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EFFECTS OF WHOLE-TREE HARVESTING ON SITE PRODUCTIVITY AND SPECIES COMPOSITION OF A NORTHERN HARDWOOD FOREST

BY

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THESIS

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ABSTRACT

EFFECTS OF WHOLE-TREE HARVESTING ON SITE PRODUCTIVITY AND SPECIES COMPOSITION OF A NORTHERN HARDWOOD FOREST

by

Gabriel Ethan Roxby

University of New Hampshire, May 2012

Whole-tree harvesting is widely used in the northeastern United States to supply biomass energy plants with fuel, but questions remain regarding its long-term sustainability. To assess its effects on the northern hardwood forests that make up a significant portion of northern New England, we conducted two regeneration surveys in 2010 and 2011 covering thirty-three small clearcuts. We measured whole-tree (WTH) and conventionally harvested (CH) sites in New Hampshire and Maine, and compared the productivity and species composition of the 10-14 year old regeneration. No significant difference was observed in height, diameter or calculated biomass of stems > 2m in height. Despite several weak patterns in individual species abundance, overall species composition did not significantly vary between WTH and CH sites. We conclude that no significant effects of residue removal from whole-tree harvesting are observed within our sample of northern hardwood sites as this point in their stand development.

INTRODUCTION

With the heightened focus on renewable energy generation in the United States, biomass energy plants are likely to become an increasingly important source for our energy needs in the near future. These facilities convert biological material into electricity or thermal energy by burning it and using the steam to power turbines. One common source of this biological material is woody residues that are generated as a byproduct of harvesting activities. In the northeastern United States, the woody material typically consists of branches, tops and other sections of the tree that are of poor form and cannot be used for any other purpose. Whole-tree harvesting (WTH) refers to the practice of removing these residues from a site in addition to the traditionally merchantable tree bole. Conventional (bole-only) harvesting (CH) removes only the bole, leaving a considerable amount of woody residue on site to decompose.

Concerns over the effects WTH has on site fertility have existed since the practice began in the 1970s (Boyle, 1976; Kimmins, 1977). Branches and foliage contain a large proportion of a tree's nutrients (White, 1974) and their removal from the site during WTH may result in nutrient depletion, especially over the long term and after multiple harvests. Nutrients can be added to a site via atmospheric deposition and mineral weathering, but will these inputs be sufficient to make up for the losses? In conventional harvesting, it is widely believed that these nutrient inputs are sufficient, and that given appropriate rotation lengths, site fertility can be maintained. How forests will respond to the additional removal of harvest residues during WTH is less certain; current research has yielded mixed results. Some studies found evidence for soil nutrient depletion (Federer et al., 1989) and productivity decline (Walmsley et al., 2009), while others failed to detect any significant treatment differences (Johnson et al., 1991; Sanchez et al., 2006).

If important nutrients removed during WTH are not replaced during the course of a typical rotation, we may expect that depletion to limit the growth of trees that recolonize the site. The nutrient requirements of trees are likely not uniform throughout their life and may peak when they are poletimber-sized (Kimmins, 1977). We may expect nutrient deficiencies to assert themselves during this time, and many of the studies detecting productivity differences find them even earlier. Removing harvest residues from a site may also change microclimate conditions on the forest floor, impacting the species of trees that are successful in regenerating. We might expect the floor of a whole-tree harvested site to contain harsher conditions than one sheltered by layers of left behind logging slash. Proe et al. (2001) found evidence for higher wind speeds and a greater range of temperatures on WTH sites as compared with those retaining harvest residues. These conditions may favor the regeneration of some species and not others, potentially having a significant effect on the composition of the next stand.

The goal of this study is to examine the effects whole-tree harvesting has on site productivity and species composition and compare them to those observed in conventionally harvested sites. To narrow the study's scope, we focus solely on northern hardwood stands 10 – 14 years old created using patch cut openings of less than 6 hectares.

Report Organization

This report consists of three chapters comparing the effects of whole-tree harvesting to those of conventional harvesting. Each chapter was written as a manuscript intended for submission to an appropriate journal; therefore they are largely independent and stand on their own. A conclusion at the end of the report discusses the combined results of all three sections and looks at possible management implications.

Chapter 2 covers productivity effects from our 2010 field season at the Bartlett Experimental Forest in Bartlett, NH. We measured four 12-year old northern hardwood sites and report on three measures of productivity: height, diameter and calculated biomass of trees greater than 2 meters (m) in height. Chapter 3 discusses productivity effects found during our 2011 field season at a variety of sites across central New Hampshire. Twenty-nine 10-14 year old northern hardwood sites were measured, and we report on the same three measures of productivity. In both chapters, we attempt to quantify and isolate the effects of spatially variable solar radiation and moose browsing on our results.

Chapter 4 discusses effects on ecological characteristics of the stands measured in 2010 and 2011. The species composition and dominance of trees >2m in height are compared across harvest treatment as a whole, and then individually by species. We describe the patterns observed across harvest treatment and compare them with those due to estimated solar radiation intensity and uncut edge tree competition. Additionally, composition of tree species <2m in height and the understory plant community richness are examined and compared across harvest treatment.

The concluding chapter summarizes our results of the previous three chapters on the effect of whole-tree harvesting on productivity and species composition. We describe the limitations of our two field studies and potential management recommendations. Finally, we suggest areas that could benefit from additional research, with the goal of determining the long-term effects of whole-tree harvesting on our forests.

CHAPTER II

WHOLE-TREE HARVESTING AND SITE PRODUCTIVITY: A NORTHERN HARDWOOD SITE TWELVE YEARS AFTER HARVEST

Introduction

The burning of wood chips to generate electricity and thermal energy at biomass energy plants has become increasingly important as the United States becomes more reliant on renewable power. In the northeastern United States in particular, with its abundant forest resources and established forest products industry, biomass energy facilities represent an attractive method for generating local renewable energy (Benjamin et al., 2009). Non-merchantable tree residues from whole-tree harvesting are commonly used to meet the demand for biomass fuel. In a typical whole-tree harvesting (WTH) operation, the bole of the tree is used for conventional purposes such as lumber or other building materials. The branches and fine twigs can be chipped and sold to a biomass energy plant, providing an additional source of revenue for the landowner. In contrast, conventional harvesting (CH) removes only the bole, and leaves the other tree components on site to decompose.

Since whole-tree harvesting began in the 1970s, there has been concern that the additional removal of nutrient rich branches and fine twigs might impair site productivity (Anderson, 1985; Boyle, 1976; Kimmins, 1977), leaving a forest that regenerates trees that are slower growing and of lesser quality. This may be undesirable, as short-term gains from the extra sale of biomass may be offset by long-term losses due to reduced growth rates. Whole-tree harvesting is currently not practiced on shallow or sandy sites on least one of the nation's national forests (White Mountain National Forest) due to these productivity concerns (W.B. Leak, personal communication). Under what circumstances can WTH be practiced sustainably?

Early research into the effects of whole-tree harvesting on site productivity focused on measuring the nutrient export resulting from the removal of harvesting materials (Wells and Jorgensen, 1979; White, 1974). Nutrient imports from weathering and atmospheric deposition can be estimated and compared with the measured exports. If the outputs exceed inputs, it can be concluded that whole-tree harvesting may eventually leave the soils of certain sites unable to regrow trees at current rates. WTH was found to be sustainable for several rotations on a rich mixed hardwoods site in Wisconsin (Boyle and Ek, 1972). However, many studies caution that nutrient deficiency might be reached on nutrient poor sites, or ones with a shorter harvest rotation age (Carey, 1980; Weetman and Webber, 1972; White, 1974). Johnson et al. (1982) and Federer et al. (1989) point to calcium as the nutrient most likely to become limiting as a result of repeated whole-tree harvesting. One potential objection to these input-output studies is the assumption that all possible residue material is removed during a whole-tree harvest. Several studies have shown that it is not operationally possible to remove all biomass residue during harvest and a surprising amount likely remains on site, either unintentionally in the form of limbs breaking or branches placed intentionally to reduce erosion on skid trails. Briedis et al. (2011) found that 15% of all harvested material (45% of residue material) generated during whole-tree harvesting operations in central Maine remained on site. A previous study of a wider variety of sites across New England indicated that 4 - 10% of all harvested material remained on site (Pierce et al., 1993).

Another research approach has focused on directly measuring the nutrient content of the soil following harvest treatment. Since WTH removes more site nutrients than CH, one would expect to find WTH soils nutrient poor relative to those that were conventionally harvested. Either the total available nutrient content of the soil or just the exchangeable fraction available to trees can be measured. In a northern hardwood forest three years following harvesting, WTH did not result in a decrease in exchangeable Mg, Ca, or K levels when compared with CH (Johnson et al., 1991). A study of an acidic, upland Sitka spruce (*Picea sitchensis*) site found a loss of short-term potassium reserves, but estimated that weathering and other inputs could sustain WTH for another thirty 50-year rotations (Goulding and Stevens, 1988). In a Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) plantation in Sweden, WTH resulted in a lowered amount of exchangeable K, Ca, Mg, Mn, and Zn (Olsson et al., 1996a), but no effect on the N or C content of the soil (Olsson et al., 1996b) as compared with conventional harvesting. Briggs et al. (2000) found that WTH followed by herbicide and pre-commercial thinning resulted in only modest losses of Ca and nitrate in comparison with an uncut control site. Vanguelova et al. (2010) found WTH decreased K and P levels, but increased C and N soil storage relative to CH treatments. At least in regards to soil nutrition, it appears that many of the effects of WTH are site specific.

In addition to the indirect methods of measuring site productivity outlined above, productivity can be directly measured, usually in the form of tree biomass, height or diameter at breast height (DBH). Several of these studies found no significant difference in productivity between CH and WTH sites (Dyck et al., 1991; Hendrickson, 1988; Saarsalmi et al., 2010; Sanchez et al., 2006; Smethurst and Nambiar, 1990; Tan et al., 2009). Whole-tree harvesting was found to decrease second stand productivity in other studies, leading to the regeneration of shorter, thinner and/or less massive trees (Egnell and Leijon, 1999; Egnell and Valinger, 2003; Proe et al., 1996; Proe et al., 1994; Scott and Dean, 2006; Walmsley et al., 2009). While one study looking at the use of WTH to thin stands mid-rotation found decreased growth relative to CH (Jacobson et al., 2000), another found no evidence for long-term treatment effect (Nord-Larsen, 2002).

While negative effects to second stand productivity have been observed in certain stands, they have not been found to be universal. In addition, all of the above studies directly measuring loss of productivity were conducted in softwood plantations in Europe or loblolly pine plantations in the southern United States. These forest types are fundamentally different than the northern hardwood forest that occupies much of northern New Hampshire, Vermont, New York and Maine. Plantations in this forest type are rare, and stands typically regenerate naturally following a harvest. No studies have examined directly the productivity of second stand northern hardwood forests following whole-tree harvesting. Despite this lack of research, the constant need to supply biomass energy plants with wood chips has resulted in the widespread use of whole-tree harvesting across the northeastern United States. Clearly, there is a need to evaluate what effects whole-tree harvesting has on the forests of this region in comparison with conventional stem-only harvesting.

Serious concerns have been raised regarding the effects on long-term productivity of whole-tree harvesting, but are these concerns valid everywhere? Does just a single whole-tree harvest constitute a degradation of site quality? If WTH can be sustained in the northern hardwoods forests, it can aid in the generation of wood chips to fuel renewable biomass energy plants. The objective of our study is to determine if productivity differences – as assessed by tree height, diameter and biomass – can be detected in northern hardwood forests 12 years following WTH and CH treatments.

Methods

Study sites were located in the Bartlett Experimental Forest in the White Mountains of New Hampshire (Figure 1). Four patch cuts between 0.9 and 2.3 hectares located in research blocks 45 and 18 were harvested in November and December of 1998. Two patches were cut using whole-tree harvesting; the other two were done conventionally. All trees in both treatments were cut using a feller-buncher and yarded using grapple skidders. Prior to harvest, a mix of hardwood species dominated the stands, including sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*) and white ash (*Fraxinus americana*). The original purpose of the cutting was to examine quality of songbird habitat with different sized opening and different levels of residue removal. However, the experimental setup allows us to compare second-stand productivity resulting from whole-tree and conventional harvest methods.

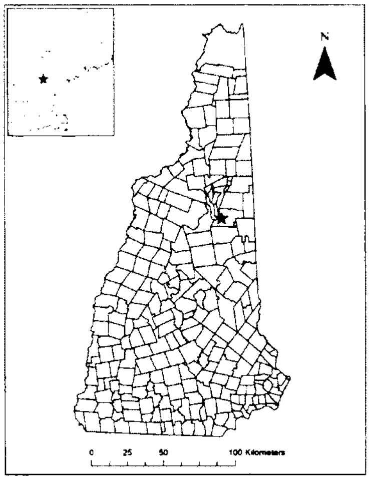

Figure 1: Location of Bartlett Experimental Forest within the state of New Hampshire and the northeastern United States (inset).

Tree species regeneration consists primarily of bigtooth aspen (*Populus grandidentata*), paper birch, yellow birch, American beech (*Fagus grandifolia*), pin cherry (*Prunus pensylvanica*) and red maple. Eastern hemlock (*Tsuga canadensis*), white ash, striped maple (*Acer pensylvanicum*) and sugar maple are found in lesser quantities. The sites are 260 to 310 meters in elevation and located on soils derived from glacial till parent material over granitic bedrock (Lyons et al., 1997). Slopes average 6-7 degrees and face either northeast (3 of the sites) or west (1 site). While the specific history of the land is not known, the Bartlett Experimental Forest is dominated by second growth forest resulting from widespread land clearing and timber harvesting in the late 1800s and early 1900s (Belcher, 1980). Much of the northeastern United States followed experienced similar land use histories (see Foster, 1992)

Preliminary Site Visits and Plot Selection

Two site visits were conducted in January and May 2010 to assess the variability of the regeneration and determine suitable sampling methods. To determine cut boundaries, a GPS position was recorded for uncut edge trees along the patch cut perimeter using a Garmin handheld GPS. The height of each edge tree was also measured using a laser rangefinder (Impulse 200 model from Laser Technology, Inc.) We expected that spatial variation in solar radiation would play a large role in forest productivity (Finzi and Canham, 2000) with areas receiving more radiation being more productive. These tree locations and heights were used to generate a model of incident solar radiation immediately following harvest (described in the next section).

A 6 x 6 meter grid of potential plots was generated within each of the patch cuts; the number of potential sample plots was therefore a function of the cut area. The total solar radiation incident on each was then calculated using the spatial solar radiation model. Potential plots in each cut were classified into one of three categories based on incident solar radiation during the growing season – high (greater than 4478 megajoules per square meter (MJ/m^2)), medium (3516 – 4478 MJ/m^2), and low (less than 3516

Table 1: Stratified random sampling of plots by radiation intensity category (see text for category definitions). Number of plots measured within each site was allocated proportionally by the composition of each cut, split by radiation category. Sites were either whole-tree (WTH) or conventionally harvested (CH) and between 0.9 and 2.3 hectares in size.

Harvest Treatment	Area (ha)	Composition of Cut by Radiation Category			Number of Plots Measured			
		Low	Med	High	Low	Med	High	Total
WTH	1.1	12%	28%	61%	4	8	18	30
CH	0.9	22%	64%	14%	7	19	4	30
WTH	2.3	5%	10%	85%	2	5	43	50
CH	1.9	6%	30%	64%	3	15	32	50

MJ/m^2). The solar radiation range and end points were selected subjectively. The fraction of potential plots in each category is a representation of the sunlight conditions that predominate in each patch cut and was used to stratify the actual sample plots we measured. Time and resource considerations constrained the total number of sample plots measured to 160; the two larger cuts were allocated 50 each and the two smaller were given 30 each. Within each cut, these sample plots were allocated in proportion to the radiation conditions of each site. For example, if 80% of the potential plots in a cut were in the high radiation category and we wanted to measure 50 total plots, 40 (0.8 * 50) would be in that high radiation category range. From among all potential plots in that category, 40 would be selected using a random number generator. This process was repeated for each radiation category in each patch cut (Table 1).

Spatial Solar Radiation Model

Using edge tree heights and positions, a model was created using ArcView GIS 3.3 to quantify the spatial variation in solar radiation present in the four Bartlett patch cuts. For each hour of a day, the model determined if a plot would be in sun or shade given the solar elevation angle, the solar azimuth angle, and the angle to the top of an appropriate edge tree. If the sun's elevation angle was greater than the angle to the top of an edge tree, that plot received that hour's worth of sunlight. The model ran incrementally through each hour of each day of the growing season (assumed to be April 1st through October 1st), and calculated the total radiation intensity (summed across all wavelengths, in MJ/m^2) a plot received. A more detailed description of how the radiation model was created step by step can be found in Appendix A. Plot radiation intensity was categorized into low (1157 – 3516 MJ/m^2), medium (3516 – 4478 MJ/m^2) and high (4478 – 5016 MJ/m^2) radiation classes.

Data Collection

Data were collected during June and July of 2010. Plot locations were found using a handheld GPS and were generally accurate to within 5 meters. Within a 2m-radius plot each tree above 2m in height was examined and recorded by species. Diameter at breast height (DBH) was measured to the nearest 0.1cm using a research grade DBH tape. Trees below 2cm DBH were rounded to the nearest 0.5cm. Height from the ground to the topmost living leaf was measured using a Senshin fiberglass telescopic height measurement pole and recorded to the nearest 3 cm (0.1 feet). A qualitative determination was made as to whether vegetation in the plot had been browsed by moose during this growing season. This was deemed necessary due to the significant differences in tree regeneration associated with annual browsing and likely unrelated to harvest treatment. By quantifying moose browse damage on each plot, we could examine the degree to which browse affected regeneration as well as the effects of harvest treatment. Due to inherent inaccuracies in GPS location and determination of the patch cut area, seven plots were located outside of the clearcut area or on logging roads and were excluded from our analysis.

Data Analysis

Tree biomass was calculated using species-specific regression equations developed by Jenkins et al. (2004). Preference was given to above-ground biomass equations from studies conducted near our study location, those with large sample sizes and those encompassing the small diameter trees in our plots (Table 2, Appendix B). Biomass is a straightforward measure of a tree's success, and was used as our primary measure of productivity. However, additional tests were conducted using mean tree height, mean tree DBH and tallest tree height as productivity measures to determine if our results were robust to this assumption. Using the statistical software JMP, we created mixed effects models to assess the amount of influence harvest treatment and solar radiation had on the productivity of tree species regeneration. Harvest treatment and solar radiation were treated as fixed effects while a variable uniquely identifying each clearcut was treated as a random effect. The addition of this random effect allowed us determine how much of the residual variance was due to within-cut variation and how much was due to cut-block effects. A similar model was created to assess the significance of our moose browse classification on tree species productivity.

Using the statistical package R, quantile regression was used to obtain an equation for the upper limit on the amount of biomass a plot can produce for given radiation levels. Since there are many unmeasured factors that may diminish the actual biomass present within a plot, fitting a line to those plots with the greatest biomass can be useful to represent a radiation-dependent upper limit of the growth rate. Given the distribution of data – a clear upper bound but with a large spread throughout - quantile regression represented a logical choice. We were unaware of any method to incorporate quantile regression into our mixed effects models, all of which fit the mean of the data. While we could have averaged all plots within a clearcut to use as our sample unit for the regression, this would yield very little statistical power as we only have two replicates of each treatment. Therefore, we decided to treat each plot as a replicate, and to acknowledge the problems associated with pseudo-replication. While the regression treats each plot as if it were independent from all others, our plots are clustered within one of only four clearcuts and likely violate this assumption. We are aware of the problems associated with this, and consider the result of this regression only in the context of the statistical tests described earlier. Statistical formulas from Thompson (2002) were used to calculate biomass per acre and stems density averages. A significance level of $P < 0.05$ was used in all tests.

Results

We measured 3,922 trees above 2m in height; maximum height was 10.5m, with a mean of 4.2m. Diameters ranged from 1.0 to 10.5 cm, with a mean of 2.3cm. Basal areas of plots averaged 11.0 m^2/ha (47.9 ft^2/acre) with a maximum of 31.9 m^2/ha (139 ft^2/acre). Biomass per acre estimates for each cut varied considerably, ranging from 6.1 to 33.4 metric tons per hectare (2.7 to 14.9 tons per acre). Trees >2m in height were densely spaced, with between 7,400 and 25,000 stems/ha (3,000 to 10,000 stems/acre).

Moose Browse

Signs of current year moose browse damage were found on 46% of CH plots but only on 13% of whole-tree harvested plots. Across both treatments, plots that had this recent damage from browsing contained trees that were significantly smaller in height (69% of unbrowsed plots), diameter (78%) and biomass (23%). A mixed effects model with moose browse category as a fixed effect showed that plots containing browsed trees were significantly less productive in all four of our measures (plot biomass $R^2 = 0.50$, $p < 0.0001$, 129 d.f.; mean height $R^2 = 0.50$, $p < 0.0001$, 65 d.f.; mean DBH $R^2 = 0.22$, $p = 0.001$, 21 d.f., tallest tree height $R^2 = 0.62$, $p < 0.0001$, 142 d.f.). As a way of removing this effect of moose browsing on regeneration and focus on the effects of harvest treatment, 44 plots (28% of total) showing signs of current year browse were excluded from our primary results on productivity below. These excluded plots were not evenly split among treatment; our results below are based on data from 69 WTH plots and 40 CH plots.

Biomass, Height and Diameter

A mixed effects model predicting plot biomass showed that WTH plots showed slightly more productive regeneration, a difference that was not statistically significant ($R^2 = 0.21$, $p = 0.47$, 1.7 d.f., Table 2). The ability of this model to determine harvest treatment differences was not strong, given the low number of replicates. Productivity effects ranging from 17% less biomass to 46% greater biomass following whole-tree harvesting are consistent with our model results, using two standard errors as our uncertainty. The same model showed that solar radiation played a significant role, with plots receiving more sunlight being more productive ($R^2 = 0.21$, $p = 0.047$, 105 d.f., Table 2). Of the remaining variance, 33% was attributable to differences between clearcut sites and the rest due to within-clearcut variability. Additional models with three different measures of productivity – mean tree height, mean tree DBH and tallest tree height – yielded similar but not identical results (Figure 2, Table 2). In no case was harvest treatment a significant predictor of productivity, and higher solar radiation was correlated with significantly higher productivity in all cases except for when mean tree DBH was used as the measure of productivity.

Table 2: Parameter estimates for the two fixed effects of mixed effects model on four productivity variables. Positive parameter estimates indicate an increase in each fixed effect is correlated with an increase in the productivity variable. The standard error reflects the uncertainty in the parameter estimate. A low p < |t| value indicates a high likelihood that a given fixed effect has significant predictive power on productivity; the degrees of freedom indicate our statistical power. Asterisks indicate statistical significance at the p < 0.05 level. Harvest treatment was treated categorically and the effects of conventional harvesting (CH) are reported as compared with whole-tree harvesting.

	Parameter estimate	Standard error	d.f.	t-ratio	p > |t|
Biomass					
Harvest Treatment[CH]	-5695.23	6178.04	1.7	-0.92	0.468
Solar Radiation	5.53	2.75	105.4	2.01	*0.047
Mean Height					
Harvest Treatment[CH]	-1.20	0.70	1.5	-1.72	0.265
Solar Radiation	0.00079	0.00039	102.5	2.04	*0.044
Tallest Tree per Plot Height					
Harvest Treatment[CH]	-2.69	1.62	1.7	-1.66	0.258
Solar Radiation	0.00162	0.00069	105.7	2.35	*0.021
Mean Tree DBH					
Harvest Treatment[CH]	-0.16	0.10	0.7	-1.49	0.445
Solar Radiation	0.00016	0.00010	63.3	1.57	0.121

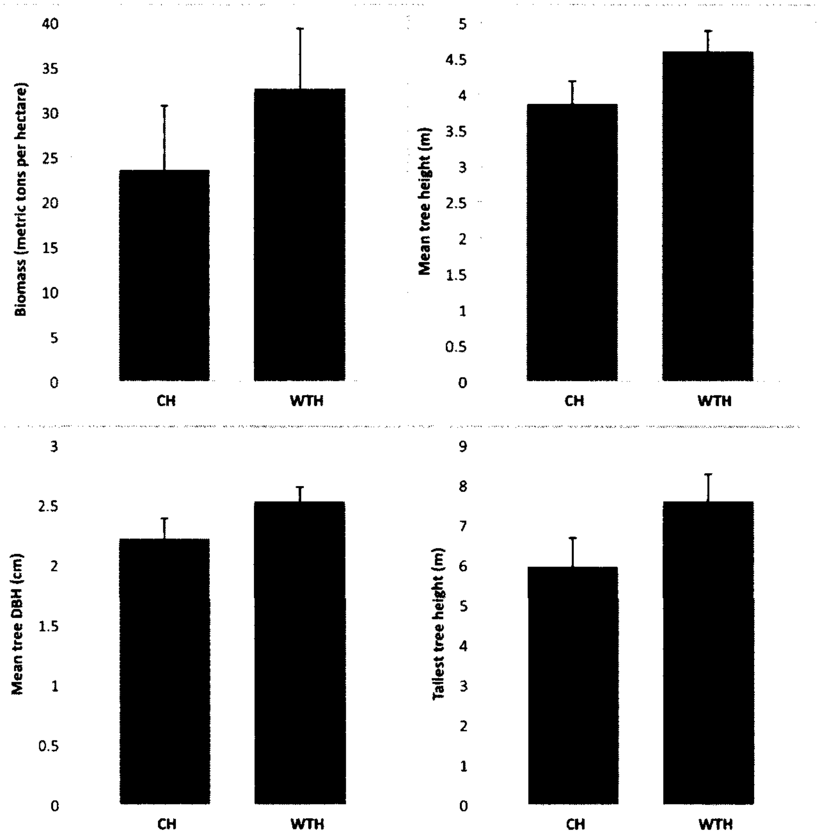

Figure 2: Productivity measures compared across harvest treatment. Error bars represent the standard error of the mean. Harvest treatment effects are not significant for any productivity measure. Data from four experimentally harvested northern hardwood sites in Bartlett Experimental Forest in Bartlett, NH.

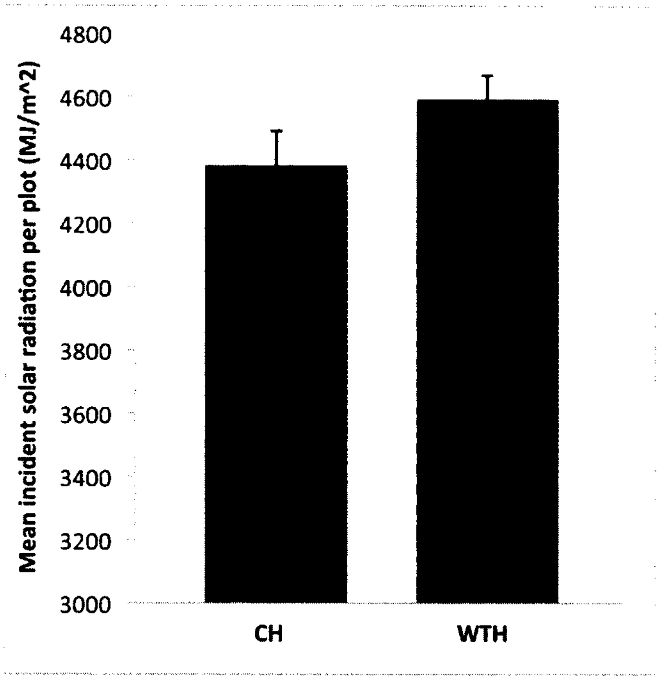

Figure 3: Estimated solar radiation per plot by harvest treatment. Differences between treatment are not statistically significant. Note that vertical axis has been scaled and does not begin at zero. Data calculated by a spatial solar radiation model created using ArcView 3.3.

Solar Radiation

Estimated solar radiation levels per plot during the growing season varied from 1600 to 5000 MJ/m^2. Largely as a result of cut shape, whole-tree harvested plots received slightly more radiation during the growing season as calculated by the spatial radiation model (t test, t=1.63, 74 d.f., p=0.11, Figure 3). Even though this difference was not statistically significant, quantile regression was used as another way to separate solar radiation from the effects of harvest treatment.

Quantile Regression

Plots of line slope and intercept vs. quantile revealed the 90th quantile to be a stable choice to represent the upper bound of the data; this is equivalent to fitting a line with 90% of the data beneath it. A two-variable regression including both radiation intensity and harvest treatment (WTH or CH) was not found to be significantly different than a simple model that only included radiation intensity (ANOVA, F=1.29, 106 d.f., p=0.26). With diameter as the independent variable instead of biomass, the result was the same, with harvest treatment adding no additional predictive power (F=0.08, 106 d.f., p=0.78). For mean tree height, a two variable quantile regression including treatment and radiation was slightly different than one including radiation alone, but did not meet our requirements for statistical significance (F=3.48. 106 d.f., p=0.065).

Discussion

No significant differences in second stand productivity are evident in our study sites 12 years following harvest treatments. A mixed effects model and quantile regression analysis showed harvest treatment had no predictive power over any of our measures of productivity. Higher biomass, height and diameter of trees in whole-tree harvested sites appear likely to be driven by a greater amount of solar radiation due to the orientation and size of the patch clearcuts. If WTH does indeed negatively affect site productivity, it is not evident on our northern hardwood sites 12 years following harvest.

These results agree with those of several other studies. Hendrickson (1988) found no difference in forest productivity four years following whole-tree and conventional harvests on an aspen (*Populus spp.*) and pine (*Pinus spp.*) stand in Ontario, Canada. Studies from New Zealand and Australia found no difference in radiata pine (*Pinus radiata*) growth three years following WTH and CH treatments (Dyck et al., 1991; Smethurst and Nambiar, 1990). WTH and CH treatment differences were similarly absent on a 10-year-old loblolly pine (*Pinus taeda*) plantation (Sanchez et al., 2006), a 3-year-old lodgepole pine (*Pinus contorta*) - Douglas fir (*Pseudotsuga menziesii*) plantation (Tan et al., 2009), and a 22-year-old Scots pine/Norway spruce plantation (Saarsalmi et al., 2010).

Additional studies have found results that contrast with ours – that whole-tree harvesting can reduce early second rotation growth. Studies of softwood plantations in England, Sweden, Wales and the southern U.S. all found WTH led to a statistically significant decrease in productivity when compared with conventional harvesting. Experiments on a Sitka spruce plantation in England showed whole-tree harvested sites yielded trees that were on average 0.8 meters shorter 10 years following harvest (Proe and Dutch, 1994). On a Scots pine/Norway spruce site in Sweden, Egnell & Vallinger (2003) found that after 24 years, WTH sites had trees with a smaller DBH (17%), lower biomass (20%) and were on average 0.6 meters shorter. Walmsley et al. (2009) found similar results 23 years following harvest in a Sitka spruce plantation in Wales. Evidence for decreased productivity was also found in loblolly pine plantations in the southern U.S., with WTH sites showing an 18% decrease in biomass as compared with CH sites (Scott and Dean, 2006). While not statistically significant, the trends revealed by our study were the reverse of this: higher second-stand biomass (39%), height (19%) and diameter (14%) on whole-tree harvested stands compared with CH sites. However, this may be primarily due to WTH plots receiving more solar radiation due to patch geometry and not necessarily a result of harvest treatment. The four previously mentioned studies finding WTH productivity declines were conducted in plantations and did not explicitly address radiation intensity. Given the uncertainty in our mixed effects model, conventionally harvested sites could contain trees ranging from 44% lower biomass to 16% higher biomass, using two standard errors as our confidence limits.

There are many differences between a naturally regenerated northern hardwood stand and a softwood plantation that may account for these discrepancies. Nutrient removal in our study sites might not be as high as in others because the harvest was conducted in winter after leaves had fallen. Leaves contain a high concentration of nutrients and harvesting trees in winter allows these nutrients to be returned to the site prior to harvest. In a softwood plantation, no matter when the harvest is conducted nutrient rich needles are removed along with the rest of the tree, potentially resulting in a higher drain on site fertility. Johnson and Curtis (2001) found some evidence for this in a meta-analysis of the effect of slash removal on C and N; softwood stands showed a higher level of depletion than hardwood stands. Additionally, the natural regeneration present in our Bartlett sites introduces more inherent variation than a highly replicated plantation. Thus, is it possible that results indicating productivity decline in the uniform conditions of a plantation are simply not yet observable in a system as variable as a naturally regenerating northern hardwoods patch cut. If that were the case, we would expect site depletion effects to eventually become observable after additional whole-tree harvests.

The most common theory put forth to explain observed productivity losses in WTH sites is that the differential loss of nutrients limits tree growth rates. However, factors besides nutrient concentration affect the ability of a stand to regenerate and grow. Slash removal in WTH can leave a forest floor more susceptible to large microclimate variations (Proe et al., 2001) possibly making it more difficult for certain tree seedlings to survive. Ground temperatures and wind speed variation could alter the relative success of different species, changing the ultimate species composition and productivity of the regenerating forest. If the species that are able to survive harsher WTH conditions do not grow as quickly as those that succeed in CH conditions, productivity of whole-tree harvested stands may suffer. If higher ground temperature fluctuations lead to increased regeneration of grasses, forbs and shrubs, these might compete with young tree seedlings for growing space and decrease productivity.

Limitations of this study lead us to urge caution about the potential for inappropriate extrapolation of our results. The sites studied have been treated a single time, and have only twelve years of growth. We cannot, therefore, comment on any long-term productivity effects of whole-tree harvesting. Additional studies are needed to see how these stands continue to develop and grow. In addition, the low level of replication of the harvest treatment (two sites per treatment) underscores the uncertainty of our results. A follow up study conducted in 2011 examined additional sites to see if our results here were common elsewhere. Examination of the residual variance in our mixed effects model on bimoass showed that 67% of the unaccounted-for variation was attributable to plot-to-plot variability within a clearcut site, suggesting that in future studies intensive site measurement may be more valuable than measuring many sites. Additional variability due to high levels of moose browse were also present in the smaller conventionally harvested cut. Twenty of the 30 plots located on this site showed signs of browse damage and were excluded from our analysis, leading to greater uncertainty in productivity estimates. While moose browse may not affect productivity of forests on a regional scale (Bergeron et al., 2011), the heavy browse of one of four of our sample sites certainly affects our results.

We also want to emphasize that our study only examines one aspect of the results of a harvest – tree growth and productivity. There are many reasons to conduct a harvest other than to grow trees quickly. Whole-tree harvesting removes fine and coarse woody debris from the site, which can have a significant effect on wildlife. Small mammals use downed logs as nesting and feeding areas, and loss of such debris can lead to decreased abundance in some cases (Loeb, 1999) but little effect in others (Bowman et al., 2000). Some bird species rely on downed woody debris to feed and nest during the breeding season, and studies have shown that experimental removal of this debris can lead to decreased bird richness and abundance (Lohr et al., 2002). Coarse woody debris is also primary habitat for many species of amphibians; retention of these materials is thought to be beneficial to their abundance and diversity (deMaynadier and Hunter, 1995).

Conclusion

Productivity differences were not observed between stands that were whole-tree harvested as compared to those that were conventionally harvested in a northern hardwoods forest 12 years following cutting. The height and biomass of regenerating stems appears to be more strongly dependent on the radiation intensity determined by the shape and orientation of the patch cut boundaries. Any loss of nutrients as a result of additional slash removal during whole-tree harvesting did not result in any productivity differences at this time. A significant amount of moose browse on one of two of the conventionally harvested stands was accounted for, but may have decreased the ability of our study to detect treatment differences. Differences between WTH and CH sites may be more prominent in highly controlled systems such as artificially regenerated softwood plantations. Additional replicates and repeated observations over time are needed to confirm or refute our results here.

Literature Cited

Anderson M. The impact of whole-tree harvesting in British forests. Quarterly Journal of Forestry (1985) 79:33-39.

Belcher CF. Logging Railroads of the White Mountains. (1980) Boston, MA: Appalachian Mountain Club.

Benjamin JG, Lilieholm RJ, Damery D. Challenges and Opportunities for the Northeastern Forest Bioindustry. Journal of Forestry (2009) 107:125-131.

Bergeron DH, Pekins PJ, Jones HF, Leak WB. Moose browsing and forest regeneration: a case study in northern New Hampshire. Alces (2011) 47:39-51.

Bowman JC, Sleep D, Forbes GJ, Edwards M. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management (2000) 129:119-124.

Boyle JR. System for Evaluating Potential Impacts of Whole-Tree Harvesting on Site Quality. Tappi (1976) 59:79-81.

Boyle JR, Ek AR. An evaluation of some effects of bole and branch pulpwood harvesting on site macronutrients. Canadian Journal of Forest Research (1972) 2:407-412.

Briedis JI, Wilson JS, Benjamin JG, Wagner RG. Biomass retention following whole-tree, energy wood harvests in central Maine: adherence to five state guidelines. Biomass and Bioenergy (2011) 35:3552-3560.

Briggs RD, Hornbeck JW, Smith CT, Lemin Jr. RC, McCormack Jr. ML. Long-term effects of forest management on nutrient cycling in spruce-fir forests. Forest Ecology and Management (2000) 138:285-299.

Carey ML. Whole tree harvesting in Sitka spruce. Possibilities and implications. Irish Forestry (1980) 37:48-63.

deMaynadier PG, Hunter MLJ. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews (1995) 3:230-261.

Dyck WJ, Hodgkiss PD, Oliver GR, Mees CA. Harvesting sand-dune forests: impacts on second-rotation productivity. In: Long-term Field Trials to Assess Environmental Impacts of Harvesting--Dyck WJ, Mees CA, eds. (1991) Rotorua, New Zealand: Forest Research Institute. 163-176.

Egnell G, Leijon B. Survival and growth of planted seedlings of Pinus sylvestris and Picea abies after different levels of biomass removal in clear-felling. Scandinavian Journal of Forest Research (1999) 14:303-311.

Egnell G, Valinger E. Survival, growth, and growth allocation of planted Scots pine trees after different levels of biomass removal in clear-felling. Forest Ecology and Management (2003) 177:65-74.

Federer CA, Hornbeck JW, Tritton LM, Martin CW, Pierce RS, Smith CT. Long-Term Depletion of Calcium and Other Nutrients in Eastern-United-States Forests. Environmental Management (1989) 13:593-601.

Finzi AC, Canham CD. Sapling growth in response to light and nitrogen availability in a southern New England forest. Forest Ecology and Management (2000) 131:153-165.

Foster DR. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology (1992) 80:753-772.

Goulding KWT, Stevens PA. Potassium Reserves in a Forested, Acid Upland Soil and the Effect on Them of Clear-Felling Versus Whole-Tree Harvesting. Soil Use and Management (1988) 4:45-51.

Hendrickson OQ. Biomass and Nutrients in Regenerating Woody Vegetation Following Whole-Tree and Conventional Harvest in a Northern Mixed Forest. Canadian Journal of Forest Research (1988) 18:1427-1436.

Jacobson S, Kukkola M, Malkonen E, Tveite B. Impact of whole-tree harvesting and compensatory fertilization on growth of coniferous thinning stands. Forest Ecology and Management (2000) 129:41-51.

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA. Comprehensive database of diameter-based biomass regressions for North American tree species (2004) Newtown Square, PA: US Department of Agriculture, Forest Service, Northeastern Research Station.

Johnson CE, Johnson AH, Siccama TG. Whole-Tree Clear-Cutting Effects on Exchangeable Cations and Soil Acidity. Soil Science Society of America Journal (1991) 55:502-508.

Johnson DW, Curtis PS. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management (2001) 140:227-238.

Johnson DW, West DC, Todd DE, Mann LK. Effects of sawlog vs. whole-tree harvesting on the nitrogen, phosphorus, potassium, and calcium budgets of an upland mixed oak forest. Soil Science Society of America Journal (1982) 46:1304-1309.

Kimmins JP. Evaluation of Consequences for Future Tree Productivity of Loss of Nutrients in Whole-Tree Harvesting. Forest Ecology and Management (1977) 1:169-183.

Loeb SC. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy (1999) 80:460-471.

Lohr SM, Gauthreaux SA, Kilgo JC. Importance of coarse woody debris to avian communities in loblolly pine forests. Conservation Biology (2002) 16:767-777.

Lyons JB, Bothner WA, Moench RH, Thompson Jr. JB. Bedrock Geologic Map of New Hampshire (1997): U.S. Department of the Interior, Geologic Survey.

Nord-Larsen T. Stand and site productivity response following whole-tree harvesting in early thinnings of Norway spruce (Picea abies (L.) Karst.). Biomass and Bioenergy (2002) 23:1-12.

Olsson BA, Bengtsson J, Lundkvist H. Effects of different forest harvest intensities on the pools of exchangeable cations in coniferous forest soils. Forest Ecology and Management (1996a) 84:135-147.

Olsson BA, Staaf H, Lundkvist H, Bengtsson J, Rosen K. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. Forest Ecology and Management (1996b) 82:19-32.

Pierce RS, et al. Whole-tree clearcutting in New England: manager's guide to impact on soils, streams and regeneration (1993): U.S.D.A. Forest Service General Technical Report NE-172.

Proe MF, Cameron AD, Dutch J, Christodoulou XC. The effect of whole-tree harvesting on the growth of second rotation Sitka spruce. Forestry (1996) 69:389-401.

Proe MF, Dutch J. Impact of Whole-Tree Harvesting on 2nd-Rotation Growth of Sitka Spruce - the First 10 Years. Forest Ecology and Management (1994) 66:39-54.

Proe MF, Dutch J, Griffiths J. Harvest residue effects on microclimate, nutrition and early growth of Sitka spruce (Picea sitchensis) seedlings on a restock site. New Zealand Journal of Forestry Science (1994) 24:390-401.

Proe MF, Griffiths JH, McKay HM. Effect of whole-tree harvesting on microclimate during establishment of second rotation forestry. Agricultural and Forest Meteorology (2001) 110:141-154.

Saarsalmi A, Tamminen P, Kukkola M, Hautajarvi R. Whole-tree harvesting at clear-felling: Impact on soil chemistry, needle nutrient concentrations and growth of Scots pine. Scandinavian Journal of Forest Research (2010) 25:148-156.

Sanchez FG, Scott DA, Ludovici KH. Negligible effects of severe organic matter removal and soil compaction on loblolly pine growth over 10 years. Forest Ecology and Management (2006) 227:145-154.

Scott DA, Dean TJ. Energy trade-offs between intensive biomass utilization, site productivity loss, and ameliorative treatments in loblolly pine plantations. Biomass and Bioenergy (2006) 30:1001-1010.

Smethurst PJ, Nambiar EKS. Effects of Slash and Litter Management on Fluxes of Nitrogen and Tree Growth in a Young Pinus-Radiata Plantation. Canadian Journal of Forest Research (1990) 20:1498-1507.

Tan X, Curran M, Chang S, Maynard D. Early Growth Responses of Lodgepole Pine and Douglas-Fir to Soil Compaction, Organic Matter Removal, and Rehabilitation Treatments in Southeastern British Columbia. Forest Science (2009) 55:210-220.

Thompson SK. Sampling. (2002) second edn. New York, NY: John Wiley & Sons, Inc.

Vanguelova E, Pitman R, Luiro J, Helmisaari HS. Long term effects of whole tree harvesting on soil carbon and nutrient sustainability in the UK. Biogeochemistry (2010) 101:43-59.

Walmsley JD, Jones DL, Reynolds B, Price MH, Healey JR. Whole tree harvesting can reduce second rotation forest productivity. Forest Ecology and Management (2009) 257:1104-1111.

Weetman GF, Webber B. The influence of wood harvesting on the nutrient status of two spruce stands. Canadian Journal of Forest Research (1972) 2:351-369.

Wells CG, Jorgensen JR. Effect of intensive harvesting on nutrient supply and sustained productivity. Presented at the Impact of Intensive Harvesting on Forest Nutrient Cycling, (1979) State University of New York, Syracuse, NY.

White EH. Whole-tree harvesting depletes soil nutrients. Canadian Journal of Forest Research (1974) 4:530-535.

CHAPTER III

WHOLE-TREE HARVESTING AND SITE PRODUCTIVITY: A LARGER SELECTION OF SITES IN NEW HAMPSHIRE AND WESTERN MAINE

Introduction

The burning of woody biomass to produce energy is a potential source of local, renewable power in northern New England. Whole-tree harvesting has the potential to provide needed wood chips to supply these biomass plants. In a whole-tree harvesting (WTH) operation, traditionally unmarketable treetops and branches can be chipped and sold. This additional income can be important to a landowner and help supply a growing renewable energy sector. However, concerns have been raised over the sustainability of whole-tree harvesting, as it removes nutrient-rich twigs, tops and low-grade woody material that would remain on site in a conventional (bole-only) harvesting (CH) operation. This additional drain on site nutrient reserves could have detrimental effects on site productivity, which may offset the benefits derived by this practice in our forests. There is a need to evaluate the potential effects of whole-tree harvesting on the future productivity of northern hardwood forests.

Concerns over long-term productivity effects of whole-tree harvesting have existed since the 1970s (Anderson, 1985; Boyle, 1976; Kimmins, 1977) when the practice first began being widely used. Early research on nutrient impacts of harvesting methods focused on comparing the amount of nutrients removed during harvest with the site's nutrient reserves. If removals are large enough, the practice of WTH could be harmful to the site and would likely impair its ability to grow trees quickly. Several studies have found cause for concern on nutrient poor sites or sites that are harvested on short rotations (Carey, 1980; Weetman and Webber, 1972; White, 1974), while others have concluded that WTH might be sustainable on richer sites (e.g. Boyle and Ek, 1972).

Johnson et al. (1982) pointed to calcium as the nutrient most likely to become limiting in an upland mixed-oak forest in Tennessee. Studies such as these that estimate system inputs and outputs may overestimate outputs by assuming that all or even most of the available residue material is removed from the site. Several studies have shown that it is not operationally possible to remove all biomass during harvest, with Briedis et al. (2011) recently finding that 15% of all harvested material (45% of residue material) generated during whole-tree harvesting operations in central Maine remained on site. A previous study of a wider variety of sites across New England measured that 4 - 10% of all harvested material remained on site (Pierce et al., 1993).

More recently, studies have looked to soil fertility for evidence of site depletion. As preferentially more nutrients are removed during whole-tree harvesting than in conventional harvesting, soil in WTH sites could become depleted over time. We might expect this effect to occur quicker in sites with nutrient poor soils. As a deficiency in one or more nutrients becomes limiting, the site's ability to grow trees will decline. Goulding and Stevens (1988) found WTH led to a short-term potassium deficiency, while Olsson et al. (1996a) showed a decrease in exchangeable K, Ca, Mg, Mn, and Zn cations. In other studies, no differences in soil nutrient content were observed. Johnson et al. (1991) found no preferential decrease in exchangeable base cations from WTH, and Olsson et al. (1996b) found no treatment effect on C and N soil content. In a meta-analysis, Johnson and Curtis (2001) suggested that harvest effects on carbon and nitrogen varied greatly by site, and that WTH was more harmful on coniferous sites than on deciduous ones. The fact that some of these studies measured *exchangeable* nutrient fractions while others measured *total* nutrient concentration may have also played some role in the discrepancy of their results.

Productivity can also be measured directly in the form of tree height, diameter or biomass. Studies of softwood plantations in Europe and the southeastern United States have found evidence of decreased second stand productivity resulting from residue removal during WTH when compared with CH (Egnell and Leijon, 1999; Egnell and Valinger, 2003; Proe et al., 1996; Proe et al., 1994; Scott and Dean, 2006; Walmsley et al., 2009). However, other studies have showed residue removal does not exert a significant effect on second stand productivity (Dyck and Skinner, 1990; Hendrickson, 1988; Saarsalmi et al., 2010; Sanchez et al., 2006; Smethurst and Nambiar, 1990; Tan et al., 2009). Once again the effect of residue removal does not seem to be universal; some sites seem to be more resilient to the removal of additional nutrients than others.

Our previous study of four patch cuts in a northern hardwood forest in the Bartlett Experimental Forest (BEF) in the White Mountains of New Hampshire showed forest productivity 12 years following harvest did not vary significantly by treatment. While initial results from that study suggested that whole-tree harvesting had weak *positive* effects of second stand productivity, we believe these results to be due to non-treatment factors. WTH plots contained less severely browsed regeneration than CH plots, and tended to receive more sunlight simply due to their size, shape and orientation. After removing heavily browsed sample plots across both treatments, mixed effects models showed that while higher radiation intensity predicted more productive regeneration, harvest treatment had no appreciable effect. Thus, twelve years following patch cutting in a northern hardwood forest, it appears residue removal in northern hardwood stands had no detectable effect on forest productivity.

With its ample forest resources and well established forest products industry, New England represents an ideal spot for the development of a biomass industry (Benjamin et al., 2009). Is widespread use of whole-tree harvesting to supply wood chips to such an industry justified or will it leave our forests depleted of nutrients and unable to grow trees at desired rates? Are the results obtained in the Bartlett Experimental Forest indicative of forest response across the northern hardwood forest of northern New England? Our previous study could not address this question due to its low level of replication (two sites per treatment) and narrow geographical sampling.

The goal of the current study was to determine if our initial findings at the BEF could be observed in a wider selection of similar northern hardwood sites. Our objectives were to (1) determine if productivity of regenerating trees is correlated with residue retention or removal and (2) determine if any correlations observed could be due to other site factors – radiation intensity, site age, clearcut size, soil type, slope and aspect. A comparison of our results with those found in the BEF gives a better picture of the effects of WTH as compared with CH as practiced in the northeastern United States.

Methods

Site Selection

Patch cut sites were selected based on their similarity to the four 12-year old patch cuts studied in 2010 in the BEF. Each site was cut using whole-tree or conventional harvesting between the years of 1997 and 2001, giving each an age of between 10 and 14 years when measured in the summer of 2011. The sites were all classified as northern hardwoods – sites with a significant softwood component were excluded. We tried to limit the size of the patch cuts to between 0.8 and 4 hectares (2 - 10 acres) during selection. However, when each cut was actually measured, several fell outside this range and were still included in our analyses. These factors were partially practical, but were also a way to minimize site variability due to factors other than harvest treatment. With each site as similar to the rest as possible, we hoped to be able to detect any productivity differences due to harvest treatment if they existed. We measured 29 sites in New Hampshire and western Maine (15 conventionally harvested and 14 whole-tree harvested) that fit our criteria.

Site Descriptions

Several site parameters varied significantly between WTH and CH treatments. Whole tree harvested areas averaged 1.8 ± 1.1 hectares in size and 11.5 ± 0.9 years in age. Canopy openings in conventionally harvested sites tended to be larger and older (t-test; size: t=3.5, 27 d.f., p=0.002; age: t=2.9, 27 d.f., p =0.007), averaging 3.3 ± 1.2 hectares and 12.7 ± 1.3 years. Sites were located between 250 and 650 meters in elevation on soils derived from glacial till parent material and classified as either well drained or moderately well drained. Bedrock underlying clearcut sites was primarily igneous, with WTH sites primarily dominated by Bethlehem Granodiorite and Ammonoosuc Volcanic Formations and CH sites containing a more heterogeneous mix of Bethlehem Granodiorite, Granite and Littleton Formations among others (Lyons et al., 1997). Plot slope averaged 6° and did not vary significantly over harvest treatment (t-test; t=0.5, 520 d.f., p=0.62). Detailed information on the land-use history of each site was not available, but prior to harvest most of the sites were second growth forest and were likely cleared for agriculture or timber harvesting in the late 1800s or early 1900s (Belcher, 1980; Foster, 1992).

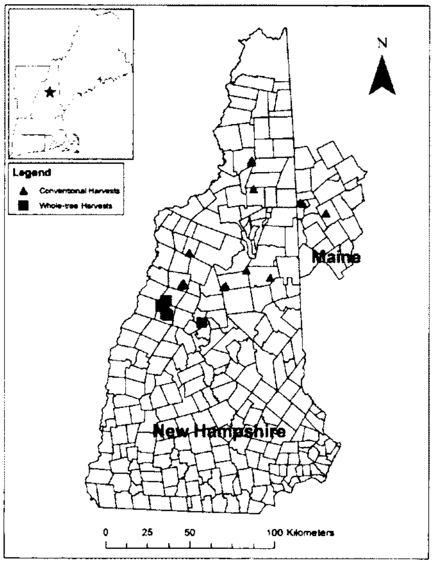

Figure 4: Locations of 14 whole-tree harvested (squares) and 15 conventionally harvested (triangles) study sites in New Hampshire and western Maine. Location within the northeastern United States is shown on the inset map.

Conventionally harvested sites were located on public lands within the White Mountain National Forest (WMNF) and were managed by the US Forest Service. However, out of concern for site degradation whole-tree harvesting is not currently practiced on the WMNF, so WTH sites were located on privately managed lands. Due to the difficulty in finding sites that met our criteria, WTH sites were heavily clustered in west central New Hampshire (Figure 4). Distance between farthest WTH sites was 26 km, as compared with the more widely dispersed CH sites (96 km separating the farthest two).

Conceptual Model

Within this paper, we hypothesize that environmental and treatment variables (measured and unmeasured) have an effect on the productivity of a sample plot. Productivity is expressed for the entire period since cutting and not on a per year basis. We assume no interaction terms, and that the productivity variables can be represented as a linear combination of our independent variables in an equation of the form

$$Y = \beta_0 + \beta_1 \cdot \chi_1 + \beta_2 \cdot \chi_2 + \ldots + \beta_n \cdot \chi_n + \varepsilon$$

where Y is one of four dependent productivity variables: sum of plot biomass, average plot tree height, maximum tree height per plot, and average per plot tree diameter; χ_n is the set of our independent variables: harvest treatment, radiation intensity, clearcut size, clearcut age, soil type, plot slope and plot aspect; β_n is a set of coefficients that reflect how each independent variable affects our estimation of each dependent productivity variable; and ε is an error term which includes the effects of unmeasured factors on the dependent productivity variables. Harvest treatment and soil type were treated as categorical variables with two possible levels and each level was assigned a numerical value – either a zero or a one. For example, if we take the harvest treatment variable to be n=1 in the above equation, $\chi_1 = 0$ for all CH plots and 1 for all WTH plots. Thus, the coefficient β_1 drops out for all CH plots and is simply a measure of how much more productive WTH plots are, independent of the other measured variables $\chi_{n\neq 1}$. Radiation intensity, clearcut size, clearcut age, slope and aspect were treated continuously, with the values of χ_n taken from GIS model calculations (radiation intensity and clearcut size), supplied by the land manager (clearcut age) or measured in the field (slope and aspect. The equation for each productivity variable Y was calculated independent of the equation for the other three productivity variables.

We define the null hypothesis H_0 – that no dependent variable has an effect on productivity – as

$$H_0 : \beta_n = 0$$

for all values of *n* at a confidence level of $p < 0.05$. In particular, we are interested in a subset of this null hypothesis, namely whether the coefficients representing the effect of harvest treatment on the four productivity variables are all equal to zero. The literature suggests either no effect or a negative effect on productivity due to whole-tree harvesting. We expected that the six other environmental independent variables (clearcut age, clearcut size, radiation intensity, soil type, slope and aspect) might have an effect on productivity as well, and each was included in the equation. In particular, we expected that clearcut age, clearcut size and radiation class would all have significant effects on productivity, with older, larger and more illuminated sites having more productive regeneration.

Data Collection

Sites were visited either once or twice between June 1st and August 11th, 2011. During the first visit, plots were located in a square grid pattern, with a spacing that varied from 27 to 49 meters (90 to 160 feet) depending on the size of the cut. Larger cuts received proportionally wider spacing, with the goal of measuring about 15 plots per cut. Midway through the field season, preliminary analysis of our results revealed additional plots were needed in cuts with a high coefficient of variation in tree height. These highly variable sites were revisited and additional plots were allocated proportional to the degree of variability exhibited in the initial visit. These supplemental transects were located between transects measured on the first visit. For sites not visited prior to preliminary analysis, plot spacing was decreased to accommodate about 30 plots per cut so these sites could be visited only once.

Within each plot the height, diameter at breast height (DBH) and species of all trees >2m in height within a 1m radius were recorded. Diameter was measured using a research grade DBH tape, and height was measured to the topmost living leaf using a Senshin fiberglass telescoping measuring rod. The slope and aspect of each plot were measured using a clinometer. Many of the plots exhibited signs of moose browse and were significantly different in appearance than those that were not browsed. In addition, a significant fraction of the plots contained grass and forb regeneration instead of trees.

Many of these plots were located along old logging roads or in wet areas. Both the browsed and non-forest areas were classified as "impaired" and excluded from subsequent analysis. Several areas within cuts contained trees far too large to have been regenerated following the cut. Plots that fell within these areas were noted as containing advanced regeneration and also excluded from our analysis.

The position and height of uncut edge trees surrounding the patch cut were recorded. Position was recorded using a Garmin handheld GPS device and height was estimated to the nearest 2m. For the initial sites, a laser rangefinder (Impulse 200 model from Laser Technology, Inc.) was used to accurately measure edge tree heights and served to check and calibrate estimation skills. These edge trees were used to accurately calculate the patch cut size and to develop a spatial solar radiation model to determine the amount of sunlight each sample plot received during the growing season.

Data Analysis

Species-specific biomass equations from Jenkins et al. (2004) were used to estimate individual aboveground tree biomass from measured diameter. For some species, many potential equations existed. When selecting which equation to use, preference was given to those developed on sites near our study location, those covering the small diameter range of trees in our sites, and those with large sample sizes. Biomass per hectare estimates for each site were calculated by dividing the total biomass present within a plot by its area and averaging over all plots within that site. T-tests were used to evaluate whether environmental variables (clearcut age, clearcut size, solar radiation intensity and plot slope) varied between WTH and CH sites. F-tests were run prior to these tests, and where variances were unequal, Welch's t-test (which does not assume equal variances) was used instead of a traditional t-test. A significance level of $P < 0.05$ was used in all tests.

Biomass values were summed and tree heights and diameters were averaged over each plot. A mixed effects model was created to determine whether choice of harvest treatment (WTH or CH) had any effect on productivity. The total amount of biomass present on each plot was used as our primary productivity measure, but three others were tested as well – mean tree height, mean tree DBH and tallest tree height. In addition to harvest treatment, six other variables were added to the model as fixed effects – clearcut age, clearcut size, radiation intensity (as calculated by the spatial radiation model, described below), soil type, plot slope and plot aspect. A variable uniquely identifying each clearcut was also added as a random effect, allowing us to determine how much of the remaining variance was due to plot variability within a site and how much was due to site-to-site variation. An additional mixed effects model was created to assess how the biomass of "impaired" plots (those that were heavily browsed or contained non-forest regeneration) compared with forested plots that were not browsed.

Quantile regression estimates of plot biomass and ANOVA tests for differences between equations were generated using R statistical software. There are many reasons why a given plot might fail to grow trees of an optimal rate, and our sampling procedure was not detailed enough to measure them all. Microclimate effects, competing vegetation during establishment and predation by wildlife are several reasons that trees within a plot may reach their growth potential. Through quantile regression, an equation that reflects only those plots that came closest to achieving this potential can be generated. We can think of this line as describing the productivity of plots that were likely not limited by unmeasured factors. The goal of this type of quantile regression was to select an appropriate quantile that accurately describes the upper bound of the data without being overly dependent on a small number of outliers.

Our mixed effects model fit the mean of the data, and we are unaware of any software that can fit the upper bound. Quantile regression estimates using each clearcut site as a replicate were highly unstable due to the low amount of sites, and were therefore not used. Treating each plot as a pseudo replicate allowed us to run meaningful quantile regressions, but violates important regression assumptions. Regression treats each plot as if it were independent from all others; our plots were clustered within one of twenty-nine clearcuts and likely violate this assumption. We are aware of the problems associated with pseudo replication and consider this regression less informative than the mixed effects model described earlier. The results of the quantile regressions do not change our conclusions, but are included to demonstrate that we find similar results using alternative methods. Tests revealed the 85th quantile to be a stable choice to represent the upper bound of each productivity measure, and two quantile regression equations were generated for each. The first considered only the six environmental variables, while the second additionally included harvest treatment (WTH or CH). ANOVA tests were run to determine whether these two equations were statistically different; this is equivalent to testing whether harvest treatment has a significant effect on productivity independent of other measured factors.

Spatial Solar Radiation Model

Using the GPS locations of measured plots and the positions and heights of edge trees, a spatial solar radiation model was created using ArcView 3.3 and ArcGIS 10.0 to predict the radiation intensity each plot would receive during the growing season. For each hour of a day, the model determined if a given plot would be in sun or shade due to the position and height of uncut edge trees around the clearcut border. If the elevation angle of the sun was greater than the angle to the top of the appropriate edge tree, the plot received that hour's worth of solar intensity. The model ran through each day of the growing season (assumed to be April 1st through October 1st) and totaled the amount of sunlight (in megajoules per square meter (MJ/m^2)) a plot received. This summed radiation intensity over the growing season was used to categorize each plot in one of three radiation categories: low (290 - 3516 MJ/m^2), medium (3516 – 4478 MJ/m^2) or high (4478 - 5049 MJ/m^2). A more detailed description of how the radiation model specifically calculates these values can be found in Appendix A. Due to GPS accuracy limitations, 16 plots inside clearcut boundaries appeared outside of them in our model; the level of solar radiation could not be accurately calculated for such plots and they were excluded from any analysis requiring a radiation intensity value.

Results

We measured 3,471 trees above 2m in height across 815 plots within our 29 study sites. Within 277 of the plots, vegetation was either severely browsed, non-forest (field, swamp, stream, road) or clearly of advanced regeneration origin; these plots were excluded from our analysis. 45% of plots within WTH sites and 27% within CH sites were excluded. The unequal distribution of these plots across harvest treatment contributed significant off-treatment variation prior to their exclusion.

The remaining 538 plots containing 2,951 trees were characterized by non-browsed forest regeneration that began its growth following harvest. Tree height averaged 4.3m with a maximum of 11.1m. Diameters ranged from 1.0 to 13.2 cm at breast height with an average of 2.5cm. Plot basal area averaged 12.5m^2/ha (54.4 ft^2/acre) and varied greatly from 0 to 71.7 m^2/ha (0 to 312.3 ft^2/acre) due to our small plot size. Aboveground biomass estimates per site ranged from 10.3 to 61.6 metric tons per hectare (4.6 to 27.5 tons per acre). Tree density ranged from 8,600 to 30,000 trees per hectare (3,500 to 12,000 trees per acre). Conventionally harvested plots on average received a higher level of solar radiation, as estimated by the spatial radiation model (t-test: $t = 3.0$, 520 d.f., $p = 0.003$, Figure 5).

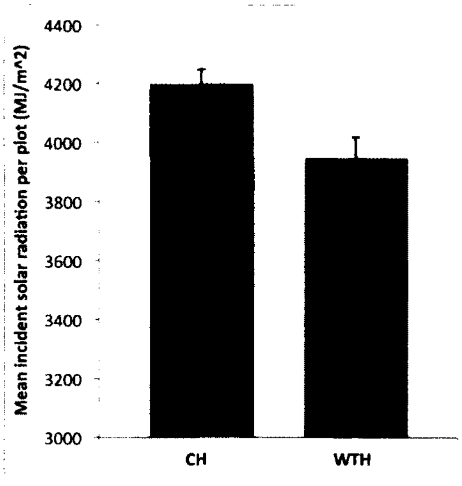

Figure 5: Estimated solar radiation per plot by harvest treatment. Error bars represent standard error of the mean. Conventionally harvested plots received significantly more solar radiation during the growing season. Note that vertical axis has been scaled to highlight this difference and does not begin at zero. Data calculated by a spatial solar radiation model using ArcView 3.3 and ArcGIS 10.0 for twenty-nine sites in central New Hampshire and western Maine.

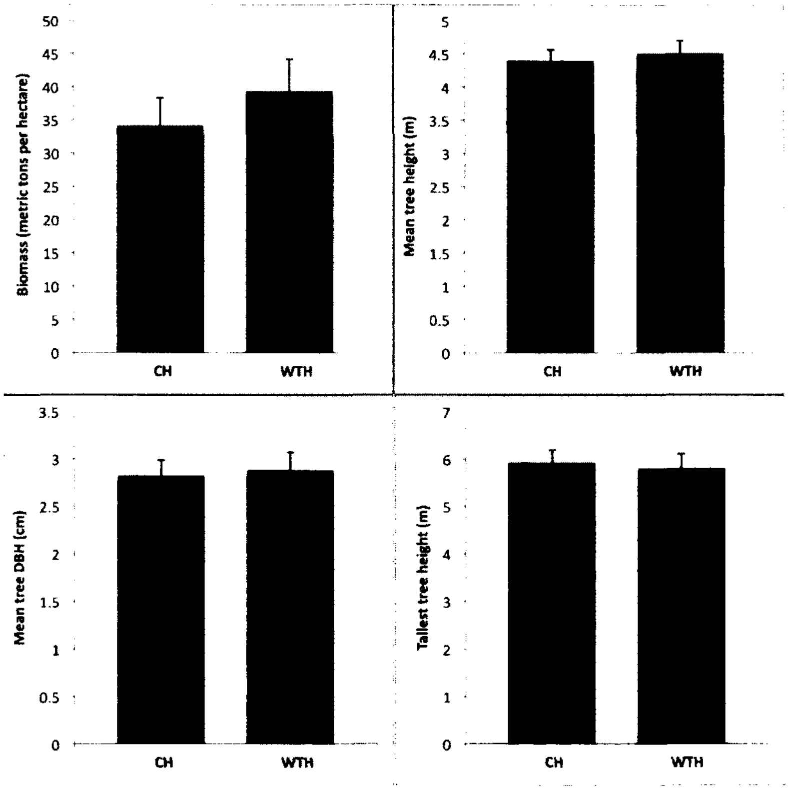

Figure 6: Productivity measures compared across harvest treatment. Error bars represent the standard error of the mean. Harvest treatment effects are not significant for any productivity measure. Data from twenty-nine northern hardwood sites in central New Hampshire and western Maine.

Height, Diameter and Biomass

A mixed effects model showed that harvest treatment did not have a strong effect on plot biomass ($R^2 = 0.10$, $p = 0.39$, 19 d.f.; Figure 6,Table). Due to the very low R-squared value, the ability of this model to predict productivity using the measured environmental and harvest variables was not strong. High uncertainty in parameter estimates meant that effects on plot biomass of whole-tree harvesting could range from a decrease of 10% to an increase of 26% when compared with the biomass of conventionally harvested plots (using two standard errors as our uncertainty). Models using mean tree height, mean tree DBH and tallest tree height as the productivity measure, yielded similar results (Figure 6, Tables 4-6); none showed that harvest treatment had a significant effect on productivity. Additionally, none of the additional six environmental variables – clearcut age, clearcut size, solar radiation intensity, soil, plot slope and plot aspect – had a significant effect on any productivity variable. Residual variance was primarily due to variability between plots within a clearcut site, with only six to nine percent of the variability due to site-to-site differences.

Regression

Two quantile regression equations were generated for each measure of productivity: one containing the six environmental variables and the second containing harvest treatment (WTH or CH) in addition to these six. If a pair of these equations was significantly different in predictive power, it suggested that harvest treatment has a significant effect on productivity independent of the other six environmental variables. The two equations were found to be not significantly different for biomass, mean height, tallest tree per plot height, or mean DBH (ANOVA; plot biomass: F=0.62, d.f.=503, p=0.43, mean height: F=0.45, d.f.=505, tallest tree per plot height: F=0.50, d.f.=504, p=0.48, p=0.50, mean DBH: F=0.91, 504 d.f., p=0.34).

Table 3: Parameter estimates for the mixed effects model on mean tree height. Positive parameter estimates indicate an increase in fixed effect is correlated with in increase in tree height. The standard error reflects the uncertainty in the parameter estimate. A low p > |t| value indicates a high likelihood that a given fixed effect has significant predictive power on tree height; the degrees of freedom and t-ratio for this test are reported as well. Harvest treatment and soil type were treated categorically and the effects on tree height of conventional harvesting (CH) and moderately well-drained till (MWDT) are reported as compared with whole-tree harvesting and well-drained till.

	Parameter estimate	Standard error	d.f.	t-ratio	p > |t|
Fixed Effects					
Harvest Treatment[CH]	-0.05604	0.11743	20.7	-0.48	0.64
Solar Radiation	-0.00007	0.00006	505.8	-1.12	0.27
Plot Slope	0.01870	0.01394	323.1	1.34	0.18
Plot Aspect	-0.00063	0.00057	255.7	-1.11	0.27
Soil Type[MWDT]	0.12708	0.13778	22.3	0.92	0.37
Clearcut Age	0.09655	0.07663	15.3	1.26	0.23
Clearcut Size	0.01461	0.03203	20.5	0.46	0.65
Random Effects	% variance				
Clearcut ID	7.2				
Residual Error	92.8				

Table 4: Parameter estimates for the mixed effects model of plot biomass. Positive parameter estimates indicate an increase in fixed effect is correlated with in increase in plot biomass. The standard error reflects the uncertainty in the parameter estimate. A low p > |t| value indicates a high likelihood that a given fixed effect has significant predictive power on plot biomass; the degrees of freedom and t-ratio for this test are reported as well. Harvest treatment and soil type were treated categorically and the effects on plot biomass of conventional harvesting (CH) and moderately well-drained till (MWDT) are reported as compared with whole-tree harvesting and well-drained till.

	Parameter estimate	Standard error	d.f.	t-ratio	p > |t|
Fixed Effects					
Harvest Treatment[CH]	-815.91	938.97	22.0	-0.87	0.39
Solar Radiation	0.34	0.49	503.6	0.69	0.49
Plot Slope	-91.19	113.90	312.0	-0.80	0.42
Plot Aspect	-8.63	4.64	247.8	-1.86	0.06
Soil Type[MWDT]	1511.35	1102.01	23.7	1.37	0.18
Clearcut Age	583.82	610.42	16.1	0.96	0.35
Clearcut Size	29.56	256.01	21.7	0.12	0.91
Random Effects	% variance				
Clearcut ID	6.6				
Residual Error	93.4				

Table 5: Parameter estimates for the mixed effects model on mean tree DBH. **Positive parameter estimates indicate an increase in fixed effect is correlated with in increase in tree DBH. The standard error reflects the uncertainty in the parameter estimate. A low p > |t| value indicates a high likelihood that a given fixed effect has significant predictive power on tree DBH; the degrees of freedom and t-ratio for this test are reported as well. Harvest treatment and soil type were treated categorically and the effects on tree DBH of conventional harvesting (CH) and moderately well-drained till (MWDT) are reported as compared with whole-tree harvesting and well-drained till.**

	Parameter estimate	Standard error	d.f.	t-ratio	p > |t|
Fixed Effects					
Harvest Treatment[CH]	-0.02915	0.11833	25.5	-0.25	0.81
Solar Radiation	-0.00004	0.00006	505.0	-0.72	0.47
Plot Slope	0.00044	0.01371	358.1	0.03	0.97
Plot Aspect	-0.00089	0.00056	300.1	-1.59	0.11
Soil Type[MWDT]	0.21856	0.13857	27.4	1.58	0.13
Clearcut Age	0.04235	0.07760	19.2	0.55	0.59
Clearcut Size	-0.02494	0.03226	25.4	-0.77	0.45
Random Effects	% variance				
Clearcut ID	8.0				
Residual Error	92.0				

Table 6: Parameter estimates for the mixed effects model on tallest tree height. **Positive parameter estimates indicate an increase in fixed effect is correlated with in increase in tree height. The standard error reflects the uncertainty in the parameter estimate. A low p > |t| value indicates a high likelihood that a given fixed effect has significant predictive power on tree height; the degrees of freedom and t-ratio for this test are reported as well. Harvest treatment and soil type were treated categorically and the effects on plot biomass of conventional harvesting (CH) and moderately well-drained till (MWDT) are reported as compared with whole-tree harvesting and well-drained till.**

	Parameter estimate	Standard error	d.f.	t-ratio	p > |t|
Fixed Effects					
Harvest Treatment[CH]	0.06077	0.18657	21.4	0.33	0.75
Solar Radiation	-0.00004	0.00009	504.9	-0.43	0.67
Plot Slope	0.01109	0.02082	362.7	0.53	0.59
Plot Aspect	-0.00032	0.00085	307.0	-0.38	0.70
Soil Type[MWDT]	0.20092	0.21815	22.9	0.92	0.37
Clearcut Age	0.05310	0.12317	16.5	0.43	0.67
Clearcut Size	0.01037	0.05086	21.3	0.20	0.84
Random Effects	% variance				
Clearcut ID	9.2				
Residual Error	90.8				

Discussion

Our study found no evidence of productivity limitation following whole-tree harvesting, in comparison with conventional bole-only methods. Mixed effects models and quantile regressions both showed that choice of harvest treatment had no significant effect on biomass, height or diameter of regenerating stems. A decrease in productivity following whole-tree harvesting is therefore not observed in our sample plots 10-14 years following a single harvest. Our concurrent study on four experimentally harvested sites in the Bartlett Experimental Forest in 2010 showed similar results. There, whole-tree harvested sites were found to have higher tree heights and diameters, but this difference was attributed to differences in radiation intensity. With radiation intensity factored out of the 2010 data, harvest treatment offered no predictive power on biomass, height or diameter.

Several studies directly measuring productivity have also found no productivity differences between whole-tree and conventional harvesting. Hendrickson (1988), working in a northern mixed forest in central Ontario, found no biomass difference in natural aspen (*Populus spp.*) or pine (*Pinus spp.*) regeneration four years following harvest treatment. No treatment differences were similarly detected in New Zealand or Australian stands of radiata pine (*Pinus radiata*) three years following harvest (Dyck et al., 1991; Smethurst and Nambiar, 1990). Productivity differences were similarly absent in a 10-year old loblolly pine plantation in the southern United States (Sanchez et al., 2006) and a 22-year old Scots pine/Norway spruce plantation in Finland (Saarsalmi et al., 2010). Our results also indicate no productivity decline resulting from residue removal, but the majority of these studies were conducted on coniferous plantations utilizing artificial regeneration techniques. These highly controlled systems are fundamentally different than the naturally regenerating northern hardwood forest where our study was conducted.

In contrast to our study and those listed above, whole-tree harvesting was found to reduce early second stand growth in several instances. Experiments on a Sitka spruce (*Picea sitchensis*) plantation found reductions in tree height 10 years following whole-tree harvest compared with trees on CH sites (Proe and Dutch, 1994). A follow-up study determined that early differences in growth rate caused heights to diverge 5-8 years following harvest and then grow at similar rates (Proe et al., 1996). Egnell and Leijon (1999) found decreased height following WTH was only evident after 7-10 years of regrowth in a Scots pine/Norway spruce stand. When the stand was revisited 24 years after initial harvest, trees on WTH sites showed reduced height (6%), DBH (17%) and biomass (20%) when compared with CH sites (Egnell and Valinger, 2003). 8-15% declines in productivity measures were reported in a Sitka spruce plantation in Wales 23 years following harvest (Walmsley et al., 2009). These studies suggest that differences in productivity manifest themselves 5-10 years following harvest and may be persistent for at least another 15 years. Although our study was conducted on stands within this timeframe (10-14 years of age), we detected no productivity decline due to whole-tree harvesting.

Differences in the way softwood and hardwood forests cycle nutrients may play a role in explaining why we detect no effects of residue removal and several other studies do. Whole-tree harvests on our northern hardwood sites were largely done in the winter after leaves had fallen. Leaves hold a large amount of nutrients, and their return to the site might mitigate nutrient losses due to whole-tree harvesting. In softwood plantations, nutrient rich needles are removed during harvest regardless of the season. In a meta analysis, Johnson and Curtis (2001) found the depletion of soil N and C following whole-tree harvesting was limited to softwood sites. However, with many studies of softwood plantations showing no productivity decline, it is likely that variability in site conditions and nutrient reserves play a large role in the effect WTH has on site productivity.

The degree of uniformity present in plantation silviculture may also play a role in detecting treatment differences. With each tree seedling of a single species starting at the same time and at the same height, the variability of tree heights throughout a stand's growth is bound to be unnaturally low. This makes detecting small treatment differences easier than in a highly variable naturally regenerating system. Plantation history may have also played a role; if soils were eroded or depleted due to intensive use, an already deficient nutrient pool may have led to slower growth rates on WTH sites. Our naturally regenerating northern hardwood sites, in contrast, have a relatively thick, nutrient rich organic layer and may be somewhat buffered from short-term nutrient depletion. The only study we could find that directly measured the effects of WTH and CH on second stand productivity in a naturally regenerating system found no treatment differences four years following harvest (Hendrickson, 1988).

Significant off-treatment variability between WTH and CH sites represents a weakness in our site selection process. However, our CH study sites were significantly larger in area and older than our WTH study sites and hence should have contained more productive regeneration. If residue removal from WTH causes of additional productivity limitation, this should have manifested itself as an even larger difference in productivity between treatments. However, WTH and CH sites in our study showed similar values for all measures of productivity.

Another important difference between treatments that is more difficult to quantify is that the clearcuts of each were likely outlined and administered somewhat differently. Conventional sites were located on public land and managed by the US Forest Service. The process of administering a harvest on public land is often a lengthy one, spanning several years from initial prescription to closing out the actual harvest. In contrast, WTH sites were located on privately managed lands and many were salvage operations following a severe ice storm in 1999. Salvage operations are inherently time-sensitive, with the damage due to the storm dictating the outline of a clearcut rather than years of careful planning. It is also possible that the storm damage on our WTH sites prior to harvest caused additional twigs and branches to fall into the stand understory and mitigate the loss of nutrients somewhat. However, the amount of residue left on site following CH would likely be significantly greater than the amount produced from storm damage.

Temporal and spatial limitations lead us to urge caution about extrapolation of our results. Our study found no effects of WTH on northern hardwood stands 10-14 years following a single harvest treatment, but cannot comment on long-term sustainability of the practice or harvests within different forest types. Many studies point to the potential for long-term depletion of soil nutrients if a site is whole-tree harvested multiple times especially on short rotations (Aber et al., 1979; Boyle et al., 1973; Federer et al., 1989; White, 1974). As whole-tree harvesting began being used widely only in the 1970s, no data exist to examine effects on site productivity over a long time scale. Long term monitoring of existing sites and the establishment of paired experimental treatments are needed to accurately describe such potential long-term effects. Our mixed effects models showed only six to nine percent of un-accounted for variance was due to variability between clearcut sites, with the rest attributed to plot variability within a site. This is likely due to our small plot sizes (1m-radius) and relatively small number of plots measured within each clearcut. This suggests that more intensive sampling (more plots per clearcut) in future studies may yield a more precise estimate of the effect of residue removal on productivity.

Even if residue removal has no impact on the tree species productivity, it may affect wildlife habitat in important ways. Small mammals feed and nest in and around coarse woody debris. Its removal from the landscape has been shown to have detrimental effects on the abundance of some mammals (Loeb, 1999) but not others (Bowman et al., 2000). A decrease in abundance and richness of bird species that utilize downed woody debris during the breeding season was noted when this woody material was experimentally removed from the landscape (Lohr et al., 2002). Retention of rotting woody debris provides primary habitat to many amphibians and is thought to be beneficial to overall amphibian abundance and diversity (deMaynadier and Hunter, 1995).

Conclusion

We find no evidence for productivity decline in a northern hardwoods forest following whole-tree harvesting as compared with similar stands that were conventionally (bole only) harvested. Height, diameter and calculated biomass did not decline due to residue removal on sites that were harvested 10-14 years ago. Previous research has found some evidence supporting our findings and some evidence suggesting productivity losses, but almost all were conducted on softwood plantations. Our study is one of the first to directly measure tree regrowth in a highly variable naturally regenerating system. While we cannot offer the final word on the sustainability of whole-tree harvesting, our study suggests that detrimental effects to productivity found by others following whole-tree harvesting might not occur in northern hardwoods forests of New Hampshire and western Maine.

Literature Cited

Aber JD, Botkin DB, Melillo JM. Predicting the effects of different harvesting regimes on productivity and yield in northern hardwoods. Canadian Journal of Forest Research (1979) 9:10-14.

Anderson M. The impact of whole-tree harvesting in British forests. Quarterly Journal of Forestry (1985) 79:33-39.

Belcher CF. Logging Railroads of the White Mountains. (1980) Boston, MA: Appalachian Mountain Club.

Benjamin JG, Lilieholm RJ, Damery D. Challenges and Opportunities for the Northeastern Forest Bioindustry. Journal of Forestry (2009) 107:125-131.

Bowman JC, Sleep D, Forbes GJ, Edwards M. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management (2000) 129:119-124.

Boyle JR. System for Evaluating Potential Impacts of Whole-Tree Harvesting on Site Quality. Tappi (1976) 59:79-81.

Boyle JR, Ek AR. An evaluation of some effects of bole and branch pulpwood harvesting on site macronutrients. Canadian Journal of Forest Research (1972) 2:407-412.

Boyle JR, Phillips JJ, Ek AR. "Whole Tree" Harvesting: Nutrient Budget Evaluation. Journal of Forestry (1973) 71:760-762.

Briedis JI, Wilson JS, Benjamin JG, Wagner RG. Biomass retention following whole-tree, energy wood harvests in central Maine: adherence to five state guidelines. Biomass and Bioenergy (2011) 35:3552-3560.

Carey ML. Whole tree harvesting in Sitka spruce. Possibilities and implications. Irish Forestry (1980) 37:48-63.

deMaynadier PG, Hunter MLJ. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews (1995) 3:230-261.

Dyck WJ, Hodgkiss PD, Oliver GR, Mees CA. Harvesting sand-dune forests: impacts on second-rotation productivity. In: Long-term Field Trials to Assess Environmental Impacts of Harvesting--Dyck WJ, Mees CA, eds. (1991) Rotorua, New Zealand: Forest Research Institute. 163-176.

Dyck WJ, Skinner MF. Potential for productivity decline in New Zealand radiata pine forests. Presented at the North American Forest Soils Conference, July 1988 (1990) University of British Columbia, Vancouver, Canada.

Egnell G, Leijon B. Survival and growth of planted seedlings of Pinus sylvestris and Picea abies after different levels of biomass removal in clear-felling. Scandinavian Journal of Forest Research (1999) 14:303-311.

Egnell G, Valinger E. Survival, growth, and growth allocation of planted Scots pine trees after different levels of biomass removal in clear-felling. Forest Ecology and Management (2003) 177:65-74.

Federer CA, Hornbeck JW, Tritton LM, Martin CW, Pierce RS, Smith CT. Long-Term Depletion of Calcium and Other Nutrients in Eastern-United-States Forests. Environmental Management (1989) 13:593-601.

Foster DR. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology (1992) 80:753-772.

Goulding KWT, Stevens PA. Potassium Reserves in a Forested, Acid Upland Soil and the Effect on Them of Clear-Felling Versus Whole-Tree Harvesting. Soil Use and Management (1988) 4:45-51.

Hendrickson OQ. Biomass and Nutrients in Regenerating Woody Vegetation Following Whole-Tree and Conventional Harvest in a Northern Mixed Forest. Canadian Journal of Forest Research (1988) 18:1427-1436.

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA. Comprehensive database of diameter-based biomass regressions for North American tree species (2004) Newtown

Square, PA: US Department of Agriculture, Forest Service, Northeastern Research Station.

Johnson CE, Johnson AH, Siccama TG. Whole-Tree Clear-Cutting Effects on Exchangeable Cations and Soil Acidity. Soil Science Society of America Journal (1991) 55:502-508.

Johnson DW, Curtis PS. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management (2001) 140:227-238.

Johnson DW, West DC, Todd DE, Mann LK. Effects of sawlog vs. whole-tree harvesting on the nitrogen, phosphorus, potassium, and calcium budgets of an upland mixed oak forest. Soil Science Society of America Journal (1982) 46:1304-1309.

Kimmins JP. Evaluation of Consequences for Future Tree Productivity of Loss of Nutrients in Whole-Tree Harvesting. Forest Ecology and Management (1977) 1:169-183.

Loeb SC. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy (1999) 80:460-471.

Lohr SM, Gauthreaux SA, Kilgo JC. Importance of coarse woody debris to avian communities in loblolly pine forests. Conservation Biology (2002) 16:767-777.

Lyons JB, Bothner WA, Moench RH, Thompson Jr. JB. Bedrock Geologic Map of New Hampshire (1997): U.S. Department of the Interior, Geologic Survey.

Olsson BA, Bengtsson J, Lundkvist H. Effects of different forest harvest intensities on the pools of exchangeable cations in coniferous forest soils. Forest Ecology and Management (1996a) 84:135-147.

Olsson BA, Staaf H, Lundkvist H, Bengtsson J, Rosen K. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. Forest Ecology and Management (1996b) 82:19-32.

Pierce RS, et al. Whole-tree clearcutting in New England: manager's guide to impact on soils, streams and regeneration (1993): U.S.D.A. Forest Service General Technical Report NE-172.

Proe MF, Cameron AD, Dutch J, Christodoulou XC. The effect of whole-tree harvesting on the growth of second rotation Sitka spruce. Forestry (1996) 69:389-401.

Proe MF, Dutch J. Impact of Whole-Tree Harvesting on 2nd-Rotation Growth of Sitka Spruce - the First 10 Years. Forest Ecology and Management (1994) 66:39-54.

Proe MF, Dutch J, Griffiths J. Harvest residue effects on microclimate, nutrition and early growth of Sitka spruce (Picea sitchensis) seedlings on a restock site. New Zealand Journal of Forestry Science (1994) 24:390-401.

Saarsalmi A, Tamminen P, Kukkola M, Hautajarvi R. Whole-tree harvesting at clear-felling: Impact on soil chemistry, needle nutrient concentrations and growth of Scots pine. Scandinavian Journal of Forest Research (2010) 25:148-156.

Sanchez FG, Scott DA, Ludovici KH. Negligible effects of severe organic matter removal and soil compaction on loblolly pine growth over 10 years. Forest Ecology and Management (2006) 227:145-154.

Scott DA, Dean TJ. Energy trade-offs between intensive biomass utilization, site productivity loss, and ameliorative treatments in loblolly pine plantations. Biomass and Bioenergy (2006) 30:1001-1010.

Smethurst PJ, Nambiar EKS. Effects of Slash and Litter Management on Fluxes of Nitrogen and Tree Growth in a Young Pinus-Radiata Plantation. Canadian Journal of Forest Research (1990) 20:1498-1507.

Tan X, Curran M, Chang S, Maynard D. Early Growth Responses of Lodgepole Pine and Douglas-Fir to Soil Compaction, Organic Matter Removal, and Rehabilitation Treatments in Southeastern British Columbia. Forest Science (2009) 55:210-220.

Walmsley JD, Jones DL, Reynolds B, Price MH, Healey JR. Whole tree harvesting can reduce second rotation forest productivity. Forest Ecology and Management (2009) 257:1104-1111.

Weetman GF, Webber B. The influence of wood harvesting on the nutrient status of two spruce stands. Canadian Journal of Forest Research (1972) 2:351-369.

White EH. Whole-tree harvesting depletes soil nutrients. Canadian Journal of Forest Research (1974) 4:530-535.

CHAPTER IV

EFFECTS OF WHOLE-TREE HARVESTING ON SPECIES COMPOSITION OF TREE AND UNDERSTORY COMMUNITIES IN A NORTHERN HARDWOOD FOREST TWELVE YEARS FOLLOWING HARVEST

Introduction

The burning of woody biomass to create electricity has the potential to supply local, renewable energy to the northeastern United States. With its well established forest products sector, ample forest resources and high percentage of land in private ownership to quickly meet market demands, New England represents an ideal location for a wood-based biomass industry (Benjamin et al., 2009). In forested regions such as the northeastern U.S., whole-tree harvesting (WTH) is commonly used to supply biomass energy plants with feedstock. During WTH, traditionally non-merchantable wood residue in the form of branches and treetops are chipped, sold, and eventually burned for energy. In conventional harvesting (CH), this residue remains on site and decomposes, returning its nutrients to the soil. In effect, WTH allows a landowner to earn additional income while supplying fuelwood to local biomass energy plants. However, the effect of residue removal during whole-tree harvesting on the future species composition and productivity of our forests is not well known.

Concerns about the effects of removing additional woody residues on the future of the forest have long been recognized (Anderson, 1985; Boyle, 1976; Kimmins, 1977). Removal of the additional nutrients contained in harvest slash may eventually leave a site unable to grow trees at its highest rate, impairing the productivity of the forest. Woody residue may provide structural benefits to wildlife, and its removal may have an effect on animals that utilize rotting woody debris as habitat. Finally, the removal of harvest slash may change the microclimate of the forest floor, altering which seeds and seedlings are ultimately successful in regenerating and affecting the species composition of the next stand.

Branches, fine twigs and needles that make up harvesting slash contain a large proportion of a tree's nutrients, and their removal could have significant effects on site fertility. The primary concern is that WTH could impair future site productivity, leaving a forest that regrows slowly or contains trees of poor quality. Studies examining soil nutrient content have found discrepant results; WTH harvesting was found to deplete certain soil nutrients on some sites (Olsson et al., 1996a; Vanguelova et al., 2010) but have no effect on others (Johnson et al., 1991; Olsson et al., 1996b). Several studies have measured productivity declines directly following WTH, finding trees that are smaller, have smaller diameters and a lower biomass than those of CH sites (Egnell and Valinger, 2003; Proe et al., 1996; Scott and Dean, 2006; Walmsley et al., 2009). However, all of these studies were conducted in softwood plantations and additional studies exist that show no productivity decline on similar sites (Dyck et al., 1991; Hendrickson, 1988; Saarsalmi et al., 2010; Sanchez et al., 2006; Smethurst and Nambiar, 1990; Tan et al., 2009). The majority of these studies do not examine ecological effects such as species composition, as most study sites utilize artificial regeneration techniques to establish the subsequent stand.

Through removal of harvest residues, WTH likely reduces the amount of fine and coarse woody debris on a forest floor, which may have negative impacts on wildlife that require decomposing wood for habitat. Effects are likely to be both site and species specific, with one study showing decreases in richness and abundance of songbirds (Lohr et al., 2002) and another showing a decrease in small mammal populations as a result of coarse woody debris removal (Loeb, 1999). Bowman et al. (2000) found rotting logs to be important to red-backed vole populations on a landscape scale, but no evidence for a link between coarse woody debris and other small mammal populations. Coarse woody debris is also an important habitat requirement for many species of salamander, and its removal from the landscape would likely have negative effects on their populations and diversity (deMaynadier and Hunter, 1995).

We might also expect the retention or removal of woody debris to have an effect on the microclimate of the forest floor following harvest. This may regulate to some degree the tree species that are able to regenerate and recolonize the site. Proe et al. (2001) found that WTH sites experienced higher wind speeds and larger temperature fluctuations when compared with sites where harvest residues were retained. These effects quickly dissipated as vegetation was re-established, but may play a significant factor in early seedling establishment during natural regeneration. In an upland hardwoods site in Tennessee, Mann (1984) found more vigorous stump sprouting following CH, but more seedling establishment following WTH. Certain species also appeared to regenerate more strongly following a certain treatment; chestnut oak (*Quercus montana*), black oak (*Quercus velutina*) and red maple (*Acer rubrum*) did best following CH while black gum (*Nyssa sylvatica*), tulip poplar (*Lireodendron tulipifera)* and sourwood (*Oxydendrum arboreum*) seemed to prefer WTH. Brakenhielm and Liu (1998) found that WTH significantly altered species composition, diversity and succession in a lichen-Scots pine forest in Sweden.

Many studies of the White Mountains of New Hampshire have correlated changes in environmental factors with changes in species composition. In a study of small canopy openings, McClure and Lee (1993) showed that gap size, gap age and position within the gap were all significant predictors of tree species composition. Leak (1976) and (1978) outlined a classification scheme based on soil parent type and drainage class and correlated each category with tree species composition in late and mid-successional stands. Lee et al. (2005) also found soil substrate to be a significant predictor, and additionally showed elevation seemed to play a major role in tree species composition. All of these studies point to the underlying effects that soil moisture and nutrient content have on regeneration. Whole-tree harvesting affects these same two factors by removing additional nutrients from the site, and likely increasing the amount of sunlight the understory receives, affecting soil moisture. This points to the potential for changes in tree species composition following WTH and natural regeneration in comparison with sites where residues are retained. We are not aware of any studies that examine the effects of residue removal or retention of the species composition of the next stand within the northeastern U.S.

With whole-tree harvesting increasingly used to meet demand for woody biomass chips, research is needed to determine the ecological effects of this practice on species composition of the regeneration. The vast majority of timber harvests in the northeastern United States rely on natural regeneration to repopulate a forested stand, and small changes to the microclimate of the forest floor may result in significant changes to species composition of the regeneration. Compositional changes in forest regeneration can alter the productivity and merchantability of the next stand of trees. The objective of this study is to determine the effects of residue removal from WTH on natural regeneration in northern hardwood sites in New Hampshire in comparison with conventionally harvested stands where residues were retained. Our focus is on the species composition and abundance of (1) trees > 2m tall, (2) tree saplings ≤ 2m tall, and (3) non-tree understory plants. We made an additional effort to determine if any effects observed could be explained by spatial variations in radiation intensity alone. Two separate studies, different in their scope, were conducted and are summarized here. The first examines all three objectives on four sites in the Bartlett Experimental Forest in the White Mountains of New Hampshire while the second examines just the first objective on 29 sites in central New Hampshire and western Maine.

Methods

Site Description and History

Sites were measured over two summers as a part of concurrent studies examining the impacts of residue removal on site productivity. Four 12-year old patch cuts in the Bartlett Experimental Forest (BEF) were measured during summer 2010 (Figure 7). These cuts were between 0.9 and 2.3 hectares (2.2 to 5.7 acres) in size and were harvested during November and December of 1998. Trees were whole-tree harvested in two of the cuts (residues removed) and conventionally harvested in the others (residues left on site). Sites were between 260 and 310 meters in elevation and located on glacial till parent material. Underlying bedrock was primarily igneous, with the highly clustered WTH sites on Bethlehem Granodiorite and Ammonoosuc Volcanic Formations. Conventionally harvested sites were more geographically well distributed, and were located over Bethelehem Granodiorite, Granite and Littleton Formations (Lyons et al., 1997). Terrain on the sites gently sloped (6-7 degrees) to the northeast (3 sites) or west (1 site). Although no measurements were made prior to harvest, timber sale reports reveal that the previous stands consisted primarily of northern hardwood tree species. Detailed information on the land-use history of each site was not available, but prior to harvest most of the sites were second growth forest and were likely cleared for agriculture or timber harvesting in the late 1800s or early 1900s (Belcher, 1980; Foster, 1992).

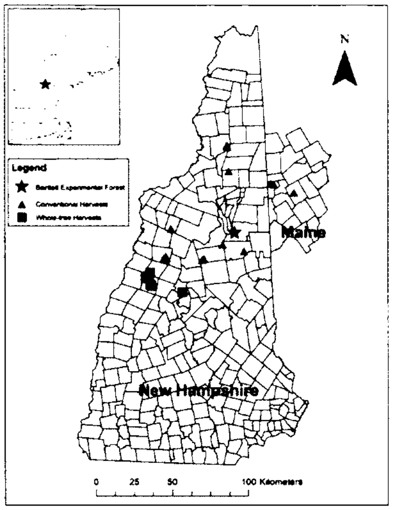

Figure 7: Map showing the location of the Bartlett Experimental Forest (star), site of the four patch cuts measured in 2010. Also shown are the 14 whole-tree harvested (squares) and 15 conventionally harvested (triangles) patch cuts measured in 2011 within New Hampshire and western Maine. Location within the northeastern United States is shown on the inset map.

Twenty-nine additional patch cuts in central New Hampshire and western Maine were measured during summer 2011 (Figure 7). These cuts were not established for research purposes as were the sites at the BEF, but were selected to be as similar to the BEF sites as possible: northern hardwood forests that were cut 10-14 years ago using patch cuts that were between 0.6 and 5.7 hectares (1.6 – 14.1 acres) in size. Fourteen whole-tree harvested and 15 conventionally harvested sites that fit these criteria were located and measured. Sites were between 250 and 650 meters in elevation, located on soils with glacial till parent material, and classified as either well or moderately well drained. No data on the species composition of previous stands were available. Conventionally harvested sites were located on US Forest Service lands in the White Mountain National Forest (WMNF) while WTH sites were located on private lands.

Whole-tree harvesting is not currently practiced on the WMNF due to concerns about nutrient depletion, especially on shallow or sandy sites (W.B. Leak, personal communication).

Data Collection

As our studies were conducted using different methods, they were analyzed separately; we will reference them using the year of the data collection (2010 or 2011).

2010 Study. The height and location of uncut trees along the edge of each patch cut were recorded during initial site visits. This information was used to accurately measure the size and shape of each patch cut and to create a model to predict radiation intensity during the growing season. This spatial solar radiation model (described in detail in a later section) was based on simple assumptions and calculated the radiation intensity expected at any point within a site based on edge tree heights and the position of the sun. We expected regeneration to vary based on spatial variation in sunlight levels (Finzi and Canham, 2000); areas that were shaded by nearby edge trees would be more likely to regenerate shade tolerant species than areas receiving full sunlight.

Using ArcView GIS 3.3, a 6x6 meter grid of potential plots was overlaid on each patch cut, creating a group of measurable plots that was dependent on patch size. For each potential plot, the radiation intensity throughout the growing season was calculated using the spatial radiation model and reported in megajoules per square meter (MJ/m^2). Potential plots were categorized as receiving high (> 4478 MJ/m^2), medium (3516 – 4478

Table 3: Stratified random sampling of plots by radiation intensity category (see text for category definitions). Number of plots measured within each site was allocated proportionally by the composition of each cut, split by radiation category. Sites were either whole-tree (WTH) or conventionally harvested (CH) and between 0.9 and 2.3 hectares in size.

Harvest Treatment	Area (ha)	Composition of Cut by Radiation Category			Number of Plots Measured			
		Low	Med	High	Low	Med	High	Total
WTH	1.1	12%	28%	61%	4	8	18	30
CH	0.9	22%	64%	14%	7	19	4	30
WTH	2.3	5%	10%	85%	2	5	43	50
CH	1.9	6%	30%	64%	3	15	32	50

MJ/m^2) or low (< 3516 MJ/m^2) amounts of radiation. Actual plots to be measured were selected using stratified random sampling using radiation categories as strata. 30 plots were allocated to each of the smaller cuts, while 50 were measured in the two larger cuts. Thus, if 60% of the potential plots were in the high radiation category and that cut was allocated 50 actual plots, 30 plots (0.6 * 50) were selected randomly from the pool of high radiation category plots to be measured. This method allowed the measured plots to be representative of the different sunlight conditions that were actually present within the cut (i.e. no radiation condition was over- or under-represented, see Table 7).

Each of the 160 plots was visited either during June or July 2010. Plot centers were located using a handheld GIS unit and were generally accurate to within 5m. Within a 2m-radius plot, the height, diameter and species of all trees taller than 2m were recorded. Diameter at breast height (DBH) was measured to the nearest 0.1 cm using a research grade DBH tape; small trees (<2 cm DBH) were estimated to the nearest 0.5 cm. Tree height to the topmost living leaf was recorded to the nearest 0.3 cm (0.1 inch) using a Senshin fiberglass measuring pole. Within a 1m-radius subplot, saplings shorter than 2m were tallied by species. We made no attempt to distinguish between saplings of seed and sprout origin. Non-tree species occurring within this subplot were also recorded.

Two plant groups were difficult to separate into species and were recorded by genus (*Carex. spp.* and *Rubus spp.);* other plants we were unable to identify were excluded from our analysis. Slope and aspect of each plot were measured using a clinometer. A qualitative assessment was made as to whether or not vegetation within the plot had been browsed by moose during the past year. This observation was made to categorize and isolate variation due to repeated moose browsing of regeneration. Seven plots were either located on logging roads or fell outside the actual cut area due to limitations in GPS accuracy and were therefore excluded from our analysis.

2011 Study. Due to research resource considerations, the sampling protocol for the 2010 study was modified for the 2011 study. Plots were located according to a square grid pattern oriented north-south or east-west, with grid spacing varying by site based on the size of the cut opening. Plot spacing varied from 27 to 49 meters (90 to 160 feet) based on an initial goal of establishing approximately 15 plots per site. Midway through the season, data analysis revealed additional plots were needed on sites with a high coefficient of variation in tree height. We revisited these patch cuts and measured 4 to 34 additional plots, proportional to the variation exhibited by the site. Grid spacing on sites not yet visited was decreased to accommodate about 30 plots per cut.

With pacing difficult due to the density of vegetation, a handheld GPS unit was used to navigate to plots along each grid transect. Within each 1m-radius plot height, diameter and species were recorded for all trees > 2m in height. Diameter at breast height was measured using a research grade DBH tape and height to the uppermost living leaf was measured using a Senshin fiberglass measuring pole. If a plot showed signs of current year browse damage or was composed of non-tree regeneration (i.e. field, road or small stream), this was noted. No measurements on tree saplings shorter than 2m or non-tree understory vegetation were made due to research resource constraints.

Spatial Solar Radiation Model

Expected radiation intensity values for each plot were calculated using the GPS locations of measured plots and the positions and heights of trees along the edge of the clearcut area. The GIS programs ArcView 3.3 and ArcGIS 10.0 were used to create this model and determine the total radiation intensity a given plot would receive during the growing season (assumed to be April 1st through October 1st). First, a list of solar elevations and azimuths was generated using the Excel program SolRad v. 1.2 (Pelletier, 2011). With this list of solar positions, the program determined trigonometrically if each plot was illuminated or shaded by trees along the clearcut edge for each hour of each day during the growing season. The radiation intensity for each hour a plot received sunlight was summed and a final value, measured in megajoules per square meter (MJ/m^2), was generated. This summed radiation was used to categorize each plot into one of three radiation categories: low (290 - 3516 MJ/m^2), medium (3516 – 4478 MJ/m^2) or high (4478 - 5049 MJ/m^2). A more detailed description of how the solar radiation model was created and calculated these values can be found in Appendix A. Radiation intensity was calculated prior to data collection in 2010 and was used to proportionally randomly stratify plots within radiation category. In 2011, radiation intensity was calculated after data collection and used in analysis only. Due to GPS accuracy limitations, 16 plots in the 2011 data set appeared outside the actual clearcut boundaries; accurate calculation of radiation intensity was therefore not possible and they were excluded from any analyses requiring a radiation value.

Data Analysis and Statistics

We chose biomass fraction – the fraction of total biomass accounted for by a single species - as the metric with which to quantify species dominance of stems > 2m in height. Biomass is a straightforward measure of the amount of resources used by a given tree and a good indicator of future tree success. Since we measured stems of all size classes, using density would have biased the results toward making small, numerous species seem dominant, when in fact they were likely suppressed and may never achieve canopy dominance. For both the 2010 and 2011 data, species dominance of stems >2m in height was calculated by averaging species' biomass fractions with other plots subject to the same treatment and within the same clearcut site. Since only four sites were measured during the 2010 season, the data were combined with the 29 sites from 2011 and treated as one data set for the majority of the statistical tests performed. However, since the 2010 season measured those four sites with a high sampling intensity, several statistical tests only using the 2010 data were run and are noted in our results.

For trees >2m in height, three treatments were tested – harvest type (WTH or CH), radiation category (low, medium or high) and edge category (within 10m of clearcut edge or > 10m from the edge). To simplify our graphs, only the most common seven species were analyzed individually. The choice of these seven represented a natural cut-off, with additional species occurring in low enough concentrations to make drawing conclusions difficult. Lesser abundant species (nine in 2010 and eleven in 2011) were grouped and graphically displayed as "other." For trees < 2m in height and understory plants (measured only in the 2010 season), only harvest treatment was tested.

Non-metric multidimensional scaling (a form of ordination) was used to assess the similarities in species composition between clearcut sites of trees > 2m in height. Input variables were the biomass fraction of each of the seven most common tree species and an eighth variable containing the summed fraction of all other less common species. The values of these variables reflected the composition of an entire clearcut site and were calculated by averaging all the measured plots of that site. With eight dimensions of variation – one for each measured variable – visualizing meaningful patterns is difficult, so ordination was used to reduce the dimensionality to make relationships easier to observe. Ordination is a common dimension reduction technique, and works to minimize the "stress" of a given configuration of replicates. The stress of a given solution is a measure of the difference between the distance of two replicates in the original dimension space and the distance between the same two in the space of reduced dimension. A low stress value shows that the ordination has accurately captured the relationships between replicates present in the original higher dimensional space. Ordination works by placing points randomly in a reduced dimensional space and then iteratively moving them in a direction that reduces the stress the most. A stable solution is reached when the calculated stress is low enough and stable over several iterations. This final result of a successful ordination places replicates with similar values close together and those that differ greatly far apart. Others have used non-metric multidimensional scaling with success to examine the effects of environmental variables and harvest intensity on species composition (Lee et al., 2005; McDonald et al., 2008; Olivero and Hix, 1998).

Ordination was run using PC-ORD v. 4.25 (McCune and Mefford, 1999) and used the Sorensen (Bray-Curtis) distance measure to calculate distance between analysis units. To obtain the appropriate number of dimensions for ordination, preliminary ordinations were run starting at a 6-D solution and stepping down to a 1-D solution. Using a random starting configuration, 20 solutions for each dimension were generated using real data. The solutions of each dimension were examined for low stress and low instability (a measure of how much the stress varies by iteration). In each test run, the 3-dimensional solution represented a stable, low stress solution. Examinations of scree plots (which plot the final stress vs. the number of dimensions) confirmed that higher dimension solutions resulted in small decreases in final stress as compared with 3-D solutions. The 3-D solution for each test was then rerun with 500 iterations and an instability criterion of 0.0001 to be sure the lowest stress, most stable solution was found. For each ordination, the proportion of the variance represented by the solution in ordination space (reduced dimension) was calculated as compared with the solution in the original space of higher dimension.

Multi-response permutation procedures (MRPP) were used to determine if tree species composition as a whole varied significantly by each of the three treatments tested – harvest treatment (WTH or CH), radiation category (high, medium or low) and edge category (edge or center). Other studies have used MRPP successfully to determine the degree that environmental variables and harvest intensity affect overall species composition (McDonald et al., 2008; Olivero and Hix, 1998). A multivariate analysis of variance (MANOVA) was used to determine whether 3-D ordination scores differed significantly by treatment. Kruskal-Wallis tests were used to determine whether individual species abundances varied significantly by treatment. For each treatment, seven Kruskal-Wallis tests were run, increasing the likelihood of falsely rejecting the null hypothesis (Type II error) that no treatment effect exists. We therefore applied the Bonferroni correction for multiple tests, which reduced our critical P value to reject the null hypothesis from 0.05 to 0.05/7 = 0.007. Species were additionally grouped by shade tolerance, and Kruskal-Wallis tests were run to determine whether each shade tolerance group varied significantly by treatment. American beech and striped maple were considered shade tolerant, red maple and yellow birch were considered mid-tolerant, and paper birch, pin cherry and bigtooth aspen were considered shade intolerant. As three Kruskal-Wallis tests were conducted for each treatment, we again applied the Bonferroni correction, reducing our critical P value for rejecting the null hypothesis from 0.05 to 0.05/3 = 0.017. Since this adjustment may be overly cautious (Gotelli and Ellison, 2004), we additionally noted non-significant Kruskal-Wallis test results with $p < 0.10$.

Saplings 0-1m and 1-2m in height were summed separately by species by harvest treatment. This value was then divided by the total area of the plots in which they were found to obtain sapling densities. Seventeen species of trees were recorded in the sapling size classes; densities of the nine most common (those with greater than 10 stems tallied total) were reported individually on our graphs. A mixed effects model was created for each species, with the number of tallied stems per plot as the dependent variable. Harvest treatment (either WTH or CH) was used as a fixed effect and a variable uniquely identifying each clearcut site was used as a random effect.

Many non-tree understory species were found in only one or two 1m-radius plots, so we focused our analyses on the most commonly occurring twelve species. In addition, any lesser abundant plants occurring in greater than three plots that showed potential differences in abundance by treatment were reported. The proportion of plots that contained each understory plant was calculated and used as a measure of that species' abundance within each treatment. Additionally, the number of species found in each plot (species richness) was calculated and used as the dependent variable in a mixed effects model. Using harvest treatment as a fixed effect and a variable uniquely identifying each clearcut site as a random effect, the mixed effects model determined whether observed differences in species richness could be attributed to harvest treatment. Unless otherwise noted, tests with a probability value of $p < 0.05$ were considered to be statistically significant. Taxonomy follows Haines (2011).

Results

Moose Browse and Non-forested Plots

Plots classified as containing primarily non-forest regeneration or those with current year browse damage (referred to hereafter as "stunted") were found to contain significantly different regeneration than those containing unbrowsed forest. F-tests showed that the sets of stunted and unbrowsed plots did not have equal variances, so Welch's t-tests (which do not assume equal variance) were used to determine whether productivity varied. Stunted plots were significantly less productive than unbrowsed forest plots (Welch's t-test; height: t=11.35, 102 d.f., p<0.001, diameter: t=4.99, 78 d.f. p<0.001, biomass: t=12.68, 129 d.f., p<0.001). Species composition and sapling abundances were also significantly altered. Since the majority of stunted plots had reduced or no tree cover, on average they contained a greater diversity of understory plants. In an effort to reduce off-treatment variation, stunted plots (44 in the 2010 season and 277 in the 2011 season) were excluded from all of our analyses. While these plots are a part of actual regeneration and contribute to the composition of regenerating forests, their occurrence is not necessarily due to harvest treatment. We will confine our analyses to a subset of the regeneration – forest unhindered by moose browse – to reduce off-treatment variation. In the 2010 study 40 CH and 69 WTH plots meet this criteria, while 358 CH and 180 WTH plots did so in the 2011 study.

Site Variables

We measured 3,922 trees in 2010 and 2,951 trees in 2011 that were > 2m in height. Trees averaged 4.3m in height, 2.4cm in DBH and were densely spaced, with between 7,400 and 30,000 trees per hectare (3,000 to 12,000 trees per acre). Estimates of aboveground biomass ranged from 6 to 62 metric tons per hectare (3 to 28 tons per acre). Estimated radiation intensity did not vary significantly by harvest treatment (t-test: t-ratio = 0.98, 31 d.f., p = 0.34). Tree species composition in all height classes was dominated by a variety of hardwood species – American beech (*Fagus grandifolia)*, yellow birch (*Betula allegheniensis)*, paper birch (*Betula papyrifera)*, striped maple (*Acer pensylvanicum)*, red maple (*Acer rubrum)*, pin cherry (*Prunus pensylvanica)* and bigtooth aspen (*Populus grandidentata).* Members of the *Rubus* genus (primarily blackberry and red raspberry) were abundant in the understory along with herbaceous plants such as *Aralia nudicaulis*, *Maianthemum canadense*, *Dennstaedtia punctilobula*, and *Trillium erectum*.

Species Composition Comparison by Harvest Treatment

Ordination on species composition of the combined data set (both seasons) yielded a 3-D solution with a final stress of 10.2 and a final instability of 0.00002. The three axes combined explained 91.3% of the variation and were > 99% orthogonal to each other. MRPP showed that harvest type did not have a significant effect on species composition as a whole, and a MANOVA on the ordinations scores confirmed this result (Table 4). Analyses of individual species abundance (summarized in Table 5 and Figure 8) indicated that no species showed a strong affinity for a specific harvest treatment. Red maple and paper birch were slightly more abundant in CH sites, but did not meet our criteria for statistical significance. American beech was found in greater quantities in WTH sites, but this difference was again not strong enough to be deemed statistically significant. Biomass fractions of pin cherry, striped maple, yellow birch and bigtooth aspen did not vary significantly by harvest treatment. When species were grouped according to their shade tolerance, none of the three tolerance groups varied in a statistically significant manner, although all were close (Table 5). When only the intensively sampled 2010 clearcuts were analyzed, none showed patterns that were statistically significant. (Table 5)

Species Composition Comparison by Radiation Category

The ordination for radiation intensity category yielded a 3-D solution with a final stress of 14.2 and a final instability of 0.006. The three axes combined accounted for explained 85.2% of the variation present originally and were > 93% orthogonal. MRPP showed that radiation intensity had no significant effect on species composition, and this was confirmed by a MANOVA on the coordinate values (Table 4). Analyses on individual species confirmed this result as well – no species showed significantly different biomass fractions between radiation categories (Table 6, Figure 9). Grouping species by shade tolerance showed similar results, with no group showing a significantly higher fraction in a radiation intensity category. When only considering data from the intensively sampled 2010 clearcuts, no species showed statistically significant patterns. Two species showed marginally significant ($p < 0.10$) patterns, with bigtooth aspen in highest concentrations in high radiation plots and red maple highest in plots of medium radiation intensity (Table 6).

Table 4: Details of MRPP and MANOVA tests showing no difference in overall tree species composition between whole-tree harvested and conventionally harvested clearcuts. Data from thirty-three 10-14 year old northern hardwood sites in central New Hampshire and western Maine.

	Multi-response permutation procedures (MRPP)		**Mulltivariate analysis of variance (MANOVA)**		
	A value	p value	Test	Value	p value
Harvest Treatment	0.015	0.119	F-test	0.171	0.199
Radiation Category	-0.006	0.823	Wilk's Lambda	0.955	0.650
Edge Category	0.005	0.189	F-test	0.087	0.156

Species Composition Comparison by Edge Category

A three dimensional ordination with a final stress of 11.8 and a final instability of 0.005 was generated for the 2011 dataset aggregated by edge category. The three axes explained 90.8% of the original variation and were > 95% orthogonal. MRPP performed on the ordination scores showed that edge category had no significant effect on species composition and this was confirmed by a MANOVA on the coordinate values (Table 4). Kruskal-Wallis tests on individual species confirmed this result as well, with no species having a significantly higher biomass fraction in the center or edge regions of clearcuts (Table 7, Figure 10). Red maple, paper birch and yellow birch were nearly significant ($p < 0.10$), with all three having higher biomass fractions in plots in the center of clearcuts, greater than 10 meters from the edge boundary. Aggregating the species according to shade tolerance reveals that tolerant species have higher abundances in edge plots while mid-tolerant species are found more often in center plots. However, these patterns do not meet our criteria for statistical significance (Table 7). When examining just the 2010 data set, bigtooth aspen and red maple showed marginally ($p < 0.10$) higher abundances within "center" plots (> 10m from clearcut edge). American beech along with shade tolerant species as a whole showed marginally higher abundances within "edge" plots. (Table 7)

Table 5: Results from Kruskal-Wallis tests to determine whether species abundance varied significantly by harvest treatment. Tests were run individually on the seven most commonly occurring species as well as on groupings by shade tolerance. Results are shown for a data set containing both 2010 and 2011 sites (left) as well as on the intensively measured 2010 sites only. For entries with a p value < 0.10, the treatment with the highest biomass fraction is noted. Data collected in central NH and western ME.

	2010 and 2011 Data Sets			**2010 Data Set Only**		
	Harvest treatment with highest biomass fraction	P value	Kruskal-Wallis test statistic	Harvest treatment with highest biomass fraction	P value	Kruskal-Wallis test statistic
American Beech	WTH	0.072	3.244	-	0.439	0.600
Bigtooth Aspen	-	0.338	0.916	-	0.121	2.400
Pin Cherry	-	0.255	1.295	-	0.439	0.600
Red Maple	CH	0.008	6.983	-	0.439	0.600
Striped Maple	-	0.640	0.219	-	0.439	0.600
Paper Birch	CH	0.010	6.572	-	0.439	0.600
Yellow Birch	-	0.678	0.172	-	0.121	2.400
Tolerants	WTH	0.052	3.784	-	0.439	0.600
Mid-Tolerants	CH	0.078	3.115	-	0.121	2.400
Intolerants	CH	0.070	3.290	-	0.121	2.400

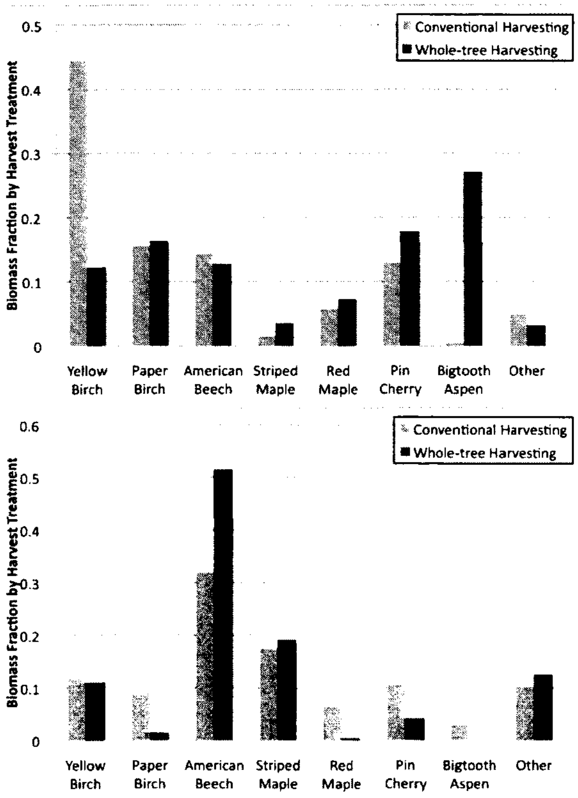

Figure 8: Differences in biomass fraction in whole-tree and conventionally harvested sites for seven most common species in the 2010 (top) and 2011 (bottom) sites. Data from 33 northern hardwood sites across New Hampshire and western Maine.

Table 6: Results from Kruskal-Wallis tests to determine whether species abundance varied significantly by radiation intensity category. Tests were run individually on the seven most commonly occurring species as well as on groupings by shade tolerance. Results are shown for a data set containing both 2010 and 2011 sites (left) as well as on the intensively measured 2010 sites only. For entries with a p value < 0.10, the radiation intensity category with the highest biomass fraction is noted. Data collected in central New Hampshire and western Maine.

	2010 and 2011 Data Sets			2010 Data Set Only		
	Radiation category with highest biomass fraction	P value	Kruskal-Wallis test statistic	Radiation category with highest biomass fraction	P value	Kruskal-Wallis test statistic
American Beech	-	0.255	2.736	-	0.215	3.076
Bigtooth Aspen	-	0.392	1.873	High	0.059	5.649
Pin Cherry	-	0.802	0.443	-	0.144	3.873
Red Maple	-	0.164	3.613	Med	0.022	7.616
Striped Maple	-	0.940	0.125	-	0.368	1.998
Paper Birch	-	0.806	0.432	-	0.375	1.962
Yellow Birch	-	0.223	2.999	-	0.931	0.144
Tolerants	-	0.204	3.183	-	0.215	3.076
Mid-Tolerants	-	0.146	3.846	-	0.741	0.598
Intolerants	-	0.860	0.302	-	0.122	4.212

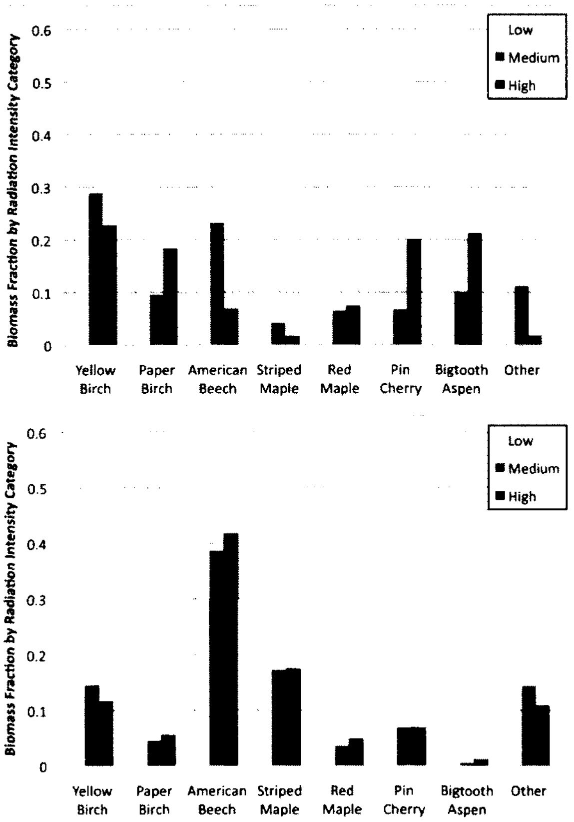

Figure 9: Differences in biomass fraction for seven most common species by plot radiation intensity category. Top graph shows results from the 2010 season; the bottom reflects the 2011 season. Light intensity for each plot was estimated and categorized using a spatial light model as described in the text. Data from 33 northern hardwood sites across New Hampshire and western Maine.

Table 7: Results from Kruskal-Wallis tests to determine whether species abundance varied significantly by edge category. Tests were run individually on the seven most commonly occurring species as well as on groupings by shade tolerance. Results are shown for a data set containing both 2010 and 2011 sites (left) as well as on the intensively measured 2010 sites only. For entries with a p value < 0.10, the edge category with the highest biomass fraction is noted. Data collected in central NH and western ME.

	2010 and 2011 Data Sets			2010 Data Set Only		
	Edge category with highest biomass fraction	P value	Kruskal-Wallis test statistic	Edge category with highest biomass fraction	P value	Kruskal-Wallis test statistic
American Beech	-	0.296	1.092	Edge	0.083	3.000
Bigtooth Aspen	-	0.130	2.297	Center	0.076	3.150
Pin Cherry	-	0.731	0.118	-	0.386	0.750
Red Maple	Center	0.012	6.379	Center	0.043	4.083
Striped Maple	-	0.555	0.349	-	0.245	1.349
Paper Birch	Center	0.069	3.301	-	0.773	0.083
Yellow Birch	Center	0.065	3.409	-	1.000	0.000
Tolerants	Edge	0.022	5.241	Edge	0.083	3.000
Mid-Tolerants	Center	0.069	3.318	-	0.564	0.333
Intolerants	-	0.164	1.936	-	0.248	1.333

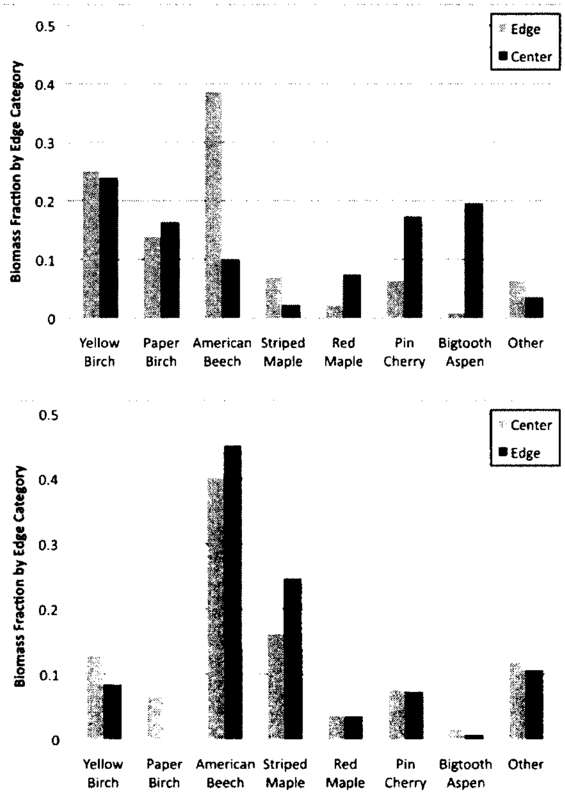

Figure 10: Differences in biomass fraction for seven most common species by plot edge category. The top graph reflects 2010 data while the bottom shows data from 2011. Plots within 10 meters of the clearcut boundary were considered "edge" plots; all others were considered "center." Data from 33 northern hardwood sites across New Hampshire and western Maine.

Species Composition of Saplings

Sapling regeneration (< 2m in height) in 2010 was dominated by yellow birch, red maple and American beech, which together accounted for 81% of stems 0-1m tall and 92% of stems 1-2m tall (Figure 11). Mixed effects models using harvest treatment as a fixed effect and a clearcut identifier as a random effect showed that residue removal did not have a significant effect on sapling density of any species in either size class (Table 8). Abundances saplings <2m in height were not measured in the 2011 study sites.

Understory Composition and Diversity

Twenty-five species of understory plants were identified in 40 CH plots and 30 within 69 WTH plots. Eleven of the twelve most abundant understory species occurred more frequently in WTH plots than in CH plots (Figure 12). *Uvularia sessilifolia* was the lone exception, being found in 18% of CH plots but only 9% of WTH plots. Of lesser abundant species, *Gaultheria procumbens* and *Monotropa uniflora* were only found on CH plots (on 8% and 10% of plots respectively). *Spinulum annotinum* was found on 9% of WTH plots but only 3% of CH plots. A mixed effects model showed that average species richness per plot was more likely to be driven by variability between clearcut sites than harvest treatment (Table 8).

Table 8: Details of mixed effects model on abundance of 0-1m and 1-2m tall saplings and understory plant richness. Dashes indicate insufficient data to perform a given test for a particular species. No tests indicate a significant effect of residue removal during WTH on sapling or understory communities. Data from four twelve-year-old patch clearcuts in the Bartlett Experimental Forest in the White Mountains of New Hampshire.

	Fixed Effect of Harvest Treatment [CH]					**Random Effect of Clearcut ID**	
	Parameter estimate	Standard error	d.f.	t-ratio	p > |t|	% variance explained	Residual
0-1m Sapling Abundance							
American Beech	1.03	0.51	1.1	2.02	0.27	7.8	92.2
Eastern Hemlock	-0.14	0.19	2.0	-0.75	0.53	4.2	95.8
Pin Cherry	-	-	-	-	-	-	-
Red Maple	-0.78	1.55	1.9	-0.50	0.67	39.8	60.2
Striped Maple	-0.03	0.11	0.8	-0.29	0.83	-	-
Sugar Maple	0.26	0.20	0.4	1.27	0.60	-	-
White Ash	0.10	0.16	0.9	0.64	0.65	-	-
Paper Birch	-0.08	0.13	1.6	-0.65	0.60	6.2	93.8
Yellow Birch	0.61	0.74	1.7	0.83	0.51	15.4	84.6
1-2m Sapling Abundance							
American Beech	0.28	0.43	1.7	0.66	0.59	5.3	94.7
Eastern Hemlock	-0.01	0.01	0.5	-0.99	0.60	-	-
Pin Cherry	-	-	-	-	-	-	-
Red Maple	-	-	-	-	-	-	-
Striped Maple	-0.02	0.04	2.0	-0.40	0.73	5.9	94.1
Sugar Maple	-	-	-	-	-	-	-
White Ash	-	-	-	-	-	-	-
Paper Birch	-	-	-	-	-	-	-
Yellow Birch	0.55	0.30	1.0	1.82	0.32	4.1	95.9
Understory Plant Community							
Species Richness	0.06	1.64	2.0	0.04	0.97	82.7	17.3

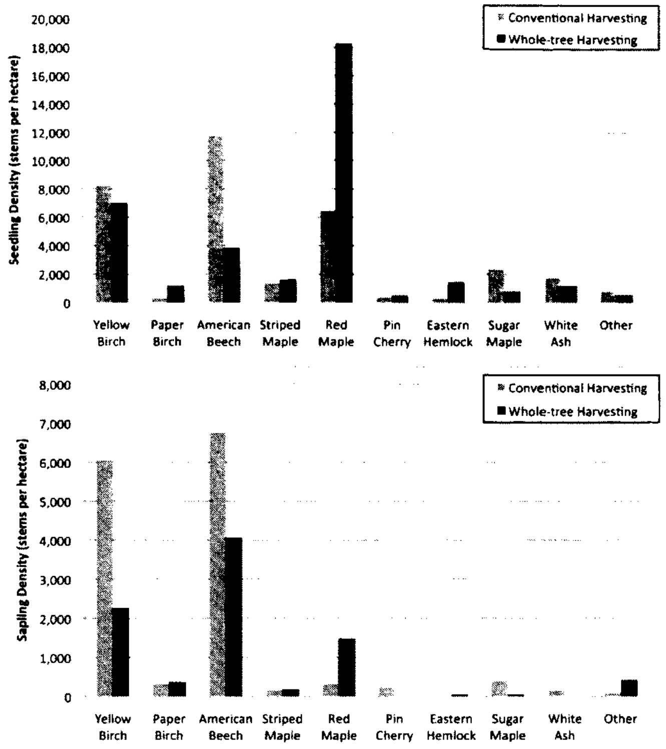

Figure 11: Densities of saplings 0-1m in height (top) and 1-2m in height (bottom) for the 2010 season by harvest treatment. Data from four experimentally harvested northern hardwood sites in the Bartlett Experimental Forest in Bartlett, NH

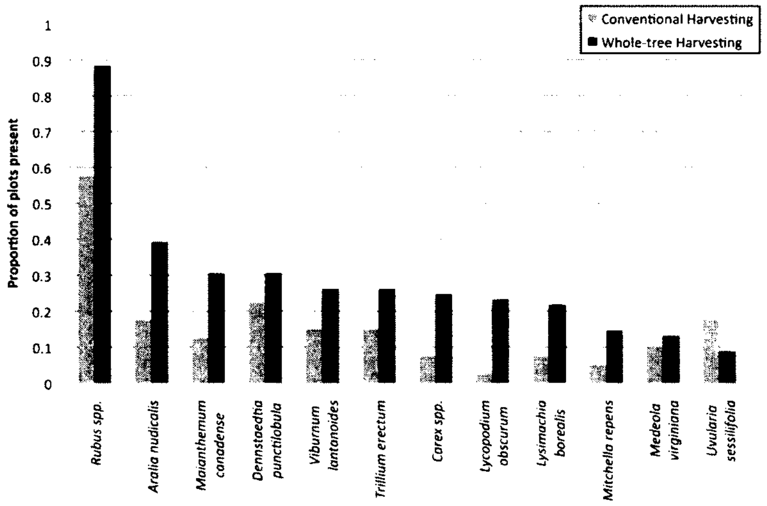

Figure 12: Proportion of plots containing the most common 12 understory plants by harvest treatment. Data from four experimentally harvested northern hardwood sites measured in 2010 in the Bartlett Experimental Forest in Bartlett, NH.

Discussion

Our data do not indicate that residue removal following whole-tree harvesting has a significant effect on the species composition or understory richness of regenerating northern hardwood forests. Ordination of both datasets using non-metric multidimensional scaling showed overall composition was not significantly different between WTH and CH clearcuts as demonstrated by MRPP results and confirmed by MANOVA tests on the ordination scores. We additionally could not detect any differences in overall species composition due to estimated plot radiation intensity or distance to clearcut edge.

Comparison of how individual species varied by harvest, radiation and edge treatments revealed several patterns of note, but none met our criteria for statistical significance. Since it is possible that our use of the Bonferroni correction is overly conservative (Gotelli and Ellison, 2004) we have noted test results with an uncorrected significance value of $p < 0.10$ and discuss how they correlate with known ecological characteristics below. Paper birch and red maple both showed higher abundances within conventionally harvested sites, while American beech was more prevalent with WTH sites. Red maple, yellow birch and paper birch all showed slightly higher abundances in "center" plots > 10m from the clearcut edge. No species showed even marginally significant ($p < 0.10$) patterns by solar radiation category.

Due to the retention of harvesting slash on CH sites, one might expect increased shading in the understory to favor trees that can regenerate in partial shade. While paper birch is thought of as shade intolerant, its seeds seem to germinate best in partial shade

(Perala and Alm, 1990), with one study showing that paper birch seeds germinated best in soil exposed to 45% of full sunlight (Logan, 1965). Paper birch produce very small, wind-driven seeds, and the increased shade under CH slash may provide a cool, moist environment in which to germinate. The exposed, highly variable ground temperatures in WTH sites (Proe et al., 2001) may not be as hospitable. The seeds produced by yellow birch are similar in size and germinate under similar conditions to those of paper birch (Perala and Alm, 1990). However, we found no significant patterns with respect to yellow birch abundance across harvest treatment. Paper birch and yellow birch abundances were slightly higher in the center of clearcuts of both harvest types. While this pattern was not statistically significant, it does confirm our knowledge of paper birch as a shade intolerant species that grows best in full sunlight.

Red maple showed higher abundances in conventionally harvested sites and in plots > 10m from the clearcut edge. However, the vast majority of the red maple stems observed in both field seasons were dense clusters of stump sprouts from cut stems. Thus, observed abundances are most likely due to differences in pre-harvest red maple abundance and probably not reflective of any true harvest treatment effect on regeneration. Bigtooth aspen showed no significant patterns over any of our three treatment variables, but its abundance was likely governed by preharvest intensities as well. Bigtooth aspen have small, wind driven seeds, but also reproduce clonally from root suckering. Many of the aspen in our study plots were extremely tall, and likely grew from root suckers from uncut trees outside of the clearcut. In contrast to our study, Hendrickson (1988) found greater aspen regeneration following WTH as compared with

CH sites in pine-aspen stands in Canada, attributing the effect to increased forest floor temperatures and sunlight due to the absence of logging slash.

American beech, a shade tolerant species that reproduces readily vegetatively from root suckering, was present in higher abundance in WTH sites. If whole-tree harvesting serves to increase the amount of sunlight present on the forest floor, we would expect it to favor shade intolerant species such as pin cherry and decrease success of shade tolerant species such as American beech. Our tentative result shows the opposite, suggesting observed patterns in American beech abundance might be due to the high degree of variability in measured regeneration.

The final two species analyzed individually, pin cherry and striped maple, showed no marginally significant patterns with respect to harvest treatment, solar radiation or proximity to clearcut edge. From knowledge of their silvicultural characteristics, we would expect pin cherry to be prominent in areas with high radiation intensity and striped maple in areas of lower radiation intensity. Our study shows no such patterns, likely an additional testament to the inherent variability present in these regenerating clearcuts.

A mixed effects model comparing sapling abundances showed no effect of residue removal on the abundance of any species. This was likely due to low statistical power, as sapling abundances were only measured in the four clearcut sites in the 2010 field season. Our statistical power was also not strong enough to detect any meaningful differences in richness of understory plants within 1m-radius plots in our 2010 season. We may expect the removal or retention of harvest materials to affect understory non-tree regeneration in one of two ways. If the retention of harvest materials in CH increases the heterogeneity of microclimate conditions on the forest floor, we might expect a greater variety of species to colonize these niches. Alternatively, harvest material retention may shade the forest floor and decrease the amount of available growing space, lowering the abundance and richness of understory regeneration.

Our study attempted to measure the effects of residue removal, radiation intensity and distance to clearcut edge on species composition, but unmeasured variables also likely played a role in our results. While we attempted to remove the effects of continual yearly moose brose by excluding browsed plots, other factors still remain. Species composition of the previous stand likely had significant impacts on the composition of the regeneration, especially for species with the ability to sprout from shallow roots or cut stumps. The spatial distribution of seed rain due to previous stand composition also likely affects our results and contributes to the patchiness of regeneration; seeds are more likely to land in locations close to their parent tree. Detailed data on the composition of the previous stand was not available for any of the stands measured.

High site variability and low statistical power also hampered our ability to draw precise conclusions, especially when comparing sapling densities and understory richness across harvest treatment. Sapling density mixed effects models indicate that 92 - 95% of the residual model variance was due to variability in sapling sizes within a given clearcut. This suggests that, to obtain a more precise estimate on sapling densities < 2m in height, future studies would be best adopting a more intensive sampling procedure within each clearcut, with > 50 plots per cut. On the other hand, 82% of the residual variance in the understory richness mixed effects model was due to variation between clearcuts. In this case, finding and measuring additional WTH and CH clearcuts would be more valuable in improving the model fit than measuring additional plots within each clearcut.

Conclusion

The data suggest residue removal has no measureable effect on the species composition of a northern hardwood forest 10-14 years following patch clearcutting. Low statistical power and small sample sizes limited our ability to draw conclusions about sapling densities and understory richness underneath overstory trees. Our results suggest the need for additional studies on the effects of residue removal on the ecology of northern hardwood forests as well as long-term monitoring of existing sites. As whole-tree harvesting becomes more common on our landscape, it becomes more vital to determine the effects of residue removal on the species composition and richness of our forests.

Literature Cited

Anderson M. The impact of whole-tree harvesting in British forests. Quarterly Journal of Forestry (1985) 79:33-39.

Belcher CF. Logging Railroads of the White Mountains. (1980) Boston, MA: Appalachian Mountain Club.

Benjamin JG, Lilieholm RJ, Damery D. Challenges and Opportunities for the Northeastern Forest Bioindustry. Journal of Forestry (2009) 107:125-131.

Bowman JC, Sleep D, Forbes GJ, Edwards M. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management (2000) 129:119-124.

Boyle JR. System for Evaluating Potential Impacts of Whole-Tree Harvesting on Site Quality. Tappi (1976) 59:79-81.

Brakenhielm S, Liu Q. Long-term effects of clear-felling on vegetation dynamics and species diversity in a boreal pine forest. Biodiversity and Conservation (1998) 7:207-220.

deMaynadier PG, Hunter MLJ. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews (1995) 3:230-261.

Dyck WJ, Hodgkiss PD, Oliver GR, Mees CA. Harvesting sand-dune forests: impacts on second-rotation productivity. In: Long-term Field Trials to Assess Environmental Impacts of Harvesting--Dyck WJ, Mees CA, eds. (1991) Rotorua, New Zealand: Forest Research Institute. 163-176.

Egnell G, Valinger E. Survival, growth, and growth allocation of planted Scots pine trees after different levels of biomass removal in clear-felling. Forest Ecology and Management (2003) 177:65-74.

Finzi AC, Canham CD. Sapling growth in response to light and nitrogen availability in a southern New England forest. Forest Ecology and Management (2000) 131:153-165.

Foster DR. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology (1992) 80:753-772.

Gotelli NJ, Ellison AM. A Primer of Ecological Statistics. (2004) Sunderland, MA: Sinauer Associates, Inc.

Haines A. Flora Novae Angliae. (2011): Yale University Press, New Haven, CT.

Hendrickson OQ. Biomass and Nutrients in Regenerating Woody Vegetation Following Whole-Tree and Conventional Harvest in a Northern Mixed Forest. Canadian Journal of Forest Research (1988) 18:1427-1436.

Johnson CE, Johnson AH, Siccama TG. Whole-Tree Clear-Cutting Effects on Exchangeable Cations and Soil Acidity. Soil Science Society of America Journal (1991) 55:502-508.

Kimmins JP. Evaluation of Consequences for Future Tree Productivity of Loss of Nutrients in Whole-Tree Harvesting. Forest Ecology and Management (1977) 1:169-183.

Leak WB. Relation of tolerant species to habitat in the White Mountains of New Hampshire (1976): U.S.D.A. Forest Service Research Paper NE-351.

Leak WB. Relationship of species and site index to habitat in the White Mountains of New Hampshire (1978): U.S.D.A. Forest Service Research Paper NE-397.

Lee TD, Barrett JP, Hartman B. Elevation, substrate, and the potential for climate-induced tree migration in the White Mountains, New Hampshire, USA. Forest Ecology and Management (2005) 212:75-91.

Loeb SC. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy (1999) 80:460-471.

Logan KT. Growth of tree seedlings as affected by light intensity I. White birch, yellow birch, sugar maple and silver maple (1965): Canadian Department of Forestry Publication No 1121. 16 pp.

Lohr SM, Gauthreaux SA, Kilgo JC. Importance of coarse woody debris to avian communities in loblolly pine forests. Conservation Biology (2002) 16:767-777.

Lyons JB, Bothner WA, Moench RH, Thompson Jr. JB. Bedrock Geologic Map of New Hampshire (1997): U.S. Department of the Interior, Geologic Survey.

Mann LK. First-year regeneration in upland hardwoods after two levels of residue removal. Canadian Journal of Forest Research (1984) 14:336-342.

McClure JW, Lee TD. Small-scale disturbance in a northern hardwoods forest: effect on tree species abundance and distribution. Canadian Journal of Forest Research (1993) 23:1347-1360.

McCune B, Mefford MJ. Multivariate analysis of ecological data, Version 4.0 (1999) Glenden Beach, Oregon, USA: MJM Software Design.

McDonald RI, Motzkin G, Foster DR. The effect of logging on vegetaion composition in Western Massachusetts. Forest Ecology and Management (2008) 255:4021-4031.

Olivero AM, Hix DM. Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. Plant Ecology (1998) 139:177-187.

Olsson BA, Bengtsson J, Lundkvist H. Effects of different forest harvest intensities on the pools of exchangeable cations in coniferous forest soils. Forest Ecology and Management (1996a) 84:135-147.

Olsson BA, Staaf H, Lundkvist H, Bengtsson J, Rosen K. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. Forest Ecology and Management (1996b) 82:19-32.

Pelletier G. SolRad - a solar position and solar radiation calculator for Excel/VBA (2011). Available at: http://www.ecy.wa.gov/programs/eap/models.html.

Perala DA, Alm AA. Reproductive ecology of birch: a review. Forest Ecology and Management (1990) 32:1-38.

Proe MF, Cameron AD, Dutch J, Christodoulou XC. The effect of whole-tree harvesting on the growth of second rotation Sitka spruce. Forestry (1996) 69:389-401.

Proe MF, Griffiths JH, McKay HM. Effect of whole-tree harvesting on microclimate during establishment of second rotation forestry. Agricultural and Forest Meteorology (2001) 110:141-154.

Saarsalmi A, Tamminen P, Kukkola M, Hautajarvi R. Whole-tree harvesting at clear-felling: Impact on soil chemistry, needle nutrient concentrations and growth of Scots pine. Scandinavian Journal of Forest Research (2010) 25:148-156.

Sanchez FG, Scott DA, Ludovici KH. Negligible effects of severe organic matter removal and soil compaction on loblolly pine growth over 10 years. Forest Ecology and Management (2006) 227:145-154.

Scott DA, Dean TJ. Energy trade-offs between intensive biomass utilization, site productivity loss, and ameliorative treatments in loblolly pine plantations. Biomass and Bioenergy (2006) 30:1001-1010.

Smethurst PJ, Nambiar EKS. Effects of Slash and Litter Management on Fluxes of Nitrogen and Tree Growth in a Young Pinus-Radiata Plantation. Canadian Journal of Forest Research (1990) 20:1498-1507.

Tan X, Curran M, Chang S, Maynard D. Early Growth Responses of Lodgepole Pine and Douglas-Fir to Soil Compaction, Organic Matter Removal, and Rehabilitation Treatments in Southeastern British Columbia. Forest Science (2009) 55:210-220.

Vanguelova E, Pitman R, Luiro J, Helmisaari HS. Long term effects of whole tree harvesting on soil carbon and nutrient sustainability in the UK. Biogeochemistry (2010) 101:43-59.

Walmsley JD, Jones DL, Reynolds B, Price MH, Healey JR. Whole tree harvesting can reduce second rotation forest productivity. Forest Ecology and Management (2009) 257:1104-1111.

CONCLUSION

No evidence of productivity decline in young northern hardwood forests was observed during our two study seasons as a result of whole-tree harvesting. Both studies actually showed WTH sites were slightly more productive, but this difference was not statistically significant and may be correlated with unmeasured site variables. In our first season, WTH sites received more sunlight than CH sites due to the shape and orientation of their clearcut boundaries. When this variable was factored out, the difference in productivity disappeared. In the second field season, a suite of environmental variables including clearcut size, clearcut age, slope, aspect, average solar radiation and soil type varied between treatment groups. When these characteristics were taken into account, statistical comparisons showed no difference in tree height, diameter or biomass. Both studies corrected for the effect of moose browse on regeneration by excluding any plots that showed signs of repeated browse damage. Plots containing non-forest regeneration were also excluded to further reduce off-treatment variation.

We also found no strong evidence for changes to overall tree species composition or understory plant richness resulting from residue removal during whole-tree harvesting. Several species showed weak patterns when analyzed individually, with American beech being more common in WTH plots and red maple and paper birch more prevalent in CH plots. Additionally, when grouped by shade tolerance, WTH clearcuts showed higher fractions of shade tolerant species such as American beech and striped maple. However, none of these patterns met our criteria for statistical significance, and may be due to high variability in clearcut regeneration. Other studies have shown species compositional differences (Mann, 1984) with one reporting an increase in aspen abundance following whole-tree harvesting (Hendrickson, 1988).

Overall, we find no evidence at this time to support concern about reduced productivity or altered species composition following WTH. Whole-tree harvesting appears to have little effect on young northern hardwood sites in New Hampshire and western Maine when compared with conventional methods. Limitations in our study design restrict the applicability of our results; we only examined northern hardwood forests 10-14 years following harvest. Evidence of productivity decline may not present itself until later in the rotation or even after several harvests, and different forest types may react differently altogether to residue removal. Additional research is needed to determine if the results observed in our studies are observed elsewhere, and if they persist throughout the duration of the rotation.

LITERATURE CITED

Aber JD, Botkin DB, Melillo JM. Predicting the effects of different harvesting regimes on productivity and yield in northern hardwoods. Canadian Journal of Forest Research (1979) 9:10-14.

Anderson M. The impact of whole-tree harvesting in British forests. Quarterly Journal of Forestry (1985) 79:33-39.

Belcher CF. Logging Railroads of the White Mountains. (1980) Boston, MA: Appalachian Mountain Club.

Benjamin JG, Lilieholm RJ, Damery D. Challenges and Opportunities for the Northeastern Forest Bioindustry. Journal of Forestry (2009) 107:125-131.

Bergeron DH, Pekins PJ, Jones HF, Leak WB. Moose browsing and forest regeneration: a case study in northern New Hampshire. Alces (2011) 47:39-51.

Bird RE, Hulstrom RL. A simplified clear sky model for direct and diffuse insolation on horizontal surfaces (1981) Golden, CO: Solar Energy Research Institute.

Bowman JC, Sleep D, Forbes GJ, Edwards M. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management (2000) 129:119-124.

Boyle JR. System for Evaluating Potential Impacts of Whole-Tree Harvesting on Site Quality. Tappi (1976) 59:79-81.

Boyle JR, Ek AR. An evaluation of some effects of bole and branch pulpwood harvesting on site macronutrients. Canadian Journal of Forest Research (1972) 2:407-412.

Boyle JR, Phillips JJ, Ek AR. "Whole Tree" Harvesting: Nutrient Budget Evaluation. Journal of Forestry (1973) 71:760-762.

Brakenhielm S, Liu Q. Long-term effects of clear-felling on vegetation dynamics and species diversity in a boreal pine forest. Biodiversity and Conservation (1998) 7:207-220.

Briedis JI, Wilson JS, Benjamin JG, Wagner RG. Biomass retention following whole-tree, energy wood harvests in central Maine: adherence to five state guidelines. Biomass and Bioenergy (2011) 35:3552-3560.

Briggs RD, Hornbeck JW, Smith CT, Lemin Jr. RC, McCormack Jr. ML. Long-term effects of forest management on nutrient cycling in spruce-fir forests. Forest Ecology and Management (2000) 138:285-299.

Carey ML. Whole tree harvesting in Sitka spruce. Possibilities and implications. Irish Forestry (1980) 37:48-63.

deMaynadier PG, Hunter MLJ. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews (1995) 3:230-261.

Dyck WJ, Hodgkiss PD, Oliver GR, Mees CA. Harvesting sand-dune forests: impacts on second-rotation productivity. In: Long-term Field Trials to Assess Environmental Impacts of Harvesting--Dyck WJ, Mees CA, eds. (1991) Rotorua, New Zealand: Forest Research Institute. 163-176.

Dyck WJ, Skinner MF. Potential for productivity decline in New Zealand radiata pine forests. Presented at the North American Forest Soils Conference, July 1988 (1990) University of British Columbia, Vancouver, Canada.

Egnell G, Leijon B. Survival and growth of planted seedlings of Pinus sylvestris and Picea abies after different levels of biomass removal in clear-felling. Scandinavian Journal of Forest Research (1999) 14:303-311.

Egnell G, Valinger E. Survival, growth, and growth allocation of planted Scots pine trees after different levels of biomass removal in clear-felling. Forest Ecology and Management (2003) 177:65-74.

Federer CA, Hornbeck JW, Tritton LM, Martin CW, Pierce RS, Smith CT. Long-Term Depletion of Calcium and Other Nutrients in Eastern-United-States Forests. Environmental Management (1989) 13:593-601.

Finzi AC, Canham CD. Sapling growth in response to light and nitrogen availability in a southern New England forest. Forest Ecology and Management (2000) 131:153-165.

Foster DR. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology (1992) 80:753-772.

Gotelli NJ, Ellison AM. A Primer of Ecological Statistics. (2004) Sunderland, MA: Sinauer Associates, Inc.

Goulding KWT, Stevens PA. Potassium Reserves in a Forested, Acid Upland Soil and the Effect on Them of Clear-Felling Versus Whole-Tree Harvesting. Soil Use and Management (1988) 4:45-51.

Haines A. Flora Novae Angliae. (2011): Yale University Press, New Haven, CT.

Hendrickson OQ. Biomass and Nutrients in Regenerating Woody Vegetation Following Whole-Tree and Conventional Harvest in a Northern Mixed Forest. Canadian Journal of Forest Research (1988) 18:1427-1436.

Jacobson S, Kukkola M, Malkonen E, Tveite B. Impact of whole-tree harvesting and compensatory fertilization on growth of coniferous thinning stands. Forest Ecology and Management (2000) 129:41-51.

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA. Comprehensive database of diameter-based biomass regressions for North American tree species (2004) Newtown Square, PA: US Department of Agriculture, Forest Service, Northeastern Research Station.

Jenness J. Radiating Lines and Points (rad_lines.avx) Extension for ArcView 3.x, v. 1.1 (2006): Jenness Enterprises. Available at: http://jennessent.com/arcview/radiating_lines.htm.

Johnson CE, Johnson AH, Siccama TG. Whole-Tree Clear-Cutting Effects on Exchangeable Cations and Soil Acidity. Soil Science Society of America Journal (1991) 55:502-508.

Johnson DW, Curtis PS. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management (2001) 140:227-238.

Johnson DW, West DC, Todd DE, Mann LK. Effects of sawlog vs. whole-tree harvesting on the nitrogen, phosphorus, potassium, and calcium budgets of an upland mixed oak forest. Soil Science Society of America Journal (1982) 46:1304-1309.

Kimmins JP. Evaluation of Consequences for Future Tree Productivity of Loss of Nutrients in Whole-Tree Harvesting. Forest Ecology and Management (1977) 1:169-183.

Lead S. Create point at all intersections between polyline themes (2004). Available at: http://arcscripts.esri.com/details.asp?dbid=12397.

Leak WB. Relation of tolerant species to habitat in the White Mountains of New Hampshire (1976): U.S.D.A. Forest Service Research Paper NE-351.

Leak WB. Relationship of species and site index to habitat in the White Mountains of New Hampshire (1978): U.S.D.A. Forest Service Research Paper NE-397.

Lee TD, Barrett JP, Hartman B. Elevation, substrate, and the potential for climate-induced tree migration in the White Mountains, New Hampshire, USA. Forest Ecology and Management (2005) 212:75-91.

Loeb SC. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy (1999) 80:460-471.

Logan KT. Growth of tree seedlings as affected by light intensity I. White birch, yellow birch, sugar maple and silver maple (1965): Canadian Department of Forestry Publication No 1121. 16 pp.

Lohr SM, Gauthreaux SA, Kilgo JC. Importance of coarse woody debris to avian communities in loblolly pine forests. Conservation Biology (2002) 16:767-777.

Lyons JB, Bothner WA, Moench RH, Thompson Jr. JB. Bedrock Geologic Map of New Hampshire (1997): U.S. Department of the Interior, Geologic Survey.

Mann LK. First-year regeneration in upland hardwoods after two levels of residue removal. Canadian Journal of Forest Research (1984) 14:336-342.

McClure JW, Lee TD. Small-scale disturbance in a northern hardwoods forest: effect on tree species abundance and distribution. Canadian Journal of Forest Research (1993) 23:1347-1360.

McCune B, Mefford MJ. Multivariate analysis of ecological data, Version 4.0 (1999) Glenden Beach, Oregon, USA: MJM Software Design.

McDonald RI, Motzkin G, Foster DR. The effect of logging on vegetaion composition in Western Massachusetts. Forest Ecology and Management (2008) 255:4021-4031.

Nord-Larsen T. Stand and site productivity response following whole-tree harvesting in early thinnings of Norway spruce (Picea abies (L.) Karst.). Biomass and Bioenergy (2002) 23:1-12.

Olivero AM, Hix DM. Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. Plant Ecology (1998) 139:177-187.

Olsson BA, Bengtsson J, Lundkvist H. Effects of different forest harvest intensities on the pools of exchangeable cations in coniferous forest soils. Forest Ecology and Management (1996a) 84:135-147.

Olsson BA, Staaf H, Lundkvist H, Bengtsson J, Rosen K. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. Forest Ecology and Management (1996b) 82:19-32.

Pelletier G. SolRad - a solar position and solar radiation calculator for Excel/VBA (2011). Available at: http://www.ecy.wa.gov/programs/eap/models.html.

Perala DA, Alm AA. Reproductive ecology of birch: a review. Forest Ecology and Management (1990) 32:1-38.

Pierce RS, et al. Whole-tree clearcutting in New England: manager's guide to impact on soils, streams and regeneration (1993): U.S.D.A. Forest Service General Technical Report NE-172.

Proe MF, Cameron AD, Dutch J, Christodoulou XC. The effect of whole-tree harvesting on the growth of second rotation Sitka spruce. Forestry (1996) 69:389-401.

Proe MF, Dutch J. Impact of Whole-Tree Harvesting on 2nd-Rotation Growth of Sitka Spruce - the First 10 Years. Forest Ecology and Management (1994) 66:39-54.

Proe MF, Dutch J, Griffiths J. Harvest residue effects on microclimate, nutrition and early growth of Sitka spruce (Picea sitchensis) seedlings on a restock site. New Zealand Journal of Forestry Science (1994) 24:390-401.

Proe MF, Griffiths JH, McKay HM. Effect of whole-tree harvesting on microclimate during establishment of second rotation forestry. Agricultural and Forest Meteorology (2001) 110:141-154.

Saarsalmi A, Tamminen P, Kukkola M, Hautajarvi R. Whole-tree harvesting at clear-felling: Impact on soil chemistry, needle nutrient concentrations and growth of Scots pine. Scandinavian Journal of Forest Research (2010) 25:148-156.

Sanchez FG, Scott DA, Ludovici KH. Negligible effects of severe organic matter removal and soil compaction on loblolly pine growth over 10 years. Forest Ecology and Management (2006) 227:145-154.

Scott DA, Dean TJ. Energy trade-offs between intensive biomass utilization, site productivity loss, and ameliorative treatments in loblolly pine plantations. Biomass and Bioenergy (2006) 30:1001-1010.

Smethurst PJ, Nambiar EKS. Effects of Slash and Litter Management on Fluxes of Nitrogen and Tree Growth in a Young Pinus-Radiata Plantation. Canadian Journal of Forest Research (1990) 20:1498-1507.

Tan X, Curran M, Chang S, Maynard D. Early Growth Responses of Lodgepole Pine and Douglas-Fir to Soil Compaction, Organic Matter Removal, and Rehabilitation Treatments in Southeastern British Columbia. Forest Science (2009) 55:210-220.

Thompson SK. Sampling. (2002) second edn. New York, NY: John Wiley & Sons, Inc.

Vanguelova E, Pitman R, Luiro J, Helmisaari HS. Long term effects of whole tree harvesting on soil carbon and nutrient sustainability in the UK. Biogeochemistry (2010) 101:43-59.

Walmsley JD, Jones DL, Reynolds B, Price MH, Healey JR. Whole tree harvesting can reduce second rotation forest productivity. Forest Ecology and Management (2009) 257:1104-1111.

Weetman GF, Webber B. The influence of wood harvesting on the nutrient status of two spruce stands. Canadian Journal of Forest Research (1972) 2:351-369.

Wells CG, Jorgensen JR. Effect of intensive harvesting on nutrient supply and sustained productivity. Presented at the Impact of Intensive Harvesting on Forest Nutrient Cycling, (1979) State University of New York, Syracuse, NY.

White EH. Whole-tree harvesting depletes soil nutrients. Canadian Journal of Forest Research (1974) 4:530-535.

APPENDICES

Appendix A: Details of the Spatial Radiation Model

A spatial radiation model was created to estimate the amount of solar radiation incident on each measured plot for the duration of the growing season. The actual procedure for calculating these values was different for our two field seasons due to different sampling protocols and a change in GIS software. Plot selection in the 2010 field season was based on the results of the spatial radiation model, which was developed using ArcView GIS 3.3. The radiation for all potential plots was calculated and stratified random sampling based on radiation level was used to select which plots were actually measured. In the 2011 season, calculation of solar radiation was done using ArcGIS 10.0 *after* plot selection and measurement. Calculation was therefore only done for plots that were actually measured, and not used during plot selection. While the specific steps taken to calculate a solar radiation value were different due to different capabilities of the GIS software, they adopt fundamentally the same procedure. Some procedures that are supported by the more recent ArcGIS 10.0 software were not available in ArcView GIS 3.3. The procedure as conducted using the most recent software is described below, and program add-on extensions that were used for the older software are noted as appropriate.

The potential plot locations for the 2010 season were generated by creating a 6 x 6 meter grid within the cut boundaries. For the 2011 season, the position and elevation of each sample point and edge tree were loaded into the GIS program from our handheld GPS unit. Using the Bearing Distance to Line tool (in ArcView GIS 3.3 an add-on extension by Jenness, 2006), 36 lines radiating outward from each sample point (at 10°

intervals) were created to represent possible azimuthal paths a solar ray could take to strike the plot. For example, the line radiating south from the plot represents the path a ray would take during the part of the day when the sun's azimuth is due south. Points representing edge trees from a given site were connected to form a clearcut outline layer representing the spatial extent of each cut. The radiating lines layer and the clearcut outline layer were then intersected to generate a layer of points corresponding to locations where a solar ray's path would intersect with the clearcut boundary (for ArcView GIS 3.3 an extension by Lead, 2004). Spatially joining the ray intersections with the clearcut outline allowed us to determine which edge tree was nearest to each intersection and could potentially block the path of solar radiation. Next, the ground distance from ray intersection to the plot center where it originated was calculated. Using this plot-to-edge distance along with the edge tree height, plot elevation and edge tree elevation, a critical shading angle was calculated for each intersection using trigonometry (Figure 13). This angle represented the minimum elevation angle the sun must be at for a given plot to receive sunlight at a given solar azimuth.

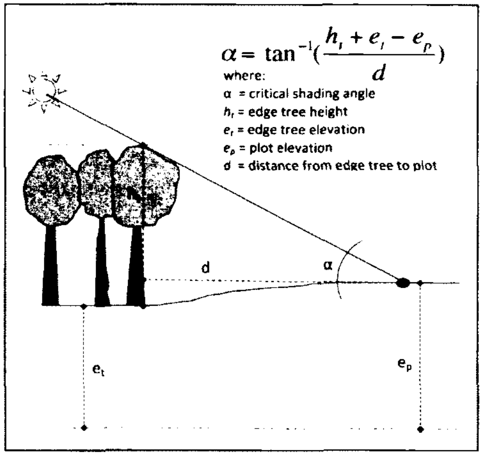

Figure 13: Diagram demonstrating calculation of the critical angle α for a given plot and a given azimuth. When the sun is above this angle, the plot receives radiation.

The Microsoft Excel worksheet SolRad v.12 (Pelletier, 2011) was used to calculate the solar elevation, azimuth and incident radiation for Bartlett, NH (lat = 44.062°, long = -71.293°, elevation = 290m) over a 183 day period from April 1^{st} 12:00AM to October 1^{st} 12:00AM, 2001. This was the actual location of our 2010 field season sites and an approximate center of sites measured during the 2011 season, so the values generated were used for data of both seasons. Default values for other parameters were used (barometric pressure = 1013, ozone thickness = 0.35, water vapor thickness = 4, aerosol optical depth at 500nm = 0.35, aerosol optical depth at 380nm = 0.35, forward scattering = 0.85, surface albedo = 0.2). Solar position and incident radiation was calculated in 15-minute increments. Global incident radiation across all wavelengths calculated using the Bird model (computed by SolRad from equations in Bird and Hulstrom, 1981) was used for all calculations. Repeated model runs demonstrated that incident radiation values over the 183-day period varied < 0.2% year-to-year, so the values from 2001 were used. The azimuth of each entry in this table was rounded to a multiple of 10 to correspond with our generated radiating lines. A script written in the programming language Avenue and run in ArcView 3.3 ran through each hour of the solRad list and determined if the sun's elevation angle was greater than the critical blocking angle at its current azimuth for each plot. If greater (meaning the sun was above the edge tree and the plot was receiving radiation), the incident radiation for that moment was added to that plot's total. The final result of the script was a list of each sampled plot and the amount of radiation that it received during the entire growing season, reported in megajoules per square meter (MJ/m^2).

Appendix B: Biomass Regression Equations

Table 9: Biomass equations based on tree diameter from Jenkins et al. (2004). Column descriptions: (1) tree species, (2) number of trees >2m in height measured in 2010 and 2011 seasons combined, (3) biomass equation used with diameter in centimeters and resulting biomass in grams, (4) coverage area of the study that determined the biomass equation, (5) and (6) diameter range over which the equation is valid, and (7) the number of sample trees used to develop the equation.

***Equation for paper birch developed using data from Minnesota, Wisconsin, New Hampshire, Maine and New Brunswick.**
****Equation for white pine developed from several equations based on data taken in New York and New Brunswick.**

Species	# Stems Counted	Biomass Equation	Area	DBH range (cm)		# Samples
				Min	Max	
American Beech	1873	$10^{2.1112+2.462*\log(d)}$	New Hampshire	1.0	63.0	14
Yellow Birch	1817	$10^{2.1047+2.4417*\log(d)}$	New Hampshire	1.0	63.0	14
Paper Birch	848	$1000*0.0882*d^{2.562}$	US & Canada*	0.0	29.5	204
Pin Cherry	762	$e^{6.9902+1.3066*\ln(d/2.54)}$	Maine	0.1	2.5	13
Striped Maple	533	$e^{7.227+1.6478*\ln(d/2.54)}$	Maine	0.1	2.5	12
Red Maple	372	$1000*e^{-2.0274+2.3199*\ln(d)}$	Nova Scotia	1.1	29.6	49
Bigtooth Aspen	314	$1000*e^{-2.32+2.3773*\ln(d)}$	Nova Scotia	1.2	33.8	30
Sugar Maple	95	$10^{2.0537+2.4793*\log(d)}$	New Hampshire	1.0	63.0	14
White Ash	94	$e^{7.1148+1.3707*\ln(d/2.54)}$	Maine	0.1	2.5	12
Black Cherry	59	$10^{1.1981+1.5876*\log(d)}$	Ohio	0.4	6.8	37
Northern Red Oak	15	$e^{7.2395+1.0216*\ln(d/2.54)}$	Maine	0.1	2.5	14
Eastern Hemlock	14	$e^{6.9159+0.70038*\ln(d/2.54)}$	Maine	0.1	2.5	11
Mountain Maple	13	$e^{7.2723+1.4835*\log(d/2.54)}$	Maine	0.1	2.5	10
Red Spruce	10	$1000*e^{-1.7957+2.2417*\ln(d)}$	Nova Scotia	1.2	31.3	37
Quaking Aspen	9	$1000*e^{-2.3778+2.4085*\ln(d)}$	Nova Scotia	0.8	26.5	26
White Pine	8	$e^{5.2831+2.0369*\log(d)}$	Eastern US	1.0	55.0	**
Grey Birch	6	$e^{-2.1053+2.3123*\log(d)}$	Nova Scotia	1.1	22.7	44
American Basswood	5	$e^{6.6585+1.223*\ln(d/2.54)}$	Maine	0.1	2.5	11