. There was no differences of total leaf area, recent 5-year basal area increment and growth efficiency 38 years after biomass harvesting. For planted trees, foliar N and C concentration were not different. Although the retained trees in shelterwood units showed a different initial response in basal area growth by biomass utilization level, the effect seems to have been temporary. Thus, the results support the author’s conclusion that there is no long-term impacts of biomass utilization on individual tree response at this study site.

Chapter 5 investigated understory recovery and changes in species composition and diversity over time. There was no difference in shrub recovery across measurement years by biomass utilization levels. Species composition was drastically shifted after the harvesting and post-harvesting treatments, but the shrub species composition recovered in 10-38 years. After 38 years, there is little evidence that shrub communities differ according to the biomass treatment history. Notably, high level of biomass utilization (without prescribed fire) resulted in the highest shrub biodiversity. These results imply that the shrub community at this study site is resilient to biomass harvesting and subsequent prescribed fire treatment.

In chapter 6, the biomass production was examined at a stand/ecosystem level. The biomass production for regenerated trees by species, shrub layers by strata, and organic matter, C, and N contents in forest floor and mineral soil layer were compared. The statistical test results indicate that there is no difference among the utilization treatments for either aboveground biomass production or soil properties 38 years
after harvest. Observed trivial differences seem to have been caused not by changes in site productivity, but rather by regeneration dynamics that followed harvesting and post-harvesting operations.

Chapter 7 proposed the best model for the bark thickness estimation of Douglas-fir trees in local scale. Segmented polynomial regression model performed the best, compared to the simple linear model and classic nonlinear model. It seems that the model can account for change in biomass allocation as the crown develops. In addition, the model indicated that bark thickness was not affected by the level of biomass utilization, although the relationship between bark thickness and site productivity is not certain.

Synthesizing these results is necessary in order to provide forest managers with an overall evaluation of biomass utilization impacts. For this, amount of biomass utilization, total soil organic matter (forest floor + mineral soil), individual tree vigor (growth efficiency for regenerated tree), total aboveground vegetation production, total (tree) regeneration biomass, and understory vegetation diversity (relative Shannon index to control) by biomass utilization treatment were compared in Table 8-1 and Figure 8-1. The high-unburned (H_U) treatment showed the best performance in this overall evaluation. Despite of its maximized biomass extraction, the H_U treatment yielded the best total regeneration tree biomass production and understory biodiversity. In addition, the total soil organic matter and total aboveground vegetation production were close to the maximum results from other treatments. In contrast, lesser intensive biomass utilization treatments showed inferior consequences. Therefore, these results altogether show that even a high intensity of biomass utilization does not produce long-term negative impacts on site productivity and biodiversity.

In conclusion, this study revealed no long-term detrimental consequences of biomass harvesting on site productivity and vegetation dynamics. The fact that the study site was a relatively productive one, and that soil disturbance was likely minimized during harvesting, should be noted. Further research at sites of lesser productivity, and in stands harvested by ground-based systems, will help fill remaining knowledge gap.
Table 8-1. Comparisons of amount of biomass utilization, total soil organic matter (forest floor + mineral soil), individual tree vigor (growth efficiency for regenerated tree), total aboveground vegetation production, total (tree) regeneration biomass, and understory vegetation diversity (relative Shannon index to control) among the biomass utilization treatments 38 years after harvesting in Coram Experimental Forest. Numbers in parenthesis represent the relative performance to the maximum performance.

<table>
<thead>
<tr>
<th>Biomass Utilization Treatment</th>
<th>Biomass Utilization (%)</th>
<th>Soil Organic Matter (Mg/ha)</th>
<th>Individual Tree Vigor (cm²/m²)</th>
<th>Total Aboveground Biomass (Mg/ha)</th>
<th>Total Regeneration Biomass (Mg/ha)</th>
<th>Understory Vegetation Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td>H_U</td>
<td>72.3 (1.00)</td>
<td>268.8 (0.93)</td>
<td>1.77 (0.94)</td>
<td>46.3 (0.98)</td>
<td>41.2 (1.00)</td>
<td>1.75 (1.00)</td>
</tr>
<tr>
<td>L_B</td>
<td>54.2 (0.75)</td>
<td>219.2 (0.76)</td>
<td>1.88 (1.00)</td>
<td>43.2 (0.92)</td>
<td>38.1 (0.92)</td>
<td>1.24 (0.71)</td>
</tr>
<tr>
<td>M_B</td>
<td>65.6 (0.91)</td>
<td>289.1 (1.00)</td>
<td>1.70 (0.90)</td>
<td>47.2 (1.00)</td>
<td>35.6 (0.86)</td>
<td>0.95 (0.54)</td>
</tr>
<tr>
<td>M_U</td>
<td>62.9 (0.87)</td>
<td>198.3 (0.69)</td>
<td>1.34 (0.71)</td>
<td>39.5 (0.94)</td>
<td>33.0 (0.80)</td>
<td>1.14 (0.65)</td>
</tr>
</tbody>
</table>
Figure Captions

Figure 8-1. Relative performances (relative to the maximum case) for amount of biomass utilization, total soil organic matter (forest floor + mineral soil), individual tree vigor (growth efficiency for regenerated tree), total aboveground vegetation production, total (tree) regeneration biomass, and understory vegetation diversity (relative Shannon index to control) among the biomass utilization treatments 38 years after harvesting in Coram Experimental Forest.
Figure 8-1.