TRENDS IN GROWTH AND SOIL NUTRIENTS FOLLOWING FIRE AND LOGGING

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ABSTRACT

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Keywords: boreal forest, calcium, carbon, clearcut, compound disturbance, conifer, deciduous, harvesting intensity, meta-analysis, mixedwood, nitrogen, phosphorus, potassium, soil nutrient dynamics, stand development, stoichiometry, temperate forest.

Understanding the impact of natural and anthropogenic disturbance on soil fertility and tree growth is critical to the sustainability of forest management, yet there remains much uncertainty regarding how both harvesting and wildfire affect soil nutrient dynamics, especially over several decades and in varying overstory types. Historically, wildfire has been the dominant stand-replacing disturbance and an important mechanism of ecosystem renewal. However, intensive forest harvesting is replacing fire as the primary disturbance in many parts of the world, sparking concerns about nutrient depletion and decreased site productivity associated with biomass removals.

I conducted a global meta-analysis of northern forest ecosystems to examine the effects of forest harvesting on total concentrations and stoichiometric ratios of soil carbon ([C]), nitrogen ([N]), and phosphorus ([P]) relative to natural, uncut control stands, and whether these effects differed as a function of harvest intensity, soil depth, overstory type, and time since harvesting. I then used an age chronosequence from 7- to 33-years-old to examine and compare the effects of clearcut harvesting and fire on soil nutrient concentrations and tree growth in three predominant upland boreal stand types (dominated by deciduous or coniferous trees, or a combination of both) during early stand development.

The results of the meta-analysis indicated that harvesting negatively affects [C], [N], and [P] in the forest floor soil layer, but has positive or neutral effects on the mineral soils layer, except for when it is coupled with fire disturbance (through post-fire salvage logging or prescribed burn following harvest), which resulted in strong, negative effects on mineral soil [C] and [N]. The negative effect of harvesting on forest floor nutrients increased with harvesting intensity. Time since harvesting had a positive effect on soil [C] and [N], but less so for [P], which likely requires more time to recover given its reliance on inputs from mineral weathering.

Our chronosequence study also highlighted the important role of stand age (i.e. time since disturbance). Although fire resulted in more dramatic effects on soil nutrient concentrations and stand basal area than harvesting in the 7-year-old stands, these differences converged in the 15- and 33-year-old stands. Similar to the meta-analysis, the effects of disturbance were most profound in the forest floor layer, and temporal trends differed between biologically controlled nutrients (C and N), which recovered rapidly and linearly, and nutrients that are more geochemically controlled (P, K, and Ca).

The results of both studies indicated that conifer stands are more sensitive to nutrient loss following disturbance than deciduous stands, and mixedwood stands are intermediate. Our findings highlight the importance of harvest intensity and rotation length on long-term soil nutrient health when managing northern forest ecosystems, particularly in conifer stands.

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NOTE TO THE READER

Each of the two chapters herein have been prepared as separate manuscripts for submission to publication. Thus, there may be some overlap in terms of definitions and descriptions. In addition, the plural form has been used to describe procedures and findings, rather than the singular form, since the manuscripts developed from each chapter were written with myself as primary author and other committee members as co-authors. Chapter 1 has been submitted to Journal of Applied Ecology and Chapter 2 is being prepared for submission to Ecological Applications.

CHAPTER ONE: INTENSIVE FOREST HARVESTING INCREASES SUSCEPTIBILITY OF NORTHERN FOREST SOILS TO NUTRIENT LOSS – A META-ANALYSIS

Introduction

In recent decades, exponential human population growth combined with peak production of fossil fuels have placed increasing pressure on worldwide forests to meet human needs, leading to intensified utilization of forest resources in many parts of the globe (Murray and King 2012, Hansen et al. 2013, Pan et al. 2013, Hoekstra and Wiedmann 2014). Forest products are an important source of renewable energy, building materials, food, and more, but forests also provide essential ecosystem services including clean air and carbon (C) sequestration. Global forest C stocks are estimated at 861 ± 66 Pg C, with approximately 383 ± 30 Pg C, or ~44%, sequestered in forest soils (Pan et al. 2011). Furthermore, anthropogenic nitrogen (N) deposition is increasing at exponential rates, posing significant risks to environmental and human health throughout the globe in geographical areas that are exposed to agricultural and industrial sources of nitrogen-containing waste (Galloway et al. 2008, Elser et al. 2009). Through canopy interception and retention, forests provide an important sink for anthropogenic N (Fenn et al. 2000). However, it remains unclear whether managed forests are equivalent to natural forests in terms of their ability to provide ecosystem services such as C and N storage. Moreover, intensive forest management regimes, such as whole-tree harvesting, which remove greater amounts of nutrients from the site in forest residues, are not fully understood in terms of impacts on forest ecosystem function, yet there is considerable concern that they will cause nutrient depletion (Vanguelova et al. 2010, Achat et al. 2015a).

Therefore, increasing our empirical understanding of the effects of harvesting on soil nutrient dynamics in forests is essential.

Interest in understanding the impacts of intensive forest harvesting practices began in the early days of mechanized harvesting, approximately 40 years ago; often with a particular emphasis on soil nutrient budgets (e.g. Weetman and Webber 1972, White 1974, Aber et al. 1978), since they are a key indicator of site fertility and ecosystem productivity (Huston and Wolverton 2009). In particular, researchers have sought to understand how intensive forest harvesting (e.g., clearcutting) affects the C and N budgets of forest soils (Raich 1983, Burger and Pritchett 1984, e.g. Mattson and Swank 1989, Carter et al. 2002, Clarke et al. 2015). Harvest intensity ranges from partial removal of the overstory in partial harvesting systems (PH) to complete removal of the overstory with branches and foliage left on site, i.e., stem-only harvesting (SOH), or complete removal of the overstory, including branches and foliage, i.e., whole-tree harvesting (WTH) (also called biomass harvesting). As harvest intensity increases from PH to WTH, successively greater amounts of forest residues are removed from the site, which may cause greater nutrient depletion. In addition, many managed forests experience compound disturbances involving both harvesting and fire; for example, prescribed burning of a site following harvest, or salvage logging following fire (HF). These compound disturbances are increasingly common due to the growing frequency and severity of forest fires at northern latitudes (Westerling et al. 2006, Boulanger et al. 2013), and may affect soil nutrient properties more significantly than either harvesting or fire alone (Kishchuk et al. 2015).

By removing some or all of the overstory canopy, forest harvesting may influence microclimate and alter plant-soil interactions in ways that potentially cause losses of nutrients and may affect whether forest soils are a net source or sink of atmospheric C (Jandl et al.

2007). For example, removal of the overstory by forest harvesting may raise soil temperatures and increase decomposition rates, potentially causing greater release of C by heterotrophic respiration (Covington 1981), or increased leaching of dissolved organic C and N, as well as ammonium (NH_4^+) and nitrate (NO_3^-) (Nieminen 2004, Jerabkova et al. 2011). Losses of N via nitrate leaching following harvesting may deplete base cations, since the latter are mobilized by the hydrogen ions released in the process of nitrate formation, which promotes their loss and may reduce site productivity (Vitousek et al. 1979). Fewer studies have investigated the response of phosphorus (P) to harvesting, but this knowledge is also essential since, like N, P limits productivity; not only in tropical ecosystems with highly weathered soils (Walker and Syers 1976, Vitousek and Farrington 1997, Hedin et al. 2003), but also in the younger, post-glacial soils found primarily in temperate and boreal ecosystems (Chapin et al. 1994). Phosphorus limitation may become more prevalent as global change processes increase the abundance of C and N relative to P through atmospheric deposition and anthropogenic emissions (Vitousek et al. 2010, Yuan and Chen 2015). Clearcutting removes significant portions of the living vegetation P pool, and this effect may be amplified in WTH compared to SOH. For example, in a mature temperate hardwood forest, stem wood and bark were found to contain 22% and 9% of the aboveground biomass P pool, respectively, while branches, twigs, and foliage were found to account for 56%, 1%, and 12%, respectively (Yanai 1998), meaning that the amount of P exported in residues during WTH would be twice or more than that of SOH. Similar to C and N, forest harvesting may also cause losses of P via leaching from higher to lower soil layers and in runoff exports (Yanai 1998, Nieminen 2004).

Though forest harvesting can result in overall losses of C and nutrients, the release of organically bound nutrients may also cause a short-lived flush of plant-available forms of nutrients (i.e. the "assart effect") that benefits site productivity in early stand development (Simard et al. 2001, Jerabkova et al. 2011). Removal of overstory biomass can also increase light and moisture availability, and any of these factors can enable rapid colonization by understory plant species with high turnover rates and therefore high inputs of litter C, and to a lesser extent N. Post-clearcut sites may favour regeneration of vascular understory plants with high turnover rates even more than sites re-establishing after fire (Hart and Chen 2008). Biological fixation by post-harvest pioneering vegetation can also enable significant inputs of N, which in turn can increase C sequestration (Johnson and Curtis 2001, Gundale et al. 2011). Depending on site conditions, rapid regeneration of pioneer tree species and advanced regeneration following harvesting may also contribute significantly to C and N inputs through litterfall and root turnover (Bradley et al. 2001, Fleming et al. 2006, Yuan and Chen 2010). However, whether these or other mechanisms enable recovery of P losses following forest harvesting is poorly understood. Unlike C and N, phosphorus is largely geochemically controlled, with its primary source being mineral weathering rather than biotic controls (Walker and Syers 1976, Vitousek and Farrington 1997). Consequently, while soil P is positively associated with soil C and N, it increases more slowly (Cleveland and Liptzin 2007), therefore the recovery of P from forest harvesting may require significantly more time than that of C or N.

Despite the abundance of studies reporting the effects of forest harvesting on soil fertility it remains unclear whether harvesting depletes soil nutrients, largely due to divergent findings in the literature. For example, several studies have concluded that WTH drastically reduces soil nutrients over time (Kaarakka et al. 2014, Mack et al. 2014), while others have found that SOH increases soil nutrients (Kishchuk et al. 2015). These discrepancies may result from differing levels of biomass removal intensity (Jones et al. 2011); however, some studies that have reported decreases in nutrients from harvesting report no differences between harvest intensities (Jerabkova et al. 2011, Slesak et al. 2011). Soil nutrient responses to harvesting also depend on the particular nutrient (Vanguelova et al. 2010, Huang et al. 2013, Grand et al. 2014) and appear to be strongly influenced by overstory composition (Jerabkova et al. 2011) and by soil layer and depth (Achat et al. 2015b). Thus, confounding factors such as soil layer (Moreno-Fernandez et al. 2015), harvest intensity, time elapsed since disturbance (Achat et al. 2015b), local site conditions - such as stand type (Johnson and Curtis 2001, Jerabkova et al. 2011), and differing experimental design appear to underlie much of the controversy.

In this paper we conduct a meta-analysis to explore the overall effect of harvesting on soil nutrient dynamics, and whether nutrient responses differ according to soil layer, harvest intensity, overstory type, and time since harvesting, focusing on northern forests (i.e. temperate and boreal), since they are driven by similar natural disturbance regimes and soil formation factors. While several reviews and meta-analyses have highlighted global trends in harvesting effects, focusing primarily on the response of C or N pools, or both (Johnson and Curtis 2001, Jerabkova et al. 2011, Achat et al. 2015a, Achat et al. 2015b, Clarke et al. 2015), here, we build on previous studies by focusing on soil C and N concentrations and their stoichiometric ratios (rather than pools), and by including data on soil P. We will also analyze a broader range of biomass removal methods and disturbance intensities, including SOH and

WTH, as well as partially harvested stands and those that have experienced compound disturbances involving fire and harvesting (e.g. salvage-logging following wildfire or prescribed burn following harvesting). Specifically, our objectives are to: a) test the effects of forest harvesting on soil C, N, and P concentrations and C:N:P ratios using the natural log response ratio (ln*RR*), which is measured as the natural logarithm of the ratio of C, N, and P concentrations and C:N:P in harvested stands to those of control stands, and b) test whether ln*RR* differs as a function of soil layer, harvest intensity, overstory type, and time since harvesting.

Methods

Data collection

We searched ISI Web of Science and Google Scholar for publications that reported the effects of forest harvesting on soil C, N, and P concentrations and ratios relative to natural, uncut stands. We used various combinations of the following search terms: 'forest harvesting', 'whole-tree harvesting', 'clear-cutting', 'stem-only harvesting', 'forest management', 'harvest intensity', 'soil nutrients', 'soil nutrient stoichiometry', 'carbon', 'nitrogen', or 'phosphorus'. We looked for additional suitable studies by following citations from relevant publications, including related meta-analyses and reviews (Johnson and Curtis 2001, Jerabkova et al. 2011, Achat et al. 2015a, Achat et al. 2015b, Clarke et al. 2015). Publications that met the following criteria were included: 1) measurements from treatment stands and from natural, uncut reference stands were reported. In some cases the control measurement was taken prior to treatment at the same site (many studies on forest harvesting use WTH stands as the treatment group and SOH as the control and, thus, were excluded), 2) the harvesting treatment (i.e. intensity of biomass removal) was fully described, 3) the time elapsed since harvesting treatment was given, 4) a description of species composition was provided (both pre- and post-treatment species composition in cases where measurements came from the same site before and following disturbance, and for both treatment and reference stands in other cases, 5) experimental location was given, and 6) sample size was reported. We focused on harvesting effects in northern forests since they represented the vast majority of studies found in our literature search, and since temperate and boreal forests are more similar in terms of natural disturbance regimes and pedogenesis than tropical forests. These criteria resulted in a total of 610 observations from 45 studies. The year of publication for studies included in our meta-analysis ranged from 1982-2015.

We collected the mean values of soil C, N, and P concentrations, pools, and ratios from each study as well as study and site characteristics, including soil layer and sampling depth, harvesting treatment (PH, SOH, WTH, HF), overstory type (broadleaf, mixedwood, or conifer), time since harvesting treatment (TSH), and study location. Studies were rejected when there were no control group measurements or when sample size was not reported; the latter only occurred in one case. When a selected publication only presented their results graphically, we used Plot Digitizer (http://plotdigitizer.sourceforge.net/) to digitally extract means and, if reported, sample variances. A majority of studies included in our database did not explicitly report stoichiometric ratios, in which case we calculated them based on the reported C, N, and P concentrations or pools from each individual study. Due to insufficient data for mineral soil observations, we were only able to analyze the effects of harvesting on [P], C:P, and N:P for the forest floor soil layer.

Data analysis

We first standardized units for all observations of soil C, N, and P concentrations to grams per kilogram (g kg $^{-1}$) and calculated C:N:P ratios using all available observations of both concentrations and pools. We measured the response of each soil nutrient parameter to harvesting disturbance using the natural logarithm of response ratio (ln*RR*) as our metric of "effect size" (Hedges et al. 1999).

$$\ln RR = \ln\left(\overline{X}_t / \overline{X}_c\right) = \ln \overline{X}_t - \ln \overline{X}_c \tag{1}$$

where $\overline{X_t}$ and $\overline{X_c}$ are the reported mean for each soil nutrient parameter in harvested treatment and control treatment, respectively.

We then used a fixed effects model in R (version 3.2.4, R Core Team 2016) with the package *metafor* and the function *rma.uni* to see whether the responses of soil [C], [N], [P], and C:N:P to harvesting differ depending on soil layer, harvest intensity, overstory type, and time since harvesting (Viechtbauer 2010). Since our data set was not sufficiently large to test all treatment combination levels amongst our categorical explanatory variables, we used bivariate models, which enabled us to test the influence of each variable separately. We also included a weighting function in our model to account for variability among studies with respect to sample size and measurement error. Following previous work (Pittelkow et al. 2015), we weighted studies by replication rather than by study variance, since the latter was not reported for a significant number of studies included in our database, thus enabling us to assign influence to each study based on the amount of replication without requiring sampling variance. According to this approach, we used the following equation, which assigns greater weight to studies with higher replication:

$$wi = \left(n_{contr} \times n_{treat}\right) \div \left(n_{contr} + n_{treat}\right) \tag{2}$$

While meta-analytic models generally assume independence between observations from included studies, many of the studies in our dataset compared multiple treatment groups with a single, common control group, making it unlikely that our data meets this assumption. Therefore, in cases where more than one observation from a given study was included in the same category, we divided the weight by the total number of observations from that study:

$$wi = \left(\left(n_{contr} \times n_{treat}\right) \div \left(n_{contr} + n_{treat}\right)\right) \div n_{total} \qquad (3)$$

Dividing the assigned weight (Eq. 2) by the total number of observations within each study (Eq. 3) both accounts for non-independence (i.e. reduces autocorrelation) and reduces the weight of more comprehensive studies (i.e. distributes the relative influence of each study more evenly) (Pittelkow et al. 2015). For example, when using Eq. 2, the weight of the study with the most replication was 60 times that of the study with the least replication, whereas when using Eq. 3, the study with maximum replication was assigned a weight only 1.38 times that of the study with the least replication. We also ran our models using weights by replication without dividing by the total number of observations, and assigning equal weight to all observations ($wi = 1$). We observed qualitatively consistent trends among these three weighting approaches; however, in this paper we report the results obtained by weighting effect size estimates by replication and dividing by the total number of observations (Eq. 2).

Results

Overall, forest floor C, N, and P concentrations were significantly, negatively affected by harvesting, with ln*RR* of -0.08, -0.14, and -0.19, respectively (Fig. 1.1a-c, Table 1.1). By contrast, [C], [N], and [P] in the mineral soil did not differ between harvested and unharvested stands, nor did the overall effect of harvesting with both soil layers pooled – except for [C], for which the negative effect persisted (Fig. 1.1a-c). Forest floor C:N ratio was also significantly, negatively affected by harvesting, but the opposite trend occurred in the mineral soil, with a significant positive response of C:N in harvested vs. control stands (ln*RR* of -0.04 and 0.05, respectively) (Fig. 1.1d). The positive effect of harvesting on C:N remained when both soil layers were analyzed together (Fig. 1.1d). Despite a relatively small number of observations, forest floor C:P was significantly positively affected by harvesting (ln*RR*: 0.04), whereas forest floor N:P did not differ between harvested and control stands (Fig. 1.1e-f).

The negative effect of harvesting on forest floor nutrient concentrations was also observed when examining harvest intensity; however, the effect was primarily non-significant, except for [C], for which there was a general negative effect of increasing harvest intensity, with WTH resulting in the greatest negative response, followed by SOH, and PH showing a significantly positive response (ln*RR*: -0.22, -0.03, and 0.05, respectively) (Fig. 1.2a, Table 1.2). We found a similar negative relationship between harvest intensity and forest floor [N] and [P], but only WTH had a significantly negative effect on forest floor [N] and SOH on forest floor [P] (ln*RR*: -0.2) (Fig. 1.2b-c). By contrast, the effect of SOH and WTH on mineral soil [C] was significantly positive (ln*RR*: 0.1 and 0.06, respectively) (Fig. 1.2d), and SOH also had a significant positive effect on mineral soil [N] (ln*RR*: 0.1) (Fig. 1.2e). Unlike harvesting alone, the compound disturbance of harvesting and fire had a very strong negative effect on mineral soil [C] and [N] (ln*RR*: -0.3 and -0.23, respectively) (Fig. 1.2d-e). Mineral soil [C] and [N] did not differ significantly between partially harvested stands and control stands (Fig. 1.2d-e). Partial harvesting had a significant positive effect on forest floor C:N whereas WTH had a significant negative effect (ln*RR*: 0.13 and -0.07, respectively), and neither SOH nor HF had a significant effect. Forest floor N:P did not differ between control stands and PH, SOH, or WTH stands (Fig. 1.2f-g). Mineral soil C:N showed a significant positive response to all harvest intensities compared to the control stands (Fig. 1.2h).

Our results also demonstrated a strong influence of overstory type on the responses of C, N, and P concentrations and ratios to harvesting. In the forest floor, this effect was most evident in conifer stands, in which there was a strong negative effect of harvesting on [C], [N], [P], and C:N (ln*RR*: -0.16, -0.18, -0.24 and -0.06, respectively). By contrast, forest floor N:P was positively affected by harvesting in conifer stands and forest floor [C] was positively affected in deciduous and mixedwood stands (ln*RR* of 0.08, 0.03, and 0.05, respectively) (Fig. 1.3a-c and 1.3f-g, Table 1.3). Forest floor [N], [P], C:N and N:P did not differ significantly between harvested and control stands. In the mineral soil there was a reverse trend in the effect of harvesting. In conifer stands, mineral soil [C], [N], and C:N were significantly, positively affected by harvesting (ln*RR*: 0.12, 0.06, and 0.06, respectively), whereas there was a significant negative effect of harvesting on mineral soil [C] and [N] in deciduous stands (ln*RR*: -0.26 and -0.13, respectively), and a marginally negative effect on mineral soil C:N in deciduous stands (Fig. 1.3d-e and 1.3h). Harvesting had no significant effects on either forest floor or mineral soil [N] and C:N (Fig. 1.3b, 1.3e-f, and 1.3h).

We found a significant, positive effect of time since harvesting on C and N concentrations in both the forest floor and mineral soil (ln*RR*: 0.004, 0.008, 0.005 and 0.008, respectively). The C:N ratio in both soil layers responded negatively to time since harvesting, contrasting with forest floor N:P and C:P ratios, which increased significantly and also displayed the greatest magnitude of effect in response to time since harvesting (ln*RR*: -0.002, -0.003, 0.05, and 0.03, respectively). Forest floor [P] did not differ significantly with time since harvesting (Fig. 1.4 and Fig. 1.5, Table 1.4)

Table 1.1. Overall effects of harvesting on soil C, N, and P concentrations and ratios.

Parameter	Predictor	ln*RR*	95% Confidence Intervals		n	*P*
			Lower	Upper		
[C]	Overall	-0.04	-0.05	-0.03	148	**<0.0001**
	Forest floor	-0.08	-0.10	-0.07	39	**<0.0001**
	Mineral soil	-0.01	-0.02	0.01	109	0.218
[N]	Overall	-0.03	-0.07	0.02	161	0.238
	Forest floor	-0.14	-0.23	-0.05	52	**0.003**
	Mineral soil	0.01	-0.04	0.06	109	0.798
[P]	Overall	-0.07	-0.16	0.03	27	0.178
	Forest floor	-0.19	-0.33	-0.04	20	**0.012**
	Mineral soil	0.03	-0.10	0.16	7	0.652
C:N	Overall	0.02	0.01	0.03	240	**0.001**
	Forest floor	-0.04	-0.06	-0.02	105	**<0.0001**
	Mineral soil	0.05	0.04	0.07	135	**<0.0001**
N:P	Overall	nd	nd	nd	nd	nd
	Forest floor	-0.03	-0.09	0.04	23	0.383
	Mineral soil	nd	nd	nd	nd	nd
C:P	Overall	nd	nd	nd	nd	nd
	Forest floor	0.04	0.02	0.06	11	**<0.0001**
	Mineral soil	nd	nd	nd	nd	nd

Abbreviations: [C] – total carbon concentration, [N] – total nitrogen concentration, [P] – total phosphorus concentration, C:N – carbon to nitrogen ratio, N:P – nitrogen to phosphorus ratio, C:P – carbon to phosphorus ratio. Significance of bold values is at $P < 0.05$.

Table 1.2. Effects of harvest intensity ($H_i = 1, 2\ldots4$) on soil C, N, and P concentrations and ratios.

Parameter	Predictor	ln*RR*	95% Confidence Intervals		n	*P*
			Lower	Upper		
Forest Floor						
[C]	Partial	0.05	0.02	0.09	9	**0.003**
	SOH	-0.03	-0.05	-0.01	22	**0.011**
	WTH	-0.22	-0.25	-0.20	6	**<0.0001**
	HF	nd	nd	nd	nd	nd
[N]	Partial	0.02	-0.24	0.27	11	0.906
	SOH	-0.12	-0.26	0.02	27	0.094
	WTH	-0.21	-0.36	0.07	12	**0.004**
	HF	nd	nd	nd	nd	nd
[P]	Partial	nd	nd	nd	nd	nd
	SOH	-0.20	-0.38	-0.03	13	**0.022**
	WTH	-0.14	-0.45	0.17	5	0.371
	HF	nd	nd	nd	nd	nd
C:N	Partial	0.13	0.05	0.21	12	**0.001**
	SOH	-0.02	-0.05	0.02	46	0.430
	WTH	-0.07	-0.10	-0.05	41	**<0.0001**
	HF	-0.06	-0.16	0.03	6	0.195
N:P	Partial	0.06	-0.08	0.19	5	0.397
	SOH	0.05	-0.05	0.15	9	0.319
	WTH	0.04	-0.11	0.18	6	0.619
	HF	nd	nd	nd	nd	nd
Mineral Soil						
[C]	Partial	0.05	-0.01	0.10	17	0.084
	SOH	0.10	0.08	0.12	40	**<0.0001**
	WTH	0.06	0.03	0.09	25	**<0.0001**
	HF	-0.30	-0.32	-0.27	27	**<0.0001**
[N]	Partial	0.00	-0.18	0.18	12	0.996
	SOH	0.10	0.02	0.17	42	**0.013**
	WTH	0.05	-0.04	0.15	28	0.269
	HF	-0.23	-0.33	-0.12	27	**<0.0001**
C:N	Partial	0.11	0.06	0.16	28	**<0.0001**
	SOH	0.07	0.04	0.10	45	**<0.0001**
	WTH	0.03	0.02	0.05	45	**0.000**
	HF	0.10	0.04	0.16	17	**0.001**

Abbreviations: [C] – total carbon concentration, [N] – total nitrogen concentration, [P] – total phosphorus concentration, C:N – carbon to nitrogen ratio, N:P – nitrogen to phosphorus ratio, C:P – carbon to phosphorus ratio. SOH – stem-only harvesting, WTH – whole-tree harvesting, HF – harvesting and fire disturbance. Significance of bold values is at $P < 0.05$.

Table 1.3. Effects of overstory type ($O_i = 1, 2, 3$) on soil C, N, and P concentrations and ratios.

Parameter	Predictor	ln*RR*	95% Confidence Intervals		n	*P*
			Lower	Upper		
Forest Floor						
[C]	DEC	0.03	-0.01	0.07	7	0.117
	MW	0.05	0.02	0.08	14	**0.002**
	CON	-0.16	-0.18	-0.14	16	**<0.0001**
[N]	DEC	-0.07	-0.27	0.13	14	0.502
	MW	-0.05	-0.30	0.20	15	0.708
	CON	-0.18	-0.30	-0.07	21	**0.002**
[P]	DEC	-0.06	-0.29	0.17	7	0.637
	MW	nd	nd	nd	nd	nd
	CON	-0.24	-0.44	-0.03	8	**0.022**
C:N	DEC	0.07	-0.01	0.15	10	0.083
	MW	0.05	-0.02	0.12	20	0.194
	CON	-0.06	-0.08	-0.04	75	**<0.0001**
N:P	DEC	-0.02	-0.14	0.10	9	0.752
	MW	nd	nd	nd	nd	nd
	CON	0.08	0.00	0.16	11	**0.059**
Mineral Soil						
[C]	DEC	-0.26	-0.29	-0.24	19	**<0.0001**
	MW	0.03	-0.01	0.06	22	0.157
	CON	0.12	0.10	0.14	68	**<0.0001**
[N]	DEC	-0.13	-0.23	-0.04	19	**0.004**
	MW	0.12	-0.10	0.33	23	0.292
	CON	0.06	0.00	0.12	67	**0.050**
C:N	DEC	-0.04	-0.08	0.00	19	0.082
	MW	-0.03	-0.10	0.03	24	0.306
	CON	0.06	0.05	0.07	92	**<0.0001**

Abbreviations: [C] – total carbon concentration, [N] – total nitrogen concentration, [P] – total phosphorus concentration, C:N – carbon to nitrogen ratio, N:P – nitrogen to phosphorus ratio, C:P – carbon to phosphorus ratio. DEC – deciduous stand, MW – mixed-wood stand, CON – conifer stand. Significance of bold values is at $P < 0.05$.

Table 1.4. Effects of time since harvesting on soil C, N, and P concentrations and ratios.

Parameter	ln*RR*	95% Confidence Intervals		n	*P*
		Lower	Upper		
Forest Floor					
[C]	0.004	0.003	0.005	39	**<0.0001**
[N]	0.008	0.000	0.015	52	**0.051**
[P]	0.007	-0.016	0.029	20	0.559
C:N	-0.002	-0.003	0.000	105	**0.038**
N:P	0.048	0.024	0.071	20	**<0.0001**
C:P	0.028	0.022	0.034	11	**<0.0001**
Mineral Soil					
[C]	0.005	0.004	0.005	109	**<0.0001**
[N]	0.008	0.004	0.011	109	**<0.0001**
C:N	-0.003	-0.004	-0.002	135	**<0.0001**

Abbreviations: [C] – total carbon concentration, [N] – total nitrogen concentration, [P] – total phosphorus concentration, C:N – carbon to nitrogen ratio, N:P – nitrogen to phosphorus ratio, C:P – carbon to phosphorus ratio. Significance of bold values is at $P < 0.05$.

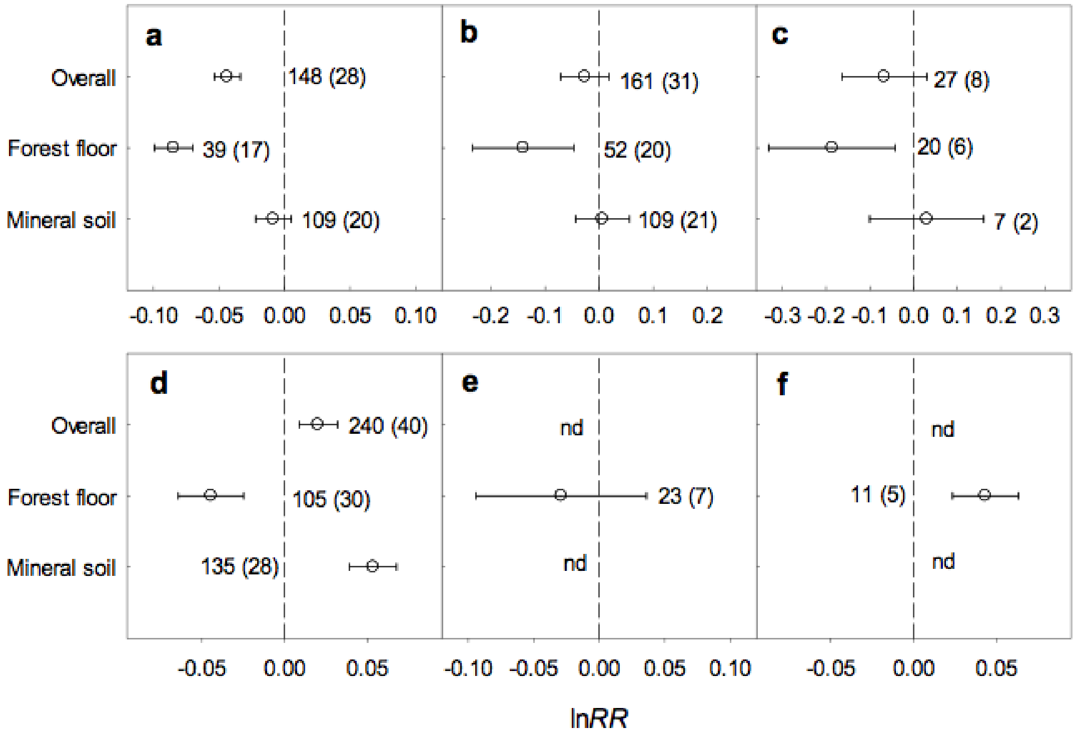

Figure 1.1. Effect size of harvesting (ln*RR*) on soil nutrient parameters overall and as a function of soil layer (forest floor or mineral soil): (**a**) total carbon concentration ([C]), (**b**) total nitrogen concentration ([N]), (**c**) total phosphorus concentration ([P]), (**d**) total carbon to total nitrogen ratio (C:N), (**e**) total nitrogen to phosphorus ratio (N:P), (**f**) total carbon to phosphorus ratio (C:P). Values are mean ± 95% confidence intervals of natural log response ratio between harvested and control (unharvested) stands. Number of observations are listed beside each variable without parentheses, number of studies are in parentheses. "nd" indicates no data.

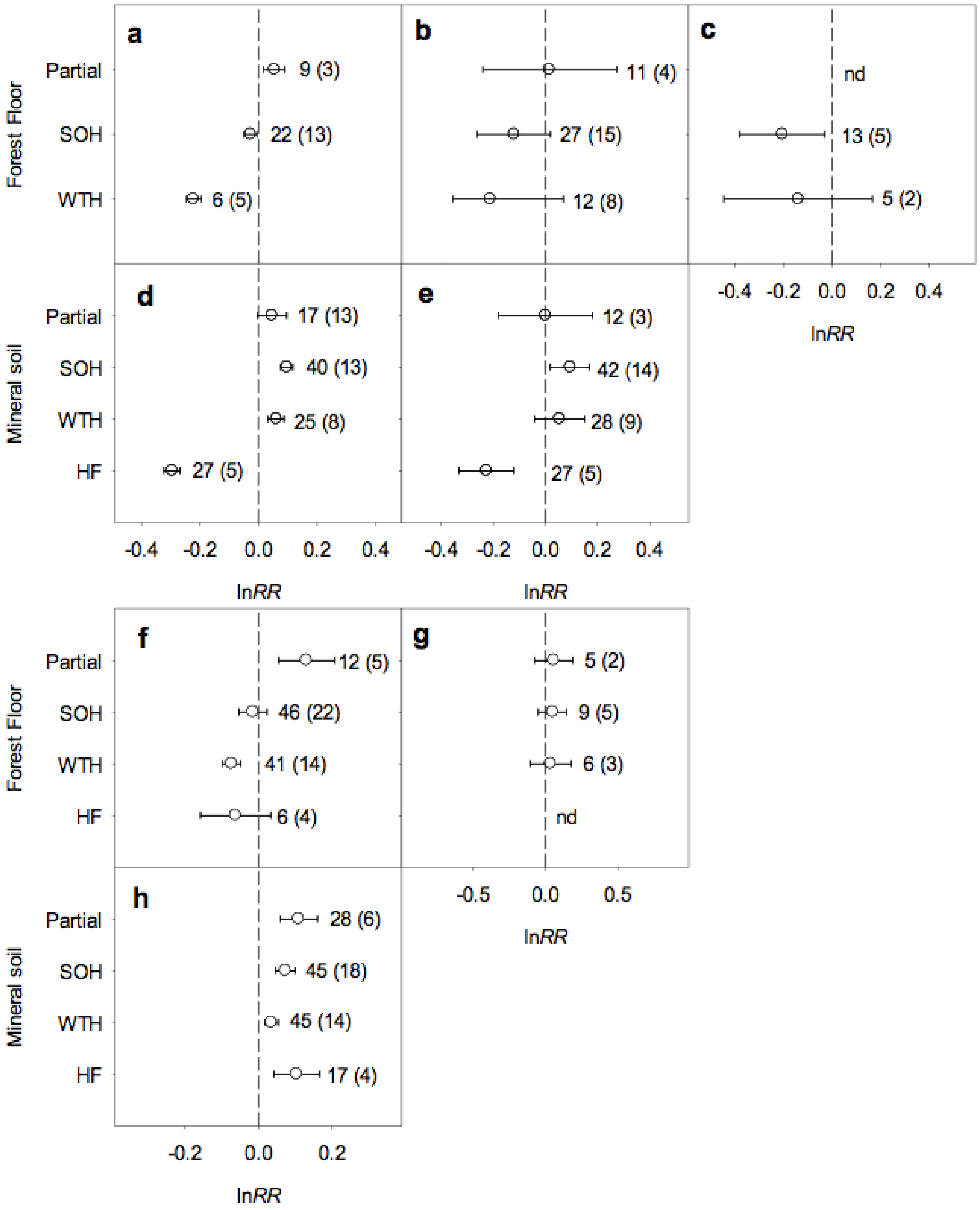

Figure 1.2. Effect size (ln*RR*) of harvesting on soil nutrient concentrations and ratios as a function of harvest intensity: (**a**) forest floor carbon concentration ([C]), (**b**) forest floor nitrogen concentration ([N]), (**c**) forest floor phosphorus concentration ([P]), (**d**) mineral soil carbon concentration ([C]), (**e**) mineral soil nitrogen concentration ([N]), (**f**) forest floor carbon to nitrogen ratio (C:N), (**g**) forest floor nitrogen to phosphorus ratio (N:P), (**h**) mineral soil carbon to nitrogen ratio (C:N). Values are mean ± 95% confidence intervals of natural log response ratio between harvested and control (unharvested) stands. Number of observations are listed beside each variable without parentheses, number of studies are in parentheses. “nd” indicates no data.

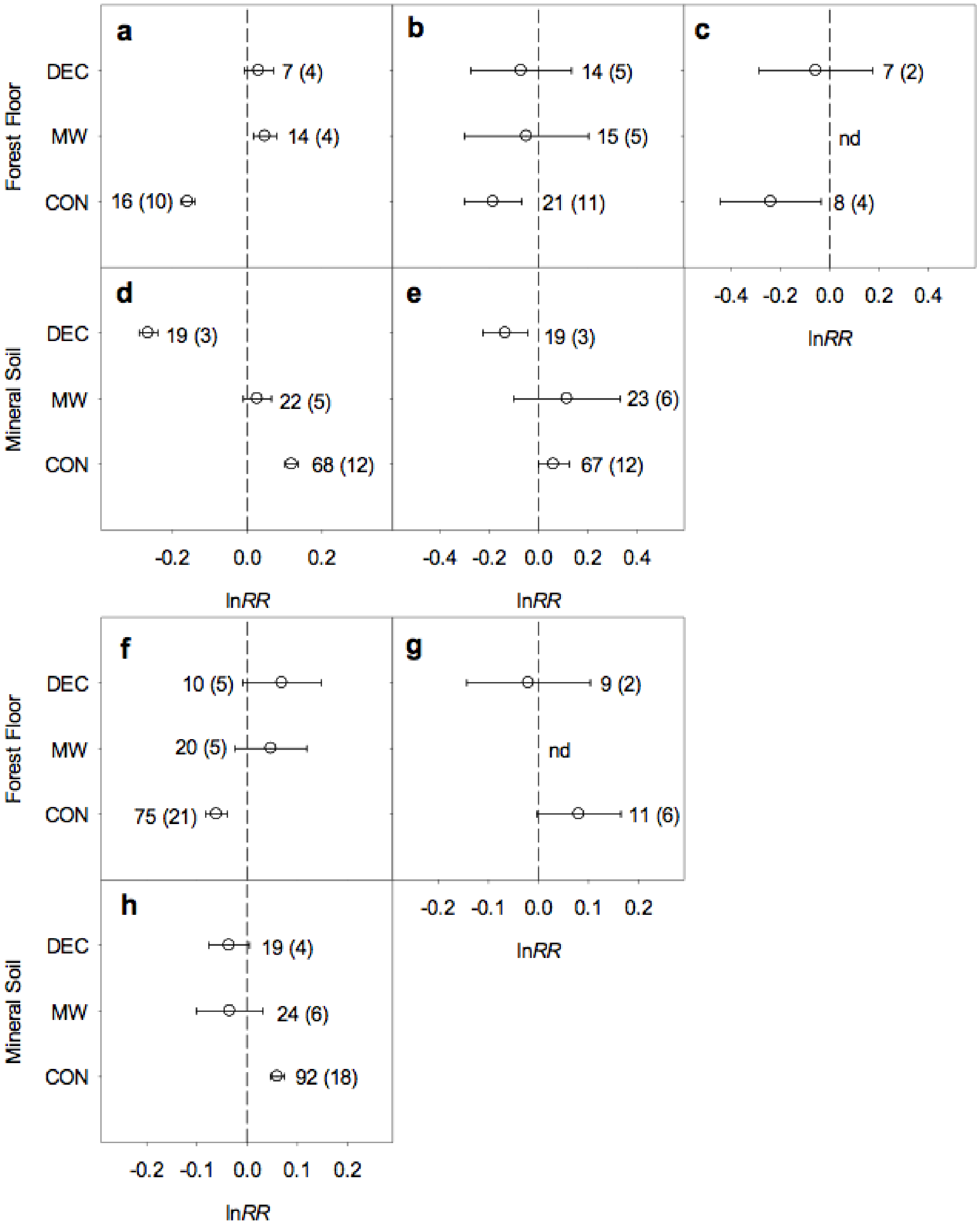

Figure 1.3. Effect size (ln*RR*) of harvesting on soil nutrient concentrations and ratios as a function of overstory type: (**a**) forest floor carbon concentration, (**b**) forest floor nitrogen concentration, (**c**) forest floor phosphorus concentration, (**d**) mineral soil carbon concentration, (**e**) mineral soil nitrogen concentration, (**f**) forest floor carbon to nitrogen ratio, (**g**) forest floor nitrogen to phosphorus ratio, (**h**) mineral soil carbon to nitrogen ratio. Values are mean ± 95% confidence intervals of natural log response ratio between harvested and control (unharvested) stands. Number of observations are listed beside each variable without parentheses, number of studies are in parentheses. "nd" indicates no data.

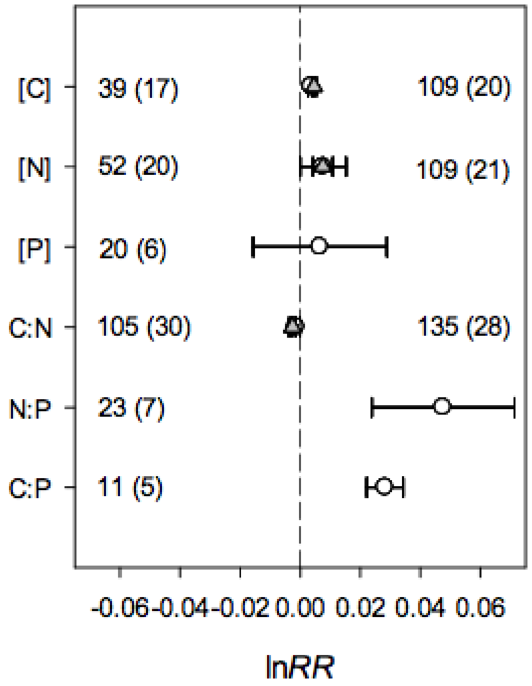

Figure 1.4. Effect size (ln*RR*) as a function of time since harvesting on soil nutrient concentrations and ratios. Circles with no fill represent forest floor response. Triangles with grey fill represent mineral soil response. Values are mean ± 95% confidence intervals of natural log response ratio between harvested and control (unharvested) stands. Number of forest floor observations are listed on the left side of each variable, and number of mineral soil observations on the right side, without parentheses, number of studies are beside and in parentheses.

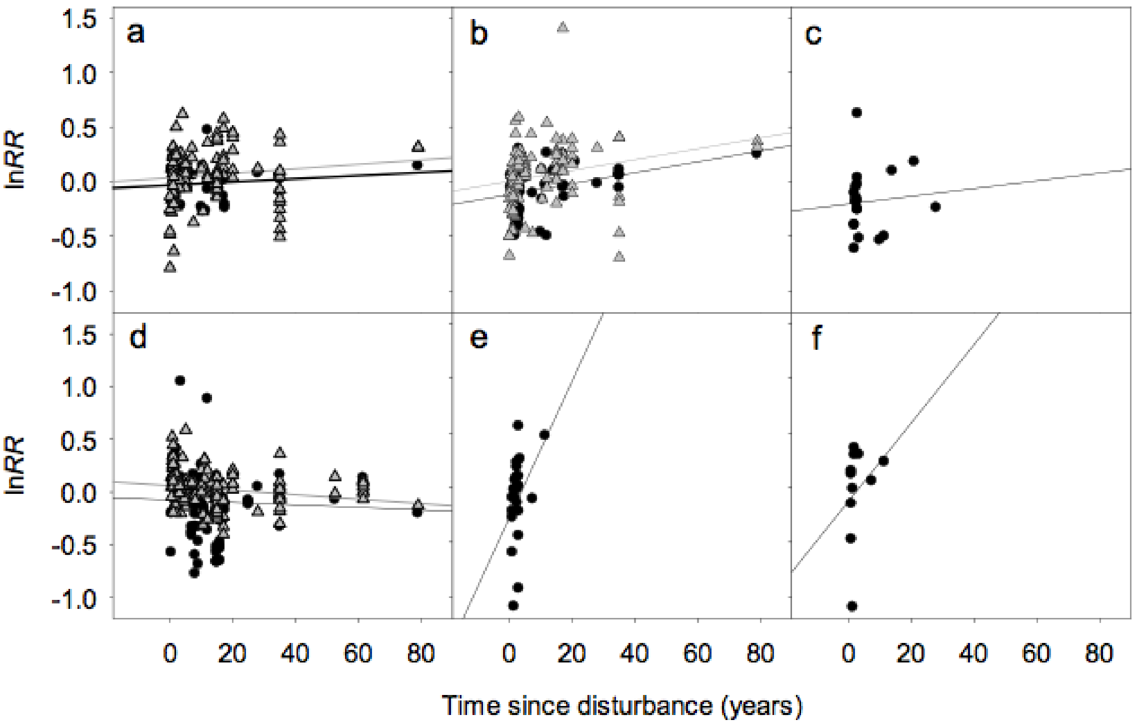

Figure 1.5. Effect size (ln*RR*) as a function of time since harvesting on soil nutrient concentrations and ratios: (**a**) total carbon concentration, (**b**) total nitrogen concentration, (**c**) total phosphorus concentration, (**d**) carbon to nitrogen ratio, (**e**) nitrogen to phosphorus ratio, (**f**) carbon to phosphorus ratio. Circles with black fill represent forest floor response. Triangles with grey fill represent mineral soil response.

Discussion

Our meta-analysis reveals that forest harvesting has a profound effect on soil nutrient dynamics, but that the nature of this effect is highly dependent on soil layer and harvesting intensity, and to a lesser extent, overstory composition type and time since harvesting.

Our analyses show a clear contrast between the effects of harvesting on the forest floor and mineral soil layers, with concentrations of C, N, and P generally being negatively affected by harvesting in the forest floor and positively affected in the mineral soil. Potential mechanisms driving the loss of nutrients from the forest floor of harvested stands include increased soil temperature and decomposition rates, and subsequent increases in heterotrophic respiration and leaching losses from upper to lower soil layers (Covington 1981, Nieminen 2004, Jerabkova et al. 2011). Correspondingly, we found a negative effect of harvesting on the forest floor C:N ratio, whereas the mineral soil C:N ratio was positively affected by harvesting. While the overall negative effect of harvesting on forest floor C, N, and P concentrations was quite clear, mineral soil nutrient concentrations did not differ as much between the harvested and control stands, suggesting mineral soil may be less susceptible to disturbance, and highlighting the role of the forest floor in buffering the effects of microclimate change from underlying soil layers. Further, our results suggest that harvesting may cause greater losses of forest floor C, N, and P than can be compensated for by mineral soil gains by way of vertical redistribution (Fig. 1.1a-c), indicating an overall net loss of nutrients from the soil. This is likely due to the rate of forest floor leaching following overstory removal exceeding the uptake ability of plant and soil biota in the mineral soil below, and subsequent losses of nutrients to very deep mineral layers or waterways (Nieminen 2004).

While harvesting had an overall negative effect on soil nutrient concentrations, this effect varied according to harvesting intensity, as similarly reported by (Achat et al. 2015b), with nutrient losses from the soil increasing with harvest intensity. This was particularly evident for forest floor C concentration, which responded positively to partial harvesting, but increasingly negatively to stem-only and whole-tree harvesting, respectively (Fig. 1.2a). Although a negative trend in forest floor N concentration with increasing harvesting intensity was also apparent (Fig. 1.2b), lack of statistical significance is consistent with (Jerabkova et al. 2011), who, while examining soil N response to partial harvest and clearcutting, found that factors other than biomass removal intensity may be more influential to N dynamics in post-harvested sites. Forest floor P was similarly negatively affected by intensive harvesting, however our meta-data did not include enough observations of the effects of partial harvesting on P concentrations to enable comparison with the negative effects of clearcutting (i.e. SOH and WTH) (Fig. 1.2c). The significant positive response of forest floor C:N to partial harvesting likely reflects the incorporation of well-decomposed C-rich litter and woody residues left behind following partial stand removal, as well as root necromass from stumps (Clarke et al. 2015). By contrast, there was a significant negative response of forest floor C:N to whole-tree harvesting, and we attribute this to increased decomposition and mineralization rates resulting from increased light and soil temperatures associated with whole-tree harvesting due to the more complete exposure of the soil (Covington 1981, Nieminen 2004).

Opposite to the forest floor soil layer, we found evidence that clearcutting (SOH and WTH) had a stronger, positive effect on soil C and N concentrations than partial harvesting in the mineral soil layer, likely due to greater leaching losses and subsequent vertical redistribution from the forest floor resulting from greater harvest intensity. However, our meta-analysis revealed striking negative effects of combined harvest and fire disturbance on mineral soil C and N concentrations, demonstrating that when the two disturbances occur in rapid succession, overall exports of C and N from the soil are greater, since we observed mineral soil gains rather than reductions following all intensities of harvesting disturbance that did not include fire (Fig. 1.2d-e). These results are in agreement with previous observations that compound disturbances reduce soil nutrients more significantly than harvesting alone (Kishchuk et al. 2015). Mineral soil C:N responded positively to all levels of harvest intensity as well as combined harvest and fire disturbance (Fig. 1.2h), likely due to vast inputs of

C to the mineral soil by way of turnover from live and dead roots from the harvested stand and the regenerating stand (Yuan and Chen 2012), as well as vertical redistribution (Achat et al. 2015b).

The influence of harvesting on soil nutrient concentration also varied according to forest overstory species composition, with the greatest negative effects occurring in the forest floor layer of conifer dominated stands (Fig. 1.3a-c). This is most likely caused by differences in chemical characteristics of coniferous versus deciduous tree species. For example, conifer species tend to have lower litterfall and root turnover and lower foliar and root N and P concentrations than deciduous species (McGroddy et al. 2004, Yuan and Chen 2009, 2010). Compared to deciduous stands, conifer stands tend to be more P-deficient (Achat et al. 2013), and conifer tree species are generally more tolerant of nutrient-poor conditions and thus more likely to establish on nutrient scarce sites (Taylor and Chen 2011). Consequently, the forest floor of conifer-dominated stands may be more susceptible to nutrient depletion from harvesting than deciduous or mixedwood stands. However, the response of the mineral soil layer to overstory composition contrasted strongly with the forest floor, where harvesting had a positive effect on mineral soil C and N in conifer stands (likely leached from the forest floor) (Covington 1981, Achat et al. 2015b), and a negative effect on C and N in deciduous stands. The losses of mineral soil N in deciduous stands may reflect greater exports via stream water or leaching to very deep soils not accounted for in our meta-analysis, since these sites are comparatively N-rich. This observation is supported by the work of (Jerabkova et al. 2011), whose meta-analysis of harvesting effects on N found that harvested deciduous forests had higher nitrate concentrations and nitrate flux relative to mixedwood or coniferous forests. Moreover, conifer tree species tend to accumulate more soil organic matter in the forest floor and less in the mineral soil, due to their shallow root systems, while the reverse trend is associated with deciduous trees (Jandl et al. 2007).

Our results show that forest floor and mineral soil C and N concentrations, as well as forest floor N:P and C:P ratios increased with increasing time since harvest (Fig. 1.4 and Fig. 1.5). This likely reflects growing inputs of C and N from regenerating vegetation following harvesting via litterfall, root mortality, understory vegetation turnover, and biological fixation (Johnson and Curtis 2001, Shrestha and Chen 2010). These results confirm that biologically controlled elements, such as C and N, accumulate quickly and efficiently following losses related to harvesting. Although our study revealed significant changes in C and N during recovery from harvesting, the magnitude of this effect was relatively small, likely due to increasing convergence between harvested and control stands over time, overshadowing the effect of time (i.e. stand development) in harvested stands. The exception was forest floor C:P and N:P ratios, which showed a much greater response than our other soil nutrient parameters, indicating that inputs of C and N are of a far greater magnitude than those of P in the first decades following harvesting. However, our data set included many more observations of C and N than of P, which spanned a longer time frame (~0-79 years for the former and ~0-28 years for the latter). Nonetheless, forest floor P concentration did not differ with time since harvesting (Fig. 1.4 and Fig. 1.5), which we attribute to the greater amount of time required for soil P to recover following losses from harvesting exports. Previous work has shown that while P is positively associated with C and N, it accumulates more slowly (Cleveland and Liptzin 2007), likely due to the differing mechanisms by which it is controlled (i.e. geochemical processes such as weathering which operate over longer time scales than many biological processes) (Walker and Syers 1976, Vitousek and Farrington 1997), thus recovery of P in the forest floor following harvesting appears to lag behind that of C and N.

Our results have shown that intensive harvesting methods, i.e., clearcutting, result in significantly greater losses of C, N, and P from forest soils compared with less intensive, partial harvesting methods and that this effect is compounded by harvesting and fire when they occur in rapid succession. However, the effect of harvesting on soil nutrients varied widely according to soil layer, overstory composition, and time since harvest. The strong, negative response of the forest floor to harvesting reflects its heightened sensitivity to land use change, but also its important role as a buffer from disturbance for the underlying mineral soil through vertical redistribution of nutrients (Jandl et al. 2007). Nonetheless, our results clearly show that while the forest floor may act as a nutrient buffer, intensive harvesting, especially when compounded with other disturbances (e.g., fire), can overwhelm the capacity of the soil to retain nutrients, leading to exports of C, N, and P from the system (Kishchuk et al. 2015). In agreement with previous work, our data further indicate that the effects of harvesting diminish with time, since young, rapidly regenerating stands, during early succession, can act as C and N sinks for decades. Thus, ensuring that harvest rotation periods are of a sufficient length in northern forests ecosystems, especially conifer dominated forest stands, may be critical for avoiding net long-term exports of soil C, N, and P, and maintaining forest ecosystem services (Jandl et al. 2007, Achat et al. 2015a, Moreno-Fernandez et al. 2015). Given that many global change processes favour the abundance of C and N, and that they appear better capable of rapidly accumulating than P following harvesting, phosphorus limitation and the decoupling of C and N from P in managed forests may be an increasing concern (Vitousek et al. 2010, Yuan and Chen 2015).

CHAPTER TWO: TEMPORAL TRENDS IN THE EFFECTS OF WILDFIRE AND HARVESTING ON SOIL NUTRIENTS AND TREE GROWTH IN THE BOREAL FOREST

Introduction

Site productivity is central to the long-term economic and ecological sustainability of forest ecosystems. During most of world forest history, fire has been the dominant natural disturbance and an important mechanism of ecosystem renewal (Attiwill 1994). However, throughout many parts of the world, forest harvesting is replacing fire as the primary disturbance (Pan et al. 2013). In managed forests, there is growing concern regarding the effect of nutrient depletion caused by over-harvesting on site productivity (Achat et al. 2015a, Achat et al. 2015b). Moreover, the effects of forest harvesting may be additive to those of fire at the landscape scale, since the frequency, intensity, and severity of forest fires appear to be increasing in temperate and boreal biomes due to global change processes, in spite of intensive forest resource extraction (Bowman et al. 2009, Boulanger et al. 2013).

Both fire and harvesting remove some or all of the forest overstory canopy, which affects site microclimate and plant-soil interactions through reduced light interception and increased surface soil temperatures, which, in turn, can stimulate nutrient decomposition and mineralization rates, leading to increased heterotrophic respiration and leaching losses (Covington 1981, Nieminen 2004). However, the effects of fire and harvesting on soil nutrients also differ in important ways (Johnson and Curtis 2001, Thiffault et al. 2007). During fire events, elemental loss occurs not only via leaching but also by transfer to the atmosphere, either by volatilization or particulate movement, or both, depending largely on the temperature required to volatilize a given element and the temperature reached during combustion

(Raison et al. 1985, Certini 2005). For example, carbon (C) and nitrogen (N) are highly volatile, whereas calcium (Ca) is not volatilized at temperatures typically reached by forest fires, but may still be exported as ash or other particulates by wind and erosion. Phosphorus (P) and potassium (K) require higher temperatures than C and N but lower than Ca. The quantity of elements released to the atmosphere during combustion can vary by orders of magnitude depending on volatility. Elements that are bound within the forest floor and other plant materials tend to volatilize at much lower temperatures (Raison et al. 1985), and their release from compounds can cause a temporary flush of plant-available nutrients for the regenerating forest stand (Simard et al. 2001, Smithwick et al. 2005). Elemental loss during harvesting is more straightforward than that of fire in the sense that exports of nutrients are directly related to the intensity of biomass removal. However, harvesting practices may affect soil nutrients and the development of the regenerating stand through additional mechanisms, such as soil compaction, vegetation management, fertilization, and physical effects related to site preparation (Roberts et al. 2005, Tan et al. 2009).

The effects of fire and harvesting on soil nutrients are further dependent on soil depth (i.e., horizon), tree species composition of the forest overstory, and time since disturbance (Johnson and Curtis 2001, Shrestha and Chen 2010). In terms of soil depth, the uppermost soil horizon, i.e., the forest floor layer, is the most susceptible to the impacts of disturbance since most fine roots, plant tissues, soil biota, and other sources of soil organic matter are concentrated within this layer. Thus, the forest floor experiences the greatest changes in nutrients following harvesting and fire and likely buffers the underlying mineral soil layers by absorbing the brunt of the effects (Achat et al. 2015b, Hume et al. 2016). Overstory composition can also strongly influence the responses of soil nutrients to fire and harvesting disturbance, especially in the forest floor, since coniferous and deciduous trees differ significantly in their litter and foliar chemical characteristics, production, and decomposition rates (Yuan and Chen 2009, Paré et al. 2013). In the boreal forest, deciduous broadleaf tree species tend to have higher growth rates and more rapid turnover of leaf litterfall and fine roots, which tend to be richer in N, K, and Ca than those of coniferous species (Laganière et al. 2010, Yuan and Chen 2010). Moreover, during the past several decades, the relative abundance of broadleaf deciduous tree species has been increasing in the boreal forest due to increasing disturbances such as harvesting, insect outbreaks, and fire (Soja et al. 2007, Laquerre et al. 2009), since these disturbances promote broadleaf tree species that reproduce vegetatively, such as trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) (Ilisson and Chen 2009, Landhausser et al. 2010).

The recovery of soil nutrients in response to disturbance varies as forest stands age (i.e. with time since disturbance), especially nutrients such as C and N, which are strongly biologically controlled and accumulate rapidly with organic matter inputs (Wardle et al. 2003). However, the recovery of nutrients that are driven mainly by geochemical inputs (e.g. weathering of primary minerals), such as P and Ca, or by both biological and geochemical mechanisms, such as K, are poorly understood, or are controversial due to conflicting results (Duchesne and Houle 2008, Maynard et al. 2014). Preliminary results for soil P suggest that it requires significantly longer to recover from fire than C or N (Hume et al. 2016), and that it is strongly, negatively affected by harvesting (Thiffault et al. 2011). While the short-term responses of soil nutrients to different disturbance types is expected to vary (McRae et al.

2001, Kishchuk et al. 2015), it remains unclear how the recovery of soil nutrients differs between harvesting and fire as stands age, especially for different forest overstory types as stands undergo succession.

Differences in the effects of fire and harvesting on soil nutrient dynamics may also influence the renewal and growth of the regenerating stands, since site resources such as soil nutrients constitute a fundamental driver of site productivity (Chen et al. 2002, Huston and Wolverton 2009). Disturbance-driven temporal trends in stand renewal and growth are also likely to vary with overstory composition, since boreal deciduous stands are associated with richer sites that have higher concentrations of N, Ca, and P, and higher cation exchange capacity than boreal coniferous stands. Moreover, inter-specific interactions among tree species change with stand development (Cavard et al. 2011), and at the stand initiation and self-thinning stages, tree species may interact predominantly through resource competition (Connell and Slatyer 1977). However, how temporal trends in soil nutrient dynamics under fire and harvesting relate to the development and productivity of regenerating stands in diverse overstory types is poorly understood.

In the Canadian boreal forest, the effects of harvesting and fire on soil nutrient dynamics and stand productivity in varying forest types is inadequately understood (see results from the eastern boreal forests (Brais et al. 1995, Mahendrappa et al. 2006, Thiffault et al. 2008), prompting recent calls for better knowledge to improve policy directive (Thiffault et al. 2010). In this paper, we examine stand growth (basal area per hectare, BA ha^{-1}) and dominant tree height (m), as well as the dynamics of soil [C], [N], [P], [K], and [Ca] in the forest floor, surface, and subsurface mineral soil, throughout early secondary succession (7-, 15-, and 33-years since disturbance), using replicated chronosequences developed in three predominant boreal overstory stand types originated from stand-replacing fire and clearcut harvesting. Specifically, we ask the following research questions: (1) How do stand growth (BA ha^{-1}) and tree height (m), as well as soil [C], [N], [P], [K], and [Ca], change over time as stands of different overstory types develop following stand-replacing fire and clearcut harvesting? (2) Do temporal trends in soil [C], [N], [P], [K], and [Ca] differ according to soil layer (i.e. forest floor, surface, and subsurface mineral soil)? Do the responses of soil nutrient concentrations to fire and harvesting correspond to their volatility? We hypothesize that: (a) the effects of disturbance origin, stand age, and overstory type will be most dramatic in the forest floor due to greater susceptibility to disturbance impacts, and since the influence of biological feedbacks decreases with soil depth (Yuan and Chen 2010, Achat et al. 2015b); (b) the nutrients that are more susceptible to volatilization will respond more dramatically to fire than to harvesting due to the effects of combustion (Simard et al. 2001, Thiffault et al. 2008); (c) tree growth and nutrient concentrations will be slower to recover from disturbance in conifer than broadleaf stands due to the chemical and functional differences between the tree species, whereas mixedwood stands will be intermediate (Paré et al. 2013); and (d) short term differences in soil nutrient concentrations, stand growth, and tree height due to disturbance origin will converge over time (Shrestha and Chen 2010, Kishchuk et al. 2015).

Methods

Study area

Our study was done in the boreal mixedwood forest north of Lake Superior, approximately 150 km northwest of Thunder Bay, Ontario, Canada, between 49°44’N to 49°65’ N and 89°16’W to 90°13’W. The closest meteorological station is in Cameron Falls, Ontario and reports a mean annual temperature of 1.9°C and mean annual precipitation of 824.8 mm (Environment Canada 2014). Surficial deposits originate from the Wisconsinan period of glaciation, which ended approximately 9,500 years ago in this region. The dominant deciduous broadleaf tree species are trembling aspen (*Populus tremuloides* Michaux) and white birch (*Betula papyrifera* Marsh.). The dominant conifer species are jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill) BSP), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.). Based on reconstruction of fire history in our study area, the average fire cycle has decreased from 295 years for the period prior to 1921, to between 96 and 156 years for the period from 1921-2008 (Senici et al. 2010). Commercial harvesting, primarily by clearcut, began in the 1970s in our study area. Study sites were selected to reflect the regional site type that is most commonly chosen for operational management: moderately deep glacial tills of the Brunisolic order with mesic moisture regime (Soil Classification Working Group 1998).

Sampling design

Our study used stratified random sampling to select sites for each combination of disturbance origin, stand age, and overstory type. We employed chronosequence methods to examine the effects of time since disturbance by locating sites with similar characteristics and developmental histories at different ages; selected to represent stages of stand development. When care is taken to ensure demonstrable successional links during site selection and replication, the chronosequence method is an effective way to study successional dynamics at decadal time scales (Walker et al. 2010). We used chronosequences that were previously established and added new sites as necessary, following the methodology of (Hart and Chen 2008). Disturbance origin was determined using harvesting and silviculture records from the forest licensee and fire records maintained by the provincial government. Suitability of stands was assessed initially by examining aerial photos and records from the provincial Forest Resource Inventory (FRI) to determine current and historical species composition and confirm that all sites succeeded from appropriate forest types. We further confirmed successional links between our sites by examining understory vegetation and soil sampling (Taylor and Chen 2011), and by consulting with local forest management experts (Paul Poschmann, *personal communication*). Records of fire events and harvesting operations for our study area enabled us to select sites from three age classes: 7, 15, and 33-years-old. These correspond roughly to the stand initiation and early and late stem exclusion (i.e. self-thinning) stages of stand development (Chen and Popadiouk 2002).

For each age category, we sampled three different overstory stand types that shared similar site conditions, including slopes of ≤ 5% and mesic moisture regime, since mesic sites in our region may be dominated by broadleaf or conifer tree species, or a mixture of both, at any stage of stand development (Taylor and Chen 2011). Similar to (Cavard et al. 2011), we confirmed the similarity of intrinsic site conditions across our chronosequences by testing for significant differences in mineral soil texture at a depth of 30-50 cm (Appendix Table A.2.1). No significant differences were found at $\alpha = 0.1$ (Appendix Table A.2.2). This enabled us to examine the effects of disturbance origin, overstory type, and time since disturbance on soil nutrients and tree growth and to represent the dominant upland stand types in the study area, including broadleaf deciduous (dominated by *Populus tremuloides*), conifer (dominated by *Pinus banksiana*), and mixedwood (composed of mixtures of mostly *Populus tremuloides* and *Pinus banksiana*). Each combination of disturbance origin, overstory type, and stand age was replicated three times, resulting in a total of 54 stands (Table 2.1).

In recent decades, harvested conifer and mixedwood stands our study area have been managed using silvicultural methods including site preparation, artificial regeneration, and vegetation management. By contrast, broadleaf deciduous stands are left to regenerate naturally without the use of the aforementioned methods. Thus overstory stand types in our harvested chronosequences differ not only in terms of tree species composition, but also in terms of post-harvest management techniques. Specifically, 7- and 15-year-old harvested stands of conifer and mixedwood overstory were scarified by disc trencher and planted with jack pine seedlings, which were released from competing vegetation by application of aerial herbicide. Deciduous stands and 33-year-old stands of all overstory types regenerated naturally (Joan Keene, *personal communication*). In order to minimize the effects of spatial structure (Legendre and Legendre 2012), we established stands of the same overstory type and age as far from one another as possible, which resulted in distances of 0.5 – 10 km. The selected stands were ≥ 1 ha in area and were visually homogeneous in terms of tree species composition.

Field measurements

We established a randomly located 0.04 ha (11.28 m radius) fixed area circular plot within each of the 54 selected study stands. The plots were located ≥ 50 m from the forest edge, in order to represent the stand, and an inventory was conducted to record the species, diameter at breast height (DBH, 1.3 m above root collar), and total height of trees. In the 33-year-old stands, all trees within each 0.04 ha (11.28 m radius) circular plot were measured. In 7- and 15-year-old stands, all trees within a 0.005 ha (3.99 m radius) circular sub-plot were measured due to very high stem density. Top tree height was determined by finding the average of the 5 tallest trees in each of the 7- and 15-year-old plots (0.005 ha), and the 40 tallest trees in each of the 33-year-old plots (0.04 ha). Stand composition was determined by calculating percentage basal area (% BA) for each species in each plot. Broadleaf and conifer trees represent 65% or more of stand composition by stem density or BA while mixedwood sites are relatively equal percentages of deciduous and conifer trees (< 65% deciduous or conifer by stem density or BA) (Table 2.1).

Within each plot, we also collected soil samples from ten random points, for each layer, using a Dutch auger. At each point, the litter and bryophyte layer was removed, depth was measured and a sample was collected for the organic layer (F and H layers), hereafter referred to as the forest floor (FF) (variable depth), and for two mineral soil layers: M1 (0-15 cm) and M2 (15-30 cm). The samples collected from the ten points within the plot were then combined according to depth to produce one composite sample for each layer at each site, resulting in a total of 54 composite samples for each of the three soil layers (162 samples in total), for laboratory analysis. In addition, we collected samples from a third mineral soil layer (M3, 30-50 cm) for particle distribution analysis to test whether intrinsic soil texture differed as a function of stand age and overstory type and thereby confirm the suitability of study stands (Cavard et al. 2011).

Table 2.1. Characteristics of 54 stands sampled in the boreal forest of Ontario, Canada.

Disturbance Origin	Stand age (years)	Over story*	Stand density (stems/ha)	Basal area (m^2/ha)	Stand composition (% BA)				
					Trembling aspen	White birch	Jack pine	Other broadleaf species‡	Spruce spp.
Fire	7	B	1533 (3182)	1 (0)	92 (2)	3 (2)	3 (2)	2 (1)	
	7	M	9200 (1001)	1 (0)	28 (3)	15 (4)	48 (7)	4 (1)	
	7	C	5933 (1360)	2 (0)	1 (1)	1 (1)	98 (1)	1 (0)	
Harvest	7	B	5000 (154)	2 (0)	88 (3)	4 (0)	1 (0)	7 (4)	
	7	M	10867 (488)	4 (0)	61 (10)	1 (1)	38 (9)		
	7	C	5933 (1103)	3 (0)		2 (1)	88 (9)		11 (8)
Fire	15	B	10242 (60)	10 (1)	89 (7)	6 (4)		5 (3)	
	15	M	5400 (693)	4 (1)	49 (6)	3 (2)	40 (5)	2 (1)	5 (4)
	15	C	4433 (405)	1 (0)	8 (5)		92 (5)		
Harvest	15	B	2542 (4795)	9 (3)	99 (1)	1 (1)			
	15	M	6817 (1379)	7 (1)	42 (5)		57 (5)	1 (0)	
	15	C	2000 (385)	1 (0)			94 (3)	1 (1)	6 (2)
Fire	33	B	1659 (54)	26 (1)	93 (3)	4 (3)	1 (1)	2 (1)	
	33	M	1400 (87)	13 (1)	52 (4)		41 (6)		7 (5)
	33	C	2051 (58)	22 (1)	3 (2)	1 (0)	96 (3)		
Harvest	33	B	1258 (35)	17 (1)	90 (3)	8 (4)	1 (0)		2 (1)
	33	M	1842 (83)	27 (1)	44 (5)	1 (1)	51 (4)		
	33	C	2375 (231)	24 (1)	1 (1)		98 (0)		1 (1)

Notes: *Overstory types: B – broadleaf, C – conifer, and M – mixed-wood.
†Values are means with 1 SE in parentheses.
‡The "Others" category includes *Salix* spp. and *Prunus pensylvanica.*
All overstory-age combinations were replicated (3 stands).

Laboratory analysis

Soil samples were analyzed for physical and chemical properties at Lakehead University in Thunder Bay, Ontario. Samples were air-dried and coarse fragments were removed using a 2 mm sieve. For the FF, M1, and M2 soil layers, chemical analyses were done with samples ground finely enough to pass through a 100-mesh (0.15 mm) sieve to ensure a uni-form sample. Total concentrations of P, K, and Ca were determined using the nitric/hydrochloric acid digestion method with inductively coupled plasma atomic emission spectrometry (ICP-AES) (Kalra and Maynard 1991). Total concentrations of C and N were analyzed by the flash dynamic combustion method, using a high temperature reactor to fully combust each sample and provide a precise measure of the quantity of elemental gases within each sample (Carter and Gregorich 2008). For the M3 layer, particle size distribution for mineral soil texture was determined by the Bouyoucos hydrometer method (Carter and Gregorich 2008).

Statistical analysis

We used three-way ANOVA to test the main and interaction effects of disturbance origin (stand-replacing wildfire and clearcut harvesting), stand age (7-, 15-, and 33-years-old), and overstory type (broadleaf, mixedwood, and conifer), on soil nutrient concentrations ([C], [N], [P], [K], and [Ca]) in the FF, M1, and M2 layers, and on tree growth (BA ha^{-1}), as well as particle size distribution of the M3 layer. We analyzed each response parameter within each soil layer (for nutrient concentration) separately using the following model:

$$Y_{ijkl} = \mu + A_i + T_j + O_k + A \times T_{ij} + A \times O_{ik} + T \times O_{jk} + A \times T \times O_{ijk} + e_{l(ijk)} \qquad (1)$$

where Y_{ijkl} is the measured response of soil nutrients, tree growth, or particle size distribution, μ is the overall mean, A is stand age (i = 1, 2, 3), T is overstory type (j = 1, 2, 3), O (k = 1, 2) is disturbance origin, and e is random sampling error from replications (l =1, 2, 3) within stand age, overstory type and disturbance origin.

We checked assumptions of normality and homogeneous variance using the Shapiro-Wilk normality test and Levene's test, and used natural log or square root transformation when necessary to meet assumptions. We examined multiple comparisons of means (α =

0.05) using Tukey's honest significant differences (HSD). We performed all statistical analyses in R version 3.3.0 (R Core Team 2016).

Results

Stand basal area (BA, m^2 ha^{-1}) differed significantly with all predictors except the three-way interaction between disturbance origin, stand age, and overstory (Table 2.2). Overall, harvested stands had greater BA than fire origin stands throughout most of our chronosequences, however when the interaction between disturbance origin and stand age was considered, stands of fire origin only differed significantly from harvested stands at 7-years-old (Fig. 2.1a-c). BA also differed significantly according to the main effect of stand age, generally increasing with time since disturbance. However, there was also a significant interaction effect of stand age and overstory type – broadleaf stands gained in BA far more rapidly than conifer stands, which did not increase significantly until the 33-year-old stands, while the increase in BA over time in mixedwood stands was intermediate to that of broadleaf and conifer stand types (Fig. 2.1a-c). There was also a significant interaction effect of disturbance origin and overstory type due to greater BA in harvested mixedwood stands than burned mixedwood stands and conifer stands of both disturbance origins (Fig. 2.1a-c). BA did not differ according to the three-way interaction between disturbance origin, stand age, and overstory type.

Most variation in tree height was driven by stand age, with significant increases at each age category, however the increase was most dramatic in the 33-year-old stands (Fig. 2.1d-f, Table 2.2). Tree height also differed according to overstory type, with significantly lower overall tree heights in conifer stands than mixedwood and especially deciduous stands.

Although tree height did not differ between the two disturbance origins, there was a significant interaction effect of disturbance origin and stand age, but this effect reflected age-driven trends – 33-year-old burned and harvested stands differed significantly from 7- and 15-year-old burned and harvested stands. Tree height also differed significantly with the interaction between overstory and stand age, due to greater tree heights in the 33-year-old broadleaf stands than 33-year-old conifer stands. The interaction between disturbance origin and overstory type had a marginally significant effect on tree height, due to shorter trees in burned conifer stands. The three-way interaction between disturbance origin, stand age, and overstory type did not affect tree height.

In the forest floor, the main effect of disturbance origin was significant for all nutrients except K, due to overall higher concentrations in harvested vs. burned stands. All forest floor nutrients also differed significantly with stand age, with concentrations generally highest in the 33-year-old stands (Fig. 2.2a-o, Table 2.2). However, as with BA, when the interaction effect of disturbance origin and stand age was considered, the two disturbance types only differed significantly in the 7-year-old stands for all forest floor nutrients (Fig. 2.2a-o). In addition, temporal trends in forest floor nutrients differed between the two disturbance types; in burned stands nutrients increased linearly, with 15-year-old stands intermediate to 7- and 33-year-old stands, whereas in harvested stands nutrients fluctuated from high concentrations in 7-year-old stands, to low in 15-year-old stands, to high again in the 33-year-old stands (Fig. 2.2a-o). Forest floor [N], [K], and [Ca] also differed significantly according to overstory type, due to significantly higher concentrations in the broadleaf stands compared to conifer stands, and intermediate concentrations in mixedwood stands (Fig. 2.2d-f and Fig. 2j-o, Table 2.2). Forest floor nutrient concentrations did not differ according to the interactions between disturbance origin and overstory type, stand age and overstory type, nor the three-way interaction between disturbance origin, stand age, and overstory type.

Table 2.2. Effects of disturbance (Di = 1, 2), stand age (Aj = 1, 2, 3), and overstory type (Tk = 1, 2, 3) on soil C, N, P, K, and Ca concentrations in post-fire and post-harvest stands.

Parameter	Disturbance		Age		Overstory	
	F	*P*	*F*	*P*	*F*	*P*
Basal area (m^2 ha^{-1})	9.74	**0.004**	173.73	**<0.001**	3.63	**0.037**
Top tree height (m)	0.084	0.774	1381.93	**<0.001**	6.46	**0.004**
Forest Floor Soil Nutrients						
C (g kg^{-1})	4.66	**0.038**	13.18	**<0.001**	0.83	0.444
N (g kg^{-1})	12.76	**0.001**	15.10	**<0.001**	3.31	**0.048**
P (g kg^{-1})	6.43	**0.016**	11.78	**<0.001**	2.15	0.131
K (g kg^{-1})	1.41	0.247	8.25	**0.001**	6.63	**0.004**
Ca (g kg^{-1})	4.14	**0.050**	4.84	**0.014**	5.96	**0.006**
Surface Soil Nutrients (0-15 cm)						
C (g kg^{-1})	1.32	0.258	3.79	**0.032**	1.10	0.345
N (g kg^{-1})	2.45	0.126	5.58	**0.008**	0.91	0.410
P (g kg^{-1})	2.22	0.145	8.92	**<0.001**	1.47	0.244
K (g kg^{-1})	1.48	0.232	18.04	**<0.001**	4.03	**0.027**
Ca (g kg^{-1})	8.16	**0.007**	3.77	**0.033**	3.32	**0.048**
Subsurface Soil Nutrients (15-30 cm)						
C (g kg^{-1})	1.06	0.311	10.59	**<0.001**	0.15	0.862
N (g kg^{-1})	1.93	0.174	6.81	**0.003**	0.82	0.447
P (g kg^{-1})	8.54	**0.006**	4.87	**0.014**	1.18	0.319
K (g kg^{-1})	0.00	0.969	45.97	**<0.001**	3.58	**0.038**
Ca (g kg^{-1})	17.14	**<0.001**	6.87	**0.003**	2.39	0.106

Abbreviations: [C] – total carbon concentration, [N] – total nitrogen concentration, [P] – total phosphorus concentration, [K] – total potassium concentration, [Ca] – total calcium concentration. Significance of bold values is at $P < 0.05$.

Table 2.2 continued.

Parameter	Disturbance × Age		Disturbance × Overstory		Age × Overstory		Disturbance × Age × Overstory	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Basal area (m^2 ha^{-1})	4.92	**0.013**	6.04	**0.006**	16.00	**<0.001**	0.48	0.750
Top tree height (m)	3.87	**0.030**	2.80	0.074	2.66	**0.049**	1.72	0.167
Forest Floor Soil Nutrients								
C (g kg^{-1})	4.78	**0.015**	0.86	0.430	1.59	0.198	0.57	0.690
N (g kg^{-1})	6.60	**0.004**	0.70	0.502	1.90	0.132	0.42	0.792
P (g kg^{-1})	3.01	0.062	0.18	0.839	1.13	0.360	0.50	0.737
K (g kg^{-1})	3.77	**0.033**	0.86	0.430	0.40	0.809	0.48	0.751
Ca (g kg^{-1})	5.04	**0.012**	0.70	0.503	1.00	0.422	0.24	0.913
Surface Soil Nutrients (0-15 cm)								
C (g kg^{-1})	0.71	0.499	0.24	0.789	1.23	0.317	0.60	0.663
N (g kg^{-1})	1.03	0.368	0.28	0.757	1.03	0.406	0.29	0.882
P (g kg^{-1})	3.11	**0.057**	0.33	0.719	2.19	0.090	0.90	0.478
K (g kg^{-1})	15.49	**<0.001**	2.26	0.119	0.47	0.759	0.36	0.833
Ca (g kg^{-1})	8.41	**0.001**	1.81	0.178	2.67	**0.048**	1.58	0.200
Subsurface Soil Nutrients (15-30 cm)								
C (g kg^{-1})	0.10	0.903	0.06	0.944	1.11	0.366	1.00	0.420
N (g kg^{-1})	0.29	0.747	0.04	0.960	0.59	0.674	1.35	0.272
P (g kg^{-1})	2.08	0.140	2.69	0.082	0.71	0.594	1.65	0.184
K (g kg^{-1})	27.64	**<0.001**	1.74	0.190	0.78	0.544	0.38	0.825
Ca (g kg^{-1})	8.59	**0.001**	2.38	0.108	0.74	0.572	0.42	0.791

Abbreviations: [C] – total carbon concentration, [N] – total nitrogen concentration, [P] – total phosphorus concentration, [K] – total potassium concentration, [Ca] – total calcium concentration. Significance of bold values is at $P < 0.05$.

In the surface (M1, 0-15 cm) and subsurface (M2, 15-30 cm) mineral soil, trends among the various nutrients were more variable than in the forest floor, and were driven primarily by stand age. Mineral soil [C] and [N] shared similar temporal trends, with the smallest concentrations in 15-year-old stands, which differed significantly from 33-year-old stands (Fig. 2.3a-f and Fig. 2.4a-f, Table 2.2). By contrast, mineral soil [P] was highest in the 15-year-old stands, which differed significantly from both the 7- and 33-year-old stands in the surface mineral soil, and from the 7-year-old stands in the subsurface mineral soil. However, surface mineral soil [P] also differed significantly according to the interaction between disturbance origin and stand age; concentrations were higher in 15-year-old burned stands than 7- and 33-year-old burned stands, whereas harvested stands fluctuated less over our chronosequences (Fig. 2.3g-i). In the subsurface mineral soil, [P] differed significantly between the two disturbance types, due to higher concentrations in harvested stands throughout most of our chronosequences (Fig. 2.4g-i, Table 2.2). Mineral soil [C], [N], and [P] did not differ according to the interaction effect of disturbance origin and overstory, stand age and overstory, nor the three-way interaction between disturbance origin, stand age, and overstory (Fig. 2.3a-i, Fig. 2.4a-i, Table 2.2).

In both mineral soil layers, [K] was greatest overall in 15-year-old stands, but differed significantly between all three age categories. Mineral soil [K] did not differ according to the main effect of disturbance origin, however, the interaction effect of disturbance origin and stand age resulted in very different temporal trends between the two disturbance types. In harvested stands, [K] was greatest in the 7-year-old stands and decreased over time, whereas in burned stands, the trend for [K] was similar to that of [P] – concentrations were small in the 7-year-old stands, increased dramatically in the 15-year-old stands, and then decreased again in the 33-year-old stands. Potassium concentration in both mineral soil layers also differed according to overstory type, with significantly greater concentrations in broadleaf than conifer stands (Fig. 2.3j-l and Fig. 2.4j-l). Mineral soil [K] did not differ with the interaction between disturbance origin and stand age, nor stand age and overstory, nor the three way interaction between disturbance origin, stand age, and overstory type (Table 2.2).

Calcium was the only nutrient that differed with the main effect of disturbance origin in the surface and subsurface mineral soil, due to overall greater concentrations in harvested stands compared to those of fire origin. However, there was also a strong interaction effect of disturbance origin and stand age in both mineral soil layers, similar to that of [K] – in harvested stands, [Ca] decreased over time, such that [Ca] in 7-year-old harvested stands was significantly higher than in the 33-year-old stands of either disturbance origin, whereas in fire origin stands, [Ca] fluctuated less with stand age but was highest in the 15-year-old stands (Fig. 2.3m-o and Fig. 2.4m-o, Table 2.2). In the surface mineral soil, [Ca] differed according to overstory type, with significantly higher concentrations in broadleaf than conifer stands, and intermediate concentrations in mixedwood stands. There was also an interaction effect of overstory and stand age in the surface mineral soil, due to high [Ca] in 7- and 15-year-old broadleaf stands (Fig. 2.3m-o), but this effect was absent in the subsurface mineral soil. The three-way interaction between disturbance origin, stand age, and overstory type did not affect [Ca] in either mineral soil layer, nor did the interaction between disturbance origin and stand age (Table 2.2).

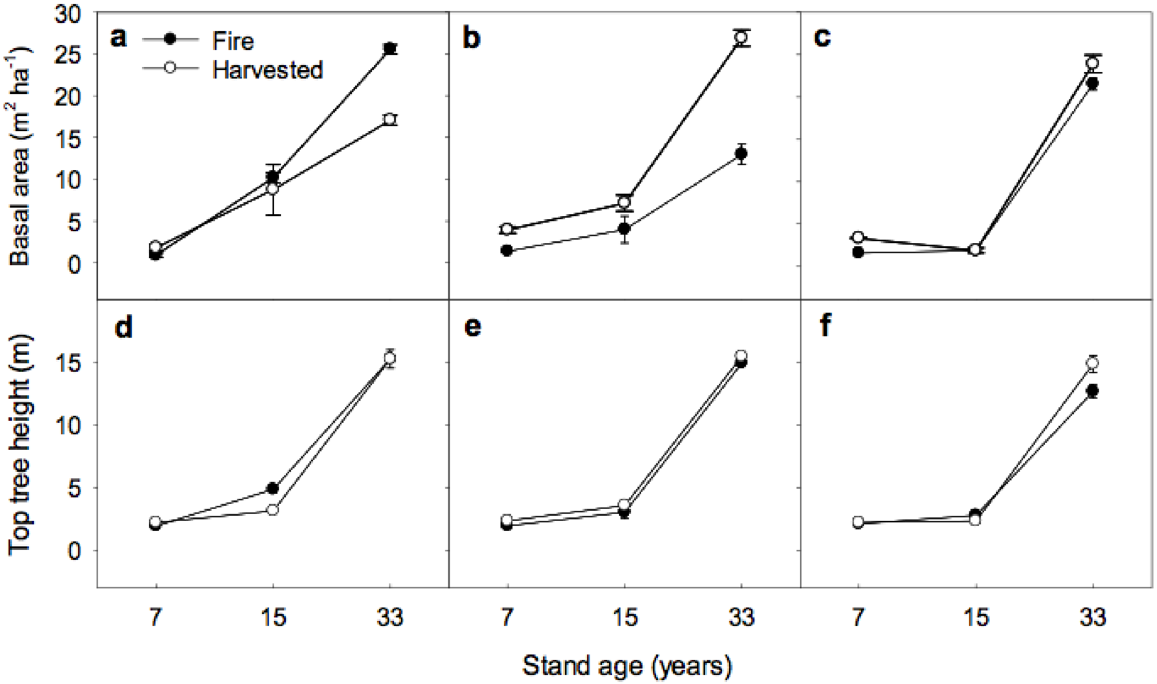

Figure 2.1. Effects of disturbance origin, overstory type, and stand age on stand growth and tree height: (**a**) stand basal area (m^2 ha^{-1}) in deciduous stands, (**b**) stand basal area (m^2 ha^{-1}) in mixedwood stands, (**c**) stand basal area (m^2 ha^{-1}) in conifer stands, (**d**) top tree height (m) in deciduous stands, (**e**) top tree height (m) in mixedwood stands, (**f**) top tree height (m) in conifer stands. Values are mean ± 1 SE.

Discussion

Our study demonstrates the important influence of disturbance origin, overstory type, and stand age on stand regeneration and soil nutrient concentrations in the boreal forest. Of the various predictors, stand age (i.e. time since disturbance) was the most influential, with significant increases of stand basal area, tree height, and forest floor nutrient concentrations over time, as well as strong temporal trends in the mineral soil that were reflective of stand development processes. In the youngest stands, we observed significant differences due to disturbance origin, with significantly smaller stand basal area and forest floor nutrient concentrations in 7-year-old burned stands compared to harvested stands of the same age (Fig.

2.1a-c, Fig. 2.2a-o). However, these same parameters no longer differed in the 15- and 33-year-old stands, indicating that the divergent short term effects of disturbance origin converged over time as stands developed, as we had hypothesized (Shrestha and Chen 2010). The exception was tree height, for which there were no discernable disturbance-driven differences, in agreement with previous boreal forest studies (Fig. 2.1d-f) (Kishchuk et al. 2015).

Our hypothesis that stand growth during early stand development following disturbance would be slower in conifer than broadleaf stands was also supported by our findings – the gain in basal area was significantly more rapid in broadleaf than conifer stands. Whereas basal area in mixedwood and especially broadleaf stands increased significantly between each of the three age categories in our chronosequences, in conifer stands it did not change until the 33-year-old stands, regardless of whether the stands originated from fire or from harvesting (Fig. 2.1a-c). Tree height was also affected by overstory – 33-year-old deciduous stands had taller trees than conifer stands of the same age (Fig. 2.1d and 2.1f). We attribute this to functional differences between coniferous and deciduous tree species in the boreal forest, such as the faster growth rates of deciduous tree species and their ability to reproduce vegetatively following disturbance. These characteristics enable regeneration to begin immediately on sites that were occupied by deciduous tree species prior to stand-initiating disturbances, whereas conifer regeneration may be delayed, which can further inhibit tree growth by enabling competing herbaceous vegetation to establish (Chen et al. 2009, Ilisson and Chen 2009, Bartels et al. 2016). Furthermore, in the boreal forest, and specifically in our study stands, competition from deciduous understory plants and trees in harvested conifer stands is often managed by silvicultural methods including site preparation, artificial regeneration, and subsequent release of conifer tree species using vegetation management, whereas harvested deciduous stands are left to regenerate naturally (Fleming et al. 2006). Thus, though we did not specifically test their impacts, the lag in basal area growth we observed in conifer stands relative to deciduous and mixedwood stands may result from a number of management interventions, in addition to functional differences between coniferous and deciduous tree species in the boreal forest. Our results for overstory type effects also suggest that competition continues to be an important driver throughout the period of early stand development represented by our chronosequences, since tree growth in mixedwood stands was intermediate to that of deciduous and coniferous stand types, rather than being more productive (Connell and Slatyer 1977, Cavard et al. 2011).

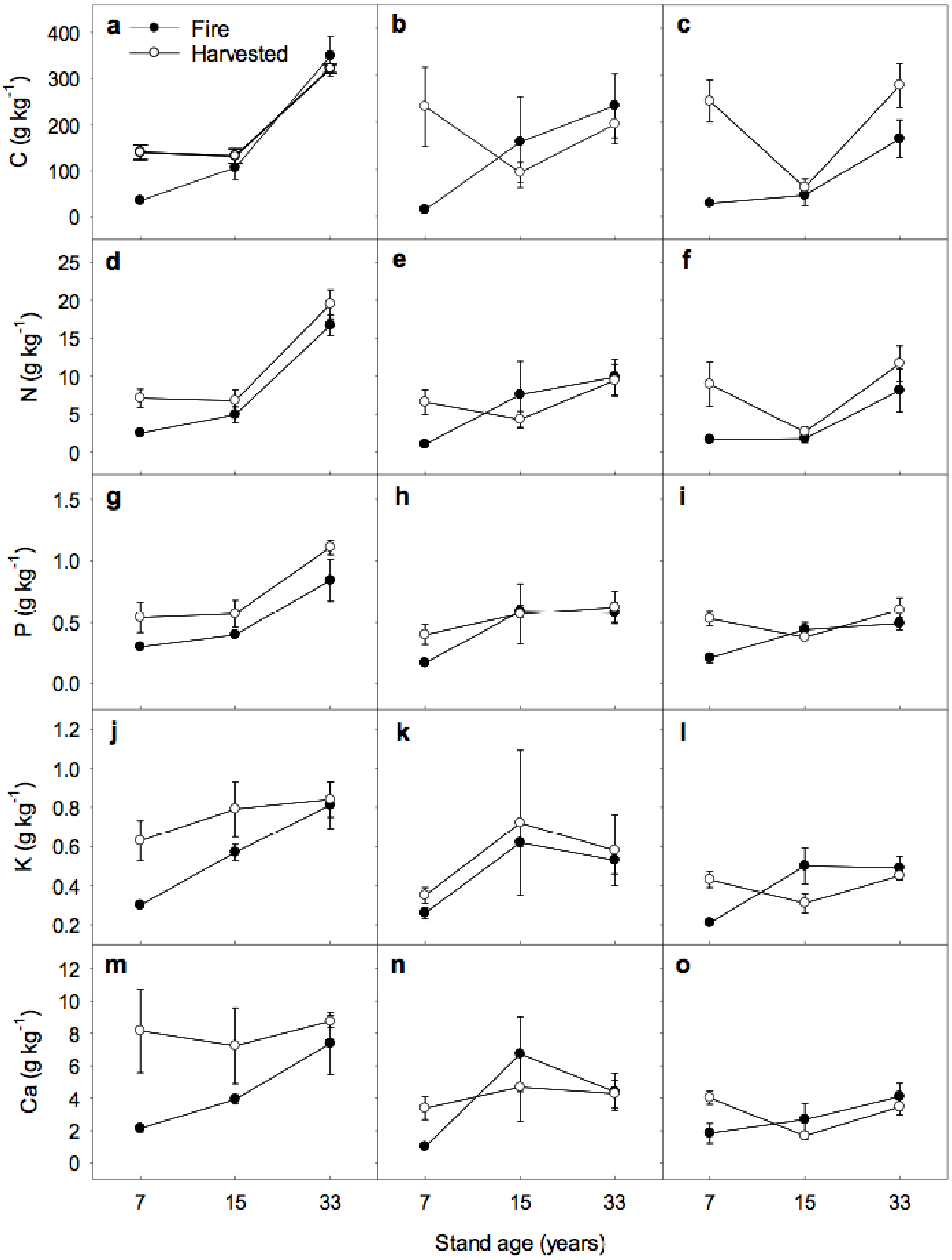

Figure 2.2. Effects of disturbance origin, overstory type, and stand age on nutrient concentrations of the forest floor: (**a**) total carbon concentration ([C]) in deciduous stands, (**b**) [C] in mixedwood stands (**c**) [C] in conifer stands, (**d**) total nitrogen concentration ([N]) in deciduous stands, (**e**) [N] in mixedwood stands, (**f**) [N] in conifer stands, (**g**) total phosphorus concentration ([P]) in deciduous stands, (**h**) [P] in mixedwood stands, (**i**) [P] in conifer stands, (**j**) total potassium concentration ([K]) in deciduous stands, (**k**) [K] in mixedwood stands, (**l**) [K] in conifer stands, (**m**) total calcium concentration ([Ca]) in deciduous stands, (**n**) [Ca] in mixedwood stands, (**o**) [Ca] in conifer stands. Values are mean ± 1 SE.

As we hypothesized, the effects of disturbance, stand age, and overstory type on soil nutrient concentrations were most pronounced in the forest floor relative to the other soil layers, due to its dynamic nature and buffering capability, and since the influence of biological feedbacks decreases with soil depth (Yuan and Chen 2010, Thiffault et al. 2011, Achat et al. 2015b). This was particularly true in the burned stands, which had the smallest concentrations of all nutrients across our entire chronosequences, especially for highly volatile C and N, for which we had hypothesized a more dramatic response to fire due to the effects of combustion. By contrast, harvested stands tended to have larger (C and N) or similar (P and Ca) nutrient concentrations in the 7-year-old vs. 15-year-old stands (Fig. 2.2a-o). These striking differences between 7-year-old burned vs. harvested stands likely reflect not only nutrient losses from forest floor combustion, but also short term gains of organic matter following harvesting due to inputs of woody residues and live and dead litter and fine roots; in agreement with previous studies comparing the effects of wildfire and harvesting (Simard et al. 2001, Thiffault et al. 2008, Kishchuk et al. 2015). Furthermore, the temporal trend of increases in total nutrient concentrations between 7- and 15-year-old burned stands vs. decreases or no change over the same time period in harvested stands suggests contrasting mechanisms of site renewal between the two disturbance origins during stand initiation. For example, (Simard et al. 2001) found a greater flush of plant-available forms of nutrients following fire despite greater overall losses, likely due to ash inputs and the release of organically bound nutrients, compared with high initial concentrations of nutrients following harvesting, likely due to increased organic matter inputs. These contrasting patterns may explain the rapid increases in stand basal area and forest floor nutrient concentrations we observed between the 7- and 15-year-old burned stands (Fig. 2.1a-c, Fig. 2.2a-o). The decreases of forest floor nutrient concentrations in harvested stands during the same time period likely reflect plant uptake and the absence or comparative scarcity of N-fixing vegetation (Fig. 2.2a-o). While we did not directly test the influence of understory vegetation, previous research in our chronosequences has shown that harvesting is correlated with higher vascular plant cover and richness, including rhizomatous species that establish rapidly with high nutrient demands, whereas wildfire is associated with several N-fixing understory vegetation species, including feather mosses and alder (Hart and Chen 2008).

Potassium was the only nutrient in the forest floor for which the main effect of disturbance origin was not significant, however 7-year-old fire stands still had significantly lower K concentrations tha harvested stands of the same age (Fig. 2.2j-l). The lack of a significant main effect of disturbance origin is likely due to the high mobility of monovalent K ions, which makes K easily lost from the forest floor immediately following disturbance, regardless of whether the loss is via leaching from harvest residues or organic matter combustion during fire. The mobility of K also means that it is easily accumulated and cycled within plant biomass, and thus is strongly biologically controlled in spite of being derived primarily from mineral weathering (Sardans and Peñuelas 2015). Indeed, K was the only soil nutrient that differed significantly according to overstory type in all three soil layers, with concentrations significantly higher in broadleaf than conifer stands, and mixedwoods intermediate, as we had hypothesized. The overstory trend was also significant for forest floor N and Ca and for surface soil Ca, thus the cycles of all three nutrients appear to be driven to varying degrees by overstory type, which we attribute to the higher acidity and lower N, K, and Ca contents of coniferous vs. deciduous trees (Fig. 2.2d-f and Fig. 2.2j-o, Fig. 2.3j-o, and Fig. 2.4j-l)

(Yuan and Chen 2009, Paré et al. 2013). In addition, there is evidence that rates of K and Ca uptake and canopy exchange may be greater in deciduous than coniferous stands (De Schrijver et al. 2007). Moreover, the K cycle, which was most strongly influenced by overstory of all the nutrients studied, is strongly tied to water use efficiency, with K more restricted in drier environments (Sardans and Peñuelas 2015). Due to their higher leaf area index and persistent foliage, conifer trees intercept and retain more precipitation in their canopies than deciduous trees, resulting in drier soils and thus providing an additional potential explanation for the lower K concentrations we observed in the forest floor, surface, and subsurface mineral soils of conifer stands in our chronosequences (Augusto et al. 2015).

In the surface and subsurface mineral soil, total concentrations of C and N followed similar trends, with the lowest concentrations found in the 15-year-old stands, and the highest concentrations in the 7- and 33-year-old stands (Fig. 2.3a-f and Fig. 2.4a-f). We attribute this to inputs of C and N in the 7-year-old stands from harvest residues or post-fire woody debris, turnover of early successional herbaceous annual plant species, and biological fixation, followed by decreases in mineral soil C and N in the 15-year-old stands due to vertical redistribution from lower to higher soil layers resulting from intense uptake by the regenerating stand, with concentrations increasing again in the 33-year-old stands due to increased woody, litterfall, and fine root inputs resulting from competition-induced mortality and high canopy closure (Johnson and Curtis 2001, Yuan and Chen 2010, Gundale et al. 2011, Chen and Shrestha 2012, Hume et al. 2016). By contrast, the temporal trends of P, K, and Ca were characterized by high concentrations in the 15-year-old stands and low concentrations in the 7- and 33-year-old stands (Fig. 2.3g-o and Fig. 2.4g-o). We attribute these inverse patterns to the differing mechanisms that drive the cycles of biologically controlled C and N vs. geochemically controlled P, K, and Ca. For example, the most striking contrasts are in the 33-year-old stands, which represent late stem exclusion stage in boreal forest succession, a highly competitive period of stand development (Chen and Popadiouk 2002). While mineral soil C and N were abundant during this stage in our chronosequences, we found very low mineral soil concentrations of P, K, and Ca. We attribute this to greater proportions of these nutrients being taken up by competing trees than can be supplied by mineral weathering, which may lead to increased exploitation of the mineral soil and subsequent vertical redistribution to the forest floor, and ultimately to regenerating vegetation as increasingly more nutrients are stored in standing biomass during rapid growth phases of boreal stand development (Yanai et al. 2005, Paré et al. 2013, Hume et al. 2016)

Overall, our study demonstrates the highly dynamic nature of the forest floor, wherein we observed strong responses in nutrient dynamics to disturbance origin, stand age, and overstory type, whereas effects were more muted in the mineral soil, reflecting the ability of the forest floor to absorb impacts and thereby provide a buffer to mineral soils (Yanai et al. 2003, Yuan and Chen 2010, Thiffault et al. 2011, Achat et al. 2015b). Our findings also suggest that fire results in more drastic short term effects – both stand basal area and forest floor nutrient concentrations were much smaller in 7-year-old burned than harvested stands. However, all of these indicators of site productivity converged between the two disturbance origins in the 15- and 33-year-old stands, which likely reflects the ability of boreal forests to recover rapidly from fire due to the flush of plant-available nutrients (Simard et al. 2001, Thiffault et al. 2007). Finally, our study points to marked differences between deciduous and conifer stands that influence the responses of tree growth and soil nutrients to disturbances over the course of early stand development (Lecomte and Bergeron 2005, Chen et al. 2009, Ilisson and Chen 2009, Taylor and Chen 2011). Tree growth in conifer stands lagged behind the other overstory types, with no significant changes in basal area until 33 years after disturbance, whereas both deciduous and mixedwood stands had significantly higher stand basal area within 15 years. Conifer stands also had smaller concentrations of K in all three soil layers, Ca in both the forest floor and surface mineral soil, and N in the forest floor, compared with deciduous stands. Mixedwood stands were intermediate. These observations indicate the higher acidity and less nutrient-rich chemistry of boreal conifer trees (Yuan and Chen 2009, Laganière et al. 2010, Paré et al. 2013, Augusto et al. 2015), and in the case of K, the persistence of the overstory effect throughout the soil layers may indicate a drier soil environment in conifer compared to deciduous stands, since the dense and persistent canopies of conifer soils are associated with greater canopy interception and retention of precipitation (Augusto et al. 2015), and the K cycle is strongly restricted by low soil moisture (Sardans and Peñuelas 2015).

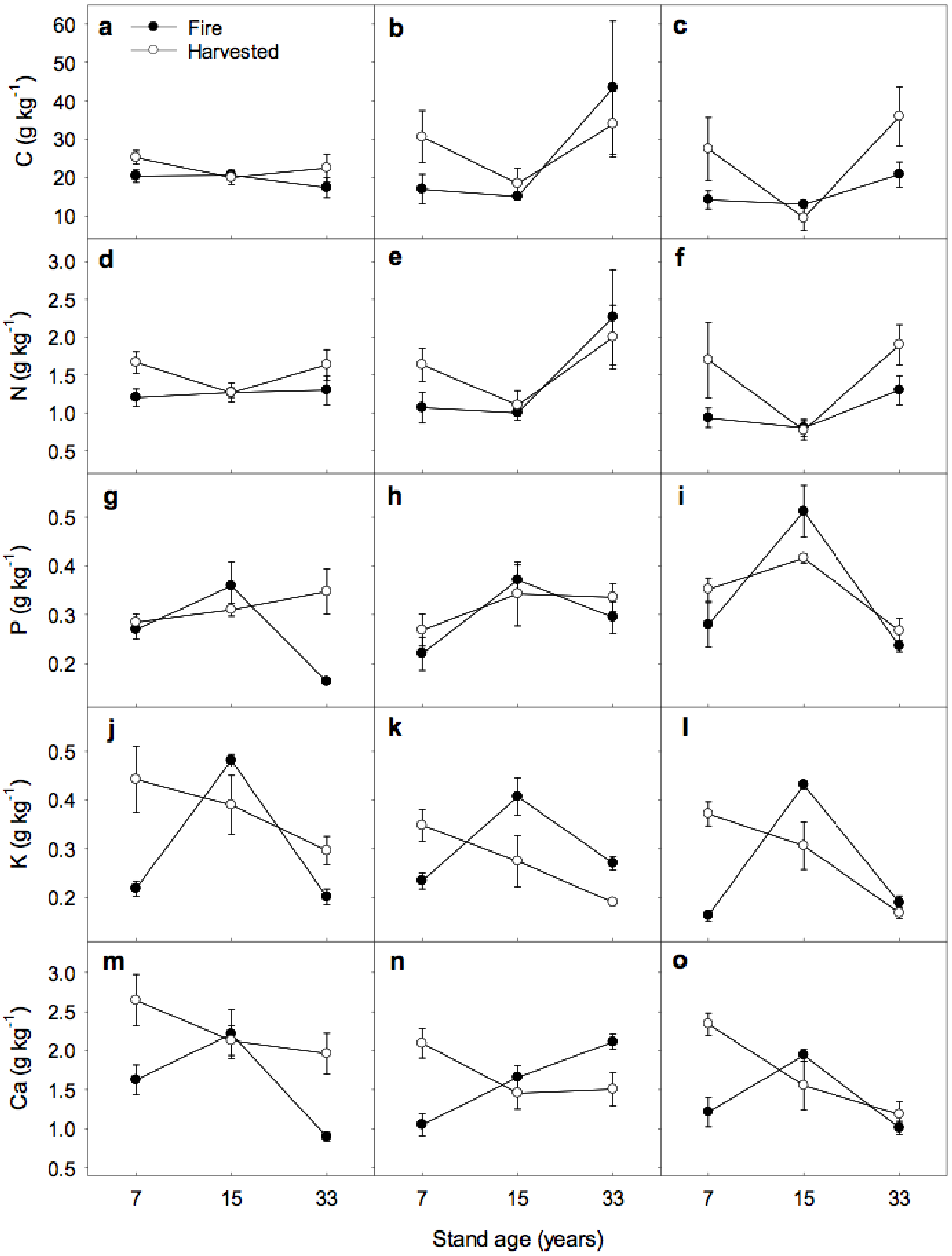

Figure 2.3. Effects of disturbance origin, overstory type, and stand age on nutrient concentrations of the surface mineral soil (M1, 0-15 cm): (**a**) total carbon concentration ([C]) in deciduous stands, (**b**) [C] in mixedwood stands (**c**) [C] in conifer stands, (**d**) total nitrogen concentration ([N]) in deciduous stands, (**e**) [N] in mixedwood stands, (**f**) [N] in conifer stands, (**g**) total phosphorus concentration ([P]) in deciduous stands, (**h**) [P] in mixedwood stands, (**i**) [P] in conifer stands, (**j**) total potassium concentration ([K]) in deciduous stands, (**k**) [K] in mixedwood stands, (**l**) [K] in conifer stands, (**m**) total calcium concentration ([Ca]) in deciduous stands, (**n**) [Ca] in mixedwood stands, (**o**) [Ca] in conifer stands. Values are mean ± 1 SE.

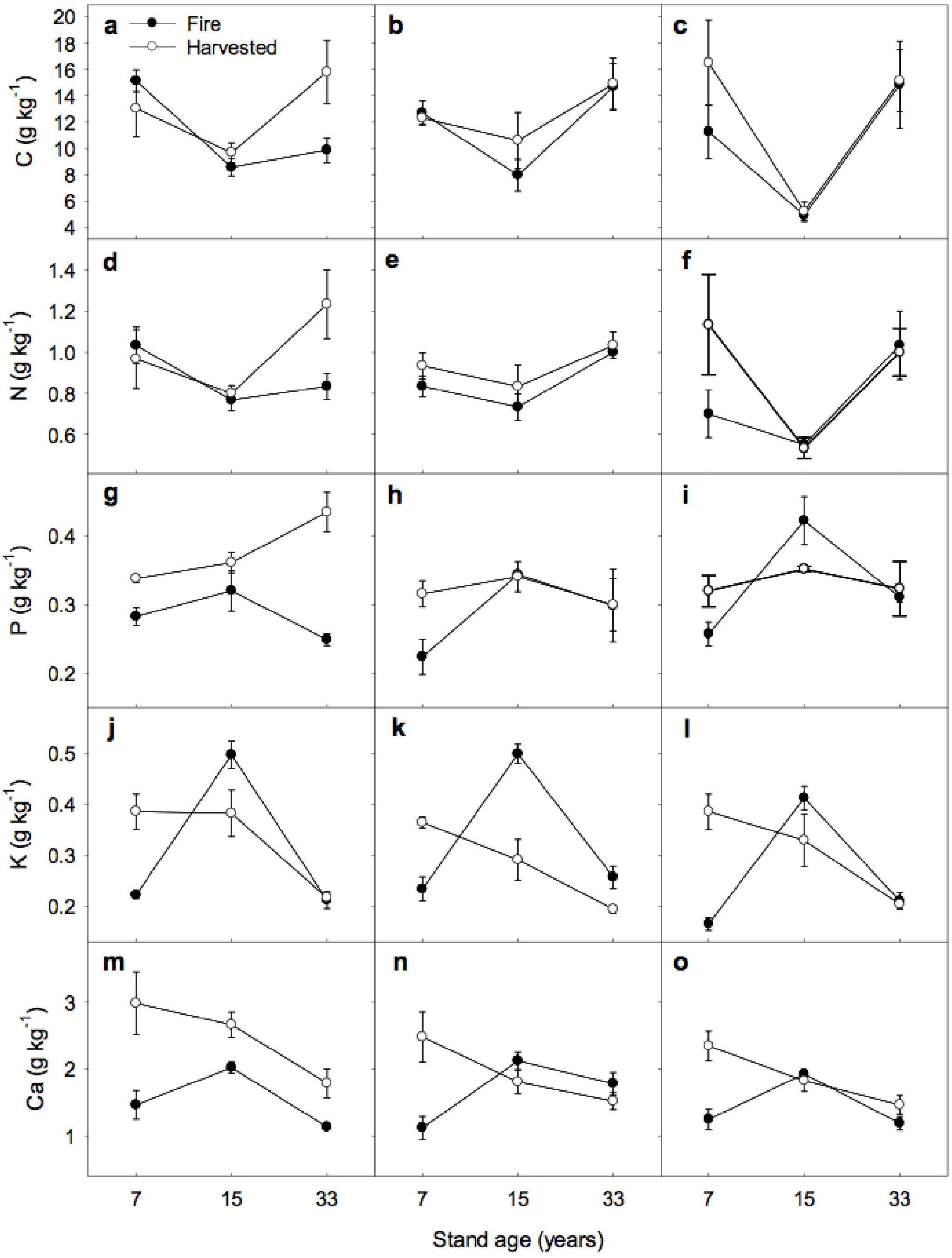

Figure 2.4. Effects of disturbance origin, overstory type, and stand age on nutrient concentrations of the subsurface mineral soil (M2, 15-30 cm): (**a**) total carbon concentration ([C]) in deciduous stands, (**b**) [C] in mixedwood stands (**c**) [C] in conifer stands, (**d**) total nitrogen concentration ([N]) in deciduous stands, (**e**) [N] in mixedwood stands, (**f**) [N] in conifer stands, (**g**) total phosphorus concentration ([P)] in deciduous stands, (**h**) [P] in mixedwood stands, (**i**) [P] in conifer stands, (**j**) total potassium concentration ([K]) in deciduous stands, (**k**) [K] in mixedwood stands, (**l**) [K] in conifer stands, (**m**) total calcium concentration ([Ca]) in deciduous stands, (**n**) [Ca] in mixedwood stands, (**o**) [Ca] in conifer stands. Values are mean ± 1 SE.

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APPENDICES

Appendix 2.1.

Table A.2.1. Particle analysis results from the mineral soil at a depth of 30-50 cm for 54 stands sampled in the boreal forest of Ontario, Canada. Values are mean ± SE.

Disturbance origin	Stand age	Overstory	Texture (%)		
			Sand	Silt	Clay
Fire	7	B	70.1 (5.8)	24.8 (6.3)	5.1 (1.1)
	7	C	78.5 (5.4)	14.3 (3.9)	7.2 (2.5)
	7	M	89.1 (1.1)	7.5 (2.1)	3.3 (1.1)
Harvested	7	B	64.1 (3.2)	27.3 (2.3)	8.6 (2.9)
	7	C	71.0 (4.4)	25.9 (4.4)	3.1 (0.2)
	7	M	81.6 (2.4)	14.6 (1.5)	3.8 (0.9)
Fire	15	B	74.1 (3.7)	19.1 (3.4)	6.9 (0.3)
	15	C	85.2 (1.8)	8.2 (1.6)	6.5 (0.5)
	15	M	81.6 (3.6)	12.2 (1.8)	6.2 (1.9)
Harvested	15	B	67.7 (4.2)	18.9 (2.1)	13.3 (4.6)
	15	C	82.1 (6.4)	10.8 (5.2)	7.1 (1.2)
	15	M	77.0 (3.0)	18.4 (2.0)	4.6 (1.0)
Fire	33	B	73.5 (1.0)	21.5 (2.1)	5.0 (1.7)
	33	C	77.1 (7.3)	16.9 (6.0)	6.0 (1.4)
	33	M	68.8 (8.6)	26.7 (8.8)	4.5 (0.3)
Harvested	33	B	68.4 (1.1)	27.2 (1.1)	4.4 (0.4)
	33	C	74.1 (3.8)	19.4 (3.7)	6.6 (0.0)
	33	M	63.6 (1.3)	27.6 (0.7)	8.8 (0.5)

Abbreviations: B – broadleaf deciduous overstory type, C – conifer overstory type, M – mixedwood overstory type.

Appendix 2.2.

Table A.2.2. Effects of stand age (A_i, $i = 1, 2, 3$) and overstory type (T_j, $j = 1, 2, 3$) on intrinsic soil texture for the mineral soil at a depth of 30-50 cm for 54 stands sampled in the boreal forest of Ontario, Canada.

Texture	Age		Overstory		Age × Overstory	
	F	*P*	*F*	*P*	*F*	*P*
Sand	2.09	0.137	4.04	0.025	2.46	0.060
Silt	3.92	0.027	3.17	0.052	2.17	0.089
Clay	1.53	0.229	1.44	0.248	1.09	0.375