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Abstract

Removals of forest biomass in the northeastern US may intensify over the coming decades due to increased demand for renewable energy. For forests to regenerate successfully following intensified harvests, the nutrients removed from the ecosystem in the harvested biomass (including N, P, Ca, Mg, and K) must be replenished through a combination of plant-available nutrients in the soil rooting zone, atmospheric inputs, weathering of primary minerals, biological N fixation, and fertilizer additions. Few previous studies (especially in North America) have measured soil nutrient pools beyond exchangeable cations, but over the long rotations common in this region, other pools which turn over more slowly are important. We constructed nutrient budgets at the rotation time scale for three harvest intensities and compared these with detailed soil data of exchangeable, organic, and primary mineral stocks of in soils sampled in 15 northern hardwood stands developed on granitic till soils in the White Mountain region of New Hampshire, USA. This comparison can be used to estimate how many times each stand might be harvested without diminishing productivity or requiring fertilization. Under 1990s rates of N deposition, N inputs exceeded removals except in the most intensive management scenario considered. Net losses of Ca, K, Mg, and P per rotation were potentially quite severe, depending on the assumptions used.

Biologically accelerated soil weathering may explain the lack of observed deficiencies in regenerating forests of the region. Sites differed widely in the long-term nutrient capital available to support additional removals before encountering limitations (e.g., a fourfold difference in available Ca, and a tenfold difference in weatherable Ca). Intensive short-rotation biomass removal could rapidly deplete soil nutrient capital, but traditional long rotations, even under intensive harvesting, are unlikely to induce nutrient depletion in the 21st century. Weatherable P may ultimately limit biomass production on granitic bedrock (in as few as 6 rotations). Understanding whether and how soil weathering rates respond to nutrient demand will be critical to determining long-term sustainability of repeated intensive harvesting over centuries.

Key words

ecosystem budget; whole-tree harvesting; sustainable forestry; soil weathering; apatite; bioenergy; calcium; phosphorus

Introduction

Deciduous forests in the northeastern United States have a long history of exploitation as a source of fuel and timber. New harvesting methods emerged in the 1970s, in which branches and low-value trees were chipped and sold as fuel rather than left on site. Studies of the increased nutrient removal associated with such harvests raised concern about the potential depletion of important nutrients, especially Ca, from forest soils (White 1974, Mann et al. 1988, Federer et al. 1989, Hornbeck et al. 1990, Adams et al. 2000). Interest in forest bioenergy has increased again recently (e.g. Malmsheimer et al. 2008, Richter et al. 2009), driven by energy price volatility and the goals of reducing net greenhouse gas emissions and dependence on imported energy.

Sustainable forestry comprises management practices that maintain the capacity of the forest to provide important ecosystem services in the future, including water quality, biodiversity, species composition, and forest productivity (Janowiak and Webster 2010, Walker et al. 2010, Berger et al. 2013). Here we address potential productivity declines due to nutrient removal in stands harvested repeatedly. From this perspective, sustainability requires that removals of nutrients from ecosystems be balanced by inputs to plant-available pools (Sverdrup and Svensson 2002, Flueck 2009). Though many forests in the northeastern USA remain productive after having been harvested and regrown twice or more, continued harvest removals and associated hydrologic losses of nutrients will eventually reduce net primary productivity unless ecosystem inputs increase above current estimates. Observations of nutrient availability and productivity in whole-tree harvested stands have yielded mixed results, at least for the relatively short time scales examined thus far (Thiffault et al. 2011). Though analogous forest systems elsewhere in the world are often fertilized to replace nutrients where biomass removals are high (e.g. northern Europe, Stupak et al. 2008), forest fertilization is not currently common in the northeastern USA.

Exchangeable nutrients have historically been considered the nutrient pool most available to plants and of greatest relevance in assessing productivity (Marschner 1995). However, exchangeable pools contain only a small fraction of the nutrients required by a regrowing forest (e.g. Likens et al. 1994; 1998). Indeed, at decadal time scales, even forests undergoing vigorous biomass accumulation appear not to deplete exchangeable soil nutrient pools (Johnson et al. 1991, 1997, Bélanger et al. 2004). More relevant to longer-term productivity is the rate of supply of these nutrients from less available pools or sources external to the ecosystem, relative to the rate needed to support regrowth (Rastetter and Shaver 1992, Craine 2009).

Nutrients enter forest ecosystems via atmospheric deposition and the weathering of geologic substrates. Nitrogen is not present in many parent materials but is also fixed microbially from the atmosphere. In regions of granitic parent material, base cations (Ca, Mg, K) are weathered primarily from silicate minerals, while the most important source of P is the accessory mineral apatite ($Ca_5(PO_4)_3(F,Cl,OH)$). Apatite can also be an important source of Ca in granitic soils (Blum et al. 2002; Nezat et al. 2004), because it weathers more rapidly than silicate minerals (Allen and Hajek 1989). Long-term weathering rates have been estimated from soil profiles in the White Mountain region (Nezat et al. 2004; Schaller et al. 2010). Weathering rate estimates are inherently variable and difficult to compare across methods and locations (Klaminder et al. 2011, Futter et al. 2012). However, weathering rates that are required to close ecosystem budgets (Likens et al. 1996, 1998, Hyman et al. 1998) are sometimes an order of magnitude greater than measured long-term rates estimated from the degree of depletion of soil profiles relative to their parent material. This discrepancy is a common finding when comparing estimates of weathering by different methods in similar soils (Table 1), despite the expectation that current rates should be lower than long-term means due to the decline in weathering rate as soils age (Taylor and Blum 1995). This discrepancy has been attributed to elevated acid deposition (Langan et al. 1995), but hydrologic Ca losses cannot be fully explained by observed acidic inputs (Hamburg et al. 2003). Rooting-zone soil weathering rates are difficult to assess at the watershed scale, where net fluxes are small relative to the large dynamic stocks, uncertainties are often large (Likens and Bormann 1995, Yanai et al. 2012), soils vary over short spatial scales, and significant chemical contributions to streamflow may occur below the rooting zone.

Another potential explanation for high apparent weathering rates is that soil weathering may be accelerated when there is increased biotic demand (Hamburg et al. 2003). The removal of large amounts of biomass over the past ~150 years is a significant new disturbance in forests of the region. Wind, ice damage, and infrequent fires have been the dominant forms of disturbance over the past 10,000 years, and generally leave most nutrient capital on site. Regrowing forests may shift resource allocation towards the acquisition of nutrients other than N, such as P (Rastetter et al. 2013). Ectomycorrhizal fungi are known to weather primary minerals (such as apatite) by etching mineral surfaces with organic acid exudates under conditions where the weathering products (such as P) are limiting (Landeweert et al. 2001; Hoffland et al. 2004; Van Scholl et al. 2008). Greatly elevated rates of apparent mineral weathering have been observed in aggrading pine mesocosms (Bormann et al. 1998, Balogh-Brunstad et al. 2008), and may occur in rapidly aggrading forest stands as well (Hamburg et al. 2003, Bélanger et al. 2004).

Research Approach and Objectives

Analyses of the sustainability of forestry practices typically compare management-induced nutrient losses to nutrient inputs via atmospheric deposition and weathering (e.g. Sverdrup and Svensson, 2002; Duchesne and Houle, 2008). Building on work by Federer et al. (1989), we extend this approach by comparing net nutrient loss per rotation to nutrient stocks, under a range of assumptions about harvest intensity and nutrient availability. Specifically, we ask:

1. What is the net nutrient balance per rotation under various harvesting scenarios?
2. How much variation exists in nutrient stocks (exchangeable, organically bound, and apatite) among stands that are ostensibly similar in species composition and soil type?
3. Assuming that exchangeable and organically bound nutrients can be depleted over multiple rotations, which nutrient eventually becomes limiting (i.e. is exhausted first) under each harvesting scenario?
4. If apatite in the rooting zone is considered available, how many additional rotations would be possible?

The first question relates directly to "strong" definitions of sustainability, whereby resource stocks must be maintained at current levels over time (e.g. Goodland and Daly, 1996; Flueck, 2009). The second question seeks to characterize variation in soil nutrient stocks at spatial scales relevant to management decisions, in order to avoid depleting ecosystems beyond critical thresholds. The third and fourth questions stem from the observation that ecosystems may continue to function normally despite some level of stock depletion.

Our approach necessarily involves many assumptions about 1) the magnitude of fluxes that are difficult to estimate across a variable landscape and 2) how fluxes will change over time with increasing nutrient stress. When simplifying assumptions must be made, we have chosen those that likely lead to an overestimation bias of the number of rotations that can be sustainably harvested in the northern hardwood region.

Methods

Study Sites

We sampled soils in 15 deciduous forest stands of varying age in the White Mountain region of central New Hampshire (Figure 1; Table 2). Dominant species included American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britton) in mature stands, and white birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), and pin cherry (*Prunus pensylvanica* L. f.) in younger stands. One site (B1) was a former pasture dominated by red spruce (*Picea rubens* Sarg.) mixed with northern hardwoods, and the area sampled at the Hubbard Brook Experimental Forest (HBEF) has red spruce and balsam fir (*Abies balsamea* L.) at higher elevations. Soils were primarily well or moderately drained, coarse-loamy, mixed-frigid typic Haplorthods developed on glacial till parent material derived from granitoid and high-grade metamorphic silicate rocks.

Sample Collection

Three 0.5 m^2 quantitative soil pits were excavated at each of 14 study sites (excluding HBEF) in 2003-4, following methods described in detail by Vadeboncoeur et al. (2012). The Oie and Oa horizons were collected in their entirety. Mineral soil samples were quantitatively excavated in several depth increments to the top of the C horizon, sieved to 12 mm in the field, weighed, homogenized, and subsampled. The top 25 cm of the C horizon was also quantitatively excavated in at least one pit per stand.

Soil data for HBEF were assembled from multiple data sets collected in three first-order watersheds on the same south-facing slope. Forest floor samples (60 pin-block samples) were collected at Watershed 6 in 2002 (Yanai et al. 2013). Mineral soils were sampled in 59 quantitative soil pits in the adjacent Watershed 5 in 1983; one from each of four elevation zones was randomly chosen for analysis (Hamburg et al. 2003). C horizon samples from Watershed 1, approximately 1 km to the east, were analyzed by Nezat et al. (2004), but sampling was not quantitative; C horizon mass in the top 25 cm was estimated as the mean of that measured in the other 14 stands.

Laboratory Analysis

Organic horizon samples were air-dried, subsampled, and dried to constant mass at 60ºC. Oa samples were sieved to 6 mm and Oie samples were milled. Mineral soil samples were air-dried and sieved to 2 mm; subsamples were oven-dried at 105ºC. Total N concentrations were measured on a CE Instruments Model NC2100 elemental analyzer. Oa and mineral soil samples were subjected to a sequential extraction procedure adapted from Nezat et al. (2007) to measure exchangeable, organic, and weatherable apatite fractions for each mineral nutrient. Each extraction step was conducted for 24 hours at 20ºC. First, exchangeable cations were extracted with 1 M NH_4Cl. Then, soil organic matter was extracted in 30% H_2O_2. Finally, each sample was extracted with 1 M HNO_3, which has been shown to congruently dissolve apatite in contact with the solution, though ~30% of total apatite may be shielded by more resistant silicate minerals (Nezat et al. 2007). Oa samples were then subjected to a final extraction in concentrated HNO_3 for 3 hours in a microwave digester. Oie samples were microwave-digested in concentrated HNO_3 rather than sequentially extracted, because they had little mineral matter. Concentrations of Ca, Mg, K, and P in all soil extracts were measured on an Optima 3300 DV ICP-Optical Emission Spectrometer. Mineral soil samples from HBEF were not subjected to the H_2O_2 extraction; P is the only element for which H_2O_2 extracts a substantial amount relative to the first (exchangeable) extraction in mineral soils. We estimated H_2O_2-extractable P at HBEF using the mean ratio of total mineral soil C:P_{H2O2} across the other 14 stands.

Scenario Description

We predicted ecosystem nutrient depletion over multiple rotations based on a range of assumptions about nutrient inputs and outputs (called scenarios I and II), harvest intensity (called scenarios a, b, and c), and the stocks of nutrients considered available to the ecosystem over multiple rotations (called scenarios 1, 2, and 3). We used combinations of scenarios to address our specific research questions, and report summarized results across the 15 stands.

The net depletion or enrichment of each nutrient was calculated as the difference between the nutrient removal per rotation and the ecosystem inputs (atmospheric deposition and soil weathering) during the rotation length. We conducted this calculation under two sets of assumptions about ecosystem inputs and outputs: I) using pedogenic time-scale average weathering inputs and assuming zero baseline streamflow output, or II) using weathering rates estimated from ecosystem budgets and hydrologic outputs (Table 3).

Ecosystem input and output data

Bulk atmospheric deposition and streamflow fluxes of all macronutrients have been monitored at HBEF since the 1960's (Likens 2012a, 2012b, 2012c); we used mean inputs and outputs for the period 1985-2004. We did not include dry deposition of N as an input, due to high landscape-scale variability (Lovett et al. 1997) and its small magnitude (e.g. 3-6% of total N inputs; Weathers et al., 2006). We included total dissolved P analyzed in bulk collector solutions, which may somewhat overstate ecosystem inputs due to the mineralization of locally derived particulate P (e.g. pollen), despite quality-control standards that exclude visibly contaminated samples (Stelzer et al. 2002).

We calculated harvest-induced leaching, which we included in all scenarios, as the cumulative 22-year difference between streamwater nutrient flux from HBEF Watershed 5 (clearcut by whole-tree harvest in 1983) and that of the adjacent reference watershed after accounting for the small pre-treatment difference between these streams (Yanai et al. 2005; Likens 2012b,c). Increases in export over the reference baseline were similar in magnitude to those measured by Hornbeck et al. (1990) throughout New England for 3 years after clearcutting.

Scenario I: We used stand-specific weathering inputs of Ca, K, Mg, and P calculated by Nezat et al. (2004) and Schaller et al. (2010), based on profile depletion relative to titanium. One stand (M5) lacked a C horizon, making it unsuitable for this approach, so we used mean weathering rates from the other 13 stands. Two others (C1 and H6) had irregular element ratio profiles for one or more nutrients; for these elements we also used mean weathering estimates. We conservatively assumed zero baseline (non-harvest-related) leaching of nutrients under this scenario.

Scenario II: We included 20-year observed streamflow losses of nutrients (Likens et al. 2012c), and also included recent budget-based weathering estimates from HBEF Watershed 6 for Ca (Likens et al. 1998) and nearby Cone Pond for K and Mg (Hyman et al., 1998). Phosphorus weathering is highly uncertain (Yanai 1992, Vadeboncoeur 2013); we estimated P weathering from the Likens et al. (1998) estimate of Ca weathering, assuming that 17% of long-term Ca weathering was in the form of apatite (as estimated by Nezat et al. 2004). This estimate of current P weathering is in the middle of estimates based on other calculation approaches (Vadeboncoeur 2013).

Biomass removal scenario data

To estimate net nutrient balances per rotation, we paired nutrient budgets under scenarios I and II with estimates of total nutrient export per harvest (in scenarios a, b, and c, below).

Scenario a: Stem-only removal on a ~100-year rotation is a common forest management practice in which merchantable saw and pulp logs are removed from a site, while branches, poor quality trees, and smaller trees are left on site, either standing or as slash. To estimate the nutrient capital removed in this type of harvest, we used the 2007 vegetation inventory from 550-745 m elevation at HBEF Watershed 6. Wood and bark contents (Siccama 2007) were summed for all trees >12.7 cm DBH to estimate nutrient removals for a heavy timber and pulpwood harvest. Basal area for this stand was 25 m^2 ha^{-1}, and estimated biomass removal was 125 dry metric tons per hectare. Biomass and nutrient content may be somewhat lower than is typical for the region (Fahey et al. 2005), but the allometry and nutrient stocks are uniquely well validated (Arthur et al. 2001).

Scenario b: A more intensive scenario is whole-tree harvesting on the same 100-year rotation. This is the same as the previous scenario, except that non-merchantable parts of trees are also removed for bioenergy use, rather than being left on site. We assumed winter harvesting of deciduous trees, with no removal of foliage. We used the same vegetation inventory as in the previous scenario to calculate the biomass stock of all trees >2 cm DBH, subtracting leaves and the small amount of slash estimated by Arthur et al. (2001). Biomass removal in this scenario is 187 dry metric tons per hectare, a 50% increase over the stem-only scenario.

Scenario c: The most intensive scenario we modeled was whole-tree harvesting on a shorter, ~35 year rotation, which would theoretically maximize the biomass harvest rate, at least over the first few harvests. To represent the biomass removed from a forest of this age, we used an inventory taken in 2011 in four stands in the Bartlett Experimental Forest that were clearcut between 1975 and 1980. Nutrient concentrations (Fatemi 2007) and allometric equations (Fatemi et al. 2011) were specific to two of these stands. Basal area averaged 32 m^2 ha^{-1}. Allowing for 40% of branch biomass to be left on site due to typical harvest inefficiency (Briedis et al., 2011; somewhat more than in the experimental W5 harvest), this harvest would yield 156 dry metric tons per hectare, about 240% as much biomass as scenario b on an annualized basis.

While we modeled removals as clearcuts for the sake of simplicity and to reduce the number of scenarios, removals associated with partial cuts on shorter rotations (e.g. 30% of basal area every 30 years) are likely at least as great as scenario a (if stem only) or b (if whole trees are removed).

Soil nutrient availability

For each study stand, we calculated "available" stocks of N, Ca, K, Mg, and P in each of three scenarios. We report the means (of 3 or more soil pits) within each stand, and the variation within and among stands is reported as coefficient of variation.

Scenario 1: We first assumed that only exchangeable and organically bound and complexed nutrient pools would become available over one to several harvest rotations. For the Oa organic nutrient content, we used the extraction with the best correlation between organic matter content and the concentration of each nutrient (the 20ºC HNO_3 extraction for K and Mg, and a microwave HNO_3 extractable for Ca and P), to avoid including the often significant silicate mineral content of the Oa horizon.

Scenario 2: Because P is the least abundant geologically derived nutrient in the soil parent material relative to biotic demand, and because apatite may be an important source of Ca to forest ecosystems in the region (Blum et al. 2002; Hamburg et al. 2003, Yanai et al. 2005) our second scenario adds 1N HNO_3-extractable apatite in the B horizon to the "available" stock of Ca and P.

Scenario 3: In the most optimistic scenario, we assumed that apatite in the top 25 cm of the C horizon was also biologically available. Federer et al. (1989) assumed that unweathered parent material became available to biological uptake only at a rate equal to the physical denudation rate. However, 5-7% of total fine root biomass mass in the 14 studied stands was found in the C horizon (Yanai et al. 2006, Park et al. 2007), which appears to be typical for the region (Donahue 1940). It is not known to what extent these roots provide access to C-horizon nutrients, but it is conceivable that carbon allocation to deep roots and mycorrhizae might increase when weathering-derived nutrients are limiting (Chapin et al. 1985, George et al. 1997, Bever et al. 2009, Smits et al. 2012).

Soil stock depletion calculations

The number of supportable rotations (N) was calculated as the ratio of the available nutrient stock (S) to nutrient removal per rotation (R), accounting for other ecosystem-scale input (F_{in}) and output (F_{out}) fluxes over the rotation length (T_R):

$$N = \frac{S}{R + T_R(F_{out} - F_{in})}$$

We used only the more conservative net nutrient budget scenario (I) for these estimates. Supportable rotations under varying harvest intensities were compared under scenarios Ia1, Ib1, and Ic1. We examined variability of depletable nutrient stocks among stands by calculating the range in the number of 100-year whole-tree harvest rotations required to deplete exchangeable plus organic nutrient stocks, and exchangeable plus organic plus apatite stocks (scenarios Ib2 and Ib3).

Results

Assembling stand-level budgets for various types of rotations shows that N inputs exceed outputs in all except the most intensive harvesting scenario (c) (Table 4). On the other hand, nutrient balances were negative (net ecosystem depletion) for Ca under all management and nutrient input-output scenarios. Magnesium and K showed net depletion under all scenarios except Ia and Ib, and P showed net depletion in all scenarios except IIa.

The nutrients examined differed in patterns of variation among stands when we examined stocks in the exchangeable fraction plus organic matter (Table 5). Nitrogen and K, which varied about twofold among stands (with CVs ~20%) showed considerably less variation than Ca, Mg, and P, which varied at least fivefold (CVs > 33%). Variation among stands in apatite stocks in the B horizon was substantially less than in the C horizon (Table 5).

The number of rotations that could be supported by the complete mineralization and uptake of all organic and exchangeable nutrients in the O and B horizons varied considerably among stands and especially among harvest scenarios (Figure 2). Calcium was most commonly predicted to be depleted first in the bole-only scenario, though K limitation was encountered first at the Bald Mountain stands. Bole-only harvesting could be supported for one to four additional rotations by these stocks. In the whole-tree harvest scenarios, Ca, K, or Mg limited production, depending on the stand, before two additional rotations were completed. In all cases, calculations based on input-output budget II (assuming observed hydrologic losses and weathering rates calculated by difference) indicated more rapid depletion of soil nutrients than the calculations based on budget I (assuming zero non-harvest-induced hydrologic output and long-term mean weathering rates from profile depletion).

Including B-horizon apatite as a P stock that could be made available via accelerated mycorrhizal weathering dramatically increased estimates of potential future production (Table 6). This limit ranges widely from six to > 40 rotations under a 100-year whole-tree harvesting rotation. However, unless the weathering of other Ca-bearing minerals also accelerates, Ca supply may present a more immediate constraint; B-horizon apatite stocks of Ca supply only an additional one to five rotations. If roots and mycorrhizal fungi were able to utilize the much larger stocks of apatite in the C horizon (an uncertain proposition, given the low density of roots at this depth), supportable 100-year whole-tree harvests would more than double in some cases, though by very little where the C horizon is shallow or poor in apatite (Table 6).

Discussion

Validity of Assumptions

Our estimates likely represent an upper bound to the number of harvests that each stand would be able to sustain without additional nutrient inputs. This is because when assumptions were needed we intentionally biased the result in this direction. For example, our use of HBEF Watershed 6 for harvestable nutrient content estimates may understate regional standing biomass nutrient stocks in mature stands, because the biomass of this stand is on the low side of regional variation (Leak and Smith 1996, Fahey et al. 2005, van Doorn et al. 2011, Reiners et al. 2012, Rastetter et al. 2013). On the other hand, errors are potentially quite large when applying allometric equations and nutrient contents beyond the areas for which they were developed (Melson et al. 2011). Biomass at stands C8 and C9 at the Bartlett Experimental Forest is 35% and 26% greater than at Watershed 6, respectively, and estimated removals under WTH range from 20% greater for P to 90% higher for Ca, indicating the potential for more rapid depletion of nutrients if these sites were cut and regained their current biomass and nutrient content in 100 years. Measurements of base cations in biomass at a similar site in Québec (Tremblay et al. 2012) fall between the HBEF and Bartlett ranges, while biomass and nutrient removals estimated for a whole-tree harvested stand of unreported age in northern NH (Hornbeck et al. 1990) were somewhat lower than the HBEF Watershed 5 estimates.

We also assumed constant atmospheric inputs into the future, which is more likely for some nutrients than for others. Widespread declines in base cation deposition (Hedin et al. 1994) generally preceded the 20-year period we used. Phosphorus deposition may also have decreased in the region, as mineral aerosols are the dominant atmospheric source of both base cations and of P (Newman 1995), and some local sources (notably road dust and fly ash) have likely decreased over the past century. N deposition has very recently declined sharply in the region (Bernal et al. 2012). Balancing removals under scenarios Ia and Ib would require deposition of 2.7 and 4.5 kg ha^{-1} y^{-1} respectively, plus enough to balance any hydrologic N losses that continue under reduced atmospheric loading. The depletion of N accumulated in SOM from elevated N deposition in the 20th century would reduce the impact of this potential future imbalance, as would biological N fixation, which has been observed in aggrading ecosystems on N-poor substrates (Bormann et al. 2002).

We assumed that the entire organic pool of nutrients was available over the relevant time scale, though the mineralization of organically bound N and P may be limited by overall OM decomposition rates. Much of this material is fairly recalcitrant, though mycorrhizal fungi under nutrient-limited conditions can be expected to allocate C to enzymes that may liberate these nutrients from complex organic substrates, even at a net energy cost (Orwin et al. 2011). Furthermore, we assumed that forest production and nutrient uptake would continue until available stocks of nutrients were fully depleted, though in reality uptake and growth would slow should this limit be approached.

Our assumption of constant nutrient content for successive tree rotations may counteract our overestimates of nutrient supply. Nutrient concentrations tend to decrease with nutrient stress in foliage, and likely also in wood and bark (DeWalle et al. 1991), though this has not been extensively studied. Species differ widely in overall wood nutrient concentrations and also in the ability to remobilize nutrients from heartwood (Meerts 2002). To the extent that some current nutrient uptake represents “luxury” uptake, i.e. uptake beyond an amount that affects production, such decreases would increase the number of potential rotations, as future nutrient exports in the biomass would be smaller than assumed in our analyses. However, for limiting nutrients, large decreases in uptake would necessarily be met by decreases in production (Craine 2009). Species composition would likely also change to favor species with greater nutrient-use efficiency.

Another possible underestimation is our use of the top 25 cm of C horizon nutrient stocks, despite C horizons which extended deeper than this at most sites (Vadeboncoeur et al. 2012). However, making efficient use of nutrients deeper than this would likely entail a large increase in root and mycorrhizal density and activity at these depths, which are not traditionally considered part of the rooting zone.

Weathering

In scenario I, our calculations conservatively assumed only the long-term, pedogenic time, mean weathering rate from observed profile depletion relative to titanium (Schaller et al. 2010). Current rates should theoretically be lower than long-term means, due to a reduction in weatherable mineral surfaces and depletion of the more rapidly weatherable minerals as soils age (Taylor and Blum 1995). However, current watershed budgets (Table 1) require a rate of soil weathering greater than the long-term mean, or the depletion of soil organic and exchangeable pools, to explain the large observed difference between outputs of base cations in streamwater and inputs in atmospheric deposition in both aggrading and steady-state stands (Likens and Bormann 1995, Romanowicz et al. 1996).

It is difficult to explain how forests are regenerating and accumulating biomass Ca while also losing Ca and other cations in streamflow at accelerated rates, unless weathering rates are elevated far above their long-term means (Hamburg et al. 2003; Yanai et al. 2005). Current biotic demand for P and base cations might exceed the long-term steady state due to prior harvest removals, early stages of ecosystem N saturation, a warming climate, and increased atmospheric CO_2 concentrations (Peñuelas et al. 2012). Alternatively, weathering below the rooting zone (which has not been monitored over time) may lead to nutrient losses and weathering rate estimates that overstate inputs available for plant uptake. Distinguishing between these possibilities has important implications for predicting nutrient balance in future rotations.

The degree to which mycorrhizal weathering of apatite in the B and C horizons can mitigate nutrient depletion and subsequent declines in productivity remains to be determined and deserves further research. Other minerals may be subject to similar processes; fungal weathering of biotite may be an important source of K and Mg to ecosystems (Wallander and Wickman

1999; Rosling et al. 2004), which may be important in stands where these nutrients are predicted to be depleted before Ca (Table 2). Feldspar minerals contain the majority of total Ca and K in granite-derived soils (Nezat et al. 2007) but less work has been done to determine whether the slower process of feldspar weathering might be influenced by biotic demand for these elements.

If apatite can be made available to trees at an accelerated rate when demand is increased, then this raises many interesting and unanswered questions. If Ca deficiency drives apatite weathering in excess of P demand, excess P may become occluded, associated with Al and Fe secondary minerals. Alternatively, if apatite is weathered at an increased rate due to biotic demand for P, Ca may leach out of the system in stream water; this process could be one explanation for the sustained elevation of streamwater of Ca from Watershed 5 at HBEF for at least 20 years following whole-tree harvesting (Yanai et al. 2005). Allocation of carbon to deeper roots and associated mycorrhizal fungi (Bever et al. 2009, Kiers et al. 2011) may represent a significant carbon cost to the trees, with implications for aboveground productivity. Allocation to mycorrhizal fungi may account for ~20% of primary production (Hobbie 2006), and appears to vary with the availability of N and P (Treseder 2004, Vadeboncoeur 2010, Vicca et al. 2012).

A better understanding of biogeochemical cycling in forests under various management regimes on a range of soils will require more geographically specific data on baseline weathering rates as well as in-situ estimates of short-term weathering rates in regenerating stands. Over the short term (one to several rotations) such data could help to differentiate sustainable from unsustainable forestry practices (see, for example, the differences between weathering scenarios I and II in Table 4). However, if weathering rates can be upregulated in response to biological demand, over the long term these rates may matter less than the nutrient capital in weatherable primary minerals. Except in cases where rapid geologic uplift and erosion continuously supply fresh parent material, an unfertilized forest can be regarded as effectively closed on a management-relevant time scale for macronutrients other than N, because removals are much greater than atmospheric inputs. By treating weathering as an unknown internal flux and examining the total weatherable pools of each nutrient we can put upper limits on the total long-term removal that a soil can ultimately support (Table 6), independent of the rate at which weathering might occur.

Implications for Management and Policy

Shorter rotations would yield more biomass in the short term, but much less biomass in the long term (Table 7) due to the higher nutrient concentrations of biomass removed, as well as fewer years of atmospheric and weathering inputs between harvests. For this reason, at any harvest intensity, longer rotation lengths would be more sustainable than shorter ones.

While we use a single value for harvest-induced leaching of nutrients across all harvest scenarios, more moderate harvesting scenarios (patch cutting, strip cutting, single-tree selection, diameter-limit cutting) may reduce overall leaching losses, even if harvests are more frequent (Hornbeck and Leak 1992). However, harvest-induced leaching accounts for only about 20% of total rotation Ca losses under the whole-tree harvesting scenario; the bulk of nutrient capital exported each rotation is in the biomass.

It is also possible, depending in part on harvest conditions, that changes in site nutrient status will affect the species composition of the regenerating forest, with consequent effects on timber value and wildlife habitat. These effects might be expected to precede declines in overall forest productivity, as species more tolerant of low-nutrient conditions become more competitive. Species changes over multiple rotations will depend not only on nutrient availability, but also on climate change, dispersal mechanics, and silvicultural practice. These effects are typically considered aspects of sustainability (Worrell and Hampson 1997), and may affect the decisions of land owners and foresters regarding the intensity of future management.

Landscape-scale variation

Our data show a high degree of variability in soil nutrient stocks at the landscape scale. All stands included in this analysis are upland sites generally representative of the type harvested in the region; half had been clearcut since 1970. Variability can be dramatic even at small spatial scales. For example, the mean coefficient of variation (CV) among the three 0.5 m^2 pits at each stand in B-horizon apatite Ca was 67%. Nezat et al. (2004) found similar variation in nutrient stocks and weathering rates across HBEF Watershed 1 (12 hectares). Much of this variation is due to the amount of soil, though total soil nutrient contents also vary with the depth of the O horizon and parent material. Thus, nutrient content increases with the depth of these horizons and decreases with the presence of coarse clasts in soil.

In this study, variation was greatest across stands separated by tens of kilometers, which is probably attributable to variation in parent material mineralogy (Figure 1). Stands with the lowest stocks of nutrients tended to be located on Conway granite, while those on other types of granitic bedrock (particularly Concord granite at Bald Mountain) had dramatically greater C-horizon Ca and P capital (Table 2). These differences reflect documented differences in apatite abundance between these lithologies (Billings and Wilson 1965). Also of relevance in glaciated landscapes is the parent material in the source region "upstream" of each stand, which may have contributed significantly to the local glacial till; in glaciated areas the till source area may be more important than underlying bedrock in predicting potential nutrient supply (Figure 1; Hornbeck et al. 1997).

Regional-scale variation

The stands in our study do not represent the full range of soil types in the region. Sustainable removal rates of Ca, for example, would be much higher in sites with carbonate-bearing parent materials. Nezat et al. (2008) characterized HNO_3-extractable Ca stocks (including both apatite and carbonates) across the northeastern United States from New York to Maine, including three of our study stands, which were generally low, especially relative to sites on carbonate-bearing sedimentary parent material. Both the HBEF and Cone Pond watersheds have lower-than-average streamwater Ca export compared with other small watersheds in northern and western New England (Hornbeck et al. 1997), suggesting generally higher Ca availability beyond the often thin granitic tills of the White Mountains.

Pairing chemical analyses of sequential extracts from soils with estimates of nutrient removal per rotation, as we have done here, allows for robust sustainability assessments across a wide variety of temperate forest ecosystems. Unfortunately, systematic data on soil mass and mineral content do not exist at a regional scale. NRCS soil classifications focus on physical and limited chemical characteristics of the soils, which provide some important information (texture, rockiness, organic concentrations) but are insufficient to address questions of long-term nutrient supply. These classifications, along with site-index guidelines relating soil texture and slope position to species composition and production (e.g. Leak 1978), are a reasonable starting place for estimating long-term production at the stand and landscape scales, but ultimately such assessments will require detailed information on soil mineralogy. Existing regional analyses classifying ecosystem sensitivity to acid deposition (e.g. Robinson, 1997) give a rough sense of parent material controls on base cation supply, but do not address soil primary P stocks. New continental-scale soil chemistry datasets (Smith et al., 2011) provide coarse but potentially useful data on regional variation in soil P and other nutrients.

Fertilization

Fertilization could be used to mitigate or reverse nutrient depletion from harvest removals. However, the possibility of short-term nutrient pulses in runoff has raised concern, especially because the most cost-effective time to fertilize is during harvesting (Stupak et al. 2008). Fertilizers and the labor required to apply them may be quite costly relative to the marginal time-discounted value of forest products removed, especially if the return interval is long. Globally, more intensive forestry regimes (predominantly plantations) often include early- and mid-rotation fertilizations to match short-term uptake demand (Fox et al. 2007; Laclau et al 2009), though rarely have whole-rotation nutrient mass balances been considered in fertilization recommendations.

Over the long term, hardened (slow-release) wood ash might be an economical alternative to mined mineral fertilizers, especially as global exploitable phosphate reserves become depleted (Smil 2000). From an ecosystem perspective, the application of locally sourced wood ash to regenerating forests is an appealing solution, as it closes the nutrient cycle. However, care must be taken regarding heavy metal mobility, appropriate application rate, and timing (Karltun et al. 2008). While gains in productivity in the current rotation may not be substantial without also adding N (Pitman 2006), our analysis indicates that returning mineral nutrients may be critical to sustaining future rotations.

Policy Implications

Forest harvest guidelines generally recommend against whole-tree harvesting at sites with wet or thin soils, steep slopes, or rare species (Stupak et al. 2008, Evans et al. 2010). Coarse sandy soils or those with a history of fire or intensive agriculture have also been suggested as indicators of vulnerability to nutrient loss (Hallett and Hornbeck 2000). Our analysis shows that such guidelines might not identify some sites that are vulnerable in the long-term to nutrient depletion; some sites that the analysis indicates are quite vulnerable to nutrient depletion were clearcut by the US Forest Service in the past several decades.

Across much of the Northeast, depending on the parent material, nutrient stocks are probably adequate to support one to several whole-tree rotations at about a 100-year interval without substantial ecosystem consequences. However, short-rotation heavy cuts have a high risk of depleting nutrient capital due to greater total biomass removal rates and shorter recovery time, and should not be considered without additional research into mineral soil weathering rates and nutrient stocks at a range of spatial and temporal scales. Currently, woody biomass prices are too low for such intensive management to be economically viable, but this situation could change rapidly if policies favoring bioenergy were adopted at the state or federal level, so it is important to ensure that best-practices guidelines recognize this risk. Biomass accumulation in stands that our analysis indicates are vulnerable to nutrient depletion are similar to that in stands throughout the region (Fatemi et al. 2011, Reiners et al. 2012), and if 100-year rotation lengths are utilized there should be little concern that whole-tree harvesting might lead to a net depletion in exchangeable base cations (Johnson et al. 1991, Bélanger et al. 2004) for the foreseeable future. However, more research is needed to determine which forests might face nutrient depletion with future harvesting and whether bioenergy can be derived from these forests into the 22nd century.

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Table 1

Long-term soil weathering rates and watershed-scale denudation rates (kg ha^{-1} y^{-1}) for granitic soil in the study region and elsewhere. Long-term weathering rates are derived from the depletion of each element relative to an immobile reference element, assuming that the C horizon represents unweathered parent material. Denudation rates are estimated from watershed budgets in which major fluxes are measured and weathering is assumed to account for the missing term required to achieve mass balance.

a) Long-term soil profile weathering rates	**Soil age (ka)**	**Ca**	**K**	**Mg**	**P**
in study region:					
Schaller et al. (2010) regional mean	14	0.59	2.11	0.33	0.043
range of 13 site rates used in this study		0.11-1.14	0.42-4.23	0.06-0.91	0.017-
Nezat et al. (2004), HBEF W1	14	1.46	4.18	0.51	0.114
in studies also reporting denudation rates (see below):					
April et al. (1986), New York	14	2.0-3.6	5.0-5.9	1.0-1.5	
Kirkwood and Nesbitt (1991), Ontario	12	2.6	2.8	1.0	
Bain et al. (2001), Scotland		0.04-0.10	0.11-0.45	0.006-0.035	
other rates for reference:					
Taylor and Blum (1995), Wyoming	11-21	1.1-1.7	1.0-1.9	0.015	
Egli et al. (2008), Switzerland and Italy	12-16	0.0-4.3	0.04-3.7	0.11-4.7	
Olsson and Melkerund (2000), Sweden & Finland	9	1.4-1.6	0.6-1.6	1.6-2.4	~0.01
Newman (1995), New Zealand	6-12				0.1-0.3

Table 1, continued

b) Denudation rates from watershed budgets	**Ca**	**K**	**Mg**	**P**
in study region:				
Bailey et al. (1996), Cone Pond	1.2-3.3			
Hyman et al. (1998), Cone Pond	2.18	1.08	1.09	
Likens and Bormann (1995), HBEF *	21.1	7.1	3.5	
Likens et al. (1998), HBEF	2.00-3.12			
Wood et al. (1984), HBEF *				1.5-1.8
in studies also reporting long-term weathering rates				
April et al. (1986), New York	3.3-23.0	0-1.3	0.3-3.6	
Kirkwood and Nesbitt (1991), Ontario	10.8	0.2	2.6	
Bain et al. (2001), Scotland	1.6		2.6	
other rates for reference:				
Marchand (1971), California	17	1.1	1.8	0.03
Lelong et al. (1990), France	2.7-11.2	2.8-6.5	2.4-5.5	
Clayton and Megahan (1986), Idaho	13.6	1.63	1.43	

* Probably greatly overestimated due to budget error (Likens et al. 1994, Likens and Bormann 1995).

Table 2

Description of the stands used in the study. "Cuts" indicates the number of times a site had been harvested as of 2004. Sites are ordered geographically from southwest to northeast (Figure 1). The "C" and "H" sites within the Bartlett Experimental Forest are ordered by stand age (youngest to oldest).

	Bedrock	Elev. (m)	FF (cm)	Depth to C (cm)	Rock vol. (%)	Age (yrs)	Cuts
BW	Concord granite	570	12	30	26	>100	~1
B1	Concord granite	490	5	36	19	~70	1
HBEF	Rangeley schist	600	7	50	18	70-100	~1
M6	Conway granite	540	5	66	34	23	2
C1	Mt Osceola granite	570	2	74	36	14	2
C2	Conway granite	340	4	73	26	16	2
H6	Conway granite	330	6*	61	17	19	2
C4	Conway granite	410	5	78	15	26	2
C6	Conway granite	460	6	38	15	28	2
H4	Conway granite	350	4	73	25	64	2
H1	Conway granite	320	5	68	14	68	2
C8	Mt Osceola granite	330	3	74	31	~120	1
C9	Conway granite	440	8	85	33	~120	1
T30	Rangeley schist	550	6	48	23	55	2
M5	Rangeley schist	630	7	48	36	26	2

* Randomly located soil pits at H6 appear to have overestimated the Oa horizon relative to more extensive pin-block samples taken across the stand in the same year (Vadeboncoeur et al. 2012). Pin-block data are reported here.

Table 3

Scenarios used in the analysis of nutrient depletion by biomass removal.

Input/output budget data scenarios

I HBEF observed precipitation inputs.

Stand-specific weathering rates from profile depletion relative to Ti.

Non-harvest-associated leaching = 0.

II HBEF observed precipitation inputs.

Weathering rates inferred from HBEF ecosystem budgets

Non-harvest-associated leaching observed at HBEF

Biomass harvest scenarios

a Stem-only removal on 100 y interval

b Whole-tree removal on 100 y interval

c Whole-tree removal on 35 y interval

Nutrient availability scenarios

1 Weathering rate assumed in I or II cannot change; only exchangeable and organically bound stocks are available over multiple rotations

2 Weathering rate may change in response to demand. Apatite in the B horizon is also available, in addition to exchangeable and organic stocks

3 Weathering rate and rooting depth may change in response to demand. Apatite in the B and top 25 cm of the C horizon are available, in addition to exchangeable and organic stocks

Table 4

Net nutrient stock changes per rotation under three scenarios of harvest intensity and two nutrient budget scenarios. These were combined to calculate net stock changes per rotation, which were applied to each site under various scenarios of nutrient availability.

	stock removed per harvest ($kg\ ha^{-1}$)				other fluxes in budget ($kg\ ha^{-1}\ y^{-1}$)				calculated net stock change per 100 years in each scenario ($kg\ ha^{-1}$)					
Scenario	a	b	c	all	all	I	II	II	Ia*	Ib*	Ic*	IIa	IIb	IIc
element	100y stem-only	100y whole-tree	35y whole-tree	harvest related leach-ing	precip input at HBEF	mean baseline weather-ing*	budget-inferred weather-ing input at HBEF	observed stream output at HBEF						
Ca	296	456	359	74	1.12	0.59	2.28	7.24	-198	-359	-1066	-754	-914	-1621
K	99	189	150	47	0.64	2.20	1.08	1.76	+137	+48	-279	-150	-240	-567
Mg	26	40	30	16	1.09	0.25	1.09	2.09	+15	+2	-74	-109	-123	-198
P	17	28	19	0	0.18	0.043	0.18	0.011	-6	-18	-44	+6	-5	-31
N	222	395	349	50	8.0	0	0	2.6	+528	+355	-340	+268	+95	-600

* For later calculations based on budget scenario I, site-specific weathering rates estimated by Schaller et al. (2010) were used rather than the means shown here as an example.

Table 5

Soil nutrient stocks measured at each site.

	exchangeable and organic thru B					apatite in B horizon		apatite in top 25cm of C horizon	
	Ca	K	Mg	P	N	Ca	P	Ca	P
BW	1125	176	153	178	5298	405	222	4985	1927
B1	546	152	80	125	5322	1114	674	5937	2581
HBEF	308	162	61	194	8608	647	534	1408	913
M6	594	199	45	109	7752	69	91	32	116
C1	274	260	28	38	3688	212	109	188	130
C2	523	214	43	56	4265	148	59	247	114
H6*	820	219	52	106	5365	625	493	697	387
C4	341	198	37	58	5051	73	61	194	150
C6	373	144	35	73	5277	136	64	405	313
H4	533	220	43	72	6895	411	365	110	68
H1	499	224	40	100	6338	179	151	262	152
C8	567	157	34	62	4143	586	390	1054	454
C9	471	174	32	104	6590	1266	850	1238	585
T30	755	278	74	116	5047	562	591	1269	757
M5	684	196	98	113	5673	657	483	0	0

* Oa horizon nutrient content estimates for site H6 are scaled to the mass difference observed between the soil pits and the more extensive pin block samples taken in the same year. N content of the Oa was measured directly on the pin block samples.

Table 6

Number of 100-year whole-tree harvest rotations required to exhaust B-horizon and B+C-horizon apatite stocks, if Ca or P ultimately limits production. Weathering of non-apatite Ca was assumed constant at long-term rates (Table 1).

	exch + org + apatite thru B (Scenario I2b)		exch + org + apatite thru C25cm (Scenario I3b)	
	Ca	**P**	**Ca**	**P**
BW	4.2	21	18	108
B1	5.1	37	23	154
HBEF	3.2	33	8.0	75
M6	1.7	10	1.8	15
C1	1.3	7	1.8	13
C2	1.8	6	2.4	11
H6	3.7	27	5.4	45
C4	1.2	6	1.7	13
C6	1.4	7	2.6	21
H4	2.5	20	2.8	23
H1	1.7	13	2.3	20
C8	3.4	21	6.4	42
C9	5.0	45	8.6	72
T30	3.2	33	6.3	67
M5	3.6	29	3.6	29

Table 7

Total biomass (dry metric tons) harvestable before nutrient exhaustion (Figure 2) from each site under budget scenario I, availability scenario 1, and each of the three harvest intensity scenarios.

site	100 y bole only	100 y whole tree	35 y whole tree
BW	578	256	172
B1	482	218	148
HBEF	355	212	140
M6	345	291	243
C1	178	143	115
C2	320	264	214
H6	475	401	262
C4	241	186	145
C6	255	200	158
H4	341	276	222
H1	274	236	202
C8	437	323	164
C9	354	265	174
T30	395	347	302
M5	445	357	286
mean	**388**	**284**	**206**

Figure 1

Location of the 15 sites used in this study. The wedge-shaped areas to the northwest of each site outline the approximate till source area for each site (Hornbeck et al. 1997). Geologic data are simplified from Lyons et al. (1997).

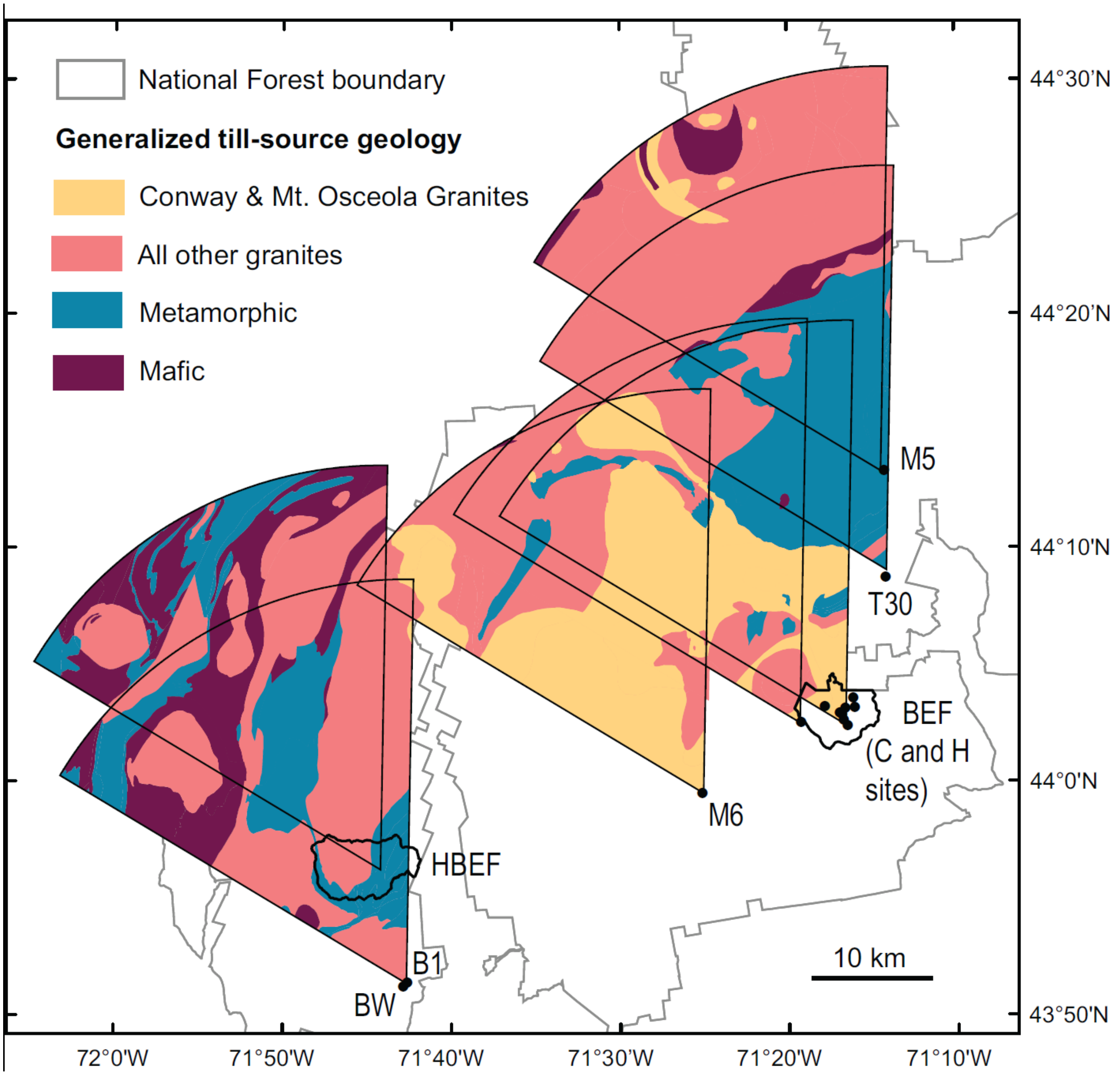

Figure 2

Times to nutrient depletion in three harvest scenarios across 15 sites, assuming that weathering proceeds at the long-term baseline value (Budget scenario I), and that only exchangeable and organically bound nutrients are available on the time scale of multiple rotations (Availability scenario 1). All three harvest scenarios are shown. Calcium is the first nutrient exhausted in all scenarios except those indicated for potassium or magnesium.