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Effect of Fertilization on Growth and Mortality of Jack Pine Growing on Poor, Sandy Soils in Michigan, USA: Implications for Sustainable Management

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Abstract: Our understanding of nutrient limitations to jack pine (*Pinus banksiana* Lamb.) growth is lacking across the Lake States of the USA (Michigan, Wisconsin and Minnesota), where this species makes up an important forest cover type on nutrient poor sands. Currently this cover type is managed using whole-tree harvesting (WTH) across large areas of state and federal forestland, which raises concerns for long-term declines in soil fertility and future productivity. In this study, I carried out a factorial fertilization experiment to better understand potential nutrient limitations to jack pine growth on excessively drained sandy soils in northern Lower Michigan. Treatments were nitrogen (N), phosphorus (P) and base cations applied singly and in all factorial combinations. In addition, I constructed input-output nutrient budgets for jack pine management in northern Lower Michigan using existing data on atmospheric deposition, weathering and harvest nutrient removals. In no case did I observe an increase in tree growth rate to fertilization, instead I observed an overall decline in growth rates, and an increase in mortality rates, in trees fertilized with N. Nitrogen-induced imbalances of foliar N: potassium (K) were strongly correlated with decreased growth in N amended plots. Together with nutrient budget analysis, which indicated that harvest removals of K greatly exceed inputs over the planned rotation, this suggests that WTH may not be sustainable over multiple rotations. Furthermore, the impacts of WTH on ecosystem K status are likely to be exacerbated over time by anthropogenic N deposition.

Keywords: nutrient limitation; nitrogen; potassium; whole-tree harvest; stem-only harvest

1. Introduction

The degree and nature of nutrient limitations to forest productivity have important implications for designing silvicultural systems that will sustain long-term soil productivity, as well as for understanding the impacts of anthropogenic nitrogen (N) deposition on forest productivity. Nitrogen availability has long been viewed as limiting the productivity of most temperate and boreal forests, a view that has been strongly supported by recent meta analyses of N addition experiments [1,2]. However, other metanalyses and reviews have indicated that co-limitation of forest productivity by phosphorus (P) may be widespread, even in high-latitude systems [3,4]. More recently, a global review of the literature on potassium (K) biogeochemistry has argued that K availability may be as limiting as either N or P for terrestrial productivity [5]. I investigated the nature of nutrient limitations to tree growth in young jack pine (*Pinus banksiana* Lamb.) plantations in Michigan, USA, in order to better understand the sustainability of current silvicultural practices, and to assess the likely response of this system to anthropogenic N deposition.

For decades, there has been great concern in the forestry literature over the prospect that large nutrient removals associated with intensive harvesting of forest residues may result in long-term

declines in soil fertility. This topic was intensively researched in the 1980s with comparisons of traditional stem-only harvesting (SOH) vs. whole-tree harvesting (WTH) (e.g., [6,7]). Interest in this topic revived in the late 2000s with increasing emphasis on intensification of forest harvesting to meet biomass energy goals (e.g., [8,9]). From the 1980s through the present day, a consistent finding has been that forests found on sandy soils with low inherent fertility are more susceptible to long-term declines in soil fertility from intensive harvesting compared to forests on finer-textured soils with greater capacity to supply base cations through weathering [6–11]. Despite this clear understanding, jack pine forests growing on extremely acidic, nutrient-poor outwash sands across the Lake States region continue to be managed with WTH. In fact, woody biomass harvesting guidelines for both the state of Michigan and the state of Wisconsin, provide special exemptions to forest residue retention guidelines for this species, allowing for WTH [12,13]. The rationale provided for this exception in both states' guidelines is that jack pine has a lower demand for nutrients, compared to other species, therefore, greater nutrient removals are unlikely to impact future forest productivity. In addition, anecdotally, foresters in this region view moisture as the overarching limiting factor on the excessively drained outwash sands where jack pine grows, and thus see nutrient availability as relatively unimportant to growth of these forests. Whereas, jack pine has been shown to be very responsive to fertilization (particularly N) in Canadian studies (reviewed by [14]), we are not aware of any studies of nutrient limitation to jack pine growth on excessively drained outwash sands in the Lake States.

Anthropogenic additions of reactive N to the global N cycle represent one of the most significant components of global environmental change [15,16]. Widespread inputs of a growth-limiting nutrient through atmospheric N deposition have been attributed with increasing forest productivity and carbon sequestration on a global basis [2,17–19]. The fact that boreal conifer forests have been traditionally viewed as being strongly limited by N [20,21], suggests that they should be particularly responsive to anthropogenic N deposition. However, other studies have indicated that coniferous trees are either less responsive to added N compared to broadleaved trees [22], or even experience growth declines in response to increased N availability [19], especially where base cation availability is low and N additions lead to imbalances or deficiencies in tree nutrition [23]. Xeric site conditions also have the potential to inhibit the response of conifer stands to N additions. Several studies have indicated that N fertilized conifers are more susceptible to drought stress compared to trees grown with lower levels of N [20,24,25], or that the response to added N can be nullified by inadequate moisture [26]. Thus jack pine in the Lake States growing at the southern limit of the species' distribution and restricted to excessively-drained sands may be less responsive to atmospheric N deposition due to the combination of low base cation availability and drought stress.

In this study, I used a factorial fertilization experiment to assess the degree to which young jack pine plantations growing on excessively drained outwash sands are limited by N, P or base cations. I expected jack pine would respond with increased growth to N fertilization, but that growth response to N would be modest in this drought stressed ecosystem, compared to responses documented for jack pine growing in less drought stressed conditions in boreal Canada. Furthermore, I expected that growth response to N would be constrained by the availability of P and base cations on these extremely coarse textured soils.

2. Materials and Methods

2.1. Study Sites and Experimental Design

I assessed nutrient limitations to growth in two young jack pine plantations located in the Highplains District of northern Lower Michigan [27]. One plantation was located in Presque Isle County (PI; 45.219°, −84.166°) and the other was located in Ogemaw County (OG; 44.473°, −84.283°). Both plantations were established by the Michigan Department of Natural Resources (MDNR) to provide breeding habitat for the endangered Kirtland's warbler (KW; *Setophaga kirtlandii*) following whole-tree harvesting of a preceding stand of mature jack pine. The PI plantation was established in

2008, whereas the OG plantation was established in 2007. Soil at the PI site is classified as a sandy, isotic, frigid Typic Udipsamment (Grayling Sand), whereas soil at the OG site is classified as a sandy, mixed, frigid, Alfic Haplorthod (Mancelona Sand). Both plantations were planted at relatively high densities (ca. 1.3 × 2.0 m spacing) in undulating rows characteristic of KW plantations [28].

On 7 May 2015, I established 24 plots at each site in a randomized complete block design with three replications. Blocks were located on level ground, in relatively homogeneous areas of the plantation determined a priori from satellite imagery. Each plot contained 25 trees (5 rows of 5 trees each), with at least a 4-tree buffer between plots. Within each block, I randomly assigned plots to one of 8 factorial fertilization treatments. Treatments were N (applied as urea), P (applied as triple superphosphate), and base cations (abbreviated B; applied as a combination of K-Mag fertilizer and pelletized gypsum (20% Ca, 16% S). Application rates were 100 kg ha^{-1} for N, 100 kg ha^{-1} for P and 100 kg K ha^{-1}, 100 kg Ca ha^{-1}, and 51 kg Mg ha^{-1} in the B treatment. In addition to the base cations, the B treatment also delivered 170 kg ha^{-1} of sulfur (S). I applied fertilizer treatments in a complete factorial combination including all interactions for a total of 8 treatments (control, N, P, B, N + P, N + B, P + B and N + P + B). Fertilizer was spread evenly by hand throughout each entire 25-tree plot; however, measurements were only conducted on the interior 9 (3 × 3) trees.

2.2. Field Measurements and Data Analysis

I measured initial tree heights of the interior 9 trees in every plot on 19–20 May 2015, prior to bud break. Heights were measured with a height pole to the nearest cm. Plots were visited again on 26 October 2015, 23 October 2016 and 19 October 2017, and trees were recorded as alive or dead and heights measured for all living trees. For simplicities sake, herein I only report cumulative height growth and cumulative mortality for the entire period May 2015 through October 2017. In addition to absolute height growth (cm), for each tree I calculated relative growth rate (RGR) using the formula:

$$\text{RGR} = (\ln H_2 - \ln H_1)/(t_2 - t_1) \tag{1}$$

where H_2 and H_1 are heights at t_2 (October 2017) and t_1 (May 2015).

On 1 November 2017, I collected foliage from three interior trees per plot that were either dominant or co-dominant in height. From each tree I collected a single shoot of new (2017) growth from the upper 1/4 of the crown, on the north side of the tree, making sure that that shoot was completely unshaded by any other branches. Shoots from the three trees were composited by plot, returned to the laboratory and dried at 65 °C. Needles were plucked from each shoot, mixed well and then pulverized to a fine powder in a ball mill. Needles were sent to a commercial lab (A & L Great Lakes Laboratories, Fort Wayne, IN, USA) for analysis of N by dry-combustion gas chromatography and of P, K, Ca and Mg by microwave-assisted nitric acid digestion and inductively-coupled plasma atomic emission spectrometry (ICP-AES).

Growth, RGR, mortality and foliar nutrient concentration data were analyzed using a Linear Mixed Model for a randomized complete block design with fixed effects of Site, N, P and B, random effects of blocks within each site, and experimental plots for factorial fertilizer assignment. We used the normal residuals as the error term. I accounted for heterogeneous variances in blocks/sites and fertilizer treatments by fitting an unequal-variance model. Mortality data were arcsine transformed prior to analysis. Dunnett-Hsu multiple comparison procedure was used to compare growth, RGR and mortality for each fertilizer treatment against the unfertilized control. As an exploratory tool to understand foliar nutrient factors that might underlie variability in tree growth among treatments, I conducted simple linear correlations of absolute growth and RGR against foliar concentrations of individual macronutrients, as well as foliar ratios of all macronutrients to N. Statistical significance for all analyses was accepted at the 0.05 level. Statistical analyses were performed using SAS version 9.3 software (©2010 SAS Institute Inc., Cary, NC, USA).

2.3. Nutrient Budgets

In order to put growth and mortality responses to fertilizer applications into a broader ecosystem and management context, I constructed basic, input-output nutrient budgets for current KW habitat management on glacial outwash landforms in northern Lower Michigan. This exercise was based on publically available environmental monitoring data (e.g., atmospheric deposition rates, soil survey data) and publications in the peer-reviewed literature. Jack pine plantations managed for Kirtland's warbler are established after whole-tree harvesting on a planned rotation length of 50 years. Therefore, I estimated the amount of N, P, K, Ca and Mg removed in whole-tree harvesting as the average of total above ground nutrient stocks for jack pine plantations on similar soils in northern Lower Michigan quantified by Alban [29]. I also estimated harvest nutrient removals from a hypothetical stem-only harvest scenario using just bolewood and bark nutrient stocks from the same source. I estimated nutrient inputs via atmospheric deposition over a 50-year rotation using total deposition data from the National Atmospheric Deposition Program [30]. These deposition estimates account for both wet and dry deposition using a combination of empirical and modeled data as described by Schwede and Lear [31]. I calculated the annual average total deposition for the study area across all 16 years of data available (2000–2015) from the National Atmospheric Deposition Program (NADP). I estimated base cation weathering rates using the "clay fraction method" [32], texture data available from the soil survey [33], and proportions of exchangeable cations in comparable soils from Rothstein and Spaulding [34]. I estimated inputs of P from weathering as 0.3 kg ha^{-1} y^{-1} based on data reported in Newman et al. [35]. For nitrogen inputs, I made the highly conservative estimate that rates of biological fixation averaged 1 kg N ha^{-1} y^{-1}. Non-symbiotic fixation alone has been estimated to average 2–3 kg N ha^{-1} y^{-1} in forest ecosystems worldwide [36], and these jack pine forests have abundant symbiotic N fixers including *Comptonia perigrina* (L.) J.M. Coult. (Myricaceae) and lichens. Because I had no data available on leaching losses of N, P, K, Ca or Mg from these ecosystems, I constructed nutrient budgets under three scenarios of assumed leaching rates: (1) 100% of annual inputs are retained (i.e., a completely closed system); (2) 2/3 of annual inputs are retained and 1/3 leached (i.e., a moderately leaky system); and (3) 1/3 of annual inputs are retained and 2/3 are leached (i.e., a highly leaky system). Under each of these scenarios, I estimated the number of years of nutrient inputs that would be required for the system to recover the nutrients removed in WTH or SOH.

3. Results

3.1. Tree Growth and Mortality

There were significant main effects of N addition ($p < 0.001$) and base cation addition ($p = 0.010$) on absolute tree growth rates over the course of the experiment. Tree growth was lower overall in plots with added N compared to plots without added N (Figure 1a), whereas tree growth was greater overall in plots with added base cations compared to plots without (Figure 1b). No other main effects or interactions had a significant effect on absolute growth rates. Dunnett's multiple comparison tests indicated that the N + P treatment had significantly lower growth than the control treatment ($p = 0.001$), but none of the other individual fertilizer treatments had growth rates significantly different from the control (Figure 1c).
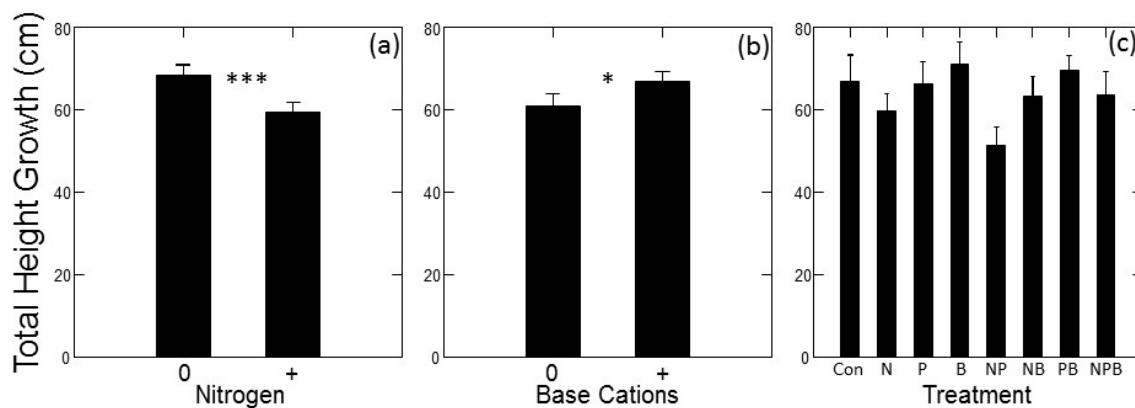
Figure 1. Absolute growth rates of jack pine (*Pinus banksiana* Lamb.) in northern Lower Michigan in response to fertilization plotted as main effects (±1 Standard Error (SE)) of N (**a**) and Base Cations (**b**) and individual factorial treatments compared to control (**c**). Data represent mean total height growth in cm from May 2015 through October 2017. For panels (**a**,**b**) horizontal axis symbols indicate treatment with ("+") and without ("0") added fertilizer. Symbols in (**a**,**b**) indicate significance of main effects, symbols in (**c**) indicate growth significantly different from the control at $p < 0.05$ (*) and $p < 0.001$ (***).

There were significant main effects of site ($p = 0.031$), N addition ($p = 0.005$) and base cation addition ($p = 0.011$) on relative growth rates over the course of the experiment. No other main effects or interactions had a significant effect on relative growth rates. Relative growth rates were higher in the OG site, solely because trees at this site were shorter at the start of the experiment: initial heights at OG averaged 160 cm (s.d. = 24.5) compared to 193 cm (s.d. = 30.1) at PI. Responses of RGR to added nutrients were essentially identical to those of absolute growth. N-amended plots had lower RGR (Figure 2a) and base cation amended plots had higher RGR (Figure 2b). Dunnett's multiple comparison tests indicated that the N + P treatment had significantly lower RGR than the control treatment ($p = 0.034$), but none of the other individual fertilizer treatments had RGR significantly different from the control.
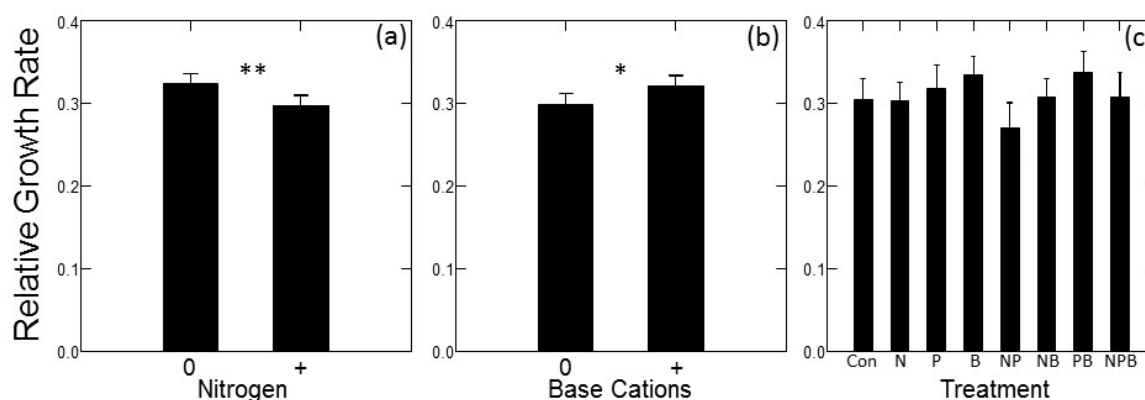

Figure 2. Relative growth rates of jack pine (*Pinus banksiana*) in northern Lower Michigan in response to fertilization plotted as main effects (±1 SE) of N (**a**) and Base Cations (**b**) and individual factorial treatments compared to control (**c**). For panels (**a**,**b**), horizontal axis symbols indicate treatment with ("+") and without ("0") added fertilizer. Symbols in (**a**,**b**) indicate significance of main effects, symbols in (c) indicate growth significantly different from the control at $p < 0.05$ (*) and $p < 0.01$ (**).

There was a significant main effect of N addition on mortality rate ($F_{1,14.1} = 6.92$; $p = 0.020$), with higher mortality in treatments with added N compared to treatments without added N (Figure 3a). No other main effects or interactions had a significant effect on tree mortality. Dunnett's multiple comparison tests also indicated that none of the individual fertilizer treatments had mortality rates significantly different from the control.
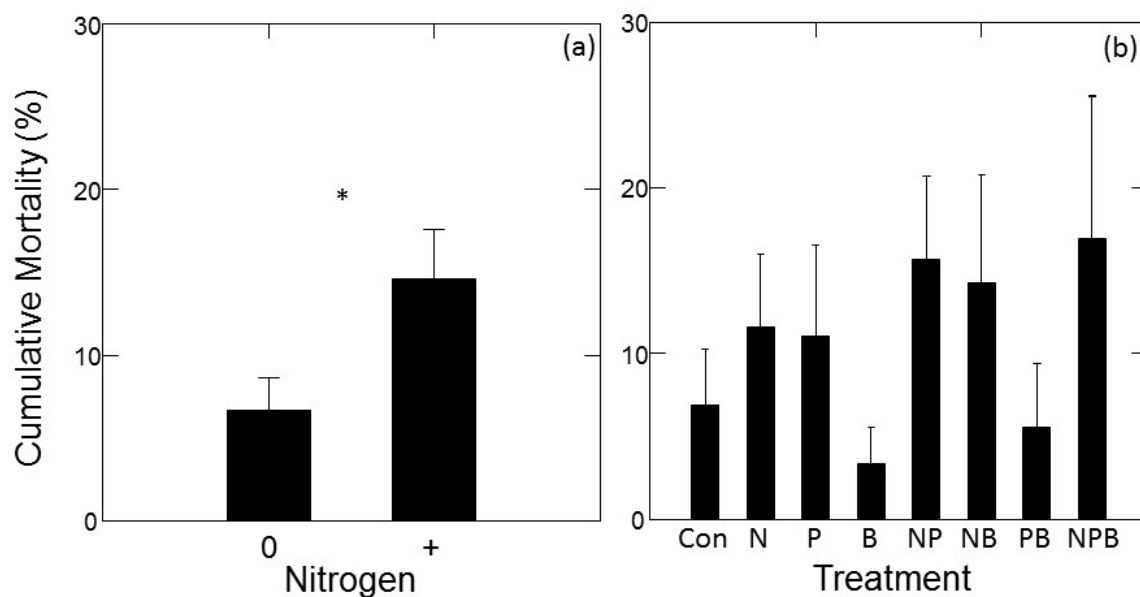
Figure 3. Mortality of jack pine (*Pinus banksiana*) in northern Lower Michigan in response to fertilization plotted as main effects (±1 SE) of N (**a**) and individual factorial treatments compared to control (**b**). Data represent mean cumulative tree mortality occurring between May 2015 and October 2017. In panel (**a**), horizontal axis symbols indicate treatments with ("+") and without ("0") added nitrogen. Symbols in (**a**) indicate significance of main effects, symbols in (**b**) indicate growth significantly different from the control at $p < 0.05$ (*).

3.2. Foliar Nutrition

Figure 4 illustrates the main effects of fertilizer treatments on foliar macronutrient concentrations; there were no significant interactive effects on any foliar nutrition parameters. Foliar N concentrations trended higher in N-amended plots; however, the main effect of N addition was not statistically significant (Figure 4a; $p = 0.086$). In contrast, addition of N tended to decrease concentrations of other macronutrients. Foliar S (Figure 4d; $p = 0.001$), foliar Ca (Figure 4e; $p = 0.011$) and foliar Mg (Figure 4f; $p = 0.004$) all declined significantly with N addition; however, the decline in foliar K with N addition was not quite statistically significant (Figure 4c; $p = 0.065$). Addition of P led to a significant decrease in foliar N (Figure 4a; $p = 0.024$) but did not significantly affect any other foliar macronutrient. Addition of base cations (and S) led to a marginally-significant increase in foliar K (Figure 4c; $p = 0.086$) and significant increases in foliar S (Figure 4d; $p < 0.001$) and foliar Mg (Figure 4f; $p < 0.001$).

As an exploratory tool to understand factors that may underlie variability in tree growth, I conducted simple linear correlations of absolute growth and RGR against foliar macronutrient concentrations and ratios of foliar N to all other macronutrients (Table 1). The ratio of N:K was the only foliar nutrition parameter that was significantly correlated with absolute growth, and it exhibited the strongest correlation with RGR. Both absolute growth and RGR declined with increasing foliar N:K ratio (Figure 4a,b). Foliar N and foliar P concentrations were significantly correlated with RGR only (Table 1); for both, RGR declined with increasing foliar nutrient concentration (Figure 4c,d). All statistically significant correlations between foliar nutrition parameters and growth are plotted in Figure 5.
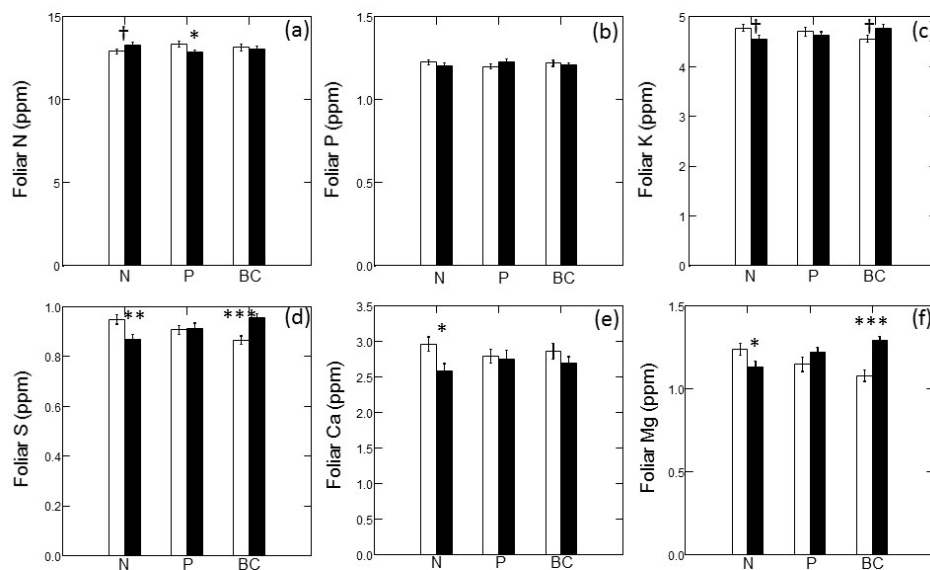
Figure 4. Foliar macronutrient concentrations of jack pine (*Pinus banksiana*) in northern Lower Michigan in response to main effects of nitrogen (N), phosphorus (P) and base cations (BC). Individual panels present data for N (**a**), P (**b**), potassium (**c**), sulfur (**d**), calcium (**e**), and magnesium (**f**). Values are means (±1 SE) for unfertilized plots (open bars) and fertilized plots (filled bars). Symbols indicate significance of main effects at $p < 0.1$ (†); $p < 0.05$ (*); $p < 0.01$ (**) *and* $p < 0.001$ (***).

Table 1. Correlation coefficients and probabilities (Bonferonni) for simple linear correlations between absolute and relative tree growth rates and foliar nutrition parameters of jack pine (*Pinus banksiana* Lamb.) in northern Lower Michigan. Statistically significant correlations are indicated by bold text. Statistically significant correlations are plotted in Figure 5.

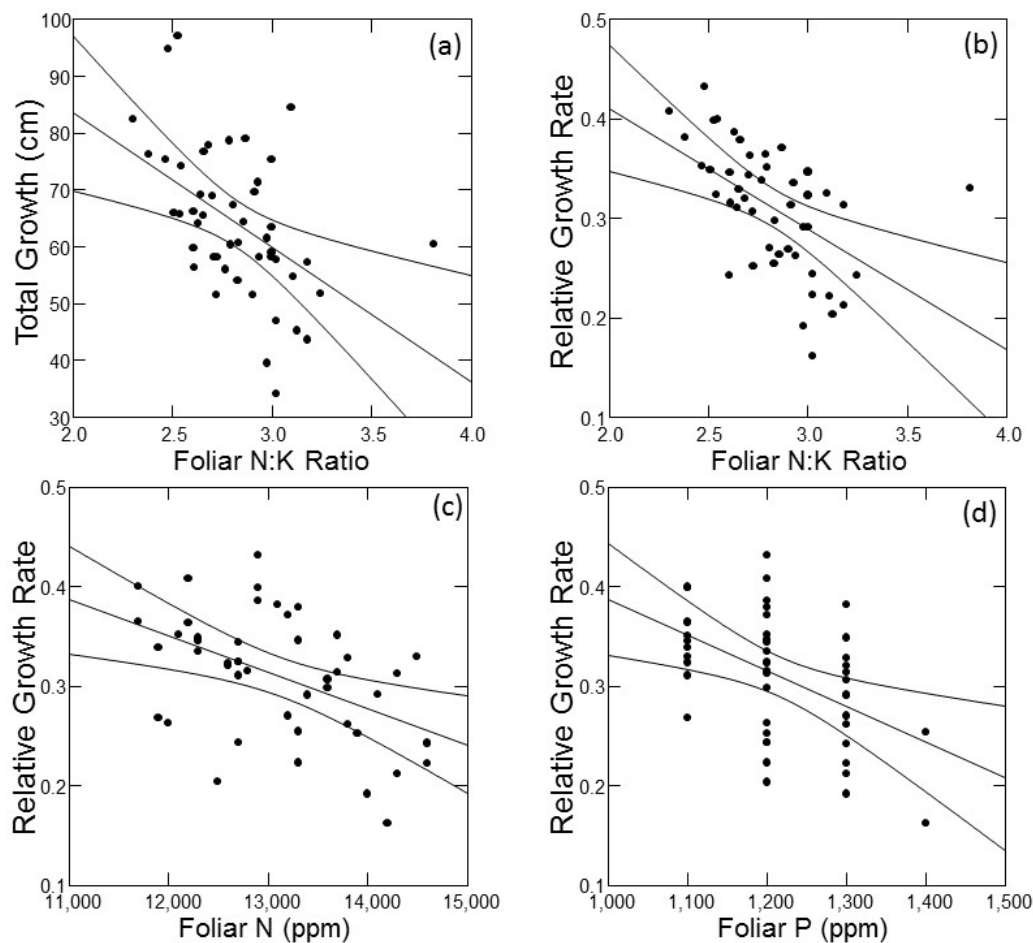| Absolute Growth (cm)	*r*	*p*
Foliar N (ppm)	−0.425	0.118
Foliar P (ppm)	−0.351	0.647
Foliar K (ppm)	0.248	1.000
Foliar S (ppm)	−0.055	1.000
Foliar Ca (ppm)	0.071	1.000
Foliar Mg(ppm)	0.131	1.000
Foliar N:P Ratio	−0.050	1.000
Foliar N:K Ratio	**−0.490**	**0.018**
Foliar N:S Ratio	−0.190	0.585
Foliar N:Ca Ratio	−0.216	1.000
Foliar N:Mg Ratio	−0.178	1.000
Relative Growth Rate		
Foliar N (ppm)	**−0.493**	**0.017**
Foliar P (ppm)	**−0.481**	**0.024**
Foliar K (ppm)	0.240	1.000
Foliar S (ppm)	−0.220	0.398
Foliar Ca (ppm)	−0.118	1.000
Foliar Mg (ppm)	0.200	1.000
Foliar N:P Ratio	0.021	1.000
Foliar N:K Ratio	**−0.526**	**0.005**
Foliar N:S Ratio	−0.059	1.000
Foliar N:Ca Ratio	−0.053	1.000
Foliar N:Mg Ratio	−0.248	1.000

Figure 5. Plots of significant correlations (from Table 1) with 95% confidence intervals between foliar nutrition parameters (*X* axes) and absolute or relative growth rates (*Y* axes) of jack pine (*Pinus banksiana*) in northern Lower Michigan. Individual panels present data for absolute growth against foliar N:K (**a**), and relative growth rate against foliar N:K (**b**), foliar N (**c**) and foliar P (**d**).

3.3. Nutrient Budgets

Results from simple, input-output nutrient budgeting are presented in Table 2. Of the five macronutrients investigated, K stood out as having the greatest imbalance between outputs and inputs. Even under the impossibly optimistic scenario of 100% retention of inputs (zero leaching losses), I estimate that it would take 73 years for weathering and deposition to replace the K removed via WTH. This exceeds the planned harvest rotation for these plantations by 23 years. Under the most "leaky" scenario (only 1/3 of annual inputs retained in the system), this estimate increased to 117 years. Under SOH, replacement times for K ranged from 35 years under the 100% retention scenario to 55 years under the 1/3 retention scenario. In contrast, even under the most pessimistic scenario (WTH, 1/3 retention), N, P and Ca removals were all replaced within the planned 50-year rotation for these plantations. Under SOH, N, P, and Ca, replacement times ranged from 8–12 years under the 100% retention scenario to 15–20 years for the 1/3 retention scenario. Replacement times for Mg were generally longer than for N, P and Ca, but only exceeded the planned harvest rotation by three years under the most pessimistic scenario of WTH with 1/3 retention.

Table 2. Estimated nutrient budgets for jack pine (*Pinus banksiana*) plantations on glacial outwash sands in northern Lower Michigan. Data below are the estimate of the number of years required for ecosystems to recover nutrients removed in either whole-tree harvesting or stem-only harvesting under three different scenarios of nutrient leaching: 100% nutrient retention, 2/3 nutrient retention and 1/3 nutrient retention (see Nutrient Budgets in Methods above for details). Scenarios under which nutrient recovery would not be achieved within the planned 50-year rotation are indicated with bold numbers.

	Nutrient Leaching Scenarios		
Whole-Tree Harvest	**100% Retention**	**2/3 Retention**	**1/3 Retention**
Nitrogen	20	28	48
Phosphorus	27	33	43
Potassium	**73**	**90**	**117**
Calcium	19	23	31
Magnesium	25	34	53
Stem-only Harvest			
Nitrogen	8	11	19
Phosphorus	10	12	15
Potassium	35	42	**55**
Calcium	12	15	20
Magnesium	14	19	30

4. Discussion

Contrary to my original expectation, I found no evidence that the availability of macro-nutrients limits the growth of young jack pine plantations on glacial outwash sands in northern Lower Michigan. None of the macronutrients, added singly or in combination, increased growth of jack pine relative to unfertilized controls (Figure 1c). These results are in sharp contrast with results from numerous jack pine fertilization studies in boreal Canada, which consistently demonstrate a strong growth response to added nitrogen, either alone or in combination with P and K (65 fertilization studies of jack pine reviewed by [14]). In contrast, I could only find a single fertilization study on jack pine in the Lake States, in which two young (7 and 11 year old) jack pine stands growing on outwash sands in northwestern Wisconsin showed no growth response to N fertilization [37]. Although data on fertilization response of jack pine in the Lake States are extremely limited, the lack of response in our study and that of McCullough and Kulman [37] is intriguing and consistent with the anecdotal reasoning of regional foresters that extreme drought stress is the overwhelming limiting factor on outwash sands of this region. It may be that the higher growing season temperatures and greater evaporative demand [38] here at the southern limit of jack pine's range constrain its responsiveness to added nutrients. Lim et al. [26] recently demonstrated that drought stress constrained the responsiveness of Scots pine (*Pinus sylvestris* L.) to nitrogen fertilization. More experimental data on the responsiveness of jack pine to fertilization across the Lake States, especially across a range of stand ages and site conditions, is needed to better understand constraints to productivity in this region.

Biomass harvesting guidelines developed by state agencies in Wisconsin and Minnesota provide special exemptions allowing for WTH of jack pine on outwash sands [12,13]. The rationale for this exception in both states' guidelines is that jack pine has a lower demand for nutrients compared to other species; therefore, greater nutrient removals are unlikely to impact future forest productivity. My finding that growth rates of young jack pine plantations do not respond to added macro nutrients is consistent with this reasoning and would seem to support the assertion that greater nutrient removals due to WTH will not result in productivity declines through future rotations. However, my analysis of nutrient input-output budgets, together with data from the fertilization study suggest that this approach may not be sustainable over the long term. Most notably, my estimates of K removals in WTH greatly exceed estimated inputs from atmospheric deposition and weathering; even assuming a perfectly closed system (no K leaching) it would take more than 70 years for deposition and weathering to replace the K removed by WTH (Table 2). Thus, it seems clear that repeated WTH of jack pine

on a 50-year rotation will lead to long-term depletion of K in these coarse, sandy soils. This finding is consistent with a recent study of Corsican pine (*Pinus nigra* Arnold) on sandy soils in Belgium, where weathering and deposition of Ca, K and P were insufficient to replace removals by WTH [39]. This finding is also consistent with increasing recognition of the global significance of K as a limiting nutrient for forest productivity and its potential sensitivity to harvest removals [5,40].

The response of tree growth, mortality and foliar nutrition to factorial fertilization treatments further supports the significance of K removals from these systems, and suggests the potential for limitation by K and other base cations to be exacerbated by N deposition. In this study, I observed a strong negative response to N fertilization, whereby plots with added N had lower rates of tree growth and higher rates of mortality compared to plots without added N (Figures 1a, 2a and 3a). In contrast, plots with added base cations had higher rates of tree growth (Figures 1b and 2b), with no significant effect on mortality. Data on foliar nutrition clearly demonstrate that N additions led to strong reductions in foliar base cation concentrations. This is consistent with a large body of literature on N saturation, which indicates that N additions to forest ecosystems can lead to deficiencies and imbalances of other nutrients, particularly base cations [23,41,42]. For K, Sardans and Peñuelas [5] reviewed 27 studies that documented impacts of N additions on K supply to plants, and consistently found enhanced K leaching, reduced foliar K concentrations and increased foliar N:K ratios. In this study, I found that foliar N:K ratio was the foliar nutrition parameter most strongly correlated with tree growth rates; suggesting that N:K imbalances may explain the reduction in tree growth induced by N fertilization.

Nutrient budget estimates (Table 2), together with N fertilization impacts on tree growth mortality and foliar nutrition (Figures 1–4), indicate the potential for long-term declines in soil fertility and forest productivity under the combined effects of WTH and atmospheric N deposition. Potassium depletion appears to be the most likely mechanism by which such a decline could occur; K removals in WTH far exceed inputs and foliar N:K imbalances appear to be an important driver of negative growth response to N additions. Potassium deficiencies and imbalances may be particularly important for jack pine in the Lake States, given the critical role of K in drought tolerance [5]. Because jack pine in the Lake States occurs at the southern limit of the species' range on excessively drained soils, drought-induced stresses will likely grow in importance as the climate warms [43]. Thus, the combination of WTH removals of K and continued atmospheric deposition of N are likely to decrease the resilience of these ecosystems to a warming climate. Whole-tree harvesting of jack pine became common in this region in the early 1980s when intensive management efforts to create young jack pine stands for the KW began [28]. Therefore, the earliest plantations established for KW will be reaching rotation age in the next 10 years. Because of the high concentrations of K in foliage relative to bolewood [29], transitioning to SOH for the next generation of KW habitat would greatly reduce the amount of K removals associated with harvesting (Table 2).

5. Conclusions

I could find no evidence that growth rates of young jack pine plantations on xeric sands are limited by availability of macronutrients. Instead, I observed a decline in growth rates, and an increase in mortality rates, in trees fertilized with N. Nitrogen-induced deficiencies of K and/or N:K imbalances appear to be the cause of the negative growth response to added N. Together with nutrient budget analysis, which indicates that harvest removals of K greatly exceed inputs over the planned rotation, this suggests that WTH may not be sustainable over multiple rotations. Impacts of WTH on ecosystem K status are likely to be exacerbated over time by anthropogenic N deposition.

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