

## Status of soil acidification in North America

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**ABSTRACT:** Forest soil acidification and depletion of nutrient cations have been reported for several forested regions in North America, predominantly in the eastern United States, including the northeast and in the central Appalachians, but also in parts of southeastern Canada and the southern U.S. Continuing regional inputs of nitrogen and sulfur are of concern because of leaching of base cations, increased availability of soil Al, and the accumulation and ultimate transmission of acidity from forest soils to streams. Losses of calcium from forest soils and forested watersheds have now been documented as a sensitive early indicator and a functionally significant response to acid deposition for a wide range of forest soils in North America. For red spruce, a clear link has been established between acidic deposition, alterations in calcium and aluminum supplies and increased sensitivity to winter injury. Cation depletion appears to contribute to sugar maple decline on some soils, specifically the high mortality rates observed in northern Pennsylvania over the last decade. While responses to liming have not been systematically examined in North America, in a study in Pennsylvania, restoring basic cations through liming increased basal area growth of sugar maple and levels of calcium and magnesium in soil and foliage. In the San Bernardino Mountains in southern California near the west coast, the pH of the A horizon has declined by at least 2 pH units (to pH 4.0–4.3) over the past 30 years, with no detrimental effects on bole growth; presumably, because of the Mediterranean climate, base cation pools are still high and not limiting for plant growth.

**Keywords:** calcium depletion; acidic deposition; base cations; red spruce; sugar maple; liming; winter injury; forest health

Studies on the effects of acidic deposition in North America increasingly point towards base cation depletion from forest soils as one of the principal mechanisms by which air pollutants can affect forest sustainability and productivity, particularly in areas where soils are inherently low in base cations and where cation reserves have been further depleted by harvesting or other past land use activities. Base cation depletion is a cause for concern because of the role these ions play in acid neutralization, and in the

case of calcium (Ca), magnesium (Mg) and potassium (K), their importance as essential nutrients for tree growth and health. In addition, depletion of base cations from the soil is the process that leads to aluminum (Al) mobilization (LAWRENCE et al. 1997). Low Ca/Al ratios in soil allows the Al to interfere with root uptake of Ca in forest soils (SHORTLE, SMITH 1988). The accumulation and ultimate transmission of acidity from forest soils to streams is of concern as is the increase in Al concentrations in surface waters.

Losses of Ca from forest soils and forested watersheds have now been documented as a sensitive early indicator of the soil response to acid deposition for a wide range of forest soils in the U.S. (LAWRENCE et al. 1999; HUNTINGTON et al. 2000). The high mobility of Ca in soils, which makes it susceptible to leaching, is a primary reason for these effects, leading to concerns for longer-term decreases in forest ecosystem productivity and function (Table 1). In addition, the relatively high fraction of total Ca supply that is exchangeable increases its susceptibility to depletion in some forest systems (ADAMS et al. 2000). For acid sensitive systems, perhaps the best indication of the chemical imbalance created by continued inputs of acid deposition is evidenced when strong acids derived from S and N ( $\text{NO}_3$  and  $\text{SO}_4$ ) cause measurable alterations in the amount of chemical elements in plant tissues (foliage, roots, and wood), such as decreasing levels of base cations (e.g. Ca), increasing levels of acidic cations (e.g. Al, Mn, and Fe), or both (SHORTLE, SMITH 1988; McLAUGHLIN, KOHUT 1992; HORSLEY et al. 2000).

Acid deposition has contributed to a regional decline in the availability of soil Ca and other base cations in many different types of forest ecosystems. Studies in New Hampshire (LIKENS et al. 1996; BAILEY et al. 1996), the Catskill Mountains in New York (LAWRENCE et al. 1999), West Virginia (ADAMS 1999), North Carolina (KNOEPP, SWANK 1994), South Carolina (MARKEWITZ et al. 1998), Ontario, Canada (WATMOUGH 2002; WATMOUGH, DILLON 2003), and Quebec, Canada (DUCHESNE et al. 2002) have documented nutrient base cation (e.g. Ca, Mg, K and others) depletion in soils due to acid deposition and forest regrowth. Resampling of forest soils in northwestern Pennsylvania shows an increase in soil acidity of 0.78 and 0.23 pH units in the O and A horizons after 36 years (DROHAN, SHARPE 1997). The high mortality rates and reduced vigor reported for sugar maples experienced in

northern Pennsylvania and Quebec, Canada over the last decade has been linked to cation depletion from those soils (DUCHESNE et al. 2002; LONG et al. 1997; HORSLEY et al. 2000; MOORE et al. 2000; DROHAN et al. 2002).

Acid deposition is also contributing to the depletion of base cations in many poorly buffered soils supporting southern pines. Soil acidification and reductions in base saturation have also been observed in highly-polluted southern California forests and chaparral ecosystems, but cation reserves are still large in these Mediterranean climate ecosystems (POTH, WOHLGEMUTH 1999). In contrast to these studies, at one site in New Hampshire researchers inferred (not direct re-measurement) no decline in Ca in the forest floor in a chronosequence study in New Hampshire (YANAI et al. 1999; HAMBURG et al. 2003). Recently it was reported that in forests growing on granitoid parent materials in New Hampshire, upstate New York, and Maine, apatite provides a source of readily weathered and plant-available Ca for forest growth (YANAI et al. 2005). Forests growing on these soil types may not be as susceptible to Ca depletion as previously predicted. At sites where there may be appreciable amounts of dolomitic parent material (JOHNSON, TODD 1998) that are accessible to trees, soil Ca may not be depleted to the extent it can be in nearby soils that lack a dolomitic source (TRETTIN et al. 1999). In the case studies cited above, and in other examples of Ca depletion in forest soils in Europe (HUNTINGTON 2000; JÖNSSON et al. 2003), it has not been possible to quantify the component of depletion attributable to anthropogenic acidic deposition versus tree uptake.

#### Base cation depletion in North American forests

A number of lines of evidence are consistent with decreasing soil Ca in recent decades. The failure of stream water quality to recover in many parts of

Table 1. Summary of linkages between acid deposition, biogeochemical processes that affect Ca, physiological processes that are influenced by Ca, and effect on forest function

Biogeochemical response to acid deposition	Physiological response	Effect on forest function
Leach Ca from leaf membrane	Reduce the cold tolerance of needles in red spruce	Loss of current-year needles in red spruce
Reduce the ratio of Ca to Al in soil and in soil solutions	Dysfunction in fine roots of red spruce blocks uptake of Ca	Decreased growth and increased susceptibility to stress in red spruce
Reduce the ratio of Ca to Al in soil and in soil solutions	More energy is used to acquire Ca in soils with low Ca: Al ratios	Decreased growth and increased photosynthate allocation to roots
Reduce the availability of nutrient cations in marginal soils	Sugar maples on drought-prone or nutrient-poor soils are less able to withstand stresses	Episodic dieback and growth impairment in sugar maple

northeastern North America in spite of major decreases in both sulfate emissions and deposition is not fully understood but has been at least partially attributed to depletion of exchangeable base cations including Ca (STODDARD et al. 1999; LIKENS et al. 1996; LAWRENCE et al. 1999). Many streams in the northeastern U.S. exhibit long-term trends of declining Ca concentrations (HUNTINGTON 2000). Streamwater Ca concentrations may be declining due to decreases in deposition of both sulfate and Ca (LYNCH et al. 2000) as well as decreases in exchangeable soil Ca (LAWRENCE et al. 1999; LIKENS et al. 1996; FERNANDEZ et al. 2003). These findings indicated that both base cation depletion and stream water chemistry were related to acid deposition in this area. The accumulation of S and N in forest soils from decades of elevated atmospheric acidic deposition will delay recovery as the gradual release of these elements continues to be a drain on the exchangeable Ca pool (DRISCOLL et al. 2001; KNOEPP, SWANK 1994). Long-term trends in stream water chemistry and sulfate deposition at several forested watersheds in North Carolina and Virginia support the hypothesis that soil retention of atmospherically-derived sulfate has decreased in recent years (RYAN et al. 1989; JOHNSON et al. 1993) supporting this mechanism for ongoing Ca depletion.

Depletion of base cations has been greater in the B horizon than in the forest floor. High Al/Ca ratios in the B horizon suppress uptake of Ca by roots in this horizon, which reduces the Ca input to the forest floor by vegetative recycling. Thus trees become more dependent on Ca uptake from the forest floor (BAILEY et al. 1996). High Al to Ca ratios in the B horizon have also contributed to Ca loss from the forest floor. As Al is transported into the forest floor through water movement (upward water table and capillary action) and biocycling, exchangeable Ca is displaced and the Al to Ca ratio is raised in the O horizon (LAWRENCE et al. 1995).

The potential for weathering re-supply of exchangeable soil Ca remains an important uncertainty because our estimates of weathering are based on indirect estimates and are usually poorly quantified (28). Some studies have concluded that it is unlikely that weathering could re-supply Ca at the rate at which outputs exceed inputs in many forests (BAILEY et al. 1996; HUNTINGTON 2000; APRIL, NEWTON 1992; JOHNSON, LINDBERG 1992; BINKLEY et al. 1989). The fact that numerous sites are exhibiting measurable decreases in exchangeable soil Ca suggests that weathering re-supply rates are insufficient to match rates of loss.

Soil acidification may increase the rate of weathering, but the incremental increase in Ca release is likely to be small in soils that are already acidic. Studies that have attempted to quantify Ca weathering rates in acidic forest soils in the eastern US generally have found that rates are low (TURNER et al. 1990; JOHNSON, LINDBERG 1992; KENNEDY et al. 2002; DIJKSTRA et al. 2003) in comparison with typical combined rates of tree uptake and soil leaching (HUNTINGTON et al. 2000). A recent study using strontium isotopes to investigate base cation nutrition in acid deposition impacted forests raises new concerns about the capacity of mineral weathering to replenish exchangeable base cations. Unpolluted temperate forests can become nutritionally decoupled from deeper weathering processes, virtually functioning as atmospherically fed ecosystems (KENNEDY et al. 2002). KENNEDY et al. (2002) showed that base cation turnover times are considerably more rapid than previously recognized in the plant available pool of soil. These results challenge the prevalent paradigm that plants largely feed on rock-derived base cations and further strengthen the hypothesis that mineral weathering will not be able to replenish cation pools depleted by atmospheric deposition and vegetative uptake.

#### **Ecosystem processes affected by calcium levels**

Plant physiological processes affected by reduced Ca availability include development of cell wall structure and growth, carbohydrate metabolism, stomatal regulation, resistance to plant pathogens, and tolerance of low temperatures (Fig. 1) (DEHAYES et al. 1999). Soil structure, macro and micro fauna, decomposition rates, and N metabolism are also important processes that are significantly influenced by Ca levels in soils. The importance of Ca as an indicator of forest ecosystem function is evidenced by its diverse physiological roles, coupled with the fact that Ca mobility in plants is very limited and can be further reduced by tree age, competition, and reduced soil water supply (MC LAUGHLIN, WIMMER 1999). The relatively rapid responses observed when restoring base cations through liming, the manual addition of basic substances such as Ca and Mg (LONG et al. 1997; MOORE et al. 2000), provides compelling evidence of the limitations imposed on forest function by excessive base cation removal (Table 1). While responses to liming have not been systematically examined in the U.S., liming has been used extensively to remediate the adverse effects of soil acidification in European forests (HUETTL, ZOETTL 1993).

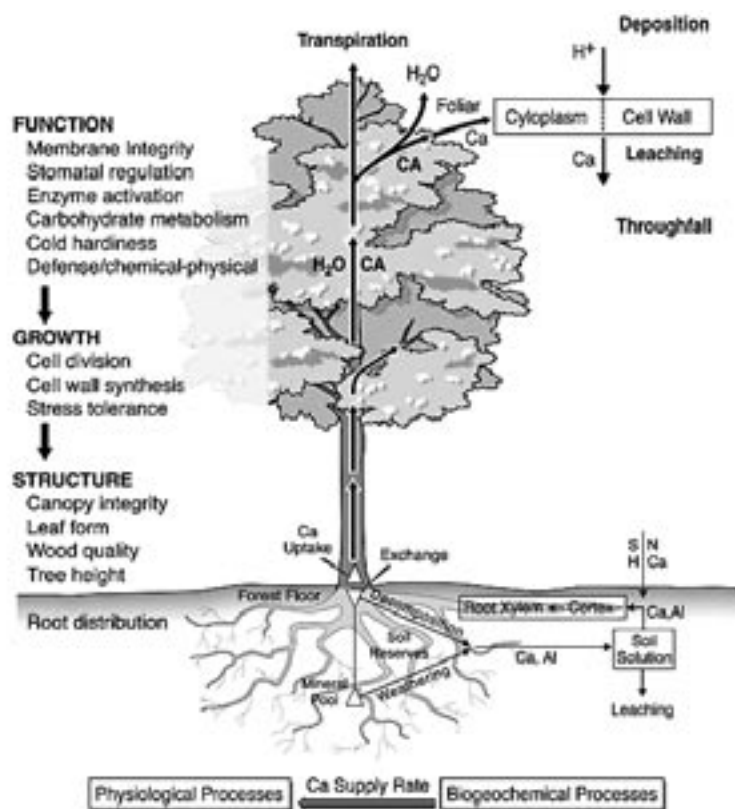


Fig. 1. Diagram showing indicators of forest physiological function, growth, and structure that are linked to biogeochemical cycles through processes that control rates of Ca supply (after McLAUGHLIN et al. 1987). Calcium plays a vital role in many different plant physiological processes that influence growth rates and the capacity of plants to resist environmental stresses such as extremes of temperature, drought, insects, and diseases. Because maintaining an uninterrupted flow of Ca from the soil to growing centers within trees is important to maintaining these functions, factors such as acidic deposition which can deplete soil Ca or interfere with Ca uptake through mobilization of soil Al are a concern for maintenance of forest health

## CASE STUDIES

### High elevation spruce fir

High elevation spruce-fir ecosystems in the eastern U.S. epitomize sensitive soil systems. Base cation stores are generally very low, and soils are near or past their capacity to retain more S or N. Deposited S and N, therefore goes straight into soil water, which leaches soil Al and Ca, Mg and other base cations out of the rooting zone. The low availability of these base cation nutrients, coupled with the high levels of Al that interfere with roots taking up these nutrients, can result in plants not having sufficient nutrients to maintain good growth and health. Acid deposition has contributed to a regional decline in the availability of soil Ca and other base cations in high elevation and mid-elevation spruce-fir forests of New York, New England and the Southern Appalachians (Fig. 2). It is estimated that tree uptake and storage of Ca and acid leaching losses are equally responsible for losses of Ca from the soil (JOSLIN et al. 1992). Red spruce growth rate declines have been observed in New York and New England at the higher elevations, as well as in portions of the southern Appalachians (McLAUGHLIN et al. 1987; EAGAR, ADAMS 1992). Red spruce forests in the highest elevations of the southern Appalachians have shown an increase in mortality in recent decades and a significant decline

in crown condition (PEART et al. 1992). Foliar Ca levels, and soil and root Ca/Al ratios are considered low to deficient over most of the southern spruce-fir region and portions of the northern region (JOSLIN et al. 1992; CRONAN, GRIGAL 1995). Reduced ratios of photosynthesis to dark respiration were found in red spruce in the southern Appalachians at high elevation sites where Ca/Al ratios in needles were low (McLAUGHLIN, KOHUT 1992). Similar physiological responses were observed in controlled studies using native soils.

A clear link has now been established in red spruce stands between acid deposition, Ca supply, and sensitivity to abiotic stress. Red spruce uptake and retention of Ca is impacted by acid deposition in two main ways: leaching of important stores of Ca from needles (DEHAYES et al. 1999); and decreased root uptake of Ca due to Ca depletion from the soil and Al mobilization (SMITH, SHORTLE 2001; SHORTLE et al. 1997; LAWRENCE et al. 1997). Mobilized Al displaces Ca from exchange sites (39). Lower Ca/Al ratios in soil can disrupt physiological processes that are important to maintaining resistance to natural stresses, such as insects, disease and climatic extremes (46,60). Red spruce must also expend more metabolic energy to acquire Ca from soils in areas with low Ca/Al ratios, resulting in slower tree growth (SMITH, SHORTLE 2001). Acid deposition leaches membrane-associated Ca from mesophyll

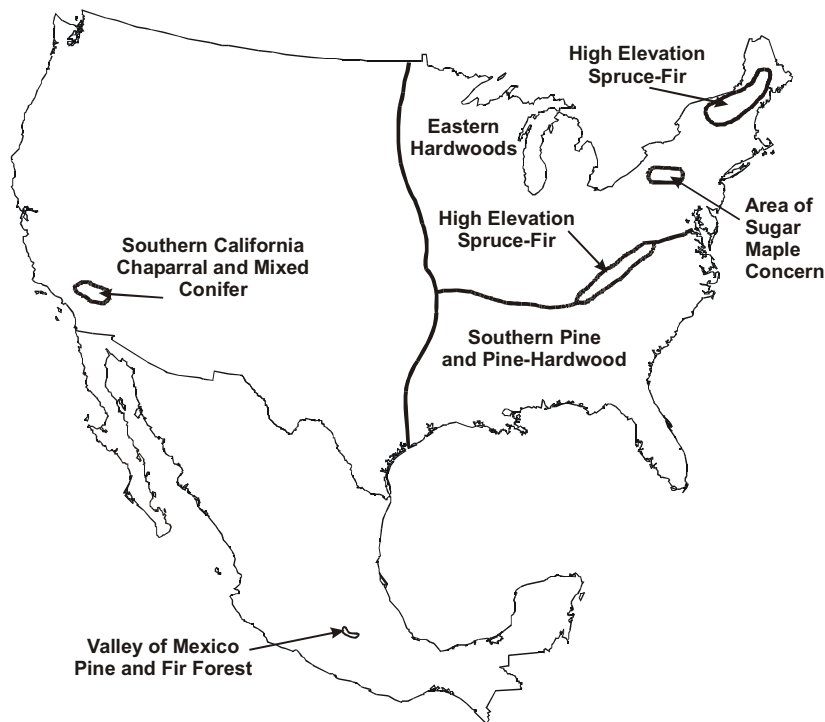


Fig. 2. Broad forest regions and study sites of North America where instances of acidic deposition effects have been reported. The area of concern for sugar maples is based on study sites in north central Pennsylvania (LYNCH et al. 2000) and regional studies (MITCHELL et al. 1994). Forest soil acidification effects have also been reported in Ontario (WATMOUGH 2002; WATMOUGH, DILLON 2003) and Quebec (DUCHESNE et al. 2002; PEART et al. 1992), Canada. The Valley of Mexico area shown is located within the Mexico City Air Basin (FENN et al. 2002)

cells of one-year old red spruce needles (SCHABERG et al. 2000), which in turn reduces freezing tolerance (DEHAYES et al. 1999). These changes increase the sensitivity of red spruce to winter injuries under normal winter conditions in the Northeast, result in the loss of needles, and impair the overall health of forest ecosystems (DEHAYES et al. 1999). Exposure to acidic clouds and acid deposition has reduced the cold tolerance of red spruce in the Northeast by 3–10°C (VANN et al. 1992; THORNTON et al. 1994).

#### Hardwood forests of the midwest and the northeast

There is a strong relationship between acid deposition and leaching of base cations from soils in hardwood forests (e.g. maple, oak), as indicated by long-term data on watershed mass balances (LIKENS et al. 1996; MITCHELL et al. 1996), plot- and watershed-scale acidification experiments in the Adirondacks (MITCHELL et al. 1994) and in Maine (NORTON et al. 1999; RUSTAD et al. 1996) and studies of soil solution chemistry along an acid deposition gradient from Minnesota to Ohio (MACDONALD et al. 1992). Although sulfate is the primary anion causing base cation leaching in eastern North America, nitrate is a significant contributor in watersheds that are N saturated as a result of N deposition (ADAMS et al. 1997). Sensitivity of hardwood soils to acid deposition is largely controlled by inherent properties and land use; unfortunately,

tools to assess present conditions or susceptibility to nutrient depletion are not readily available or widely applicable.

Although there is no conclusive evidence that forest growth over the majority of this forest type has to date been adversely affected by acid deposition, some forested areas within this region may be impacted by current rates of cation leaching. Depletion of base cations, as a result of leaching, combined with low rates or replacement by weathering and reduced levels of atmospheric deposition of base cations will delay or preclude recovery of some hardwood forest soils following reductions in acid deposition. A comparison of rates of removal of Ca by various harvesting techniques with exchangeable Ca pools in forest soils in West Virginia has revealed that removal rates equal or exceed soil exchangeable pools for approximately half of these soils, even under the least intensive removal strategies (ADAMS et al. 2000). Thus harvesting has the potential to greatly accelerate losses currently experienced by leaching on low cation soils.

Unusually high sugar maple crown dieback and mortality have been observed across the Allegheny Plateau in northern Pennsylvania since the 1980's (Fig. 2) (KLOB, MCCORMICK 1993). The decline is attributed to multiple stress, with poor soil nutrient base cation status a predisposing factor, and stress due to multiple defoliation by native insects the agent leading to the decline. Additions of Ca and Mg by lime application to plots located on nutrient poor

sites significantly improved sugar maple survival, crown vigor, tree growth, and seed production, whereas, black cherry and American beech were unaffected by the treatment (LONG et al. 1997). On both limed and unlimed plots, sugar maple growth was positively correlated with the concentration of Ca and Mg in leaves and negatively correlated with the concentration of Al and Mn (LONG et al. 1997). Declining stands are associated with low levels of nutrient base cations in soil, low foliar concentrations of Mg and Ca, high levels of Al and Mn in the soil, and two or more incidents of defoliation by native insects over a ten year period (HORSLEY et al. 2000). Presently there is no supporting evidence that cation depletion has adversely affected other hardwood species.

The same intensity of defoliation did not cause mortality in stands with adequate nutrient base cations in the soil (HORSLEY et al. 2000). Soil nutrient base cation status is related to amount of weatherable minerals in the soil, with low amounts found in unglaciated areas with highly weathered soils and higher amounts found in glaciated areas with geologically more recent soil parent material (HORSLEY et al. 2000). The role of acidic deposition in base cation depletion has not been quantified in this region, but is likely a contributing factor since northern Pennsylvania has received some of the highest levels of acidic deposition in the country over the past 40 years (LYNCH et al. 2000). However, site-specific data on changes in soil nutrient base cation pools is limited. Resampling of forest soils in northwestern Pennsylvania originally sampled in the 1960's showed an increase in soil acidity (DROHAN, SHARPE 1997).

#### **Southern pine and pine-hardwood forests**

Significant impacts of acid deposition have not been detected over extensive forested areas in the southern pine and pine-hardwood region. Acid deposition is contributing to the depletion of base cations in many poorly buffered soils supporting southern pines and may over the long term (decades), have adverse effects on productivity (RICHTER et al. 1994). It appears that reduced emissions have resulted in less soil-adsorbed sulfate (MARKEWITZ et al. 1998). However, N deposition is expected to increase tree growth, at least in the short term, in some N deficient soils.

Currently it is estimated that about 59% of the pine forest of the southeast have soils that are low enough in base cations to be susceptible to acidification by cation leaching due to acid deposition and 10% of

the soils are considered extremely acidic (RICHTER et al. 1995). While these impacts will likely have negative long term consequences, the inputs of atmospheric sources of N to many of the former agricultural soils with depleted N reserves, which currently support southern pine forests, should be expected to have small cumulative effects that are positive.

#### **Mixed conifer and chaparral in southern California**

While soil acidification has not been a major ecological concern in the highly-polluted forests and chaparral watersheds in the Los Angeles, California Air Basin (Fig. 2), the limited available data strongly suggest that some soils have acidified by as much as two pH units in the past 30 years (FENN, POTH 1996; WOOD et al. 1992). Mineral soil pH values at a mixed conifer forest site in the highly polluted western San Bernardino Mountains are on average approximately 4.0, compared to historical pH values greater than 6.0 in this same area (ARKLEY et al. 1977). Similar increases in acidification were not detected in the forest sites with relatively low air pollution exposure (FENN, POTH 1996). Similarly, pH values generally ranged from 6.3 to 7.3 in a survey of chaparral soils completed in 1973 in the Angeles National Forest. In 1990 pH values in a survey of the same region were generally within the range of pH 4.6 to 5.7 (WOOD et al. 1992; WOOD 1994). Soil acidification due to atmospheric deposition in southern California is presumably from N deposition, because S deposition is low in this region (FENN et al. 2000).

#### **Pine/fir forests in the Valley of Mexico**

High levels of N and S deposition occur in pine/fir forests south and southwest of the Mexico City metropolitan area (FENN et al. 1999). However, because of the moderately high base saturation of these soils, soil pH changes due to atmospheric deposition have been relatively mild, especially in *Pinus hartwegii* stands that are characterized by highly open canopy cover. Under *Abies religiosa* stands, which have a dense canopy cover and high leaf area, atmospheric deposition is much higher and corresponding decreases in base cation pools in soil, base saturation and pH (WATMOUGH, HUTCHINSON 1999) are also greater than under pine. K and Mn levels in foliage of a fir plantation were at deficiency levels at a high pollution site (LÓPEZ-LÓPEZ et al. 1998). Likewise, Ca and K concentrations in pine and fir foliage were lower at a high pollution site than a site upwind of

Mexico City (GOMEZ-GUERRERO, HORWATH 2004). Concentrations of base cations (Ca, K, Mg) in soil were lower and Al concentrations were higher at a high pollution site, particularly under fir canopies. Although atmospheric deposition in parts of southern California and near Mexico City are as much as several-fold higher than in eastern North America (FENN et al. 1999, 2003), soil properties in the two latter regions have buffered soil acidification responses to a much greater degree than observed in forests with more cation depleted and highly weathered soils. For example, base saturation of the upper mineral horizons in the most polluted sites in southern California and the Valley of Mexico are yet relatively high, 35–80% and 22–43%, respectively (FENN et al. 1996; GOMEZ-GUERRERO, HORWATH 2004).

### CONCLUSIONS

Increasing evidence indicates that Ca depletion is a primary mechanism of acidic deposition effects on forests in eastern North America. Forests growing on highly weathered base-poor soils are most at risk. Sugar maple and red spruce declines in eastern North America are associated with low base cation pools, particularly low levels of soil Ca. Although few remediation studies have been done in North America, liming improved soil base cation status and tree health and vigor of sugar maple in sensitive areas. Red spruce is impacted by low root uptake of Ca (due to soil Ca depletion and Al mobilization) and leaching of Ca from needles. Acid deposition induced leaching of membrane-associated Ca from mesophyll cells of one-year old red spruce needles reduces freezing tolerance, leading to increased winter injury in the northeast. Low foliar Ca in high elevation spruce in the southeast has been associated with reduced efficiency of carbohydrate production in response to high levels of acid deposition. Trends of declining exchangeable Ca pools in forest soils of the northeast and southeast raise concerns about long term sustainability of these forests in the face of continuing acidic deposition, particularly in areas of repeated timber harvesting. The highest acidic deposition inputs in North America are in forests downwind of Los Angeles and Mexico City. Air pollution gradient studies and temporal trends in forests near these two urban areas indicate that soil pH and base cation concentrations have decreased in these forests, but base cation pools are still abundant. Nitrogen saturation responses such as elevated nitrate export in runoff and plant physiological effects of ozone and excess N are the

major concern in these forests growing on highly buffered soils.

### References

- ADAMS M.B., 1999. Acidic deposition and sustainable forest management in the central Appalachians, USA. *Forest Ecology and Management*, 12: 17–28.
- ADAMS M.B., ANGRADI T.R., KOCHENDERFER J.N., 1997. Stream water and soil solution responses to 5 years of nitrogen and sulfur additions at the Fernow Experimental Forest, West Virginia. *Forest Ecology and Management*, 95: 79–91.
- ADAMS M.B., BURGER J.A., JENKINS A.B., ZELAZNY L., 2000. Impact of harvesting and atmospheric pollution on nutrient depletion of eastern US hardwood forests. *Forest Ecology and Management*, 138: 301–319.
- APRIL R., NEWTON R., 1992. Mineralogy and mineral weathering. In: JOHNSON D.W., LINDBERG S.E. (eds.), *Atmospheric Deposition and Forest Nutrient Cycling*, Ecological Studies 91. New York, Springer-Verlag: 378–425.
- ARKLEY R.J., GERSPER P.J., GLAUSER R., 1977. General description of ecosystem properties: Soils. In: MILLER P.R., ELDERMAN M.J. (eds.), *Photochemical Oxidant Air Pollution Effects on a Mixed Conifer Forest Ecosystem: A Progress Report*. Ecological Research Series, EPA-600/3-77-104. Corvallis, Oregon, U.S. Environmental Protection Agency: 19–28, 264–299.
- BAILEY S.W., HORNBECK J.W., DRISCOLL C.T., GAUDETTE H.E., 1996. Calcium inputs and transport in a base-poor forest ecosystem as interpreted by Sr isotopes. *Water Resources Research*, 32: 707–719.
- BINKLEY D., VALENTINE D., WELLS C., VALENTINE U., 1989. An empirical model of the factors contributing to 20-yr decrease in soil pH in an old-field plantation of loblolly pine. *Biogeochemistry*, 8: 39–54.
- CRONAN C.S., GRIGAL D.F., 1995. Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. *Journal of Environmental Quality*, 24: 209–226.
- DEHAYES D.H., SCHABERG P.G., HAWLEY G.J., STRIMBECK G.R., 1999. Acid rain impacts calcium nutrition and forest health: alteration of membrane-associated calcium leads to membrane destabilization and foliar injury in red spruce. *BioScience*, 49: 789–800.
- DIJKSTRA F.A., VANBREEMEN N., JONGMAN A.G., DAVIES G.R., LIKENS G.E., 2003. Calcium weathering in forested soils and the effect of different tree species. *Biogeochemistry*, 62: 253–275.
- DRISCOLL C.T., LAWRENCE G.B., BULGER A.J., BUTLER Y.J., EAGAR C., LAMBERT K.F., LIKENS G.E., STODDARD J.L., WEATHERS K.C., 2001. Acidic deposition in the Northeastern United States: sources and inputs, ecosystem effects, and management strategies. *BioScience*, 51: 180–198.

- DROHAN J.R., SHARPE W.E., 1997. Long-term changes in forest soil acidity in Pennsylvania, USA. *Water, Air, and Soil Pollution*, 95: 299–311.
- DROHAN P., STOUT S.L., PETERSEN G., 2002. Sugar maple (*Acer saccharum* Marsh.) decline during 1979–1989 in northern Pennsylvania. *Forest Ecology and Management*, 170: 1–17.
- DUCHESNE L., OUIMET R., HOULE D., 2002. Basal area growth of sugar maple in relation to acid deposition, stand health, and soil nutrients. *Journal of Environmental Quality*, 31: 1676–1683.
- EAGAR C., ADAMS M.B., 1992. *The Ecology and Decline of Red Spruce in the Eastern United States*, Ecological Studies 96. New York, Springer-Verlag: 417.
- FENN M.E., POTH M.A., 1996. Preliminary evidence of nitrogen saturation in the San Bernardino Mountains in Southern California. In: COX R., PERCY K., JENSEN K., SIMPSON C. (compilers), *Proceedings of the IUFRO Air Pollution and Multiple Stresses 16<sup>th</sup> International Meeting for Specialists in Air Pollution Effects on Forest Ecosystems*. Sept. 7–9, 1994, Fredericton, New Brunswick, Canada: 97–102.
- FENN M.E., POTH M.A., JOHNSON D.W., 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. *Forest Ecology and Management*, 82: 211–230.
- FENN M.E., DE BAUER L.I., QUEVEDO-NOLASCO A., RODRIGUEZ-FRAUSTO C., 1999. Nitrogen and sulfur deposition and forest nutrient status in the Valley of Mexico. *Water, Air, and Soil Pollution*, 113: 155–174.
- FENN M.E., POTH M.A., SCHILLING S.L., GRAINGER D.B., 2000. Throughfall and fog deposition of nitrogen and sulfur at an N-limited and N-saturated site in the San Bernardino Mountains, southern California. *Canadian Journal of Forest Research*, 30: 1476–1488.
- FENN M.E., DE BAUER L.I., HERNÁNDEZ-TEJEDA T., 2002. *Urban Air Pollution and Forests: Resources at Risk in the Mexico City Air Basin*. Ecological Studies 156. New York, Springer-Verlag: 387.
- FENN M.E., HAEUBER R., TONNESEN G.S., BARON J.S., GROSSMAN-CLARKE S., HOPE D., JAFFE D.A., COPELAND S., GEISER L., RUETH H.M., SICKMAN J.O., 2003. Nitrogen emissions, deposition, and monitoring in the western United States. *BioScience*, 53: 391–403.
- FERNANDEZ I.J., RUSTAD L.E., NORTON S.A., KAHL J.S., COSBY B.J., 2003. Experimental acidification causes soil base-cation depletion at the Bear Brook Watershed in Maine. *Soil Science Society of America Journal*, 67: 1909–1919.
- GOMEZ-GUERRERO A., HORWATH W.R., 2004. Unpublished data on soil properties at Desierto de los Leones (high pollution) and Zoquiapan (low pollution), two forest sites in the Valley of Mexico.
- HAMBURG S.P., YANAI R.D., ARTHUR M.A., BLUM J.D., SICCAMA T.G., 2003. Biotic control of calcium cycling in northern hardwood forests: Acid rain and aging forests. *Ecosystems*, 6: 399–406.
- HORSLEY S.B., LONG R.P., BAILEY S.W., HALLETT R.A., HALL T.J., 2000. Factors associated with the decline disease of sugar maple on the Allegheny Plateau. *Canadian Journal of Forest Research*, 30: 1365–1378.
- HUETTL R.F., ZOETTL H.W., 1993. Liming as a mitigation tool in Germany's declining forests – reviewing results from former and recent trials. *Forest Ecology and Management*, 61: 325–338.
- HUNTINGTON T.G., 2000. The potential for calcium depletion in forest ecosystems of southeastern United States: review and analysis. *Global Biogeochemical Cycles*, 14: 623–638.
- HUNTINGTON T.G., HOOPER R.P., JOHNSON C.E., AULENBACH B.T., CAPPELLATO R., BLUM A.E., 2000. Calcium depletion in a southeastern United States forest ecosystem. *Soil Science Society of America Journal*, 64: 1845–1858.
- JOHNSON D.W., LINDBERG S.E., 1992. *Atmospheric Deposition and Forest Nutrient Cycling*. Ecological Studies 91. New York, Springer-Verlag: 707.
- JOHNSON D.W., SWANK W.T., VOSE J.M., 1993. Simulated effects of atmospheric sulfur deposition on nutrient cycling in a mixed deciduous forest. *Biogeochemistry*, 23: 169–196.
- JOHNSON D.W., TODD D.E., 1998. The effects of harvesting on long-term changes in nutrient pools in a mixed oak forest. *Soil Science Society of America Journal*, 62: 1725–1735.
- JOSLIN J.D., KELLY J.M., VAN MIEGROET H., 1992. Soil chemistry and nutrition of North American spruce-fir stands: evidence for recent change. *Journal of Environmental Quality*, 21: 12–30.
- JÖNSSON U., ROSENGREN U., THELIN G., NIHLGÅRD B., 2003. Acidification-induced chemical changes in coniferous forest soils in southern Sweden 1988–1999. *Environmental Pollution*, 123: 75–83.
- KENNEDY M.J., HEDIN L.O., DERRY L.A., 2002. Decoupling of unpolluted temperate forests from rock nutrient sources revealed by natural <sup>87</sup>Sr/<sup>86</sup>Sr and <sup>84</sup>Sr tracer addition. *Proceedings of the National Academy of Sciences*, 99: 9639–9644.
- KLOB T.E., McCORMICK L.H., 1993. Etiology of sugar maple decline in four Pennsylvania stands. *Canadian Journal of Forest Research*, 23: 2395–2402.
- KNOEPP J.D., SWANK W.T., 1994. Long-term soil chemistry changes in aggrading forest ecosystems. *Soil Science Society of America Journal*, 58: 325–331.
- LAWRENCE G.B., DAVID M.B., SHORTLE W.S., 1995. A new mechanism for calcium loss in forest floor soils. *Nature*, 378: 162–165.
- LAWRENCE G.W., DAVID M.B., BAILEY S.W., SHORTLE W.C., 1997. Assessment of calcium status in soils of red



- spruce forests in the northeastern United States. *Biogeochemistry*, 38: 19–39.
- LAWRENCE G.B., DAVID M.B., LOVETT G.M., MURDOCH P.S., BURNS D.A., STODDARD J.L., BALDIGO B.P., PORTER J.H., THOMPSON A.W., 1999. Soil calcium status and the response of stream chemistry to changing acidic deposition rates in the Catskill Mountains of New York. *Ecological Applications*, 9: 1059–1072.
- LIKENS G.E., DRISCOLL C.T., BUSO D.C., 1996. Long-term effects of acid rain: Responses and recovery of a forest ecosystem. *Science*, 272: 244–246.
- LONG R.P., HORSLEY S.B., LILJA P.R., 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. *Canadian Journal of Forest Research*, 27: 1560–1573.
- LÓPEZ-LÓPEZ M.A., VELÁZQUEZ-MENDOZA J., VELÁZQUEZ-MARTINEZ A., GONZÁLEZ-ROMERO V., CETINA-ALCALÁ V.M., 1998. Estado nutrimental de *Abies religiosa* en una área con problemas de contaminación ambiental. *Agrociencia*, 32: 53–59.
- LYNCH J.A., BOWERSOX V.C., GRIMM J.W., 2000. Acid rain reduced in Eastern United States. *Environmental Science and Technology*, 34: 940–949.
- MacDONALD N.W., BURTON A.J., LIECHTY H.O., WHITER J.A., PREGITZER K.S., MROZ G.D., RICHTER D.D., 1992. Ion leaching in forest ecosystems along a Great Lakes air pollution gradient. *Journal of Environmental Quality*, 21: 614–623.
- MARKEWITZ D., RICHTER D.D., ALLEN H.L., URREGO J.B., 1998. Three decades of observed soil acidification in the Calhoun Experimental Forest: Has acid rain made a difference? *Soil Science Society of America Journal*, 62: 1428–1439.
- McLAUGHLIN S.B., DOWNING D.J., BLASING T.J., COOK E.R., ADAMS H.S., 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the eastern United States. *Oecologia*, 72: 487–501.
- McLAUGHLIN S.B., KOHUT R., 1992. The effects of atmospheric deposition on carbon allocation and associated physiological processes in red spruce. In: EAGAR C., ADAMS M.B. (eds.), *Ecology and Decline of Red Spruce in the Eastern United States*. Ecological Studies 96. New York, Springer-Verlag: 338–384.
- McLAUGHLIN S.B., WIMMER R., 1999. Tansley Review No. 104: Calcium physiology and its role in terrestrial ecosystem processes. *New Phytologist*, 142: 373–417.
- MITCHELL M.J., DAVID M.B., FERNANDEZ I.J., FULLER R.D., NADELHOFFER K., RUSTAD L.E., STAM A.C., 1994. Response of buried mineral soil bags to experimental acidification of forest ecosystem. *Soil Science Society of America Journal*, 58: 556–563.
- MITCHELL M.J., RAYNAL D.J., DRISCOLL C.T., 1996. Biogeochemistry of a forested watershed in the central Adirondack Mountains: Temporal changes and mass balances. *Water, Air, and Soil Pollution*, 88: 355–369.
- MOORE J.-D., CAMIRE C., OUMET R., 2000. Effects of liming on the nutrition, vigour, and growth of sugar maple at the Lake Clair Watershed, Quebec, Canada. *Canadian Journal of Forest Research*, 30: 725–732.
- NORTON S.A., KAHL J.S., FERNANDEZ I.J., HAINES T.A., RUSTAD L.E., NODVIN S., SCOFIELD J.P., STRICKLAND T., ERICKSON H., WIGGINGTON P., LEE J., 1999. The Bear Brook Watershed, Maine, (BBWP) USA. *Environmental Monitoring and Assessment*, 55: 7–51.
- PEART D.R., NICHOLAS N.S., ZEDAKER S.M., MILLER-WEEKS M.M., SICCAMA T.G., 1992. Condition and recent trends in high-elevation red spruce populations. In: EAGAR C., ADAMS M.G. (eds.), *Ecology and Decline of Red Spruce in the Eastern United States*, Ecological Studies 96. New York, Springer-Verlag: 125–191.
- POTH M.A., WOHLGEMUTH P., 1999. Geography, geology, geomorphology and forest soils. In: MILLER P.R., McBRIDE J.R. (eds.), *Oxidant Air Pollution Impacts in the Montane Forests of Southern California: A Case Study of the San Bernardino Mountains*. Ecological Studies 134. New York, Springer-Verlag: 7–27.
- RICHTER D.D., MARKEWITZ D., WELLS C.G., ALLEN H.L., APRIL R., HEINE P.R., URREGO B., 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. *Ecology*, 75: 1463–1473.
- RICHTER D.D., MARKEWITZ D., 1995. Atmospheric deposition and soil resources of the southern pine forest. In: FOX S., MICKLER R.A. (eds.), *Impact of Air Pollutants on Southern Pine Forests*. Ecological Studies 118. New York, Springer-Verlag: 315–336.
- RUSTAD L.E., FERNANDEZ I.J., DAVID M.B., MITCHELL M.J., NADELHOFFER K.J., FULLER R.D., 1996. Experimental soil acidification and recovery at the Bear Brook Watershed in Maine. *Soil Science Society of America Journal*, 60: 1933–1943.
- RYAN P.F., HORNBERGER G.M., COSBY B.J., GALLOWAY J.N., WEBB J.R., RASTETTER E.B., 1989. Changes in the chemical composition of stream water in two catchments in the Shenandoah National Park, Virginia, in response to atmospheric deposition of sulfur. *Water Resources Research*, 25: 2091–2099.
- SCHABERG P.G., DEHAYES D.H., HAWLEY G.J., STRIMBECK G.R., CUMMING J.R., MURAKAMI P.F., BORER C.H., 2000. Acid mist, soil Ca and Al alter the mineral nutrition and physiology of red spruce. *Tree Physiology*, 20: 73–85.
- SHORTLE W.C., SMITH K.T., 1988. Aluminum-induced calcium deficiency syndrome in declining red spruce trees. *Science*, 240: 1017–1018.
- SHORTLE W.C., SMITH K.T., MINOCHA R., LAWRENCE G.B., DAVID M.B., 1997. Acidic deposition, cation mobilization, and biochemical indicators of stress in healthy red spruce. *Journal of Environmental Quality*, 26: 871–876.

- SMITH K.T., SHORTLE W.C., 2001. Conservation of element concentration in xylem sap of red spruce. *Trees – Structure and Function*, 15: 148–153.
- STODDARD J.L. et al., 1999. Regional trends in aquatic recovery from acidification in North America and Europe. *Nature*, 401: 575–578.
- THORNTON F.C., JOSLIN J.D., PIER P.A., NEUFELD H., SEILER J.R., HUTCHERSON J.D., 1994. Cloudwater and ozone effects upon high elevation red spruce: A summary of study results from Whitetop Mountain, Virginia. *Journal of Environmental Quality*, 23: 1158–1167.
- TRETTIN C.A., JOHNSON D.W., TODD D.E. JR., 1999. Forest nutrient and carbon pools: a 21-year assessment. *Soil Science Society of America Journal*, 63: 1436–1448.
- TURNER R.S., COOK R.B., VAN MIEGROET H., JOHNSON D.W., ELWOOD J.W., LINDBERG S.E., HORNBERGER G.M., 1990. Watershed and lake processes affecting surface water acid-base chemistry. In: *Acid Deposition: State of Science and Technology*, Rep. 10, National. Acid Precipitation Assessment Program, Washington, D.C., Nov. 1990: 1–167.
- VANN D.R., STRIMBECK G.R., JOHNSON A.H., 1992. Effects of ambient levels of airborne chemicals on freezing resistance of red spruce foliage. *Forest Ecology and Management*, 51: 69–79.
- WATMOUGH S.A., 2002. A dendrochemical survey of sugar maple (*Acer saccharum* Marsh) in south-central Ontario, Canada. *Water, Air, and Soil Pollution*, 136: 165–187.
- WATMOUGH S.A., HUTCHINSON T.C., 1999. Change in the dendrochemistry of sacred fir close to Mexico City over the past 100 years. *Environmental Pollution*, 104: 79–88.
- WATMOUGH S.A., DILLON P., 2003. Calcium losses from a forested catchment in south-central Ontario, Canada. *Environmental Science and Technology*, 37: 3085–3089.
- WOOD H.B., 1994. Unpublished data on soil pH trends (1973 to 1990) in chaparral ecosystems in the San Gabriel Mountains, southern California.
- WOOD H.B., OLIVIER K.L., RYAN T.M., 1992. Surface soil acidification in smog-polluted chaparral ecosystems in the San Gabriel Mountains, California. *Bulletin of the Ecological Society of America*, 73: 392.
- YANAI R.D., SICCAMA T.G., ARTHUR M.A., FEDERER C.A., FRIEDLAND A.J., 1999. Accumulation and depletion of base cations in forest floors in the northeastern United States. *Ecology*, 80: 2774–2787.
- YANAI R.D., BLUM J.D., HAMBURG S.P., ARTHUR M.A., NEZAT C.A., SICCAMA T.G., 2005. New insights into calcium depletion in northeastern forests. *Journal of Forestry*, 103: 14–20.

## Stav acidifikace půdy v Severní Americe

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**ABSTRAKT:** Acidifikace lesní půdy a vyčerpávání kationtů živin byly zaznamenány pro několik lesních oblastí Severní Ameriky, zejména pak na východě USA včetně severovýchodu a v centrálních oblastech Apalačského pohoří, ale rovněž v některých částech jihovýchodní Kanady a jihovýchodu USA. Pokračující regionální přísun dusíku a síry má význam kvůli vyluhování bazických kationtů, zvýšené dostupnosti půdního Al a akumulaci a nakonec přenosu acidity z lesní půdy do vodotečí. Ztráty vápníku z lesních půd a zalesněných povodí byly nyní zaznamenány jako citlivý časný ukazatel a funkčně signifikantní reakce na kyselou depozice pro široké rozpětí lesních půd v Severní Americe. U smrku červeného *Picea rubens* byla zjištěna jasná vazba mezi kyselou depozicí, změnami v zásobě vápníku a hliníku a zvýšenou citlivostí na zimní poškození. Zdá se, že vyčerpání vápníku přispívá k ústupu javoru na některých půdách, zejména pak vysoké míry mortality pozorované v severní Pensylvánii během posledního desetiletí. Zatímco reakce na vápnění nebyla v Severní Americe sys-

tematicky zkoumána, obnovení bazických kationtů prostřednictvím vápnění zvýšilo přírůst výčetní základny javoru cukrodárného a úroveň vápníku a hořčíku v půdě a listí. V pohoří San Bernardino v jižní Kalifornii poblíž západního pobřeží pH horizontu A kleslo za posledních 30 let o nejméně dvě jednotky pH (na pH 4,0–4,3) bez škodlivého vlivu na přírůst kmene. Pravděpodobně vlivem vnitrozemského klimatu je zásoba bazických kationtů stále vysoká a neomezuje růst rostlin.

**Klíčová slova:** vyčerpání vápníku; kyselá depozice; bazické kationty; smrk červený; javor cukrodárný; vápnění; zimní poškození; zdraví lesa

Acidifikace lesních půd a vyčerpání kationtů živin byly hlášeny pro několik zalesněných oblastí v Severní Americe, hlavně na východě USA včetně severovýchodu a centrálních oblastí Apalačského pohoří, ale také v částech jihovýchodní Kanady a jihu USA. Pokračující oblastní vstup dusíku a síry mají význam kvůli vyluhování bazických kationtů, zvýšené dostupnosti půdního Al a akumulaci a nakonec přenosu acidity z lesních půd do vodotečí. Ztráty vápníku z lesních půd a zalesněných povodí byly nyní doloženy jako citlivý časný ukazatel a funkčně závažná reakce na kyselou depozici pro širokou paletu lesních půd v Severní Americe. Studie o účincích kyselé depozice stále více ukazují na vyčerpání bazických kationtů z lesních půd jako jeden z nejdůležitějších mechanismů, jímž atmosférické imise mohou ovlivnit udržitelnost a produktivitu lesa zejména v oblastech, kde jsou půdy neodmyslitelně chudé na bazické kationty a kde zásoba kationtů byla dále ochuzena těžební činnostmi nebo předešlými aktivitami využití půdy. Vyčerpání bazických kationtů je příčinou znepokojení kvůli úloze, kterou tyto kationty mají v neutralizaci kyselin, a v případě vápníku (Ca), hořčíku (Mg) a draslíku (K) jejich významu jako nezbytných živin pro růst a zdraví dřevin. Kromě toho vyčerpání bazických kationtů z půdy je proces, který vede k mobilizaci hliníku (Al). Nízký poměr Ca/Al v půdě dovoluje, aby Al zasahoval do příjmu Ca kořeny v lesních půdách. Akumulace a přenos acidity z lesních půd do vodotečí mají význam, protože roste koncentrace Al v povrchových vodách.

Rostoucí důkazy naznačují, že vyčerpání Ca je primárním mechanismem vlivů kyselé depozice na lesy ve východních oblastech Severní Ameriky. Lesy

rostoucí na půdách chudých na báze vystavených vlivu povětrnosti jsou nejvíce v ohrožení. Hynutí javoru cukrodárného a smrku červeného na východě Severní Ameriky je spojeno s nízkou zásobou bazických kationtů, zejména pak nízkou úrovní půdního Ca. I když v Severní Americe bylo provedeno málo studií týkajících se nápravy, vápnění zlepšilo stav bazických kationtů v půdě a zdraví a vitalitu javoru cukrodárného v citlivých oblastech. Smrk červený je ovlivňován nízkým příjmem Ca kořeny (vlivem vyčerpání Ca v půdě a mobilizací Al) a vyluhováním Ca z jehličí. Kyselá depozice vyvolala vyluhování Ca z mezofylu buněk jednoletých jehlic smrku červeného vedoucí ke zvýšenému zimnímu poškození na severovýchodě Severní Ameriky. Nízký obsah Ca v jehličí smrku ve velkých nadmořských výškách na jihovýchodě Severní Ameriky je spojen s redukcí schopností produkce sacharidů v reakci na vysokou úroveň kyselé depozice. Tendence klesajících zásob výměnného Ca v lesních půdách severovýchodu a jihovýchodu Severní Ameriky zvyšuje zájem o dlouhodobou udržitelnost těchto lesů přes pokračující kyselou depozici zejména v oblastech opakující se těžby dříví. Nejvyšší vstupy kyselé depozice v Severní Americe se vyskytují v lesích ve směru větru od Los Angeles a Mexico City. Výzkum gradientů znečištění ovzduší a časové trendy v lesích blízko těchto dvou městských oblastí naznačují, že pH půdy a koncentrace bazických kationtů v těchto lesích se snížily, avšak zásoba bazických kationtů je stále bohatá. Odezva saturací dusíku, jako je zvýšené vynášení nitrátů v odtoku, fyziologické účinky ozonu na rostliny a nadbytek N, jsou hlavním problémem v těchto lesích rostoucích na vysoce pufovaných půdách.

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