

# Assessing the Threat That Anthropogenic Calcium Depletion Poses to Forest Health and Productivity

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## Abstract

Growing evidence from around the globe indicates that anthropogenic factors including pollution-induced acidification, associated aluminum mobility, and nitrogen saturation are disrupting natural nutrient cycles and depleting base cations from forest ecosystems. Although cation depletion can have varied and interacting influences on ecosystem function, it is the loss of calcium (Ca) that may be particularly limiting to tree health and productivity. Calcium plays unique roles in plant cell function, including environmental signal transduction processes that allow cells to sense and respond to stress. Considering this, Ca depletion could impair plant response systems and predispose trees to reduced growth and increased decline. Controlled experiments with red spruce (*Picea rubens* Sarg.) and other tree species provide mechanistic support for the hypothesis that Ca deficiencies predispose trees to decline. Importantly, several examples of species declines in the field also suggest that injury is often greater when Ca depletion and stress exposure co-occur.

Connections between contemporary species declines and Ca depletion highlight the need for monitoring forests for indicators of change, including Ca loss. Direct measures of soil and plant Ca concentrations provide one traditional means of assessing the Ca status within forests. Although these measures are often valuable, substantial variation among soils and species and a lack of comparative historical data provide obstacles to the use of these measures for evaluating Ca depletion across the landscape. An alternative approach for assessing Ca depletion is to model critical loads and exceedances of pollutant additions that lead to

net losses in Ca pools and likely disrupt ecosystem Ca cycles within forests. For example, spatial associations of Ca cycling and loss to broad-scale data on forest health and productivity were recently conducted for portions of the Northeastern United States. A steady-state ecosystem process model was coupled to extensive spatial databases and used to generate maps identifying forest areas likely to experience Ca depletion. Sustainable Ca supplies in forest ecosystems are functions of forest type, timber extraction intensity, prior land use, atmospheric deposition rates, and site factors including climate, hydrology, soil mineral type and weathering rates. Considering the unique vulnerability of Ca to leaching loss and its vital role in supporting tree stress response systems, the model focused on how changes in Ca pools may influence forest health conditions. Initial comparisons within New England indicated that the model-based Ca deficiency metric was a good predictor of field-based indicators of forest health and productivity. Models such as this show promise for evaluating the threat Ca depletion poses to forest health and productivity in an integrated and spatially explicit manner in North America. This approach has already proven valuable to policymakers and managers in Europe when evaluating alternative pollution reduction or mitigation options.

**Keywords:** Anthropogenic depletion, calcium, critical loads, stress response, sustainable nutrient supply, tree health.

## Anthropogenic Cation Depletion

Cations are naturally occurring, positively charged elements that are important constituents of soils and surface waters and play unique and critical roles in biological systems. Among many functions, cations serve as important co-factors influencing the activity of biomolecules, act to modify charge balances within cells and organelles, and serve as signaling agents that help regulate cell physiology (Buchanan and others 2000, Marschner 2002). In forested ecosystems, the presence and availability of cations is governed through the interplay of numerous natural processes, including atmospheric additions, mineral weathering, soil

formation, plant uptake and growth, forest stand dynamics, and leaching losses (Likens and others 1998). However, mounting evidence indicates that a variety of anthropogenic factors are altering biogeochemical cycles and depleting base cations such as calcium (Ca) and magnesium (Mg) from terrestrial ecosystems. Chief among these drivers of cation loss are processes directly or indirectly associated with atmospheric pollution.

### Pollutant Drivers

Through industrial activity and the increased combustion of fossil fuels over the past century, humans have dramatically increased gaseous emissions of sulfur dioxide ( $\text{SO}_2$ ), nitrogen oxides ( $\text{NO}_x$ ), and ammonia ( $\text{NH}_3$ ) and particulate emissions of acidifying compounds (Driscoll and others 2001). Recent pollution controls have reduced emissions of sulfur (S)-based compounds in Europe and North America, resulting in moderate reductions in S deposition, but there has been little change in nitrogen (N) deposition (Driscoll and others 2001, UNECE 2005). In contrast to North America and Europe, with rapid economic development and economic growth, Asia—and most notably China—has significantly increased fossil fuel combustion in recent years (Liu and Diamond 2005). As a result, emissions of  $\text{SO}_2$ ,  $\text{NO}_x$ ,  $\text{NH}_3$ , and associated compounds have increased greatly in the region (Carmichael and others 2002, Liu and Diamond 2005, Richter and others 2005). In fact, pollutant deposition of S and N compounds now affects a quarter of China's land area, making China one of the countries most influenced by these pollutants (Feng and others 2002, Jianguo and Diamond 2005).

Through the atmospheric conversions of  $\text{SO}_2$  and  $\text{NO}_x$  to the acids  $\text{H}_2\text{SO}_4$  (sulfuric) and  $\text{HNO}_3$  (nitric) as well as the release of hydrogen ions ( $\text{H}^+$ ) during the oxidation of ammonium ( $\text{NH}_4^+$ ) by soil microbes, S- and N-based pollutants act to acidify forest systems (Driscoll and others 2001). Among other impacts, this acidification increases the leaching of base cations from soils (Kirchner and Lydersen 1995; Likens and others 1996, 1998; Schulze 1989), and enhances the availability of aluminum (Al), which reduces base cation availability for plant uptake (Cronan and Scholfield 1990, Lawrence and others 1995). In addition to the atmospheric

production of acids from pollutant constituents, N inputs can lead to N saturation (the availability of N in excess of biological demand), which can deplete cations as excess N leaches from forest soils (Aber and others 1998). It has even been hypothesized that pollution-associated climatic warming could enhance rates of natural acidifying process, further exacerbating soil cation loss (Tomlinson 1993). In addition to pollution-associated cation loss, a side effect of existing pollution controls has been the reduced emission of particulates that contain base cations such as Ca (Hedin and others 1994). Reduced inputs and increased removals of cations from forests have resulted in net depletions that have been documented in a variety of ways, including long-term changes in stream chemistry, the analysis of archived soils, and the chemical analysis of tree xylem cores.

### Evidence From the Field

Long-term data of stream water chemistry at watersheds such as those at the Hubbard Brook Experimental Forest, New Hampshire, have documented changes consistent with the pollution-induced leaching of base cations from soils (Likens and others 1996, 1998). Early stream monitoring revealed an increasing flush of base cations (Ca and Mg) that paralleled  $\text{SO}_4^{2-}$  and  $\text{NO}_3^-$  concentrations—evidence that pollutant inputs were leaching stored soil cations into surface waters (Likens and others 1996, 1998). However, after 1970, mass balance calculations identified ever-reducing concentrations of cations, particularly Ca, coincident with decreases in  $\text{SO}_4^{2-}$  and  $\text{NO}_3^-$ —a pattern suggesting the depletion of available cations following long-term leaching (Likens and others 1996, 1998). The connection between cation losses and pollutant inputs was reinforced by data indicating that these same trends in stream chemistry occur in old-growth forests where the potentially confounding effects of land use disturbance (and associated acidification) were avoided (Martin and others 2000). Furthermore, European data indicate that the largest losses of Ca and Mg occur at sites with the most acid loading (Kirchner and Lydersen 1995).

Calculated reductions in soil cation storage inferred from the chemical analysis of stream water have recently

been bolstered by studies from the United States and Europe that directly measured reductions in soil Ca storage following long-term exposures to acidic deposition. Bailey and others (2005) measured the cation concentration of soils at four forested sites in the Allegheny Mountains of Pennsylvania in 1997 and compared these to data from archived soil samples from these same sites collected in 1967. At all four sites there were significant reductions in Ca and Mg concentrations and pH over the two sample periods, and, at most sites, documented losses of Ca and Mg were much larger than could be accounted for by biomass accumulation—suggesting leaching losses as a more likely cause. In a separate analysis, Lawrence and others (2005) measured the cation contents of soil samples collected in 1926, 1964, and 2001 near St. Petersburg, Russia. They found that concentrations of exchangeable Ca in the upper 30 cm of soil decreased about tenfold from 1926 to 1964 but remained stable thereafter. In contrast, exchangeable Al showed a small decrease in the upper 10 cm of soil from 1926 to 1964, but a tenfold increase in the upper 30 cm from 1964 to 2001. They interpreted these results as reflecting a two-stage acidification process: (1) from 1926 to 1964 when inputs of acidity were neutralized by the replacement of exchangeable Ca by H, and (2) from 1964 to 2001 when the neutralization of continued acidic inputs shifted from cation exchange to weathering of solid phase Al (Lawrence and others 2005). Here, too, changes in soil Ca concentrations were not attributable to biomass accumulation of Ca, but appeared better related to pollution-induced soil Ca depletion.

Consistent with measured reductions in soil Ca, several studies have noted reduced Ca concentrations in the stemwood of trees following the advent of elevated pollution loading (Bondietti and others 1990, Likens and others 1996, Shortle and others 1995). An initial increase in Ca concentration is often noted within wood for the decades with the greatest increases in acidic deposition that likely mobilized soil cations, increasing their availability for root uptake and leaching loss (e.g., Shortle and others 1995). However, the reduction in stemwood Ca in recent decades may better reflect the long-term depletion of Ca from soils (Shortle and others 1995). Importantly, reductions in Ca concentrations

within wood also suggest that pollution-induced changes in soil Ca levels are being transferred to living organisms.

### **Potential Contributions from Harvesting**

In addition to pollution-associated depletion, tree harvests have the potential to exacerbate cation depletion within forests if they contribute to net cation losses that exceed long-term inputs (Adams 1999, Federer and others 1989, Huntington 2000, Mann and others 1988, Nykvist 2000). Sequestration in aboveground woody biomass is an important cation sink within forest systems (Federer and others 1989, Mann and others 1988), and this is particularly true for Ca, which is highly concentrated in woody cell walls (Marschner 2002). Because of this, tree harvests can lead to the disproportionate removals of Ca relative to other cations (e.g., Adams 1999, Federer and others 1989). Harvests can also affect nutrient cycling through increased site acidification and leaching (Federer and others 1989), and reduced stocking following harvest may diminish stand-level transpiration and associated Ca uptake, further promoting Ca loss via leaching (Hornbeck and others 1993). In addition, varying methods of harvest can differentially alter Ca loss. For example, in one study, whole-tree (stems and branches) harvests removed up to 530 kg/ha, whereas sawtimber sales (bole wood only) removed about 442 kg/ha (Mann and others 1988). The frequency of tree harvest may also influence overall cation removal. Calculations from one study estimated a 15-percent loss of Ca from leaching even with no harvest, a 28-percent loss of Ca with one harvest (at 80 years), and a 41-percent Ca loss for an equal-intensity harvest performed in two stages: once at 40 years and once at 80 years (Adams 1999).

### **Calcium Depletion as a Biologically Unique Threat**

Although the depletion of any of the essential base cations can have varied and interacting influences on ecosystem function, the loss of Ca may be particularly limiting to tree health because the unique distribution and physiology of Ca suggests that the depletion of this key cation could specifically weaken plant stress response systems and predispose trees to decline.

## Calcium Distribution and Physiology

In contrast to many cations, Ca is highly compartmentalized within plant cells and tissues, and this partitioning is a defining characteristic of its physiological function. Although Ca is an essential micronutrient, it is toxic in its free form within the cell cytoplasm because it precipitates with inorganic phosphate (e.g., Bush 1995, Knight 2000). Thus, in order to assure phosphate availability for energy metabolism and other essential processes, Ca is actively pumped from the cytoplasm and is sequestered in inaccessible locations and chemical forms, including insoluble oxalate crystals outside the plasma membrane (Fink 1991). Because Ca can only exist in very low concentration in the cytoplasm, it is functionally immobile in the phloem (which relies on cytoplasmic transport). Thus, unique to other cations, Ca cannot be redistributed within plants to overcome localized deficiencies.

Localized concentrations of Ca support at least two important functions: (1) they add to the structural stability of cell walls and membranes, and (2) labile Ca is a key constituent in the pathway that allows cells to sense and respond to environmental stimuli and change (Marschner 2002). This second function appears particularly relevant to tree health concerns related to Ca depletion. Ca serves as an important second messenger in the perception and transduction of environmental and stress signals (Bush 1995, Pandey and others 2000, Roos 2000, Sanders and others 1999). Because extremely little free Ca exists in the cytoplasm of cells, environmental stimuli that temporarily alter the permeability of the plasma membrane allow labile Ca to flow into cells along a steep concentration gradient (Sanders and others 1999). Once in the cytoplasm, Ca quickly binds to Ca-specific proteins such as calmodulin, which then initiate a chain of physiological modifications (e.g., changes in enzyme activity, gene transcription, etc.) that help cells adjust to the environmental conditions that triggered the response cascade. This entry of Ca into the cytoplasm acts as a messenger of environmental information for cells and appears to be an essential first step in triggering a wide range of physiological responses needed by plants to successfully adjust to environmental change or defend against pests and pathogens. Numerous independently

conducted studies have concluded that Ca plays a critical message perception and transduction role in response to an array of environmental stresses, including low temperature (DeHayes and others 1997, 1999; Monroy and others 1993), drought (Sheen 1996), fungal infections (Hebe and others 1999), and insect infestations (McLaughlin and Wimmer 1999).

## Implications to Forest Health

Given the fundamental role Ca plays in plant stress response systems, biological Ca depletion could create a scenario analogous to the suppression of animal immune systems (Schaberg and others 2001). For example, there are numerous circumstances (e.g., HIV infection, chemotherapy treatment, etc.) that impair the normal function of human immune systems. An immuno-compromised person may appear, feel, and ostensibly function as if they were healthy. Nonetheless, when exposed to a disease agent, they can experience declines in health that are exaggeratedly large relative to a person with a fully functioning immune system. In this same way, it is possible that depletions of biologically available Ca could suppress the ability of plants to adequately sense and respond to changes in their surroundings and make them more vulnerable to decline (Figure 1). This suppression would predispose plants to disproportionate decline following exposure to perhaps even normal levels of stress (e.g., pathogens or drought) that would otherwise pose no catastrophic threat if biological response systems were fully functional. Importantly, under this scenario plants might initially appear to be normal and healthy even though their biological response systems were compromised (Schaberg and others 2001).

## Experimental Evidence of Tree Health Impacts

Although based on basic understandings of the distribution and physiology of Ca in plants, experimental evidence that Ca deficiencies could reduce stress tolerance in trees has only recently surfaced. This evidence was first documented for the well-studied phenomenon of winter injury in red spruce, but was later shown to be relevant to other tree species and stresses other than freezing injury.

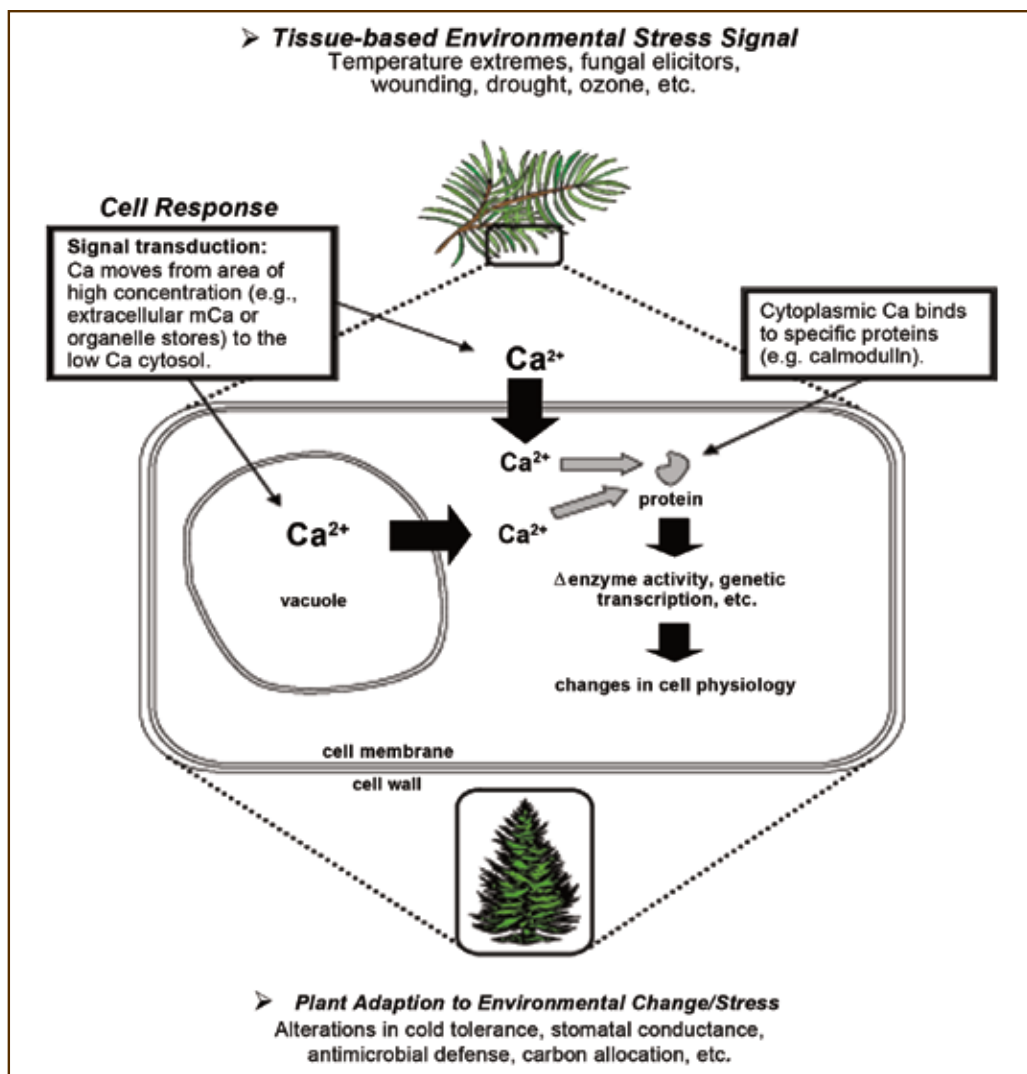


Figure 1—Schematic representation of how biological calcium (Ca) depletion may suppress plant stress response systems and predispose trees to decline. Environmental stimuli (e.g., a stress event) triggers the movement of Ca from areas of high concentration (i.e., extra-cellular and organelle pools) into the cytoplasm where Ca concentrations are 100 to 1,000 times lower. Once in the cytoplasm, Ca can bind to and activate Ca-specific protein complexes that interact with other cellular components (existing enzymes, DNA, etc.) to modify cell physiology in response to the instigating environmental cue. Depletion of biologically labile Ca may perturb signal transduction and diminish the ability of plants to sense and respond to environmental change/stress (Schaberg and others 2001).

### Mechanism of Red Spruce Winter Injury

Red spruce winter injury is the reddening and mortality of the foliage in late winter followed by its abscission in late spring (DeHayes 1992). Injury is caused by freezing and is likely the result of various stresses, including low temperatures (DeHayes and others 1990), freeze-thaw cycles (Hadley and Amundson 1992, Lund and Livingston 1998),

and rapid freezing (Perkins and Adams 1995). The current-year foliage of red spruce is more vulnerable to injury than older foliage age classes or foliage from sympatric species because it is less cold tolerant (DeHayes and others 1990). In addition, certain anthropogenic inputs such as acidic or prolonged N deposition can further reduce foliar cold tolerance and increase the risk of freezing injury (Schaberg

and DeHayes 2000). Heavy foliar loss and potential bud mortality from winter injury disrupts the carbon economies of trees, leading to growth declines and potential mortality (DeHayes 1992, Lazarus and others 2004). Winter injury was linked to the widespread decline of red spruce observed in the Northeastern United States from the 1960s through the 1980s (Friedland and others 1984, Johnson 1992), and severe winter injury events persist within the region (Lazarus and others 2004).

Beginning in the late 1980s, a series of studies were published showing that acid mist exposure significantly reduced the cold tolerance of red spruce current-year foliage, increasing the risk of foliar winter injury (e.g., DeHayes and others 1991, Fowler and others 1989, Vann and others 1992). The physiological mechanism for this acid-induced reduction in cold tolerance remained unresolved, however, until a new method for measuring Ca specifically associated with cellular membranes was used in conjunction with controlled acid mist exposure experiments. Using these new methods for measuring membrane-associated Ca (mCa), a series of experiments documented that acid mists preferentially leached mCa from the outside of mesophyll cells, whereas other cations and forms of Ca were leached less, presumably because they were concentrated within the protective membrane barrier of cells (DeHayes and others 1999, Jagels and others 2002, Jiang and Jagels 1999, Schaberg and DeHayes 2000, Schaberg and others 2000). Furthermore, these studies showed that this loss of mCa destabilized membranes, depleted a source of Ca needed for stress signaling, reduced foliar cold tolerance, and predisposed trees to the secondary freezing injury responsible for decline (DeHayes and others 1999, Schaberg and DeHayes 2000, Schaberg and others 2000). Later work verified that soil-based Ca depletion initiated the same mechanistic sequence of physiological disruptions documented for foliar Ca leaching (Schaberg and others 2002).

### Pertinence to Other Tree Species and Stressors

The bulk of experimental evidence elucidating the influence of Ca depletion on tree nutrition and stress response has involved winter freezing injury of red spruce. However,

recent evidence indicates that the same basic mechanism of physiological disruption documented for this species and syndrome are pertinent to other tree species and stressors. For example, Schaberg and others (2001) treated red spruce, eastern hemlock (*Tsuga Canadensis* (L.) Carr.), balsam fir (*Abies balsamea* (L.) Mill.), and eastern white pine (*Pinus strobus* L.) seedlings with acid mist and compared the nutritional and physiological responses of the newly evaluated species to those well-documented for red spruce. Although there was insufficient tissue to make all measurements on each species, results showed that acid mist reduced mCa levels (in eastern hemlock), decreased cell membrane stability (in balsam fir), and reduced foliar cold tolerance (in white pine) similar to red spruce (Schaberg and others 2001). In a separate experiment with red spruce, Borer and others (2005) examined the influence of acid mist exposure on stomatal closure following tissue desiccation—a stress response to drought that is also dependent on Ca signaling (Knight 2000). Red spruce seedlings were exposed to pH 3 or 5 mists and then measured for foliar Ca concentrations and rates of stomatal closure as foliage desiccated following shoot harvest. As with past experiments, acid mist exposure reduced the Ca available in foliage, but here the loss of Ca was also accompanied by a 15 percent slower rate of stomatal closure as tissues desiccated (Borer and others 2005). Results of experimental trials like this support the theory that anthropogenic Ca depletion could deplete biological Ca pools enough to suppress stress response systems and predispose trees to decline.

### Field Evidence of Influences on Tree Health

Controlled experiments like the ones outlined above have provided valuable insights into the biological mechanism through which Ca depletion may influence tree physiology and health. However, such studies by themselves do little to inform us of the threat Ca depletion may pose to native forests. Instead, evidence from numerous field studies has supported experimental findings and implicated Ca depletion as a contributing factor in the real-world decline of tree species in the United States and abroad.

### Winter Injury of Red Spruce

The role that foliar winter injury has played in red spruce decline in Northeastern United States and adjacent Canada has long been understood (see DeHayes 1992). In addition, experimental evidence has provided a detailed understanding of the mechanism through which acid deposition can deplete biologically available Ca and predispose foliage to damage (see “Mechanism of Red Spruce Winter Injury”). However, it was only following the severe winter injury event of 2003 that evidence indicated that acid deposition exposure in the field influences winter injury expression across the landscape. Lazarus and others (2006) measured the degree of foliar winter injury among dominant and codominant red spruce trees at multiple elevations (plots) at 23 sites in Vermont and adjacent States and used regression analyses to evaluate how injury varied with plot elevation, latitude, longitude, slope, and aspect. They found that injury was significantly greater in western portions of the study area, west-facing slope, and higher elevations—areas that have historically received higher levels of acidic and N deposition (Lazarus and others 2006). Although these findings support the hypothesis that acidic or N deposition or both act on a landscape scale to exacerbate winter injury, it was an ancillary evaluation that more specifically implicated Ca depletion as a modifier of injury expression in 2003. Hawley and others (2006) measured foliar nutrition and winter injury of red spruce on two watersheds at the Hubbard Brook Experimental Forest in New Hampshire: one a reference watershed that has undergone considerable Ca loss attributed to acid deposition-induced leaching (Likens and others 1996, 1998), and another watershed that was fertilized with  $\text{CaSiO}_3$  in 1999 to replace lost Ca. Dominant and codominant red spruce on the Ca-addition watershed had significantly more Ca in their foliage and experienced about one-third the foliar injury of comparable trees on the reference watershed (Hawley and others 2006).

### Sugar Maple Decline

Sugar maple (*Acer saccharum* Marsh.) decline has been documented throughout parts of the Northeastern United States and Quebec over many recent decades (Allen and others 1992a, Kelley 1988, Mader and Thompson 1969,

Wilmot and others 1995). These declines have been characterized using various measures, including crown deterioration, increased leaf chlorosis, and reduced growth. Stress factors such as drought (Payette and others 1996), freezing (Robitaille and others 1995), and insect defoliation (Allen and others 1992b) have been implicated with the decline and mortality of sugar maple. Regardless of stressor, decline has also been associated with deficiencies or imbalances of various elements including N, phosphorous (P), potassium (K), Mg, manganese (Mn), or Ca (Bernier and Brazeau 1988, Horsley and others 2000, Mader and Thompson 1969, Ouimet and Fortin 1992, Paré and Bernier 1989, Wilmot and others 1995). Although the specific elements associated with decline can differ among sites, deficiencies in Ca have been highlighted as a potential contributor to sugar maple decline in recent studies throughout the region (e.g., Ellsworth and Liu 1994, Ouimet and Camiré 1995, Wilmot and others 1996), in part because experimental additions of Ca or lime or both have been shown to reduce decline symptoms (Long and others 1997, Moore and others 2000, Wilmot and others 1995).

Consistent with these observations, Schaberg and others (2001) hypothesized that sugar maple decline may be another example of Ca depletion's influence on tree stress response systems and health (Figure 2). Variations in maple decline symptoms (crown condition and basal area growth) coinciding with differences in soil Ca status across a range of sites are consistent with this hypothesis (Schaberg and others 2006). However, as with red spruce, controlled additions of Ca at the Hubbard Brook Experimental Forest have provided a more specific test of the influence of Ca depletion on sugar maple health. For example, Juice and others (2006) compared the nutrition, reproductive success, and physiology of sugar maple seedlings on the reference and Ca-addition watersheds there. They found that seedlings on the Ca-treated watershed had higher root and foliar Ca concentrations, experienced greater survivorship, existed in greater densities, and had higher foliar chlorophyll concentrations than seedlings on the reference watershed (Juice and others 2006). Mycorrhizal colonization of seedlings was also greater in the treated than the reference watersheds (Juice and others 2006). In another study, Huggett

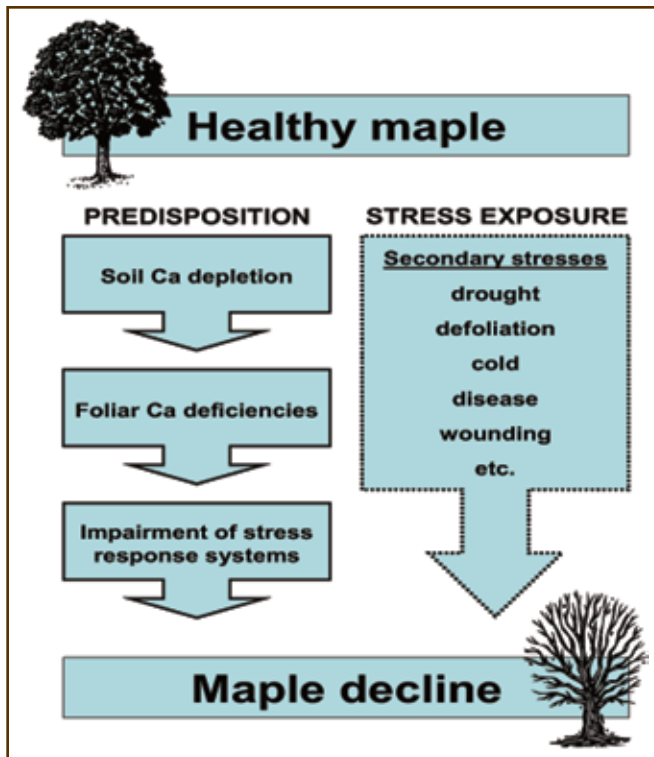


Figure 2—Proposed mechanism of sugar maple decline. This depicts how Ca deficiency may suppress stress response systems and predispose trees to decline following exposure to stress factors reported to contribute to sugar maple decline in the Eastern United States and Canada (Schaberg and others 2001).

and others (2007) surveyed and wounded forest-grown sugar maple trees in a replicated Ca manipulation study at Hubbard Brook. Similar to past studies, this study found that Ca addition increased foliar Ca levels and resulted in improved crown vigor, reduced branch dieback, and greater basal area growth among trees (Huggett and others 2007). However, new were findings that Ca addition particularly improved the growth release of trees following a severe ice storm and significantly increased stem wound closure—a capacity particularly important to a species that is regularly wounded as part of maple sugar production (Huggett and others 2007). These new findings are particularly noteworthy because they more specifically test the influence of Ca nutrition on the ability of sugar maple trees to respond to environmental change (release from competition) and stress (wounding).

### Anthracnose Damage to Flowering Dogwood

Acidic deposition exposure significantly increases the susceptibility of flowering dogwood (*Cornus florida* L.) trees to injury by the fungal pathogen dogwood anthracnose (*Discula destructive* Redlin) (Anderson and others 1993, Britton and others 1996). Furthermore, controlled studies have implicated acid-induced nutrient deficiencies in this altered disease susceptibility (Britton and others 1996). Elevated disease susceptibility has also been associated with environmental conditions (e.g., shade, low temperatures, wet cool summers, etc.) that result in low transpiration rates and thereby reduce the accumulation of Ca in plants (McLaughlin and Wimmer 1999). The association of Ca deficiency and anthracnose susceptibility is also supported by an increased resistance to this disease following lime application (USDA FS 1991). Based on this and other evidence, McLaughlin and Wimmer (1999) proposed that Ca deficiencies driven by low soil Ca concentrations, low transpiration rates or accelerated foliar leaching, or both, reduce the natural resistance of dogwood to anthracnose infection.

### Emerging Examples in the United States and Europe

In addition to the well-established connections between Ca depletion and tree health outlined above, new associations between the Ca status and health of trees periodically emerge—particularly in regions that experience continued pollution-induced Ca leaching. Differences in the susceptibility of eastern hemlock trees to damage by the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) in the Northeastern United States may provide an example of this. The HWA is a small, aphid-like insect that was likely introduced to the mid-Atlantic States from Asia in the 1950s and has since expanded its range and influence, devastating hemlock forests over an ever-widening portion of eastern hemlock's native range (Orwig and Foster 1998). Although it was first believed that little or no variation in susceptibility to HWA damage existed among hemlock trees (McClure 1995), recent work has shown that differences in site conditions and the presence of other stressors are associated with differential damage and decline (Orwig and Foster



1998, Sivaramakrishnan and Berlyn 1999). In particular, Pontius and others (2006) recently concluded that foliar chemistry was linked to the infestation and susceptibility of eastern hemlock to HWA. Among other evidence, results of a regional monitoring effort showed that concentrations of Ca, K, N, and P were strongly correlated with HWA densities (a driving factor in hemlock decline). From this and other findings, they hypothesized that, whereas foliar N and K concentrations may influence hemlock decline through an alteration in insect behavior due to palatability issues, Ca and P concentrations may deter severe HWA damage through an alteration in tree physiology (Pontius and others 2006). Experimental tests are needed to assess whether these changes in physiology involve Ca-induced alterations in plant stress response systems.

Evidence of acid deposition damage to forest health and productivity in Europe is anything but new or emerging. Indeed, media attention and resulting public concern about the possible connection between pollution exposures and forest death (Waldsterben) helped spur initial efforts to control acidifying pollution additions (Kakebeeke and others 2004). Research eventually identified pollution-induced cation depletion (particularly Mg and Ca) as an instigating component of forest decline (Schulze 1989). Although the mechanism through which acid deposition influences the health of European forests has not been explicitly defined, it is generally agreed that it acts as a predisposing agent, weakening forests and making them more susceptible to damage by other stresses including insect attack, extreme climate events, or storm damage (Materna and Lomský 2002, UNECE 2005). This scenario is strikingly similar to the Ca depletion and stress response suppression hypothesis developed primarily using evidence from declines in the United States (Schaberg and others 2001). In fact, a recent example of forest damage in Europe that is thought to be predisposed by pollution exposure involves the reddening and abscission of foliage of Norway spruce in the late winter, presumably due to freezing injury (Lomský and Šrámek 2002, Materna 2002). Patterns of injury (preferentially impacting the youngest foliage with the intensity and extent of damage increasing with elevation, Lomský and Šrámek 2002, Materna 2002) are identical to those documented

for red spruce winter injury (DeHayes 1992, Lazarus and others 2004), which has been mechanistically linked to Ca depletion (see “Mechanism of Red Spruce Winter Injury”).

## **Limitations of Current Indicators of Calcium Depletion**

Evidence from laboratory experiments and a growing number of field assessments indicate that anthropogenic Ca depletion may pose a unique threat to forest health and productivity. In particular, connections between contemporary species declines and Ca depletion highlight the need to monitor forests for indicators of change, including Ca loss. Direct measures of soil and plant Ca concentrations provide one traditional means of assessing the Ca status of forests. Although often valuable, these measures alone may not support a comprehensive and practical assessment of the biological threat posed by Ca depletion across the landscape for several reasons. Chief among these are difficulties associated with the high spatial variability of Ca storage and availability within forest soils, substantial differences in Ca uptake and nutritional requirements among tree species, and a lack of historical data to serve as a reference to gauge the timing and extent of Ca depletion.

## **Soils**

As noted in “Evidence From the Field” (p. 38), direct evidence of cation depletion is limited to a few retrospective studies that were able to use archived soil samples and contemporary measurements of the exact field locations to determine changes in soil chemical properties (Bailey and others 2005, Lawrence and others 2005). These studies, in combination with a 9-year watershed acidification study in Maine that showed sizable reductions in exchangeable Ca and Mg compared to the control watershed (Fernandez and others 2003), and long-term watershed mass balance observations (Likens and others 1996), support the theoretical basis of cation depletion due to acid deposition (Reuss 1983). However, application of these results to larger landscapes is highly problematic because of the large spatial variability of soil properties. Plant-available Ca status within soils is primarily determined by the mineralogy of the parent material from which the soil was formed and the

period of time that the rooting zone has been exposed to weathering. Thus, the underlying parent material and soil classification information are useful in identifying regions that may be at risk to Ca depletion (e.g., areas of the White Mountains in New Hampshire or the Adirondacks in New York). However, within susceptible regions, soil properties are highly variable, both vertically and horizontally, which make it challenging to conduct site-specific evaluations. This spatial variability can be dealt with by using a large sample size and sampling the soil by genetic horizon (Bailey and others 2005); however, this requires the assistance of trained soil scientists and incurs high costs for analysis. Consequently, collection of soil nutrition data to support regional assessments would be expensive and requires the expenditure of considerable time and effort. In part to overcome the inherent difficulties in assessing soil nutrition, but also considering the theoretical value of assessing living organisms when considering biological deficiency thresholds, vegetation chemistry has also been monitored to test for Ca deficiencies.

## Vegetation

Ca deficiency thresholds for trees in native forests exist for some species with established nutritional vulnerabilities. For example, based on greenhouse (Swan 1971) and field studies (Borer and others 2004, DeHayes and others 1999), minimal sufficiency and deficiency Ca thresholds have been determined for red spruce foliage (1200 and 800  $\mu\text{g g}^{-1}$ , respectively). The deficiency threshold is associated with reduced cold tolerance and growth and increased winter injury of trees (Borer and others 2004, DeHayes and others 1999, Swan 1971). Similarly, based on surveys of forest-grown trees, a foliar Ca deficiency threshold of about 5000  $\mu\text{g g}^{-1}$  has been established for sugar maple (e.g., see Kolb and McCormick 1993). Foliar Ca concentrations below this threshold have been associated with increases in crown dieback and reduced growth of trees (Schaberg and others 2006), reduced growth following overstory release, and impaired stem wound closure (Huggett and others 2007). However, an analysis of these thresholds reveals that threshold concentrations are not uniform among species and can differ greatly (here more than fivefold).

Obviously, not all tree species access or require Ca in equal amounts. Depending on tree rooting habits (e.g., depth of roots, possible mycorrhizal association, etc.), access to soil Ca can differ greatly. Furthermore, perhaps because Ca cycling within forests has historically been adequate to amply supply this critical nutrient, specific thresholds of Ca depletion have been developed for only a few key species (such as red spruce and sugar maple). Even for well-studied species, internal chemical sequestration of Ca (e.g., the precipitation of Ca as insoluble oxalate crystals within cell walls; Fink 1991), may mask biological Ca deficiencies and complicate the establishment of universally relevant deficiency thresholds. Indeed, discovery of the mechanism through which acid deposition reduces the cold tolerance of red spruce foliage relied on the differentiation of biologically labile Ca from total foliar pools in order to remove the confounding influence of foliar Ca sequestration (DeHayes and others 1999, Schaberg and others 2000). Thus, owing to great species-to-species variation in Ca nutrition and use, combined with questions of tissue sequestration and biological availability, foliar assessments of Ca are not universally valuable in assessing Ca deficiency. However, despite limitations, measurements of foliar Ca concentrations may have value if conducted as part of monitoring efforts to gauge spatial and temporal changes in Ca nutrition, thereby assessing trends in Ca accrual or depletion.

## Lack of Historical Data

One-time measures of soil or plant Ca concentrations can provide useful information of the current status of a site, particularly if Ca concentrations are clearly aberrant relative to limited established standards. However, short of this, they provide little insight into trends in Ca availability or potential disruptions in Ca cycling. In contrast, repeated measures (and the archiving of samples to allow for reanalysis should measurement protocols change over time) provide baseline data needed to make necessary trend assessments. To date, comparatively few such databases and archives have been established. Long-term research at the Hubbard Brook and other experimental forests (e.g., Adams 1999, Likens and others 1996, 1998), as well as a few recent studies (notably Bailey and others 2005, Lapenis and others

2004, Lawrence and others 2005) highlight the unique benefit of repeated measures for detecting meaningful changes in Ca nutrition. Recognition of the value of such data sets has bolstered efforts to compile broad nutritional data sets that encompass a variety of sites, tree species, and time periods (e.g., see the foliar chemistry database compiled by the Northeastern Ecosystem Research Cooperative: <http://www.folchem.sr.unh.edu/>), and establish sample archives as described by Lapenis and others (2004) and Lawrence and others (2005). However, given practical (especially funding) limitations, even if such data sets and archives were dramatically expanded, appropriate historical data would exist for just a fraction of the land area impacted by pollution loading. Thus, alternatives for assessing the location and extent of Ca depletion across the landscape must be developed, tested, and employed.

### **Critical Loads as an Alternative Approach**

Given the limitations of static measures of Ca status, an alternative approach has been developed that models the level of pollutant additions that will likely lead to net losses in Ca pools within forests, therefore disrupting Ca cycling and leading to reduced plant Ca availability, and the physiological consequences described above.

#### **Description and Overview**

The critical load of a pollutant is classically defined as a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge (Nilsson and Grennfelt 1998). This definition implies some sort of measurable threshold value of ecosystem condition (termed the critical limit) that is demonstrably influenced by the pollutant(s) in question. The critical load is the pollutant deposition load, which can be shown to perturb a system such that the critical limit condition is attained. In the context of the adverse impacts of S and N deposition, many different critical limits have been proposed based on values of the Ca/Al ratio of soil water, the Ca/Al ratio of soil exchange sites, soil percentage base saturation, soil water nitrate concentrations, and soil and plant carbon (C)/N ratios. The relationship between

pollutant loading and the value of the ecosystem condition being evaluated can be established empirically or by mechanistic modeling. For mechanistic modeling, both steady-state and dynamic-process models have been employed. Important modeling considerations are appropriate data availability at the spatial scale desired and the existence or lack of data that can be used for dynamic model calibration and evaluation.

### **Examples from Europe and Canada**

In 1984, a protocol to the UNECE 1979 Convention on Long-Range Transboundary Air Pollution was established providing for long-term financing of the Cooperative Program for Monitoring and Evaluation of the Long-Range Transmission of Air-Pollutants in EUROPE (EMEP) (<http://www.unece.org/env/lrtap/welcome.html>). This protocol permitted the development of the scientific and administrative structure necessary for coordinated evaluation of critical loads and exceedances for acidifying pollutants in Europe. For over a decade, European countries have used the critical loads concept to set emissions reduction targets for S and N under the UNECE Convention on Long-Range Transboundary Air Pollution (Posch and others 1995). Initially, the critical loads for S and N were developed for effects on freshwater aquatic ecosystems. This work was rapidly expanded to include the developing understanding of the role of S and N deposition in producing European forest declines.

Canada followed Europe's lead and developed critical loads modeling programs first for aquatic and then forest ecosystems (Ouinmet and others 2001, 2006) that have been incorporated into the periodic Canadian Acid Rain Assessments (Morrison and others 2005). Until recently, few have attempted to apply the critical loads approach to large forest landscapes in the United States.

### **Application to New England**

One approach for applying the concept of critical loads to assessing the sensitivity of forests to Ca depletion grew out of the work of the Conference of New England Governors and Eastern Canadian Premiers (NEG/ECP). In 1998, the NEG/ECP developed an Acid Rain Action Plan that

called for (among 44 action items) a regional assessment of the sensitivity of Northeastern North American forests to current and projected S and N emissions levels. This assessment was intended to identify the location and extent of forested areas most sensitive to continued S and N deposition and estimate deposition rates required to maintain forest health and productivity under current rates of forest resource utilization.

### Conference of New England Governors and Eastern Canadian Premiers

Considering the unique vulnerability of Ca to leaching loss and its vital role in supporting tree stress response systems, the model focuses on how atmospherically deposited S and N act to produce changes in Ca pools that may influence forest health conditions. Review of the literature (discussed above) indicated that the most appropriate critical limit that could be modeled as a function of S and N deposition was whether an ecosystem could maintain a sustainable supply of the nutrient base cations Ca, Mg, and K or if the system was experiencing long-term depletion of these elements. Systems in a chronic state of cation depletion will eventually exhibit the Ca deficiency-related problems discussed above. Because the goal of the assessment was to provide estimates of the forest area potentially impaired if pollution remained at current S and N deposition levels, a steady-state modeling approach was selected. It was determined that adequate estimates of the parameters required for steady-state modeling could be developed regionwide at an appropriate spatial scale, whereas the data requirements for dynamic modeling could only be met in a few locations. It is anticipated that the results of the steady-state modeling assessment will direct future data collection efforts to high-value, high-risk areas where the cost of data collection for dynamic modeling may be justified.

A steady-state ecosystem process model was coupled to extensive spatial databases and used to generate maps identifying forest areas likely to experience Ca depletion (Miller 2005, 2006; Ouimet and others 2006). Sustainable Ca supplies in forest ecosystems are functions of forest type, timber extraction intensity, prior land use, atmospheric

deposition rates, and site factors including climate, hydrology, and soil mineral weathering rates (NEG/ECP 2001). The ecosystem model and several submodels simulate these processes. The crucial determinant of an ecosystem's ability to tolerate S and N deposition without declining Ca supplies is the rate at which primary minerals (e.g., hornblende, plagioclase, calcite) chemically decompose, liberating the nutrient cations  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and  $\text{K}^{+}$  to plant-available pools and, thus, replenishing nutrients lost via timber removals and acid-induced leaching. A geochemical model based on the work of Sverdrup and Warfvinge (1993) was used to estimate the weathering rate of primary minerals. Considerable field and modeling efforts were required to develop the spatial data layers needed to apply this model to the New England region. The annual demand for nutrients required to regrow the biomass exported via harvesting was estimated from timber extraction rates and wood-nutrient content. This information was generally available for the New England States from combinations of State and Federal sources. Atmospheric deposition of S, N, chloride (Cl), Ca, Mg, sodium (Na), and K was estimated for a 5-year period (1999-2003) in order to provide some smoothing of year-to-year variations in climate and patterns of atmospheric transport. Total deposition, including precipitation, cloud droplet interception, and dry deposition, was estimated using atmospheric chemistry data from the US NADP, CASTNet, and NOAA-AirMon deposition monitoring networks and Ecosystems Research Group, Ltd.'s High-Resolution Deposition Model (Miller 2000, Miller and others 2005, NEG/ECP 2001).

Although only results for Vermont and New Hampshire are presented here as examples, this assessment methodology has been applied to all of New England. Critical loads of S plus N ranged widely in New Hampshire and Vermont (0 to 21  $\text{keq ha}^{-1} \text{y}^{-1}$ ) as a result of the diverse geology and climate of the region (Figure 3). Areas of Ca-rich rocks and soil materials scattered throughout the region support the highest critical loads, often in excess of 3  $\text{keq ha}^{-1} \text{y}^{-1}$ . The lowest critical loads were found primarily in northern New Hampshire where soils are developed in thin and patchy tills derived from base-poor rocks. The range of S deposition was between 3.2 and 18.9 (average 5.1)  $\text{kg ha}^{-1} \text{y}^{-1}$  and N

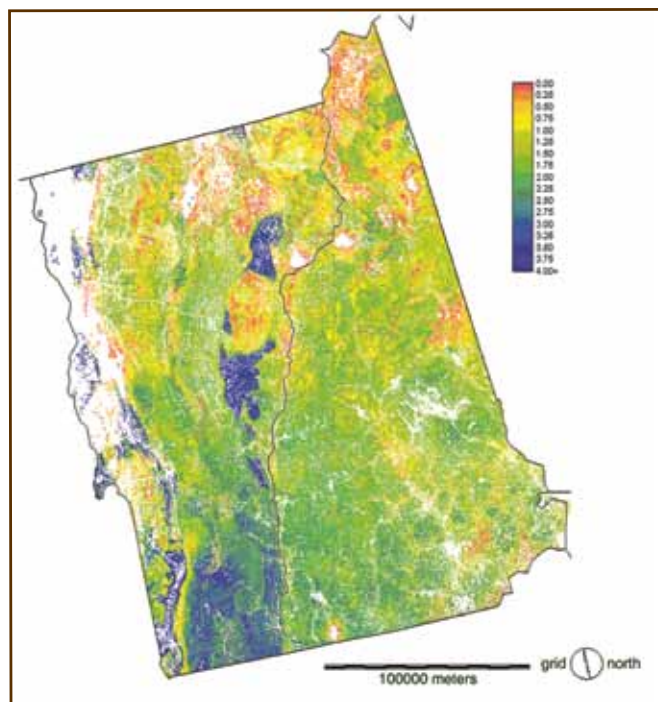


Figure 3—Critical loads of sulfur plus nitrogen to upland forests; S + N atmospheric deposition rates higher than the critical load result in greater exports of nutrient cations ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^{+}$ ) than inputs of these nutrients, leading to the eventual deterioration of soil fertility, forest health, and forest productivity. Critical loads are expressed in kilo-equivalents per hectare per year in this map of New Hampshire and Vermont; N deposition includes both ammonium + nitrate forms. White areas depict locations with nonforested land or water.

deposition (ammonium + nitrate) ranged between 3.3 and 25.2 (average 8.4)  $\text{kg ha}^{-1} \text{y}^{-1}$ , producing an aggregate acidifying and nutrient-leaching potential of 0.43 to 2.7 (average 0.92)  $\text{keq ha}^{-1} \text{y}^{-1}$  (Figure 4). The highest elevation areas received the highest S + N deposition from orographically enhanced precipitation and cloud water inputs. Deposition was also high in the southern and western parts of the region owing to proximity to emission sources.

Using critical load and atmospheric deposition estimates, a deposition index can be calculated to help evaluate the relative risk for ecosystem health problems resulting from Ca limitation (Figure 5). The deposition index is calculated as the ecosystem critical load minus the atmospheric deposition. In this index, positive values reflect the capacity of a forest ecosystem to tolerate additional acidic deposition, whereas negative values correspond to the reduction in S and N deposition required to eliminate

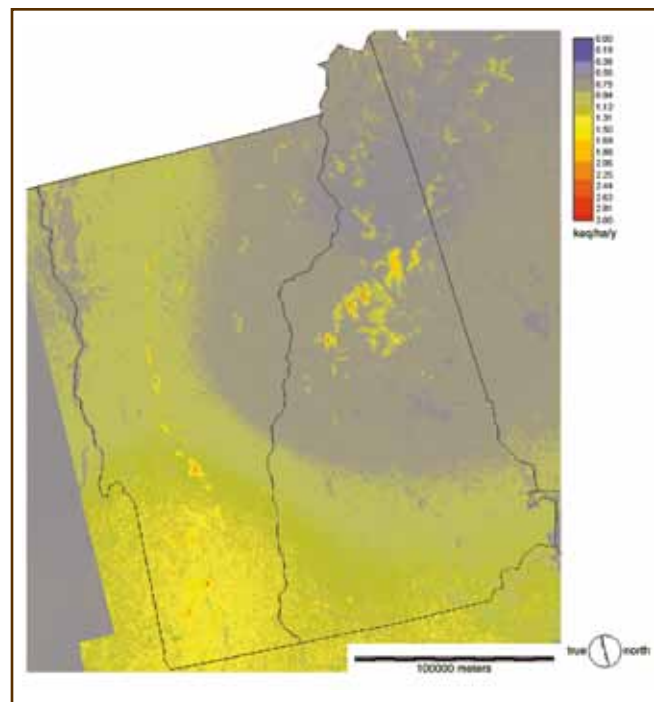


Figure 4—Average annual atmospheric deposition of sulfur and nitrogen (1999-2003). Total deposition (particle +  $\text{SO}_2$  + precipitation + cloud water) expressed in terms of kilo-equivalents of charge per hectare per year in this map centered on New Hampshire and Vermont; N deposition includes both ammonium + nitrate forms. This represents the total base-neutralizing and cation-leaching power of S and N atmospheric deposition.

present or deter the development of nutrient limitations. Atmospheric deposition of S and N during 1999-2003 exceeded the critical load in approximately 18 percent of the forested area of NH and 30 percent of the forested area in VT (Figure 5 and Figure 6). Critical loads were frequently exceeded where deposition was moderate (Northeast) to high (South) and where critical loads are low. An additional 10 percent of the forested area in each State experienced deposition rates during 1999-2003 that were less than 0.2  $\text{keq ha}^{-1} \text{y}^{-1}$  below the critical load. Some locations within these areas with shallower soils and more intense harvesting than the average values used in this assessment are likely to also be at risk of Ca depletion.

Forest tree species occupy different portions of the landscape as a function of climate, soil conditions, and land use history. This distribution results in some types of forests being more severely impacted than others by the nutrient

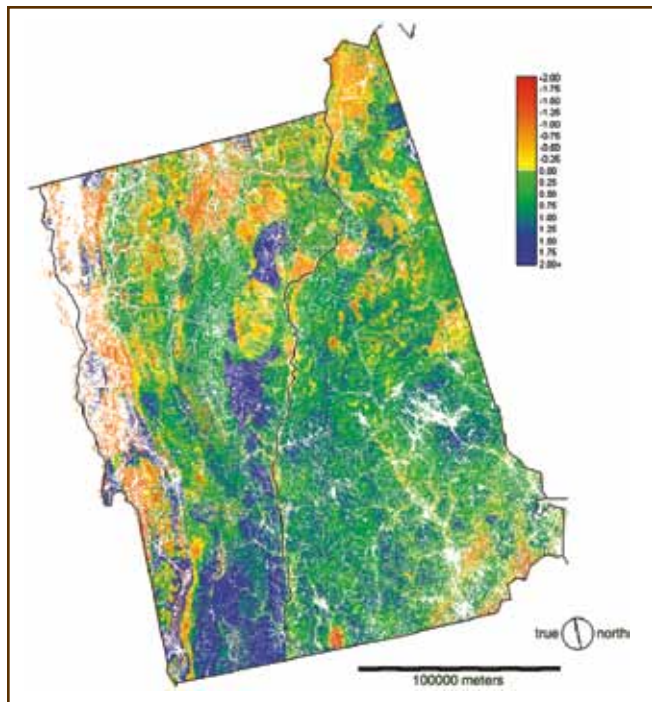


Figure 5—The deposition index for atmospheric sulfur and nitrogen deposition (1999–2003) with respect to Ca depletion. Positive values of the deposition index reflect the capacity of a forest ecosystem to tolerate additional acidic deposition. Negative values of the index correspond to the reduction in S and N deposition required to eliminate present or deter the development of nutrient limitations. Red-orange-yellow areas in this map of New Hampshire and Vermont indicate current S and N atmospheric deposition rates greater than the critical load. The deposition index is expressed in terms of kilo-equivalents of charge per hectare per year. N deposition includes both ammonium + nitrate forms. White areas represent areas with nonforested land or water.

cation depletion caused by S + N deposition. For example, critical loads are exceeded in 49.6 percent of New Hampshire's central hardwood forests, but in just 2 percent of the State's northern hardwood forests. This discrepancy exists because the central hardwood forests (6.1 percent of total forest area) tend to occur more frequently on poor sandy soils. The northern hardwood forest (18.9 percent of forest area) occurs on somewhat richer sites. Stands dominated by sugar maple (11.4 percent of forest area) occupy mid-elevation sites and have the highest Ca requirement of the northern hardwood forest variants. We estimate that the critical load is exceeded in 39.8 percent (88 167 ha) of New Hampshire's sugar maple stands, and deposition is within 10 percent of the critical load in an additional 3.6 percent (7826 ha).

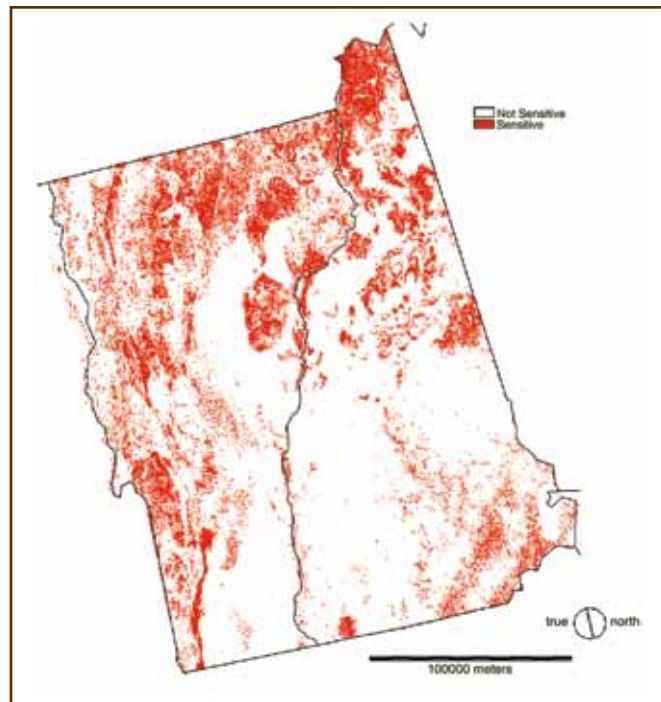


Figure 6—Areas with sulfur plus nitrogen deposition in excess of the critical load. Red-shade shows areas in New Hampshire and Vermont where S+N deposition exceeded the critical load, and forests would be likely to experience Ca depletion under 1999–2003 deposition rates.

### Relationships to Forest Health

The model-based nutrient deficiency metric appears to be a good predictor of independent, on-the-ground indicators of current forest health and productivity. For oak and pine forests in Massachusetts, tree height and canopy transparency were significantly related to foliar Ca levels and to the modeled rate of base cation depletion. Canopies were more transparent and grew to lower heights where base cation depletion rates were higher, and foliar Ca status was lower. At these same sites, root-zone soil base saturation, pH, and Ca/Al ratio were correlated with modeled base cation depletion rates. A separate evaluation also showed promising results: a comparison of model results with multiple-year aerial surveys of forest damage in Vermont indicated that both the frequency of damage and size of damaged areas were related to modeled base cation depletion. Forests in Vermont also showed greater canopy transparency and higher percentages of trees with chronic dieback where modeled base cation depletion rates were higher.



The critical loads framework can also be used to assess the recovery of ecosystems owing to changes in pollution levels and management strategies. Miller (2005) estimated that the cation depletion that likely previously occurred in 126 000 ha of forest in New Hampshire and 133 775 ha in Vermont was probably reversed by the 36-percent reduction in S deposition that occurred in the region from the late 1990s to the early 2000s. These forest areas should be experiencing recovery of base cation pools.

### **Development and Relevance of Future Models**

Initial results like those described for New Hampshire and Vermont indicate that models of critical loads and forest sensitivity show real promise in helping to empirically define the threat posed to forests in an integrated and spatially explicit manner. Risk assessment will be assisted by the expansion and refinement of existing data sets and models, as well as the development of more detailed dynamic models applicable to specific, high-interest sites. Ultimately, refined models should help policymakers and managers improve their analyses and recommendations regarding possible options to prevent or mitigate anthropogenic Ca depletion across the forested landscape.

### **Steady State versus Dynamic Models**

Steady-state models are most appropriate for regional studies because of their lower data requirements. Steady-state models can provide reasonable estimates of long-term average Ca depletion rates covering large areas at a reasonable cost. These models can provide estimates of the extent, location, and average intensity of base cation depletion. Where additional measures of base cation pools are available or can be obtained, comparison of steady-state depletion rates with base cation pools can provide first-order estimates of the time to ecosystem degradation or recovery (Miller 2005).

Dynamic models offer important insight into how and when ecosystem changes will occur in response to changes in pollution loadings and management activities. However, dynamic models are data intensive and require calibration and evaluation data that take years to obtain at considerable

expense. Calibrated dynamic models are typically only applicable to the specific locations for which they were calibrated. Thus, dynamic models seem most appropriate for assessment of high-value or high-interest sites where the additional cost of data gathering can be justified. Dynamic models may be used opportunistically where suitable pre-existing data exist; however, great care must be taken to understand how representative such opportunistic studies are of the broader landscape.

### **Policy Implications**

First and foremost, modeling approaches such as those involving the estimation of steady-state or dynamic critical loads could be of benefit to policymakers when evaluating the possible consequences of various pollution mitigation options as they relate to Ca cycling, forest health, and productivity. Analyses of trends in data from the field have been used to evaluate whether implementation of Phase I of the Clean Air Act Amendments of 1990 resulted in sufficient reductions in pollutant inputs to protect environmental resources (e.g., Butler and others 2001, Likens and others 2001). However important, this retrospective approach does little to inform decisionmakers of the possible future or long-term impacts of pollutant deposition. In contrast, a noted benefit of critical loads and associated forest sensitivity modeling is the flexibility provided to project trends forward and estimate the location and extent (steady state) and timing (dynamic models) of pollution-induced impacts. Furthermore, these models can be used to estimate differences in pollution loads and impacts among various pollution reduction plans, thereby allowing for a more detailed and reasoned analysis among policy alternatives.

### **Management Implications**

Results from modeling efforts may also inform resource managers regarding the need for possible intervention and protective strategies to reduce or mitigate the impacts of air pollution. For example, forest sensitivity maps could be used to identify forest tracts where N or S loads remain above critical loads and where liming may be needed to sustain the health and productivity of forests. In recent decades, lime has been routinely applied to forests in

Europe to counter pollution-induced losses of base cations (e.g., Materna 2002, Meiwes 1995, Saarsalmi and Mälkönen 2001), and experimental trials in the United States have shown reductions in decline symptoms when sugar maple forests received lime applications (Long and others 1997, Moore and others 2000, Wilmot and others 1996). However, lime addition can be costly and difficult to apply over forest landscapes. Modeling results could help identify areas of particular vulnerability to Ca depletion and better target regions where interventions such as lime addition may be most beneficial and cost effective. Another management option is to modify harvesting intensity in particularly vulnerable areas by extending rotation lengths or limiting the biomass removed (stem only vs. whole-tree harvesting). A reduction in harvesting intensity could be used to lower the export of Ca from the forest during the time required for air pollution reductions to be achieved.

## Worldwide Relevance

Concerns about the influence of Ca depletion on forest health exist for industrialized regions around the world including Europe, Eastern North America, and increasingly China (Driscoll and others 2001, Duan and others 2000, Kirchner and Lydersen 1995, Likens and others 1996, Schulze 1989, Tao and Feng 2000). Growing experimental evidence and examples from the field indicate that the threat posed to forest ecosystems from anthropogenic Ca depletion is real and potentially widespread. Knowledge of the influence of pollution loading on the cation pools that sustain forest health and productivity provides further scientific grounding and impetus for policymakers to modify existing pollution control measures. In addition, an increased recognition of the potential consequences of Ca depletion has functional relevance to managers in the field. Especially in regions with low inherent soil fertility or high precipitation leaching, or both, management options that either add Ca to systems or decrease its removal are increasingly being examined and employed. Indeed, in some tropical forests where native precipitation-based leaching has historically been high, and pollution-induced acidity is on the increase, sustainable forestry is not currently possible without the

addition of Ca after logging (Nykqvist 2000). The output of tested models that simulate the complexities of Ca cycling could greatly enhance the capabilities of policymakers and managers to integrate the influences of factors adding to or removing Ca from forest ecosystems. As such, these models could play a critical role in guiding adaptive policy and management decisions that prevent or mitigate pollution-induced damage to forest ecosystems.

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