Assessment of calcium status in Maine forests: review and future projection

T.G. Huntington

Abstract: Forest harvesting and acidic deposition can cause substantial decreases in the calcium (Ca) inventory of forest soils if such losses are not replenished through mineral weathering, atmospheric deposition, or fertilization. The net balance between losses and gains defines the forest Ca status. Site-specific studies have measured Ca pools and fluxes in Maine forests, but no synthesis has been published. In this paper, I review the literature on forest Ca and assess the current status and potential future trends. Forest soils in Maine are currently at lesser risk of Ca depletion compared with many forest soils in the central and southeastern United States, because levels of acidic deposition and rates of Ca accumulation in trees are lower in Maine. The rate of Ca accumulation in trees is reduced in Maine as a result of lower growth rates and a higher proportion of conifer trees that require less Ca than hardwoods. However, field-scale biogeochemical studies in Maine and New Hampshire, and regional estimates of harvest removals and soil inventories coupled with low weathering estimates, indicate that Ca depletion is a realistic concern in Maine. The synthesis of site-specific and regional data for Maine in conjunction with the depletion measured directly in surrounding areas indicates that the Ca status of many forest soils in Maine is likely declining. Ca status could decrease further in the future if forest growth rates increase in response to climate trends and recovery from insect-induced mortality and excessive harvesting in recent years. Proposed climate change induced reductions in spruce and fir and increases in hardwoods would also increase the risk of Ca depletion.

Résumé : La récolte de matière ligneuse et les dépôts acides peuvent causer des diminutions substantielles des réserves de calcium (Ca) dans les sols forestiers si de telles pertes ne sont pas comblées par l'altération des minéraux, les dépôts atmosphériques ou la fertilisation. Le bilan net des pertes et des gains représente le statut en Ca de la forêt. Des études spécifiques dans différents sites ont mesuré les pools et les flux de Ca dans les forêts du Maine mais aucune synthèse n'a été publiée. Dans cet article, l'auteur révise la littérature sur le Ca dans les sols forestiers et évalue le statut actuel et les tendances futures potentielles. Les sols forestiers du Maine sont pour l'instant moins à risque d'appauvrissement en Ca comparativement à plusieurs sols forestiers du centre et du sud-est des É.-U. parce que le niveau de dépôts acides et le taux d'accumulation de Ca dans les arbres sont plus faibles dans le Maine. Le taux d'accumulation de Ca dans les arbres est réduit dans le Maine en raison du taux de croissance plus faible et d'une plus forte proportion de conifères qui requièrent moins de Ca que les feuillus. Toutefois, les études biogéochimiques à l'échelle de la parcelle au Maine et au New Hampshire ainsi que les estimations régionales d'exportation due à la récolte et les réserves dans les sols couplées aux faibles estimations d'altération indiquent qu'il est réaliste de s'inquiéter de l'appauvrissement en Ca dans le Maine. La synthèse des données spécifiques à différents sites et des données régionales pour le Maine concurremment à l'appauvrissement mesuré directement dans les régions environnantes indique que le statut de Ca dans plusieurs sols forestiers du Maine est vraisemblablement en déclin. Le statut de Ca pourrait se détériorer davantage dans le futur si le taux de croissance des forêts augmente en réponse à l'évolution du climat, à la récupération de la mortalité causée par les insectes ainsi qu'à la récolte excessive des dernières années. Les réductions en épinette et en sapin causées par les changements climatiques appréhendés accompagnées d'augmentations des feuillus accroîtraient aussi le risque d'un appauvrissement en Ca.

[Traduit par la Rédaction]

Introduction

The assessment of the long-term effects of atmospheric acid deposition on aquatic and forest ecosystems is an ongoing effort supported by several federal government agencies, including the Environmental Protection Agency, the US Geological Survey, and the USDA Forest Service (National Acid Precipitation Assessment Program (NAPAP) 1998). The objective of these efforts is to better understand ongoing acidification and to evaluate responses to reductions in emissions of sulfur dioxide resulting from implementation of the Clean Air Act and its amendments. The National Atmospheric Deposition Program – National Trends Network (NADP–NTN) is part of the National Acid Precipitation Assessment Program (NAPAP) that tracks trends in atmospheric deposition. Analysis of deposition data in conjunction with data on water quality, soil chemistry, and forest nutrient cycling is used for regional syntheses to assess current status and trends. The objective of this assessment is to synthesize data on deposition and forest biogeochemistry to determine current forest soil Ca

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T.G. Huntington. US Geological Survey, 196 Whitten Road, Augusta, ME 04330-6021, USA (e-mail: thunting@usgs.gov).

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Table 1. Sites of forest biogeochemical investigations in Maine.

Site	Lat. (N)	Long. (W)	Exchangeable Ca (kg·ha^{-1}) Oe+Oa	Exchangeable Ca (kg·ha^{-1}) Mineral soil	Total Ca <2 mm (kg·ha^{-1})	Wet deposition input Ca (kg·ha^{-1}·year^{-1})	Hydrologic loss Ca (kg·ha^{-1}·year^{-1})	Tree uptake Ca (kg·ha^{-1}·year^{-1})
Howland*	45°10′	68°40′	156	53.3	59 600	0.22	3.2	6.1
Burnt Mill Brook, Lower†	44°23′	70°58′	546	445	na	0.54	na	na
Burnt Mill Brook, Upper*	44°23′	70°58′	245	366	na	0.54	na	na
Acadia – Cadillac Creek‡	44°20′	68°13′	102	107	na	0.86	na	na
Acadia – Hadlock Creek‡	44°19′	68°17′	75	63	na	0.86	na	na
Weymouth Point§	45°57′	69°19′	208	184	10 800	1.00	14.3	7.69
East Bear Brook‖	44°52′	68°06′	180	78	na	0.78	14.5	na

Note: na, not applicable.
*Fernandez et al. (1993) and Johnson and Lindberg (1992).
†G.B. Lawrence (unpublished data) and NADP deposition data.
‡I.J. Fernandez (unpublished data) and NADP deposition data.
§Briggs et al. (2000), Hornbeck et al. (1990), Federer et al. (1989), Smith et al. (1988).
‖I.J. Fernandez (unpublished data; soils), Norton et al. (1999).

status and future trends in the context of ongoing environmental change in Maine forest ecosystems.

Recent analyses have evaluated impacts of timber harvesting and acidic deposition on soil base cation status in the southeastern United States (Huntington 2000), east-central United States (Adams et al. 2000), northern United States (Federer et al. 1989), and central Ontario, Canada (Watmough and Dillon 2003). Analysis of base cation input–output budgets in these studies indicated that cation depletion could be a significant concern for the long-term maintenance of soil fertility and forest health and productivity at many sites. Ca depletion is of concern for a variety of reasons related to the many critical roles that Ca plays in tree physiology and the likelihood that Ca limitation will adversely influence many aspects of forest function (McLaughlin and Wimmer 1999; DeHayes et al. 1999; Schaberg et al. 2001). McLaughlin and Wimmer (1999) review evidence that Ca limitation adversely influences disease resistance, wound repair, frost hardiness, and lignin synthesis in trees. DeHayes et al. (1999) review the evidence that reduced Ca availability can affect development of cell wall structure and growth, carbohydrate metabolism, stomatal regulation, resistance to plant pathogens, and tolerance of low temperatures.

This paper will review recent literature related to Ca depletion at regional and site-specific scales. Biogeochemical studies at specific sites in Maine will be discussed and related to regional-scale data to assess trends at broader spatial scales. This review will evaluate current status and trends and provide a perspective on how future changes in forest growth rate, climate, and species composition could affect Ca status.

Materials and methods

In this assessment, data on atmospheric deposition, stream water chemistry, soil chemistry, and forest nutrient accumulation were compiled from various sources at regional and site-specific scales. Atmospheric deposition data were compiled from the National Atmospheric Deposition Program (NADP 2003). Stream water chemistry data were compiled from US Geological Survey and University of Maine records. Soil data were compiled from results of the Direct/Delayed Response Program (DDRP) (Turner et al. 1993) and the Natural Resource Conservation Service (NRCS) Pedon database. Forest nutrient accumulation was estimated using USDA Forest Service Forest Inventory Analysis (FIA) data combined with published estimates of stemwood nutrient concentrations. Site-specific data were obtained from small watershed studies in Maine (Table 1).

Atmospheric deposition

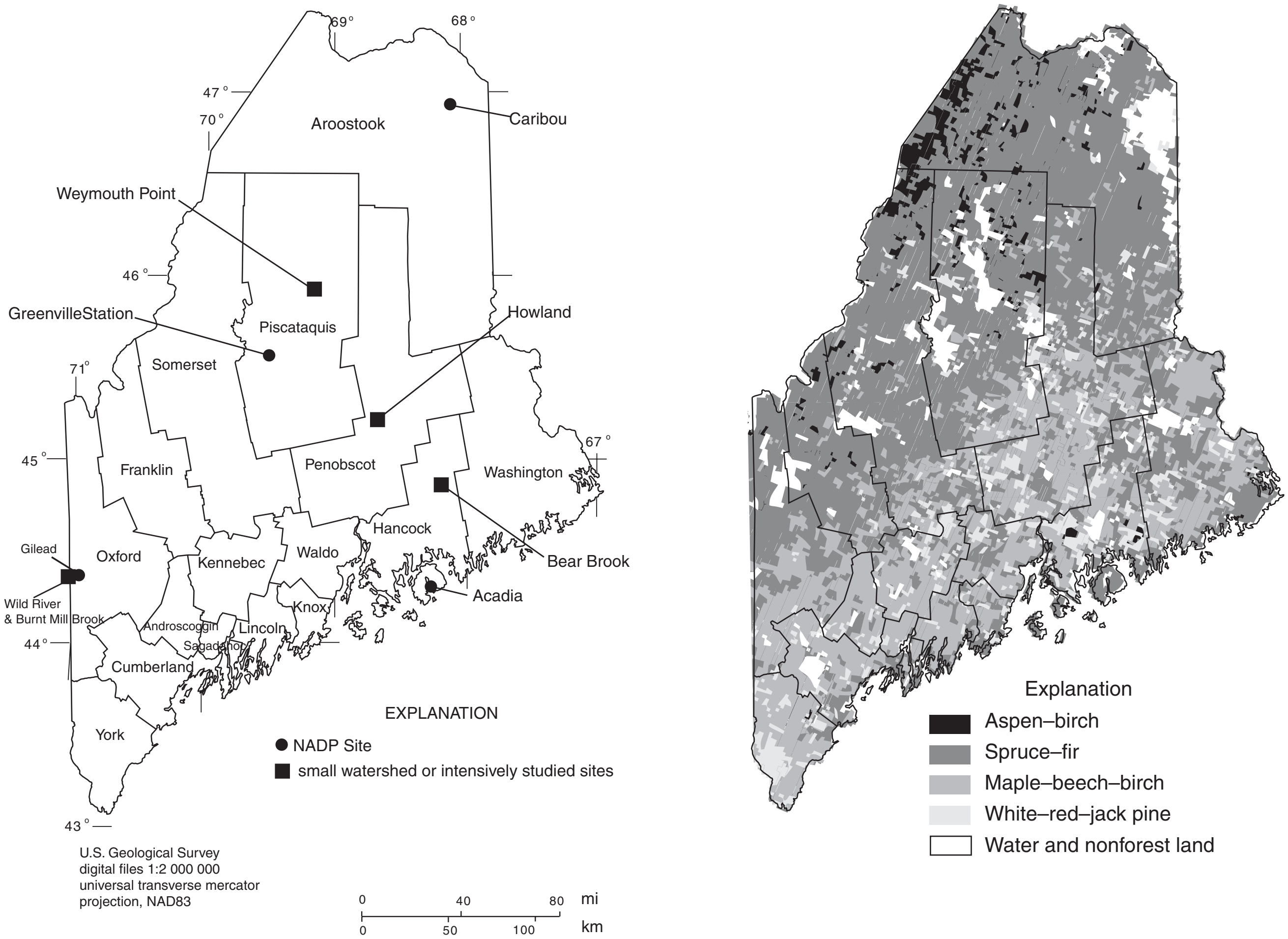
Data on atmospheric wet deposition were compiled from the National Atmospheric Deposition Program – National Trends Network (NADP–NTN) (Peden 1986; James 1993). There are four sites in Maine with approximately 20 years of records each that were used in this analysis (Fig. 1). Based on just four stations in Maine that do not include any high-elevation sites, the spatial pattern appears to be relatively uniform, with the exception of somewhat elevated levels of both sulfate (SO_4) and Ca near the coast (Lynch et al. 2000). Dry deposition of Ca is difficult to measure and has been poorly quantified compared with data on the wet deposition of Ca. Dry deposition of SO_4 and nitrate (NO_3) have been estimated somewhat more systematically using throughfall (Joslin and Wolfe 1992) or eddy correlation modeling techniques with ambient air concentrations (Hicks et al. 1991). Previous studies (Church et al. 1989; Lindberg et al. 1990) have suggested that dry deposition of SO_4 and Ca could be estimated by assuming dry:wet deposition ratios of 1:1 for SO_4 and 1.7:1 for Ca and Mg. This analysis used these ratios to estimate total deposition and used 1.7:1 for Mg.

Annual atmospheric deposition (kilograms per hectare per year) time-series data were tested for monotonic temporal trends using Kendall's τ nonparametric trend test. The slope of these trends were estimated using the Thiel/Sen slope estimation (median of all possible pairwise slopes) (Helsel and Hirsch 1992). A locally weighted scatterplot smooth (LOWESS) (Helsel and Hirsch 1992) curve was plotted using a weighting function of 66% of the period of record for graphical interpretation of the trend.

Forest nutrient accumulation

Net annual Ca accumulation in merchantable wood was estimated from the FIA measurements of net annual growth

Fig. 1. Map showing counties in Maine, approximate locations of NADP sites and small watershed or intensively studied sites, and predominant forest types by county. Forest cover modifed from the US Geological Survey and US Forest Service 2000 forest cover types, in the National Atlas of the United States (http://nationalatlas.gov). Data were derived from Advanced Very High Resolution Radiometer (AVHRR) composite images recorded during the 1991 growing season.



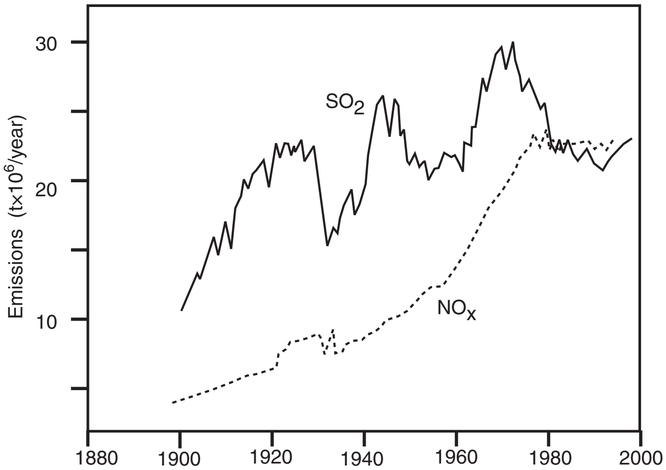
(biomass accumulation) multiplied by published estimates of Ca concentration of bole wood for the predominant tree species. The FIA involves periodic assessment of the status and use of forest resources throughout the United States. Forest inventories in Maine were conducted over 2- to 3-year periods ending in 1959, 1972, 1982, and 1995 (Ferguson and Longwood l960; Powell and Dickson 1984; Griffith and Alerich 1996). Growth rates prior to 1959 were estimated from radial area increments obtained from tree cores during the 1959 inventory. The FIA data were used in conjunction with data on Ca concentration of wood and bark to estimate the rate of Ca accumulation and removal in harvested wood products.

The FIA database retrieval system was queried using the geographic unit method within Maine to retrieve summary net annual growth statistics between the last two published inventories in 1981 and 1995. FIA data were retrieved as average annual growth of merchantable timber (wood volume that is removed during harvest per unit area) between the two most recent measurements for all plots within specified geographical areas. Average net annual growth is defined as the change in growing stock volume of all growing stock components of growth. The components of growth are accretion, in-growth, mortality, and cull increment on all remeasured plots. Accretion is the growth of trees that were tallied in the previous inventory. In-growth refers to trees that were tallied in the current inventory but were too small in diameter to be tallied in the previous inventory. Mortality refers to trees that were tallied in the previous inventory but were dead in the current inventory. Cull increment refers to any increase between inventories of live tree biomass that does not contain merchantable timber. Average net annual growth is calculated as

$$\begin{aligned}\text{Average net annual growth}\\ &= \text{accretion} + \text{ingrowth} - \text{mortality}\\ &\qquad - \text{cull increment}\end{aligned}$$

Forest growth statistics are most reliable when the geographic area is large enough to include a sufficient number of plots. Timberland area and growth data were retrieved by county or geographic unit. Several counties were retrieved as geographic units because the timberland areas in those counties were so small that estimates of growth are problematic. The data were summarized by three major forest types: hard-

Fig. 2. Historical pattern of sulfur dioxide (SO_2) and nitrogen oxides (NO_x) emissions in the United States for all sources (1900–1998). Data source: Nizich et al. (1995) and US EPA (2000).



wood, spruce–fir, and pine-dominated types. For this analysis, the oak–pine type was assigned to the hardwood-dominated type. Retrievals were also made by state for selected states in the eastern United States to compare growth rates across a gradient in mean annual temperature (MAT).

To convert from wood volume to wood mass, average specific gravities of 0.47 and 0.54 g·cm^{-3} were used for the dominant softwood and hardwood (soft and hard hardwood) species, respectively (Clark et al. 1986; US Forest Service 1972). The following wood plus bark elemental compositions for the merchantable wood removed were assumed on the basis of published values: 0.1% Ca for pine-dominated forest types, 0.23% Ca for spruce–fir-dominated types, and 0.69% Ca for hardwood-dominated types (Young et al. 1965; Dyer 1967; Young and Carpenter 1967; Switzer and Nelson 1972; Chase and Young 1978; Young et al. 1980; Johnson et al. 1988; Johnson and Henderson 1989; Johnson and Todd 1990; Johnson and Lindberg 1992; Fernandez et al. 1993).

Results and discussion

Trends in emission and atmospheric deposition

The historical pattern of sulfur dioxide emissions (Nizich et al. 1995; US EPA 2000) indicates that SO_4 deposition increased from 1955 to 1970, then decreased until about 1995, and has been constant since 1995 at levels comparable to the 1940–1955 period (Fig. 2). Contrary to the trends showing large reductions in emissions of sulfur dioxide, nitrogen oxides and ammonium emissions have been constant from 1970 to 1998 (Lynch et al. 2000; US EPA 2000). Trends in wet atmospheric deposition for sites in Maine and all of the eastern United States have been summarized recently by Lynch et al. (2000). SO_4 and base cation concentrations in precipitation decreased significantly from 1983 to 1997 throughout New England. Decreases in SO_4 concentration are thought to be a direct response to emission reductions associated with the Clean Air Act and its amendments (Lynch et al. 2000). Decreases in SO_4 concentration of precipitation have resulted in comparable decreases in atmospheric deposition.

The annual rate of atmospheric wet deposition of SO_4, Ca, and Mg decreased in Maine from 1980 through 2000 (Table 2, Fig. 3) continuing the same trends reported by Lynch et al. (2000). In contrast, the annual rate of atmospheric wet deposition of NO_3 did not change during this same period (Table 2). The trends in deposition (Table 2) converted into equivalence units result in average decreases of 0.76, 1.0, and 8.8 equiv.·ha^{-1}·year^{-1} for Ca, Mg, and SO_4, respectively. Over this same time period the deposition of NO_3 decreased at a rate of 5.0 equiv.·ha^{-1}·year^{-1} (Kendall trend test, $P <$ 0.016 at all four sites). The other major ions, Cl, NH_4, and K showed no consistent trends over time (data not shown). The timing of the decrease in deposition of Ca, Mg, and SO_4 is not identical. The decrease in SO_4 is apparent for the 1980–2000 period (Fig. 3). The decrease was fairly steady at most sites until 1995, with a pronounced flattening of the trend at most sites. In contrast, the timing of the decrease in deposition of Ca and Mg indicates a substantially more rapid rate of decline in the 1980s than after 1990.

During the 1980s and 1990s, SO_4 deposition in Maine was generally lower, typically by 30%–50%, than in most of the remainder of the northeastern United States and is similar to that in the southeastern and central United States (Lynch et al. 2000). Mountainous sites are known to receive higher rates of deposition because of higher precipitation and cloud-water deposition; however, there are no NADP sites at high elevation in Maine. The NADP data also indicate that Maine's extensive coastal zone receives elevated deposition of salts in marine aerosols, as do many coastal regions in the United States (Lynch et al. 2000). Coastal areas also receive elevated levels of K, Mg, Ca, and SO_4 at rates 1.5–3 times higher than observed at inland low-elevation sites (Lynch et al. 2000). On an absolute basis, the increases on the coast are approximately 300 equiv.·ha^{-1}·year^{-1} for Na and Cl, 90 equiv.·ha^{-1}·year^{-1} for SO_4, and in the range of 5–20 equiv.·ha^{-1}·year^{-1} for K, Mg, and Ca. The net effect of these coastal influences is to increase the potential for leaching losses of exchangeable soil Ca through ion exchange.

Stream chemistry

Streams draining small forested watersheds in Maine are generally low in Ca and are thought to be sensitive to acidification because they are low in ionic strength and weakly buffered (Kahl et al. 1991). Streams are not chronically acidic but usually experience episodic acidification during storms and snowmelt. There is little information on trends in stream chemistry in Maine, but where available it indicates declining Ca concentrations in recent years (Clow and Mast 1999; Fernandez et al. 2003). Stream-water acidification has been implicated in the deterioration of fish habitat in the eastern United States and Canada (Bulger et al. 1995; Watt et al. 2000).

Two surveys provide a fairly broad picture of the distribution of major ion chemistry in streams draining small forested watersheds in Maine and adjacent New England states. In one survey of 70 headwater streams, approximately 50% of the streams had Ca concentrations <125 μequiv.·L^{-1} (Fig. 4) (Rustad et al. 1994). In a broader regional survey for streams draining small forested watersheds primarily in New Hampshire,

Table 2. *P* values for Kendall's τ trend tests for the null hypothesis that τ = 0 (no systematic trend over time) and corresponding Thiel/Sen slope estimates for annual deposition of selected ions at four National Atmospheric Deposition Program – National Trends Network sites in Maine.

		Ca		Mg		NO_3		SO_4	
Site	Period	*P* value	Slope	*P* value	Slope	*P* value	Slope	*P* value	Slope
Caribou	1981–2001	0.053	–0.007	<0.0001	–0.0073	0.33	–0.036	0.0003	–0.38
Bridgton	1981–2001	0.053	–0.014	0.046	–0.0086	0.80	–0.025	<0.0001	–0.408
Greenville	1980–2001	0.0004	–0.020	0.0004	–0.0078	0.59	–0.017	<0.0001	–0.404
Acadia National Park	1979–2001	0.051	–0.020	0.183	–0.025	0.63	–0.0053	<0.0001	–0.532

Note: Trends are measured in kilograms per hectare per year.

Vermont, and northwestern Massachusetts, Hornbeck et al. (1997) found similar results with data from 159 streams (Fig. 4).

The linkage between trends in acidic deposition and trends in stream chemistry has been studied in the northeastern United States, Canada, and Europe. The failure of stream-water alkalinity to recover in spite of significant decreases in acidic deposition has been widely reported (Kirchner and Lydersen 1995; Likens et al. 1996; Lawrence et al. 1999; Stoddard et al. 1999; Watt et al. 2000; Stoddard et al. 2003). Calcium depletion plays a key role in this linkage because investigators frequently cite Ca depletion as a likely cause of the lack of positive stream response. In most cases, declines in SO_4 deposition have been accompanied by declines in SO_4 concentration in stream water, but base cation concentrations in stream water have also declined, resulting in no appreciable improvement in alkalinity (Stoddard et al. 2003).

Long-term monitoring of surface-water chemistry has revealed downward trends in Ca concentrations in many small streams in forested areas in the eastern United States (Stoddard et al. 1999; Huntington 2000) and in lakes in Canada (Couture 1995; Jeffries et al. 1995) and New York (Driscoll et al. 1995; Stoddard et al. 1999). These trends are consistent with soil Ca depletion and with decreasing acid anion inputs. These observations are also consistent with the hypothesis that watersheds draining areas of base-poor soils and parent materials are more likely to show signs of Ca depletion than those draining areas having more Ca-rich mineral content (Hornbeck et al. 1997).

The stream chemical record provides clear evidence for declines in SO_4 and base cation concentrations that were expected on the basis of decreases in SO_4 deposition. Because the collection of stream chemical data begins towards the end of the historical increase in sulfur emission, we do not know whether the stream-water Ca increased in response to increasing SO_4 deposition, as has been suggested from results of modeling studies (Cosby et al. 1985) and dendrochemical analyses (Bondietti et al. 1990). We also do not know what the stream-water Ca concentrations were prior to elevated anthropogenic sulfur emissions. Sulfur emissions decreased by about 34% between 1970 and 1998, and SO_4 and Ca concentrations in stream water both decreased by about 36% over the same period.

The timing of the decreases in stream-water SO_4 and Ca concentrations are similar and consistent with the conceptual model that decreases in acid anion deposition will result in parallel decreases in stream-water Ca concentration. At the Wild River near Gilead, Maine (Mast and Turk 1999) and at Hubbard Brook, New Hampshire (Likens et al. 1998), stream-water concentrations of Ca and SO_4 were variable but not trending downwards from the mid-1960s when the records begin until the early 1970s, when the levels of both Ca and SO_4 begin monotonic decreases. Episodic acidification is a common phenomenon in low-order streams in Maine (Haines et al. 1990; Kahl et al. 1992; Norton et al.1999), and in such areas may be indicative of higher sensitivity to Ca depletion than in areas where episodic acidification is not observed. Haines et al. (1990) observed that concentrations of Ca in stream water decreased during storms with increasing discharge but did not fall as much as some other bedrock-derived elements, leading to the conclusion that a considerable amount of Ca is released from the soil through ion exchange.

Stream-water Ca concentrations below 100–150 $\mu equiv.\cdot L^{-1}$ are considered low from the standpoint of sensitive aquatic biota. Of particular interest with regard to the problem of Ca depletion is the observation that aquatic biota tolerate lower pH and higher reactive Al concentrations in waters with higher Ca concentrations (Baker et al. 1990). Experiments have shown that Ca additions stimulate positive effects on sensitive aquatic biota when natural waters have Ca levels in the range of 100–150 $\mu equiv.\cdot L^{-1}$. At higher Ca levels, biological membranes are less permeable and less susceptible to damage caused by low pH or elevated Al (Baker et al. 1990). The Atlantic salmon resource in the Southern Upland (Atlantic Coast) area of Nova Scotia has been adversely affected by acidic deposition in combination with low Ca concentration (Watt 1997; Department of Fisheries and Oceans 2000).

Trend analyses for stream-water elemental concentrations at Wild River indicate that Ca plus Mg declined significantly during the period 1966–1996 by about 1.1 $\mu equiv.\cdot L^{-1}\cdot year^{-1}$, and SO_4 concentration decreased by 1.0 $\mu equiv.\cdot L^{-1}\cdot year^{-1}$ (Clow and Mast 1999). At Wild River the aggregate decline in base cation concentrations was marginally larger than that for acid anions, so decreases in base cations may not be attributed solely to decreases in acid anions and may indicate possible soil Ca depletion. At East Bear Brook in Maine, stream-water Ca concentrations decreased from 1987 through 2001 at a rate of about 2.0 $\mu equiv.\cdot L^{-1}\cdot year^{-1}$, and this decrease is "likely attributable to declines in SO_4 deposition in the region" (Fernandez et al. 2003).

Soils data

Data from Maine that can be used to characterize soil Ca inventory for forest soils are limited. Cumulative distribution plots (CDP) (Fig. 5) generated from DDRP and NRCS soil

Fig. 3. Historical pattern of atmospheric wet deposition of Ca, Mg, and SO4 at four sites in Maine. Lines are simple linear regressions for the Greenville site.

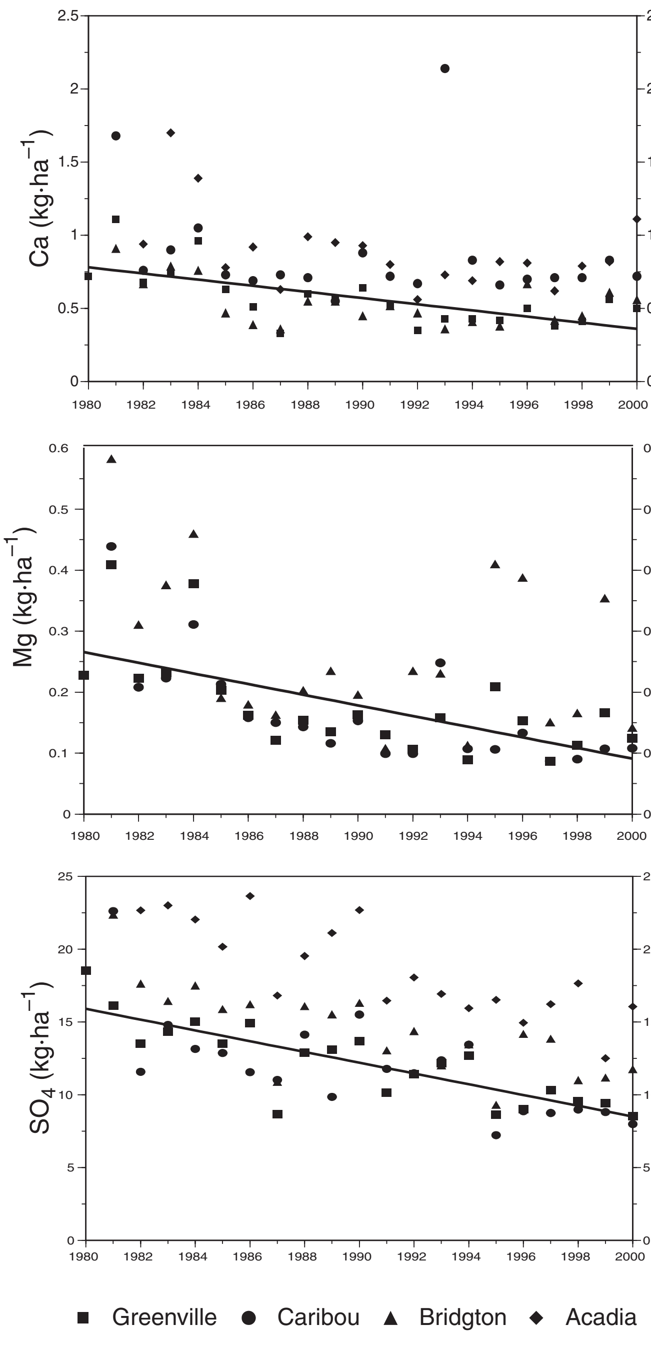
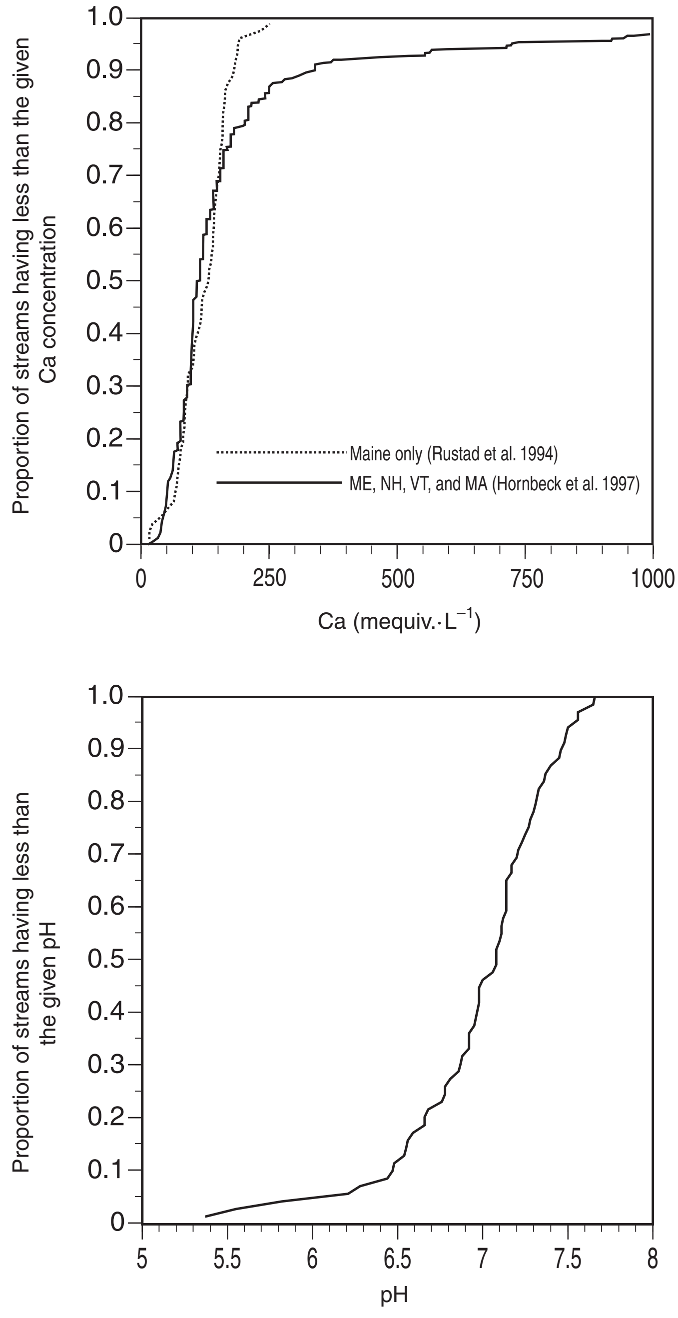


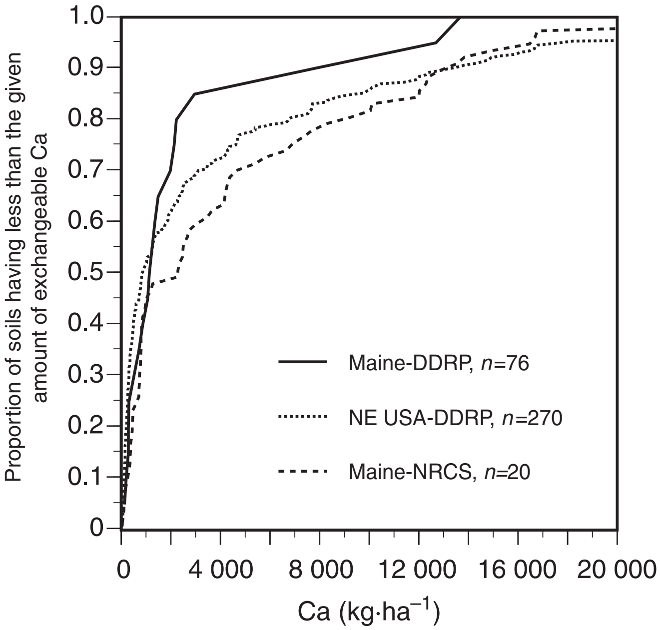
Fig. 4. Cumulative distribution plots for stream-water Ca concentration for streams in Maine, New Hampshire, Vermont, and western Massachusetts; and pH in Maine.



characterization data sets suggest that the majority of Maine forest soils are quite low in exchangeable Ca. About 50% of soils analyzed have <2000 kg Ca·ha^{-1} and 45% have <1000 kg Ca·ha^{-1}. Exchangeable Ca inventories in forest soils in Maine are comparable to those in other northeastern states (Fig. 5). These soil Ca inventories are also comparable to those found in Coastal Plain regions and somewhat higher than those found in the Southern Blue Ridge Province (Huntington 2000). The NRCS pedons did not include exchangeable Ca in the O horizons. Based on data from intensively studied sites in Maine (Table 1, see following paragraph), it is likely that the forest floor could provide an additional 100–500 kg Ca·ha^{-1} that would bring the totals for the NRCS pedons somewhat closer to those shown in the DDRP data (Fig. 5).

Intensive nutrient cycling studies that included soil characterization have been conducted at at least five sites in Maine (Table 1). These sites have very low exchangeable soil Ca inventories that are substantially lower than the median, as inferred from the CDF plots based on regional forest soil data (Fig. 5). This may be because these sites are gener-

Fig. 5. Cumulative distribution plots for exchangeable-soil Ca from Direct/Delayed Response Program and Natural Resource Conservation Service data.



ally associated with smaller headwater catchments that have thinner soils with higher coarse-fragment volumes than is characteristic of the median of the population of soils sampled in the DDRP and by the NRCS.

The soil characterization data (Fig. 5, Table 1) are consistent with low quantities of exchangeable Ca in Maine forest soils and support concerns about Ca depletion in northeastern forests through harvest removal and acid deposition (Smith et al. 1986; Federer et al. 1989; Driscoll et al. 2001). Fewer data are available on total Ca in the mineral soil (<2-mm fraction), but some data from Maine (Table 1) and other sites in the northeastern United States (Federer et al. 1989; Hornbeck et al. 1990; Johnson and Lindberg 1992) indicate that there are large supplies (typically >10 000 kg Ca·ha^{-1} that will eventually be released upon weathering. This component of a forest ecosystem's Ca inventory is highly bedrock specific but is generally considered to be much higher on glacial till of the northeastern United States than in the highly weathered mountainous and Piedmont terrains of the southeastern United States (Huntington 2000).

Forest growth and accumulation of Ca into merchantable wood

The predominant forest types in Maine during the 1995 inventory were hardwoods (39 183 km^2) and spruce–fir (24 325 km^2) (Table 3). The spruce–fir forest type group includes forest types dominated by red spruce, northern white-cedar, balsalm fir, black spruce, white spruce, or tamarack, singly or in combination. Common associates include paper birch, red maple, aspen white pine, hemlock, yellow birch, and sugar maple. Pine-dominated types occur on 5075 km^2. Much of Maine forest land contains a mixture of species that are typed on the basis of the abundance of larger trees. Hardwood types are predominantly beech–maple–birch, with lesser amounts of aspen–birch and still smaller amounts of oak–hickory and elm–ash–cottonwood types.

Hardwood, spruce–fir, and pine forest type groups incorporated Ca into merchantable wood at estimated average annual rates of 5.9, 1.6, and 1.6 kg Ca·ha^{-1}·year^{-1}, respectively, during the period 1982–1995 (Table 3). The accumulation rates varied markedly depending upon forest type and the growth rate in each county or geographic unit. The variation in growth rate is strongly affected by spruce budworm (*Choristoneura fumiferana*) mortality and cutting history. This is particularly evident in counties having high areas of spruce–fir type, such as Aroostook, Piscataquis, and Somerset Counties, which had very low total growth and Ca accumulation. The unexpectedly high rate of Ca accumulation for the spruce–fir type in the Casco Bay unit may be a result of errors associated with the small sample size for this unit (Table 3).

The rate of Ca accumulation into merchantable wood was estimated for the Southern Blue Ridge, Piedmont, and Coastal Plain ecoregions of the southeastern United States (Huntington 2000). Accumulation rates in those regions were substantially higher than estimated for Maine. Less than 5% of the counties in the Southern Blue Ridge and Piedmont ecoregions had Ca accumulation rates <6 kg Ca·ha^{-1}·year^{-1}, and 50% of the counties in those regions had accumulation rates >10 kg Ca·ha^{-1}·year^{-1}. The coastal plain region that contains more pine-dominated types had 23% of the counties, with Ca accumulation rates <6 kg Ca·ha^{-1}·year^{-1}, and 50% of the counties had accumulation rates >8 kg Ca·ha^{-1}·year^{-1}. The main reasons for the generally higher Ca accumulation rates in the Southeast are significantly higher growth rates and a higher proportion of hardwoods in the Southeast.

The rate of forest growth and nutrient accumulation in Maine has been quite variable over the last several decades because of the unbalanced age-class structure, spruce budworm epidemic, and variable harvesting rates. The age-class structure is a result of spruce budworm outbreaks of 1909–1929 and 1972–1986, periods of concentrated harvest activity, and episodes of abandonment of agricultural lands (Main State Forest Service (MSFS) 1998). A balanced age-class structure would have equal number of acres in each age-class, but in Maine the imbalance results in periods of substantially greater or lesser harvesting and forest growth rate. Forest inventories ending in 1959, 1972, 1982, and 1995 indicated that forest growth rates averaged about 2.52 m^3·ha^{-1}·year^{-1} during 1959–1972 compared with 1.75 m^3·ha^{-1}·year^{-1} during 1982–1995 (MSFS 1998). The lower growth rate in the latter period is a result of extensive spruce budworm mortality and intensive cutting preceding and during the period. The growth reduction occurred primarily in softwoods rather than in hardwoods (Table 4). Individual species data indicate that the growth reduction occurred primarily in balsam fir and red spruce, the species most affected by the spruce budworm outbreak (Table 5).

Bondietti et al. (1990) analyzed red spruce from several locations in Maine including the Penobscot Experimental Forest, Beddington, Kossuth, and Saddleback Mountain. An anomalous increase in red spruce stemwood Ca concentration beginning in the mid-1900s was followed by an anomalous decrease in the late 1900s. Both trends are consistent with trends in radial increment and SO_4 emissions (Nizich et al. 1995; US EPA 2000) and together are consistent with the

Table 3. Forest area, net annual growth, and Ca uptake into merchantable wood during the 1982–1995 period, calculated by geographic unit and forest type.

	Area (km^2)			Growth ($m^3 \times 10^3 \cdot year^{-1}$)			Ca uptake ($kg \cdot ha^{-1} \cdot year^{-1}$)		
County or unit†	Hardwood	Spruce–fir	Pine	Hardwood	Spruce–fir	Pine types	Hardwood	Spruce–fir	Pine types
Aroostook	8 172	6 913	104	1183	422	40	5.39	0.67	1.78
Hancock	1 532	1 614	316	427	574	113	10.39	3.91	1.68
Penobscot	3 858	2 839	794	804	880	190	7.76	3.41	1.12
Piscataquis	5 007	3 750	182	453	96	48	3.37	0.28	1.24
Somerset	5 801	3 332	390	614	224	144	3.94	0.74	1.74
Washington	2 321	2 796	478	325	354	85	5.22	1.39	0.83
Western Maine	6 123	1 979	776	1070	317	294	6.51	1.76	1.78
Capitol	3 057	995	697	481	351	197	5.86	3.88	1.33
Casco Bay	3 311	108	1338	889	212	594	10.00	21.64	2.09
State wide‡	39 183	24 325	5075	6243	3430	1709	5.94	1.55	1.58

Note: Average net annual growth (change in growing stock volume) is for growing stock components of growth (accretion + ingrowth – mortality – cull increment) on all remeasured plots. Data modified from Griffith and Alerich (1995).

†Geographic Units are as follows: western Maine: Franklin and Oxford Counties; Capitol: Knox, Lincoln, Waldo, and Kennebec Counties; Casco Bay: Androscoggin, Cumberland, Sagadahoc, and York Counties.

‡State-wide data are calculated from state-wide timber area and growth data by dominant forest type.

Table 4. Annual average timberland area, growth, growth rate over the inventory period for hardwood and softwood, and total forest growth rate for Maine forest land.

	Hardwood			Softwood			Total forest
Period	Area ($ha \times 10^6$)	Growth ($m^3 \times 10^6$)	Growth rate ($m^3 \cdot ha^{-1} \cdot year^{-1}$)	Area ($ha \times 10^6$)	Growth ($m^3 \times 10^6$)	Growth rate ($m^3 \cdot ha^{-1} \cdot year^{-1}$)	Growth rate ($m^3 \cdot ha^{-1} \cdot year^{-1}$)*
1959†	na	na	na	na	na	na	2.52
1959–1971‡	2.89	4.02	1.39	3.95	13.9	3.52	2.93
1972–1981‡	2.87	5.77	2.01	4.03	7.56	1.87	1.96
1982–1995§	3.92	6.23	1.59	2.94	5.18	1.76	1.75

*Modified from MSFS (1998). Data for the period ending in 1959 were estimated from radial area increment data derived from tree cores because this was the first systematic inventory. Length of record for growth rate estimate was not specified.

†Ferguson and Longwood (1960).

‡Powell and Dickson (1984).

§Griffith and Alerich (1995).

Table 5. Annual average growth over the indicated inventory periods for selected tree species or species groups in Maine.

	Annual average growth ($m^3 \times 10^6$)		
Species	1959–1971	1972–1981	1982–1995
Balsam fir	5.01	0.00	–0.20
Tamarack	0.00	0.00	0.11
Spruce (all)	5.26	3.31	1.70
Pine (all)	1.96	1.81	1.71
Northern white-cedar	0.43	1.35	0.87
Hemlock	1.31	1.03	0.98
Soft maples (red)	0.91	1.00	1.89
Sugar maple	0.69	0.71	0.84
Yellow birch	0.19	0.54	0.51
Paper birch	0.54	1.10	0.50
Beech	0.33	0.16	0.74
White ash	0.19	0.27	0.30
Aspen	0.46	1.62	0.98
Red oak	0.24	0.38	0.47
Total timberland area ($ha \times 10^6$)	6.84	6.84	6.87

hypothesis that increases in acidic deposition in the mid-1900s resulted in mobilization of exchangeable soil Ca, followed by depletion of exchangeable soil Ca and reduced availability in the late 1900s. Similar trends in Ca concentrations in eastern hemlock, Fraser fir, and yellow birch indicated that these trends were not restricted to red spruce.

Temporal patterns in Ca and Al concentrations of red spruce stemwood have suggested a potential depletion of soil Ca in the northeastern United States (Shortle et al. 1997). This temporal pattern included a transient increase in stemwood Ca concentration during the period 1950–1970, which could have resulted from cation mobilization in response to the high levels of acidic deposition during that period (Shortle et al. 1997). Further evidence of Ca depletion in northeastern US forest soils comes from use of Sr isotope ratios as tracers to distinguish atmospheric versus mineral sources of Ca (Bailey et al. 1996; Kennedy et al. 2002). In one study, 50%–60% of the soil-exchangeable and stemwood Ca in red spruce, balsam fir, and heart leaf paper birch (*Betula cordifolia* Reg.) stands in the Adirondack Mountains, New York, was of atmospheric origin suggesting depletion of Ca from mineral sources (Miller et al. 1993).

Site-specific studies

Biogeochemical input–output analyses at a small forested catchment near Weymouth Point in Maine have indicated that Ca depletion is likely an ongoing problem (Smith et al. 1986; Federer et al. 1989; Hornbeck et al. 1990; Briggs et al. 2000). The parent material at the Weymouth Point site is till that contains a significant amount of Ca in primary minerals. The soils are Aquic Haplorthods and Aeric Hapalquepts, which are typical of the region's lower lying, poorly drained soils. Harvest removals and soil leaching at Weymouth Point were estimated to be about 8 and 14 kg $Ca{\cdot}ha^{-1}{\cdot}year^{-1}$, respectively (Table 1). Briggs et al. (2000) reported that soil solutions collected at 50 cm depth had average Ca concentrations of about 80–100 $\mu equiv.{\cdot}L^{-1}$, or about 72% of the average stream-water concentration (125 $\mu equiv.{\cdot}L^{-1}$) for the reference catchment. This suggests that stream water contains a significant fraction of Ca originating from the surface 50 cm of soil and that the weathering of deeper till materials does not dominate the stream signal.

Biogeochemical analyses at the Howland research site in Maine have also suggested that outputs exceed inputs, indicating Ca depletion (Table 1). At the Howland site, Ca accumulation into merchantable wood and leaching losses substantially exceed inputs from atmospheric deposition (Johnson and Lindberg 1992; Fernandez et al. 1993). The Howland site is low in exchangeable soil Ca so that it is at risk of Ca depletion unless weathering can replenish exchangeable soil Ca. These input–output imbalances imply that Ca depletion is ongoing because the rate of chemical weathering is probably too slow to replenish exchangeable soil pools in these environments (Federer et al. 1989; Johnson and Lindberg 1992; Bailey et al. 1996; Kennedy et al. 2002).

Mass-balance studies at three other sites in Maine are incomplete, but Ca deposition input levels are low and soil-exchangeable inventories are low (Table 1), so if typical forest accumulation rates and soil leaching rates apply, these sites may also be experiencing Ca depletion. At Bear Brook, soil water leaching through lower soil horizons had average Ca concentrations of about 70 $\mu equiv.{\cdot}L^{-1}$ (Fernandez et al. 1999), which is similar to the concentrations used to calculate leaching losses at Weymouth Point and Howland. Annual runoff rates at Bear Brook (0.88 m) (Kahl et al. 1999) are also typical of central Maine, so leaching losses at the site are likely to be similar to those estimated at Howland and Weymouth Point. Although there is very limited site-specific data on rates of soil leaching, the data in Table 1 for three sites in Maine and data for sites in New Hampshire (Likens et al. 1998) and New York (Johnson and Lindberg 1992) demonstrate that leaching removes several times more Ca than is replaced through atmospheric deposition.

The Bear Brook Watershed Manipulation Project in Maine (BBWM) is an ongoing watershed-scale experimental treatment in which NH_4SO_4 is applied bimonthly to West Bear Brook at elevated levels (three to four times ambient levels of the early 1990s) following a 3-year pretreatment period (1987–1989). Stream chemistry has been monitored regularly since 1987 (Norton et al. 1999). A second reference catchment (East Bear Brook) received no experimental additions and likewise has been monitored regularly since 1987. Following NH_4SO_4 additions, stream-water Ca and Mg concentrations and annual export increased in the treated catchment until 1995 and declined between 1995 and 2001 (Fernandez et al. 2003). Soil Ca depletion was estimated as the Ca inventory in the reference watershed minus the treated watershed. This estimated depletion is balanced by the cumulative excess Ca export in stream water from the treated watershed over the period of study (Fernandez et al. 2003).

Weathering replenishment of soil-exchangeable Ca

One of the largest uncertainties regarding the long-term impact of acidic deposition on the availability of Ca at most sites in Maine is the rate of weathering replenishment. Many studies have attempted to determine whether the rate of mineral weathering replenishment is adequate to replace base cations on the soil-exchange complex that are lost through tree accumulation and soil leaching. Unfortunately, there are no direct measurements for the determination of in situ weathering rates. It is noteworthy that the Howland site in Maine had very low rates of Ca weathering release under controlled laboratory conditions compared with that of several other sites in the eastern United States (April and Newton 1992). Assessments of weathering replenishment usually rely on a variety of inferential methods including isotopic methods (Bailey et al. 1996; Miller et al. 1993; Dijkstra et al. 2003; Nezat et al. 2004), temporal patterns of Ca concentrations in stemwood (Bondietti et al. 1990; Shortle et al. 1997), or changes in soil-exchangeable Ca over time. Direct soil remeasurement studies in northeastern North America have documented significant decreases in exchangeable Ca (Johnson et al. 1994; Lawrence et al. 1995; Likens et al. 1996; Drohan and Sharpe 1997; Watmough and Dillon 2003). Using inferential methods, these studies indicate that for many sites, with soils similar to those in Maine, weathering rates have not been sufficient to replenish soil-exchangeable Ca. Earlier studies in the northeastern United States (Federer et al. 1989; Hornbeck et al. 1990; Briggs et al. 2000), east-central United States (Adams et al. 2000), and southeastern United States (Huntington 2000) have reached similar assessments.

The majority of the soils of Maine are typified by Spodosols of relatively low base saturation and low total exchangeable bases (50% have <3 $cmol{\cdot}(kg\ of\ base\ cations)^{-1}$) (Fernandez 1992). Little SO_4 is retained in these soils, thereby providing an abundant source of mobile anions as a mechanism for base cation leaching (Kahl et al. 1991). Although it is difficult to quantify, anthropogenic increases in acidic deposition during the 20th century are thought to have accelerated cation leaching losses (Binkley et al. 1989; Johnson et al. 1991; Robarge and Johnson 1992).

Two recent studies have suggested that weathering of small amounts of the Ca-rich mineral apatite may be an important source of Ca in northeastern US forest soils (Blum et al. 2002; Hamburg et al. 2003). Apatite dissolves more readily than other more abundant Ca-bearing minerals and likely occurs widely in crystalline rocks of the northeastern United States (Nezat et al. 2004). Nezat et al. (2004) estimated that in watershed 1, Hubbard Brook, New Hampshire, about 20% of the Ca in the parent material was in apatite and a minimum of between 12% and 22% of the Ca lost from the watershed was derived from the weathering of apatite. In spite of the importance of this mineral source, Nezat et al. (2004) concluded that "The present-day loss of base cations from the watershed, calculated by watershed mass balance, exceeds the long-term weathering rate, suggesting that the pool of exchangeable base cations in the soil is being diminished".

In an unpolluted temperate forest on thin (<50–60 cm) unglaciated soils overlying saprolite, the dominant trees were found to feed almost exclusively on biologically cycling atmospherically derived Ca, rather than Ca derived from min-

Table 6. Mean annual temperature (near geographic centroid of state), timberland area, and forest growth rate for selected states in the eastern United States.

State*	Mean annual temperature (˚C)†	Timberland area (ha×10^6)	Growth rate (m^3·ha^{-1}·year^{-1})
Maine (Orono)	5.85	6.87	1.66
New York (Utica)	7.26	6.24	2.68
Connecticut (Falls Village)	8.32	0.73	1.78
Massachusetts (Clinton)	8.78	1.20	2.30
Pennsylvania (State College)	9.65	6.43	2.78
Maryland (College Park)	12.75	0.98	4.01
Virginia (Charlottesville)	13.42	6.26	3.84
North Carolina (Salisbury)	14.99	7.58	4.33
South Carolina (Colombia)	17.36	5.04	2.95
Georgia (Milledgeville)	17.37	9.64	4.56
Florida (Ocala)	19.28	5.93	3.31

*Location of temperature record.
†Mean annual temperature at USHCN station at location listed in column 1 for period of record (late 1800s or early 1900s through 1994).

eral weathering in the underlying saprolite (Kennedy et al. 2002). Kennedy et al. (2002) showed that the temperate forests they studied can become nutritionally decoupled from deeper weathering processes, whereby the accumulation of base cations in trees relies largely on atmospherically deposited and biologically cycling sources.

Calcium status in the future

In this paper, Ca accumulation was estimated using data collected during 1982–1995, which was a period of substantially lower growth rate than that experienced historically (Table 4) (MSFS 1998). If the growth rate returns to more typical values of about 2.72 m^3·ha^{-1}·year^{-1} (mean of the pre-1959 and 1959–1971 periods), compared with 1.75 m^3·ha^{-1}·year^{-1} during 1982–1995 (Table 4), it would represent an increase in growth of about 56%. A 56% increase in growth occurring in the spruce–fir forest type would result in an increase from 1.55 (in 1995) to 2.42 kg Ca·ha^{-1}·year^{-1}.

Increased intensity of harvest removals including whole-tree harvesting and shifts towards shorter rotations result in increased removal of Ca and Mg in aboveground biomass and through leaching (Adams 1999). Timber management practices that disturb the soil or biogeochemical processes that interfere with normal plant Ca accumulation have the potential to result in increased Ca losses. Timber harvesting activities in forests in New England have been shown to result in elevated soil leaching losses that persist for a few years until aggrading vegetation reestablishes normal accumulation rates (Likens et al. 1998; Briggs et al. 2000).

Systematic changes in temperature and precipitation (Keim et al. 2003; Groisman et al. 2001), growing season length (Cooter and LeDuc 1995; Frich et al. 2002), and several hydrologic variables are all consistent with earlier spring warming and conditions likely to result in increases in forest growth rate (Table 6). Recent studies in Maine indicate ongoing changes in lake ice-out date (Hodgkins et al. 2002), river ice-out date (Dudley and Hodgkins 2002), timing of high spring flow (Hodgkins et al. 2003), and the ratio of snow to total precipitation (Huntington et al. 2004), all of which are consistent with trends towards earlier spring warming, particularly during the last three decades of the 20th century. On average, these trends suggest that the growing season lengthened by 1 week to 10 days during the 20th century. Within a given climatic regime and soil environment, forest growth rate is thought to be limited by nitrogen availability. Elevated nitrogen deposition in recent decades has been proposed as the cause of increased forest growth rates (Townsend et al. 1996). Forest growth rate may also increase in response to ongoing increases in atmospheric CO_2 concentration (Idso 1999).

Warming trends are likely to result in profound changes in forest species composition. Under current projections for climate change in this century, spruce–fir and northern hardwood forest types would be completely displaced by oak- and pine-dominated ecosystems (Iverson and Prasad 1998). Changes in forest species composition can potentially influence the rate of Ca accumulation in two ways. Changes in composition that result in replacement of slower growing trees with faster growing trees will increase the rate of Ca accumulation. Any changes that result in replacement of trees such as spruce, fir, northern white-cedar, or white pine, which take up relatively low amounts of Ca, by hardwood species that take up substantially higher amounts of Ca, will accelerate Ca depletion. The effect on depletion of hardwood replacement of softwoods could be mitigated somewhat by "tighter" nutrient cycling in hardwoods that would result in lower leaching losses. Because of the large differences in Ca accumulation rates by hardwood compared with conifer species, significant increases in the hardwood land base would be the single most important factor in increasing the rate of Ca depletion.

Conclusions

Maine forests currently have a lower level of risk for Ca depletion or declining Ca status than southeastern US forests because of lower levels of Ca accumulation in trees and acidic deposition. Levels of acidic deposition in Maine are lower than those found in many eastern US forests, and levels of soil-exchangeable Ca are intermediate compared with those of other regions. The current rate of Ca accumulation into merchantable wood throughout Maine forests is substantially lower than that in the southeastern United States because of low forest growth rates and a high proportion of conifer species that incorporate less Ca into merchantable wood in Maine. In spite of a lower risk of Ca depletion in Maine forests, the balance of evidence from site-specific and regional data indicate that the Ca status may be declining. Additionally, a variety of circumstances could result in large increases in the rate of net Ca depletion in Maine forests, putting them at greater risk in the future. Maine's forests have experienced exceptionally low growth rates in recent decades but growth rates are expected to return to more typical levels. Climate change, including warming and lengthening of the growing season, will likely accelerate the rate of Ca accumulation into merchantable wood. There is also concern that changes in forest species composition may result in higher rates of Ca accumulation. Together, these trends could lead to accumulation rates that are more comparable with those currently observed in the southeastern United States, which would increase the risk of Ca depletion in Maine. Continued monitoring of acidic deposition, forest growth and composition, stream chemistry, and, over the longer term, soil chemistry, is needed to monitor Ca status and ecosystem health.

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