Effects of forest biomass harvesting on soil productivity in boreal and temperate forests — A review

Article *in* Environmental Reviews · September 2011

DOI: 10.1139/a11-009

Effects of forest biomass harvesting on soil productivity in boreal and temperate forests — A review

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Abstract: Concerns about climate change and the desire to develop a domestic, renewable energy source are increasing the interest in forest biomass extraction, especially in the form of logging residues, i.e., tree tops and branches. We reviewed the literature to determine the site and soil conditions under which removal of logging residues along with the stem (i.e., whole-tree harvesting), especially at clearcut, results in negative impacts on soil productivity compared with conventional stem-only harvesting in boreal and temperate forests. Negative impacts of biomass harvesting on soil nutrient pools (e.g., nitrogen, phosphorus and base cations) and soil acid-base status are more frequent in the forest floor than in the mineral soil. In the first years post-harvest, however, biomass harvesting has the greatest potential to influence tree survival and growth, either positively or negatively, through its effects on microclimate and competing vegetation. Later in the rotation, impaired nitrogen and (or) phosphorus nutrition on whole-tree harvested sites has been shown to reduce tree growth for at least 20 years in some stands. Biomass removal can also reduce the concentrations of base cations in soils and foliage, but this has not, to date, been shown to affect tree productivity. There are no consistent, unequivocal and universal effects of forest biomass harvesting on soil productivity. However, climate and microclimate, mineral soil texture and organic C content, the capacity of the soil to provide base cations and phosphorus, and tree species autecology appear to be critical determinants of site sensitivity to biomass harvesting. Rigorous, long-term experiments that follow stand development through a rotation will facilitate the identification of categories of site or stand conditions under which negative impacts of biomass harvesting are likely.

Key words: forest biomass, whole-tree harvesting, soil productivity, tree nutrition, stand productivity.

Résumé : Les préoccupations au sujet des changements climatiques et la volonté de développer des sources d'énergie domestique renouvelable augmentent l'intérêt pour l'extraction de la biomasse forestière, surtout sous la forme de résidus de coupe, c.-à-d., les cimes et les branches des arbres. Les auteurs ont conduit une revue de littérature pour déterminer les conditions de site et de sol pour lesquelles l'enlèvement des résidus de coupe en plus de la tige (c.-à-d., la coupe par arbre entier), surtout lors de coupes à blanc, conduit à des impacts négatifs sur la productivité des sols comparativement à la récolte conventionnelle du tronc seulement, en forêts boréales et tempérées. Les impacts négatifs de la récolte de la biomasse sur les réserves du sol en nutriments (p. ex. azote, phosphore et cations basiques) et sur le statut acidité-alcalinité apparaissent plus fréquents dans l'humus que dans le sol minéral. Cependant, au cours des premières années suivant la récolte, le prélèvement de la biomasse montre le plus fort potentiel pour influencer la survie des arbres et leur croissance, soit positivement soit négativement, par ses effets sur le microclimat et la végétation compétitrice. Plus tard dans la révolution, on observe que pour certains peuplements, une nutrition amoindrie en azote et (ou) phosphore sur les sites avec coupe par arbre entier réduit la croissance des arbres pendant au moins 20 ans. Le prélèvement de la biomasse peut également réduire les teneurs en cations basiques dans les sols et le feuillage, mais ceci ne semble pas se traduire en effet sur la productivité. Il n'y a pas d'effets non équivoques et universels de la récolte de la biomasse sur la productivité des sols. Cependant, le climat et le microclimat, la granulométrie du sol, sa teneur en C organique, sa capacité á fournir les cations basiques et le phosphore, ainsi que l'autécologie des espèces semblent constituer des déterminants importants de la sensibilité des sites à la récolte de la biomasse. Des expériences rigoureuses, conduites à long terme pour suivre le développement des peuplements tout au long de la révolution, faciliteront l'identification des catégories de sites ou les conditions des peuplements pour lesquels des impacts négatifs sont susceptibles de se développer.

Received 28 April 2011. Accepted 25 May 2011. Published at www.nrcresearchpress.com/er on 23 August 2011.

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Mots-clés : récolte totale des arbres, coupe par arbre entier, productivité du sol, nutrition des arbres, productivité des peuplements.

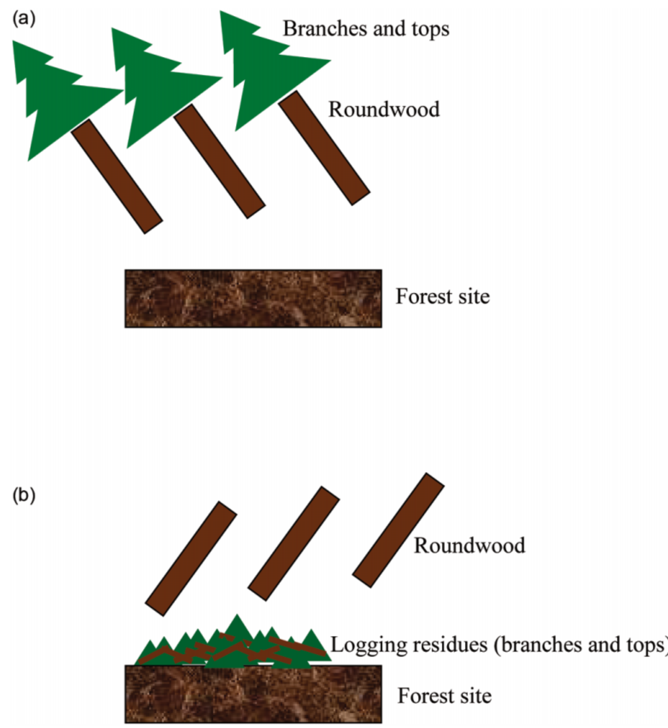
[Traduit par la Rédaction]

Introduction

Biomass from forests and byproducts from the manufacturing of traditional forest products are increasingly used to generate a range of bioproducts, of which bioenergy is currently the most common. Forest bioenergy offsets greenhouse gas (GHG) emissions because biomass is renewable. The International Panel on Climate Change (IPCC) has concluded that "[i]n the long term, a sustainable forest management strategy aimed at maintaining or increasing forest carbon stocks, while producing an annual sustained yield of timber, fibre or energy from the forest, would generate the largest sustained mitigation benefit to reduce carbon emissions" (Nabuurs et al. 2007). The use of domestic, low-grade forest biomass to replace imported energy sources also increases energy security (Lunnan et al. 2008). Furthermore, the production of new and diverse forest bioproducts enhances forest sector competitiveness and hence rural economic and social health. Although it has a low energy density, forest biomass needs a low input of additional energy for its production, harvesting, transportation, and conversion, and thus yields a high energy output : input ratio relative to other energy crops (Hakkila and Parikka 2002).

The term "forest biomass" includes primary residues, generated during forest operations such as site preparation, salvage logging, thinning, and final felling; secondary residues, produced during industrial wood transformation processes; tertiary residues that originate from demolition, construction, and packaging processes; and traditional firewood (Röser et al. 2008). Primary residues are currently the largest potential source of new feedstock for bioenergy in northern temperate and boreal forests (Röser et al. 2008). Of these, logging residues (i.e., tree tops and branches produced during commercial roundwood harvesting operations) are an accessible and economical source of forest biomass. During harvesting operations, logging residues are either already piled at the roadside where they are burned or left to rot, or are left on the forest site and hence only need retrieval. Removal of roundwood, branches, and tops from a forest site, either in one pass (harvesting and skidding of the whole tree) or in two passes (harvesting, delimbing, and skidding of the stem, followed by recovery of the branches and tops) is called whole-tree harvesting (WTH), according to the nomenclature used by Röser et al. 2008 and Hakkila and Parikka 2002 (Fig. 1*a*). WTH operations have been conducted for over three decades in many boreal and temperate forests. The reasons for such intensive biomass harvesting (i.e., economics of operations or removal of new energy feedstocks) and the end-use of this biomass (i.e., left at the roadside or processed into products) will continue to change over time, but have no bearing on the implications of forest biomass removal for biological processes. Technological advances driven by bioproduct markets will undoubtedly increase both the number of sites from which residues are removed, and the proportion of biomass that will be removed from a site in the future. Therefore, the resilience of forest sites to the increased removal of logging residues, especially during clearcutting, is a significant concern.

Fig. 1. Schematic description of harvesting treatments. (*a*) Whole-tree harvesting: removal of roundwood, tops, and branches of trees. (*b*) Stem-only harvesting: removal of roundwood; logging residues (i.e., tree tops and branches) are left on the forest site.



The key biological question resulting from increased utilization of forest biomass in WTH is whether the incremental removal of branches and tops causes undesirable environmental impacts compared with the removal of roundwood alone (i.e., stem-only harvesting (SOH); Fig. 1*b*). A subsidiary question is what defines site resilience or sensitivity to these impacts, and whether this can be related to easily measured, monitored, and mappable site variables (Scott and Dean 2006). There is a wide range of possible impacts of the incremental removal of tops and branches on soil, biodiversity, water, and air (Lattimore et al. 2009). Of these impacts, those on soil productivity, i.e., the capacity of a forest soil to sustain a growing forest, have been studied the most. WTH removes greater amounts of organic matter and nutrients from sites compared with SOH, raising concerns about soil productivity (Dyck et al. 1994; Burger 2002; Blanco et al. 2005; Raulund-Rasmussen et al. 2008). Experimental field trials have shown that WTH can have a wide range of short- to medium-term effects on soil properties and forest productivity that are often negative, but sometimes positive. The duration of most experiments, however, is less than three decades in boreal and temperate forests, which is less than one stand rotation (Raulund-Rasmussen et al. 2008). Nutrient budgets and ecosystem modelling have also been used to study the consequences of WTH (e.g., Belyazid et al. 2006; Akselsson and Westling 2005; Akselsson et al. 2007*a*, 2007*b*; Duchesne and Houle 2008). These tools are useful for studying the impacts of harvesting over one or several rotations across a wide range of site and forest conditions. They do tend to simplify forest ecosystem functioning to a limited number of parameters (e.g., soil nutrient balance). The choice of factors included in such models is thus constrained by the modellers' ability to articulate and quantify processes influencing soil and site productivity and by the lack of long-term empirical data for model calibration, testing, and verification.

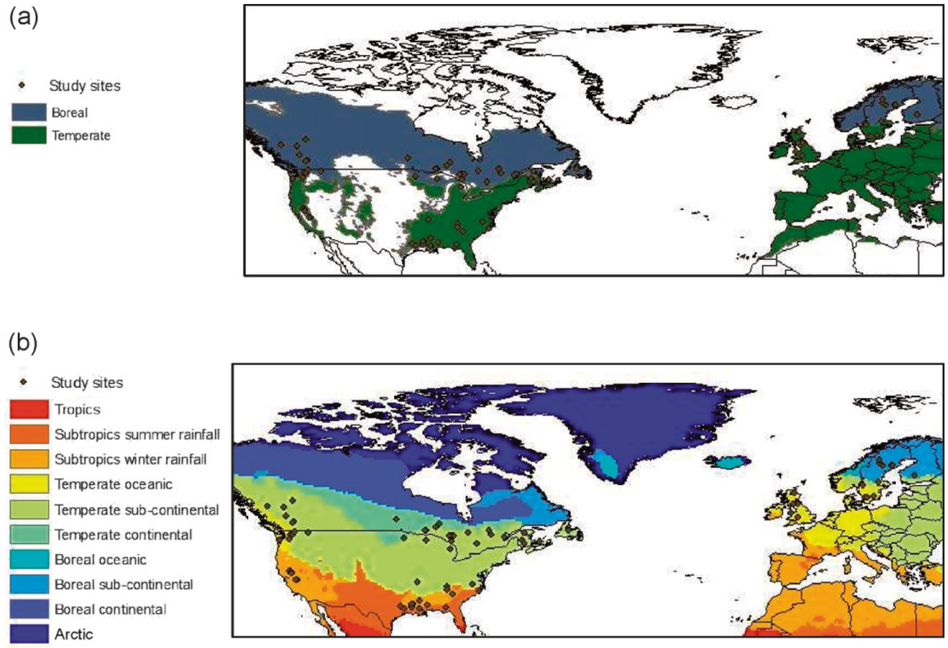
Environmental concerns over increased biomass utilization for bioenergy have resulted in a proliferation of new information about the ecological impacts of this practice. A number of jurisdictions are, therefore, developing legislation and recommendations that classify sites and stands according to their suitability for biomass harvesting, and restrict or regulate harvesting on some sites (Stupak et al. 2008; Evans and Perschel 2009). A re-examination of this topic is warranted to facilitate the development and validation of biomass harvesting guidelines based on the best available science. Previous reviews have focussed on the influence of biomass harvesting on soil (e.g., Morris and Miller 1994; Grigal 2000; Burger 2002; Raulund-Rasmussen et al. 2008). In addition, Johnson and Curtis (2001) and Nave et al. (2010) used meta-analyses to study the impacts of residue removal on soil carbon and nitrogen. These syntheses give background and context to the work presented here, which compiles empirical field trial results to search for trends in WTH effects on a range of soil productivity indicators across site and stand gradients as succession progresses over time. The objectives of this review are thus to (*i*) determine the specific impacts of WTH, especially at clearcutting, on soil productivity indicators (i.e., on the status of carbon, nutrients, and acidity–alkalinity in the soil) as well as tree foliar nutrition and growth and (*ii*) identify the site and soil conditions under which WTH is most likely to have negative effects on soil productivity compared with SOH, to assist in the development of prescriptive indices of site and soil suitability to WTH. In this review, the effects of WTH are interpreted relative to SOH; this review is not an assessment of the impacts of harvesting per se relative to a control (i.e., no harvest) as the aim was to examine the incremental pressure caused by increased removal of forest biomass in the form of logging residues.

Materials and methods

The geographical focus of our review was on forests from the boreal and temperate forest biomes as defined by the World Wildlife Fund classification (Fig. 2*a*) growing under temperate, boreal, and subtropical (i.e., southeastern US) climates of North America and Europe, as defined by the FAO–UN classification (Fig. 2*b*). We searched the peer-reviewed literature using keyword searches within the online reference databases ISI Web of Science, BIOSIS, Agricola, and CAB Direct. Keyword search strings were combinations of terms such as: forest, biomass, logging, harvest, clearcut, whole-tree harvesting, stem-only harvesting, soil productivity. We targeted studies that used field trials comparing WTH and SOH treatments because they represent the realized effects of biomass removal on the ecosystem. The list of studies included in our review is listed in Table 1. Long-term field trials that have been repeatedly sampled over several years, as well as retrospective studies and chronosequences, were included in this review. There can be significant limitations associated with studies that use space-for-time substitutions to examine changes in ecological processes through succession (Dyck and Cole 1994; Johnson and Miyanishi 2008), but broad trends can be detected and hypotheses generated by identifying common patterns among studies with varying levels of inferential power. Our primary focus was the impact of clearcutting with WTH, but thinning studies were also examined when appropriate. Finally, findings from modelling studies were considered when their larger spatial and temporal scope complemented the empirical studies used in the review, and they were also used to demonstrate convergence or divergence in results from field and modelling studies, but model outputs were not treated as empirical data.

Soil, tree nutrition, and growth data from relevant studies, including data extracted from figures using DataThief® software, were expressed as response ratios by dividing values from WTH plots by those from SOH plots; response ratios greater than 1.0 thus indicate an increase following WTH relative to SOH, and response ratios less than 1.0 indicate a decrease following WTH relative to SOH. Where possible, values from individual plots and individual soil horizons or depths were used rather than overall averages; as a result, multiple observations from a single study may be plotted in the same figure. The layout of experimental designs from each paper was respected when calculating response ratios (e.g., when data were available WTH and SOH plots from the same block in a randomized block design were compared with each other). Response ratios were calculated and plotted over time-since-harvest to reveal temporal trends for soil organic carbon, nitrogen, phosphorus and exchangeable base cations, foliar nutrients, and tree survival and height. The published results of statistical analyses as carried out in the individual papers, comparing the effects of WTH and SOH on soil properties, tree nutrition, and growth, are summarized in tables. Results from each journal article (numbers indicate references listed in Table 1) are displayed in one or more rows in a table and columns represent years since harvesting. In the text, reference numbers of articles listed in Table 1 are indicated in brackets. The colour of cells within the tables indicates the results of statistical tests comparing the effects of WTH and SOH (i.e., SOH > WTH, SOH < WTH, SOH = WTH) as reported in the studies for a given year since harvesting. These figures and tables are used to examine temporal trends in treatment effects by compiling the results of studies taken at different times from different geographical locations, and thus our results must be interpreted with caution; for example, stands of a similar age may not necessarily have reached the same successional stage because there can be considerable variation in rotation length among species and sites. To represent as broad a perspective on the potential implications of WTH for soil productivity and include as many studies as possible, we chose not to use meta-analytical

Fig. 2. Location of study sites included in the review by: (*a*) forest biomes (according to the World Wildlife Fund classification available from http://www.worldwildlife.org/science/ecoregions/delineation.html) and (*b*) thermal climates (according to the Food and Agriculture Organization – United Nations global climate classification available from http://www.fao.org/sd/EIdirect/climate/EIsp0002.htm).



tools, which often require the exclusion of studies that use unconventional analytical techniques or that provide limited metadata.

Results and discussion

Soil carbon

The direct impact of WTH on soil carbon stocks and its implications for global C cycling are critical concerns. A relatively large proportion of total ecosystem C is stored in forest soils; some estimates suggest that soil C accounts for more than 80% of total ecosystem C in boreal forests and more than 60% in temperate forests (Dixon et al. 1994; Malhi et al. 1999). Soil C also has a strong influence on soil fertility: organic matter generally improves soil structure, soil water retention, and nutrient availability, and is a substrate for soil biota that perform critical ecological functions such as decomposition and nutrient cycling (Fisher 1995; Van Cleve and Powers 1995). WTH returns smaller quantities of organic matter to the soil than SOH and thus reduced soil C contents are generally expected following WTH compared with SOH. Indeed, the process-based ecosystem model CENTURY 4.0 suggests that soil C could be reduced by about 32% if WTH rather than SOH is used in the boreal forests of central Canada under harvest rotations of 100 years for a 500-year period (Peng et al. 2002). Validation of these modelled results is not possible because there are no field studies that compare the effects of WTH and SOH on soil C beyond two decades.

Results from field-based studies surveyed for this review show no clear impact of WTH on soil C, with approximately half of the calculated response ratios having values below 1.0, and half having values above 1.0 (Fig. 3), although negative effects of WTH tend to be most frequent in the forest floor, with 70% of response ratios below 1.0. Stands from the boreal biome tend to be more negatively affected than stands from the temperate biome: 70% and 44% of the reponse ratios were below 1.0 for the boreal and temperate biomes, respectively. Only four of the 14 studies in Table 2 reported significant differences in soil C between SOH and WTH. Three of the studies in which significant treatment effects were reported are located in boreal stands and one is located in a temperate deciduous stand on ultisolic soils. A meta-analysis examining the effects of residue management on soil C and N found negligible differences associated with harvesting treatment in hardwood and mixed forests, although significant positive effects of biomass retention in SOH were observed in coniferous forests (Johnson and Curtis 2001). A more recent meta-analysis by Nave et al. (2010) reported no significant impacts associated with harvesting intensity on soil C storage in temperate forests across wide gradients of soil and stand type.

Of the studies in which significant effects were observed, WTH reduced the concentration or content of forest floor C to values corresponding to between 44% and 92% of that in SOH stands. In mineral horizons, significant treatment effects were observed only at one boreal site with inherently low concentrations of soil organic matter (i.e., mineral soils from outwash plains in northern Quebec with less than 1% organic C; Thiffault et al. 2006 [45]). Absence of significant treatment effects on other sites could be due to the fact that mineral soils with inherently high organic matter content can inhibit sorption of new C (Ussiri and Johnson 2004). Thus logging residues could be a significant source of organic matter only in coarse-textured C-poor soils.

To examine the relationship between mineral, soil-inherent, organic C and biomass harvesting, soil C contents (Mg/ha) were calculated on a 10 cm basis for each data point in Fig. 3. When available, published values of bulk density were used to convert soil carbon concentrations to soil C

Table 1. Studies comparing the effects of stem-only and whole-tree harvesting on soil properties, foliar nutrition, and tree growth in boreal and temperate forests.

No.	Reference	In Tables	Biome*	Climate*	Soil types†	Common tree species (Species code)	Location
1	Ares et al. 2007	9, 10	T	T	andisol	*Pseudotsuga menziesii* (**Fd**)	WA, USA
2	Bélanger et al. 2003	2, 7, 8	B	T	podzol	*Picea mariana* (**Sb**)	QC, Canada
3	Belleau et al. 2006	2, 3, 4, 6, 7, 8	B	T	luvisol	*Populus tremuloides* (**At**)	QC, Canada
4	Carter et al. 2002	2, 3, 4	T	S	ultisol	*Pinus taeda* (**Pt**)	LA & TX, USA
5	Egnell and Leijon 1999	10	B/T	B/T	podzol	*Picea abies* (**Sn**) and (or) *Pinus sylvestris* (**Ps**)	Sweden
6	Egnell and Valinger 2003	10	T	T	podzol	*Pinus sylvestris* (**Ps**)	S Sweden
7	Emmett et al. 1991*a*	5	T	T	podzol	*Picea sitchensis* (**Ss**)	Wales, UK
8	Emmett et al. 1991*b*	4	T	T	podzol	*Picea sitchensis* (**Ss**)	Wales, UK
9	Fleming et al. 2006*a*	4	B	T	podzol	*Pinus banksiana* (**Pj**)	ON, Canada
10	Fleming et al. 2006*b*	10	B/T	T/S	various	Various	North America
11	Goulding and Stevens 1988	7	T	T	gleysol, podzol	*Picea sitchensis* (**Ss**)	Wales, UK
12	Hassett and Zak 2005	4, 10	B/T	T	luvisol, podzol	*Populus tremuloides* (**At**)	MI, USA
13	Hendrickson 1988	9, 10	B	T	podzol	Mixedwoods, including *Acer rubrum* (**Mr**), *Betula papyrifera* (**Ep**), and *Populus tremuloides* (**At**)	ON, Canada
14	Hendrickson et al. 1989	2, 3, 5, 8	B	T	podzol	Mixedwoods, including *Acer rubrum* (**Mr**), *Betula papyrifera* (**Ep**), and *Populus tremuloides* (**At**)	ON, Canada
15	Hope 2006	10	B	T	luvisol	*Pseudotsuga menziesii* (**Fd**) and *Pinus contorta* (**Pl**)	BC, Canada
16	Johnson and Todd 1998	3, 4, 6, 7, 9	T	T	ultisol	Mixed deciduous, including *Prunus serotina* (**Cb**), *Quercus prinus* (**Qp**), *Acer rubrum* (**Mr**), and *Quercus rubra* (**Qr**)	TN, USA
17	Johnson et al. 2002	2	T	T/S	ultisol, brunisol, podzol	Mixed deciduous or *Pinus*-dominated	NC, SC & TN, USA
18	Kabzems and Haeussler 2005	2, 10	B	T	gleysol	*Populus tremuloides* (**At**)	BC, Canada
19	Laiho et al. 2003	2	T	S	ultisol, luvisol, vertisol	*Pinus taeda* (**Pt**)	LA & NC, USA
20	Li et al. 2003	2, 3, 4	T	S	ultisol	*Pinus taeda* (**Pt**)	NC, USA
21	Mahendrappa et al. 2006	5, 10	T	T		*Picea glauca* (**Sw**) and *Pinus strobus* (**Pw**)	PEI, Canada
22	Mann 1984	10	T	T	ultisol	Mixed deciduous dominated by *Quercus* species	TN, USA
23	Mann et al. 1988		T	T/S	ultisol, brunisol	Mixed deciduous or *Pinus*-dominated	NC, SC & TN, USA
24	Mattson and Swank 1989	2, 4	T	T	brunisol, ultisol	Mixedwoods dominated by *Quercus* species	NC, USA
25	McInnis and Roberts 1994	10	T	T		*Abies balsamea* (**Bf**), *Picea rubens, Picea mariana*, *Picea rubens x mariana* (**Srm**), *Acer rubrum* (**Mr**), and *Betula papyrifera* (**Ep**)	NB, Canada
26	Nykvist and Rosén 1985	7, 8	B/T	B/T	podzol	*Picea abies* (**Sn**) and (or) *Pinus sylvestris* (**Ps**)	Sweden
27	Olsson et al. 1996*a*	7, 8	B/T	B/T	podzol	*Picea abies* (**Sn**) or *Pinus sylvestris* (**Ps**)	Sweden
28	Olsson et al. 1996b	2, 3, 4	B/T	B/T	podzol	*Picea abies* (**Sn**) or *Pinus sylvestris* (**Ps**)	Sweden
29	Olsson et al. 2000	9	B/T	B/T	podzol	*Picea abies* (**Sn**) or *Pinus sylvestris* (**Ps**)	Sweden
30	Piatek and Allen 1999	3, 4	T	T	ultisol	*Pinus taeda* (**Pt**)	NC, USA
31	Powers et al. 2005	2, 4, 10	B/T	T/S	various	Various	North America
32	Proe and Dutch 1994	9, 10	T	T	gleysol	*Picea sitchensis* (**Ss**)	UK
33	Proe et al. 1999	9, 10	T	T	gleysol	*Picea sitchensis* (**Ss**)	UK
34	Proe et al. 2001	10	T	T	podzol, gleysol	*Picea sitchensis* (**Ss**)	UK
35	Roberts et al. 2005	9, 10	T	T	andisol	*Pseudotsuga menziesii* (**Fd**)	WA, USA
36	Sanchez et al. 2006*a*	3, 6, 9, 10	T	S	ultisol, luvisol, vertisol	*Pinus taeda* (**Pt**)	LA & NC, USA
37	Sanchez et al. 2006*b*	2, 3	B/T	T/S	various	Various	North America

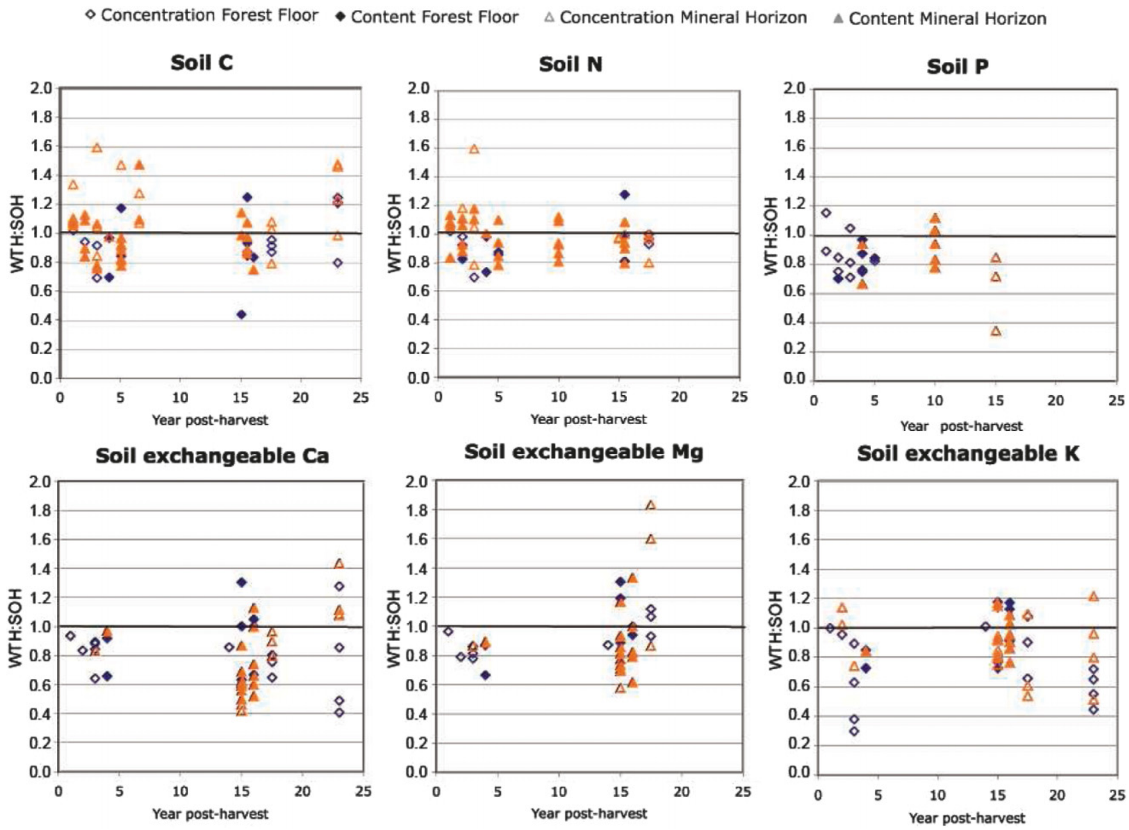
Table 1 (*concluded*).

No.	Reference	In Tables	Biome*	Climate*	Soil types†	Common tree species (Species code)	Location
38	Scott and Dean 2006	10	T	S	ultisol, luvisol	*Pinus taeda* (**Pt**)	LA, MS, TX & GA, USA
39	Sikström 2004	9, 10	B	T	podzol	*Picea abies* (**Sn**)	W Sweden
40	Staaf and Olsson 1991	8	B/T	B/T	podzol	*Picea abies* (**Sn**) or *Pinus sylvestris* (**Ps**)	Sweden
41	Staaf and Olsson 1994	5	T	T	podzol	*Picea abies* (**Sn**)	SW Sweden
42	Stevens and Hornung 1990	5	T	S	podzol	*Picea sitchensis* (**Ss**)	Wales, UK
43	Stevens et al. 1995	5	T	S	podzol	*Picea sitchensis* (**Ss**)	Wales, UK
44	Strahm et al. 2005	5	T	T	andisol	*Pseudotsuga menziesii* (**Fd**)	WA, USA
45	Thiffault et al. 2006	2, 3, 7, 8, 9	B	T	podzol	*Picea mariana* (**Sb**), *Pinus banksiana* (**Pj**) or *Abies balsamea* (**Bf**)	QC, Canada
46	Titus and Malcolm 1991	3, 6	T	T	gleysol	*Picea sitchensis* (**Ss**)	NE England, UK
47	Titus and Malcolm 1992	5	T	T	gleysol	*Picea sitchensis* (**Ss**)	NE England, UK
48	Titus et al. 1998	5	B	T	podzol, gleysol	*Betula papyrifera*	NL, Canada
49	Vitousek and Matson 1985	3, 4	T	T	ultisol	*Pinus taeda* (**Pt**)	NC, USA
50	Wall 2008	2, 3, 5, 6, 7, 8	B	B	podzol	*Picea abies* (**Sn**)	Central Finland
51	Walmsley et al. 2009	7, 8, 10	T	T	podzol	*Picea sitchensis* (**Ss**)	Wales, UK
52	Waters et al. 2004	10	B	T	various	*Pinus banksiana* (**Pj**), *Abies balsamea* (**Bf**), *Picea glauca* (**Sw**), and *Picea mariana* (**Sb**)	MB, Canada
53	Zabowski et al. 2000	10	B/T	T	brunisol, andisol	*Pseudotsuga menziesii* (**Fd**) or *Pinus contorta* (**Pl**)	WA, USA

*B, boreal; T, temperate; S, subtropical. Biomes were classified according to the World Wildlife Fund classification. Climates were classified according to the FAO–UN global climate classification.

†Where possible, the Canadian system of soil classification was employed (Soil Classification Working Group 1998); however, the American system of soil classification (Soil Survey Staff 2006) was used for ultisols and andisols because there are no Canadian equivalents.

Fig. 3. Response ratios (WTH:SOH) of soil organic carbon, soil nitrogen, soil phosphorus, and soil exchangeable cations.



content (Mg/ha). The relationship between the soil C content in WTH stands and the calculated response ratios for soil C (Fig. 4) suggest that WTH tends to cause reduced soil C contents in soils that are already poor in organic matter (i.e., those with <10 Mg/ha of C in a soil sample of 10 cm thickness). These datapoints corresponded to sandy-textured soils or to deeper soil horizons. Thus logging residues might be a more significant source of organic matter in coarse-textured and (or) C-poor soils.

On the other hand, decade-long observations of 26 LTSP sites suggest that site-specific responses of mineral soil C to harvest residue removal are rather explained by climatic factors (Powers et al. 2005 [31]): C from surface residues on sites in moderate and warmer climates is mainly respired as CO_2 and very little C is incorporated into the soil, while much of the C in residues can eventually accumulate in the soil under wetter and cooler conditions (typical of many boreal ecosystems) (Powers et al. 2005 [31]).

Despite the observations described above, detecting statistically significant differences in soil C in the field is often difficult. Studies surveyed by Yanai et al. (2003) were unable to detect treatment differences in forest floor C smaller than 15%–20%. In fact, only one of the studies we reviewed reported a significant treatment difference in soil C that was less than 20% (Bélanger et al. (2003) [2]). Based on treatment differences in the quantity of C returned to the soil in logging residues, the mass of soil C per unit area in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) stands in Sweden was expected to increase by 61%–76% after SOH compared with WTH, however, no treatment differences were detected in the field 15–16 years after harvest (Olsson et al. 1996*b* [28]). Empirical treatment-related differences in C pools are probably blurred, to some degree, by the overwhelming effect of harvesting on ecosystem C pools, independent of the intensity of residue removal (Olsson et al. 1996*a* [27]). High spatial variability of soil C content (Yanai et al. 2003), temporal changes in soil C through stand rotation and inputs of organic matter from decaying roots and litterfall, can also obscure treatment effects.

Soil total nitrogen

Field-based studies revealed a slight tendency towards reduced soil N following WTH on soil total N, with 58% of the plotted response ratios having values lower than 1.0 (Fig. 3). Negative effects of WTH were most frequently observed in the forest floor, with more than 80% of ratios having values below 1.0 whereas, for the mineral soil, response ratios were evenly distributed above and below 1.0. Only four of the 14 studies reviewed reported that WTH significantly reduced soil N relative to SOH (Table 3). WTH reduced forest floor N content or concentration to between 70% and 85% of that with SOH in three of these studies 2–5 years post-harvest. Mineral soil N was significantly reduced by WTH in only one study, in which the N content of surface (0–10 cm) mineral soils in 10-year-old subtropical pine-dominated stands in Louisiana was 81% of that in stands harvested by SOH (Sanchez et al. 2006*b* [37]). There are a number of possible explanations for the frequent lack of significant differences in the effects of SOH and WTH on soil N; although organic N is presumably mineralized and released to the soil during the decomposition of harvesting residues, this N could be rapidly taken up by the regen-

Table 2. Studies examining the impact of whole-tree (WTH) and stem-only harvesting (SOH) on soil carbon.

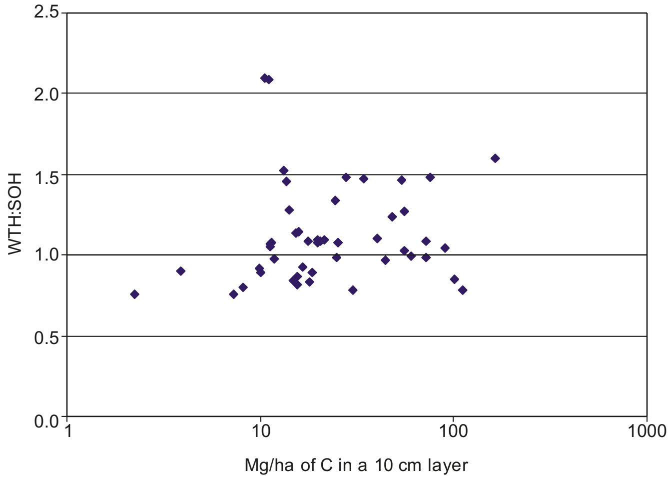
		Year post-harvest																						
Ref		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
	Units	**FOREST FLOOR**																						
2	%			●																				
3	g·kg^{-1}	○	○																					
14	% or t·ha^{-1}			○																				
17*	Mg·ha^{-1}															●	●							
19	kg·m^{-2}					○																		
28*	Mg·ha^{-1}															○	○							
45*	%															○	○	○	○	○	○			
50†	L or FH; Mg·ha^{-1}				●																			
51†	%																							○
	Total sample depth/ horizon; units	**MINERAL SOIL**																						
2	0–20 cm; %			○																				
3	0–10 cm; g·kg^{-1}	○	○																					
4	0–15 or 0–60 cm; Mg·ha^{-1}	○	○	○																				
14	0–20 cm; % or t·ha^{-1}			○																				
17*	0–30, 45, or 100 cm; Mg·ha^{-1}															○	○							
18	0–10 cm; %	○				○																		
19	0–30 cm; kg·m^{-2}					○																		
20	0–10 cm; Mg·ha^{-1}					○																		
24*	0–60 cm; % or g C·m^{-2}					○	○	○	○															
28*	0–20 cm; Mg·ha^{-1}															○	○							
37	0–20, 30, or 40 cm; Mg·ha^{-1}					○																		
45*	0–20 cm; %															●	●	●	●	●	●			
50†	0–10 cm; Mg·ha^{-1}				○																			
51†	B horizon; %																							○

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study. Refer to original papers for complete details.

*Statistical analyses were performed on data representing more than a single post-harvest year.

†Organic matter, rather than C, was estimated using loss on ignition.

Fig. 4. Relationship between mineral soil organic carbon response ratios (WTH : SOH) and mineral soil organic C content in WTH stands. Mineral soil C contents (Mg/ha) were calculated on a 10 cm basis for each data point in Fig. 3, using available published values of bulk density to convert soil C concentrations to content. Soil organic C content is plotted on a logarithmic scale.



erating vegetation, leached from the site, immobilized by microbes or diluted by the large reservoir of N already in the soil (Olsson et al. 1996*b* [28]; Powers et al. 2005 [31]).

At the stand level, variables related to N-cycling processes and microbial activity may be more sensitive to biomass removal and hence provide a more meaningful index of the effects of harvesting on soil N availability than total soil N pools (Binkley and Hart 1989; Table 4). For example, higher C : N ratios in the forest floor microbial community (Belleau et al. 2006 [3]) and in the forest floor itself (Olsson et al. 1996*b* [28]) were observed 2 and 15–16 years after WTH, respectively, despite less consistent treatment differences in total forest floor N. In a thinning experiment, Smolander et al. (2008) found slightly lower amounts of easily mineralizable C and N when whole trees, rather than delimbed stems, were removed. Changes in soil N availability related to biomass removal could have a number of causes. Fifteen months after harvesting a Sitka spruce (*Picea sitchensis*) plantation in northern Wales, for example, harvesting residues at the soil surface enhanced soil microbial N pools and stimulated rates of decomposition (Emmett et al. 1991*b* [8]) and nitrification (Emmett et al. 1991*a* [7]); this effect appeared to be related to both inputs of fresh organic material and improved microclimatic conditions (i.e., greater soil moisture and fewer temperature fluctuations; Emmett et al. 1991*b* [8]). Nevertheless, intrinsic natural variations in soil organic matter content and microclimate (Li et al. 2003 [20]) and harvesting per se, irrespective of residue management (e.g., Mattson and Swank 1989 [24]; Olsson et al. 1996*b* [28]; Brais et al. 2002; Hassett and Zak 2005 [12]; Belleau et al. 2006 [3]) could be the overriding factors controlling N cycling processes, at least at the stand level.

There are concerns in regions where atmospheric N deposition is elevated that harvest residues left on site could contribute to excess accumulation of N in the soil and N leaching, which can alter soil chemistry and biodiversity, and reduce water runoff quality (Aber et al. 1989). In this situation, biomass harvesting can be a means of reducing N load to forest soils (Fenn et al. 1998; Akselsson et al. 2007*a*). Modelling studies of Swedish forests have suggested that the intensity of harvesting can have a strong impact on the N budget. In areas with high levels of N deposition, SOH could cause an accumulation of mineral N in the soil and an increased risk of leaching (Akselsson and Westling 2005). Accordingly, eight of the ten field studies in Table 5 show that retention of harvesting residues was associated with significantly elevated rates of N leaching compared with residue removal; leaching losses of NO_3^- or $NO_3^- + NH_4^-$ were between 1.4 and 16 times higher with SOH than with WTH 1–5 years post-harvest (but see Titus and Malcolm 1992 [47]). Higher rates of mineral N leaching after SOH could be attributed to (*i*) direct (inorganic N) or indirect (organic N) inputs of N via leaching from residues into the soil, (*ii*) suppression of regrowth by harvesting residues and, as a consequence, lower rates of N uptake by vegetation, and (or) (*iii*) altered microclimatic conditions that favour increased N mineralization under residues (i.e., higher temperature and moisture, protection from freezing and thawing; Stevens and Hornung 1990 [42]; Emmett et al. 1991*a* [7]; Titus and Malcolm 1992 [47]; Titus et al. 1997). Absolute differences in N leaching after WTH and SOH are generally small, as observed by Mann et al. (1988 [23]) for a range of hardwood and conifer stands across the US. In addition, elevated N leaching associated with SOH relative to WTH frequently disappears within 3–5 years of harvesting (Table 5); harvesting intensity is thus unlikely to cause a significant overall difference in N leaching relative to the impacts of harvesting per se. Decreased rates of N leaching often coincide with the expansion of understory vegetation after harvesting (Staaf and Olsson 1994 [41]). Rapid nutrient accumulation in sprouts and herbaceous species has been shown to be a key mechanism for nutrient retention in ecosystems in the first years following harvesting in a variety of temperate ecosystems (e.g., northern hardwoods, Marks and Bormann 1972, Boring et al. 1981; loblolly pine, Cox and Van Lear 1984). Furthermore, microbial immobilization within harvesting residues can act as a N sink, thus reducing N losses through leaching, particularly in coniferous forests (Vitousek and Matson 1985 [49]; Wall 2008 [50]). In ecosystems where N cycles more rapidly and NO_3 production is generally higher, however, microbial immobilization could be less important in retaining N after disturbance than N uptake through revegetation (Vitousek and Matson 1985 [49]).

Soil phosphorus

Phosphorus availability is an important issue for soil productivity in zones with highly weathered soils, such as New Zealand, Australia, Brazil, and the southeastern US (Comerford et al. 2002). For example, WTH reduced the extractable P contents of ultisolic soils in Louisiana and North Carolina to between 79% and 89% of those in SOH plots (Sanchez et al. (2006*a* [36]). The impact on soil phosphorus availability has typically been of less concern than the impact of harvesting on N in most boreal and temperate forests because they are generally found on recently glaciated soils with abundant unweathered minerals and higher concentrations of available P. Nonetheless, nutrient budgets suggest that WTH can remove five times as much P as SOH in northern hardwood stands (Yanai 1998), and up to seven times as much P in bor-

Table 3. Studies examining the impact of whole-tree (WTH) and stem-only harvesting (SOH) on soil total nitrogen.

		Year post-harvest																			
Ref		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Units	**FOREST FLOOR**																			
3	g·kg^{-1}	○	○																		
14	mg·kg^{-1}			●																	
28*	kg·ha^{-1}															○	○				
45*	%															○	○	○	○	○	○
46	mg·g^{-1} or kg·ha^{-1}		○			●															
50	L or FH; kg·ha^{-1}				●																
	Total sample depth; units	**MINERAL SOIL**																			
3	0–10 cm; g·kg^{-1}	○	○																		
4	0–15 cm or 0–60 cm; kg·ha^{-1}	○	○	○																	
14	0–20 cm; mg·kg^{-1}			○																	
16	0–45 cm; mg·kg^{-1}															○					
20	0–10 cm; Mg·ha^{-1}					○															
28*	0–20 cm; kg·ha^{-1}															○	○				
30	0–15 cm; g·kg^{-1}															○					
36	0–30 cm; kg·ha^{-1}										●										
37	0–20, 30, or 40 cm; kg·ha^{-1}					○															
45*	0–20 cm; %															○	○	○	○	○	○
49*	0–15 cm; %	○	○																		
50	0–10 cm; kg·ha^{-1}				○																

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study.

*Statistical analyses were performed on data representing more than a single post-harvest year.

Table 4. Studies examining the impact of whole-tree (WTH) and stem-only harvesting (SOH) on soil biota and N cycling processes.

			Year post-harvest															
Ref			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Variable	**Units**	**FOREST FLOOR**															
3	Microbial C/N		○	■														
28*	C/N									■							○	○
3	Basal respiration	μg CO_2-C·g^{-1}·h^{-1}	■	○														
	qCO_2	μg CO_2-C·mg^{-1} C_{mic}	○	○														
9	CO_2 efflux	μmol CO_2·m^{-2}·s^{-1}			○	○	○											
3	Microbial C	μg·g^{-1}	○	○														
	Microbial N	μg·g^{-1}	○	○														
8	Microbial biomass	μg N·g^{-1}; g N·m^{-2}	●															
	Decay rate	%	●															
		Total sample depth; units	**MINERAL SOIL**															
3	Microbial C/N	0–10 cm	○	○														
16	C/N	0–45 cm															○	
28*	C/N	0–5 cm								○							■	■
30	C/N	0–15 cm															○	
4	Net N-min. - field	0–15 cm; kg·ha^{-1}·mo^{-1}	○	○														
12	Gross N-min. - lab	0–10 cm; mg N·kg^{-1}·d^{-1}								○	○	○						
	Gross N-imm. - lab									○	○	○						
20	Net N-min. - field	0–10 cm; kg·ha^{-1}					○											
30	Net N-min. - field	0–15 cm; kg·ha^{-1}															●	
31	Net N-min. - lab	0–20 cm; mg·kg^{-1}										○						
49	Net N-min.-field	0–15 cm;	○	●														
	Net N-min.-lab	0–15 cm;	○	●														
3	Basal respiration	0–10 cm; μg CO_2-C·g^{-1}·h^{-1}	○	○														
	qCO_2	0–10 cm; μg CO_2-C·mg^{-1} ·C_{mic}	○	○														
4	CO_2 efflux	g CO_2·m^{-2}·d^{-1}	○															
24*	CO_2 efflux	0–60 cm; kg C·ha^{-1}			○	○	○	○	○	○								
3	Microbial C	0–10 cm; μg·g^{-1}	○	○														
	Microbial N	0–10 cm; μg·g^{-1}	○	○														
4	Microbial biomass	0–15 cm; Log_{10} CFU·g^{-1}	○															
12*	Microbial biomass	0–10 cm; ng PLFA C·g^{-1} soil								○	○	○						
	Enzyme activity	0–10 cm; nmol·g^{-1}·h^{-1}								■	■	■						
49	Microbial N*	0–15 cm; μg·g^{-1}	○	○														

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study.

*Statistical analyses were performed on data representing more than a single post-harvest year.

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Table 5. Studies examining the impact of whole-tree (WTH) and stem-only harvesting (SOH) on mineral N leaching.

			Year post-harvest										
Ref	N-form	Horizon or depth; units	0	1	2	3	4	5	6	7	8	9	10
7	NO_3^-	25 cm; g N·m^{-2}	■	●									
14	NO_3^-	base of LFH; mg·L^{-1}			●	○							
		100 cm; mg·L^{-1}			●	○							
21	NO_3^-	base of LFH; kg·ha^{-1}		●	●	○	○	○	○				
		100 cm; kg·ha^{-1}		●	●	○	○	○	○				
41	NO_3^-	30 cm; mg·L^{-1}	○	●	●	○	○	○					
42	$NO_3^- + NH_4^+$	base of L; mg N·L^{-1}	●	●	●	●							
		Base of O; mg N·L^{-1}	○	●	●	●							
		A, B or C; mg N·L^{-1}	○	●	●	●							
43	$NO_3^- + NH_4^+$	base of L; mg·L^{-1} or kg·ha^{-1}	■	○	●	●	●						
		base of O; kg·ha^{-1}	○	○	○	○	○						
		C horizon; mg·L^{-1}	○	○	○	●	●						
44	NO_3^-	100 cm; mg·L^{-1}				○	●	○					
47	NO_3^-	base of LFH; mg·L^{-1}	■		■			○					
48	$NO_3^- + NO_2^-$	50 cm; kg·ha^{-1}	○	●	●	●							
50	NO_3^-	base of LFH; mg·dm^{-3}	○	○	○	○							

Note: Where possible, the effect of harvesting on nitrate leaching is reported; otherwise, N-form is indicated in the table. Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study.

eal coniferous stands (Paré et al. 2002). Indeed, Fig. 3 shows that soil P levels are generally reduced after WTH relative to SOH, regardless of glacial history: 84% of response ratios were below 1.0. Furthermore, two of the three studies reviewed in Table 6 reported significant reductions in total P, while three of the four reviewed studies reported significant reductions in extractable P.

Phosphorus can leach from logging residues into the forest floor during the first few years after harvest. Approximately one third of the P bound in logging residues was leached into the soil within a year of harvesting a Sitka spruce stand in Wales (Stevens et al. 1995 [43]). Most of the P leached from harvesting residues is retained in the soil profile (Stevens et al. 1995 [43]; Wall 2008 [50]). Extractable P and (or) total P levels in the forest floor of WTH plots were 75%–85% of those in SOH plots 2–5 years after treatment application in studies from Sweden and the UK. This pattern was probably caused by surface litter inputs following SOH, rather than immobilization of P leached from harvesting residues (Titus and Malcolm 1991 [46]; Wall 2008 [50]).

Soil base cations (Ca, Mg, and K)

Fewer studies have examined the impacts of harvesting intensity on soil base cations than on N and C. Nevertheless, a number of studies, some dating back to the early 1970s (e.g., Boyle et al. 1973), have used theoretical nutrient budgets to predict the impacts of different intensities of harvesting on soil base cation pools in temperate and boreal stands. In general, WTH is expected to cause a greater drain on base cation reserves than SOH and a net depletion of base cation pools over the long term. Calcium is typically considered the nutrient most at risk of depletion (e.g., Johnson et al. 1982, 1988; Federer et al. 1989), but Mg and K are also of concern (Sverdrup and Rosén 1998; Joki-Heiskala et al. 2003). The tree species harvested also appear to have a substantial effect on theoretical budgets: stands dominated by species with higher rates of nutrient uptake and greater standing biomass tend to be most negatively affected by WTH (Paré et al. 2002; Akselsson et al. 2007*b*).

Several recent nutrient budget modelling studies have also examined the combined effects of harvesting and acidic atmospheric deposition on soil base cation pools. Modelled nutrient budgets indicate that even SOH is unsustainable in large parts of Sweden and Finland because of leaching losses of Ca and Mg from the soil caused by atmospheric deposition (Sverdrup and Rosén 1998; Joki-Heiskala et al. 2003; Akselsson et al. 2007*b*). Calculations for 21 catchments in Norway, Germany, and eastern regions of North America have led to similar conclusions (Watmough et al. 2005). In contrast, a study modelling the nutrient budget of a boreal stand in Quebec in an area with low amounts of acidic deposition indicated that K, rather than Ca or Mg, was most sensitive to depletion (Duchesne and Houle 2006). According to this model, tree uptake would be the main pathway for K loss from the soil on these sites; given the small amount of K in these base-poor, shallow soils, K pools would probably be depleted by any intensity of harvesting (Duchesne and Houle 2006), but would be particularly sensitive to WTH (Duchesne and Houle 2008).

In agreement with nutrient budget studies, field trials frequently reveal that WTH reduces the concentration and content of exchangeable cations in the soil, with more than 70% of reponse ratios having values below 1.0, especially during the first decade after harvest (Fig. 3). Significant differences in the effects of WTH and SOH on levels of exchangeable Ca, Mg, and K were reported in five out of eight, six out of seven, and five out of nine field trials, respectively (Table 7), covering a wide array of soil, stand, and climatic conditions up to 23 years post-harvest (e.g., Nykvist and Rosén 1985 [26]; Walmsley et al. 2009 [51]). Where significant effects were reported, the concentrations or contents of exchangeable base cations in soils from WTH stands varied from 46% to

Table 6. Studies examining the impacts of whole-tree (WTH) and stem-only harvesting (SOH) on extractable and total phosphorus.

			Year post-harvest														
Ref			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Form	**Units**	**FOREST FLOOR**														
3	Total	g·kg^{-1}	○														
46	Total	mg·g^{-1} or kg·ha^{-1}		●			●										
50	Total	L or FH; kg·ha^{-1}				●											
3	Extractable	mg·kg^{-1}	○	○													
50	Extractable	L or FH; kg·ha^{-1}				●											
		Total sample depth; units	**MINERAL SOIL**														
3	Total	0–10 cm; g·kg^{-1}	○														
50	Total	0–10 cm; kg·ha^{-1}				○											
3	Extractable	0–10 cm; mg·kg^{-1}	○	○													
16*	Extractable	0–45 cm; mg·kg^{-1}															●
36	Extractable	0–30 cm; kg·ha^{-1}										●					
50	Extractable	0–10 cm; kg·ha^{-1}				○											

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study.

*Authors suggest that treatment differences may be spurious.

86% of the values measured in SOH stands (see contradictory results in Walmsley et al. 2009 [51] for Ca and in Olsson et al. 1996*a* [27] for Mg). Significant reductions in base cation levels were most frequently observed in the forest floor (Table 7). The strength of treatment effects in mineral soils may depend, in part, on the degree to which cation exchange sites are saturated with aluminum; high levels of aluminum saturation suppress base cation reactions. Indeed, Bélanger et al. (2003 [2]) proposed that high levels of aluminum saturation in coarse-textured boreal mineral soils were the reason that harvest residue retention had no significant effect on soil cation levels in mineral horizons. In a Swedish study, SOH increased exchangeable base cation levels in mineral soils relative to WTH only on sites with the lowest levels of exchangeable acidity (Olsson et al. 1996*a* [27]).

Field trials are particularly effective at highlighting differences in cycling patterns among base cations, particularly between the divalent Ca and Mg ions and the monovalent K ions. For example, Ca and Mg are embedded within large organic molecules in plant tissues and are therefore not easily leached from organic material; furthermore, they can be more strongly retained by most soil colloids because they are divalent. Owing to their low mobility in soils and slow release during decomposition (Edmonds 1987), Ca and Mg leached from harvesting residues can be effectively immobilized on cation exchange sites, thereby creating marked treatment differences in the pools of Ca and Mg in the soil (Table 7). In contrast, K is found in ionic form within plant tissues; as a result, K tends to be rapidly leached from harvesting residues and poorly retained in the soil owing to its monovalence, leading to lower rates of recovery and high losses in streamwater (Stevens et al. 1995 [43]; Olsson et al. 1996*a* [27]). Consequently, higher concentrations of K in soils from stands harvested by SOH are not as common (Fig. 3; Table 7). The implications of these differences are demonstrated in Olsson et al. (1996*a* [27]), who reported that nutrient recoveries from logging residues (defined as the percentage of the quantity of nutrients immobilized in the soil relative to the quantity of nutrients from logging residues) were several times lower for K (0%–15%) than for Ca (>60%) and Mg (>40%) 15–16 years post-harvest. The retention of harvesting residues may thus not be as efficient a means of conserving exchangeable K pools in the soil as it is for conserving exchangeable Ca and Mg.

Johnson and Todd (1998 [16]) used field trials to test hypotheses raised by theoretical nutrient budgets examining the implications of WTH and SOH for nutrient pools in mixed oak stands in Tennessee, USA (Johnson et al. 1982). Contrary to expectations, leaching losses and uptake by regenerating vegetation on WTH sites did not deplete soil exchangeable Ca pools within 15 years of harvesting, although WTH did reduce these pools relative to SOH. Calcium from nonexchangeable or deeper exchangeable reserves in the soil or bedrock probably compensated for harvesting-related losses in soil Ca on these sites. This underlines the fact that predictions of changes in ecosystem processes based solely on unvalidated model projections or theoretical budgets should be considered with caution (Johnson and Todd 1998 [16]).

Soil acidity–alkalinity status

The role of WTH in acidifying forest soils is coupled with the issue of reduced base cation pools. Whole-tree harvesting permanently deprives the soil of a large proportion of the base cations that have accumulated in vegetation during rotation, whereas SOH returns most of them to the soil through decomposition, thus counteracting some of the acidification associated with forest growth (Nilsson et al. 1982; van Breemen et al. 1983). According to Staaf and Olsson (1991 [40]), the influence of biomass harvesting on soil acidity should be most pronounced and appear earliest on productive sites (which produce the most slash and support the highest rates of decomposition), and be weaker but endure for longer periods on low productivity sites. Acidification associated with WTH can be of particular concern in regions subjected to high rates of atmospheric acid deposition. For forests in southwestern Sweden (an area with highly productive forests and elevated levels of atmospheric pollution), the increased

Table 7. Studies examining the impacts of whole-tree (WTH) and stem-only harvesting (SOH) on exchangeable (*a*) calcium, (*b*) magnesium, and (*c*) potassium.

		Years post-harvest																						
Ref		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
(*a*)																								
	Units	**FOREST FLOOR**																						
2	cmol$_c$·kg^{-1}			○																				
3	cmol$_c$·kg^{-1}	○	○																					
26*	meq·100 g^{-1}						●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
27*	L or FH; kg·ha^{-1}															●	●							
45*	cmol·kg^{-1}															●	●	●	●	●	●			
50	L or FH; kg·ha^{-1}				●																			
51	cmol$_c$·kg^{-1}																							○
	Total sample depth or horizon; units	**MINERAL SOIL**																						
2	0–20 cm; cmol$_c$·kg^{-1}			○																				
3	0–10 cm; cmol$_c$·kg^{-1}	○	○																					
16	0–45 cm; cmol$_c$·kg^{-1}															●								
27*	0–20 cm; kg·ha^{-1}															●	●							
45*	0–20 cm; cmol·kg^{-1}															○	○	○	○	○	○			
50	0–10 cm; kg·ha^{-1}				○																			
51	B horizon; cmol$_c$·kg^{-1}																							■
(*b*)																								
	Units	**FOREST FLOOR**																						
2	cmol$_c$·kg^{-1}			●																				
3	cmol$_c$·kg^{-1}	○	●																					
26*	meq·100 g^{-1}						●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		
27*	L or FH; kg·ha^{-1}															■	■							
45*	cmol·kg^{-1}															○	○	○	○	○	○			
50	L or FH; kg·ha^{-1}				●																			
	Total sample depth; units	**MINERAL SOIL**																						
2	0–20 cm ; cmol$_c$·kg^{-1}			○																				
3	0–10 cm ; cmol$_c$·kg^{-1}	○	○																					
16	0–45 cm ; cmol$_c$·kg^{-1}															●								
27*	0–20 cm ; kg·ha^{-1}															●	●							
45*†	0–20 cm ; cmol·kg^{-1}															■	■	■	■	■	■			
50	0–10 cm ; kg·ha^{-1}				○																			
(*c*)																								
	Units	**FOREST FLOOR or ORGANIC HORIZON**																						
2	cmol$_c$·kg^{-1}			○																				
3	cmol$_c$·kg^{-1}	○	○																					
26*	meq·100 g^{-1}						○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○		
27*	L or FH ; kg·ha^{-1}															○	○							
45*	cmol·kg^{-1}															○	○	○	○	○	○			
50	L or FH ; kg·ha^{-1}					●																		

Table 7 (*concluded*).

(*c*)												
51	$cmol_c \cdot kg^{-1}$											●
	Total sample depth or horizon	**MINERAL SOIL**										
2	$cmol_c \cdot kg^{-1}$			●								
3	$cmol_c \cdot kg^{-1}$	○	○									
12	0–75 cm ; $mg \cdot kg^{-1}$		○									
16†	0–45 cm ; $cmol_c \cdot kg^{-1}$					●						
27*	0–20 cm ; $kg \cdot ha^{-1}$					○	○					
45*	$cmol \cdot kg^{-1}$					●	●	●	●	●	●	
50	0–10 cm ; $kg \cdot ha^{-1}$				○							
51	B horizon ; $cmol_c \cdot kg^{-1}$											○

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study.

*Statistical analyses were performed on data representing more than a single post-harvest year.

†Authors suggest that treatment differences may be spurious.

acidity associated with WTH, averaged over a forest rotation, could be equivalent to that associated with acidic atmospheric deposition (Nilsson et al. 1982). In contrast, similar estimates for low fertility boreal black spruce (*Picea mariana*) stands in northern Quebec indicated that the increased acidity induced by WTH could be less than 20% of that caused by acidic deposition (Bélanger et al. 2003 [2]). Modelling studies have also demonstrated that the long-term sustainability of the acid–base status of Quebec's boreal forest soils could depend, in large part, on reduced air pollution and only marginally on forest management strategies (Thiffault et al. 2007).

Field trials used to validate modelled rates of soil acidification show that biomass removal has a much smaller influence on soil acidity than expected from theoretical assessments (Staaf and Olsson 1991 [40]). Accordingly, only two of eight field studies reported that WTH caused significant reductions in forest floor pH (to between 93% and 98% of that in SOH stands) and only three of eight studies showed significant effects of harvesting treatments on other indicators of forest floor acidity (exchangeable acidity, base saturation or ratio of exchangeable base cations: aluminum; Table 8). Significant treatment effects on mineral soil acidity were even less common and consistent. Ecosystem processes that mediate the influence of biomass removal on soil acidity are apparently not taken into account in theoretical acidity budgets and therefore predicted rates of soil acidification after WTH are hardly ever fully realized. For example, Wall (2008 [50]) observed that the soil was actually slightly more acidic under heaps of logging residues because of increased rates of nitrification. Likewise, soil pH was roughly the same 15–16 years after WTH and SOH in boreal forests in Quebec (Thiffault et al. 2006 [45]). The lack of a treatment effect on soil pH might be attributed to the production and persistence of organic acids produced in logging residues and then leached into the soil; this phenomenon may be typical of forests in colder climates, and could have balanced any acidifying effects of residue removal (Thiffault et al. 2006 [45]). Staaf and Olsson (1991 [40]) observed that the relationship between pH and exchangeable acidity tends to be curvilinear, flattening out below a certain pH (pH_{water} = 4.2 in their study). Soil pH may thus not be very sensitive to changes in soil acid–base status in acidic soils; instead, a substantial increase in exchangeable acidity could be needed to trigger a significant change in soil pH. Indeed, Bélanger et al. (2003 [2]) found that other indicators of acidity, such as the ratio of exchangeable base cations: aluminum, were more likely to show a treatment response than soil pH.

Tree foliar nutrition

Chemical analyses of the soil environment do not always correlate closely with the availability of nutrients to plants (Fisher and Binkley 2000). As stated by Stone (1979), no generalizations can be made about the soil supply of nutrients as a whole for tree nutrition and growth: each element has its own unique chemistry in the soil and its own rate and magnitude of circulation through organic material, soil, and vegetation. As a result, tree foliar analysis can be an invaluable tool for assessing effects of management on the availability of individual nutrients.

From Fig. 5 it can be seen that WTH frequently causes

Table 8. Studies examining the impacts of whole-tree (WTH) and stem-only harvesting (SOH) on soil acidity.

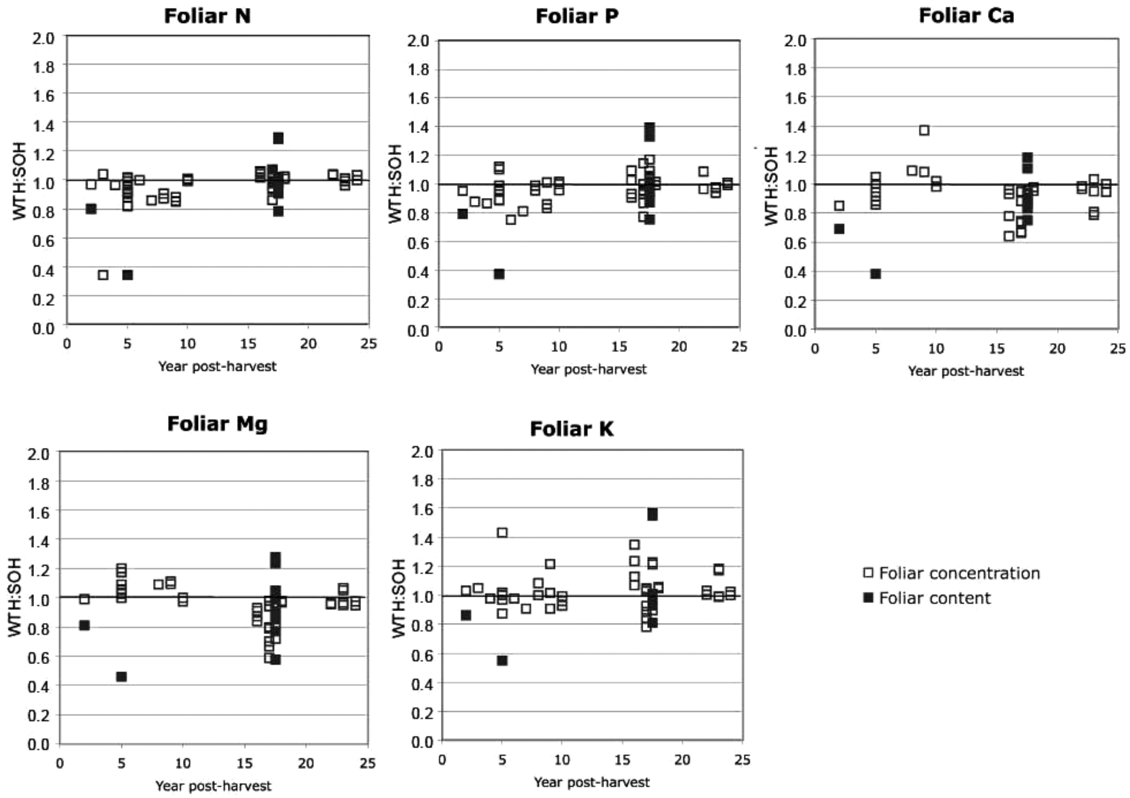
Ref			Years post-harvest																						
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
	Variable	**Horizon ; units**	**FOREST FLOOR**																						
2	pH				○																				
3	pH		○	○																					
14	pH				○																				
26*	pH																●	●	●						
40*	pH	L or FH							●	●	●														
45*	pH																								
50	pH	L or FH				○																			
51	pH																								○
3	EA	cmol(+)·kg^{-1}	○	○																					
40	EA	FH; μeq·g^{-1}							●	●	●														
2	BS	%			○																				
3	BS	%	○	○																					
27*	BS	L or FH; %																●							
45	BS	%																			○				
2	Ca_e/Al_e				●																				
	Mg_e/Al_e				●																				
	K_e/Al_e				●																				
45	BC_e/Al_e																				○				
		Total sample depth or horizon; units	**MINERAL SOIL**																						
2	pH	0–20 cm			○																				
3	pH	0–10 cm	○	○																					
14	pH	0–20 cm			○																				
40*	pH	0–10 cm							○	○	○														
45*	pH	0–20 cm																			○				
50	pH	0–10 cm				○																			
51	pH	B horizon																							○
3	EA	0–10 cm; cmol(+)·kg^{-1}	●	●																					
40	EA	0–10 cm; μeq·g^{-1}							●	●	●														
2	BS	0–20 cm; %			○																				
3	BS	0–10 cm; %	○	○														●							
27*	BS	0–20 cm; %																			■				
45†	BS	0–20 cm; %																							
2	Ca_e/Al_e	0–20 cm			○																				
2	Mg_e/Al_e	0–20 cm			○																				
2	K_e/Al_e	0–20 cm			○																				
45†	BC_e/Al_e	0–20 cm																			■				

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study. . BS indicates base saturation, EA indicates exchangeable acidity, BC_e/Al_e indicates the ratio of exchangeable base cations (Ca_e + Mg_e + K_e) to exchangeable Al.

*Statistical analyses were performed on data representing more than a single post-harvest year.

†Authors suggest that treatment differences may be spurious.

Fig. 5. Response ratios (WTH:SOH) of foliar nitrogen, foliar phosphorus, foliar calcium, foliar magnesium, and foliar potassium.



lower foliar N relative to SOH, particularly in the first decade post-harvest. Moreover, 6 of 10 studies revealed significant negative impacts of WTH in foliar N in at least one tree species on at least one sampling date, with foliar N contents or concentrations reduced by WTH to between 34% and 88% of those in stands established after SOH (Table 9*a*). A limited number of site conditions are represented among the reviewed studies; however, field trials on podzols [13, 29, 39, 45] and gleysols at higher latitudes [32, 33] were generally associated with significant negative effects of WTH on foliar N, while trials on andisols, vertisols and ultisols in the U S [1, 16, 35, 36] were not (Table 9*a*). There does not appear to be a clear relationship between harvesting-related changes in soil N pools and foliar N levels: (*i*) Thiffault et al. (2006 [45]) and Olsson et al. (1996*b* [28], 2000 [29]) observed improved foliar N nutrition after SOH but no change in soil N pools, although lower soil C:N ratios and a small shift towards more N-demanding species in SOH treatments in the Swedish experiment could indicate increased N availability (Olsson et al. (1996*b* [28]; Olsson and Staaf 1995); (*ii*) conversely, Sanchez et al. (2006*a* [36]) reported significantly reduced soil N contents with WTH but no significant change in foliar N concentrations; and (*iii*) Kranabetter et al. (2006) observed that hybrid white spruce (*Picea glauca* ×*engelmannii*) and lodgepole pine (*Pinus contorta*) saplings with the highest foliar N concentrations could be found growing in soils with the lowest total N pools and N mineralization rates. The response of regenerating stands to harvesting treatments is thus probably better explained by looking at processes governing both nutrient uptake and nutrient supply in soils.

Monitoring of foliar nutrition across a range of boreal and temperate sites in Sweden for more than two decades after harvesting showed that treatment differences in foliar N and P tend to appear early in the rotation but can disappear after the first decade (Olsson et al. 2000 [29] in Table 9). This trend can also be observed in Fig. 5: during the first 10 years post-harvest, 79% and 86% of response ratios are below 1.0 for N and P, respectively, but beyond 10 years post-harvest, response ratios are almost evenly distributed above and below the 1.0 line. Elevated levels of foliar N early in stand development after SOH can be associated with increased tree growth and a concomitant decrease in the foliar concentrations of other nutrients, through dilution effects (Proe et al. 1999 [33]; Olsson et al. 2000 [29]). Dilution effects are particularly evident for K, which can be rapidly leached from harvesting residues and soils; high concentrations of soil NO_3 and (or) delays in revegetation are often associated with SOH and may further reduce the retention of K within the soil. As a result, there could be little additional K to meet the need caused by increased tree growth arising from the release of N from decomposing residues and, consequently, foliar K concentrations can decline following SOH (Proe et al. 1999 [33]; Olsson et al. 2000 [29]). Evidence of this dilution effect can be seen in Fig. 5 for K where foliar concentrations or contents were often greater in WTH stands than in SOH stands (55% of plotted ratios above 1.0), and also for Mg during the first decade after harvest (80% of ratios above 1.0).

In contrast, Ca (and, to a lesser degree, Mg) originating from decomposing residues tends to enhance foliar nutrition; this effect may be most significant several years after harvest when the influence of residue retention on foliar N concentrations has subsided (Fig. 5; Tables 9*c* and 9*d*): beyond 10 years post-harvest, 85% and 78% of the calculated re-

Table 9. Studies examining the impacts of whole-tree (WTH) and stem-only harvesting (SOH) on tissue (*a*) nitrogen, (*b*) phosphorus, (*c*) calcium, (*d*) magnesium, and (*e*) potassium.

(a)

Ref	Spp.*	Sample type; units	Years post-harvest																							
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
			DECIDUOUS																							
13[†]	Mr	Foliage + wood; $mg \cdot g^{-1}$				○																				
	Ep	Foliage + wood; $mg \cdot g^{-1}$				○																				
	At	Foliage + wood; $mg \cdot g^{-1}$				●																				
16[†]	Cb	Foliage; $g \cdot kg^{-1}$																	○							
	Qp	Foliage; $g \cdot kg^{-1}$																	○							
	Mr	Foliage; $g \cdot kg^{-1}$																	○							
	Qr	Foliage; $g \cdot kg^{-1}$																	○							
			CONIFEROUS																							
1	Fd*	Foliage; %			○	○	○																			
29[§]	Sn	0 or 1 yr foliage; $mg \cdot g^{-1}$								●	●							○						○	○	
	Ps	0 or 1 yr foliage; $mg \cdot g^{-1}$									●	●							○	○					○	○
32	Ss	Whole tree; $kg \cdot ha^{-1}$									●															
		Foliage; %			○	○		○	○	○	○	○														
33	Ss	Foliage; % or content		○			●																			
35[‡]	Fd	Current year foliage; %			○																					
36	Pt	2nd yr foliage; $g \cdot kg^{-1}$										○														
39	Sn	0 or 1 yr foliage; $mg \cdot g^{-1}$				●																				
45[§]	Sb	0 or 1 yr foliage; $mg \cdot g^{-1}$ or content															○	○	○	○	○	○				
	Pj	0 or 1 yr foliage; $mg \cdot g^{-1}$ or content															●	●	●	●	●	●				
	Bf[‖]	0 or 1 yr foliage; $mg \cdot g^{-1}$ or content															■	■	■	■	■	■				

(*b*)

Ref	Spp.*	Sample type; units	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
			DECIDUOUS																							
16[†]	Cb	Foliage; $g \cdot kg^{-1}$																	○							
	Qp	Foliage; $g \cdot kg^{-1}$																	○							
	Mr	Foliage; $g \cdot kg^{-1}$																	○							
	Qr	Foliage; $g \cdot kg^{-1}$																	○							
			CONIFEROUS																							
29[‖]	Sn	0 or 1 yr foliage; $mg \cdot g^{-1}$								●	●							○						○	○	
	Ps	0 or 1 yr foliage; $mg \cdot g^{-1}$									○	○							○	○					○	○
32	Ss	Whole tree; $kg \cdot ha^{-1}$									●															
		Foliage; %			○	○		○	○	○	○	○														
32	Ss	Foliage; % or content		○			●																			
36	Pt	2nd yr foliage; $g \cdot kg^{-1}$			○																					
39	Sn	0 or 1 yr foliage; $mg \cdot g^{-1}$										○														
45[§]	Sb	0 or 1 yr foliage; $mg \cdot g^{-1}$ or content				○											○	○	○	○	○	○				

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Table 9 (*continued*).

(*b*)																	
	Pj	0 or 1 yr foliage; mg·g^{-1} or content							●	●	●	●	●	●			
	Bf[‖]	0 or 1 yr foliage; mg·g^{-1} or content							■	■	■	■	■	■			
(*c*)																	
		DECIDUOUS															
13[†]	Mr	Foliage + wood; mg·g^{-1}		○													
	Ep	Foliage + wood; mg·g^{-1}		○													
	At	Foliage + wood; mg·g^{-1}		●													
16	Cb	Foliage; g·kg^{-1}									●						
	Qp	Foliage; g·kg^{-1}									●						
	Mr	Foliage; g·kg^{-1}									●						
	Qr	Foliage; g·kg^{-1}									○						
		CONIFEROUS															
29[¶]	Sn	0 or 1 yr foliage; mg·g^{-1}				○	○			●					○	○	
	Ps	0 or 1 yr foliage; mg·g^{-1}					■	■			○	○				○	○
33	Ss	Foliage; % or content	●		●												
36	Pt	2nd yr foliage; g·kg^{-1}						○									
39	Sn	0 or 1 yr foliage; mg·g^{-1}		○													
45[§]	Sb	0 or 1 yr foliage; mg·g^{-1} or content							●	●	●	●	●	●			
	Pj	0 or 1 yr foliage; mg·g^{-1} or content							●	●	●	●	●	●			
	Bf[¶]	0 or 1 yr foliage; mg·g^{-1} or content							●	●	●	●	●	●			
(*d*)																	
		DECIDUOUS															
13[†]	Mr	Foliage + wood; mg·g^{-1}		○													
	Ep	Foliage + wood; mg·g^{-1}		○													
	At	Foliage + wood; mg·g^{-1}		●													
16[†]	Cb	Foliage; g·kg^{-1}									○						
	Qp	Foliage; g·kg^{-1}									○						
	Mr	Foliage; g·kg^{-1}									●						
	Qr	Foliage; g·kg^{-1}									●						
		CONIFEROUS															
29[§]	Sn	0 or 1 yr foliage; mg·g^{-1}				○	○			●					○	○	
	Ps	0 or 1 yr foliage; mg·g^{-1}					○	○			○	○				○	○
33	Ss	Foliage; % or content	○					□									
36	Pt	2nd yr foliage; g·kg^{-1}						○									
39	Sn	0 or 1 yr foliage; mg·g^{-1}		○													
45[§]	Sb	0 or 1 yr foliage; mg·g^{-1} or content							●	●	●	●	●	●			

Table 9 (*concluded*).

(*d*)																					
	Pj	0 or 1 yr foliage; mg·g^{-1} or content										●	●	●	●	●	●				
	Bf‖	0 or 1 yr foliage; mg·g^{-1} or content										■	■	■	■	■	■				
(*e*)																					
		DECIDUOUS																			
13†	Mr	Foliage + wood; mg·g^{-1}			■																
	Ep	Foliage + wood; mg·g^{-1}			○																
	At	Foliage + wood; mg·g^{-1}			○																
16†	Cb	Foliage; g·kg^{-1}												●							
	Qp	Foliage; g·kg^{-1}												○							
	Mr	Foliage; g·kg^{-1}												○							
	Qr	Foliage; g·kg^{-1}												○							
		CONIFEROUS																			
29§	Sn	0 or 1 yr foliage; mg·g^{-1}							■	■			■						■	■	
	Ps	0 or 1 yr foliage; mg·g^{-1}								○	○			■	■					○	○
32	Ss	Whole tree; kg·ha^{-1}								●											
		Foliage; %		○	○		○	○	○	○	○										
33	Ss	Foliage; % or content	○								□										
36	Pt	2nd yr foliage; g·kg^{-1}									○										
39	Sn	0 or 1 yr foliage; mg·g^{-1}			○																
45§	Sb	0 or 1 yr foliage; mg·g^{-1} or content										○	○	○	○	○	○				
	Pj	0 or 1 yr foliage; mg·g^{-1} or content										●	●	●	●	●	●				
	Bf§	0 or 1 yr foliage; mg·g^{-1} or content										■	■	■	■	■	■				

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study. Spp. indicates species.

*Refer to Table 1 for tree species codes.

†Only most common tree species shown.

‡Both SOH and WTH treatments received vegetation control.

§Statistical analyses were performed on data representing more than a single post-harvest year.

‖Authors suggest that treatment differences may be spurious.

¶Ca content in current-year needles was increased by WTH at one site but all other significant effects showed reduced foliar Ca contents and concentrations with WTH.

sponse ratios are below 1.0 for foliar Ca and Mg. A study examining the influence of harvesting intensity on the foliar nutrition of black spruce, balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*) on a range of sites in Quebec demonstrated that enhanced foliar levels of Ca and Mg in the presence of logging residues were particularly evident in stands regenerated on soils with low total elemental contents of these elements (Thiffault et al. 2006 [45]). WTH can thus more readily cause nutrient deficiencies for regenerating stands in soils developed from parent materials with a mineralogy poor in base cations.

Stand establishment and early growth

The influence of harvesting intensity on tree growth and stand productivity can be particularly complex because site-specific post-harvest changes in microclimate, nutrient and water availability, and other vegetation can all play significant roles in determining treatment effects. The limiting factors for tree growth are also highly dependent on site conditions and species characteristics, and change through time with the growth of the stand. There is therefore considerable variation among studies in the observed response of tree growth and stand productivity to harvesting treatments (Fig. 6; Tables 10*a* and 10*b*), all the more because the studies encompass a range of regeneration methods (e.g., natural regeneration by seed, resprouting, and planting). Seedling survival is almost always improved by WTH, relative to SOH; the only notable exceptions occurred in stands that also received vegetation control or soil compaction treatments (Fig. 6). Three out of six studies reported that WTH caused significant improvements in the survival of at least one tree species on at least one sampling date (to between 109% and 150% of that following SOH; Table 10*a*). A further five out of six studies found significant positive or negative effects on regeneration density. Tree height did not show a consistent treatment response early in stand development, although there is a trend toward reduced height growth with WTH after approximately 15 years (Fig. 6). In the 5 out of 12 studies that reported significant treatment effects, WTH reduced seedling heights to between 72% and 94% of that in SOH stands (with one transient exception, in Egnell and Leijon 1999 [5]). Three out of five studies also reported that WTH reduced seedling diameter to between 90% and 97% of that in stands harvested by SOH (Table 10*b*). Significant treatment effects on other growth response variables (e.g., basal area, stand density, growth rates) were less consistent.

The positive or negative effects of logging residues on stand establishment and early growth are often linked to microclimatic conditions and interactions with the competing vegetation (Proe et al. 1999 [33]). For example, WTH operations often cause disturbance and mixing of the soil that can, in turn, create better planting conditions, enhance the establishment of natural regeneration (Mann 1984 [22]; Hendrickson 1988 [13]; McInnis and Roberts 1994 [25]; Waters et al. 2004 [52]; Fleming et al. 2006*b* [10]), and increase the survival and growth of young seedlings (Morris and Miller 1994). The removal of harvesting residues with WTH exposes surface soils to solar radiation, which can warm the soil earlier in the spring, effectively extending the growing season; this could be particularly beneficial where growing seasons are short (e.g., on high-elevation or high-latitude sites), but could be of little consequence on sites with long growing seasons (Proe et al. 1994; Zabowski et al. 2000 [53]). Indeed, WTH is more likely to cause increased tree heights in boreal stands than in temperate stands: in Fig. 6, 70% of the calculated response ratios from sites in the boreal biome are above 1.0, but only 35% of those from sites in the temperate biome are above 1.0.

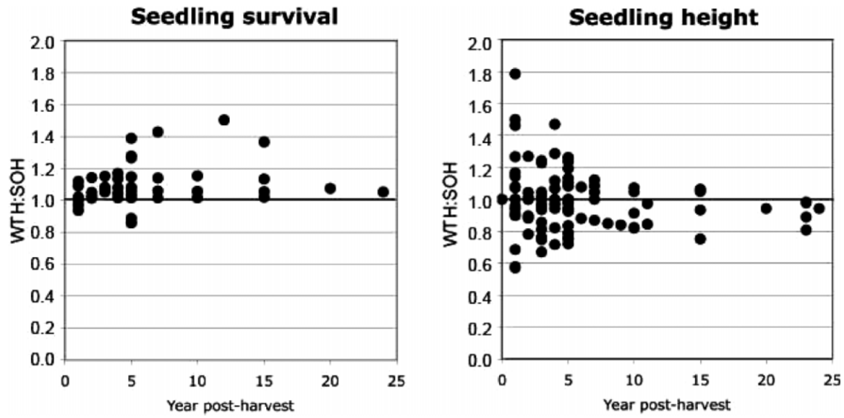
Retention of harvesting residues can also facilitate seedling growth by improving the microclimate under some site conditions. For example, residues can provide shelter and reduce wind speeds around seedlings on exposed upland sites (Proe and Dutch 1994 [32]). Residue retention can also reduce surface soil temperatures and moisture loss from direct evaporation or evapotranspiration; this effect may be particularly important on drier, less productive sites with inherently low levels of soil organic matter (Roberts et al. 2005 [35]). The moderating effect of harvesting residues on ground surface air temperatures can also reduce seedling stress when surface temperatures approach the upper limit for net positive photosynthesis under warmer climates (Zabowski et al. 2000 [53]), and provide favourable microsites for the germination of tree species that are particularly sensitive to drought stress and heat damage, such as white spruce (*Picea glauca*; Waters et al. 2004 [52]). Under colder conditions, harvesting residues can protect seedlings from frost damage (Fleming et al. 2006*b* [10]). In a 23-year-old Sitka spruce plantation in Wales, negative effects of WTH on tree height were observed on sun- and wind-exposed sites, but not on physically sheltered sites; no correlation could be found between tree growth and soil chemistry on these sites (Walmsley et al. 2009 [51]). Retention of residues has also been shown to suppress the establishment of weeds, thus reducing competition (Stevens and Hornung 1990 [42]; Fahey et al. 1991; Proe and Dutch 1994 [32]). In fact, direct weed control, which can influence moisture, light, and nutrient availability, appears to produce much larger and more consistent positive effects on seedling growth during the first years after seedling establishment than any harvest residue treatment, especially in warm–humid climates and on highly productive sites (Roberts et al. 2005 [35]; Fleming et al. 2006*b* [10]; Ares et al. 2007 [1]).

Stand productivity

Differences in nutrient availability following WTH or SOH usually affect the growth and productivity of the regenerating stand several years after harvest, when growing trees are less influenced by microclimate and competition from accompanying vegetation, but have increasing nutrient requirements as the stand approaches crown closure. After five years post-harvest, most of the calculated response ratios for seedling height are below 1.0 (Fig. 6). This is in accordance with the conceptual model of Fleming et al.[1], which describes the evolving constraints to growth through stand development (Fig. 7). For example, an unfavourable microclimate and competition from weeds reduced the height growth of Sitka

[1]Article: Assessing temporal response to forest floor removal: evolving constraints on initial stand development. Accepted for publication in *Forest Science*.

Fig. 6. Response ratios (WTH : SOH) of tree height and tree survival.



spruce seedlings in the early years of plantation establishment on WTH sites in the UK; however, growth losses after 10 years were attributed to the higher nutrient removals associated with WTH (Proe and Dutch 1994 [32]). A related study on these sites demonstrated the absence of nutrient deficiencies in the first two years after stand establishment and height growth losses related to reduced N availability by years 3 to 5 (Proe et al. 1999 [33]). Reductions in the height and basal area of Scots pine (to 94% and 83%, respectively, of that in SOH treatments) were also attributed to reduced N supply on 24-year-old WTH sites in southern Sweden (Egnell and Valinger 2003 [6]). This experiment was located 4° north of the study by Proe et al. (1999 [33]), which may explain why treatment differences only became apparent later in the rotation (i.e., 12 years after stand establishment). Interestingly, trees on sites where stems and branches were removed but needles were left on the ground showed a similar pattern of growth to trees on SOH sites up to year 15, but then became similar to that on WTH sites. This suggests that additional N from residues was supplied primarily by mineralization of foliage up to 15 years after plantation establishment and that the beneficial effects of woody residue retention appeared later (Egnell and Valinger 2003 [6]). Thinning experiments have also demonstrated that losses in tree productivity resulting from WTH, relative to SOH, can be attributed to reduced nutrient (especially N) supply 3–10 years after treatment (Sterba 1988; Jacobson et al. 1996, 2000), although these effects can disappear by year 10 (Nord-Larsen 2002). Thus, N deficiency is the most frequent cause of growth losses identified in field studies, at least in northern forests, which suggests that WTH affects processes related to the availability of N in the soil and (or) the uptake of N from the soil. Nevertheless, both nutrient uptake and tree growth are dependent on interactions among several nutrients rather than a single growth-limiting nutrient (e.g., Ingestad 1979). Thus, the influence of harvesting treatments on the supply and uptake of other nutrients (e.g., base cations) is worth investigating.

Despite the number of studies showing significant differences in the growth response of trees following SOH and WTH in the UK and Nordic countries, 10-year results from the North America-wide long-term soil production (LTSP) study did not reveal uniform, unequivocal impacts of forest biomass removal on tree productivity (Powers et al. 2005 [31]). Reductions in the volume growth of loblolly pine (*Pinus taeda*) on some LTSP sites located on highly weathered soils were reported 5 and 10 years post-harvest and were probably caused by reduced P availability. The magnitude of treatment response on these temperate–subtropical sites was related to pre-harvest soil P availability (Mehlich III P), with the poorest sites showing the greatest declines in growth following WTH, that is, a decrease of more than 50% in total tree biomass relative to SOH (Scott et al. 2004; Scott and Dean 2006 [38]). However, Powers et al. (2005 [31]) speculated that P (and possibly N) deficiencies caused by intensive biomass removal are probably transient and will be corrected by inputs from root decay and high rates of internal cycling as the stands approach crown closure. This is consistent with the findings of Egnell and Valinger (2003 [6]), in which growth losses associated with the removal of logging residues have subsided over time, probably because of tighter nutrient cycles and the decay of coarser litter both above- and belowground. Depending on site location, atmospheric N inputs could also alleviate nutrient limitations induced by WTH (Nord-Larsen 2002). However, the impacts of several rotations of WTH on soil nutrient resources remain to be seen.

Large differences can also exist among species' responses to harvesting treatments. Lodgepole pine growing in a 12-year-old LTSP experiment in central British Columbia, for example, maintained adequate foliar N nutrition and high tree productivity regardless of the intensity of organic material removal, whereas hybrid white spruce was more sensitive to changes in the soil environment (Kranabetter et al. 2006). Host-specific ectomycorrhizal *Suillus* species appeared to enhance lodgepole pine's capacity to access N from the soil, which could explain its relative lack of response to organic matter removal treatments on this site. Similarly, both the height and basal area of Norway spruce were reduced by WTH in 15-year-old plantations in Sweden, but treatment effects were much less consistent for Scots pine (Egnell and Leijon 1999 [5]). In Quebec, Thiffault et al. (2006 [45]) and Paré et al.[2] observed that black spruce was not affected by harvesting intensity, whereas jack pine growing on the same sites demonstrated significant differences in foliar nutrition and growth between SOH and WTH. Differences in juvenile growth rates as well as species-specific patterns of nutrient

[2]Personal communication, 2011.

Table 10. Studies examining the impacts of whole-tree (WTH) and stem-only harvesting (SOH) on (*a*) regeneration and (*b*) growth.

(*a*)

			Years post-harvest																							
Ref	Spp.*	Variable; units	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Fd	Survival; %	○	○	○	○	○																			
5[†]	Ps	Survival; %	○	○	○	○	○		○			■		■	■	■	■									
	Sn	Survival; %	○	○		○	○		○			○					○									
6	Ps	Survival; %	○	○	○	○	○		○			○					○					○				○
10[‡]	Var.	Survival; %					■																			
39	Sn	Survival; %	■	■	■	■	■	■																		
53	Pl	Survival; %	○																							
25	Bf	% of precut density	○																							
	Srm	% of precut density	○																							
	Mr	% of precut density	■																							
	Ep	% of precut density	■																							
13	At	Sprout density; stems·ha^{-1}		■		■																				
	Mr	Sprout density; stems·ha^{-1}		■		○																				
18	At	Sprout density; stems·ha^{-1}	○	○	○	○	■																			
22[‡]	Var.	Sprout density; stems·cm^{-1} of stump diameter diameter	●																							
51	Ss	Density; trees·ha^{-1}																							○	
52	Pj	Density; trees·ha^{-1}	○		○																					
	Bf	Density; trees·ha^{-1}	○		○																					
	Sw	Density; trees·ha^{-1}	○		●																					
	Sb	Density; trees·ha^{-1}	○		○																					

(*b*)

Ref	Spp.*	Variable; units	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
5[†]	Ps	Basal area; m^2·ha^{-1}										○		□	□	□	□									
	Sn	Basal area; m^2·ha^{-1}										○					●									
6[†]	Ps	BA (+ bark); m^2·ha^{-1}										○					●					●				●
	Ps	BA (– bark); m^2·tree^{-1}					○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●
39	Sn	Basal area; cm^{-2}·seedling^{-1}					■																			
51	Ss	Basal area; m^2·ha^{-1}																							○	
1	Fd	Basal diameter; mm			○		●																			
10[‡]	Var.	Basal diameter; cm					●																			
35[‖]	Fd	Diameter at 15 cm; mm		○	○																					
13	At	Diameter at 1.3 m; cm				○																				
	Mr	Diameter at 1.3 m; cm				○																				
51	Ss	Diameter at 1.3 m; cm																							●	
35[‖]	Fd	Diameter growth; mm·yr^{-1}		■	●																					
1	Fd	Height; cm	○	○	○	○	○																			
5[†]	Ps	Height; cm	○	○	○	○	■		○			○		○	○	○	○									
	Sn	Height; cm	○	○	○	○	○		○			●					●									
6	Ps	Height; m					○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●
13	At	Height; m		○		○																				

Table 10 (*concluded*).

(*b*)

	Mr	Height; m		○		○																				
15	Fd	Height; cm			○																					
	Pl	Height; cm			○																					
18	At	Height of dominants; cm	○	○	○	○	○																			
	Sw	Height; cm	○	○	○	●	●																			
21	Sw	Height; cm					○						○													
	Pw	Height; cm					○						○													
22[‡]	Var.	Sprout height; cm	○																							
32	Ss	Height; m			○			○	○	●	●	●														
33	Ss	Height; cm	○	○	●	●	●																			
35[‖]	Fd	Height; cm		○	○																					
39	Sn	Height; m	○	○	○	○	○	○																		
51	Ss	Height; m																							○	
53	Pl	Height; cm	○		○		○																			
35[‖]	Fd	Height growth; $cm \cdot yr^{-1}$		○	●																					
39	Sn	Height growth; $m \cdot yr^{-1}$	○	○	○	○	○	○																		
32	Ss	Rel. height growth; $cm \cdot cm^{-1}$							○	○	○	○														
33	Ss	Dry weight; $g \cdot tree^{-1}$	○	●	●	●	●																			
6	Ps	Relative dry weight; %																								○
12[†§]	At	Tree biomass; $Mg \cdot ha^{-1}$								○	○	○														
23	Var.	Tree biomass; $kg \cdot ha^{-1}$										□	○	○	●	●										
34	Ss	Tree biomass; $g \cdot tree^{-1}$				■																				
32	Ss	Tree biomass; $kg \cdot ha^{-1}$									●															
6[†]	Ps	Volume (– bark); $m^3 \cdot tree^{-1}$					○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
10[‡]	Var.	Volume index; $m^3 \cdot ha^{-1}$					○																			
36	Pt	Stand volume; $m^3 \cdot ha^{-1}$										○														
39	Sn	Stem volume; $cm^{-3} \cdot tree^{-1}$					■																			

Note: Black circles indicate that WTH reduced values compared with SOH, black squares indicate that WTH increased values compared with SOH, empty squares indicate contradictory effects, and empty circles indicate no treatment difference. Results have been compressed – black circles, black squares and empty circles indicate that a treatment difference was detected in at least one depth increment, horizon, site or unit of measurement included in a study. Spp. indicates species, BA (+ bark) indicates basal area including bark, BA (– bark) indicates basal area inside bark, Var. indicates various species, Rel. indicates relative.

*Refer to Table 1 for tree species codes.

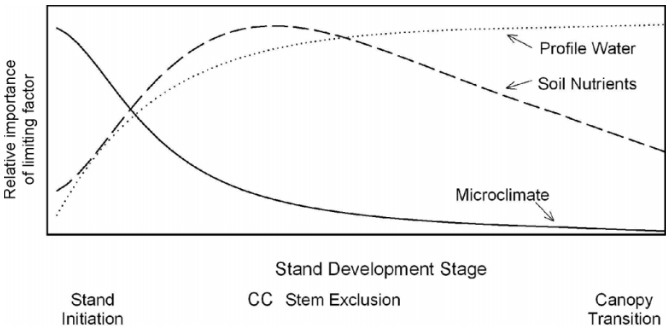
[†]Statistical analyses were performed on data representing more than a single post-harvest year.

[‡]Only overall analyses of all species and sites are summarized here.

[§]Stands dominated by trembling aspen, but biomass estimate includes white spruce, balsam fir, red maple, and (or) red oak.

[‖]Both SOH and WTH treatments received vegetation control.

Fig. 7. Conceptual diagram depicting temporal patterns of relative importance of limiting factors to stand productivity. Taken from: Fleming et al. (accepted for publication in *Forest Science*). CC denotes canopy closure.



acquisition and retention could explain this variability in response to harvesting intensity (Thiffault et al. 2006 [45]).

Overall, it is notable that treatment differences in tree growth and survival were more commonly found in European than in North American trials. It is not known, however, whether this is because of differences in management practices, disturbance histories, and (or) biophysical resources (i.e., soils and underlying geological formations). The fact that the UK trials mentioned in this review are in second-rotation stands on afforested sites using non-native species limits the applicability of findings to other regions. Similarly, the more intensive management practices in many Nordic forests over several rotations (e.g., multiple entries for thinning over a rotation) could amplify harvesting effects, at least until North American stands have passed through several more rotations.

Summary and identification of gradients in sensitivity to forest biomass harvesting

This review examined the available literature to determine the conditions under which WTH alters soil nutrient availability and tree growth compared with conventional SOH. The studies reviewed here encompass a large range of sites with various land-use histories, disturbance histories, and rates of atmospheric deposition, which can amplify, moderate or, at the very least, complicate the effect of WTH on soil productivity. Thus, it is not possible to define universal and definitive prescriptive indices of site sensitivity to forest biomass harvesting with the data currently available. Also, availability of research results is skewed towards studies on even-aged coniferous stands; therefore conclusions of the review may need to be further validated and refined for other forest types (e.g., uneven-aged deciduous stands).

Nevertheless, the data show that the responses of the various components of soil productivity to WTH can vary along gradients in (*i*) climate and microclimate, (*ii*) mineral soil texture and organic C content, (*iii*) soil base cation mineralogical content, (*iv*) soil P availability, and (*v*) autecology of regenerating species. These gradients could be used to classify forest ecosystems according to their sensitivity and (or) suitability to biomass removal. Below, we briefly discuss the influence of these factors on soil productivity.

Climate and microclimate

Climate and microclimate are critical considerations for forest biomass harvesting. They can either improve or impair tree productivity, depending on the specific limiting factors to tree growth on the site (e.g., solar radiation, moisture, frost) and the sensitivity of the regenerating species to extreme microclimatic conditions (e.g., drought, heat damage), particularly during stand establishment. For example, the almost universally positive influence of WTH on seedling survival (Table 10*a*; Fig. 6) is probably strongly linked to improvements in microclimate. In contrast, WTH-related changes in microclimate had less consistent and frequently negative effects on growth (Table 10*b*; Fig. 6), although tree height was frequently enhanced by WTH in boreal forests. Such treatment responses are not indicators of changes in the inherent capacity of the soil to support forest growth per se; however, given that nutrient supply only becomes a limiting factor to tree growth after the stand initiation phase, as seedling nutrient uptake requirements increase (Ingestad 1987), the overarching objective for ensuring the adequate growth of seedlings in the first years of plantation establishment should be to obtain optimal microclimatic conditions (management of harvesting residues is one tool for achieving this) once other risks to soil quality have been minimized.

The influence of climate and microclimate on biomass harvesting-related changes in soil properties is less clear. Of the studies included in this review, soil C concentration and content were significantly reduced by WTH only in boreal and subtropical climates. There were no obvious differences between biomes or among climates in the effect of WTH on other soil nutrient pools or foliar nutrients compared with SOH.

Mineral soil texture and organic C content

Soil texture and organic C content are other important factors determining a site's suitability for intensive biomass harvesting. Given that soil texture is a key determinant of both soil organic matter content and forest productivity (Vance 2000), it is a useful (though not exclusive; see Callesen et al. 2005 and Scott and Dean 2006 [38]) proxy for predicting soil C storage, moisture retention, and nutrient release capacity. Given the crucial role that organic matter plays in mediating soil physical, chemical, and biological properties and processes, the influence of biomass harvesting on soil C storage in coarse-textured and inherently C-poor soils is of particular concern. Organic matter losses through fire or intense silvicultural treatments have been considered more critical on coarse-textured soils (Page-Dumroese et al. 2000). Moreover, a boreal forest with a C-poor, coarse-textured soil was the only site to show strong, significant reductions in mineral soil C following WTH (Thiffault et al. 2006 [45]). Residues can provide a significant source of organic matter for regulation of soil temperature and water availability on those sites (Roberts et al. 2005 [35]).

Base cation mineralogy

Compared with SOH, WTH can reduce the availability of base cations, notably Ca and Mg, in the forest floor, although treatment differences are rarely significant in the mineral soil. Nevertheless, it also causes lower base cation foliar concentrations in trees. Based on the gradient of sites in Thiffault et al. (2006 [45]), the negative influence of WTH is expected to be strongest in soils with a limited capacity to provide base cations through weathering; soil mineralogy and clay content can thus be proxies for the capability of forest soils to release base cations (Callesen and Raulund-Rasmussen 2004; Callesen et al. 2005). The role of parent material mineralogy in mediating post-harvest changes in soil productivity has not been investigated in other studies, so, it is not possible to validate this hypothesis on a larger scale at this time; however, the availability of base cations as weathering products is considered a relevant indicator of site resilience in other contexts (e.g., susceptibility of sugar maple to decline in Bailey et al. 2004). Finally, it should be noted that the base cation status of soils with intrinsically high levels of exchangeable acidity may not be improved by residue retention because saturation in aluminum can prevent the retention of base cations released from logging residues on cation exchange sites in the soil (e.g., Bélanger et al. 2003). Large inputs of base cations from logging residues or other soil amendments (e.g., lime), or a change in the tree species composition of the stand, could also modify the acidity–alkalinity balance of the soils.

The degree of soil acidification and base cation depletion caused by biomass removal in field studies tends to be much less than expected from theoretical assessments. To date, theoretical nutrient or acidity budgets have been poor predictors of the actual effects of forest biomass harvesting on soil productivity (e.g., Johnson and Todd 1998 [16]). Furthermore, there is no evidence that the impacts of biomass removal on base cations cause reduced tree growth, at least within the time-scale covered by the studies reviewed here, and correlations between base cation nutrition and tree growth are generally weak (Fisher and Binkley 2000). However, impaired base cation (especially Ca) availability has been associated with a decrease in tree vigour and susceptibility to environmental stresses, such as freezing and drought (DeHayes et al. 1999; McLaughlin and Wimmer 1999; Schaberg et al. 2001). In addition, other critical ecosystem components could be more sensitive to changes in soil base cation pools than tree growth is. For example, effects on snails (Hamburg et al. 2003) and aquatic fauna in lakes (Jeziorski et al. 2008) could have cumulative, long-term, unpredictable implications for ecosystem health.

P availability

Biomass removal has been shown to reduce both total and available P pools. Depressed P nutrition and lower growth rates can be caused by reductions in soil P availability following intensive biomass removals in pine stands growing on highly weathered soils in the southeastern US. The greatest growth losses occur on sites with low preharvest levels of available P, suggesting that site sensitivity to forest biomass harvesting may vary along a gradient of soil P availability.

Autecology of regenerating species

Species traits related to sensitivity to microclimatic extremes, especially during seedling establishment, have been shown to determine stand response to removal of forest biomass (e.g., Fleming et al. 2006*b* [10]). Traits related to sensitivity to changes in N supply could also be important drivers. In many cases, reduced tree growth following WTH has been attributed to N limitation, although these effects are only weakly associated with changes in soil N pools per se. Instead, N-related growth responses to biomass removal appear to be species-specific rather than site-specific. Some tree species are more sensitive to changes in the soil nutritional environment, while other species have developed strategies that allow them to maintain relatively stable N nutrition and growth over a wider range of soil conditions (e.g., Périé and Munson 2000; Bothwell et al. 2001). Detailed research is needed to more closely examine changes in soil nutrient cycling patterns following biomass harvesting and the implications of these changes for tree nutrition and growth as well as the nutrient (especially N) uptake dynamics of individual tree species.

Other considerations

Significant differences in the effects of WTH and SOH are most frequently detected in the forest floor and more rarely in mineral soil. This underlines the role of the forest floor as a nutrient reservoir and mediator against disturbance (e.g., by buffering, to some extent, the acidification of deeper soil layers). Based on results from the LTSP study, Powers et al. (2005 [31]) concluded that harvesting intensity is of little consequence to soil productivity compared with forest floor removal. Indeed, the maintenance of the forest floor on the site during harvesting can be essential if the beneficial effects of logging residues on soil fertility are to be fully realized (Bélanger et al. 2003 [2]); however, this does not preclude further manipulation of the forest floor during site preparation (e.g., displacing, loosening, breaking or mixing to enhance decomposition and nutrient mineralization, improve seedbed quality, and reduce competition with the surrounding vegetation; Prescott et al. 2000).

Residue removal treatments that facilitate seedling survival and growth by improving microclimatic conditions in the first few years of stand establishment may be associated with nutrient deficiencies and growth losses in subsequent years. Thus, management decisions must balance these two potentially conflicting outcomes. Not mentioned in this review, but also worthy of consideration, is the increased risk of pest infestation when logging residues, which can provide breeding habitat, are left on site (see review by Schroeder 2008). Growth losses associated with forest biomass harvesting could be transient, lasting perhaps a decade or less in temperate climates or in areas with large nutrient inputs from the atmosphere, and could last more than two decades in colder climates or in areas with low levels of atmospheric nutrient deposition. According to the conceptual model of Fleming et al.[3] (Fig. 7), stands can enter a state of nutrient limitation within 5–20 years of establishment which may last as long as the stand is accumulating nutrients and biomass in living trees. Thus, any reduction in nutrient availability caused by residue removal could influence stand development long after canopy closure. Longer-term monitoring is required to better understand the temporal dynamics of post-harvest changes in soil productivity. As stated by Comerford et al. (1994), longer-term research should aim to predict the consequences of harvesting practices on inherent soil quality, i.e., whether

[3]Article: Assessing temporal response to forest floor removal: evolving constraints on initial stand development. Accepted for publication in Forest Science.

harvesting elicits a Type 1 response (in which nutrient deficiencies and growth losses are transient and the inherent productivity of the site remains unchanged) or a Type 2 response (in which nutrient deficiencies and growth losses are large and sustained; see model developed by Snowdon and Waring (1981, 1984).

Conclusion

Whole-tree harvesting, in which tree branches and tops are removed in addition to the stem, alters soil productivity under some site and stand conditions. This review encompassed a large range of climates, soils, forest sites, and silvicultural trends; generalizations are thus difficult to make. Nevertheless, this review demonstrates that site sensitivity can vary along gradients in (*i*) climate and microclimate, (*ii*) mineral soil texture and organic C content, (*iii*) soil mineralogy, (*iv*) P availability, and (*v*) the autecology of regenerating species, especially traits related to sensitivity to microclimatic extremes and to changes in N supply. Field trials that cover a range of conditions along a gradient of one of the above factors would allow us to refine and prioritize these factors, and facilitate the identification of threshold values or categories of site or stand conditions, for which negative impacts of biomass harvesting are likely. Future studies that measure and report such information would improve cross-site comparisons and aid in the examination of relationships between site conditions and biomass harvesting-related losses in soil productivity. At present, the longest-term data comparing the effects of SOH and WTH on soil productivity are from 24-year-old stands; longer-term field measurements may highlight other crucial determinants of site sensitivity to forest biomass harvesting. Future work will include formal meta-analyses to compile data from independent studies and place confidence limits around estimates of effect size, to discriminate among subsets of data, and to compare variability within and among studies (Curtis and Wang 1998; Nave et al. 2010).

Finally, the implications of biomass removal for biodiversity were not addressed here, although they have been the subject of several studies (e.g., Battigelli et al. 2004; Eaton 2006; Jonsell 2008), a recent review (Bunnell and Houde 2010), and a meta-analysis (Riffell et al. 2011). A consideration of the effects of biomass harvesting on soil biota and saproxylic species, for example, should provide greater insight into the impacts of harvesting treatments on ecological processes relevant to soil productivity (e.g., the functioning of soil trophic food-webs, organic matter decay, and nutrient uptake and release).

Acknowledgements

We thank Rob Fleming of the Canadian Forest Service for his insightful comments, and Antti Wall of the Finnish Forest Research Institute for sharing his compilation of references with us. We also acknowledge Gustaf Egnell and Bengt Olsson of the Swedish University of Agricultural Sciences, Umeå, from whom we drew inspiration for our data display. Our work was partially funded by the Program for Energy Research and Development (PERD) of the government of Canada (grant to D. Paré and B. Titus) and by the Fonds québécois de la recherche sur la nature et les technologies (grant to S. Brais). K. Hannam contributed to this work as an Natural Sciences and Engineering Research Council of Canada visiting fellow.

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