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Matthew A. Vadeboncoeur

University of New Hampshire - Main Campus, matt.vad@unh.edu

Steven P. Hamburg

Environmental Defense Fund

Ruth D. Yanai

SUNY College of Environmental Science and Forestry

Joel D. Blum

University of Michigan

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1 **Abstract**

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

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

28 **Key words**

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

31 **Introduction**

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

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

56 Exchangeable nutrients have historically been considered the nutrient pool most available
57 to plants and of greatest relevance in assessing productivity (Marschner 1995). However,
58 exchangeable pools contain only a small fraction of the nutrients required by a regrowing forest
59 (e.g. Likens *et al.* 1994; 1998). Indeed, at decadal time scales, even forests undergoing vigorous
60 biomass accumulation appear not to deplete exchangeable soil nutrient pools (Johnson *et al.*
61 1991, 1997, Bélanger *et al.* 2004). More relevant to longer-term productivity is the rate of

62 supply of these nutrients from less available pools or sources external to the ecosystem, relative
63 to the rate needed to support regrowth (Rastetter and Shaver 1992, Craine 2009).

64 Nutrients enter forest ecosystems via atmospheric deposition and the weathering of
65 geologic substrates. Nitrogen is not present in many parent materials but is also fixed
66 microbially from the atmosphere. In regions of granitic parent material, base cations (Ca, Mg,
67 K) are weathered primarily from silicate minerals, while the most important source of P is the
68 accessory mineral apatite ($\text{Ca}_5(\text{PO}_4)_3(\text{F},\text{Cl},\text{OH})$). Apatite can also be an important source of Ca
69 in granitic soils (Blum *et al.* 2002; Nezat *et al.* 2004), because it weathers more rapidly than
70 silicate minerals (Allen and Hajek 1989). Long-term weathering rates have been estimated from
71 soil profiles in the White Mountain region (Nezat *et al.* 2004; Schaller *et al.* 2010). Weathering
72 rate estimates are inherently variable and difficult to compare across methods and locations
73 (Klaminder *et al.* 2011, Futter *et al.* 2012). However, weathering rates that are required to close
74 ecosystem budgets (Likens *et al.* 1996, 1998, Hyman *et al.* 1998) are sometimes an order of
75 magnitude greater than measured long-term rates estimated from the degree of depletion of soil
76 profiles relative to their parent material. This discrepancy is a common finding when comparing
77 estimates of weathering by different methods in similar soils (Table 1), despite the expectation
78 that current rates should be lower than long-term means due to the decline in weathering rate as
79 soils age (Taylor and Blum 1995). This discrepancy has been attributed to elevated acid
80 deposition (Langan *et al.* 1995), but hydrologic Ca losses cannot be fully explained by observed
81 acidic inputs (Hamburg *et al.* 2003). Rooting-zone soil weathering rates are difficult to assess at
82 the watershed scale, where net fluxes are small relative to the large dynamic stocks, uncertainties
83 are often large (Likens and Bormann 1995, Yanai *et al.* 2012), soils vary over short spatial
84 scales, and significant chemical contributions to streamflow may occur below the rooting zone.

85 Another potential explanation for high apparent weathering rates is that soil weathering
86 may be accelerated when there is increased biotic demand (Hamburg *et al.* 2003). The removal
87 of large amounts of biomass over the past ~150 years is a significant new disturbance in forests
88 of the region. Wind, ice damage, and infrequent fires have been the dominant forms of
89 disturbance over the past 10,000 years, and generally leave most nutrient capital on site.
90 Regrowing forests may shift resource allocation towards the acquisition of nutrients other than
91 N, such as P (Rastetter *et al.* 2013). Ectomycorrhizal fungi are known to weather primary
92 minerals (such as apatite) by etching mineral surfaces with organic acid exudates under

93 conditions where the weathering products (such as P) are limiting (Landeweert *et al.* 2001;
94 Hoffland *et al.* 2004; Van Scholl *et al.* 2008). Greatly elevated rates of apparent mineral
95 weathering have been observed in aggrading pine mesocosms (Bormann *et al.* 1998, Balogh-
96 Brunstad *et al.* 2008), and may occur in rapidly aggrading forest stands as well (Hamburg *et al.*
97 2003, Bélanger *et al.* 2004).

98 ***Research Approach and Objectives***

99 Analyses of the sustainability of forestry practices typically compare management-
100 induced nutrient losses to nutrient inputs via atmospheric deposition and weathering (e.g.
101 Sverdrup and Svensson, 2002; Duchesne and Houle, 2008). Building on work by Federer *et al.*
102 (1989), we extend this approach by comparing net nutrient loss per rotation to nutrient stocks,
103 under a range of assumptions about harvest intensity and nutrient availability. Specifically, we
104 ask:

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

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

119 Our approach necessarily involves many assumptions about 1) the magnitude of fluxes
120 that are difficult to estimate across a variable landscape and 2) how fluxes will change over time
121 with increasing nutrient stress. When simplifying assumptions must be made, we have chosen

122 those that likely lead to an overestimation bias of the number of rotations that can be sustainably
123 harvested in the northern hardwood region.

124 **Methods**

125 ***Study Sites***

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

136 ***Sample Collection***

137 Three 0.5 m² quantitative soil pits were excavated at each of 14 study sites (excluding
138 HBEF) in 2003-4, following methods described in detail by Vadeboncoeur *et al.* (2012). The
139 Oie and Oa horizons were collected in their entirety. Mineral soil samples were quantitatively
140 excavated in several depth increments to the top of the C horizon, sieved to 12 mm in the field,
141 weighed, homogenized, and subsampled. The top 25 cm of the C horizon was also quantitatively
142 excavated in at least one pit per stand.

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

151 *Laboratory Analysis*

152 Organic horizon samples were air-dried, subsampled, and dried to constant mass at 60°C.
153 Oa samples were sieved to 6 mm and Oie samples were milled. Mineral soil samples were air-
154 dried and sieved to 2 mm; subsamples were oven-dried at 105°C. Total N concentrations were
155 measured on a CE Instruments Model NC2100 elemental analyzer. Oa and mineral soil samples
156 were subjected to a sequential extraction procedure adapted from Nezat *et al.* (2007) to measure
157 exchangeable, organic, and weatherable apatite fractions for each mineral nutrient. Each
158 extraction step was conducted for 24 hours at 20°C. First, exchangeable cations were extracted
159 with 1 M NH₄Cl. Then, soil organic matter was extracted in 30% H₂O₂. Finally, each sample
160 was extracted with 1 M HNO₃, which has been shown to congruently dissolve apatite in contact
161 with the solution, though ~30% of total apatite may be shielded by more resistant silicate
162 minerals (Nezat *et al.* 2007). Oa samples were then subjected to a final extraction in
163 concentrated HNO₃ for 3 hours in a microwave digester. Oie samples were microwave-digested
164 in concentrated HNO₃ rather than sequentially extracted, because they had little mineral matter.
165 Concentrations of Ca, Mg, K, and P in all soil extracts were measured on an Optima 3300 DV
166 ICP-Optical Emission Spectrometer. Mineral soil samples from HBEF were not subjected to the
167 H₂O₂ extraction; P is the only element for which H₂O₂ extracts a substantial amount relative to
168 the first (exchangeable) extraction in mineral soils. We estimated H₂O₂-extractable P at HBEF
169 using the mean ratio of total mineral soil C:P_{H₂O₂} across the other 14 stands.

170 *Scenario Description*

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

176 The net depletion or enrichment of each nutrient was calculated as the difference between
177 the nutrient removal per rotation and the ecosystem inputs (atmospheric deposition and soil
178 weathering) during the rotation length. We conducted this calculation under two sets of
179 assumptions about ecosystem inputs and outputs: I) using pedogenic time-scale average

180 weathering inputs and assuming zero baseline streamflow output, or II) using weathering rates
181 estimated from ecosystem budgets and hydrologic outputs (Table 3).

182 *Ecosystem input and output data*

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

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

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

204 *Scenario II:* We included 20-year observed streamflow losses of nutrients (Likens *et al.*
205 2012c), and also included recent budget-based weathering estimates from HBEF Watershed 6 for
206 Ca (Likens *et al.* 1998) and nearby Cone Pond for K and Mg (Hyman *et al.*, 1998). Phosphorus
207 weathering is highly uncertain (Yanai 1992, Vadeboncoeur 2013); we estimated P weathering
208 from the Likens *et al.* (1998) estimate of Ca weathering, assuming that 17% of long-term Ca
209 weathering was in the form of apatite (as estimated by Nezat *et al.* 2004). This estimate of

210 current P weathering is in the middle of estimates based on other calculation approaches
211 (Vadeboncoeur 2013).

212 *Biomass removal scenario data*

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

215 *Scenario a:* Stem-only removal on a ~100-year rotation is a common forest management
216 practice in which merchantable saw and pulp logs are removed from a site, while branches, poor
217 quality trees, and smaller trees are left on site, either standing or as slash. To estimate the
218 nutrient capital removed in this type of harvest, we used the 2007 vegetation inventory from 550-
219 745 m elevation at HBEF Watershed 6. Wood and bark contents (Siccama 2007) were summed
220 for all trees >12.7 cm DBH to estimate nutrient removals for a heavy timber and pulpwood
221 harvest. Basal area for this stand was 25 m² ha⁻¹, and estimated biomass removal was 125 dry
222 metric tons per hectare. Biomass and nutrient content may be somewhat lower than is typical for
223 the region (Fahey *et al.* 2005), but the allometry and nutrient stocks are uniquely well validated
224 (Arthur *et al.* 2001).

225 *Scenario b:* A more intensive scenario is whole-tree harvesting on the same 100-year
226 rotation. This is the same as the previous scenario, except that non-merchantable parts of trees
227 are also removed for bioenergy use, rather than being left on site. We assumed winter harvesting
228 of deciduous trees, with no removal of foliage. We used the same vegetation inventory as in the
229 previous scenario to calculate the biomass stock of all trees >2 cm DBH, subtracting leaves and
230 the small amount of slash estimated by Arthur *et al.* (2001). Biomass removal in this scenario is
231 187 dry metric tons per hectare, a 50% increase over the stem-only scenario.

232 *Scenario c:* The most intensive scenario we modeled was whole-tree harvesting on a
233 shorter, ~35 year rotation, which would theoretically maximize the biomass harvest rate, at least
234 over the first few harvests. To represent the biomass removed from a forest of this age, we used
235 an inventory taken in 2011 in four stands in the Bartlett Experimental Forest that were clearcut
236 between 1975 and 1980. Nutrient concentrations (Fatemi 2007) and allometric equations
237 (Fatemi *et al.* 2011) were specific to two of these stands. Basal area averaged 32 m² ha⁻¹.
238 Allowing for 40% of branch biomass to be left on site due to typical harvest inefficiency (Briedis
239 *et al.*, 2011; somewhat more than in the experimental W5 harvest), this harvest would yield 156
240 dry metric tons per hectare, about 240% as much biomass as scenario b on an annualized basis.

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

245 ***Soil nutrient availability***

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

249 *Scenario 1:* We first assumed that only exchangeable and organically bound and
250 complexed nutrient pools would become available over one to several harvest rotations. For the
251 Oa organic nutrient content, we used the extraction with the best correlation between organic
252 matter content and the concentration of each nutrient (the 20°C HNO₃ extraction for K and Mg,
253 and a microwave HNO₃ extractable for Ca and P), to avoid including the often significant silicate
254 mineral content of the Oa horizon.

255 *Scenario 2:* Because P is the least abundant geologically derived nutrient in the soil
256 parent material relative to biotic demand, and because apatite may be an important source of Ca
257 to forest ecosystems in the region (Blum *et al.* 2002; Hamburg *et al.* 2003, Yanai *et al.* 2005) our
258 second scenario adds 1N HNO₃-extractable apatite in the B horizon to the “available” stock of
259 Ca and P.

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

269 *Soil stock depletion calculations*

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

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

273
274 We used only the more conservative net nutrient budget scenario (I) for these estimates.
275 Supportable rotations under varying harvest intensities were compared under scenarios Ia1, Ib1,
276 and Ic1. We examined variability of depletable nutrient stocks among stands by calculating the
277 range in the number of 100-year whole-tree harvest rotations required to deplete exchangeable
278 plus organic nutrient stocks, and exchangeable plus organic plus apatite stocks (scenarios Ib2 and
279 Ib3).

280 **Results**

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

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

291 The number of rotations that could be supported by the complete mineralization and
292 uptake of all organic and exchangeable nutrients in the O and B horizons varied considerably
293 among stands and especially among harvest scenarios (Figure 2). Calcium was most commonly
294 predicted to be depleted first in the bole-only scenario, though K limitation was encountered first
295 at the Bald Mountain stands. Bole-only harvesting could be supported for one to four additional
296 rotations by these stocks. In the whole-tree harvest scenarios, Ca, K, or Mg limited production,
297 depending on the stand, before two additional rotations were completed. In all cases,

298 calculations based on input-output budget II (assuming observed hydrologic losses and
299 weathering rates calculated by difference) indicated more rapid depletion of soil nutrients than
300 the calculations based on budget I (assuming zero non-harvest-induced hydrologic output and
301 long-term mean weathering rates from profile depletion).

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

311 **Discussion**

312 ***Validity of Assumptions***

313 Our estimates likely represent an upper bound to the number of harvests that each stand
314 would be able to sustain without additional nutrient inputs. This is because when assumptions
315 were needed we intentionally biased the result in this direction. For example, our use of HBEF
316 Watershed 6 for harvestable nutrient content estimates may understate regional standing biomass
317 nutrient stocks in mature stands, because the biomass of this stand is on the low side of regional
318 variation (Leak and Smith 1996, Fahey *et al.* 2005, van Doorn *et al.* 2011, Reiners *et al.* 2012,
319 Rastetter *et al.* 2013). On the other hand, errors are potentially quite large when applying
320 allometric equations and nutrient contents beyond the areas for which they were developed
321 (Melson *et al.* 2011). Biomass at stands C8 and C9 at the Bartlett Experimental Forest is 35%
322 and 26% greater than at Watershed 6, respectively, and estimated removals under WTH range
323 from 20% greater for P to 90% higher for Ca, indicating the potential for more rapid depletion of
324 nutrients if these sites were cut and regained their current biomass and nutrient content in 100
325 years. Measurements of base cations in biomass at a similar site in Québec (Tremblay *et al.*
326 2012) fall between the HBEF and Bartlett ranges, while biomass and nutrient removals estimated

327 for a whole-tree harvested stand of unreported age in northern NH (Hornbeck *et al.* 1990) were
328 somewhat lower than the HBEF Watershed 5 estimates.

329 We also assumed constant atmospheric inputs into the future, which is more likely for
330 some nutrients than for others. Widespread declines in base cation deposition (Hedin *et al.* 1994)
331 generally preceded the 20-year period we used. Phosphorus deposition may also have decreased
332 in the region, as mineral aerosols are the dominant atmospheric source of both base cations and
333 of P (Newman 1995), and some local sources (notably road dust and fly ash) have likely
334 decreased over the past century. N deposition has very recently declined sharply in the region
335 (Bernal *et al.* 2012). Balancing removals under scenarios Ia and Ib would require deposition of
336 2.7 and 4.5 kg ha⁻¹ y⁻¹ respectively, plus enough to balance any hydrologic N losses that continue
337 under reduced atmospheric loading. The depletion of N accumulated in SOM from elevated N
338 deposition in the 20th century would reduce the impact of this potential future imbalance, as
339 would biological N fixation, which has been observed in aggrading ecosystems on N-poor
340 substrates (Bormann *et al.* 2002).

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

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

357 decreases in uptake would necessarily be met by decreases in production (Craine 2009). Species
358 composition would likely also change to favor species with greater nutrient-use efficiency.

359 Another possible underestimation is our use of the top 25 cm of C horizon nutrient
360 stocks, despite C horizons which extended deeper than this at most sites (Vadeboncoeur *et al.*
361 2012). However, making efficient use of nutrients deeper than this would likely entail a large
362 increase in root and mycorrhizal density and activity at these depths, which are not traditionally
363 considered part of the rooting zone.

364 ***Weathering***

365 In scenario I, our calculations conservatively assumed only the long-term, pedogenic
366 time, mean weathering rate from observed profile depletion relative to titanium (Schaller *et al.*
367 2010). Current rates should theoretically be lower than long-term means, due to a reduction in
368 weatherable mineral surfaces and depletion of the more rapidly weatherable minerals as soils age
369 (Taylor and Blum 1995). However, current watershed budgets (Table 1) require a rate of soil
370 weathering greater than the long-term mean, or the depletion of soil organic and exchangeable
371 pools, to explain the large observed difference between outputs of base cations in streamwater
372 and inputs in atmospheric deposition in both aggrading and steady-state stands (Likens and
373 Bormann 1995, Romanowicz *et al.* 1996).

374 It is difficult to explain how forests are regenerating and accumulating biomass Ca while
375 also losing Ca and other cations in streamflow at accelerated rates, unless weathering rates are
376 elevated far above their long-term means (Hamburg *et al.* 2003; Yanai *et al.* 2005). Current
377 biotic demand for P and base cations might exceed the long-term steady state due to prior harvest
378 removals, early stages of ecosystem N saturation, a warming climate, and increased atmospheric
379 CO₂ concentrations (Peñuelas *et al.* 2012). Alternatively, weathering below the rooting zone
380 (which has not been monitored over time) may lead to nutrient losses and weathering rate
381 estimates that overstate inputs available for plant uptake. Distinguishing between these
382 possibilities has important implications for predicting nutrient balance in future rotations.

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

387 1999; Rosling *et al.* 2004), which may be important in stands where these nutrients are predicted
388 to be depleted before Ca (Table 2). Feldspar minerals contain the majority of total Ca and K in
389 granite-derived soils (Nezat *et al.* 2007) but less work has been done to determine whether the
390 slower process of feldspar weathering might be influenced by biotic demand for these elements.

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

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

417 *Implications for Management and Policy*

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

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

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

436 *Landscape-scale variation*

437 Our data show a high degree of variability in soil nutrient stocks at the landscape scale.
438 All stands included in this analysis are upland sites generally representative of the type harvested
439 in the region; half had been clearcut since 1970. Variability can be dramatic even at small spatial
440 scales. For example, the mean coefficient of variation (CV) among the three 0.5 m² pits at each
441 stand in B-horizon apatite Ca was 67%. Nezat *et al.* (2004) found similar variation in nutrient
442 stocks and weathering rates across HBEF Watershed 1 (12 hectares). Much of this variation is
443 due to the amount of soil, though total soil nutrient contents also vary with the depth of the O
444 horizon and parent material. Thus, nutrient content increases with the depth of these horizons
445 and decreases with the presence of coarse clasts in soil.

446 In this study, variation was greatest across stands separated by tens of kilometers, which
447 is probably attributable to variation in parent material mineralogy (Figure 1). Stands with the

448 lowest stocks of nutrients tended to be located on Conway granite, while those on other types of
449 granitic bedrock (particularly Concord granite at Bald Mountain) had dramatically greater C-
450 horizon Ca and P capital (Table 2). These differences reflect documented differences in apatite
451 abundance between these lithologies (Billings and Wilson 1965). Also of relevance in glaciated
452 landscapes is the parent material in the source region “upstream” of each stand, which may have
453 contributed significantly to the local glacial till; in glaciated areas the till source area may be
454 more important than underlying bedrock in predicting potential nutrient supply (Figure 1;
455 Hornbeck *et al.* 1997).

456 *Regional-scale variation*

457 The stands in our study do not represent the full range of soil types in the region.
458 Sustainable removal rates of Ca, for example, would be much higher in sites with carbonate-
459 bearing parent materials. Nezat *et al.* (2008) characterized HNO₃-extractable Ca stocks
460 (including both apatite and carbonates) across the northeastern United States from New York to
461 Maine, including three of our study stands, which were generally low, especially relative to sites
462 on carbonate-bearing sedimentary parent material. Both the HBEF and Cone Pond watersheds
463 have lower-than-average streamwater Ca export compared with other small watersheds in
464 northern and western New England (Hornbeck *et al.* 1997), suggesting generally higher Ca
465 availability beyond the often thin granitic tills of the White Mountains.

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

478 continental-scale soil chemistry datasets (Smith et al., 2011) provide coarse but potentially useful
479 data on regional variation in soil P and other nutrients.

480 *Fertilization*

481 Fertilization could be used to mitigate or reverse nutrient depletion from harvest
482 removals. However, the possibility of short-term nutrient pulses in runoff has raised concern,
483 especially because the most cost-effective time to fertilize is during harvesting (Stupak et al.
484 2008). Fertilizers and the labor required to apply them may be quite costly relative to the
485 marginal time-discounted value of forest products removed, especially if the return interval is
486 long. Globally, more intensive forestry regimes (predominantly plantations) often include early-
487 and mid-rotation fertilizations to match short-term uptake demand (Fox et al. 2007; Laclau et al
488 2009), though rarely have whole-rotation nutrient mass balances been considered in fertilization
489 recommendations.

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

498 *Policy Implications*

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

506 Across much of the Northeast, depending on the parent material, nutrient stocks are
507 probably adequate to support one to several whole-tree rotations at about a 100-year interval
508 without substantial ecosystem consequences. However, short-rotation heavy cuts have a high

509 risk of depleting nutrient capital due to greater total biomass removal rates and shorter recovery
510 time, and should not be considered without additional research into mineral soil weathering rates
511 and nutrient stocks at a range of spatial and temporal scales. Currently, woody biomass prices
512 are too low for such intensive management to be economically viable, but this situation could
513 change rapidly if policies favoring bioenergy were adopted at the state or federal level, so it is
514 important to ensure that best-practices guidelines recognize this risk. Biomass accumulation in
515 stands that our analysis indicates are vulnerable to nutrient depletion are similar to that in stands
516 throughout the region (Fatemi et al. 2011, Reiners et al. 2012), and if 100-year rotation lengths
517 are utilized there should be little concern that whole-tree harvesting might lead to a net depletion
518 in exchangeable base cations (Johnson et al. 1991, Bélanger et al. 2004) for the foreseeable
519 future. However, more research is needed to determine which forests might face nutrient
520 depletion with future harvesting and whether bioenergy can be derived from these forests into the
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522

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860 **Table 1**

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

a) Long-term soil profile weathering rates	Soil age (ka)	Ca	K	Mg	P
<i>in study region:</i>					
Schaller et al. (2010) regional mean	14	0.59	2.11	0.33	0.043
<i>range of 13 site rates used in this study</i>		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
<i>in studies also reporting denudation rates (see below):</i>					
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	
<i>other rates for reference:</i>					
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
<i>in study region:</i>				
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
<i>in studies also reporting long-term weathering rates</i>				
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	
<i>other rates for reference:</i>				
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	

867

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

869 **Table 2**

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

874

	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

875

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

878 **Table 3**

879 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 T_i .

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

880 **Table 4**

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

Scenario	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)					
	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	baseline weather- ing*	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

883

884 * 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

885 as an example.

886 **Table 5**

887 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

888

889 * Oa horizon nutrient content estimates for site H6 are scaled to the mass difference observed between the soil pits

890 and the more extensive pin block samples taken in the same year. N content of the Oa was measured directly on the

891 pin block samples.

892

893 **Table 6**

894 Number of 100-year whole-tree harvest rotations required to exhaust B-horizon and B+C-
 895 horizon apatite stocks, if Ca or P ultimately limits production. Weathering of non-apatite Ca was
 896 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
	<hr/>		<hr/>	
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

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898

899 **Table 7**

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

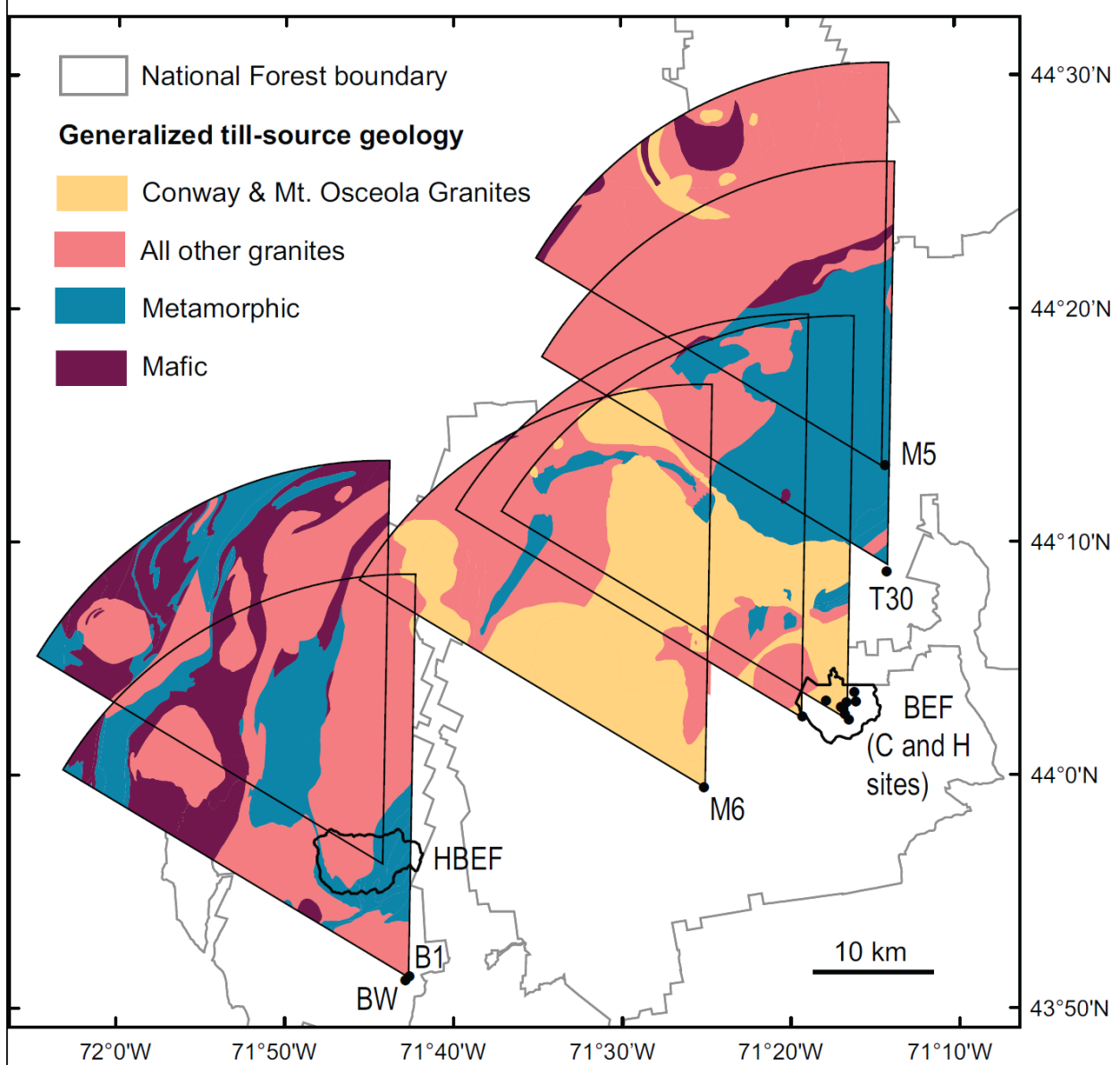
site	100 y bole only	100 y whole tree	35 y whole tree
BW	578	256	172
B1	482	218	148
HBEF	355	212	140
M6	345	291	243
C1	178	143	115
C2	320	264	214
H6	475	401	262
C4	241	186	145
C6	255	200	158
H4	341	276	222
H1	274	236	202
C8	437	323	164
C9	354	265	174
T30	395	347	302
M5	445	357	286
mean	388	284	206

902

903 **Figure 1**

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

907

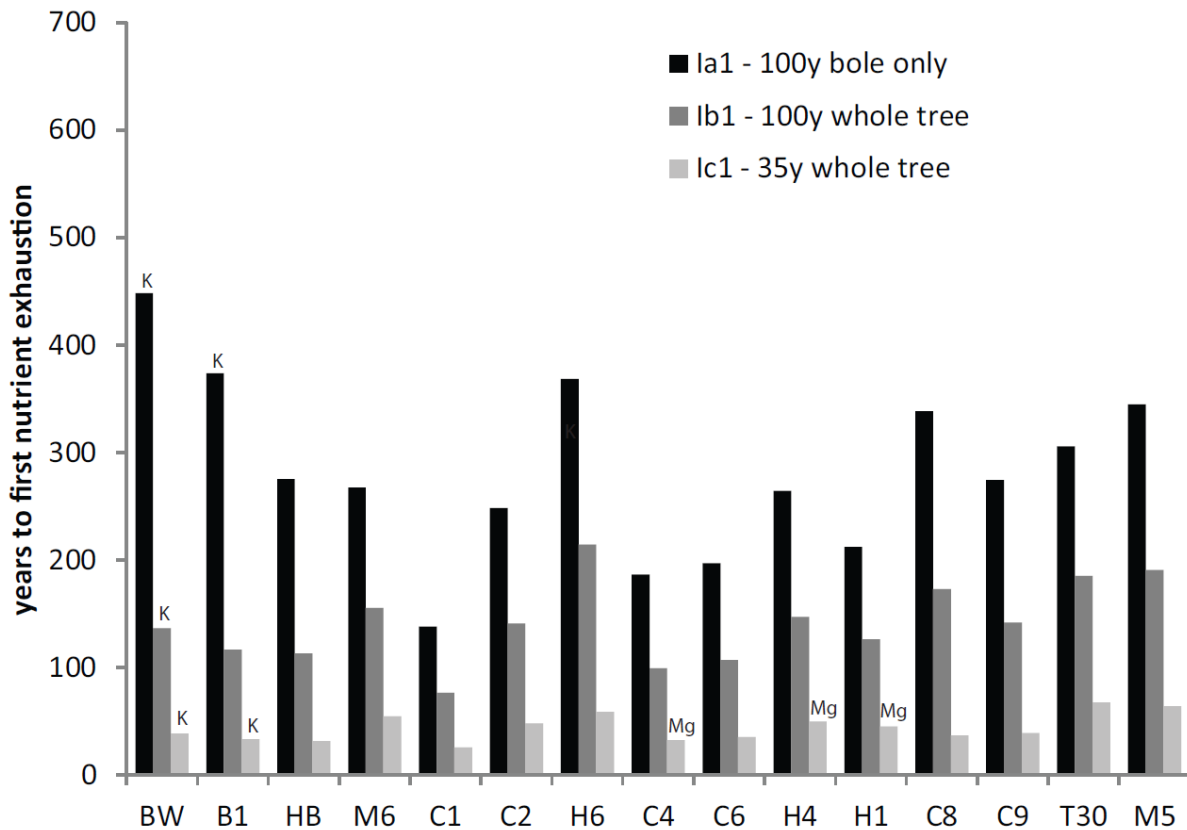


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910 **Figure 2**

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

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