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Sustainable Forest Management in a Disturbance Context: A Case Study of Canadian Sub-Boreal Forests

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1. Introduction

In many forests, timber harvesting is displacing natural disturbance (e.g., wildfire, wind, insects and disease) as the major agent of ecosystem disturbance. There is a growing concern over the impacts of intensive timber harvesting on the long-term site productivity (Nambiar et al., 1990; Nambiar and Sands, 1993; Johnson, 1994). The significant yield decline of Chinese fir (*Cunninghamia lanceolata* [Lamb] Hook) in southern China (Yu, 1988; Sheng and Xue, 1992) and of radiata pine (*Pinus radiata* D. Don) in southeastern Australia (Keeves, 1966; Squire, 1983) and New Zealand (Whyte, 1973) after several forest-harvest rotations exemplifies this concern, and the issue has gained renewed attention as interest has grown in forest certification, biodiversity, protection, forest carbon management and sustainability. A key issue in the discussion of sustainability is the comparability in ecological impacts between timber harvesting and natural disturbance (e.g., wildfire, insects, and disease). Much of the focus in this discussion has been on the characteristics that clear-cutting and natural disturbance have in common (Hammond, 1991; Keenan and Kimmins, 1993). However, the debate has frequently been frustrated by the lack of an adequate description of the range of ecological effects of both natural disturbance and forest harvesting. A variety of recent initiatives in forest policy in both the United States and Canada have emphasized natural disturbance processes and their structural consequences as models of forest management (Lertzman et al., 1997). However, implementing this approach is often limited by our incomplete understanding of natural disturbance regimes (Lertzman and Fall, 1998; Perera and Buse, 2004). Many studies have demonstrated importance of wildfire disturbance in forest ecosystems (Attiwill, 1994; Lertzman and Fall, 1998). If natural disturbance is fundamental to the development of forest ecosystems, then our management of natural areas should be based on an understanding of disturbance processes (Attiwill, 1994; Poff et al., 1997; Richter et al., 1997; Andison, 2000; Johnson et al., 2003)). This also highlights that ecological impacts of harvesting must be evaluated within a broad disturbance context. In the British Columbia (BC) interior forest ecosystems that are described as having a natural disturbance type maintained by frequent stand-initiating fires, forest managers are

particularly interested in understanding natural wildfire disturbances in order to maintain the ecological patterns and functions of these forests (Parminter, 1998; Kimmins, 2000; Wei et al. 2003). In these areas, wildfire disturbance is part of natural ecosystem processes, and its functions are, from a long-term perspective, part of natural variability. Lodgepole pine forest (*Pinus contorta ssp. latifolia* Engelm. ex S. Wats.) is a major type of forests in the central interior of BC, and concerns have been expressed over potential impacts of intensive timber harvesting on long-term site productivity (Kimmins, 1993; Wei et al., 1997).

Both timber harvesting and wildfire disturbances can vary substantially in size, intensity, severity, frequency and internal heterogeneity, greatly complicating comparisons of the effects of different disturbance types. The differences relate to differences in forest type, topography, timing of the disturbance, local management methods, and management objectives (Lertzman and Fall, 1998; Parminter, 1998). From a nutrient perspective, a major difference between timber harvesting and wildfire disturbance is the biomass of woody debris (WD) left in the ecosystem, and the quantity of nutrients removed.

WD, particularly coarse woody debris (CWD), has been shown to be an important structural and functional element in many forested ecosystems (Lambert et al., 1980; Sollins, 1982; Harmon et al., 1986; Spies et al., 1988). It provides a key habitat component (especially large logs) for many forms of wildlife (Reynolds et al. 1992). Studies by Harvey et al. (1981) and Harvey et al. (1987) showed that organic materials, especially humus and buried residue in the advanced stage of decay, are excellent sites for the formation of ectomycorrhizal root tips. Graham et al. (1994) used ectomycorrhizal activity as a primary indicator of a healthy forest soil. Further, CWD may play a significant role in long-term nutrient cycling; it can be an important site for asymbiotic nitrogen fixation, and it acts as a source of slow nutrient release during its long period of decay.

This paper summarizes a series of our research and publications in lodgepole pine forests in the sub-boreal regions of British Columbia, Canada. The objectives of this study are: (1) to quantify the difference in the mass and nutrients of woody debris remaining immediately following harvesting and wildfire disturbances; (2) to evaluate long-term implications of those differences in site productivity; and (3) to determine the management strategies for achieving sustainability of long-term site productivity in lodgepole pine forests in the BC interior.

2. Study area

The study area is located west of Williams Lake in the Chilcotin plateau of interior British Columbia (52°-53°N, 123°-124°W) in the very dry and cold subzone of the Sub-Boreal Pine Spruce biogeoclimatic zone (SBPSxc). Average monthly temperatures range from -13.8°C in January to +11.6°C in July. The mean daily temperature is below 0°C from November to March. Average annual precipitation is 464 mm, of which 195 mm is snow. Soils are well drained brunisols and luvisols of sandy or sandy loam texture. Soil parent material is primarily glaciofluvial or morainal. The forest is relatively pure lodgepole pine with trembling aspen (*Populus tremuloides* Michx) in some of the newly disturbed stands. White spruce (*Picea glauca* (Moench) Voss) is the theoretical climax tree species over most of the SBPS. In the very dry and cold SBPSxc subzone area, however, the abundance of pine regeneration and the virtual absence of spruce regeneration on zonal sites suggests that lodgepole pine is the climatic climax tree species (Steen and Demarchi, 1991). Lodgepole pine grows relatively slow under such a dry and cold subzone. Average diameter and height are 17.8 cm and 14.4 m in mature stands, respectively.

Wildfire is a common, natural disturbance which cycles this type of forest about every 100 - 125 years (mean fire return interval in the SBPS Zone, J. Parminter, Ministry of Forests, Victoria, British Columbia). Other natural disturbance agents such as mountain pine beetles (*Dendroctonus ponderosae* Hopk) and dwarf mistletoe (*Arceuthobium americanum* Nutt) are common in the study area. The former can cause extensive tree mortality, and much of the harvesting in the study area was in stands where some (about 5-25%) of the dominant trees had been killed by mountain pine beetles. Dwarf mistletoe does not usually kill lodgepole pine but can cause severe losses of volume production.

There are two types of timber harvesting including stem-only harvesting (SOH) and whole-tree harvesting (WTH) applied in lodgepole pine forests in the central interior of British Columbia. WTH removes most of the above-ground woody biomass including crown materials while SOH removes most of the above-ground woody biomass but leaves crown materials on the site. Concern has focused on the ecological impacts of the removal of nutrient-rich crown materials, and in WTH such removal may result in considerably more site nutrient depletion. For this study, we included both harvesting methods.

3. Methods

A combination of field investigation with ecosystem modeling was used for this study. The purpose of the field survey is to quantify the differences immediately following wildfire disturbance and harvesting, while the ecosystem modeling is to evaluate the long-term implication of those differences in site productivity. The ecosystem model FORECAST, or its forerunner FORCYTE, has been used as a management evaluation tool in several types of forest ecosystems (Sachs and Sollins, 1986; Kellomäki and Seppälä, 1987; Wang et al., 1995; Wei and Kimmins, 1995; Morris et al., 1997; Wei et al., 2000; Seely et al., 2002; Welham et al., 2002). The model was specifically designed to examine the impacts of different management strategies or natural disturbance regimes on long-term site productivity. A brief description of the FORECAST model approach is presented in the next section; details are found in Kimmins (1993); Seely et al., (1999); and Kimmins et al., (1999).

3.1 Field investigation

WD in this study includes CWD and fine woody debris (FWD). We define CWD as woody stems ≥ 2.5 cm diameter and FWD as woody stems < 2.5 cm diameter. We investigated FWD as well as CWD as the former should account for the major difference in WD loading between SOH and WTH sites.

3.1.1 Measurements of mass of above-ground WD

Thirteen plots (five for WTH and four each for wildfire disturbance and SOH) with records of the time of disturbance were located, interspersed across the study area. Most selected plots were harvested or burned within less than 20 years ago, with an exception of the plot burned in 1961. It was not possible to locate more fire-killed plots because no records are available for the fires occurred 30 years ago, and because recent fire protection in the area has limited the number of fire disturbances.

The line intersect sampling method was employed to quantify WD volume (McRae et al., 1979). This involves 3 lines (each 30 m in length) laid out in an equilateral triangle. The triangular layout is used to minimize bias in situations where the logs are not randomly

oriented and to cover the variation in WD distribution. Five triangles were randomly set up in each plot. The more details on measurements and calculations were described by Wei et al. (1997).

3.1.2 Measurements of decay of above-ground WD

Changes of wood density in WD for early and medium decay classes on both fire-killed and harvested sites were used to estimate WD decay coefficients. We assumed that WD decay follows a single-exponential decay equation (Fahey, 1983; Busse, 1994):

$$y_t = y_0 * e^{-k * t}$$

where y_t is wood density in WD after decay of t years, y_0 is initial wood density at year 0, and k is the decay coefficient. Using this equation, we estimated k values for early and medium decay classes on both fire-killed and harvested sites, which enable us to compare differences in WD decay between these two types of disturbance. No attempt was made to measure k values for advanced WD because of lack of data on years of decay in advanced WD on the study sites.

WD in the plot burned in 1961 can obviously be classified as medium and advanced decay classes after 33 years of decay, depending on the degree of contact with ground. The mean decay rate of these advanced decaying woody materials in this plot was estimated based on the above equation. This rate was assumed to be the rate for advanced decaying WD carried over from pre-disturbance forests in order to estimate the advanced WD loading in the year right after disturbances in all selected plots.

3.1.3 Estimates of below-ground WD

The stump-breast height diameter table from Omule and Kozak (1989) was used to estimate DBH values from the measured stump diameters for the SOH and WTH sites. A DBH - height equation was established in adjacent uncut stands to estimate heights of stands prior to disturbances. The validated equations and biomass component ratios from Comeau and Kimmins (1989), along with estimated H and DBH were then used to estimate above- and below-ground biomass of each plot before harvesting for harvested sites. For the fire-killed sites, these biomass parameters were estimated using the decomposition model developed in this study and the biomass component ratios from Comeau and Kimmins (1989). The below-ground biomass component includes fine and coarse roots.

3.1.4 Quantification of nutrient removals

In order to quantify the amount of nutrients removed by different disturbances, samples of the different decay and size classes of CWD and WD (from two plots of each disturbance), fresh woody materials, living needles and fresh litter (from neighboring uncut stands of above sampling plots) were collected to analyze N and P nutrient concentrations.

Total N and P losses through harvesting were estimated from data on the biomass removed and nutrient concentrations therein. The biomass removed by harvesting was calculated from the estimated total biomass before disturbances and total WD mass left after harvesting. Total N and P losses through wildfire were estimated using assumed % loss of forest floor and foliage due to burning. Because wildfires in the study area are very variable in intensity and severity of impact, a range of severities was assumed. Based on our

observations, we assumed a range of wildfire severities from 25% to 85% loss of both forest floor and foliage. It was also assumed that, on average, 10% of branch mass was lost during the fire. The average loading of the forest floor (L and F layers) biomass in mature lodgepole pine forests in the study area was $14.5 (\pm 3.3) \text{ Mg} \cdot \text{ha}^{-1}$.

3.1.5 Measurement of asymbiotic nitrogen fixation rates in woody debris and forest floor

Measures of nitrogenase activity were used as an index of nitrogen fixation, based on an adaptation of the acetylene reduction assay (Hardy et al., 1973). Sampling was carried out on five occasions (August 22 and September 25, 1994, and May 15, June 18 and July 20, 1995) at the three study sites. From an analysis of historical weather data and preliminary sample tests, we believe that no nitrogen fixation activities occur from November to April due to low temperature. The more details on measurements and calculations were described by Wei et al. (1998).

3.1.6 Statistical analyses

Homogeneity of variances and normality of distributions of data sets were checked. Data that were not homogeneous (CWD, total WD and nitrogen fixation rates) were logarithmically transformed prior to analysis. Using SYSTAT version 5.0 (Wilkinson, 1990), analyses of variance (ANOVA) were performed on WD variables (e.g., above-ground CWD and total WD), nitrogen fixation rates and moisture contents (%). Where there was a significant difference, means of measured variables were compared between WTH, SOH and wildfire disturbances using the Turkey test.

3.2 Ecosystem modeling

3.2.1 A brief description of the ecosystem model FORECAST

The ecosystem management simulation model FORECAST uses the hybrid simulation approach. The model employs empirical data, from sites of different nutritional quality, which describe tree and plant biomass accumulation over time and plant tissue nutrient concentrations. These data form the basis from which the rates of key processes are estimated, such as canopy function (photosynthesis), carbon allocation responses to changing resource availability (nutrients), competition-related mortality (largely competition for light), and rates of nutrient cycling. FORECAST, which accounts explicitly for changes in nutritional site quality over time caused by various simulated autogenic successional processes and types (allogenic and biogenic) of disturbance, was designed for the evaluation of forest management strategies in forests where potential net primary production is limited by nutrient availability, and in which nutrient availability is altered by management or natural disturbance events. The more details on the FORECAST model and model calibration were described by Kimmins et al. (1999) and Wei et al. (2003).

3.2.2 Defining the disturbance scenarios and sustainability indicators

Characteristics of disturbance can be best described by the frequency (return intervals for wildfire and rotation lengths for harvesting) and intensity (severity for wildfire and utilization levels for harvesting) of disturbance. Based on input from local ecologists and soil scientists, we defined three severity categories (low, medium, high) and three fire

return intervals (40, 80, 120 years) for wildfire simulations, and two utilization levels (SOH, WTH) and three rotation lengths (40, 80, 120 years) for harvesting simulations. A description of those severity and utilization categories is given in Table 1. Each scenario was then simulated commencing with the initial ECOSTATE file described in Wei et al. (2003). The unrealistically short 40-year rotation length was included in the study in order to compare harvesting at this frequency with fire, and because it helps to define a response curve (Powers et al., 1994).

Four output parameters (production, mass of decomposing litter, total available soil nitrogen and nitrogen removal) were used in the assessment of the sustainability of site productivity. Total production is a direct indicator of achieved productivity, while decomposing litter, total available soil nitrogen and nitrogen removal are indirect indicators of site productivity potential. Woody debris, as part of decomposing litter, is also a source of asymbiotic nitrogen fixation (Wei and Kimmins, 1998), and can protect soil from erosion and play an important role in maintaining some aspects of biodiversity (Harmon et al., 1986; Hunter, 1990).

Disturbance	Severity*	Biomass burned or removed for each component (%)							
		Stemwood	Stembark	Branch	Foliage	Large root	Medium root	Small root	Cones
Wildfire	Low (Fire-L)	0	10	10	20	0	0	10	10
	Medium (Fire-M)	15	60	50	60	20	20	20	60
	High (Fire-H)	50	95	95	100	30	30	60	95
Harvesting	SOH	90	90	0	0	0	0	0	0
	WTH	90	90	90	90	0	0	0	90

Table 1. Definition of disturbance severity for both wildfire and harvesting for simulations of lodgepole pine forests (*Fire-L: low severity fire; Fire-M: medium severity fire; Fire-H: high severity fire; SOH: stem-only harvesting; WTH: whole-tree harvesting)

4. Results and discussion

4.1 Differences immediately following disturbances

4.1.1 Difference in WD mass between SOH, WTH and wildfire disturbances

There were significant differences in above-ground CWD ($p < 0.001$) and total WD mass ($p < 0.001$) between the fire-killed and the harvested sites that we sampled. The greatest CWD and WD mass was created by wildfire while the lowest was left on the WTH sites; wildfire left about 3 to 5 fold more above-ground WD on the sites than did clearcutting. No significant differences in above-ground CWD and total WD mass were detected between SOH and WTH (Table 2), except the difference in above-ground FWD ($p < 0.001$) (Table 2). However, the means of CWD and WD mass were greater on the SOH sites than on the WTH sites.

Timber harvesting removed far more above-ground WD than did the wildfire disturbance that was investigated. In the case of a severe wildfire, the difference would be much less. However, harvesting did leave between 18% (WTH) and 24% (SOH) of total above-

ground WD on the sites. These above-ground WD retention percents on the harvested sites were higher than we expected. This is because a relatively high proportion of the living stems in the stands that were studied were smaller than the utilization criteria; more than 92% of above-ground WD on the harvested sites was contributed by woody material with a diameter less than 15 cm, which was the lower limit for utilization on these sites. The remaining WD was contributed by small quantities of logs in advanced decay stages that were a carryover from previous natural disturbances, and unharvested low-quality trees.

There were no significant differences in below-ground WD mass between the three types of disturbance (Tables 2). The amount of below-ground WD was similar to the amount of above-ground WD on the harvested sites, and was about 30% of the above-ground mass on the fire-killed sites. This suggests that below-ground WD makes an important contribution to total WD loading on the disturbed sites in the study area.

Diameter size class (cm)	Mass of WD (Mg.ha ⁻¹)		
	WTH	SOH	Wildfire
0.0 -- 0.49	0.25(0.0)	0.63(0.0)	0.49(0.0)
0.5 -- 0.99	0.75(0.1)	1.78(0.2)	1.37(0.1)
1.0 --2.49	1.61(0.1)	3.60(0.5)	2.77(0.3)
2.5 -- 4.99	1.28(0.1)	2.67(0.2)	2.53(0.1)
5.0 -- 6.99	1.73(0.2)	3.83(0.6)	4.34(0.4)
≥ 7.0	11.71(1.3)	15.51(2.3)	91.09(7.3)
advanced decay	1.88(0.3)	3.68(1.4)	1.29(0.3)
stump	1.62(0.1)	1.96(0.4)	0.00
above-ground CWD	18.22(1.2) ^a	27.65(1.6) ^a	99.25(4.2) ^b
above-ground FWD	2.61(0.1) ^a	6.01(0.4) ^b	4.63(0.2) ^b
total above-ground WD	20.83(1.1) ^a	33.66(2.2) ^a	103.88(4.3) ^b
total below-ground WD	31.98(1.9) ^a	31.53(2.2) ^a	37.12(1.6) ^a
total WD	52.81(3.0) ^a	65.19(4.1) ^a	141.00(5.8) ^b

Table 2. Comparison of woody debris (WD) mass (Mg.ha⁻¹) in the year immediately following disturbance between stem-only harvested (SOH), whole-tree harvested (WTH) and wildfire-killed sites, based on modification of the field data to account for mass losses due to decomposition since disturbance (Note: FWD: fine woody debris; CWD: coarse woody debris; standard error of the mean is in parentheses; the sample size (n) is 25 for WTH, and 20 for others; means with the same letter within a row are not significantly different (*p* > 0.05) from each other (the Tukey test))

Timber harvesting removed most of the above-ground biomass, but like natural disturbances it left all below-ground biomass on site. The below-ground biomass (total roots) in lodgepole pine stands accounts for an important portion of total tree biomass,

ranging from 20% on mesic sites to 28% on xeric sites (Comeau and Kimmins, 1989). This below-ground biomass may play an important role in long-term site productivity on these disturbed sites because our data show that asymbiotic nitrogen fixation rates in below-ground WD are significantly higher than in above-ground WD (see the section on asymbiotic nitrogenase fixation). Most WD studies have ignored below-ground WD, which may result in an incomplete understanding of the post-disturbance role of WD in forest ecosystems.

4.1.2 Above-ground CWD decay

The single-exponential decay coefficient (k) is an indicator of the rate of the decay process (Swift et al., 1979). The higher the k value, the faster CWD decays. Table 3 showed that, when CWD is in early or medium decay stages (data limited to about <30 years of decay since disturbance in this study), k values associated with above-ground CWD on the harvested sites were significantly higher ($p < 0.001$) than those on the fire-killed sites. These differences were attributed to the degree of contact between CWD and ground. CWD after harvesting generally has full contact with the ground, while CWD after wildfire disturbance experiences a long period of time before fully reaching the ground (from snag to partial suspended CWD and finally to fully ground-contact CWD). Decomposition is accelerated when logs are in contact with the ground, probably as a result of higher moisture content and increased interaction with the soil fauna and microflora.

Decay class	Years of decay*	Treatment		Sample size (n)
		Harvested	Fire-killed	
Early	5 - 10	0.021 (0.004)a	0.004 (0.001)b	16
Medium	20 - 30	0.018 (0.005)a	0.009 (0.002)b	12

Table 3. Single-exponential decay coefficients (k) for 10-20 cm diameter above-ground coarse woody debris (CWD) of different decay classes on both harvested and fire-killed sites (Wei et al. 1997) (Note: Means with the same letter within a row are not significantly different ($p > 0.05$) from each other (t-tests); standard error of the mean is shown in parentheses; *data on various years of wood decay was grouped into two time classes as shown in the table)

4.1.3 Nutrient losses through harvest or wildfire

The differences in nutrient removal between the three disturbances are presented in Table 4. The nutrient removals associated with timber harvesting generally were within the range of estimated wildfire removals; the P removal by WTH was equal to the largest value estimated for wildfire losses. WTH removed more N and P nutrients (about 2-fold) than SOH harvesting did, confirming that SOH is the more nutrient-conserving of the two harvesting methods.

Wildfire removes nutrient-rich crown material and forest floor, but leaves most large woody material in the ecosystem. In contrast, timber harvesting removes most large woody material, but leaves the nutrient-rich forest floor and part of the crown materials, depending on harvesting technique (e.g., SOH vs. WTH). Our estimates on N loss by wildfire, based on consumption of woody and litter materials, are reasonable due to volatilization and particulate convection. However, P loss by wildfire may be overestimated because P in

burned material may be lost as fly-ash, or simply added to the ground as ash. No attempt was made in this study to compare the nutrient losses through soil leaching process following the SOH, WTH and fire disturbances. However, nitrogen leaching losses after harvesting or wildfire disturbances are believed to be low in these dry interior ecosystems.

Nutrient variables	Disturbance types		
	WTH	SOH	Wildfire
N			
total removed ¹	97.8 (3.9)	57.0 (4.6)	50.0 (1.5) ~~ 166.7 (4.8) ³
removal ratio ²	0.31 (0.01)	0.18 (0.01)	0.15(0.01) ~~ 0.49(0.02)
P			
total removed	8.8 (0.4)	5.2 (0.4)	2.8 (0.1) ~~ 9.5 (0.5)
removal ratio	0.44 (0.01)	0.26 (0.01)	0.13(0.01) ~~ 0.44(0.02)

Table 4. Estimated nutrient losses (kg.ha⁻¹) caused by stem-only harvesting (SOH), whole tree harvesting (WTH) and wildfire (from Wei et al. 1997)(Note: Standard error of the mean is shown in parentheses; ¹. total removed is the amount of nutrients removed during disturbance; ². the removal ratio is the amount of nutrients removed during disturbance divided by total amount of nutrients in biomass (above and below-ground biomass and forest floor) prior to disturbance; ³. the range given here is based on an assumed range of fire severities: see text for explanation)

4.1.4 Asymbiotic nitrogenase activity in decaying wood, forest floor and soil

The nitrogen fixation rate in dead root was significantly higher than in the other substrates examined (Table 5), and the rate in mineral soil was the lowest. Table 5 also showed that nitrogen fixation rates in more advanced decay wood (medium or advanced decay classes) were significantly higher than in early decay wood. The difference in nitrogen fixation rates between medium and advanced decay wood was not significant. The nitrogen fixation rate in May 15, 1995 was the lowest, due to low temperature, among all other sampling dates.

The differences between early and medium decay classes of WD for both wildfire-killed and harvested sites indicate that nitrogen fixation activity increases as wood decay progresses (Table 5). However, there was little change in activity between medium and advanced decay stages on the wildfire-killed sites, suggesting that the increase in activity may only occur during the early stages of decay and then reach a steady level, depending on moisture content. The nitrogen fixation activity associated with dead roots was the highest among all substrates we studied (Table 5) probably due to the high moisture content of this material. The lowest activity occurred in mineral soil probably because of insufficient carbon substrates and low moisture content and also because soil weights more per volume. The nitrogen fixation activity in stumps and litter was higher than that in soil and early decaying stems.

Rates of nitrogen fixation in our study are generally consistent with other measures in northern forest ecosystems (Jurgensen et al., 1987 and 1989; Hendrickson, 1988; Harvey

et al., 1989; Sollins, 1982; Roskoski, 1980). Cushon and Feller (1989) found much lower values; aerobic conditions during incubation in their assay might be responsible for this deviation.

Substrate	Nitrogen fixation rates (nm C ₂ H ₄ g ⁻¹ day ⁻¹)					
	Aug. 22, 94	Sept. 25, 94	May 15, 95	June 18, 95	July 20, 95	mean
Fire-killed sites						
decaying wood						
early	2.60 (0.10)	1.27 (0.32)	0.00	1.86 (0.91)	0.92 (0.30)	1.33 (0.36) ^c
medium	3.91 (0.92)	3.85 (0.71)	0.14 (0.10)	10.94 (2.66)	9.00 (3.32)	5.58 (1.14) ^b
advanced	6.32 (1.72)	8.69 (1.49)	0.33 (0.20)	12.05 (6.40)	2.81 (0.71)	5.64 (1.61) ^b
dead roots	11.40 (2.82)	14.87 (4.56)	1.23 (0.46)	37.15 (16.1)	10.94 (3.11)	15.1 (4.75) ^a
branches	4.70 (2.20)	4.96 (1.98)	0.00	0.29 (0.24)	0.00	1.99 (0.75) ^c
floor litter	6.92 (3.11)	7.10 (2.02)	0.00	8.75 (4.11)	4.23 (1.52)	5.40 (1.43) ^b
humus	1.33 (0.32)	0.10 (0.03)	0.21 (0.20)	7.05 (3.47)	1.68 (1.30)	2.07 (0.87) ^c
mineral soil	0.00	0.05 (0.03)	0.00	0.50 (0.10)	0.00	0.11 (0.04) ^d
Harvested sites						
decaying wood						
early	3.22 (0.30)	3.62 (1.14)	0.00	3.49 (0.88)	0.72 (0.24)	2.21 (0.74) ^c
medium	3.90 (1.01)	3.60 (1.20)	0.00	10.70 (2.56)	7.37 (2.10)	5.20 (1.10) ^b
advanced	10.02 (3.07)	1.76 (0.52)	0.60 (0.40)	10.11 (2.72)	9.11 (3.82)	6.32 (1.24) ^b
dead roots	11.90 (3.01)	10.38 (1.34)	6.20 (0.31)	11.34 (1.29)	13.52 (5.94)	10.7 (2.01) ^a
branches	3.01 (0.80)	5.57 (1.67)	1.41 (2.01)	1.06 (0.14)	2.57 (1.01)	2.72 (0.98) ^c
floor litter	12.1 (2.05)	8.30 (2.89)	2.30(2.21)	1.20 (0.22)	4.30 (1.12)	5.64 (1.47) ^b
humus	1.13 (0.24)	0.34 (0.15)	0.49 (0.28)	2.28 (0.89)	0.41 (0.31)	1.16 (0.37) ^c
mineral soil	0.10 (0.05)	0.15 (0.07)	0.00	0.00	0.10 (0.10)	0.07 (0.03) ^d

Table 5. Estimated nitrogenase activity for each substrate and sampling time and the mean nitrogenase activities for all sampling dates in 1994-1995 (from Wei et al. 1998) (Note: Each value is the mean and (the standard error) of 4 samples; means with the same letter within a column are not significantly different ($p > 0.05$) from each other (the Tukey test))

4.2 Long-term implications of these differences in sustainability of productivity

4.2.1 Impacts of disturbance frequencies (rotation length or intervals)

As expected, the total productivity over a 240-year simulation increased with the length of the interval for all disturbance types (Figure 1a). This is clearly related to lower nitrogen losses over the 240-year simulation period (Figure 1b) and consequently more nitrogen and

forest floor accumulation (Figures 1c,d, respectively). This indicates, as expected, that the sites we studied would be more productive under less frequent disturbance by the regimes defined in this study.

The rate of increase in productivity between disturbance scenarios varies, with a sharp increase from intervals of 40 years to intervals of 80 years, but only a modest increase from 80 years to 120 years. This reflects not only the difference in percentage change in interval length between these two scenarios, but a decrease in stem mass accumulation at stands ages greater than 80 years. The combined effects of genetically-determined, age-related decline in growth rates and the altered geochemical balance at longer disturbance intervals results in a declining sensitivity of total productivity to disturbance frequency at intervals longer than 80 years.

Figure 1a also shows that the difference in total productivity between the five disturbance types becomes progressively smaller as the disturbance interval increases, suggesting that these lodgepole pine ecosystems are fairly resilient in the face of a disturbance interval of 120 years. This is particularly evident for timber harvesting (SOH and WTH) and low-severity wildfire disturbance. However, rotation lengths of longer than 120 years may not be suitable from a timber management perspective because (1): they lead to little gain of productivity within a rotation, and a decline of total productivity over the 240-year simulation period; and (2) they increase problems with mistletoe. Therefore, we conclude that 120 years would be the upper limit for rotation length in terms of maximization of site productivity for the medium quality site.

The trend of site productivity over multiple consecutive rotations is a useful indication of sustainability. Figure 2 shows that with a harvest (WTH, SOH) or low-severity wildfire interval of 80 years or longer, site productivity is sustainable over a 240-year simulation. In contrast, site productivity at 40-year frequency is only sustainable with SOH; the other four scenarios were not shown to be sustainable (Figure 1a and Table 6). Therefore, 80 years appears to be the lower limit of sustainable rotation lengths of the three examined for the management system that we simulated, and 80 to 120 years would probably be the range of suitable rotation lengths for medium quality sites in the study area. Simulations at intermediate rotation lengths would be needed to define sustainable rotation length more accurately.

Lodgepole pine forests in the study area are thought to have been recycled for thousands of years under natural wildfire return intervals of about 100-125 years. This is similar to the disturbance interval that was estimated by this simulation to be sustainable, and suggests that the study of natural disturbance regimes can be helpful in designing sustainable management strategies. However, although the average wildfire return interval is 100 -125 years in the study sites, its variability is very high, ranging from 40 to 200 years (Pojar, 1985). This is much different from human-caused disturbance such as timber harvesting which tends to apply roughly equal harvest frequencies in a specific type of forest. The variability in frequency of natural disturbance may be important for the maintenance of certain ecosystem values because it affects the dynamics of WD loading and stand structures. Our study has demonstrated that both above-ground and below-ground WD plays an important role in the nitrogen economy in these lodgepole pine forests. The implications of this natural disturbance variability for other ecological attributes, such as wildlife habitat, remain unknown and are beyond the scope of this study, as are the implications of imposing a more uniform disturbance frequency.

Fig. 1. (a-d). Four simulation output indicators (total productivity, total nitrogen removal, available soil nitrogen and forest floor mass) under five disturbance scenarios on a site of medium quality over a period of 240-year simulation (from Wei et al. 2003)

Fig. 2. Dynamics of site productivity under fiver disturbance scenarios on a site of medium quality over a simulation period of 240 years (from Wei et al. 2003)

In some forest types, and depending on how it is done, clear-cut harvesting reverts the ecosystem to an earlier stage of the sere (defined as the sequence of plant and animal communities which successively occupy a site over a period of time). However, in some forests, or with some techniques, clear-cutting may simply recycle the existing seral stage, promptly replacing the mature trees with young trees of the same species with little or no change in the understory. In other forests, clear-cutting in the absence of fire and soil disturbance may accelerate succession by facilitating earlier development of the subsequent seral stage. This generally involves the release of shade-tolerant seedling of the next seral stage. Clear-cutting in pure lodgepole pine forests in the study area generally tend to recycle the existing seral stage.

Disturbance Interval (years)	Disturbance Severity				
	Fire-L	Fire-M	Fire-H	SOH	WTH
40	1157	847	709	1457	1275
80	1745	1525	1349	1887	1801
120	1942	1843	1734	2034	2002

Table 6. Difference in total tree productivity (Mg/ha) between disturbance severity scenarios and between disturbance interval scenarios over a period of 240-year simulation (from Wei et al. 2003) (Note: Abbreviations are given in Table 1)

4.2.2 Impacts of disturbance severities

Figures 1a-d show that medium and high-severity wildfire had the largest impact on most of the simulated indicators. Total productivity (Figure 1a) and total soil nitrogen (Figure 1c) are much less for the moderate and severe fire simulations than for the harvested or low-severity wildfire simulations. This reflects the greater loss of N in the medium and high-severity wildfire simulations (Figure 1b).

The simulations suggest that timber harvesting (SOH, WTH) is a relatively nutrient conservative disturbance compared to wildfire. All simulated indicators for the harvesting treatments are within the range of the wildfire treatment (Figures 1a-d), and close to those for the low-severity wildfire treatment. These simulation results support one of the conclusions from our field investigation of the differences between harvested and fire-killed stands in the study area: the nutrient removals caused by harvesting were within the estimated range of nutrient removals caused by wildfire.

The difference in all indicators between SOH and WTH treatments declined as the rotation lengths increased (Figures 1a-d). There is only a minor difference in total productivity over the 240-year simulation at a rotation of 120 years. This suggests that both WTH and SOH are acceptable harvesting methods for the maintenance of long-term site productivity in these lodgepole pine forests if a rotation of 120 years is used. However, the simulations suggest that WTH could reduce productivity by up to 20% compared with SOH if the rotation length was as short as 40 years. SOH is a more nutrient conservative harvest method because it leaves more of the relatively nutrient-rich crown materials on the ground, and should be used instead of WTH for rotations less than 80 years. Our results from both simulation (Figure 1d) and field studies demonstrate that the total mass of decomposing organic matter on wildfire-killed sites, particularly for long-interval, lower-severity wildfires, would be much higher than on harvested sites. This reflects the larger accumulation of aboveground CWD on the wildfire-killed sites, and slower decomposition of this material on fire sites than on harvested sites because much of it is suspended above the ground on branch-stubs on the burned sites. The WD left on the harvested sites is smaller in diameter and in closer contact with the ground, resulting in faster decomposition and, therefore, lower persistence. The lower level of decomposing litter on high-severity wildfire sites (Figure 1d) is attributed to much larger loss of forest floor and crown materials compared with lower severity fire. Because of these differences, harvesting conserves nutrients more than wildfire does at time of disturbance. However, because decomposing

litter on wildfire sites consists largely of persistent WD that supports asymbiotic nitrogen fixation, even severely burned sites eventually recover from nutrient losses caused by fire. WD may also play an important role in providing wildlife habitat and microclimatic shelter for regeneration.

Fig. 3. Simulation of the mass of decomposing woody debris (WD) in above-ground and below-ground over three consecutive 80-year rotations in a stem-only harvested lodgepole pine forest (from Wei et al. 2003)

WTH has been a common harvesting method in the study area. SOH has been applied recently as a result of concern over nutrient removal caused by WTH. While SOH leaves much more of the fine woody debris (<2.5 cm) and crown materials on the ground, both SOH and WTH leave the same mass of stump and root systems (Wei et al., 1997). In harvested lodgepole pine forests, the mass of this largely unseen below-ground WD is normally much greater than the mass of the visible above-ground WD (Figure 3), and asymbiotic nitrogen fixation associated with the former is much higher than for the latter due to its higher moisture content. From a nitrogen perspective, below-ground WD in these forests is more important than above-ground WD, and consequently, the N-fixation associated with below-ground WD reduces the nutritional significance of differences in aboveground debris loading between SOH and WTH sites. The importance of this belowground tree biomass also suggests that complete tree harvesting, which includes

removal of stumps, major roots, and all above-ground biomass, would require much longer rotations for it to be sustainable.

4.2.3 Interactive effects of disturbance severity and frequency:

The ecological rotation concept

Sustainability in stand level forestry involves non-declining patterns of change. Such non-declining patterns require a balance between the frequency and severity of disturbance, and the resilience of the ecosystem in question. An ecological rotation is defined as the period required for a given site managed under a specific disturbance regime to return to an ecological state comparable to that found in pre-disturbance condition, or to some new desired condition that is then sustained in a non-declining pattern of change. Too short a recovery period for a given disturbance and ecosystem recovery rate, or too large a disturbance for a given frequency and recovery rate, can cause reductions in future forest productivity and other forest values (Kimmins, 1974). Stand level sustainability can thus be achieved by using the design of management on ecological rotations. However, estimating the length of ecological rotations is difficult, and will generally require the use of an ecosystem management simulation model.

The ecological rotation concept asserts that stand level sustainability can be achieved under several different combinations of disturbance severity and disturbance frequency, for a given level of ecosystem resilience. Figure 2 shows that stemwood production is sustained over successive rotations for SOH-40 year and WTH-80 year harvest disturbances, and sustained production for low fire-80 year and medium fire-120 year combinations. The low fire-40 year, medium fire-80 year and the high fires-120 year combinations all show about the same degree of decline in productivity. These results support the concept of ecological rotations, and suggest the ecological rotation could be a useful template for the design of sustainable stand level forestry. Managers may either choose harvest frequency based on economic, technical or other social/managerial considerations and then limit the degree of ecosystem disturbance required by ecological rotation for the site in question with the chosen frequency. Alternatively, they may choose the level of ecosystem disturbance (type of harvest system; severity of post harvest site treatment), but then be constrained in terms of how frequently this can be applied (e.g. the rotation length). If neither of these alternatives is acceptable, they can increase ecosystem resilience by means of silvicultural interventions.

Our FORECAST simulation results suggest that, from a nitrogen-related productivity perspective, the ecological rotation of the medium quality site would average about 100 years, with a possible range of 80 –120 years. However, the ecological rotation should be evaluated in a broader context than soil fertility and site productivity. It should also be calculated for attributes such as understory vegetation, wildlife habitat, and soil physical and chemical conditions.

The ecological rotation for soil fertility is site-specific (Kimmins, 1974). For example, on a site receiving nutrients in seepage water or having large reserves of readily weatherable soil minerals, even substantial losses of nutrients may be replaced relatively rapidly. Similarly, on a site with very slow replacement and/or poorly developed nutrient accumulation mechanisms, even a small loss of nutrients may require a substantial period for replacement. The concept of ecological rotation is defined and applied at the stand level. As noted above, sustainable management at this spatial scale implies non-declining patterns of change,

rather than unchanging conditions. As a consequence, no single value or ecological process can be supplied from any one stand continuously. The objectives of sustainable management in terms of even-flow of values must, therefore, be evaluated at the landscape level. This requires that models such as FORECAST be incorporated into landscape level models such as HORIZON (Kimmins et al., 1999).

5. Conclusion

Timber harvesting has substantially reduced the mass of above-ground CWD compared with natural wildfire disturbance in lodgepole pine forests in the central interior of British Columbia. There were no significant differences in above-ground CWD and total WD between SOH and WTH sites, but there was a significant difference in the mass of FWD between these two types of harvesting. WD on the harvested sites decays more rapidly and persists for less time due to its smaller size and closer contact with the ground, compared with those on the fire-killed sites. Below-ground WD is an important component of total WD in terms of its mass loadings and associated nitrogen fixation activities. It should be given greater consideration in future investigations of the role of WD, particularly in the dry interior forests of British Columbia.

Both measured and simulated nutritional impacts of timber harvesting were within the simulated range of impacts caused by the wildfire defined in this study. They were similar to the simulated long-interval, low-severity wildfire regimes. Either of the current timber harvesting methods (SOH or WTH) can maintain long-term site productivity in the study area if rotations of 80-120 years are used. Shorter rotations should use SOH. Because of lack of validation, application of these simulation results must be cautious and adaptive.

This research also demonstrates that the combination of field measurement with ecosystem simulation is a useful and effective approach for evaluating sustainability of long-term forest productivity.

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The concept of forest sustainability dates from centuries ago, although the understanding of sustainable forest management (SFM) as an instrument that harmonizes ecological and socio-economic concerns is relatively new. The change in perspective occurred at the beginning of the 1990s in response to an increased awareness of the deterioration of the environment, in particular of the alarming loss of forest resources. The book collects original case studies from 12 different countries in four continents (Africa, America, Asia and Europe). These studies represent a wide variation of experiences from developing and developed countries, and should clarify the current status of SFM worldwide and the problems associated with its implementation.

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