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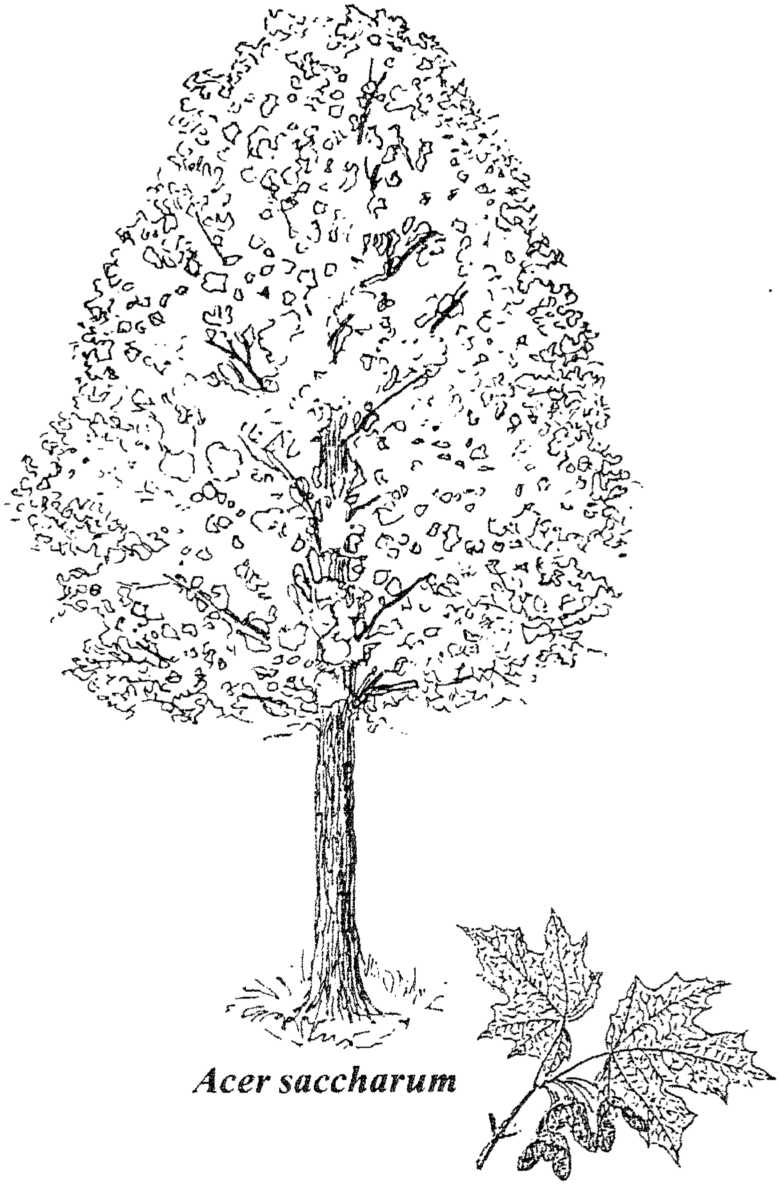
Sugar Maple Ecology and Health: Proceedings of an International Symposium

June 2-4, 1998
Warren, Pennsylvania



Acer saccharum

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Sugar Maple Ecology and Health: Proceedings of an International Symposium

June 2-4, 1998
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Edited by:
Stephen B. Horsley
Robert P. Long

Sponsored by:
USDA Forest Service, Northeastern Research Station
Pennsylvania State University, School of Forest Resources
State University of New York, College of Environmental Sciences and Forestry
Pennsylvania Department of Conservation and Natural Resources
New York Department of Environmental Conservation

Preface

Sugar maple (*Acer saccharum* Marsh.) is a signature species in the northern hardwood forest of the northeastern and north central United States and eastern Canada. The species has been sought for its hard wood, sweet sap, and flaming fall foliage. Sugar maple biology has been the subject of much scientific study, yet despite a tremendous collective effort, many aspects of its ecology and health are not well understood.

During the past four decades, declines of sugar maple have occurred throughout its range. Each decline event has been the subject of intense research. The declines were ephemeral, preventing a complete understanding of conditions and causes. The most recent decline in Pennsylvania was the impetus to organize an international symposium on sugar maple ecology and health.

Speakers from the United States and Canada were invited to share their research and explore a variety of topics concerning sugar maple history and ecology, recent sugar maple declines, nutrient and belowground dynamics in northeastern forests, and interactions of forest health with biotic and abiotic stressors. Posters also were contributed. Attending scientists, natural resource professionals, and land managers participated in two days of talks and discussions and a day-long field trip to sugar maple decline research sites in northwestern Pennsylvania and southwestern New York.

Conference speakers and poster presenters were invited to submit abstracts, popular summaries, or complete manuscripts on the work presented at the conference. Abstracts and popular summaries have been reviewed by the conference co-editors; complete manuscripts received additional peer review.

Stephen B. Horsley and Robert P. Long
Conference Co-editors
USDA Forest Service, Northeastern Research Station,
Warren, PA, and Delaware, OH, respectively

Acknowledgments

We thank the many people who helped make the conference successful. In addition to the conference co-editors, the organizing committee included Douglas Allen, State University of New York, College of Environmental Science and Forestry; David DeWalle, Environmental Resources Research Institute and School of Forest Resources, Pennsylvania State University; and Scott Bailey, Northeastern Research Station, Durham, New Hampshire. The conference organizers also acted as session moderators. Wendy Snaveley, Kathy Sweeney, Susan Stout, Harry Steele, Vonley Brown, Barbara McGuinness, Todd Ristau, David Saf, and Ernest Wiltsie Northeastern Research Station, Warren, Pennsylvania, helped with local arrangements. Carol Calvin, Northeastern Research Station, Delaware, Ohio, prepared the conference logo. Stephen Wingate, Allegheny National Forest, Michael Fay and Stephen Smith, New York Department of Environmental Conservation, Paul Lilja and Thomas Hall, Pennsylvania Department of Conservation and Natural Resources, and Scott Bailey and Richard Hallett, Northeastern Research Station, Durham, New Hampshire, helped with the field trip. Ann Oroszi, Northeastern Research Station, Delaware, Ohio, provided clerical support.

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Sugar Maple: Its Characteristics and Potentials

Ralph D. Nyland[1]

Abstract

Sugar maple dominates the northern hardwood forest, but grows over a broader geographic area. Conditions of soil and climate largely limit its distribution, and account for its less continuous cover along fringes of the range. Sugar maple regenerates readily following a wide range of overstory treatments. Success depends upon its status as advance regeneration, particularly under strategies favorable to less shade-tolerant species. In even-aged stands, trees of upper canopy positions grow well following release by cutting. Those of lower canopy positions do not. In uneven-aged stands, both small and large trees respond well to release. Diameter-limit cutting removes the best trees, often leaving stands in poor condition for growth and health. Damage to trees by natural agents and logging commonly leads to discoloration and decay, and often to dieback. Within the range of northern hardwoods, sugar maple seems generally healthy. Exceptions include stands damaged by defoliation, logging, and similar agents.

Requirements for Ecologic Success

To persist over ecologic time, a species must become established at available sites; survive, grow and develop successfully under prevailing edaphic, climatic, and biologic conditions; produce viable seed in quantity and frequency for establishment at critical times; and endure. Its range expands when seed moves to favorable sites in new areas.

In this context, *site* means the interacting biotic and abiotic factors that determine the potential for a species or tree to become established and develop. Important factors include:

1. the periodicity of extended shortages or excesses of moisture;
2. deficiencies or excesses of nutrients due to the parent material, with uptake influenced by available moisture;
3. mechanical damage by wind, ice and snow, and vertebrate animals (including people);
4. defoliation and other activities by insects and other invertebrates, and effects of fungi and disease organisms; and
5. physical and chemical interference and competition from existing or co-establishing vegetation.

These affect the form, vigor, and growth of individual trees and groups of trees. They also may influence the potential for flowering and pollination, seed development and dispersal, and embryo viability and germination.

Altogether, site factors influence tree success at three levels:

1. across the geographic range of a species, with the best sites likely toward the center of that area;
2. across environmental gradients within the geographic range, based upon soil, climate, and critical biota; and
3. across a single location, with variations of micro-site features that affect young trees before the root systems integrate soil across a larger local space

Generally, species and individual trees best adapted to the local site conditions and competitive effects have the highest vigor, grow the best, and occur in the upper crown positions within a cohort. Further, these trees may suffer fewer environmental stresses over time, live longer, and develop to larger sizes. Sugar maple (*Acer saccharum* Marsh.) exemplifies these principles within its range.

Ecologic Characteristics of Sugar Maple

Sugar maple is a major component of the northern hardwoods forest type group, including six distinct hardwood forest cover types and one mixed hardwood-conifer type (Eyre 1980). It occurs in lesser amounts or occasionally in two other eastern hardwood cover types, three oak-dominated forest cover types, five central hardwoods forest cover types, two boreal hardwood cover types, and six eastern conifer cover types. The current geographic range extends from the Maritimes in Canada westward across the Great Lakes region to the prairie, and southward into Missouri, Tennessee, Virginia, Pennsylvania, northern Maryland and Delaware, and southern New England. Small outliers occur farther south, and in northeastern South Dakota (Figure 1).

Sugar maple accounts for 50% or more of the basal area in northern hardwood stands. The most contiguous area of this cover type currently runs from northern Ohio and Pennsylvania through southern Ontario and Quebec, and eastward through northwestern Massachusetts into western Maine. Northern hardwoods also grow extensively in southern Ohio and west-central Indiana, and along the Appalachians in eastern West Virginia. More dispersed major blocks intermix with other forest cover types around the Great Lakes in Michigan, Wisconsin, Minnesota, and western Ontario; and from central Maine eastward through the Maritimes (Figure 1). This broad region has a generally cool and moist climate, a growing season of 80-260 days, and well-distributed precipitation throughout that period (Godman 1965; Eyre 1980; Godman *et al.* 1990).

Since the early 1900's, northern hardwoods have naturally reforested many former agricultural sites within their natural range, and probably in fringe areas as well. As a consequence, many areas formerly supporting only widely dispersed and disconnected remnant woodland patches now have large tracts of unbroken northern hardwood forest

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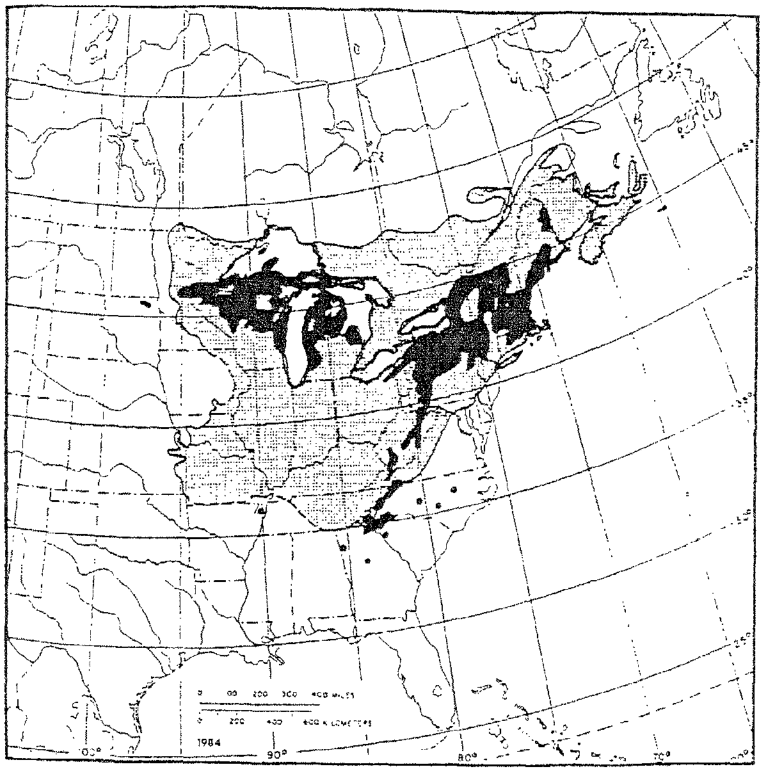

Figure 1.—The geographic range of northern hardwoods (black) in the United States, in comparison to the distribution of sugar maple (stippled) (after Shantz and Zon 1924; Godman *et al.* 1990).

(Nyland *et al.* 1986; Zipperer *et al.* 1988, 1990). Overall, from 1963 to 1992 northern hardwoods increased from approximately 13 to 19 million ha (32 to 46 million ac) (Quigley and Morgan 1969; Powell *et al.* 1993). At upland sites, the naturally reforested stands often contain pure sugar maple, or sugar maple mixed with some white ash (*Fraxinus americana* L.) or another common associate. On more poorly drained soils, red maple (*Acer rubrum* L.) has become dominant, along with white ash and American elm (*Ulmus americana* L.). The reforested stands generally have an even-aged character. Other woodlands commonly contain a broader array of species, and many have an uneven-aged character. (e.g., Nyland *et al.* 1986; Zipperer *et al.* 1990).

The range of northern hardwoods overlaps that of Spodosol and Inceptisol soils (Figure 2). Sugar maple also extends across a major area of Alfisols lying south of the Great Lakes, but primarily on fertile, mesic sites (Smith 1995). It grows in sands through silt loams, but develops best in fairly deep, moist, fertile, well-drained loam soils having ample growing season soil moisture. These conditions enhance leaf litter decomposition, helping to enrich the soil. Sugar maple does poorly in dry soils, and will not occur on wet sites (Godman 1965; Leak 1978; Godman *et al.* 1990). The fine feeding roots develop mainly within or near the organic horizons. They, and the mycorrhizal associations on them, react to variations in soil moisture and texture, and events that sharply reduce overstory shading can affect their development and survival (Fayle 1965; Kessler 1966; Allen 1987).

In the southern portion of its range, sugar maple is important on the highest quality oak sites, moist (but not wet) flats, and in ravines or coves. To the north it dominates mesic ridges between poorly drained areas, the warm upper slopes with good drainage and a middle or better range of pH, and enriched benches and coves. Along with the importance of bedrock and till sources on current soil, best growth occurs at sites with organic material incorporated into the mineral horizons. American beech (*Fagus grandifolia* Ehrh.) often replaces sugar maple on the drier sites, especially at the more northern latitudes. Red maple dominates the poorly drained soils throughout much of the natural range for sugar maple. At high elevations and toward the northern part of their range, northern hardwoods converge with boreal forests. Aside from soil, climate largely limits the distribution of sugar maple in elevation, as well as longitude and latitude. Conditions become too cold to the north, too warm to the south, and too dry to the west (Godman 1965; Post 1969; Hosie 1973; Leak 1978, 1980; Godman *et al.* 1990; Farrar 1995; Heisey 1995).

Biologic Attributes of Sugar Maple

Sugar maple produces some seed by age 50. Amounts increase thereafter, with production related to tree size and stand density (e.g., tree vigor). Large diameter (past 100 years) trees often produce vast quantities. In sawtimber stands, production varies from some seed annually, to medium or better crops in slightly more than one-half of the years within the range of northern hardwoods. Good crops

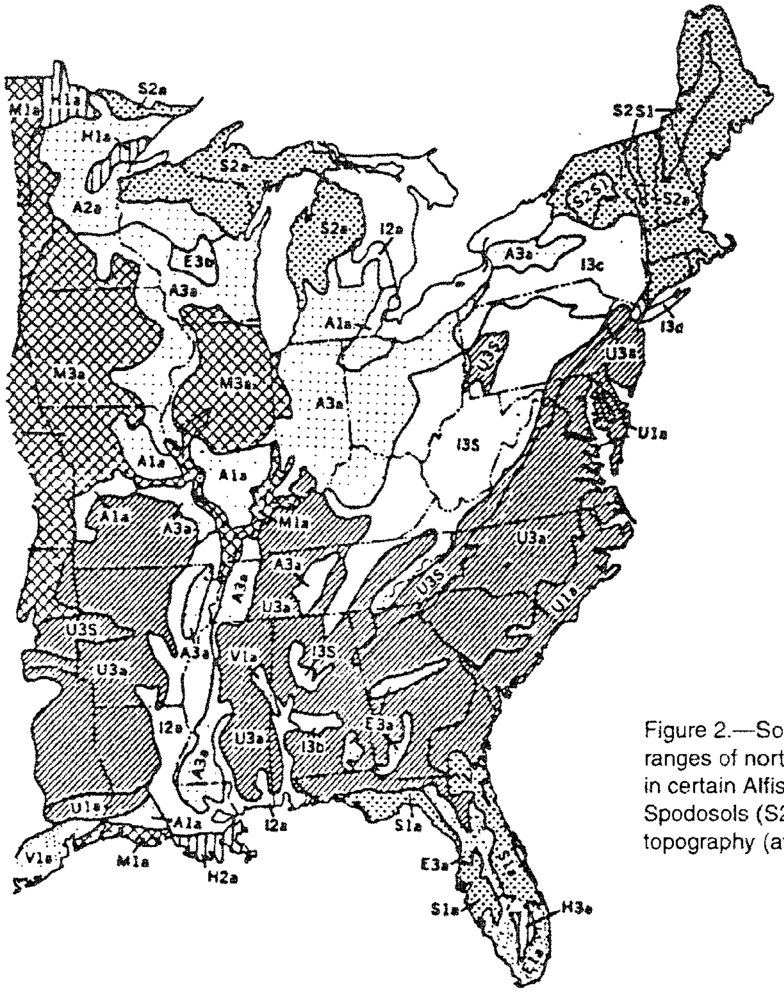

Figure 2.—Soil orders of northeastern United States. The ranges of northern hardwoods and sugar maple largely occur in certain Alfisols (A2a and A3a), Inceptisols (I3a and I2a), and Spodosols (S2a and S2S1) on gentle to steeply sloping topography (after US Soil Conserv. Soc. 1975).

often occur in successive years, with only occasional failures (Godman 1965; Tubbs 1969; Godman and Mattson 1976; Godman *et al.* 1990; Garrett and Graber 1995). At least among developing even-aged stands of seed-bearing ages in Pennsylvania at the fringe of northern hardwoods, annual seed production varies widely, with good seed years only every 7-8 years (Grisez 1975, Long *et al.* 1997).

Seeds will glide up to 107 m (350 ft) down wind into openings, but most fall much closer in closed stands (Godman *et al.* 1990; Nyland 1996). They stratify naturally over winter within the leaf litter. Most germinate the first year under favorable conditions. The high germination capacity commonly results in a carpet of seedlings following good seed years, given favorable environmental conditions during the spring and early growing season. The strong radicle readily penetrates a heavy leaf litter, so that a high proportion of germinants survive if the forest floor remains reasonably moist. Even small and light overstory disturbances, or other events that brighten the understory, trigger regeneration underneath residual stands at mesic sites. Once established, advance seedlings and saplings may persist for many years. They develop rapidly following either partial or complete overstory removal, especially at sites with good moisture and available nitrogen. In addition, young trees, small saplings, and large seedlings readily sprout. These sources, coupled with well-developed advance regeneration, often maintain sugar maple as an important component of new stands where more rapidly growing species also regenerate (Godman 1965; Trimble *et al.* 1986; Godman *et al.* 1990; Tryon *et al.* 1992; Wang and Nyland 1993; Walters and Reich 1997).

Sugar maple shows considerable genetic variability. Sources from warm, dry portions of the range have greater drought resistance than seedlings from cooler and moister sites. Local and individual genetic variation also affects height growth and degree of apical dominance (Kriebel 1969). Also, tests suggest significant genetic effects on individual tree diameter and height growth, and survival. Early responses provide a good indicator of long-term height development (Schuler 1994).

Repeated browsing by ungulates, hare, and rabbits may destroy sugar maple seedlings, making regeneration difficult by any silvicultural method. Also, stands subjected to protracted intense browsing may develop understories of interfering plants that can prevent successful regeneration of sugar maple in both even- and uneven-aged stands. These include ferns and grasses (Tubbs 1973; Marquis 1987), or a dense beech understory (Richards and Farnsworth 1971; Kelty and Nyland 1981; Marquis *et al.* 1984, 1992; Marquis 1987) or striped maple. Failure to control these plants will lead to a failure of sugar maple and other desirable species following cutting to a wide range of densities, and after clearcutting (Richards and Farnsworth 1971; Kelty and Nyland 1981; Marquis *et al.* 1984, 1992). The reproduction method must reduce these obstacles (site preparation and reduction of animal density) to insure success (Kelty and Nyland 1981; Sage 1987; Marquis *et al.* 1992; Horsley 1994; Nyland 1997). For large areas, applications using a skidder-mounted mist blower prove most efficient for controlling an interfering understory (Sage 1987; Horsley 1994).

Growth and Development

On suitable sites, sugar maple lives for 300-400 years, reaching more than 30 m (100 ft) tall and 89-102 cm (35-40 in) dbh (Westveld 1933; Eyre and Zillgitt 1953; Blum 1961; Leak 1975). It annually increases about 0.3 m (1 ft) in height for the first 30-40 years, but little after 140-150 years (Godman *et al.* 1990). Frequent breakage by ice, snow, wind, and logging often limits useable length to about 8-12 m (25-40 ft) at many high elevation and northern latitude sites (Nyland 1989). These injuries commonly lead to discoloration of wood present at the time of injury, and decay may develop in some cases (Shigo 1966).

Large trees add about 2.54 cm (1 in) of diameter per decade in unmanaged stands. Increment even of old trees will increase following release by cutting. In managed uneven-aged stands and even-aged ones of intermediate ages, radial increment of good-vigor trees will increase in proportion to the degree of release (intensity of cutting), and may average 5-8 cm (2-3 in) per 10 years (Nyland 1989). Mortality will decrease inversely with residual density (Eyre and Zillgitt 1953; Gilbert *et al.* 1955; von Althen *et al.* 1994; Majcen 1995; Pothier 1996). Yet net stand-wide production increases in stands thinned down to 60% relative density, due in part to the reduction of mortality losses (Nowak 1996). Also, individual residual tree diameter growth increases following thinning in even-aged stands. But the degree generally correlates with tree size and crown canopy position (Stone 1986; Marquis 1991; Nyland *et al.* 1993). Low vigor trees of intermediate and overtopped positions continue to grow at relatively slow rates, even following fairly heavy release (Figure 3a). By contrast, small (young) trees in managed uneven-aged communities have well developed crowns and good vigor (Kenefic and Nyland 1998). Their radial growth (Figure 3b) and height will increase appreciably if cutting regulates the spacing and density across size classes (Eyre and Zillgitt 1953; Gilbert *et al.* 1955; Mader and Nyland 1984; Donoso *et al.* 1998).

Some Factors Affecting the Health and Condition of Sugar Maple

Several insects, fungi, diseases, and environmental phenomenona affect sugar maple. Few actually kill the trees. They may reduce the vigor, decrease the value for products, or structurally weaken the bole. Sugar maple borer has this effect. Some fungi like *Armillaria* kill sugar maple, and heavy defoliation over successive years may result in mortality. But defoliation mostly kills low-vigor trees, and root diseases and

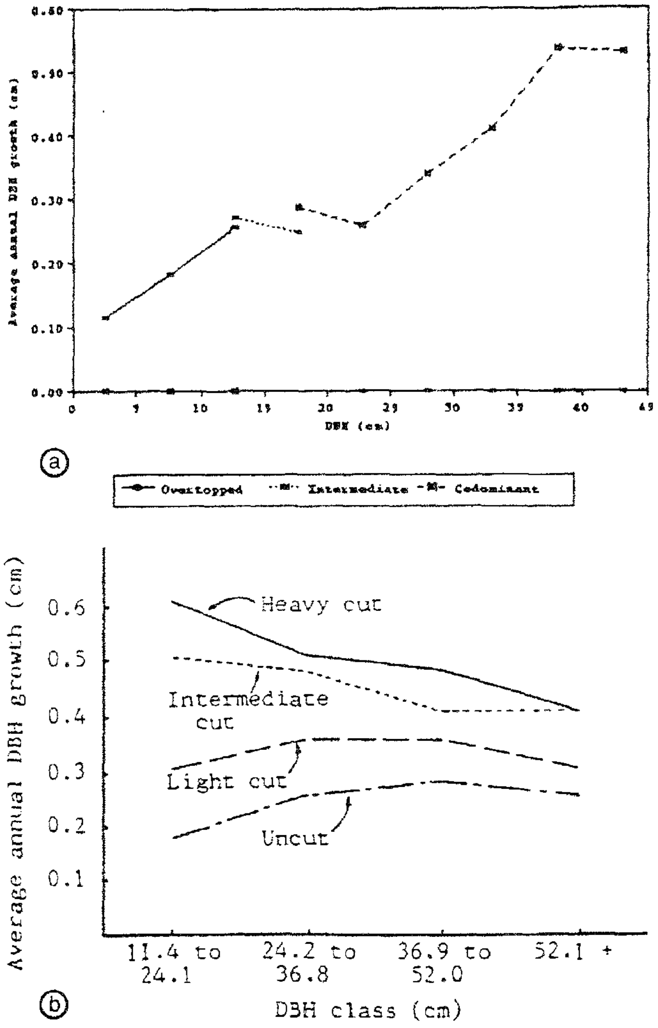

Figure 3.—Growth of sugar maple trees following release. a. After thinning in even-aged stands, radial increment correlates with crown position and tree diameter, with best increment among trees that initially grew in upper-canopy positions (after Lareau 1985; Nyland *et al.* 1993). b. After selection system treatments that cut across the diameter classes in uneven-aged stands, the growth of small trees increases in proportion to the intensity of cutting, and dramatically so at relatively low residual density (after Eyre and Zillgitt 1953).

other fungi commonly enter through wounds to a tree (Allen 1987; Shigo 1966; Shortle 1987). Breaking branches >8 cm (>3 in) diameter and removal of bark from >970 cm^2 (>150 in^2) of the bole triggers discoloration of the wood present and may lead to decay if wood-rotting fungi colonize through the wounds (e.g., see Shigo 1966). Such large wounds appear to increase the chance of measurable decay within 20-25 years (Hesterberg 1957; Silverborg 1959; Ohman 1970; Nyland and Gabriel 1971; Nyland *et al.* 1976).

Landowners cannot prevent damage during storms and actions of fungi. They can spray to protect against defoliation. And they can control injuries from logging and other stand uses to some degree (Nyland 1989). Precluding skidding on saturated soils prevents root wounds that serve as entry courts for diseases and also reduce the size of a root system and its moisture absorption and carbohydrate storage capacities. These injuries can lead to dieback during periods of stress (Shigo 1985; Manion 1991; Cote and Ouimet 1996).

Several assessments suggest either a recent increase of diebacks and declines in sugar maple (Lachance *et al.* 1995; Cote and Ouimet 1996; Auclair *et al.* 1996; Auclair *et al.* 1997), a pattern of periodic growth depressions and recoveries over long time periods (Payette *et al.* 1996), or no anomalies (Lane *et al.* 1993; Hopkin and Dumond 1994; Heisey 1995). Reported problems commonly occur along outer portions of the range for northern hardwoods (e.g., northern Pennsylvania, Quebec, and the Maritimes). Evaluations implicate factors like drought, heat, insect attacks, stand maturation, freezing, freezing-thawing cycles, injuries, soil nutrients, other natural stresses, tree social status within the community, and forest management practices. As with other species, most likely a complex of site factors influence the success of sugar maple, and multiple factors determine its vigor and condition (Houston 1981; Stolte 1997).

Forest health specialists commonly suggest that trees of high vigor better withstand a variety of harmful agents. Appropriate tending to reduce inter-tree crowding and maintaining large and full crowns may help to make sugar maple more resistant, and more resilient in recovery (Boyce 1948; Hawley and Stickel 1948; Graham 1952). Silviculture will not prevent damage during widespread outbreaks of insects or major disease incidents (Baskerville 1975; Wood 1988). Yet a variety of health maintenance measures should become routinely incorporated into the silvicultural system for a stand. These include (after Belanger and Malac 1980; Belanger 1981; Nyland 1996):

1. use of an appropriate reproduction method and the requisite site preparation to insure an abundance of species suited to the site;
2. timely tending to control stand density and insure high tree vigor;
3. selection of sound, vigorous, and well-developed trees as residual growing stock;
4. timely salvage and sanitation cutting to remove weakened and badly injured trees, and to reduce risks to damaging insects and fungi;
5. setting an appropriate life span for an age class;
6. appropriately siting and designing skid trails to minimize affects on soil and residual trees;
7. scheduling skidding and other machine operations for seasons when the soil will support the equipment without rutting and root damage;
8. careful practice in logging to minimize injuries to residual trees; and
9. continual monitoring of potential health problems and their causes to allow prompt response as needs arise

These measures represent part of a landowner's integrated health management program.

Silviculture for Sugar Maple Dominated Stands

Silviculture either regenerates mature age classes, or tends those of intermediate ages. Foresters use both activities to establish and maintain some particular set of ecologically desirable plant community attributes. Uses that serve economic interests derive from those conditions. In this context, foresters use timber harvesting to implement the planned silvicultural treatments. When removals allow a commercial sale, landowners can manage the habitat for indigenous plants and animals, maintain essential hydrologic and other important ecologic functions, influence visual qualities, and serve many other purposes without major investments (Nyland 1996).

Several biologic and ecologic characteristics facilitate the regeneration of sugar maple throughout much of its range, and make it responsive to later management. Important ones include (after Bourdo 1969):

1. consistent and abundant seed production;
2. good dispersion from the parent tree once seeds mature;
3. ready germination and establishment of seedlings;
4. sprouting from stumps of both small and larger trees;
5. a high tolerance to shading;
6. good rates of diameter and height growth at high light levels;
7. strong growth response following release from competition;
8. high resistance to many harmful agents; and
9. good recovery following crown breakage by ice, snow, wind, and logging

Since sugar maple dominates northern hardwood stands, its silviculture parallels that for the forest type as a whole.

Considerations for Regeneration

The extent that sugar maple reforested former agriculture sites and cut-over forest stands attests to the ease of securing natural regeneration under a wide variety of seedbed and residual stand conditions. Yet in forested areas, regeneration often fails on skid trail surfaces devoid of an organic cover and humus, even if seeds fall on them and germinate (Walters and Nyland 1989; Wang and Nyland 1996). A leaf litter does not impede penetration of the radicle following germination (Godman *et al* 1990). Favorable moisture and nutrient supplies in the humus sustain the seedlings until their root systems develop.

Sugar maple seedlings develop best at about 13-45% of full sunlight. Once well established, they persist for many years under even heavy shade (Logan 1965; Tubbs 1969), and respond to release by overstory cutting. If well developed, advance seedlings survive and grow better following complete or heavy overstory removal. For stands lacking such seedlings, clearcutting may delay establishment and development of a new cohort, and shelterwood method commonly proves more effective (Tubbs 1977a, 1977b). Having seedlings greater than 0.3 m (1 ft) tall also speeds cohort development following partial overstory disturbance (Leak and Wilson 1958; Metzger and Tubbs 1971; Mader and Nyland 1984).

Advance seedlings of good vigor grow in proportion to the degree of release, reaching about 1.8 m (6 ft) in 12 years and 3.0 m (10 ft) in 20 years on good sites with full sunlight. Less shade-tolerant associates may grow twice as rapidly, making the advance status of sugar maple critical to insuring its place in the main canopy of even-aged stands (Wang 1990; Wang and Nyland 1996). Depending on how long they grew under shade prior to release, sugar maple saplings reached 3.0 m (10 ft) in 18-23 years after selection system cutting to 17 m^2/ha (75 ft^2/ac). Low light levels under this and higher stocking make conditions unfavorable for faster-growing less shade-tolerant species, so sugar maple commonly dominates the new age class (Tubbs 1969; Nyland 1997; Donoso *et al.* 1998). However, dense interfering plants (e.g., American beech) or intensive and protracted browsing (e.g., white-tailed deer) can preclude success following any cutting strategy.

Uneven-aged Silviculture

Selection system controls the density within different size (age) classes to sustain stand conditions and volume production over successive cutting cycles, the patterns of regeneration across a stand, and the growth and quality of residual trees. At regular intervals, landowners remove excess immature trees to maintain a specified residual number per size (age) class, and harvest the economically or ecologically mature ones to regenerate a new cohort across a fixed proportion of the stand area. Failure to incorporate regeneration, tending, and harvest simultaneously makes the result unpredictable, the residual conditions less consistent over time, and the yields less regular (Nyland 1987; Nyland *et al.* 1993; Nyland 1996).

Research and experience provided guidelines (Table 1) for selection system based upon an 8-12 yr cutting cycle (Eyre and Zillgitt 1953; Arbogast 1957; Gilbert and Jensen 1958; Leak *et al.* 1969). Simulation methods suggest other alternatives for longer treatment intervals, different stand conditions, and various landowner objectives (Hansen and Nyland 1987; Hansen 1987; Nyland 1996). Appropriately structured stands grow between 0.6 and 0.7 m^2/ha/yr (2.5 and 3.0 sq ft/ac/yr) for basal area (Eyre and Zillgitt 1953; Blum and Filip 1963; Leak *et al.* 1969; Mader and Nyland 1984), and 2.2 and 3.2 m^3/ha/yr (200-300 bd ft/ac/yr) of sawtimber volume (Eyre and Zillgitt 1953; Leak *et al.* 1969; Mader and Nyland 1984). Differences in production largely reflect the variation in tree heights across regions and sites. Generally, growth provides sufficient yields for another operable cut at the intended interval.

Partial cutting in uneven-aged stands commonly causes broken branches and basal wounds, and may destroy some trees. The incidence will be proportional to the numbers of trees in a size class, and ones with major injuries may comprise about one-fifth of the residual basal area. Repeated partial cutting might maintain a base level of physical defect in a stand managed with any type of partial cutting strategy (Nyland and Gabriel 1971); Nyland *et al.* 1976; and Nyland 1989).

Even-aged Silviculture

Treatments to regenerate a new age class and tend older ones never occur simultaneously in even-aged communities. So landowners often treat conditions found at a given time, rather than following a pre-planned management strategy for an entire rotation. Most landowners consider pre-commercial treatments financially unacceptable, and delay the first entry for 50-60 years, when they can do a commercial thinning. For this, foresters use an appropriate relative density guide to plan the residual stocking and method for thinning based upon the numbers of trees, their sizes, the basal area, and the species composition (Leak et al. 1969; Roach 1977; Tubbs 1977b; Marquis *et al.* 1984). Most guides recommend leaving increased levels of residual basal area as a stand matures, generally targeted at 60-70% relative density. This threshold insures full site utilization and high net volume production over a thinning cycle, while inhibiting epicormic branching and promoting natural pruning due to inter-tree shading. Stands become ready for another thinning when relative density regrows to about 80% (Leak *et al.* 1969; Roach 1977; Marquis 1986; Stout 1987; Nowak 1996).

Taking about two-thirds of the basal area from below the mean stand diameter, and the remainder from larger trees (crown thinning), concentrates the growth potential onto trees of upper canopy positions (Roach 1977; Marquis et al. 1984). Conversely, cutting the largest trees removes the best growing and volume-producing ones (Marquis 1986; Nyland *et al.* 1993). In fact, simulation work indicates that best sawtimber production will accrue in thinned stands having about 60% of the residual basal area in sawtimber-sized trees, and reduced to B-line relative density as represented on the appropriate stocking guide (Solomon 1977). Such

Table 1.—Alternate residual diameter distributions for selection system under different length cutting cycles (After Eyre and Zillgitt 1953; Arbogast 1957; Gilbert and Jensen 1958; Leak *et al.* 1969; Hansen and Nyland 1987; Hansen 1987 and Nyland 1996).

Diameter class Cm	8-12 yrs M²/ha	15 yrs M²/ha	20 yrs M²/ha	25 yrs M²/ha
5-13	2.5	2.3	2.3	2.3
14-28	4.5	5.7	4.5	6.8
29-43	6.8	8.0	6.8	5.7
44+	6.8	3.4	2.3	-
Total	20.6	19.4	15.9	14.8

thinnings increase the sawtimber yields by 50-100% for rotations of 90-125 years (Solomon and Leak 1986). Thinnings that favor trees of upper canopy positions should not cause extensive logging damage if the contractor carefully controls the skidding and uses appropriate machinery (Nyland 1986, 1989).

Both clearcutting and shelterwood methods effectively regenerate new even-aged communities of northern hardwoods when applied appropriately. Sugar maple will arise largely from advance seedlings and small saplings (Jensen 1943; Wendel and Trimble 1968; Grisez and Peace 1973; Marquis et al. 1984, 1992; Tubbs 1977a). Consequently, for stands lacking adequate advance regeneration, managers should use the shelterwood method. Some regeneration guides (e.g., Tubbs 1977a) recommend leaving some mature trees in place until each hectare averages at least 2025 (5000/ac) desirable trees >0.9 m (>3 ft) tall. If landowners find these already in place, they can remove the complete overstory in a single operation (Marquis 1967; 1987; Roberge 1977; Walters and Nyland 1989).

Shelterwood method seed cutting can leave from 11.5 m^2/ha (50 ft^2/ac) or less (Curtis and Rushmore 1958; Richards and Farnsworth 1971; Leak and Solomon 1975; Kelty and Nyland 1981), to as much as 21 m^2/ha (90 ft^2/ac) (Metzger and Tubbs 1971). Generally, 7 to 18 m^2/ha (30 to 80 ft^2/ac) gives acceptable stocking of desirable species, although sugar maple grows best under 7-9 m^2/ha (30-40 ft^2/ac) (Kelty 1987). *Rubus* will dominate most sites where cutting removes one-half or more of the basal area. That poses no problems in eastern regions, where the tree regeneration emerges from the berry bushes by the 6th or 7th year (Kelty and Nyland 1981; Kelty 1987; Walters and Nyland 1989). In the upper Lake States, dense *Rubus* and herbaceous plants may delay the development of sugar maple regeneration (Metzger and Tubbs 1971; Tubbs 1977a), so guides suggest leaving a 60% crown cover (Tubbs 1977b). Time to a removal cutting depends on the stocking of residual seed trees and the rate that regeneration develops. Strip and patch clearcutting may provide acceptable alternatives. Patch size, strip width, and the orientation of either will influence shading patterns and seed dispersal (Marquis 1965a, 1965b; Lees 1987; Nyland 1996)).

Diameter-limit Cutting

Deliberate silviculture controls the growth, composition, and character of forest stands. It also leaves the best trees as growing stock and future sources of seed. Yet many landowners routinely do diameter-limit cutting that removes the salable products with little regard for the nature, density, or distribution of residual trees or the regeneration that follows. Because sugar maple regenerates so readily, at least some seedlings become established even after these exploitive cuts, given a seed source and no interference from browsing or existing vegetation. And while the inconsistent responses and reduced long-term economic value should make diameter-limit cutting undesirable, it remains popular (Nyland 1992; Nyland *et al.* 1993).

Actual effects differ between even- and uneven-aged stands. In the latter, diameter-limit cutting removes the older age classes, and does not necessarily degrade the younger ones. In even-aged communities it leaves low vigor trees of poor growth potential (Marquis 1991; Nyland *et al.* 1993). These often develop extensive epicormic branching after exposure by heavy cutting, and many die back as well. In most cases, diameter-limit cutting leaves an unevenly distributed or patchy residual stand with both high-density patches and areas having little stocking (Nyland 1996).

Often, contractors who do diameter-limit cutting also use little care with the skid trails, and continue to operate on saturated soils. This causes deep rutting, and damage to the root systems of adjacent residual trees. The combination of low-vigor trees and root damage may lead to later dieback in times of environmental stress (e.g., Cote and Ouimet 1996; Manion 1991).

Some Other Important Considerations

Sugar maple has regenerated and then developed to at least moderate ages under a wide range of environmental conditions and management strategies. In fact, since the early 1900's, it has reforested extensive area within the original range, primarily on lands once cleared for agriculture. This resulted in a major consolidation of forests in areas earlier supporting primarily small and widely-scattered remnant stands (Nyland *et al.* 1986; Zipperer *et al.* 1988, 1990). Available records also suggest that during the same period, northern hardwoods spread into areas and sites where they occurred infrequently or not at all early in the 20th Century (Quigley and Morgan 1969). Further, in at least some areas of continuous forest cover and disturbed by only one of a few timber harvests (Whitney 1990; De Steven *et al.* 1991):

1. sugar maple's abundance, importance, and stature increased in stands where it occurred as a limited but noticeable part of the upper canopy in pre-settlement times;
2. sugar maple's distribution widened through regeneration onto sites where earlier it did not occur, or grew as a minor component; and
3. sugar maple's prominence as an overstory tree increased in stands where it persisted primarily in the understory in the absence of important natural or human stand-altering disturbances

As an illustration, in western portions of the Allegheny Plateau of Pennsylvania, sugar maple was a minor component of old-growth stands, and limited primarily to the understory except along upper slopes of the valleys (Hough 1936; Whitney 1990). Following cutting of the old-growth, sugar maple became a more important component of the replacement stands where it had originally occurred as a minor component of the overstory. The cutting also increased the areal extent of forest community types that have sugar maple as an important upper-canopy tree (Whitney 1990).

Recently, observers have reported declines of sugar maple, commonly in fringe portions of the range of northern hardwoods (Figure 2). This suggests that the current condition of sugar maple may reflect local or regional growing conditions, with incidents of poor health in localities with marginal soils and climate. This may include sites where sugar maple occurred only as a minor species in the earlier forests. On a broader range of sites, local diebacks may emanate from physical damage to trees by natural and human causes, and the poor social status of individual trees prior to release by heavy cutting and other modes of stand disturbance. Often the diebacks become apparent during later times of stress (U.S. For Serv. 1979; Houston 1981; Manion 1991; Cote and Ouimet 1996; Stolte 1997). At least in part, this sugar maple conference serves as a forum to examine such possibilities.

Markets for low value and small diameter trees often dictate the management strategy for sugar maple. Landowners can easily sell large-diameter logs of good quality, and can profitably cut among the smaller diameter classes and in younger stands if they have outlets for fiber products (e.g., pulpwood and firewood) as well. Otherwise, they must usually invest in cull removal and small-tree tending, and most have historically opted not to spend the money. Instead, they often revert to diameter-limit cutting.

While diameter-limit cutting has become widespread, northeastern North America does have many examples of silviculture in stands dominated by sugar maple. New research will continue to illuminate the opportunities for influencing stand development and character through silvicultural practice. Still, the management of sugar-maple dominated stands appears at an important juncture. In the absence of better ways to promote deliberate silviculture, landowners seem destined to repeat the exploitive practices historically used across millions of hectares of northern hardwood forest. Under those circumstances, ecologic and economic outcomes may become increasingly less optimal, and forest health issues more common. Only time will tell.

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Sugar Maple: Abundance and Site Relationships in the Pre- and Post- Settlement Forest

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Abstract

A review of the available historical evidence provides a picture of sugar maple's site relationships in the presettlement forest and its changing status over the last 300 years. Sugar maple was widely distributed throughout the Northeast during the presettlement period. It was particularly abundant on the richer, better drained, silt-rich sites. A comparison of the early land survey records and more recent forest inventory data suggests that sugar maple has increased its abundance on a variety of sites, including a number of more marginal sites. The resulting off-site conditions may partially explain sugar maple's recent decline and its inability to exploit some old field sites.

Introduction

There is an increasing recognition that humans are an integral part of many ecosystems (Grumbine 1997). This has generated an interest in quantifying the degree to which humans have altered those ecosystems. The cutting and forest clearance accompanying European settlement entailed a major reorganization of North America's forests (Whitney 1994). Sugar maple *Acer saccharum* Marsh., was and is a dominant of the beech-sugar maple forest region and the hemlock-white pine-northern hardwood forest region, which cover much of the northeastern United States (Braun 1950). The present paper represents a brief overview of sugar maple's occurrence in the presettlement forest, its relationship to various site factors and its response to European settlement. I will start by summarizing our knowledge of existing sugar-maple site relationships and presettlement site relationships. I will then compare the early land survey records with more recent twentieth century forest inventory data to gain an idea of sugar maple's changing abundance. I will close with a brief discussion of some of the management implications of sugar maple's exacting site requirements and its postsettlement increase.

Existing Soil-site Relationships

Although sugar maple occupies a variety of sites, it makes its best growth on moderately fertile soils that are deep and well-drained (Godman 1957). Brand (1985) noted that sugar maple was associated with the more nutrient rich sites across a wide variety of U.S. Forest Service plots in Michigan and Minnesota. It dominates the melanized silt-rich, loamy, often gentle or moderately sloping soils of the Midwest and New England (Archambault and others 1989; Leak 1978; Lindsey 1998; Pregitzer and Barnes 1984; Wilde 1976). It is particularly abundant on lower slope positions or coves that are enriched by leaf litter, colluvium, or nutrient rich water moving from upslope (Leak 1982; Pregitzer and others 1983; Smith 1995). Foresters have recognized it as an overstory dominant of the fertile *Acer/Arisaema, Acer/ Osmorhiza-Hydrophyllum, Acer/Viola*, and *Quereus rubra-Acer saccharum/Caulophyllum* site types (Archambault and others 1989; Pregitzer and Barnes 1984; Smith 1995).

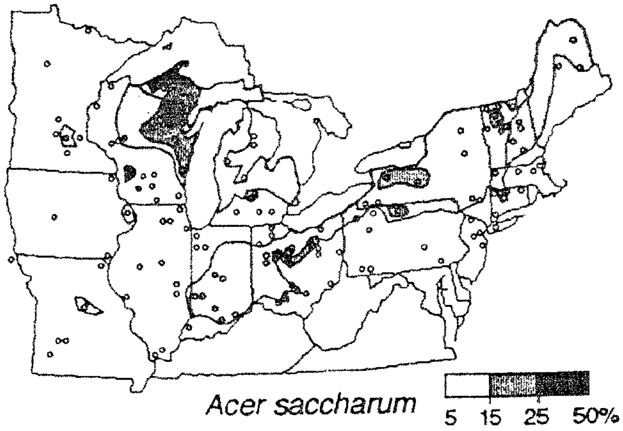

Figure 1.—Map showing abundance of sugar maple in presettlement forest as percent of trees noted in early land survey records. Each circle represents a land survey record, generally encompassing a township or a county. Slightly modified from Whitney (1994).

Most weathered soils in the unglaciated portion of sugar maple's range are low in extractable nutrient base cations. As a result it is not surprising that south of the glacial border, sugar maple reaches its best development on soils that are influenced by base cations in the bedrock (Bailey and others 1999; Nigh and others 1985; Pearson 1962), the addition of silt on terraces and floodplains or nutrient enriched seep water from upslope (Jennings 1936).

Presettlement Abundance And Site Relationships

Counts of witness or corner trees in the early land survey records have frequently been employed to assess the abundance of various tree species in the presettlement forest (Whitney 1994). Although they are subject to surveyor and sampling biases, most investigators believe that they provide a fairly reliable quantitative estimate of the species composition of the forest (Bourdo 1955; Whitney 1994). A compilation of these records in the Northeast (Figure 1) indicates that although sugar maple was well distributed throughout the region, it infrequently accounted for more than 15 percent of the witness trees even in the glaciated portion of its range. Here again it was associated with more fertile site conditions. Sugar maple probably reached its greatest abundance in the hemlock-northern hardwood forest region of northern Wisconsin and the Upper Peninsula

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Table 1.—Relative density or percent representation of all trees reported in pre- and post- settlement (twentieth century) forests.

Location	Presettlement	Postsettlement	Source
N. Maine	5.4	6.5	Lorimer 1977
N. Vermont (Chittenden Co.)	15.8[a]	23.5	Siccama 1971
Catskill Mts., NY	12.8	23.2	McIntosh 1962 McIntosh 1972
N. Pennsylvania (Allegheny Natl. Forest)	5.3	13.3	Whitney 1990
N. lower Michigan (Crawford Co.)	2.1	6.0	Whitney 1987
N. Wisconsin (T35N, R14E)	29.3	43.6	Stearns 1949
S. Wisconsin (Cadiz Twp.)	3.4	28.2	Sharpe and others 1987
Northeastern Ohio (Wayne Co.)	4.2	6.0	Whitney and Somerlot 1985
Northwestern Ohio	8.9	9.5	Gysel 1944

[a] Upper estimate of percentage as includes some red maple a well as sugar maple.

of Michigan directly to the west of beech's range limit. On the richer, loamy soils of the region (Albert 1995; Barrett and others 1995), it occasionally accounted for over 50 percent of the trees reported (Bourdo 1955). Sugar maple was also abundant (15 to 20 percent of the trees) in the more calcareous till derived soils of upstate New York south of Lake Ontario (Marks and others 1992). Braun (1950) stated that the boundary between the mixed mesophytic forest region and the beech-maple forest region coincides with the Wisconsin glacial boundary. In northeastern Ohio, however, sugar maple was fairly common (18% of the trees present) on the alkaline (10-15% carbonate) late Wisconsinian Hiram till. Its abundance dropped precipitously to 3.5 percent on the older more deeply leached (no natural lime within 5 feet) late Wisconsinian Hayesville and Navarre tills (Bureau and others 1984; White 1967; Whitney 1982). On the more acidic, residual soil south of the glacial border, sugar maple represented only 2.6 percent of the trees. Here it was confined to lower slope positions and the richer alluvial soils of floodplains (Whitney 1982). Sugar maple was likewise rare (<2 percent of the trees) and confined to the richer, more calcareous soils of the valley floors in the unglaciated Ridge and Valley Province of central Pennsylvania (Abrams and Ruffner 1995).

Soil texture and nutrients appear to have been major determinants of sugar maple's abundance in the Midwest. Sugar maple was positively associated with the richer loams and sandy loams of the morainal areas of northern lower Michigan (Harman and Nutter 1973; Whitney 1986) and the Upper Peninsula of Michigan (Barrett and others 1995). Sugar maple was a sure sign of rich, fertile soils to the early settlers (Whitney 1994). In southern Michigan, Indiana and northern Ohio, sugar maple exhibited a preference for the richer, somewhat finer textured (silt and clay rich) loams of the till plains and the end moraines (Crankshaw and others 1965; Dodge 1987; Kapp 1978; Medley and Harman 1987; Whitney 1982). Sugar maple is a fairly drought-sensitive species (Bahari and others 1985). Its shift to the finer textured loam in the lower Midwest may have compensated for the greater evaporative stress to the south.

Drainage and landscape position also influenced sugar maple's occurrence on the beech and sugar maple dominated till plains. As it requires an adequate air supply for the growth of its roots, it reached its greatest abundance on the better drained soils of the swells and the slopes of the till plains. Beech was more a species of the poorly drained swales (Gilbert and Riemenschneider 1980; Lindsey 1998; Shanks 1953).

Changing Status

Comparisons of sugar maple's abundance in the early land survey records with more recent forest surveys suggests that sugar maple has at least maintained and in many cases increased it relative density in the postsettlement forest (Table 1). It showed major gains relative to other species in northern Vermont, in the Catskills, in northwestern Pennsylvania, in Michigan, and in Wisconsin. Significant increases were also noted in the relative importance value (another measure of abundance (Ward 1956)) of sugar maple in the Gogebic Iron Range of northern Wisconsin (Mladenoff and Howell 1980), and in a variety of soils in northern lower Michigan (Harmon and Nutter 1973). The increase has variously been attributed to the cessation of fire (Sharpe and others 1987), to sugar maple's ability to resprout when cut and its prolific seed production (White and Mladenoff 1994) and to sugar maple's plasticity and its ability to reproduce and grow successfully in the understory as well as large and small gaps in the canopy (Canham 1988; Frelich and Lorimer 1991; Stearns 1949). Although sugar maple is very sensitive to crown and ground fires (Simpson and others 1990), other disturbances in the form of blowdowns or the death of a canopy tree favored sugar maple in the presettlement forest (Frelich and Lorimer 1991; Hough and Forbes 1943). Likewise sugar maple's shade tolerance and its vigorous seed and sprout reproduction made it "the most aggressive reproducer" of the cutover northern hardwood forest (Illick and Frontz 1928).

Management Implications

Sugar maple's high site requirements (Hornbeck and Leak 1992) and its significant postsettlement increase on a variety of soils and sites (Harman and Nutter 1973) suggests that sugar maple may now occupy a number of marginal sites, i.e., sandy nutrient poor soils, shallow acidic soils on ridges, and soils with impeded drainage. Sugar maple typically has slow growth, deteriorates at an early age, or succumbs to fungi and cankers on these sites (Nowak 1996; Ward and others 1966; Wilde 1976). "Off-site" conditions may partially explain the recent decline of sugar maple on a number of acidic shallow, nutrient poor sites across the Northeast (Horsley and others, this volume; Kolb and McCormick 1993; Wargo and Auclair 1999[1]).

Sugar maple is a fairly nitrophilous species. Sugar maple reached its greatest abundance in Indiana's presettlement forests on soils with a high total (Kjeldahl) soil nitrogen level (Crankshaw and others 1965). Nitrogen availability and nitrogen mineralization rates are high in most woodland ecosystems dominated by sugar maple (Pastor and others 1982; Zak and Pregitzer 1990). Several investigators have suggested a deficiency of nitrogen could limit sugar maple's establishment on many old field sties, where plowing and erosion reduced the organic matter and nitrogen content of the soil (Ellis 1974; Lennon and others 1985). Much of the marginal farmland of the northeastern United States has been abandoned over the last 100 years (Whitney 1994). Sugar maple's exacting site requirements could explain its inability to capture many of these old field sites relative to its more successful but less nitrogen demanding congener, red maple.

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History of Sugar Maple Decline

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Abstract

Only a few episodes of sugar maple dieback or decline were recorded during the first half of the 20th Century. In contrast, the last 50 years have provided numerous reports of both urban and forest dieback/decline. In the late 1950s, a defoliation-triggered decline, termed maple blight, that occurred in Wisconsin prompted the first comprehensive, multidisciplinary study of a sugar maple decline. That research, and other investigations since, provided the conceptual framework for a model of sequential, stress-initiated cause and effect for dieback/decline disease. Many cases of urban maple dieback/decline have been attributed to soil compaction, drought, impeded soil water availability, or toxic effects of road deicing salt. Most cases of forest or sugarbush decline have been associated with the initiating stresses of insect defoliation or drought, singly or in concert. Mortality of stressed trees is often caused or hastened when roots or twigs are invaded by opportunistic, secondary organisms, especially the root rot fungi *Armillaria* spp. (and probably *Xylaria* sp.). In the past two decades, freezing of roots associated with periods of thaw-freeze and of deep cold, especially when snow cover was minimal or lacking, have been correlated with major decline episodes in eastern Canada and northern New England and New York. An hypothesis that dieback results when death of roots leads to transpiration-stress and vessel cavitation is supported by observations that dieback/decline episodes attributed to droughts appear correlated temporally with prior root-freeze events. Such events are now believed responsible for the serious maple dieback/decline problems in southern Quebec in the 1980-1990s that at first were hypothesized to result from atmospheric deposition. While atmospheric deposition has been discounted as a direct cause of maple declines, the long-term and perhaps complex effects on tree health of deposition-hastened changes in soil chemistry, especially in areas with soils susceptible to acidification, are the primary subjects of current investigations.

Introduction

Sugar maple (*Acer saccharum* Marsh.) has many highly valued qualities. Its long life, pleasing form, and brilliant fall color have made it a favored tree for gracing dooryards and roadsides from New England to the Lake States. Its hard, but easily-worked, light-colored wood is widely used for flooring, furniture, and many specialty products. Wood with uniquely figured patterns, including "bird's eye", "curley", or "fiddleback" is highly prized for fine woodworking. Further, the romanticism and economic values associated with spring sapflows and maple sugaring are as strong today as in colonial times.

Certain ecophysiological characteristics of sugar maple have made it easy to exploit these values. Sugar maples fruit prolifically; seeds, which mature in the fall, are readily dispersed by wind and germinate the following spring. Well over 5,000,000 seeds per acre are common in good seed years and, establishment is often highly successful. Carpets of young seedlings are common, and the ability of shade-suppressed seedlings and saplings to respond when released has enabled the species to become a predominant component of many forest types. Sugar maple does best on deep soils that are moderately coarse-textured, moist and well-drained (Godman et al. 1990).

Sugar Maple Declines

Although records are lacking, it is highly probable that sugar maple has long experienced serious episodes of dieback/decline. Many of the environmental stresses affecting today's forests occurred in pre-European settlement times; droughts, insect defoliation, fire, damaging winds, and ice storms were no strangers to those early forests. Although opinions vary, the effects of these disturbances, especially, perhaps, fire and windstorms, created mosaics of both uneven-aged and even-aged forests of differing successional stages (Clawson 1983, Loucks 1983). Old, uneven-aged stands contained a high proportion of mature and overmature trees—those considered most susceptible to many of the stress factors that trigger declines. As colonization ensued, activities such as logging, clearing, burning, pasturing, and sugaring intensified dramatically. Areas best suited for tree growth were often those most desired for agricultural uses. Much of the old growth forest was removed, especially during the latter half of the 19th century. Reestablishment of forests on land withdrawn from agriculture has resulted in large areas of relatively even-aged forests that, during the latter half of the 20th century purportedly began reaching an age of increased susceptibility to stress events.

While a few reports of maple dieback/declines appeared in the first half of the 20th century (Hartley and Merrill 1915; Marsden 1950; McKenzie 1943), it was not until after 1950 that accounts of such problems become numerous. Several reviews present the chronologies and presumed causes of sugar maple dieback/decline episodes (e.g. Allen et al. 1992; Houston 1985, 1987; McIlveen et al. 1986; Millers et al. 1989; Sinclair 1964; Westing 1966). The purpose of this brief paper is not to restate what was presented in those reviews, but, rather, to discuss the main themes that seem most pertinent to the present situation.

The Nature of Sugar Maple Dieback/decline

One conceptual model of sugar maple dieback/declines in forest situations was structured around the premise that disease manifestation (progressive crown dieback sometimes leading to continued tree decline and death) results when one or more predisposing (sensu stricto) stress

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factors reduces resistance to invasion by opportunistic, secondary-action organisms that result in death of tissues—sometimes of trees (e.g. Houston 1981, 1992). This model evolved initially from research on "maple blight", a dieback/decline of sugar maple in northeastern Wisconsin, triggered by insect defoliation (Anonymous 1964, Giese et al. 1964). A complex of insects including several species of leafrollers and the maple webworm, *Tetralopha asperatella* (Clem.) caused severe defoliation on about 10,000 acres in the mid-late 1950s (Giese and Benjamin 1964). Dead and dying trees and saplings usually were attacked aggressively by *Armillaria* sp. (Houston and Kuntz 1964). Severely damaged stands, prior to being defoliated, had low basal area and density, and a high proportion (> 50%) of sugar maple. During the 10 months prior to the onset of mortality, the region had below-normal precipitation (-8.3 inches) (Skilling 1964).

Later studies elsewhere confirmed the defoliation stress/*Armillaria* association and clarified the biochemical basis for the lowered resistance of defoliation-affected tissues to attack by this opportunist (Parker and Houston 1971; Wargo 1972; Wargo et al. 1972;Wargo and Houston 1974). Another opportunist, *Steganosporium ovatum* (Pers.) S.J. Hughes, appeared to hasten the death of defoliation or drought-stressed twigs and branches (Hibben 1959, Wargo and Houston 1974). Research on several other stress-initiated problems (e.g., Appel and Stipes 1984, Ehrlich 1934, Houston 1994a, Schoeneweiss 1981a, b, Wargo 1977, 1983) has validated the chronological and spatial premises of the following simple, general model for dieback/decline diseases:

> 1. Healthy trees + stress → Altered trees (tissues) (dieback begins)
>
> 2. Altered trees + more stress → Trees (tissues) altered further (dieback continues)
> •
> •
> •
> n. Severely altered trees (tissues) + organisms of secondary action → Trees (tissues) invaded. (Trees lose ability to respond to improved conditions, decline, and perhaps die.)

For the defoliation-triggered sugar maple dieback/declines just described, the model would be:

> 1. Healthy sugar maple trees + defoliation → Sugar maples altered (dieback begins)
> •
> •
> •
> n. Altered trees + *Stegonosporium ovatum* → Twig dieback accelerated + *Armillaria* sp. → Roots, root collars invaded, trees decline, die.

In these statements, the numbers refer to sequential episodes of stress events and host response; "n" indicates that at some point or degree of host change, organisms of secondary action are able to invade altered tissues successfully. The model above indicates that although host changes sufficient to allow organism attack can occur after a single severe stress event, such changes usually follow multiple or repeated events. Arrows are to be read as "leads to".

The statements of this model can be construed as summaries of several important relationships:

i) Dieback of trees or tissues often results from the effects of the stress factor(s) alone. With abatement of stress, and in the absence of significant colonization by saprogens or secondary insects, dieback often ceases and trees recover. The dieback phase can be viewed as a survival mechanism whereby the tree adjusts to its recently encountered adverse environment.

ii) Stress alone, if sufficiently severe, prolonged, or repeated, can cause continued or repeated dieback and even death. Numerous reports exist of tree mortality following either unusually severe and prolonged drought or episodes of severe defoliation, especially if repeated, perhaps even in the same growing season. Even one severe defoliation occurring concomitantly or sequentially with drought can result in high tree mortality.

iii) Usually, however, the decline phase, wherein vitality lessens and trees succumb, is the consequence of organism invasion of stress-altered tissues. Recovery from this phase depends on many factors including the vitality of the tree, the particular tissues invaded, the relative aggressiveness of the organism(s), and the degree of invasion.

iv) Where and when the dieback phase occurs is closely related to where and when the triggering stress(es) occurs. The decline and mortality phase is related, in addition, to the temporal and spatial distributions of the organisms of secondary action.

These summary statements point out the inherent difficulty in separating "dieback" from "decline". Such a separation seems difficult and arbitrary—for most dieback/declines reflect complex continuums of host responses to successive and/or multiple events.

Temporal-spatial Patterns of Sugar Maple Dieback/declines

Comparisons of reported major episodes of sugar maple dieback/decline provide a picture of when and where trees have been affected and the stress factors or events that triggered them. For example, sorting the reports listed by Millers et al. (1989) by place, i.e., by urban or roadside (Table 1) vs. forest or sugarbush (Table 2), reveals that in eastern U.S., the few early (pre-1950) episodes were limited to urban/roadside problems that were triggered (as have subsequent problems in these arenas) by the effects of such stresses as drought, road deicing salt, soil compaction, and occasionally by *Verticillium* wilt, *Phytopthora* and *Fusarium* cankers, and *Armillaria* root disease (Table 1).

Table 1.—Chronology of dieback, decline, mortality problems of sugar maple reported for roadside or urban situations (adapted from Millers et al. 1989).

Dates	Location	Cause
1912-13	Washington DC - New England	drought
1939-49	Massachusetts	drought, defoliation
1956-58	Lake States	drought, *Verticillium*, *Phytopthora*, *Armillaria*
1950-60	Northeast	drought, salt, defoliation
mid-60's	Michigan	drought, salt
1968-70	Northeast	salt, pollution (?)
1975-78	Maine	mech., soil comp., pollution (?)
1976	Lake States, Northeast	drought, salt, compaction
1977-82	Wisconsin	*Fusarium*, *Phytopthora*
1978-81	Minnesota	drought, *Verticillium* wilt
1982	Missouri	?
1984-86	Iowa	?

Table 2.—Chronology of dieback, decline, mortality problems of sugar maple reported for forest trees and sugarbushes (adapted from Millers et al. 1989).

Dates	Location	Cause
1951-54	NY, VT	defoliation (Forest tent)
1956-58	MA	drought
1958-62	WI	defoliation/*Armillaria* (leaf rollers, webworm)
1958-62	Lake States	high water tables
1950-60's	Northeastern US	drought, etc.
1957-67	CT	defoliation, (gypsy moth, spanworm)
1968-71	NY, ME	defoliation (saddled prominent)
1973	PA	defoliation (forest tent caterpillar)
1977	MI	defoliation (forest tent caterpillar, saddled prominent)
1978-81	MN	drought
1980-82	NY	defoliation (forest tent caterpillar)
1981-85	NH	defoliators
1984	MN, MI	drought, *Agrilus*
1984	NY	defoliation
1984-85	PA	defoliation, poor sites, thrips, anthracnose
1985	MA	?
1984-86	VT	defoliation (forest tent caterpillar)
1988-89	WI, MN	drought
1980-90	Quebec, NY	thaw-freeze, root-freeze

In contrast, the principal stress factors reported as triggers of major dieback/decline problems of forest and sugarbush, (noted only since 1951 in U.S.), are insect defoliation and drought, singly or in concert. Saprogens involved in forest decline situations have included *Armillaria* spp., *Agrilus* spp. and anthracnose fungi (Table 2).

Accounts of maple dieback/decline from Canada generally have paralleled those from the U.S. Thus, except for episodes of dieback in the Beauce region of southern Quebec in 1932 (Pomerleau 1944) and elsewhere from 1937 to 1949 (especially from 1946 to 1949) (Pomerleau 1953), and in Ontario in 1947 (McIlveen et al. 1986), few accounts appeared prior to 1950. Most of the early episodes were triggered by insect defoliation, but a few were associated with the drought periods of the 1930s and later.

Since 1950, episodes of maple dieback/decline associated with insect defoliation, drought, logging, and more recently, with root freezing have increased in number. The relationship between root freezing (associated with deep soil freezing during times of low or absent snow cover) and the onset of dieback has received increasing attention in Canada and northeastern U.S. (e.g. Lachance 1985, Bauce and Allen 1991), has been replicated experimentally (Pomerleau 1991, Robitaille et al. 1995), and has been proposed as a major factor triggering maple decline in eastern Canada (e.g. Auclair et al. 1992). Drought and root freezing have been proposed as causes of irreversible cavitation in sapwood vessels that, in turn, prevents water movement (Auclair 1993, Auclair et al. 1992, Sperry et al. 1988, Tyree and Sperry 1989). Impairment of water conduction is believed to be responsible for crown dieback.

Usually, close examination of dieback/decline problems, even in remote areas, has revealed evidence for the prior occurrence of stress factors that singly, or in combination, are known to initiate dieback and also to render tissues susceptible to opportunists whose attacks can prevent recovery and hasten tree decline. Prior management practices (e.g., thinning) (Kelley 1988) and climatic episodes (e.g. drought) (Allen 1987, Bauce and Allen 1991) have been correlated with increased mortality following defoliation. It is probable that variations in trees' response to stress can occur locally due to differences in genotypes, local differences in tree vigor, patterns of stress occurrence, presence or absence or vigor of opportunistic organisms, or variations in site quality.

Sometimes imbedded within the maple decline complexes are two diseases caused by primary pathogens: *Verticillium* wilt, a vascular disease caused by *Verticillium dahliae* Kleb. which has been noted only in urban situations, and sapstreak, also a vascular disease, caused by *Ceratocystis virescens* (Davidson) C. Moreau, which rarely has been observed other than in forests and sugarbushes. Although caused by a primary pathogen, sapstreak should be considered part of the decline complex based on symptomotology and the facts that (1) injuries to roots or root collars are necessary as infection courts for *C. virescens*, and (2) tree mortality is almost always associated with attacks by *Armillaria* sp. or *Xylaria* sp. (Houston 1993, 1994b). The importance of injuries for sapstreak infection creates a close temporal-spatial relationship between human activities and disease development. Thus, most diseased trees are located adjacent to skid trails or woods roads, and they develop symptoms within 1 to 4 years after infection. Recognized in North Carolina and Tennessee in the late 1930s and early 1940s (Hepting 1944), sapstreak was not reported from the Lake States until 1960 (Kessler and Anderson 1960) or from the northeast until 1964 (Houston and Fisher 1964). Whether recent increases in reported cases of sapstreak represent increases in disease incidence or in disease recognition is not known.

The ability of sugar maple to dominate favorable forest sites was noted earlier. Sometimes, however, this species colonizes sites unfavorable for later growth and development. For example, stands of sugar maple have developed on many abandoned fields in New England and New York. It is on these sites, often too wet, too dry, or nutrient impoverished, and along roadsides, that many sugar maple decline problems have occurred. Favoring sugar maple on wet, cool, bottom lands can create an unstable situation, as the species is neither long-lived nor vigorous on wet or dry soils and is extremely sensitive to abiotic or biotic stresses under such conditions. Widening and paving roads certainly have affected roadside maples adversely, and the added insult of road salt has created an intolerable environment for this mesically adapted, nutrient demanding species (LaCasse and Rich 1964). Trees along roadsides are prone to damage from drought events not sufficiently severe to affect forest trees.

Ironically, it was the dieback and deterioration of roadside trees that prompted a major research program on maple decline in Massachusetts in the early-mid 1960s (Westing 1966). Forest researchers were put in the position of trying to characterize a problem that at that time did not exist in the forests of Massachusetts. From this effort, however, came the initial thrust to understand soil nutrient - maple tree condition relationships (Mader and Thompson 1969).

The Stresses

Defoliation.—Effects of defoliation are addressed elsewhere in this symposium. Comments here are limited to pointing out that the consequences of defoliation stress were intensively investigated in studies of maple blight in Wisconsin (Anonymous 1964, Giese et al. 1964). Research on this problem comprised the first truly multidisciplinary investigation of a sugar maple decline. Those investigations, together with several since (Bauce and Allen 1991, Parker and Houston 1971, Wargo 1972, Wargo and Houston 1974) revealed the complex nature of host response and secondary organism attacks that characterize a dieback/decline disease and as described earlier, provided the model used as a framework for study of dieback/decline diseases of many tree species (Houston 1981, 1992).

Defoliation can affect all age classes, and even young trees exhibit twig and branch dieback that can progress with repeated defoliations. Death of young defoliated trees is usually the consequence of root invasions by opportunists, especially *Armillaria* sp. Such killing attacks of young trees may occur in forest situations, even after a single defoliation, where abundant and vigorous opportunist populations occur. Where such populations are absent, tree mortality may not occur, even after repeated defoliations (e.g., Gregory and Wargo 1986, Parker and Houston 1971).

Drought.—Throughout this century, drought has been cited as a cause or a possible contributing factor of maple dieback/decline (Bauce and Allen 1991, Griffin 1965, Hartley and Merrill 1915, Hibben 1962, 1964, Marsden 1950, Ohman 1969, Sinclair 1964, Skelly and Wood 1966, Skilling 1964, Westing 1966). Beginning in the 1950s, notable episodes of maple dieback/decline occurred during or following periods of severe water shortage (e.g., Table 2). Observations that defoliation episodes, that are coincident or closely followed by drought are especially devastating (e.g. Allen 1987), are paralleled by the recent analyses by Auclair et al. (1996) suggesting that the effects of root freezing are especially damaging if followed by drought. Dieback/decline appears to result when desiccation of branches and refoliating tissues (following defoliation), or of the first spring flush of leaves (following winter root freeze), is enhanced when conducting tissues are injured or killed by cavitation. The biochemical changes in sugar maple caused by drought and defoliation are similar (Parker 1970), and these changes favor growth and invasion by *Armillaria* spp. (Wargo 1972, Wargo and Houston 1974). Thus, because of their effects on host-defense systems, combinations of stress factors render trees exceptionally vulnerable to lethal attacks by opportunistic organisms.

Extremes of Temperature.—In northern Wisconsin, fall frosts killed immature leaves and terminal buds that formed after a midsummer defoliation and thus contributed to branch and twig dieback (Houston and Kuntz 1964). Other cold events also have been associated with maple dieback and decline. Episodes of thaw-freeze and of deep cold during snow-free winter periods were associated with diebacks of sugar maple and other species (e.g. Pomerleau 1944, 1991). These events apparently occurred commonly in the first half of this century yet, major diebacks did not occur during that time, presumably because tree populations were relatively young (Auclair et al. 1992, Auclair et al. 1996). Thus, forest maturation is postulated as a key factor preconditioning trees to climatic injury and dieback (Auclair et al. 1996, 1997). The recent re-recognition that root freezing is an important factor in northern forests stems largely from the work by Auclair and coworkers (e.g., Auclair et al. 1992, 1996) in Quebec, and by Bauce and Allen (1991) in New York. Auclair et al.'s (1996) analysis of climate data suggests that episodes of forest dieback are correlated with heat and drought stress but only after forests have been affected by root-freezing events. According to Auclair et al. (1996), crown dieback reflects drought effects in trees injured previously by freezing.

Acidic Deposition.—In the 1980s concern arose that atmospheric deposition, especially acidic deposition, was causing sugar maple decline in Ontario, Quebec, and Vermont (Carrier 1986, McLaughlin et al. 1985, Vogelmann 1982, Vogelmann et al. 1985). Surveys and studies showed damage to sugar maple on a number of sites with soils deemed highly susceptible to acidification (e.g., the Muskoka area in southern Ontario, the Beauce region of southern Quebec and Camel's Hump in Vermont). Observers promoting acid-deposition hypotheses tended to dismiss such factors as defoliator outbreaks, climatic events such as early thaws or droughts, or disturbances caused by harvesting or tapping as the primary or sole cause. Attention was focused narrowly on atmospheric deposition. Subsequently, it was realized that the rather sudden appearance of dieback and decline in the Canadian forests was not the result of a direct effect of acid deposition, but rather a consequence of one or a combination of several factors previously associated with dieback/declines, especially the winter freeze-thaw events during periods of little snow cover (e.g., Pitelka and Raynal 1989, Auclair et al 1992). Concern remains that acidic deposition may play a role in certain cases of sugar maple decline, especially as it may influence the chemistry of soils susceptible to acidification over the long term. That concern is strongly demonstrated by the emphasis placed on soil chemistry relationships at this symposium.

Synthesis

The fact that few major episodes of maple dieback/decline occurred during the first half of the 20th Century suggests that either there were fewer or less severe predisposing stresses, or that the forests then were more resistant or resilient to such stress. Arguments for the latter seem most plausible if, as Auclair et al. (1996, 1997) suggest, younger trees are less susceptible than mature ones to cavitation-inducing climatic events. Correlations of dieback episodes and a number of weather/climate indices, both local and global, support that hypothesis (Auclair et al. 1996, 1997). The paucity of reported sugar maple dieback episodes early in this century, even though there were frequent and severe winter-thaw-freeze and root-freeze events, as well as significant drought periods, presumably stems from the fact that in most northern hardwood forests, maple had not reached its susceptible age (= commercial maturity) of 100 years (Auclair et al. 1996) or 150 years (Millers et al. 1989) following the massive harvesting that occurred between 1860 and 1890. Under this scenario, forest (species) maturation would seem critical.

On the other hand, old-age may be less critical when stresses other than climate extremes are involved. Defoliation was the initiator of maple blight, but fall frosts, drought, and root pathogens, especially *Armillaria* sp. were all involved in the dieback, decline, and mortality of defoliated trees. Outbreaks of a unique suite of defoliators began in "young" stands soon after unusually heavy harvesting of older trees had opened up the forest and stimulated sapling growth. As the insect populations increased and spread, all ages were defoliated—and all ages suffered heavy mortality. Perhaps forest stand "maturation" is not only a matter of physiological predisposition to cavitation of individual trees, but also of the abundance and condition of secondary-organism populations within "mature" stands.

Whether, or how, outbreaks of defoliating insects are associated with the climate measures utilized by Auclair et al. (1996) needs to be determined. Populations of some defoliators are favored by hot, dry summers, and the concomitant or successive occurrence of defoliation and drought has proven disastrous to sugar maple (Allen 1987). Finally, it is clear that natural changes in soil chemistry, especially acidification, when augmented by acidic deposition, may significantly affect growth and tree resistance to stresses and opportunistic organisms. How such edaphic factors influence or are influenced by the stress factors known to severely affect sugar maple remains unclear.

Conclusion

Most of the maple dieback/declines that have been studied intensively were initiated by severe, acute stress factors, such as defoliation, drought, or winter root freezing. The concomitant or sequential occurrence of these in various combinations contributes strongly to the acuteness and severity of host responses.

Understanding of cause-effect relationships and underlying mechanisms is increasing. For example, the emerging hypothesis that dieback following certain stresses is a consequence of vessel column cavitation is balanced by climate models which suggest that cavitation may not be especially serious unless followed by severe drought. These concepts must be evaluated in light of current understanding of the role of secondary-action organisms as agents that impair recovery and cause mortality of stressed trees.

The focus now and for the immediate future, and which is emphasized in this symposium, is on soil relationships. It is clear, however, that knowledge gained from the past needs to be carefully interpreted in light of what already is known here about histories of management, drought, defoliation, and root pathogens. All of these factors are part of the picture. From the point-of-view of a forest dieback/decline researcher, it does not get any better than this!

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A Ten-Year Regional Assessment of Sugar Maple Mortality

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Abstract

The North American Maple Project (NAMP) monitored annual sugar maple mortality from 1988 through 1997 in Maine, Massachusetts, New Brunswick/Nova Scotia, New Hampshire, New York, Ontario, Quebec, Vermont, and Wisconsin. Annual mortality in Minnesota, Ohio and Pennsylvania was evaluated for 1992 through 1997. When data from the dominant/codominant and intermediate/suppressed crown levels were combined, average annual mortality (% trees) ranged from 1.9% (New York) to 0.3% (New Brunswick/Nova Scotia) in sugarbushes (SBs) and 1.9% (New Hampshire) to 0.4% (Wisconsin) in maple stands not managed for syrup production (NSBs). In general, mortality of dominant/codominant sugar maple was lower than in the intermediate/suppressed crown position. Average annual mortality was not significantly different among each of three elevational categories or among each of three deposition levels for wet sulfate or wet nitrate. Mortality in plot-clusters located >300 m elevation and exposed to high levels of wet nitrate (>20 kg/ha/yr) or wet sulfate (>27.5 kg/ha/yr) deposition was significantly greater in both SBs and NSBs compared to mortality in plot-clusters exposed to high levels of deposition but located <300 elevation (SB: >300 m 2.2%, <300 m 0.6%; NSB: >300 m 1.1%, <300m 0.3%). A number of small, but statistically significant ($p \leq 0.05$), differences in mortality occurred among three ecological Divisions, three Provinces and three Sections in the U.S., and three Ecozones and four Ecoregions in Canada. Within 13 geographic regions (states and provinces), two crown positions, two management categories, three levels of elevation, three deposition levels for both wet nitrate and wet sulfate, and 18 biophysical regions, annual sugar maple mortality documented by the NAMP was similar to mortality reported in the literature for typical northern hardwood stands. Mortality in SBs was similar to that in NSBs.

Introduction

The North American Maple Project (NAMP) was initiated in 1988 in response to public concern for the condition and sustainability of the sugar maple (*Acer saccharum* Marsh) resource. An earlier paper (Allen et al. 1992) reported on the crown condition of overstory sugar maple monitored during the first three years (1988-1991) of the project. More recently, Allen et al. (1995) summarized changes in crown condition for 1988 through 1995 and presented an overview of mortality. Here we examine nine years of sugar maple mortality (1989 through 1997) in the context of geographic regions (states and provinces), crown position, management category, levels of atmospheric deposition, elevation, and ecological unit. We address the hypothesis that sugar maple mortality which occurred in the NAMP plots during this period is within the range expected for the stand and site conditions included in the study.

Methods

The general methods used to select, establish and measure plot-clusters (Millers et al. 1991) changed little during the ten-year history of the NAMP (Allen et al. 1995). Stands were selected systematically to facilitate frequent visits, to cover a variety of sugar maple sites, to encompass a range of atmospheric deposition levels, and to assure long-term integrity. A cluster of five 20 x 20 m permanent plots was established in each stand. To qualify, a stand had to have an overstory that contained 50% or more sugar maple, 50-150 years old. All trees $\geq$ 10 cm diameter at breast height (1.4 m) were evaluated annually for crown condition and survival. Analyses of sugar maple mortality are presented as annual percent tree loss resulting from "natural" mortality. That is, we did not include loss of trees that were deemed healthy but died or were removed as a direct result of some forest management related activity, such as road building or thinning. Natural mortality constitutes a baseline for determining losses ostensibly due to natural stresses. The occurrence and extent of natural disturbances (e.g., insect defoliation, drought, wind damage, etc.) were incorporated into the database for each plot-cluster and used to establish the temporal occurrence and extent of stresses.

Annual mortality was determined by monitoring the number of trees surviving from one year to the next:

Annual Plot-Cluster Mortality=

$$\frac{[(\text{number of live trees in year t-1}) - (\text{number of live trees in year t})] \times 100}{\text{number of live trees in year t-1}}$$

Plot-cluster mortalities were then averaged within each year to obtain annual mortalities for the various strata. The strata were based on region (state, province, country), elevation, deposition level, and ecotype (Table 1). Estimates of wet sulfate and wet nitrate deposition for each plot-cluster were interpolated using deposition maps (5 kg/ha isopleths) provided by Environment Canada and the U.S. National Atmospheric Deposition Program/National Trends Network Coordination Office. UTM coordinates located each site relative to the nearest isopleth or monitoring station. Mortality figures are based on 7,569 dominant/codominant (D/C) and 3,885 intermediate/suppressed (I/S) sugar maples (N = 11,454) monitored annually between 1988 and 1997 (Table 2). Two-way comparisons were made with the t-test, and analysis of variance (ANOVA) in conjunction with Tukey's test for multiple comparisons. Prior to analysis all data were tested for homoscedasticity. Alpha was set at 0.05 as a nominal indicator of significance for all comparisons.

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Table 1.—Ecological variables used to stratify NAMP data on sugar maple mortality

VARIABLE	CATEGORIES	NUMBER OF PLOT-CLUSTERS
Elevation	High >450 M	39
	Medium 300-450 m	71
	Low < 300 m	53
	Divisions	
Biophysical Units	Warm Continental	25
United States	Warm Continental Regime Mts.	60
(McNab and Avers 1994)	Hot Continental	21
	Provinces	
	Eastern Broadleaf Forest (Continental)	17
	Laurentian Mixed Forest	25
	Adirondack New England Mixed Forest	60
	Sections	
	White Mountains	17
	New England Piedmont	13
	Green Taconic, Berkshire Mts.	23
Canada	**Ecozones**	
(Ecological Stratification	Atlantic Maritime	24
Working Group 1995)	Boreal Shield	16
	Mixed Wood Plain	18
	Ecoregions	
	Algonquin-Lake Nipissing	6
	Appalachian	14
	Lake Erie Lowland	6
	Manitoulin-Lake Simcoe	8
	Northern New Brunswick Uplands	5
	Southern Laurentians	8
Wet Sulfate Deposition	High >27.5 kg/ha/yr	24
	Medium 17.6-27.5	192
	Low <17.6	49
Wet Nitrate Deposition	High >20 kg/ha/yr	37
	Medium 16-20	71
	Low <16	57
Forest Management	Sugarbush	
	U.S.	53
	Canada	31
	Nonsugarbush	
	U.S.	53
	Canada	28

Table 2.—Regional distribution of plot-clusters and number of sugar maples monitored by NAMP

REGION	NO. PLOT-CLUSTERS IN 1988	INITIAL AVE.(RANGES) BASAL AREA (m^2/ha)	NUMBER OF LIVE SUGAR MAPLES BY CROWN POSITION (1988) DOMINANT/ CODOMINANT	INTERMEDIATE/ SUPPRESSED	INITIAL NO. LIVE SUGAR MAPLES
Maine	18	29.1 (20.2-40.8)	726	455	1,181
Massachusetts	10	27.9 (15.4-36.2)	453	175	628
Michigan	10	24.1 (17.8-31.0)	194	78	272
Minnesota [a]	8	24.4 (24.5-31.5)	221	238	459
New Brunswick/ Nova Scotia	11	22.7 (12.9-31.0)	856	116	972
New Hampshire	6	24.6 (15.2-36.5)	257	121	378
New York	18	24.8 (15.7-35.5)	645	438	1,083
Ohio [a]	6	33.7 (28.3-39.9)	141	120	261
Ontario	24	26.8 (15.4-40.3)	928	434	1,362
Pennsylvania [a]	6	29.1 (21.6-36.4)	173	112	285
Quebec	24	27.6 (17.4-35.6)	1,285	594	1,879
Vermont	26	27.6 (12.2-43.4)	1,054	588	1,642
Wisconsin	18	24.9 (15.7-32.4)	636	416	1,052
TOTAL	185		7,569	3,885	11,454

[a]Plot-clusters were not established in these regions until 1992, the remainder were initiated in 1988.

Results

Canada vs United States

Percent sugar maple mortality in the NAMP plot-clusters by crown position from 1989 through 1997 was similar in both Canada and the United States, except in a few cases. Generally, mortality of dominant/codominant (D/C) trees was similar in both sugarbushes (SB) and non-sugarbushes (NSB). However, in four of nine years (1989, 1990, 1992, 1997), mortality of intermediate/suppressed (I/S) sugar maples in Canada's sugarbush (SB) plot-clusters exceeded that of sugar maple in the dominant/codominant crown position. During the remaining five years, average mortality in both crown positions was approximately equal (Table 3).

Mortality of understory sugar maple in U.S. SBs exceeded that in the overstory in seven of nine years; mortality in the two crown positions was approximately the same in 1992 and 1997. Sugar maple mortality in the intermediate/ suppressed crown class for NSBs always exceeded overstory mortality in both countries.

In 1989, mortality of intermediate/suppressed maples in U.S. SBs (4.0%) was more than four times that which occurred in the dominant/codominant crown class (0.8%). Comparative mortality for the two management categories was more dissimilar in the intermediate/suppressed crown position compared to the dominant/codominant trees. For Canadian SBs, annual mortality of dominant/codominant maple ranged from 0.4% (1993) to 0.9% (1995) and intermediate/ suppressed losses varied from 0.4% (1994) to 2.4% (1990). Comparative figures for maple in U.S. SBs were, D/C: 0.3% (1990) to 1.3% (1995) and, I/S: 1.0% (1993) to 4.0% (1989).

Differences in the nine-year average annual tree mortality when SB and NSB data within each country were combined

Table 3.—Average annual mortality (% trees) of sugar maple for NAMP plot-clusters in Canada and the United States (1989-1997) by management category and crown position)

COUNTRY	MANAGEMENT CATEGORY[a]	CROWN POSITION[b]	YEAR								
			1989	1990	1991	1992	1993	1994	1995	1996	1997
CANADA	SB	D/C	0.5	0.5	0.8	0.6	0.4	0.5	0.9	0.9	1.1
		I/S	1.2	1.5	0.8	2.4	0.5	0.4	1.0	0.9	2.3
	NSB	D/C	0.4	0.4	0.6	0.6	0.3	0.3	0.8	0.3	0.3
		I/S	2.1	2.2	1.3	1.4	1.8	1.6	1.6	1.2	1.1
U.S.	SB	D/C	0.8	0.3	0.8	0.9	0.6	0.7	1.3	0.7	0.7
		I/S	4.0	1.6	1.5	1.0	1.0	1.1	2.7	1.6	0.8
	NSB	D/C	0.8	0.3	0.6	0.5	0.8	0.4	0.7	0.5	0.3
		I/S	2.7	1.7	2.3	1.3	1.0	0.8	1.8	1.6	2.4

[a] SB = sugarbush, NSB = non-sugarbush
[b] D/C = dominant/codominant; I/S = intermediate/suppressed

were similar in both dominant/codominant (Can.: 0.6 ± 0.1%, U.S.: 0.7 ± 0.1%) and intermediate/suppressed (Can.: 1.4 ± 0.1%, U.S.: 1.7 ± 0.2%) crown positions and were significantly different between crown positions in each country.

Average annual mortality of dominant/codominant maples for the nine-year period was significantly lower than losses of intermediate/suppressed for both Canadian SBs (D/C: 0.7 ± 0.1%, I/S: 1.3 ± 0.2%, $p=0.046$) and NSBs (D/C: 0.5 ± 0.1%, I/S: 1.6 ± 0.1%, $p=0.0001$). Similarly, the average annual nine-year sugar maple mortality in U.S. dominant/codominant maples was significantly lower than that of intermediate/suppressed maples in both SBs (D/C: 0.8 ± 0.1%, I/S: 1.7 ± 0.3%, $p=0.0258$) and NSBs (D/C: 0.5 ± 0.1%, I/S: 1.7 ± 0.2%, $p=0.0004$).

Regional Mortality

Mortality data from the 10 states and four provinces included in the NAMP represent sugarbushes and nonsugarbushes which exist under a variety of geographic locations and site conditions. Cooperators are interested in viewing the condition of their stands relative to those in other jurisdictions. Examining regional differences is the first step in identifying unusual levels of mortality that may be linked to local disturbances.

Total average annual sugar maple mortality (i.e., all crown positions combined) for SBs within regions ranged from 0.3% in New Brunswick/Nova Scotia to 1.9% in New York (Table 4). Mortality in NSBs was lowest in Michigan (0.2%) and highest in New Hampshire (1.9%). Mortality in the understory of SBs was significantly higher than that in the overstory only in Massachusetts, New Hampshire and Vermont. In 9 of 12 regions, mortality in the understory of NSBs was significantly higher than overstory mortality (Table 4).

Overstory mortality for SBs in New York and Quebec was significantly higher than mortality in their respective NSBs (Table 5). In Massachusetts, mortality of dominant/codominant sugar maple was significantly lower in SBs compared to NSBs. For all other regions, there were no statistically significant differences in mortality of overstory sugar maples between management categories (Table 5). Similarly, in only three regions was mortality of intermediate/suppressed trees significantly different when comparing NSBs with SBs; Massachusetts, New Brunswick and New Hampshire (Table 5).

Mortality of dominant/codominant maples in SBs was higher in New York (1.8 ± 0.3) compared to mortality of overstory maple in all other regions and significantly higher than mortality in 8 of 12 regions (the eight regions: MA, NB/NS, PA, ON, WI, VT, NH, and ME). Overstory mortality in Massachusetts (0.1 ± 0.1) was significantly lower than this mortality in New York and Quebec. Average annual mortality levels for dominant/codominant trees in NSBs were statistically similar between management categories for all regions and varied from zero to 0.8% (Table 5).

There were no statistical differences in average annual mortality of understory sugar maple in SBs among the 13 regions. In NSBs, mortality in this crown position was significantly higher in New Hampshire (4.6 ± 1.1) compared to seven regions (MI, WI, ON, NY, ME, VT, QU) but not statistically different from mortality in Pennsylvania, Massachusetts, NB/NS, and Minnesota (Table 5).

Influence of Elevation

When data from SB and NSB management categories were combined, beginning with the original sample in 1988 (Table 1), average annual sugar maple mortality was significantly lower in the dominant/codominant crown level compared to the intermediate/suppressed level for plot-clusters in all three elevation categories; high (D/C: 0.5 ± 0.1%, I/S: 2.0 ± 0.2%), medium (D/C: 0.8 ± 0.1%, I/S: 1.8 ± 0.3%) and low (D/C: 0.5 ± 0.1%, I/S: 1.1 ± 0.2%). Mortality of dominant/codominant trees at medium elevations (0.8 ± 0.1%) was

Table 4.—Average (± S.E.) annual mortality (% trees) of dominant/codominant and intermediate/suppressed sugar maples by management category (1988-1997)

REGION	SUGARBUSH			NON-SUGARBUSH		
	Dom./ Codom.	Inter./ Supp.	TOTAL	Dom./ Codom.	Inter./ Supp.	TOTAL
Maine	0.8 ± 0.2	3.0 ± 1.4	1.3 ± 0.1	0.6 ± 0.2	1.8 ± 0.5	0.9 ± 0.2
Massachusetts†	0.1 ± 0.1a	1.4 ± 0.4b	0.4 ± 0.2	0.7 ± 0.2a	2.9 ± 0.5b	1.4 ± 0.2
Michigan	0.8 ± 0.3	1.2 ± 0.5	1.0 ± 0.3	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Minnesota‡	0.8 ± 0.3	1.0 ± 0.1	0.9 ± 0.2	0.0 ± 0.0a	1.9 ± 0.7b	1.0 ± 0.3
New Brunswick/ Nova Scotia	0.2 ± 0.1	0.6 ± 0.3	0.3 ± 0.1	0.5 ± 0.2a	2.5 ± 0.4b	0.7 ± 0.2
New Hampshire	0.6 ± 0.1a	1.8 ± 0.4b	1.0 ± 0.2	0.7 ± 0.1a	4.7 ± 1.1b	1.9 ± 0.3
New York	1.8 ± 0.3	2.0 ± 0.7	1.9 ± 0.3	0.5 ± 0.1a	1.5 ± 0.4b	0.9 ± 0.2
Ohio‡	0.9 ± 0.3	0.3 ± 0.2	0.6 ± 0.2	—	—	—
Ontario	0.4 ± 0.1	1.7 ± 0.6	0.6 ± 0.1	0.4 ± 0.1a	1.1 ± 0.2b	0.7 ± 0.1
Pennsylvania‡	0.3 ± 0.3	0.6 ± 0.2	0.5 ± 0.3	0.4 ± 0.2	3.1 ± 1.2	1.2 ± 0.4
Quebec	1.2 ± 0.2	1.3 ± 0.2	1.3 ± 0.1	0.5 ± 0.2a	1.9 ± 0.3b	0.9 ± 0.1
Vermont	0.5 ± 0.2a	1.4 ± 0.2b	0.9 ± 0.1	0.8 ± 0.3a	1.9 ± 0.3b	1.2 ± 0.2
Wisconsin	0.4 ± 0.1	0.8 ± 0.2	0.6 ± 0.1	0.2 ± 0.1a	0.9 ± 0.2b	0.4 ± 0.1

† different letters in the same row signify a statistically significant difference at α=0.05 between the dominant/codominant and intermediate/suppressed comparisons within a region and management category.
‡ plot-clusters were not established in these regions until 1992; average mortality is for 1993-1997.

Table 5.—Average (± S.E.) annual sugar maple mortality (% trees) for management categories within sugar maple crown positions (1988-1997)

	DOMINANT/CODOMINANT		INTERMEDIATE/SUPPRESSED	
REGION	SB ± SE	NSB ± SE	SB ± SE	NSB ± SE
Maine	0.8 ± 0.2	0.6 ± 0.2	3.0 ± 1.4	1.8 ± 0.5
Massachusetts†	0.1 ± 0.1a	0.7 ± 0.2b	1.4 ± 0.4a	2.9 ± 0.5b
Michigan	0.8 ± 0.3	0.2 ± 0.1	1.2 ± 0.5	0.1 ± 0.1
Minnesota‡	0.8 ± 0.3	0.0 ± 0.0	1.0 ± 0.1	1.9 ± 0.7
New Brunswick/ Nova Scotia	0.2 ± 0.1	0.5 ± 0.2	0.6 ± 0.3a	2.5 ± 0.4b
New Hampshire	0.6 ± 0.1	0.7 ± 0.1	1.8 ± 0.4a	4.7 ± 1.1b
New York†	1.8 ± 0.3a	0.5 ± 0.1b	2.0 ± 0.7	1.5 ± 0.4
Ohio‡	0.9 ± 0.3	—	0.3 ± 0.2	—
Ontario	0.4 ± 0.1	0.4 ± 0.1	1.7 ± 0.6	1.1 ± 0.2
Pennsylvania‡	0.3 ± 0.3	0.4 ± 0.2	0.6 ± 0.2	3.1 ± 1.2
Quebec†	1.2 ± 0.2a	0.5 ± 0.2b	1.3 ± 0.2	1.9 ± 0.3
Vermont	0.5 ± 0.2	0.8 ± 0.3	1.4 ± 0.2	1.9 ± 0.3
Wisconsin	0.4 ± 0.1	0.2 ± 0.1	0.8 ± 0.2	0.9 ± 0.2

† different letters signify a statistically significant difference at α=0.05 between the sugarbush/non-sugarbush comparisons within a region and mortality type.
‡ plot-clusters were not established in these regions until 1992; annual average mortality is for 1993-1997.
SB=sugarbush, NSB=non-sugarbush.

significantly higher than dominant/codominant mortality at both high (0.5 ± 0.1%) and low (0.5 ± 0.1%) elevations. Mortality of intermediate/suppressed maples was significantly higher at high elevations (2.0 ± 0.2%) than mortality in this crown position at low elevations (1.1 ± 0.2%). When data from all crown positions were combined, mortality for both SBs and NSBs was similar at high, medium and low elevations (Fig. 1).

Nitrate Deposition

There were no significant differences in average annual percent mortality of sugar maple in SBs compared to NSBs from 1989 through 1997 when D/C and I/S crown positions were combined in areas of high (SB: 1.3 ± 0.3%, NSB: 0.8 ± 0.1%), medium (SB: 1.0 ± 0.1%, NSB: 1.0 ± 0.1%) and low (SB: 0.8 ± 0.1%, NSB: 0.8 ± 0.1%) levels of nitrate deposition. Mortality of intermediate/suppressed sugar maples was significantly higher than mortality in the dominant/codominant crown position at all deposition levels; high (SB: 1.6 ± 0.3%, NSB: 0.8 ± 0.2%), medium (SB: 1.6 ± 0.2%, NSB: 0.6 ± 0.1%) and low (SB: 1.7 ± 0.1%, NSB: 0.4 ± 0.1%). There were no statistically significant differences in total (D/C and I/S combined) average annual mortality of sugar maple when compared among the three deposition categories for wet nitrate in either SBs or NSBs.

Sulfate Deposition

There were no significant differences in average annual percent mortality of sugar maples in SBs compared to NSBs from 1989 through 1997 when D/C and I/S crown positions were combined for plot-clusters in areas of either high (SB: 1.3,± 0.3%, NSB: 0.7 ± 0.1%), medium (SB: 1.0 ± 0.1%, NSB: 1.0 ± 0.1%) or low (SB: 0.7 ± 0.1%, NSB: 0.7 ± 0.1%) wet sulfate deposition. In plot-clusters ostensibly exposed to high levels of sulfate deposition, there was no statistically significant difference in mortality of dominant/codominant maples (0.8 ± 0.2%) compared to maples in the intermediate/suppressed crown position (1.4 ± 0.4%). However, percent mortality of intermediate/suppressed maples was significantly higher than mortality of dominant/codominant trees in areas exposed to medium (SB: 1.7 ± 0.2%, NSB: 0.7 ± 0.1%) and low (SB: 1.6 ± 0.4%, NSB: 0.5 ± 0.1%) deposition levels. There were no statistically significant differences in total (D/C and I/S combined) average annual mortality of sugar maple when compared among the three wet sulfate deposition categories in either SBs or NSBs.

Interaction Between Elevation and High Levels of Deposition

To further examine the possibility that elevation may have influenced the association between atmospheric deposition and maple mortality, sugar maples in plot-clusters exposed to high levels of both wet nitrate and wet sulfate deposition were reclassified into one of two categories; those at >300m elev. (viz., high and medium elevation classes combined), and those at <300m elev. For high sulfate deposition, 12 plot-clusters occurred at elevations >300m, 11 plot-clusters were <300m. Twenty plot-clusters located at >300m and 16 at <300m were subjected to high levels of nitrate deposition. There were no significant differences in average annual percent tree mortality between SBs and NSBs in either the high+med (SB: 2.2 ± 0.6%, NSB: 1.1 ± 0.1%) or low (SB: 0.6 ± 0.1%, NSB: 0.3 ± 0.1%) elevation categories for areas receiving high levels of wet nitrate deposition (>20 kg/ha/yr). Similarly, when SB and NSB management categories were combined, there were no significant differences in mortality between crown positions at either elevation: high+med – D/C: 1.2 ± 0.3%, I/S: 2.2 ± 0.5%; Low – D/C: 0.4 ± 0.1%, I/S: 0.7 ± 0.2%. Within SBs when crown positions were combined, average annual mortality was significantly greater at elevations >300m (2.2%) compared to that of stands occurring at <300m (0.6%) (Fig. 2). Similarly, in NSBs there was significantly greater mortality at high+med elevations (1.1%) compared to low elevations (0.3%) (Fig. 2). Mortality of intermediate/suppressed sugar maples when data from SBs and NSBs were combined was significantly greater in the high+med (2.2%) category compared to low elevations (0.7%), and there was significantly more mortality in the dominant/codominant crown position at high+med elevations (1.2%) than at low elevations (0.4%).

In like manner, mortality from plot-clusters exposed to high levels of wet sulfate deposition (>27.5 kg/ha/yr) were stratified by combining data from high and medium elevations (i.e., >300m) and comparing it to sugar maple mortality in plot-clusters at low elevations (<300m). When data from both D/C and I/S crown positions were combined, there was no statistical difference in average annual tree mortality of sugar maple when comparing SBs and NSBs at either high+med. (SB: 2.2 ± 0.7%, NSB: 1.0 ± 0.2%) or low elevations (SB: 0.5 ± 0.1%, NSB: 0.3 ± 0.1%). Mortality in the dominant/codominant and intermediate/suppressed crown positions were statistically similar for both high+med (D/C: 1.2 ± 0.3%, I/S: 2.2 ± 0.8%) and low (D/C: 0.4 ± 0.1%, I/S: 0.6 ± 0.3%) elevations. Maple mortality within SBs and NSBs when crown positions were combined was significantly higher at high+med elevations compared to mortality at <300m (Fig. 3). This can be attributed mainly to the fact that when management categories were combined mortality of dominant/codominant trees (1.2%) was significantly higher at the higher elevations compared to maples in this crown position below 300m (0.4%).

Ecological Units (U. S.)

NAMP plot-clusters in the United States are distributed over 46 Ecological Sections, five Provinces and four Divisions as mapped by Keys et al. (1995) and described by McNab and Avers (1994). The Canadian component of this project encompasses 13 Ecoregions and three Ecozones (Ecological Stratification Working Group 1995). For the purpose of examining sugar maple mortality, small sample sizes (i.e., few plot-clusters) in many ecological units limited comparative analyses in the U.S. to three Divisions and three Provinces in the Humid Temperate Domain and three Sections in the Adirondack New England Mixed Forest-Coniferous Forest-Alpine Meadow Province (Table 6). Sample size for the Canadian portion of NAMP permits mortality comparisons between three Ecozones and six Ecoregions (Table 7).

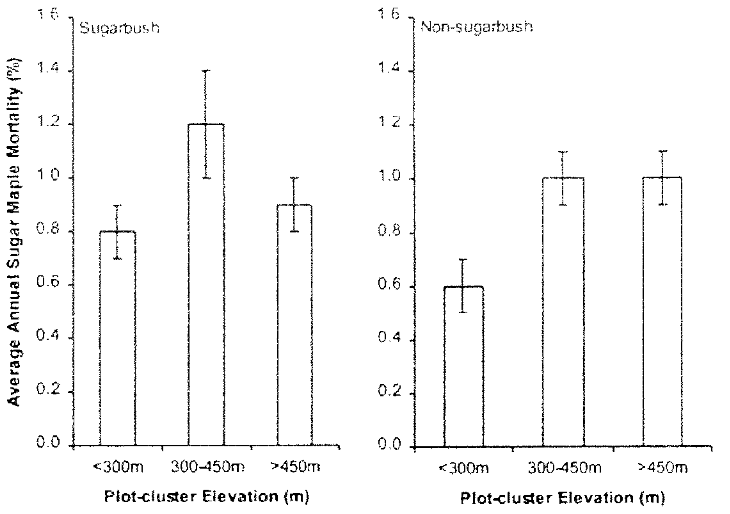

Fig. 1. Total (D/C and I/S crown positions combined) average (± SE) annual mortality (% trees) of sugar maple for SBs and NSBs in three elevational categories

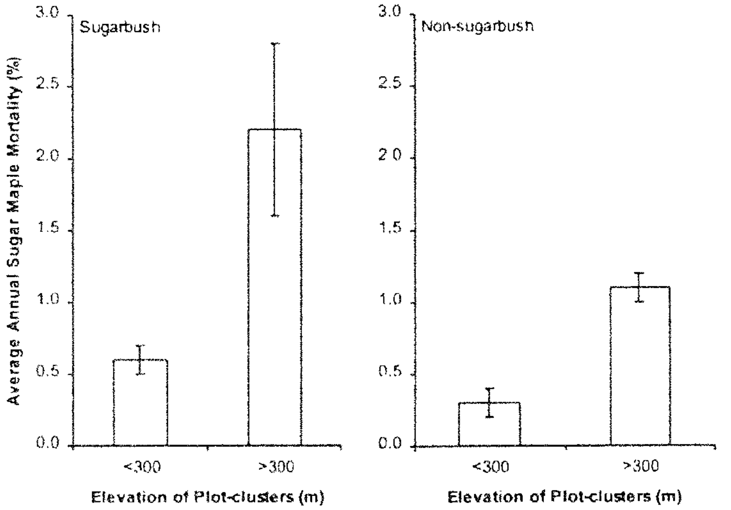

Fig. 2. Total (D/C and I/S crown positions combined) average (±SE) sugar maple mortality (% trees) for SBs and NSBs in plot-clusters occurring at high-medium (>300m) and Low (<300m) elevations in regions exposed to high (>20 kg/ha/yr) levels of wet nitrate deposition.

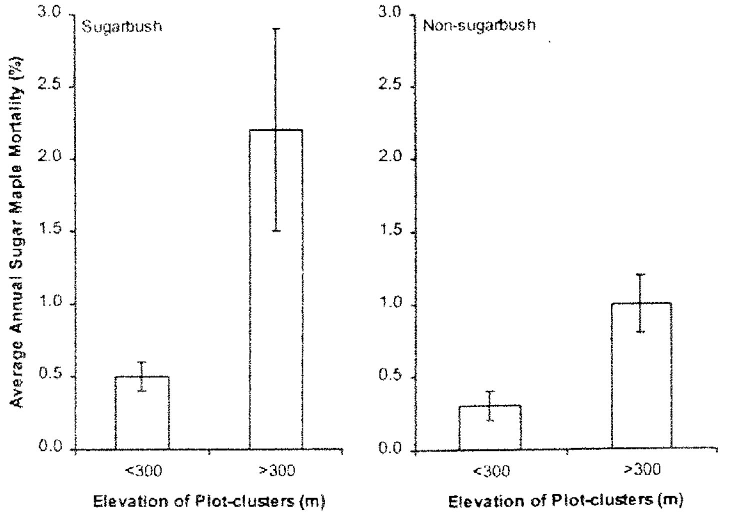

Fig. 3. Total (D/C and I/S crown positions combined) average (±SE) annual sugar maple mortality (% trees) for SBs and NSBs in plot-clusters occurring at high+medium (>300m) and low (<300m) elevations exposed to high (>27.5 kg/ha/yr) levels of wet sulfate deposition.

Table. 6.—Original (1988) number of live sugar maples monitored by NAMP in each of eight ecological regions, two management categories and two crown positions in the United States

		No. of Sugar Maples by Crown Position	
Ecological Classification[a]	Management Category (No. Plot-Clusters)[b]	Dom./Codom.	Interm./Supp.
Warm Continental Division (210)	SB (13)	818	550
	NSB (12)	885	591
Warm Continental Regime Mts (M210) Division	SB (29)	841	333
	NSB (31)	843	467
Hot Continental Division (220)	SB (12)	332	159
	NSB (9)	246	171
Laurentian Mixed Forest Province (212)	SB (13)	818	550
	NSB (12)	885	591
Adirondack New England Mixed Forest Province (212)	SB (29)	841	333
	NSB (31)	843	467
White Mts. Section (M212A)	SB (8)	337	251
	NSB(9)	322	182
East. Broadleaf Forest (Continental) Province (222)	SB (9)	210	114
	NSB (8)	213	155
New England Piedmont Section (M212B)	SB (7)	344	137
	NSB (6)	225	160
Green Taconic, Berkshire Mts. Section (M212C)	SB (11)	404	167
	NSB (12)	572	316

[a] Source: McNab and Avers 1994. Numbers are codes for ecological units.
[b] SB = sugarbush, NSB = nonsugarbush.

U.S. Ecological Divisions

Average annual percent tree mortality was similar for comparisons of SBs and NSBs when D/C and I/S crown positions were combined for plot-clusters located in the Warm Continental (WC) and Warm Continental Regime Mountain (WCRM) Divisions (Fig. 4). In the Hot Continental (HC) Division, annual mortality was significantly higher in SBs compared to NSBs (Fig. 4). Mortality of intermediate/suppressed sugar maples was significantly higher than that of dominant/codominant trees in both the WC (I/S: 0.9 ± 0.1%, D/C: 0.4 ± 0.1%) and WCRM (I/S: 2.3 ± 0.4%, D/C: 0.8 ± 0.1%), but did not differ statistically in HC (I/S: 1.1 ± 0.3%, D/C: 0.7 ± 0.1%). Combined mortality for SBs in WC (0.6%) was significantly lower than SB mortality in WCRM (1.3%). In NSBs, combined mortality was significantly higher in WCRM (1.1%) than in WC (0.7% and HC (0.6%) (Fig. 4).

U.S. Ecological Provinces

There were no significant differences in the overall (D/C and I/S crown categories combined) average annual percent tree mortality between SBs and NSBs in either the Laurentian Mixed Forest (LM, SB: 0.6 ± 0.1%, NSB: 0.7 ± 0.1%) or the Adirondack New England Mixed Forest (ANE, SB: 1.3 ± 0.2%, NSB: 1.1 ± 0.1%) Provinces. Mortality in the Eastern Broadleaf Forest (Continental) Province (EBFC), however, was significantly higher in SBs (1.2 ± 0.3%) compared to NSBs (0.4 ± 0.1%). Annual mortality of intermediate/suppressed maples was significantly higher than mortality of dominant/codominant trees in ANE and LM (data not shown). Mortality of sugar maple in the dominant/codominant crown position was statistically similar in all three regions (data not shown). Mortality of intermediate/suppressed sugar maples in ANE (2.3%) was significantly

Table. 7.—Original (1988) number of live sugar maples monitored by NAMP in each of nine ecological regions, two management categories and two crown positions in Canada

		No. of Sugar Maples by Crown Position	
Ecological Classification[a]	Management Category (No. Plot-Clusters)[b]	Dom./Codom.	Interm./Supp.
Atlantic Maritime Ecozone (AM)	SB (14)	943	262
	NSB (10)	670	188
Boreal Shield Ecozone (BS)	SB (8)	398	201
	NSB (8)	397	218
Mixed Wood Plain Ecozone (MW)	SB (9)	286	136
	NSB (9)	361	137
Algonquin-Lake Nipissing Ecoregion (ALN)	SB (3)	142	68
	NSB (3)	136	80
Appalachian Ecoregion (APP)	SB (7)	401	191
	NSB (7)	370	145
Lake Erie Lowland Ecoregion (LEL)	SB (3)	68	51
	NSB (3)	110	29
Manitoulin-Lake Simcoe Ecoregion (MLS)	SB (4)	137	70
	NSB (4)	141	70
Northern New Brunswick Uplands Ecoregion (NNBU)	SB (4)	305	38
	NSB (1)	51	7
Southern Laurentians Ecoregion (SL)	SB (4)	187	118
	NSB (4)	213	112

[a] Ecological Stratification Working Group 1995.
[b] SB = sugarbush, NSB = nonsugarbush.

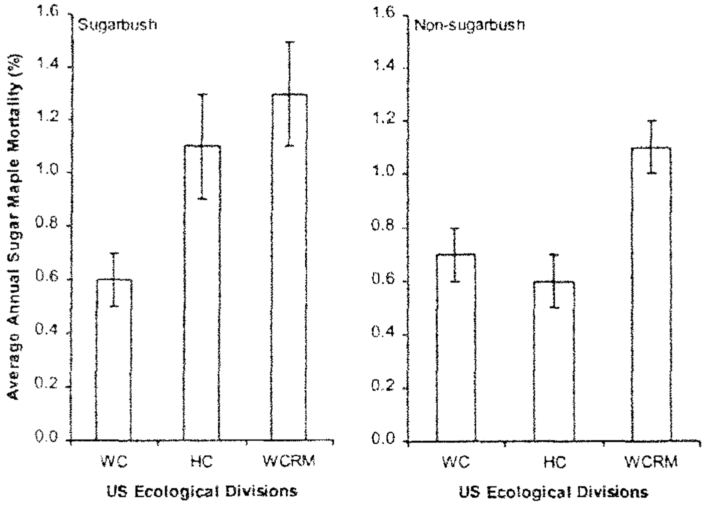

Fig. 4.—Total (D/C and I/S crown positions combined) average (± SE) annual sugar maple mortality (% trees) for SBs and NSBs in three ecological Divisions in the United States; WC = Warm Continental, HC = Hot Continental, WCRM = Warm Continental Regime Mountains.

higher than mortality at this crown position in either LM (0.9%) or EBFC (0.9%). Total average annual mortality (crown positions combined) among these Provinces was not significantly different for SBs (range 0.6 - 1.3%), but in NSBs overall mortality was significantly higher in ANE compared to LM and EBFC (Fig. 5).

U.S. Ecological Sections

The distribution of NAMP plot-clusters permits a comparison of three Sections within the Adirondack New England Mixed Forest-Conifer Forest-Alpine Meadow Province: White Mountains (WM); New England Piedmont (NEP); and Green, Taconic, Berkshire Mountains (GTBM). Sections are the smallest ecological units in the U.S National Hierarchical Framework for which NAMP sample sizes permit reasonable comparisons, and it is at this level that comparisons are most meaningful (McNab and Avers 1994).

There was no statistically significant difference between the 9-year average annual mortality of sugar maple in SBs compared to NSBs when both D/C and I/S crown positions were combined for WM, NEP or GTBM (Fig. 6). For SBs, combined mortality in both WM and NEP was significantly higher than combined mortality in GTBM. There were no significant differences in NSB mortality between Sections when crown levels were combined (Fig. 6). In all three Sections, mortality in the intermediate/suppressed crown position was significantly higher than that of overstory trees (Fig. 7). Mortality of trees within dominant/codominant and intermediate/suppressed crown positions was similar among the three Sections (Fig. 7).

Ecological Units (Canada)

Canadian Ecozones

Average annual mortality of sugar maple in Atlantic Maritime Ecozone (AM) SBs (0.6%) was significantly lower than maple mortality in NSBs (0.8%). There were no significant differences between management categories for either the Boreal Shield or the Mixed Wood Plains Ecozones (data not shown). When SB D/C and I/S crown positions were combined, mortality in BS (1.2%) was significantly higher than comparable mortality in either AM (0.6%) or MW (0.8%) (Fig. 8). Similarly, total mortality in NSBs was significantly higher for the BS Ecozone (1.1%) compared to AM (0.8%) or MW (0.5%) (Fig. 8). Mortality of intermediate/suppressed sugar maple was significantly higher than that of dominant/codominant maple in AM (I/S: 1.4 ± 0.2%, D/C: 0.4 ± 0.1%) and BS (I/S: 2.3 ± 0.5%, D/C: 0.7 ± 0.4%) but not in MW (I/S: 0.7 ± 0.1%, D/C: 0.6 ± 0.1%). There were no statistically significant differences among Ecozones in mortality of dominant/codominant sugar maples (data not shown). However, mortality of intermediate/suppressed trees was significantly higher in BS (2.3%) compared to mortality at this crown level in either AM (1.4%) or MW (0.7%).

Canadian Ecoregions

Total (D/C and I/S crown positions combined) sugar maple mortality in SBs and NSBs was similar within all six Ecoregions (data not shown). When SB D/C and I/S crown positions were combined, average annual mortality of sugar maple in the Southern Laurentians (SL) Ecoregion was significantly higher than mortality in the Northern New Brunswick Uplands (NNBU) region (Fig. 9). Likewise, in NSBs the only statistically significant difference in total mortality among Ecoregions occurred between SL and NNBU (Fig. 9). In three regions (ALN, APP, MLS), mortality of overstory D/C maple was significantly lower than understory I/S mortality (Fig. 10). Mortality of dominant/codominant trees in SL was significantly higher than mortality at this crown level in MLS or NNBU (Fig. 10). Intermediate/suppressed mortality in SL was significantly higher than understory I/S mortality in either the LEL or NNBU Ecoregions (Fig. 10).

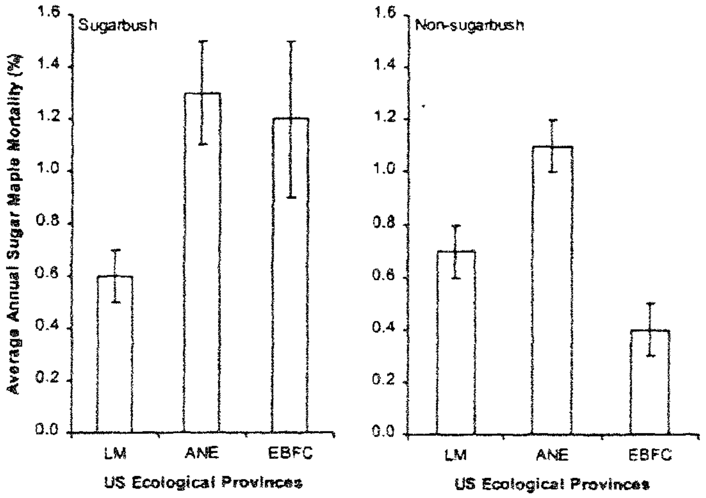

Fig. 5.—Total (D/C and I/S crown positions combined) average (± SE) annual sugar maple mortality (% trees) for SBs and NSBs in three ecological Provinces in the United States; LM = Laurentian Mixed Forest, ANE = Adirondack New England and Mixed Forest, EBFC = Eastern Broadleaf Forest (Continental).

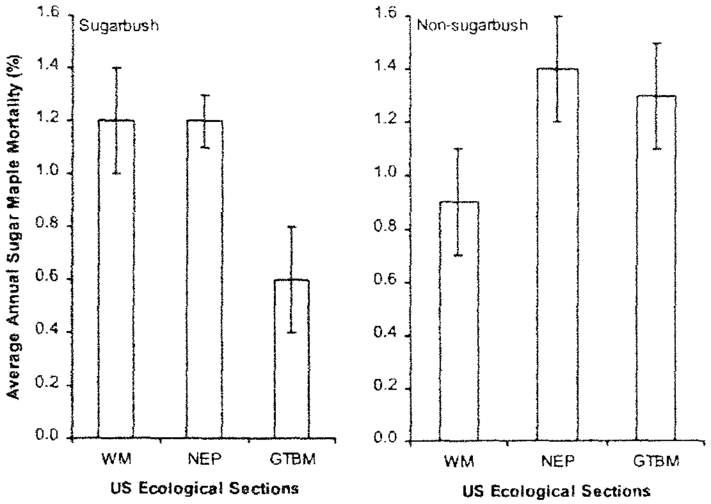

Fig. 6.—Total (D/C and I/S crown positions combined) average (± S.E.) annual sugar maple mortality (% trees) for SBs and NSBs in three ecological Sections in the United States; WM = White Mountains, NEP = New England Piedmont, GTBM = Green, Taconic, Berkshire Mountains.

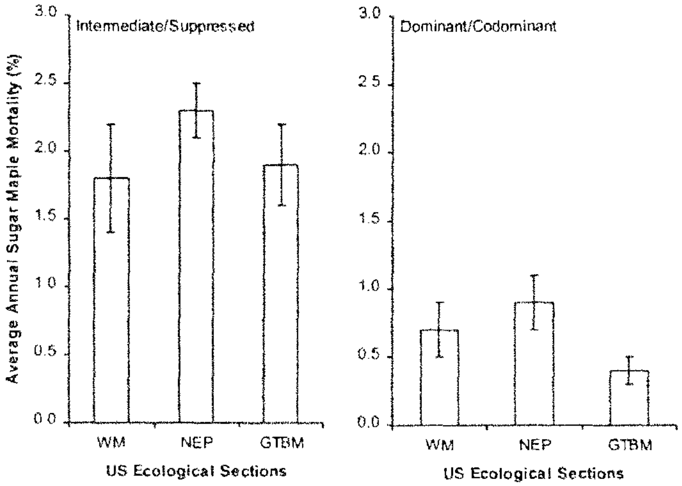

Fig. 7.—Average (± SE) sugar maple mortality (% trees) for intermediate/suppressed and dominant/codominant trees in three ecological Sections in the United States; WM = White Mountains, NEP = New England Piedmont, GTBM = Green, Taconic, Berkshire Mountains.

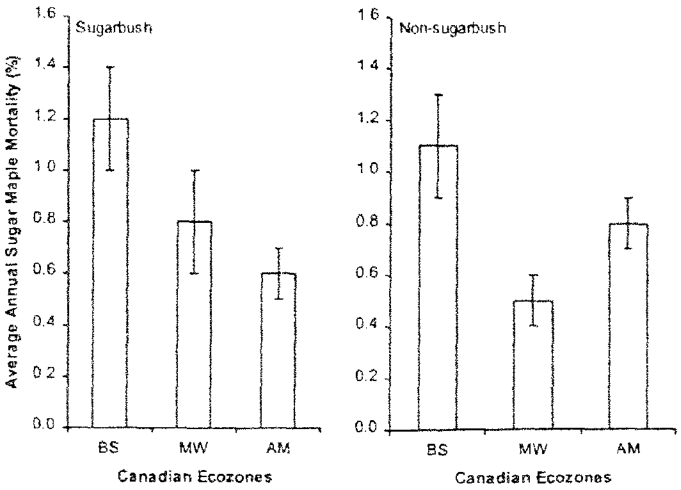

Fig. 8.—Total (D/C and I/S crown positions combined) average (± SE) annual sugar maple mortality (% trees) in three Canadian Ecozones: Boreal Shield (BS), Mixed Wood Plains (MW) and Atlantic Maritime (AM).

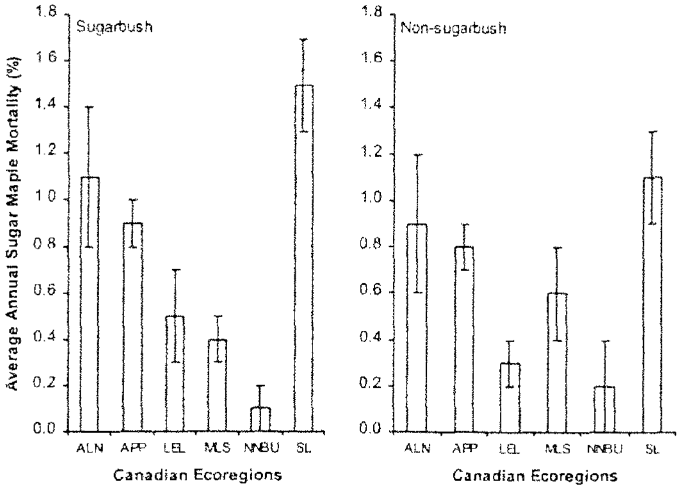

Fig. 9.—Total (D/C and I/S crown positions combined) average (± S.E.) annual percent sugar maple mortality (% trees) for SBs and NSBs in six Canadian Ecoregions; Algonquin-Lake Nipissing (ALN), Appalachians (APP), Lake Erie Lowland (LEL), Manitoulin-Lake Simcoe (MLS), Northern New Brunswick Uplands (NNBU) and Southern Laurentians (SL).

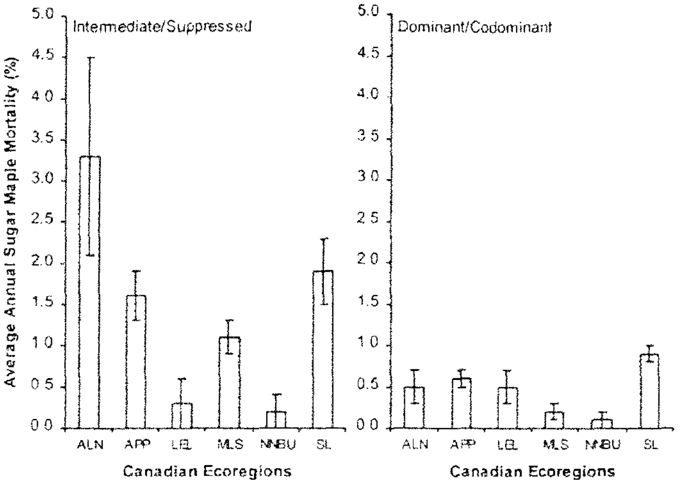

Fig. 10.—Average (± SE) annual sugar maple mortality (% trees) for intermediate/suppressed and dominant/codominant trees in six Canadian Ecoregions; Algonquin-Lake Nipissing (ALN), Appalachians (APP), Lake Erie Lowland (LEL), Manitoulin-Lake Simcoe (MLS), Northern New Brunswick Uplands (NNBU), and Southern Laurentian (SL).

Discussion

Results of monitoring and evaluating sugar maple mortality in the NAMP plot-clusters should be viewed with the understanding that stands were selected on the basis of regional location, accessibility, condition (age, species mix), and security (assurance of long-term use). In other words, sites were not picked at random and, in a statistical sense, results may be biased and not generally applicable to the maple resource. In our view, this does not detract from the ability to identify a normal or expected threshold of mortality in the absence of disturbance. Neither does it hinder evaluation of the immediate and long-term consequences of natural disturbances in terms of annual mortality or changes in crown condition of sugar maple, nor does it disallow comparison of ecological conditions included within the study. Long-term, quality controlled monitoring and subsequent evaluation is requisite to developing a baseline with which to compare changes following stress. Similarly, this type of monitoring is necessary to identify causes of unusual mortality and to facilitate early detection of potentially harmful effects (Spellerberg 1991).

The results, analyses and discussion are specific to sugar maple even though other species occur in all plot-clusters. Therefore, total tree mortality (i.e., all species combined) for each stand may be slightly higher than the values given for each crown level and when crown levels are combined. For example, at nine of the ten sites where monitoring was initiated in 1988 (Table 2), sugar maple comprises 75% to 92% of the dominant/codominant trees in SBs and 63% to 80% in NSBs. In Wisconsin, sugar maple constitutes only 56% of the overstory in SBs and 38% in NSBs.

When sugar maple mortality from NAMP plot-clusters in the United States and Canada are combined (Fig. 11), a clear pattern emerges in both SBs and NSBs. Average annual percent mortality of intermediate/suppressed trees consistently exceeds or approximates that of dominant/

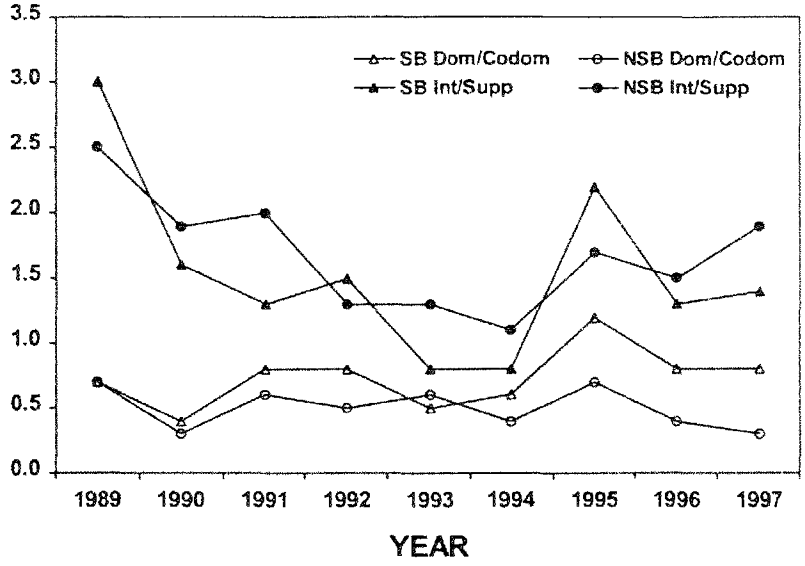

Fig. 11.—Annual natural mortality (% trees) of sugar maple (1988-1997) in Canadian and U.S. plot-clusters combined according to management category (SB = sugarbush, NSB = non-sugarbush) and crown position.

codominant trees; in SBs the difference in annual average mortality between crown positions was as much as 1% to 3%. The pattern of mortality within each crown position is very similar for both countries. With two exceptions (Ohio - SBs, Michigan - NSBs), this pattern of higher mortality in the intermediate/suppressed crown position is a consistent, though not always statistically significant, pattern when viewed at the regional level (Table 4).

Differential mortality between crown levels is expected given the more intense competition for light, moisture and soil nutrients typically experienced by trees in the understory (Peet and Christensen 1987). In all likelihood, this discrepancy is enhanced because the dominant/codominant trees are at a competitive advantage for resources disproportionate to their size (Weiner and Thomas 1986). The variation in crown level mortality within each country and within each state and province results from many factors, the most important of which are variation in stocking (Leak 1961, 1970; Solomon 1977), uneven moisture conditions (Stephens and Waggoner 1980, Hopkin and Dumond 1994), species characteristics (Westoby 1984), stage of stand development (Franklin et al. 1987), and nutrition and stress conditions (Long et al. 1997; Horsley et al. this volume). In a five-year study of mortality in a *Fagus-Magnolia* forest, Harcombe and Marks (1983) were able to demonstrate only a weak relation between death rate and stand density, suggesting that between-tree competition was not merely related to density. Indeed, in only three NAMP regions was the nine-year average annual percent sugar maple mortality positively and significantly correlated with stand basal area: New Brunswick/Nova Scotia ($r = .750$, $p = 0.012$), New York ($r = 0.604$, $p = 0.008$) and Quebec ($r = 0.520$, $p = 0.009$). The correlation coefficients indicate that even in these three examples, site and species characteristics are important, because only 27% to 56% of the variation in the dependent variable is explained by stand density alone.

One of the major questions of concern to NAMP is how total sugar maple mortality (i.e., the average annual mortality when crown positions are combined) compares with mortality of northern hardwoods reported in the literature in the absence of disturbance. A look at comparative differences or similarities is especially meaningful because the NAMP sites cover a broad geographic range for sugar maple. Total mortality in SBs (col. 4, Table 4) ranged from a high of 1.9%/yr in New York to 0.3%/yr in NB/NS. NSB mortality was highest in New Hampshire (1.9%/yr) and lowest (0.2%/yr) in Michigan (col. 7, Table 4). There are several reports of annual mortality for different broadleaved species and combinations of species in the eastern U.S. and Canada (Table 8). Two, dealing specifically with sugar maple, indicate that mortalities of <1% (Hall 1995) to 1.2% (McLaughlin et al. 1996) are typical. Kelley and Eav (1987) reported 0.5% mortality for dominant/codominant sugar maple in Vermont. Mortality in this crown position varied from 0.1% (Massachusetts) to 1.8% (New York) in NAMP SBs and 0% (Minnesota) to 0.8% (Vermont) in NSBs (Table 4). Levels of total mortality reported for eastern hardwoods range from <1% to 3.2% (Table 8). The annual mortality reported in this paper refers solely to sugar maple; therefore, mortality for the NAMP sites might be slightly higher if all species were included. Also of interest is the comparative mortality of sugar maple in SBs compared to NSBs. The hypothesis of interest here is that stands subjected to management and tapping activities associated with the maple syrup industry are subjected to repeated physical stresses which may increase annual mortality compared to less intensively managed forests. Mortality of dominant/codominant sugar maple in only two regions was significantly higher in SBs compared to NSBs; New York (1.8% vs 0.5%) and Quebec (1.2% vs 0.5%). In Massachusetts, mortality in NSBs (0.7%) was significantly higher than in SBs (0.1%). Mortality in the lower crown position was significantly higher for NSBs in Massachusetts (I/S: 2.9%, D/C: 1.4%), New Brunswick/Nova Scotia (I/S:

Table 8.—Examples of normal or expected annual mortality (% trees) for eastern hardwoods

Source	Mortality
Frelich and Lorimer (1991)	So. Appalachian, old growth mixed mesophytic, 0.6-1.0%; Lake States, old growth sugar maple/hemlock, 0.6-0.7%
Hall (1995)	Canada, sugar maple, <1%
Hall (1996)	Canada, mixed woodland plains, 0-3.2%
Hall et al. (1996)	Canada, temperate broadleaved forests and woodlands, 1-3%
McLaughlin et al. (1996)	Ontario, sugar maple, 1.2%
Buchman (1983)	Lake States, major tree species, 2.6%/yr for saplings and 0.3%/yr for poles and small sawtimber
Kelley et al. (1992)	VT, northern hardwoods, upper canopy <1%
Stephens and Waggoner (1980)	CT, mixed hardwood forests; moist site, 1.2-1.4%; medium site 1.2-2.0%; dry site 0.8-2.0%
Waring and Schlesinger (1985 ref. therein)	Generally 1-2%
Leak (1970)	NH, second growth northern hardwoods, high stocking-1.4%; med. Stocking-0.3%; low stocking-0%
Kelley and Eav (1987)	VT, dominant/codominant maple mortality, 0.5
Abrell and Jackson (1977)	IN, old growth beech-maple, 1.2%

2.5%, D/C: 0.6%) and New Hampshire (I/S: 4.7%, D/C: 1.8%) (Table 4). The relatively high average annual mortality of sugar maples in New York's SBs, and overall mortality in this region compared to other regions when data from management categories and crown levels were combined, can be attributed to an unusually severe windstorm (Pendrick 1996) that eliminated a majority of the trees in one plot-cluster in 1995. At this site, approximately 65% of the understory and 35% of the overstory maples were lost due to this one disturbance (Fig. 12). Eliminating this plot-cluster from the analysis reduces New York's annual average mortality to approximately 1.1%. Total mortality in New Hampshire (1.4%) was the second highest of the 13 regions and can be attributed mainly to relatively high losses in the intermediate/suppressed crown position in NSBs (4.6%, Table 5).

Currently, there is growing interest in the effects of atmospheric pollution on sugar maple growth and mortality. The evidence presented to date is equivocal because underlying mechanisms are poorly understood (Foster 1989). Contradictory results also confuse the issue. Bernier and Brazeau (1988), for example, speculated that a combination of P and K deficiency play a major role in maple decline. However, reports from Quebec (Payette et al. (1996), Pennsylvania (Brooks 1994) and Ontario (Hart 1991) suggest the impact of atmospheric deposition is minor, and the key factors are a combination of insect defoliation and drought (Kolb and McCormick 1993). Other evidence suggests winter weather conditions that promote deep soil frost reduce sugar maple growth (Bauce and Allen 1991), may initiate maple decline (see Auclair this volume) or alter soil solution chemistry in ways that are detrimental to maple condition (Boutin and Robitaille 1995).

We do not have on-site measures of wet sulfate or wet nitrate deposition for the NAMP plot-clusters and had to classify stands according to deposition levels determined at the nearest monitoring site (Allen et al. 1995). It seems reasonable, however, that if atmospheric conditions relative to these two elements had a major influence on maple crown condition or mortality, detectable changes in both would appear in regions receiving relatively high levels of sulfate or nitrate deposition compared to regions receiving relatively low exposure.

To examine this hypothesis, plot-clusters were first stratified by elevation, under the assumption that due to orographic uplift atmospheric deposition in eastern North America tends to increase with elevation (Lovett and Kinsman 1990, Garner et al. 1989). Differences in annual percent sugar maple mortality between the three elevation categories were significantly greater for dominant/codominant maples in plot-clusters located at mid-elevations compared to mortality in this crown position at either high or low elevations, and for intermediate/suppressed maples mortality was significantly greater at high compared to low elevations. When total (D/C and I/S crown levels combined) plot-cluster mortality was examined by deposition level regardless of elevation, there were no significant differences between deposition categories for either nitrate or sulfate. Only in SBs was

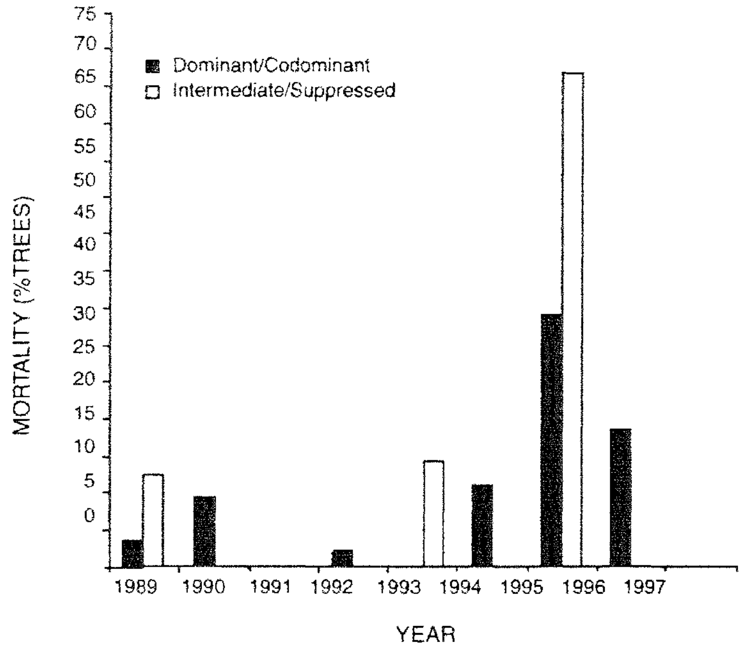

Fig. 12.—Annual mortality (% trees) of sugar maple for the Altmire Bros. Sugarbush in New York (1989-1997).

mortality above 300m (1.1%) significantly higher than mortality below 300m (0.3%). Whether differences described above are biologically significant can not be determined. These subtle differences may become more obvious when plot-clusters experience severe disturbances (Horsley et al. this volume). However, since the beginning of the NAMP several plot-clusters have experienced severe drought and heavy defoliation, yet unusual levels of mortality have not materialized. Studies in states that do not have significant sources of pollution (e.g., Vermont, Tennessee and North Carolina) may not show strong trends in precipitation chemistry with elevation (Scherbatskoy and Bliss 1984). Neither Mielke et al. (1991) working along a pH gradient in Wisconsin nor Linzon's (1987) studies of maple decline on acidic compared to calcareous soils in Ontario demonstrated significant differences in the condition of sugar maple under these ranges of conditions.

Assessment of sugar maple mortality across the range of ecological units examined by NAMP revealed no differences that appear biologically significant. These regions are described on the basis of predominant biotic and abiotic features that control or modify inputs of solar energy, precipitation and nutrients; for example, climate, geology, soils, water and vegetation. Different units are identified or described through spatial differences in a combination of these characters (Smith and Carpenter 1996, Ecological Stratification Working Group 1995). The generally similar condition of sugar maple throughout such a broad range of soils, parent geology and climate suggests that if atmospheric deposition is affecting maple or the sites on which it exists, the effect or effects are subtle and not reflected in crown condition (Allen et al. 1995) or differential mortality. Only long-term monitoring that documents the occurrence and extent of stresses and provides well-structured, chronologically collected data (Stout 1993) will determine whether what appear to be negligible affects are exacerbated by stress complexes.

Results from the 233 stands that have been monitored by NAMP for the past six to nine years indicate that in these northern hardwood stands maple crowns are in good condition (Allen et al. 1995) and mortality occurs at levels generally associated with normal stand development. Similarly, independent studies in Canada (Hall 1996, Hopkin and Dumond 1994), Vermont (Kelley and Eav 1987), and Wisconsin (Mielke et al. 1991) have been unable to document unusual levels of sugar maple mortality. However, studies in northwestern and north central Pennsylvania outside the area monitored by the NAMP plot clusters show unusual levels of sugar maple mortality (Kolb and McCormick 1993; Laudermilch 1995; McWilliams et al. 1996; Horsley et al. this volume).

Nevertheless, we recognize that in some regions extensive sugar maple mortality has occurred during the past four decades (Table 9). It is important to examine these events in order to identify the factor or factors that precipitated unusual levels of mortality and, more importantly, to distinguish causes related to human activities from those which are not directly related to human intervention. Since the classic study of maple blight in Wisconsin during the early 1960s (Giese et al. 1964), very few maple declines have been investigated with scientific rigor involving a structured look at cause and effect. However, anecdotal information is available for many episodes, provided by

Table 9.—Examples of physical and biological stresses associated with sugar maple decline

Source	Example
NH Dept. Res. And Econ. Develop. 1998 [a]	Central NH, Cardigan Mt.; 1,013 ha; cutting history; maple now on sites not previously occupied; 640-670 m elev.; *Heterocampa guttivitta*; frequent ice damage; shallow soils
Payette et al. 1996	So. Quebec; drought in combination with *Malacosoma disstria*
Rhodes 1997	Northeastern PA; 15-30% mort. On 44,145 ha >30% mort. On 27,540 ha; *M. disstria, Alsophila pometaria, Ennomos subsignarius*, anthracnose
Penn. Dept. Environ. Res. 1985	Northwestern PA; 1,215 ha; >640 m elev., *A. pometaria*; history of heavy logging
NYS Dept. Environ. Cons. 1982[a]	SE NY; 81,000 ha; *M. disstria*; drought; mort. 95% in many stands
Gross 1981a	So. Ontario; 16% mort.; *M. disstria*, site conditions, weather
Can. For. Serv. 1980	So. Ontario; >50% mort.; 8,500 ha; *M. disstria*
Giese et al. 1964. U.S. Dept. Of Agric. 1964.	NE Wisc.; 4,050 ha; 2-33% mort. Overstory. 1-56% mort. Understory; cutting hist. favored intolerants; drought killed hemlock; hem./hdwd. stand converted to maple; defoliator complex
Wink 1998[a]	North. NY, Tug Hill Plateau; 48,600 ha; 17-20% mort.; *M. disstria*; highgrading

[a] Data on file, unpublished.

professionals with knowledge of local forest types, past land use practices and disturbance histories for the areas involved. We should pay attention to these observations, because several common threads connect past episodes of sugar maple mortality.

Several recent reviews of sugar maple decline and mortality cataloged these events (e.g., Barnard et al. 1990, McIlveen et al. 1986, Millers et al. 1989). The examples chosen here (Table 9) are some of the best documented incidents of true maple declines and not merely examples of temporary crown dieback resulting from a single, short-term stress. The two predisposing factors mentioned most frequently relate to stand composition and site condition. In most instances, affected stands are predominantly sugar maple as a consequence of selective cutting, which often allows maple and other shade tolerant species to dominate sites (Nyland 1986) where historically it may have constituted a relatively small percentage of the stand. Of course, under favorable site and stand conditions sugar maple naturally attains dominance, largely due to its long life, prolific seed production, extreme shade tolerance, and persistence in the understory. These characteristics account for its ability to quickly exploit gaps in the overstory and sustain this position (Abrell and Jackson 1977). Site seems to become particularly critical when, as a consequence of either selective cutting or natural events, northern hardwood stands that are predominantly sugar maple occur at elevations where soils are thin and trees are exposed repeatedly to adverse weather events.

The most common inciting event is insect defoliation, occasionally exacerbated by drought (Kolb and McCormick 1993). Forest tent caterpillar, *Malacosoma disstria* Hubner, has been most frequently associated with maple decline and mortality, but the literature also indicates that saddled prominent, *Heterocampa guttivitta* (Walker); fall cankerworm, *Alsophila pometaria* (Harris); and elm spanworm, *Ennomos subsignarius* (Hubner) have played inciting roles as well.

Acknowledging and addressing factors that have been consistently associated with maple decline and mortality is important, because they are manageable and predictable. That is, in most situations applying appropriate silvicultural methods to alter stand conditions (encourage sugar maple on appropriate sites, maintain species diversity, optimize stand density) and maintaining conscientious pest management strategies (annual monitoring and evaluation, appropriate controls) will lower the susceptibility of northern hardwood forests to sugar maple decline.

Conclusions

During the mid- to late 1980s, the general public was inundated by sensational press describing maple decline as "a catastrophe in the making" (Jones 1986), a "mysterious plague destroying a way of life" (Pawlick 1985) and that, in general, we were "losing our forests to acid rain" (Kappel-Smith 1985). These claims were made without the benefit of long-term observations and adequate scientific investigation. After monitoring the condition of sugar maple from a variety of site conditions and geographic locations, we conclude that levels of mortality observed in plots maintained by the North American Maple Project are within normal bounds reported for a variety of broadleaved forests, including those dominated by sugar maple.

Mortality of dominant/codominant sugar maple in stands actively managed for sap production (sugarbushes) is similar to that of stands that have not been as intensively managed.

Unusual levels of mortality associated with forest declines in the past have been associated generally with a combination of nonanthropogenic biotic and abiotic stresses, and forest management activities that decrease tree diversity, or damage residual trees during stand intervention. Most forest declines can be explained by documenting the extent, timing and nature of on-site disturbances combined with a knowledge of land use history. Continued quality controlled monitoring is necessary to reveal what, if any, long-term effects may result from changes in soil chemistry and to determine whether these changes magnify the impact of other stresses.

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Spatial Relationships Between Sugar Maple (*Acer saccharum* Marsh), Sugar Maple Decline, Slope, Aspect, and Atmospheric Deposition in Northern Pennsylvania

Patrick Drohan, Susan Stout, and Gary Petersen[1]

Popular Summary

Sugar maple decline began to affect Allegheny Plateau forests in the early to mid-1980s. The forests of the region were exposed to several stresses in the period from 1985-1996, including droughts during 1988, 1991, and 1995. Additionally, both native and exotic insects reached epidemic levels during this period (see, for example, Rhoads, 1993). Other documented stresses in the region include past and present harvesting practices (Allen and others 1992), herbivory by deer (Tilghman 1989), and low soil nutrient availability (Long et al. 1997, DeWalle and Swistock 1997) possibly associated with soil acidification (Hendershot and Jones 1989).

Examination of sites experiencing sugar maple decline has yielded much valuable information about the potential causes of decline but has not provided estimates of the relative abundance of declining sugar maple sites or their spatial distribution within northern Pennsylvania. Nor did these studies provide an opportunity to contrast declining sugar maple stands with those that are not declining across a large geographic area. These estimates are desirable from both policy and scientific perspectives.

The long-term goal of our research is to characterize sites with sugar maple decline across northern Pennsylvania. In this preliminary work, our objectives were:

- to determine if the decline could be detected using data collected by the USDA Forest Service Forest Inventory and Analysis program (FIA) between 1978 and the late 1980s (Alerich 1993); and,
- to characterize the relative abundance of sugar maple decline and the sites on which declining and healthy sugar maple was found in the late 1980s across northern Pennsylvania.

This paper reports preliminary results from our study.

Methods

We limited our study to the Pennsylvania portions of the Northern Unglaciated Allegheny Plateau Section (212G) and the Northern Glaciated Allegheny Plateau Section (212F) of Bailey's Ecoregions and Subregions of the United States (Bailey and others 1994). These regions are characterized by northern hardwood forests and encompass the range of reports documenting sugar maple decline within Pennsylvania (Laudermilch 1995; McWilliams et al. 1996).

We excluded points in which overall basal area fell below the threshold of continuous forest cover ($9.2\ m^2\ ha^{-1}$) and those in which sugar maple basal area was insufficient for analysis ($2.3\ m^2\ ha^{-1}$). We found that 248 plots met these criteria (Figure 1); 140 plots were located in unglaciated Section 212G and 108 in glaciated Section 212F. Locations recorded at the center of each FIA plot were entered into a geographic information software program to create a map of stand locations and to provide points for later analysis.

FIA plot coordinates for this preliminary study consisted of actual longitudes and latitudes rounded to the nearest 100 seconds. The imprecision of FIA plot locations limited our preliminary analysis to variables (such as slope and aspect) measured directly at sample locations by FIA or to variables whose spatial resolution was compatible with plot location accuracy.

Several variables were chosen from the FIA database to determine the health status of the sugar maple population as measured in 1989. These variables were sugar maple basal area mortality in 1989 (SMBAM) and sugar maple basal area change 1978-1989 (SMBAC-we added any sugar maple basal area cut during the period to the 1989 value). We also calculated the percent dead sugar maple basal area (PDSMBA) (sugar maple basal area mortality as a percent of total living and dead sugar maple basal area), and percent sugar maple basal area change (PSMBAC) (sugar maple basal area change as a percent of basal area in 1979).

We used K Means Cluster Analysis (Minitab Inc. 1994) with these four variables to determine whether the data would cluster into healthy and declining subpopulations with sufficient separation for analysis. For slope and aspect, we tested for differences between clusters and between glacial regions as well as within region using the non-parametric Kruskal-Wallis test. Kruskal-Wallis contrasts use variable ranks rather than variable values in tests of significance. Therefore, we examined the differences in medians wherever rank difference suggested statistical significance to determine whether the differences were likely to be biologically meaningful (Minitab Inc 1994).

Wet deposition data, based on a spatially explicit model for Pennsylvania (Lynch et al. 1995), were obtained in digital format for 1987-1989 (NO_3, NH_4, SO_4, H, Ca, and Mg ($kg\ ha^{-1}\ yr^{-1}$)). We used the mean deposition over the three-year period for each element for our tests. Again, the Kruskal-Wallis test was used to contrast the deposition rankings of healthy and declining clusters across the state and within each glacial region.

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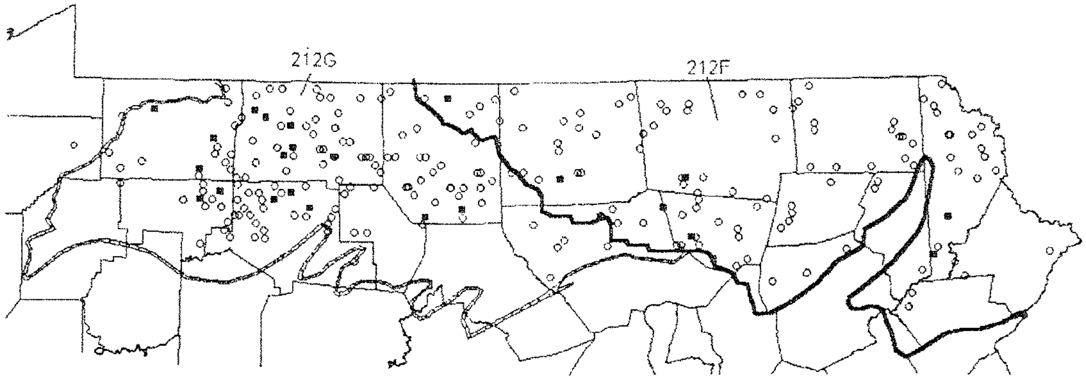

Figure 1.—Map showing the 248 FIA plot locations and the health status assigned by K-means cluster analysis (○healthy cluster, ■declining cluster). The map shows political boundaries and ecoregion boundaries (the solid line shows the boundary of glaciated Section 212F and the thin double line shows the boundary of unglaciated Section 212G).

Results and Discussion

Clustering for Health Status

Our best separation using cluster analysis resulted in the two populations seen in Figure 1 (223 healthy stands and 25 declining stands). This was achieved with all four standardized health variables (SMBAM, F=298; SMBAC, F=111; PDSMBA, F=458; PSMBAC, F=31) in the cluster analysis. Percent dead sugar maple basal area (PDSMBA) was the strongest variable contributing to the clustering. There were 123 members of the healthy cluster and 17 members of the declining cluster (about 12%) in Ecoregion 212G, the unglaciated section, and 100 members of the healthy cluster and 8 (about 7%) members of the declining cluster in Ecoregion 212 F, the glaciated area. While this difference suggests that there is a tendency towards a higher proportion of declining cluster members in the unglaciated section, the difference is not significant (p=0.22).

The declining cluster included stands with 1989 measurement period basal areas ranging from 9.2 $m^2 ha^{-1}$ to 38.9 $m^2 ha^{-1}$, with a median of 25.9 $m^2 ha^{-1}$ (Table 1). Percent dead sugar maple basal area ranged from 20 to 80 percent, with a median of 33 percent. In the healthy cluster, 1989 measurement period basal area ranged from 9.2 $m^2 ha^{-1}$ to 41.7 $m^2 ha^{-1}$, with a median of 25.9 $m^2 ha^{-1}$. In this cluster, percent dead sugar maple basal area ranged from 0 to 26 percent, with a median of 0 percent. Figure 2 shows percent dead sugar maple basal area in the two clusters plotted against their case number in the file.

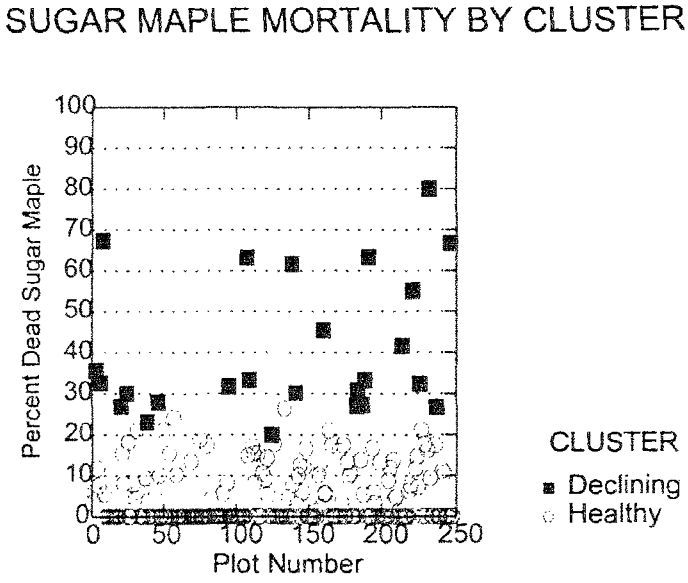

Figure 2.—Percent dead sugar maple basal area in the healthy and declining clusters (○healthy cluster, ■declining cluster).

Both the proportion of the stands with decline and the characteristics of the declining cluster are comparable to results found by Horsley et al. (this volume) in their study of topographic gradients in northern Pennsylvania and southwestern New York. Six of the 43 plots that they examined (14%) were declining; all of these plots had a percent dead sugar maple basal area in excess of 20 percent, and all the plots in their healthy cluster had percent dead sugar maple basal area less than 20 percent. All of the plots in the Horsley et al. declining cluster occurred within the unglaciated region, but our analysis detected no difference in the rate of decline between regions. Our study area extends further east and west than the Horsley et al. study, specifically including a larger portion of the glaciated region.

Table 1.—Medians, means (± standard deviation) of selected characteristics as measured or calculated from data collected during the 1978 and 1989 measurement cycle from plots in the healthy and declining clusters used for this analysis. SMBA = Sugar maple basal area.

Cluster	Basal area (m^2 ha^{-1})	SM BA (m^2 ha^{-1})	Change in SM BA (m^2 ha^{-1})	SM BA mortality (m^2 ha^{-1})	% change, SM BA	% Dead SM BA
All stands medians	25.9	6.9	1.2	0.0	14	0
means (±SD)	25.6(±7.3)	8.0(±5.2)	1.4(±2.2)	0.7(±1.2)	24(±46)	8(±14)
1 – healthy medians	25.9	7.0	1.4	0.0	17	0
means (±SD)	25.6(±7.2)	8.3(±5.3)	1.7(±1.8)	0.4(±0.6)	30(±46)	4(± 6)
2 – declining medians	25.9	4.4	2.1	2.8	-21	33
means (±SD)	25.2(± 8.2)	5.2(± 3.3)	-2.3(± 1.9)	3.3(± 1.9)	-22(± 16)	41(± 17)
212F-glaciated medians	24.5	6.3	1.7	0.0	18	0
means (±SD)	24.7(±7.6)	8.3(±5.8)	1.7(±2.1)	0.5(±1.0)	33(±56)	6(±12)
212G-unglaciated medians	26.7	7.0	0.9	0.2	10	3
means(±SD)	26.4(±7.0)	7.8(±4.8)	1.1(±2.2)	0.8(±1.3)	18(±36)	10(±15)

Table 2.—Percent of sugar maple plots on each aspect by ecological subsection.

Region	Aspect			
	North	South	East	West
Entire State	39	14	31	16
Glaciated 212F	38	12	29	21
Unglaciated 212G	39	16	33	11

Table 3.—Median deposition for several ions for healthy and declining clusters, and the p value for the Kruskal Wallis test of differences between clusters. For the Kruskal-Wallis test, the values of a variable are transformed to ranks (ignoring group membership) to test that there is no shift in the center of the groups (that is, the centers do not differ). Thus, a low p value indicates that the groups differ in rank for a particular deposition variable.

Ion deposited	Median deposition, healthy cluster (kg ha^{-1} yr^{-1})	Median deposition, declining cluster (kg ha^{-1} yr^{-1})	Kruskal Wallis p
Ammonium	2.6	2.9	0.02
Calcium	1.1	1.3	0.04
Hydrogen	0.66	0.74	0.02
Magnesium	0.21	0.22	0.23
Nitrate	18.7	20.5	0.02
Sulfate	29.4	33.7	0.02

Slope and Aspect

Sugar maple distribution across four main aspects (N, S, E, and W) was similar for all three areas studied: the entire state, the glaciated region, and the unglaciated region (Table 2). North and east aspects contained 70 percent of the sugar maple plots across the two regions.

Plots in this study occurred on slopes ranging from 0 to 62 percent (median = 16). In the glaciated region, percent slope ranged from 0 to 52 percent (median = 15) and in theunglaciated region, 0 to 62 percent (median = 17). No differences were detected between the distributions of slope steepness (percent) (p=0.645) or aspects (p=0.291) by glacial region. Nor were there significant differences across the state (slope p=0.283, aspect p=0.291), within the glaciated region (slope p=0.958, aspect p=0.863), or within the unglaciated region (slope p=0.214, aspect p=0.313) in the distributions of slope or aspect between healthy and declining populations of sugar maple. These results are consistent with the observations of Whitney (1990) and Abrams and Ruffner (1995) who found increases in sugar maple abundance from presettlement times to the present. Comparisons are difficult because of slight differences in data form and organization. Using data from the early settlement period in a study area that spanned the glacial, ecoregional border, Abrams and Ruffner (1995) found that sugar maple preferred stream valleys and north-facing coves. Whitney (1990), working with presettlement data from the Allegheny National Forest (ANF), within the unglaciated ecoregion, found that sugar maple had a marked preference for plateau top landscape positions with slopes [8 percent. In an old-growth area on the ANF, Hough and Forbes (1943) found that sugar maple was more abundant on north-facing slopes.

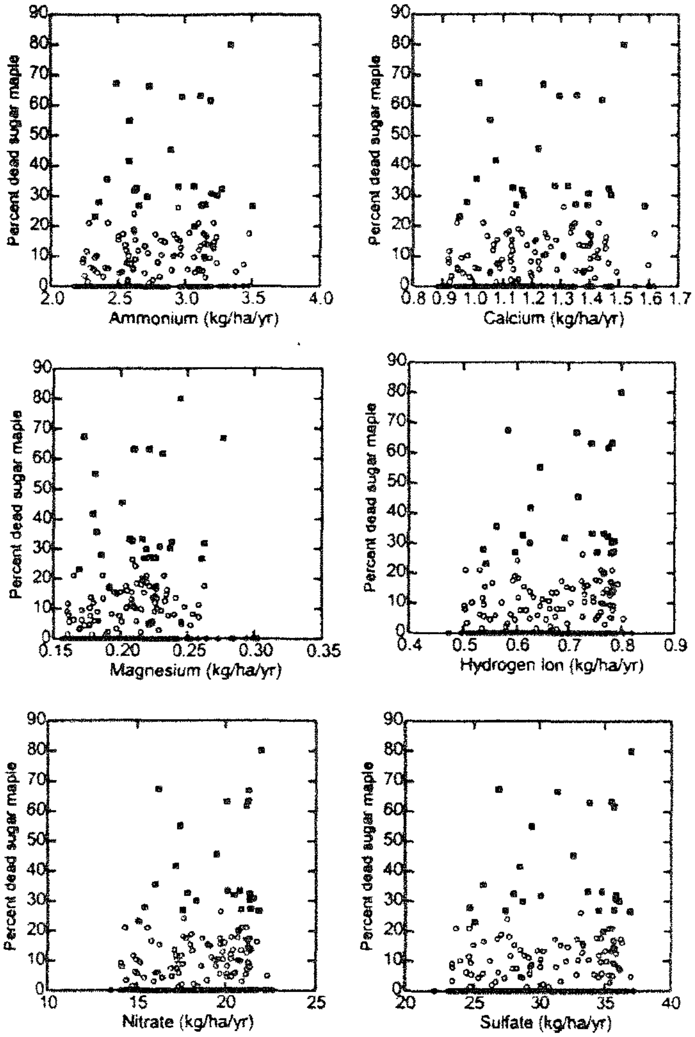

Figure 3.—Percent dead sugar maple basal area vs. each of the deposition variables examined in this study (○healthy cluster, ■declining cluster). Deposition values are mean annual kg ha^{-1} for the period 1987-1989.

Deposition Variables

Nitrate, ammonium, sulfate, and calcium deposition falls on a distinct gradient from high levels in northwestern Pennsylvania to lower levels in northeastern Pennsylvania (Lynch et al. 1995). The spatial pattern of magnesium deposition is different from that of other elements, with a secondary peak deposition level near the eastern end of the Northern Tier.

Significant differences were found across the state between healthy and declining stands for all deposition variables (p=0.02 through 0.04) except magnesium (p=0.23). Median differences in deposition values were small in all cases (Table 3). The same pattern was found within the unglaciated region. Within the glaciated region, differences between plots in the healthy cluster and those in the declining cluster were not significant (p= 0.296). Figure 3 shows the relationship between dead sugar maple basal area and each of the deposition variables for both ecoregions, including healthy and declining cluster plots.

This exploratory analysis of the correlation between deposition levels and sugar maple decline showed relationships that achieved statistical significance, but are associated with differences in actual deposition values that are unlikely to have biological meaning.

Future Work

Future work on this project will include both additional analysis at the large geographic scale reported here and analysis of intensive field-sampled data from a subset of these plots. At the large scale, we plan to test for differences between declining and healthy plots with respect to historical defoliations, elevation, and topographic position with the 248 plots. We also plan to develop much more intensive site characterizations for a sub-sample of these plots. During the summer of 1998, a crew from the Pennsylvania State University collected data at thirty of the 248 plots used in this study. They sampled soil and vegetation at 15 plots with various levels of percent dead sugar maple basal area and 15 plots with no dead sugar maple.

At each plot, the crew remeasured basal area following the methods set by the FIA program during the previous survey in 1989, collected foliage for chemical analysis, and collected cores from three trees. Other data included: slope and aspect (8-pt. scale), topographic position, tree vigor, dieback and transparency, forest floor and soil characteristics, and ground vegetation. Analysis of soil and rock physical and chemical properties and foliar chemistry will allow us to detect much more specific characteristics that distinguish plots in the healthy cluster from those in the declining cluster.

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Factors Associated with Rapid Mortality of Sugar Maple in Pennsylvania

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Abstract

Mortality of sugar maple and red maple was observed throughout Pennsylvania in 1995 following an outbreak in 1994 by forest tent caterpillar and elm spanworm on sugar maple and red maple, respectively. Symptoms of leaf anthracnose caused by *Discula campestris* (Pass.) were observed during the refoliation period from July through September 1994; the refoliation of crowns of affected trees was extremely poor or almost non-existent. Subsequent mortality and tree condition were monitored in 15 sugar maple stands located in Bedford, Blair, Lycoming, Potter, Sullivan, Susquehanna, Tioga, and Wayne counties from 1995-1997. Initial mortality was 12.3% in 1995; by 1997 cumulative mortality was 19.9% (salvaged timber excluded). The role of multiple stress factors in relation to mortality is discussed.

Introduction

Unusual levels of sugar maple (*Acer saccharum* Marsh.) crown dieback and tree mortality have been observed across the northern-tier counties of Pennsylvania since the early to mid-1980s (Kolb and McCormick 1993, Quimby 1997). In some cases, tree decline has been characterized by slow crown deterioration and eventual mortality occurring over five or more years; in other cases the crown dieback and mortality process occurs relatively rapidly in only a year or two. Defoliation, drought, and other climatic events have been associated with decline and mortality of sugar maple elsewhere (Giese et al. 1964, Gross 1991, Bauce and Allen 1991, Allen et al. 1992a and 1992b, Payette et al. 1996, Robitaille et al. 1995, Auclair et al. 1997). Recently, we had an opportunity to document a sequence of events which resulted in rapid mortality of sugar maple in Pennsylvania.

In May-June 1994, an outbreak of forest tent caterpillar (*Malacosoma disstria* Hhbner) on sugar maple was responsible for extensive defoliation of northern hardwood stands throughout Pennsylvania. Affected areas included the northern-tier counties of Bradford, Columbia, Luzerne, Lycoming, McKean, Sullivan, Susquehanna, Tioga, and Wayne and the southcentral counties of Blair and Bedford. Based on estimates from aerial surveys conducted by the Pennsylvania Bureau of Forestry (Quimby 1995 and 1996), forest tent caterpillar defoliated approximately 283,000 hectares. An additional 93,280 hectares were defoliated in areas infested by both forest tent caterpillar and elm spanworm (*Ennomos subsignaria* Hubner) on sugar maple and red maple, respectively. Subsequent refoliation of trees in affected stands was poor; trees exhibited extensive crown dieback, and foliage transparency in the range of 80 to 95+% was estimated.

In August 1994 visual inspection of foliage from affected sugar maple and red maple trees revealed symptoms of anthracnose presumably caused by the fungal pathogen *Discula campestris* (Pass.) (Hall 1995). Symptoms observed during the refoliation period were leaf blight, expansive necrotic leaf lesions characteristic of anthracnose, leaf cupping, extensive necrosis of succulent twig and bud tissue, lack of terminal bud formation, and extensive twig and branch dieback. In 1994 a study was initiated to evaluate the impact of the defoliation by forest tent caterpillar followed by anthracnose on sugar maple mortality in the years following the initial outbreak.

Methods

In November 1994, plots were established in 15 sugar maple stands for a multiyear monitoring study to record changes in tree crown condition and mortality following heavy (30-50%) to severe (50+%) defoliation by forest tent caterpillar and damage by *Discula campestris*, the sugar maple anthracnose fungus, during the subsequent refoliation period. Verification of damage by *Discula campestris* was based on the presence of bud and twig symptoms on samples taken from sugar maples within or near each study plot between September and late October 1994. Twig samples were collected and incubated in a moist chamber to induce fungal sporulation; subsequent cultures of *Discula campestris* were made from symptomatic twigs. Isolates of *Discula campestris* were tested for pathogenicity on sugar maple seedlings. After confirmation of anthracnose damage within a stand, a study plot, including 30 to 50 sugar maple trees that had been damaged by both forest tent caterpillar and *Discula campestris*, was established. Most of the sampled trees were of either dominant or codominant crown class. A total of 546 trees among the 15 plots was monitored. These plots were revisited in late May and early June 1995, 1996, and 1997 to collect data on tree mortality, percent crown dieback, percent live crown cover, foliage condition, foliage distribution and size, insect defoliation, and anthracnose activity.

Results

Only tree mortality and crown dieback are presented. Table 1 lists annual and cumulative mortality for 1995-97. In 1995, sugar maple mortality among all plots was 12.3% (67 of 546 trees), though initial tree mortality was high in four stands located in Lycoming, Sullivan, and Wayne Counties. Most residual tree crowns were damaged, and many were in fair to poor condition in most stands. Two plots located in

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Table 1.—Percentage of sugar maple mortality associated with 1994 defoliation by *Malacosoma disstria* and anthracnose caused by *Discula campestris* for 15 stands located in eight* Pennsylvania counties.

	Year		
Mortality category	1995	1996	1997
Annual	12.3 (67/546)**	8.1 (39/479)	0.7 (3/427)
Cumulative	12.3 (67/546)	19.4 (106/546)	19.9 (109/546)
Salvage healthy	-	-	2.7 (15/546)
Salvage unhealthy	-	-	15.2 (83/546)
Total salvage	-	-	17.9 (98/546)

*Bedford, Blair, Lycoming, Potter, Sullivan, Susquehanna, Tioga, and Wayne.
**Actual mortality figures presented for each category with the numerator representing dead trees and the denominator representing the study population.

Table 2.—Percentage of crown dieback in sugar maple due to the 1994 outbreak of forest tent caterpillar and anthracnose caused by *Discula campestris* on 15 study plots in Pennsylvania.

	Percent crown dieback by year		
Dieback class*	1995	1996	1997
0-15%	48.9**	57.7	79.9
20-30%	9.9	14.9	13.1
35+%	41.2	27.4	7.2

*Dieback class based on Sugar Maple Management Highlights for the Region from the North American Maple Project (Anonymous 1997).
**Percentage based on the number of standing live trees at the time of data collection; salvaged trees are not included.

Table 3.—Percentage of crown dieback in sugar maple stands* due to the 1994 outbreak of forest tent caterpillar and anthracnose where cumulative tree mortality was below 2%.

	Percent of crown dieback		
Dieback class**	1995	1996	1997
0-15%	74.2*** (242/326)	74.5 (240/322)	78.7 (251/319)
20-30%	11.3 (37/326)	11.8 (38/322)	9.7 (31/319)
35+%	13.2 (43/326)	9.9 (32/322)	9.7 (31/319)

*Data reflects nine stands which remain under study beyond 1997.
**Dieback class based on Sugar Maple Management Highlights for the Region from the North American Maple Project (Anonymous 1997).
***Percentage based on the number of standing live trees at the time of data collection.

Sullivan County on the Wyoming State Forest (Dry Run and Slab Run) each with 50 trees had 13 and 36 dead trees, respectively. Of the remaining live trees, 18 and 11 trees, respectively, had crown dieback of 80% or more. Only three additional trees died in these stands in 1996, but crown dieback was 80% or more in 22 and 8 trees, respectively. By 1996, 52 trees were dead, 30 trees had crown dieback >80%, and only 8 trees were healthy with dieback <25%. These stands were subsequently marked for salvage and removed from the current study after 1996. One plot in Wayne County on Pennsylvania State Game Lands #159 was the location where forest tent caterpillar and anthracnose were first observed and confirmed in 1994. Of the 30 trees in this plot, 4 died in 1995 and 7 in 1996. Crown dieback was >80% on 22 of 30 trees in 1995 and 14 of 19 living trees in 1996. The latter plot was marked for salvage in 1996 and removed from this study.

In 1995 two plots with 30 trees each, one in private ownership at Franklin Forks, Pennsylvania, in Susquehanna County and the other owned by the Rockport Gun Club in Wayne County, had only 1 dead tree among the 60; crown dieback of >80% was observed on 7 and 4 trees, respectively. In 1996 salvage at the Franklin Forks stand resulted in removal of 4 healthy trees and 12 trees in poor health; salvage at the Rockport Gun Club resulted in removal of 8 healthy trees, though some showed symptoms of crown dieback. These plots also were removed from the study in 1996.

Table 1 lists mortality data for the study to date. Total cumulative mortality due to natural causes for the 15 plots was 109 trees out of 546 sampled trees (19.9%). Salvage operations in 1996 and 1997 removed 98 of 546 trees (17.9%) of which 15 (2.7%) were healthy and 83 (15.2%) were in poor health. Natural mortality and salvage of trees with extensive dieback resulted in the removal of 35.1% (192/546) of the study population within three years of the forest tent caterpillar and anthracnose outbreak.

To illustrate the impact of insect defoliation and anthracnose on crown dieback, we used information developed through the North American Maple Project (NAMP) to categorize tree health among easily determined dieback classes (Anonymous 1997). Table 2 shows the tree distribution among three crown dieback classes. Trees in the 0-15% dieback class represent those with the greatest probability of long-term survival, while those with >35% dieback have a lower probability of survival. From 1995 to 1997, the proportion of trees in the 0-15% dieback class increased, while those in the >35% dieback class decreased.

Table 3 illustrates crown dieback distribution for 1995-97 among the nine stands which remained under study after 1997. Tree mortality in these stands was low. In 1995, only 4 dead trees were observed among the remaining study population of 326 trees; 3 additional trees died in 1996 and 3 more in 1997. Cumulative mortality for 1995-97 was 3%, and incidence of trees with severe dieback (>80%) for the 1995-97 period was 4.9%. Over the three years of data collection, tree crowns had less dieback and appeared to be recovering. Since 1994 there has been little or no additional insect defoliation or anthracnose damage. However, a severe drought from late June through September 1995 may have contributed to tree mortality and crown damage expression in 1996.

Discussion

High mortality and extensive crown dieback were evident within ten months of the initial defoliation. Subsequent crown recovery in residual trees was apparent by 1996 and has since improved throughout the remaining 9 stands under study. Many factors may interact to account for apparently high mortality rates following defoliation (Houston 1981). These include site factors such as soils that are excessively or poorly drained, high stand density, prior defoliation (Houston 1981, Bauce and Allen 1991), and defoliation followed by anthracnose outbreaks (Heichel et al. 1972). Unfortunately, these factors along with predefoliation crown condition could not be determined in this study. Adverse environmental factors such as drought or frost also may contribute to tree mortality following defoliation (Houston 1981). While defoliations occurred in May and June, previous research has shown that June defoliations were the most severe, resulting in the fastest and greatest amount of crown damage (Wargo 1981). In the current study, defoliation was followed by precipitation patterns that ensured moist conditions over an extended period, providing a favorable environment for anthracnose infestations (Heichel et al. 1972, Neely and Himelick 1963). During subsequent refoliation attempts, emergent leaves and subtending twigs were attacked by the anthracnose fungus which prevented any significant canopy refoliation until seasonal leaf drop in early November 1994. Therefore, affected trees with insufficient photosynthetic leaf area might not produce sufficient carbohydrate reserves to survive the winter and produce new foliage in the next growing season (Wargo 1981). Alternatively, trees with sufficient carbohydrate reserves that were not consumed during initial foliation and refoliation might survive, but would be expected to exhibit damage to residual crowns.

Other maple decline studies have noted mortality or increased crown dieback associated with secondary organisms such as the root and collar rotting fungus *Armillaria mellea* (Vahl:Fr.) P. Kumm. or the twig and branch fungus *Steganosporium ovatum* Corda. Both of these organisms may hasten the death or increase the amount of crown dieback of already stressed trees (Wargo 1981, Houston et al. 1990). There are no previous reports of the interaction between forest tent caterpillar and *Discula campestris* with the fungus acting to accelerate mortality. However, Heichel et. al. (1972) describes a field experiment where red oak and red maple saplings were manually defoliated to simulate gypsy moth or elm spanworm defoliation; during the subsequent refoliation period, emergent leaves and twigs exhibited anthracnose symptoms followed by severe twig dieback in both species. The observations of Heichel et al. (1972) suggest that insect defoliation and anthracnose can occur simultaneously to cause severe damage to tree crowns and could be a contributing factor when assessing tree decline. Given the difficulty of examining and sampling the crowns of mature trees, the role of anthracnose diseases may have been previously overlooked or attributed to other factors, including insect defoliation.

While there are many reports of long-term sugar maple mortality, only a few studies have monitored mortality rates during decline events. In the Allegheny National Forest, 340 stands surveyed in 1994, approximately ten years after initiation of sugar maple decline, revealed 28% of the sugar maple basal area (trees >2.5 cm dbh) were dead (McWilliams et al. 1996). Precise mortality rates cannot be calculated because no pre-decline data was available from these plots. Averaged across seven states and four provinces, the six-year average annual mortality rate for sugar maple in all crown classes was 0.9% for 165 plots located in sugarbushes and nonsugarbushes monitored in the North American Maple Project (Allen et al. 1995). In New England, annual mortality rates (over ten years) for sugar maple in northern hardwood stands ranged from 0.14% to 2.75% or 0.0009 to 0.0204 m^2yr^{-1} of basal area (Solomon 1977). In our study, mortality was greatest (12.3%) the year following the defoliation and anthracnose infestations; average annual mortality was 6.6% from 1995 to 1997. By 1997, annual mortality was only 0.7%, suggesting that the 1995 and 1996 mortality was episodic and by 1997 rates had returned to those found by Allen et al. (1995) and Solomon (1977). Periodic occurrences of high levels of annual mortality will influence forest composition, age structure, and stand density with irregular patterns in time and space across the landscape. Long-term annual monitoring of tree health may help to understand the influence of specific stressor events on mortality patterns.

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Impact of Forest Liming on Growth, Vigor, and Reproduction of Sugar Maple and Associated Hardwoods

Robert P. Long, Stephen B. Horsley and Paul R. Lilja[1]

Popular Summary

Introduction

In 1985 a long-term study was initiated by the Pennsylvania Bureau of Forestry and the Northeastern Research Station to evaluate factors impeding regeneration of Allegheny hardwoods (Auchmoody, unpublished). The major factors suspected of limiting regeneration were high soil aluminum levels associated with low soil pH (typically 3.6 to 4.2 in surface mineral soils), deer browsing, and interfering vegetation such as hayscented fern (*Dennstaedtia punctilobula* (Michx.) Moore) and striped maple (*Acer pensylvanicum* L.). At that time, overstory sugar maple (*Acer saccharum* Marsh.) decline was just beginning to become a serious problem on the Allegheny Plateau. Subsequently, sugar maple decline became widespread across the unglaciated Allegheny Plateau in northwestern and north central Pennsylvania. A secondary objective of the study was to determine the effects of treatments on the growth and vigor of the three principal overstory species, sugar maple, American beech (*Fagus grandifolia* L.), and black cherry (*Prunus serotina* Ehrh.), and to evaluate the effects of treatments on sugar maple flower and seed production, and seedling regeneration. Results of this study through 1993 have been reported elsewhere (Long et al. 1997), and this report will summarize results through 1996 or 1997.

Methods

Four replications of the study are located in the Susquehannock State Forest in Potter County,Pennsylvania on the unglaciated Allegheny Plateau. The study design was a split-plot with fencing (to exclude deer) the whole plot treatment and dolomitic lime (22.4 megagrams per hectare), herbicide (glyphosate), lime+herbicide, and untreated controls as the subplot treatments. Each of the 32 subplots was 45 meters X 45 meters. Herbicide to control interfering vegetation was applied with a backpack mist blower at a rate of 2.2 kg a.i. per hectare in August 1985. In October 1985, dolomitic limestone was applied with a tractor-spreader. In winter of 1985-1986, all stands were thinned to 50 percent relative density to provide lighting conditions sufficient to stimulate growth of regeneration, and in spring 1986 the electric fencing was installed.

Changes in soil chemistry were monitored by sampling soils in all 32 subplots by 2.5 centimeter increments to a depth of 15 centimeters in each year from 1986-1989 and in 1993 and 1996. Similarly, overstory growth and vigor were measured each year from 1986 to 1990 and in 1993, 1996 (growth and vigor), and 1997 (vigor only). Sugar maple flower and seed crops were evaluated each spring and fall since 1987. Mid-crown foliage chemistry was evaluated by sampling overstory sugar maples (27 trees in limed plots, 27 trees in unlimed plots) in August 1994. Sugar maple seedling regeneration was monitored in nine permanently marked 1.13 meter radius plots in each treatment plot. Where tests of statistical significance are mentioned, 0.05 was the nominal indicator of significance.

Results

Soil Chemistry

Soil chemistry was dramatically altered by the dolomitic limestone application. To simplify presentation, results are summarized for the 0-5 centimeter depth, the 5-10 centimeter depth, and the 10-15 centimeter depth. Exchangeable Ca increased in the 0-5 cm depth in 1986 to 1873 mg kg^{-1} in limed plots compared with 340 mg kg^{-1} in unlimed plots. By 1996, exchangeable Ca concentration was 2800 mg kg^{-1} in limed plots compared with 360 mg kg^{-1} in unlimed plots at the 0-5 centimeter depth. Similarly, exchangeable Mg at the 0-5 centimeter depth increased to 337 mg kg^{-1} in limed plots compared with only 50 mg kg^{-1} in unlimed plots in 1986; Mg continued to increase in limed plots to a high of 929 mg kg^{-1} in 1996. There was a downward wave of changes in elemental concentrations in limed plots induced by direct addition of Ca and Mg or by pH changes. KCl extractable Al was reduced significantly only in the upper 0-5 centimeter depth in the first few years of the study, but by 1993 and 1996 there was evidence of decreasing Al concentrations even at the deeper depths. Exchangeable Mn also decreased in response to increased soil pH in the limed plots, although there was an anomalous increase in Mn at the 0-5 centimeter depth for unlimed plots in 1996. Both P and K decreased in response to liming, but only at the 0-5 centimeter depth. Soil pH responded rapidly to lime addition, increasing to 5.28 in limed plots in 1986 compared with only 3.70 in unlimed plots. Acidity changes also were evident at the 5-10 cm depths by 1987 in limed plots. By 1996, the upper 5 centimeter pH value averaged 6.30 in limed plots and 3.70 in unlimed plots.

Vigor and Growth Responses

Overstory crown vigor was estimated by two observers and rated on a scale from 1=dead to 6=healthy using the system of Mader and Thompson (1968). For American beech and black cherry, liming did not improve vigor (Figure 1). Beech bark disease was detected in the plots early in the study and trees started to die by 1987 or 1988. There also were droughts in 1988, 1991, and 1995 which likely affected tree vigor, and these were followed by elm spanworm (*Ennomos subsignaria* Hubner) defoliations in 1993 and 1994. While

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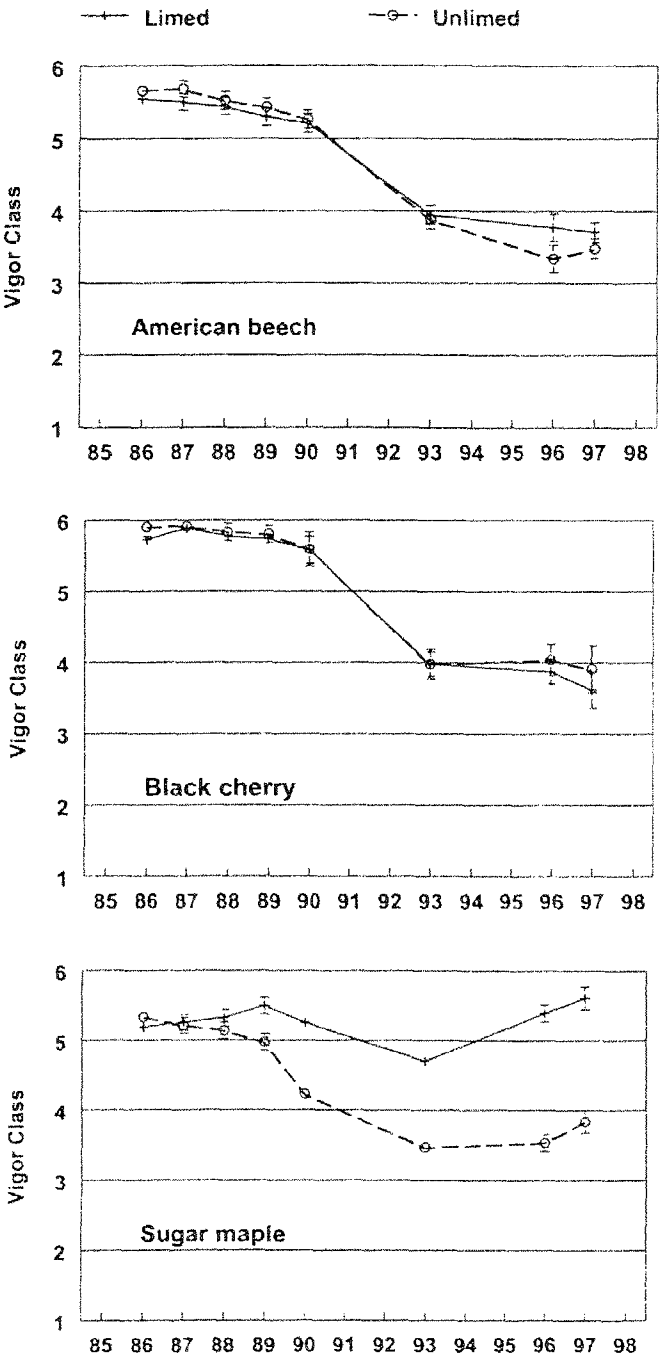

Figure 1.—Mean vigor ratings in limed and unlimed plots.

elm spanworm has a broad host range, beech is a preferred species for spanworm feeding. Overall beech vigor decreased from 5.6 in 1986 to 3.5 in 1997 (Figure 1). Black cherry has suffered similarly, with mean vigor averaging 5.7 through 1988 and then declining to 5.5 by 1990 and to 3.8 in 1993 as a result of elm spanworm defoliation. In addition, black cherry was affected by cherry scallop shell moth (*Hydria prunivorata* Ferguson) in 1995 and trees were slow to recover through 1997.

Sugar maple vigor shows a different response (Figure 1). There was some initial indication of an increase in sugar maple vigor for limed trees from 5.1 in 1986 to 5.3 in 1989, but this was not statistically significant ($p>0.05$). However, by 1990, a trend of decreasing sugar maple vigor was evident for both limed and unlimed trees, but the limed trees maintained significantly higher vigor by 1993. By 1996 and 1997, vigor for both limed and unlimed sugar maple increased. For limed trees mean vigor in 1997 was 5.6, the highest mean vigor for the duration of the study, compared with 3.8 for unlimed trees. As with beech and black cherry, sugar maple vigor of both limed and unlimed trees was negatively affected by droughts in 1988, 1991, and 1995 and by elm spanworm defoliations in 1993 and 1994. We speculate that in the absence of these stressors, sugar maple in limed plots would have continued to increase in vigor after 1989.

The progression of mortality in the course of the study is similar to the vigor results. By 1997 (12 years after treatment applications), mean mortality based on plot means shows sugar maple mortality in the unlimed plots was 18% while in limed plots it was only 9%. For beech there was no significant difference in mean mortality between limed plots (14 percent) and unlimed plots (17 percent). For black cherry, mean mortality was 15 percent on limed plots and only 10 percent on unlimed plots, but these differences were not statistically significant.

Cumulative mortality, by 1997, based on individual tree data rather than plot means showed sugar maple mortality on unlimed plots was 24 percent compared with only 9 percent on limed plots. For beech cumulative morality was 25 percent on limed plots and 24 percent on unlimed plots. Black cherry mortality was higher on limed plots, 11 percent, compared with unlimed plots, 4 percent, suggesting that liming may be deleterious to black cherry.

Growth responses indicate that liming did not significantly affect mean basal area increment of beech or black cherry through 1996 (Figure 2). However, for black cherry, there is again the suggestion that limed trees have been growing more slowly. For sugar maple, basal area growth for limed and unlimed trees started to diverge as early as 1990, but was not significantly different until 1993 when limed trees averaged 890 square centimeters of basal area and unlimed trees averaged 845 square centimeters of basal area. By 1995, unlimed sugar maple increased slightly in growth rate, while limed trees continued to accelerate in growth rate (Figure 2). Over the course of the study (1986-1996), limed sugar maple increased in basal area by 24 percent and unlimed trees by only 11 percent, and mean annual basal area increment for sugar maple averaged 19.5 square centimeters per year for limed trees and 8.6 for unlimed trees.

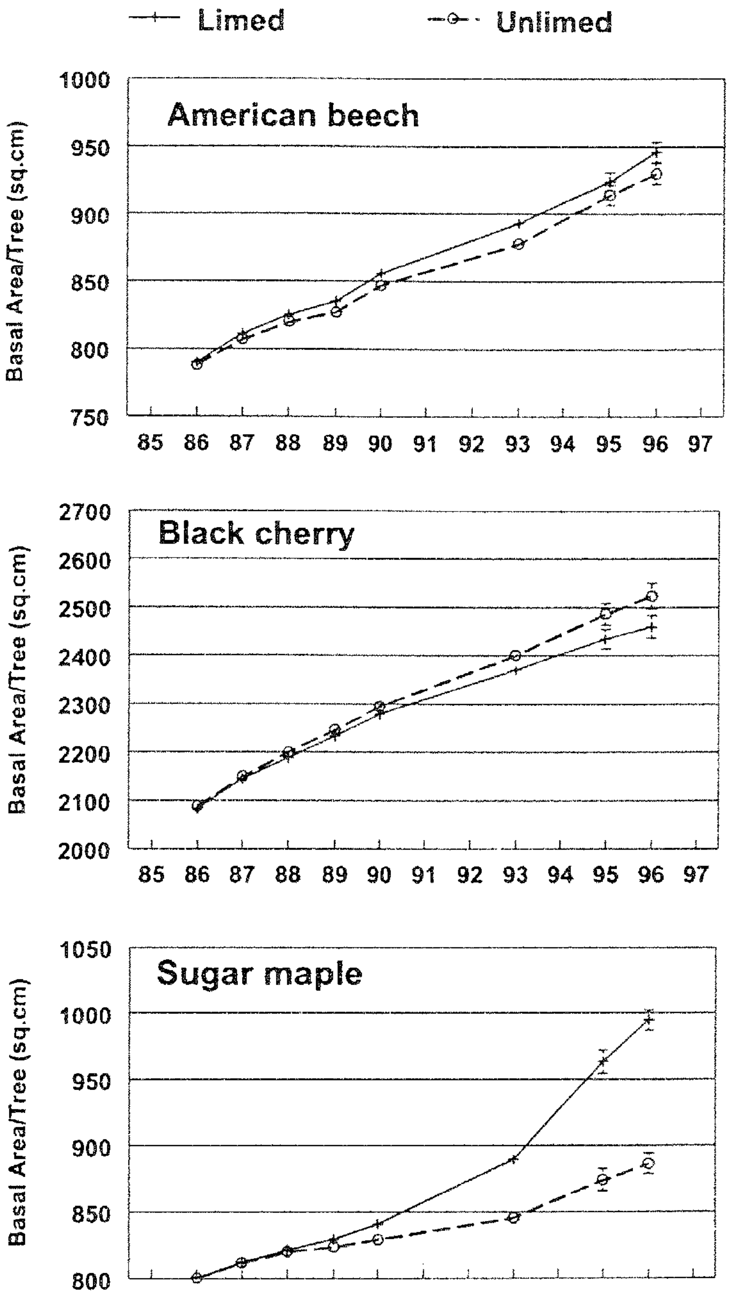

Figure 2.—Mean basal area per tree in limed and unlimed plots from 1986 to 1996. Plotted values are corrected by covariance analysis for differences in initial basal area.

Foliage Chemistry

In 1994, mid-crown foliage samples were obtained from 54 sugar maple trees, 27 in limed and 27 in unlimed plots. Foliage chemistry reflected many of the changes observed in soil chemistry. Foliar Ca levels were doubled to 8777 mg kg^{-1} in limed trees compared with only 4031 mg kg^{-1} in unlimed trees, and Mg concentrations increased fourfold to 2655 mg kg^{-1} in limed trees compared with only 617 mg kg^{-1} in unlimed trees. Both Al and Mn concentrations were reduced in foliage from limed trees compared with unlimed trees, likely due to the pH-induced decrease in availability of these cations. Foliar P concentrations were unaffected by liming, while K concentrations decreased from 7136 mg kg^{-1} in unlimed trees to 4811 mg kg^{-1} in limed trees. The decreased foliar K concentration probably indicates soils were overlimed, and, based on results from other studies, K may now be nearing a deficiency threshold in limed plots. Molar ratios of Ca:Al were 75 in foliage from unlimed trees and 233 from limed trees.

Correlations between soil and foliage nutrients provide some additional insights into nutrient relationships. There were significant positive correlations between exchangeable K, Ca, Mg, Mn and Al and corresponding foliar chemical concentrations. Correlations of overstory vigor measurements from sampled trees with soil chemical constituents revealed a negative correlation between vigor and soil Al concentrations (r=-0.59) while soil Ca and Mg were positively correlated with vigor (r=0.52 and 0.54, respectively). The foliar molar Ca:Al ratio was also positively correlated with overstory vigor (r=0.64) suggesting that low Ca:Al ratios are associated with low sugar maple vigor.

Flower and Seed Crops

Sugar maple flower and seed crops were also affected by liming, but not by fencing or herbicide. Lime increased the size, but not the frequency of sugar maple flower and seed crops. Three sugar maple flower crops were initiated during the study in 1988, 1989 and 1992. The 1988 flower crop did not develop into an appreciable seed crop though differences between limed and unlimed trees were statistically significant (p<0.001 for flower crops; p=0.13 for seed crops). To assess flower crops, the percent of crown with flowers was rated on about 200 trees, using a scale where 0=no flowers present, 1 percent=trace flowering, and 5-100 percent estimated to the nearest 5 percent class. In 1989 and 1992, the percent of crown with flowers increased from 22 percent (1989) to 225 percent (1992) in trees on limed plots compared with unlimed trees. Seed crops were rated with a different scale where 0=no seed, 1=trace-5 percent, 2= 6-25 percent, 3=26-50 percent, 4=51-75 percent, and 5=76-100 percent of crown with seed. Lime increased the mean seed crop rating from 2.8 (unlimed trees) to 3.8 (limed trees) in 1989 and from 0.6 to 2.8, respectively, in 1992. Sugar maple seed crop frequency was unaffected by lime application; over the past 31 years area-wide seed crops have appeared the year following summer drought events when the mean June-July Palmer Drought Severity Index (PDSI) became more negative than -1. Seed crop size, even on limed plots, was only 5 to 15 percent of that found in the Lake States and New England (Curtis 1959, Godman and Mattson 1976, Graber and Leak 1992). Thus, seed supply appears to be an important factor influencing sugar maple regeneration.

Sugar Maple Regeneration

Prior to 1990, there were few sugar maple seedlings on plots in any treatment; those present typically were <5 centimeters tall and did not survive from year to year. Cohorts of sugar maple seedlings occurred on study plots in 1990 and 1993 following the seed crops in 1989 and 1992, respectively. These seeds fell into vegetation established 5 to 8 years earlier. Unfenced areas typically were dominated by ferns, grass, striped maple and birch (*Betula spp.*), which are all species that are low in preference to deer or resilient to repeated deer browsing. Fenced areas were dominated by a variety of tree species and by *Rubus*.

Establishment of sugar maple seedlings was positively correlated with overstory sugar maple basal area and with grass abundance. There was more sugar maple basal area on unfenced than on fenced plots; basal area was equally distributed on lime and herbicide treatment plots. There was more grass ground cover on unfenced, limed, and herbicided plots than on fenced, unlimed, and unherbicided plots. Sugar maple seedlings were more abundant on unfenced and limed plots; herbicide made no difference.

Survival of sugar maple seedlings during the 24 months following cohort appearance in 1990 and 1993 was affected by liming and herbicide, but not by fencing. Survival was higher on limed and herbicided treatments.

Mean height of the tallest sugar maple seedling was also increased by lime application; fencing and herbicide had no effect. Seedlings on both limed and unlimed plots were buried in vegetation established prior to sugar maple seedling appearance, so the data probably do not reflect the growth potential of sugar maple.

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Sugar Maple Seedling Anatomy and Element Localization at Forest Sites with Differing Nutrient Levels

Carolyn J. McQuattie, Robert P. Long, and Thomas J. Hall[1]

Abstract

Sugar maple (*Acer saccharum* Marsh.) seedlings often have poor survival on acidic unglaciated portions of the Allegheny Plateau. Greater survival is found after lime treatment of unglaciated sites or on glaciated areas of the Plateau. The difference in survival rate may depend in part on the acidity or chemical composition of the soil. From a 1993 seedling cohort, survival after 2 years was 70 percent on limed plots (surface mineral soil pH=5.4) compared with 35 percent on more acidic unlimed plots (surface mineral soil pH=3.8) (Horsley and Long, unpublished data). A third site, Dodge Hollow (DH), on nearby glaciated soils had an abundant 1993 sugar maple seedling cohort and surface mineral soil pH was 4.0. Comparison of foliar nutrient levels showed significantly higher concentrations of base cations in foliage from seedlings on limed plots but significantly higher Mn and a lower Ca:Al ratio in foliage from unlimed plots (Horsley and Long, unpublished data). At DH foliar base cation concentrations were similar to those from the limed plot, but high foliar Mn concentration and a low Ca:Al ratio was comparable to foliage from the unlimed plot. An anatomical study was conducted to compare differences in mycorrhizal colonization, root and foliar anatomy, and the location of potentially toxic elements (Mn, Al) in seedlings from these 3 forest sites with differing soil chemical characteristics. In June and August 1996, 10 seedlings each from limed, unlimed, and DH sites were collected. Root and foliar tissues from each seedling were chemically processed for examination by light and transmission electron microscopy, and by energy-dispersive x-ray microanalysis. Remaining root systems (>80 percent of total) were chemically preserved in the field for later mycorrhizal assessment. Roots and foliar tissues for transmission electron microscopy and x-ray analysis were thin-sectioned and examined in a JEOL transmission electron microscope coupled with a Link Systems x-ray analyzer. In June, mycorrhizal colonization of roots was highest at the limed site, lowest at the unlimed site, and intermediate at DH (66, 21 and 45 percent, respectively). In August, colonization at the unlimed and DH sites was similar (approximately 35 percent) but lower than colonization at the limed site (61 percent). By light microscopy, roots from the unlimed site had an irregular outline and contained increased amounts of dense compounds in endodermal and stele cells compared to roots from the other sites. Dense staining is often associated with accumulation of phenolics or defensive compounds. Precipitates analyzed by x-ray analysis in root xylem and cortical cells (June collection) from the unlimed site were composed of Mn, and dense material observed by transmission electron microscopy in leaf chloroplast membranes was similar to Mn toxicity injury observed in sugar maple seedlings under controlled conditions (McQuattie and Schier, unpublished data). Aluminum was detected in mycorrhizal fungal hyphae (associated with P) in roots from the unlimed site and occasionally at DH. Precipitates containing Al in petiole and midvein vascular cells were found in foliage collected from the unlimed site only. In contrast, Ca and/or Si precipitates were found in foliar and root cell walls in seedlings from all sites, indicating a common chemical composition in these cellular sites. By transmission electron microscopy, starch grains were observed in leaf chloroplasts from all sites in June, whereas in August starch was prominent only in leaf blades from the unlimed site. In August, large starch grains were seen in roots of seedlings from DH. Starch grains were not observed in roots from limed and unlimed plots possibly indicating starch storage had not commenced for these seedlings. Overall, potential indicators of stress were most often seen in seedlings from the unlimed site: low early-season mycorrhizal colonization, Mn compounds in root cells, Al precipitates in leaf cells, and altered patterns of starch accumulation in leaves and roots.

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Factors Contributing to Sugar Maple Decline Along Topographic Gradients on the Glaciated and Unglaciated Allegheny Plateau

Stephen B. Horsley, Robert P. Long, Scott W. Bailey, Richard A. Hallett and Thomas J. Hall[1]

Popular Summary

In the early to mid 1980s, foresters began to notice a reduced level of sugar maple health characterized by unusual mortality of large trees, decreased crown vigor and crown dieback. Affected trees most often were located on the upper slopes of unglaciated sites; sugar maple on the lower slopes of unglaciated sites and in any landscape position on glaciated sites seemed less affected or unaffected. These observations were made against a background of unusual levels of insect defoliation and untimely climatic events (Drohan and Stout this volume).

During the past 30 years, declines of sugar maple have been reported in Massachusetts, Ontario, Quebec, Vermont, New York and Pennsylvania (Kolb and McCormick 1993). While defoliation and other stress factors also seem to be involved in each of these situations, nutrient deficiencies, particularly of base cations including Ca, Mg and K, seem to be a common thread in all of these declines. Recently, Long et al. (1997; this volume) reported that addition of dolomitic limestone at four high elevation unglaciated sites in north central Pennsylvania resulted in significantly increased sugar maple survival, crown vigor, diameter and basal area increment, flower and seed crop production. Black cherry and American beech were unaffected by lime addition. Lime significantly increased foliar concentrations of Ca, Mg, the Ca:Al and Mg:Mn molar ratios and decreased foliar concentrations of potentially toxic Al and Mn. On unlimed plots, trees with high crown vigors had higher foliar concentrations of Ca and Mg than trees with moderate crown vigor. And for all trees, mean BAI was positively correlated with foliar concentrations of Ca and Mg and negatively correlated with foliar concentrations of Al and Mn. Overall, the study showed that Ca and Mg supplies and perhaps those of potentially toxic ions like Al and Mn were important for health and growth of sugar maple.

Northwestern and north central Pennsylvania and southwestern New York lie at the boundary of the Wisconsin and earlier glacial advances. Areas to the north were glaciated as recently as 12,000 to 21,000 years ago; those south of the terminal moraine are older and have not been glaciated. Soils on glaciated portions of the Allegheny Plateau are Inceptisols and generally have higher supplies of base cations than the Ultisols found on unglaciated areas, but the distribution of Ca, Mg, Al and Mn with topographic position was not known.

In the present study, we investigated the relationship between sugar maple health and 1) glacial history, 2) topographic or physiographic position, 3) site (elevation, aspect) and stand characteristics (species composition, structure, density), 4) disturbance history (management, defoliation), and 5) foliar nutrition.

Methods

A series of plots was established in stands along topographic gradients at 19 sites across the glaciated and unglaciated portions of the Allegheny Plateau in northwestern and north central Pennsylvania and southwestern New York. In 1995, plots were established on upper, mid- and lower topographic positions at 5 sites; these were supplemented in 1996 with plots on upper and lower topographic positions at 14 additional sites. In all there are 43 stands; 18 on glaciated soils and 25 on unglaciated soils. In each stand, we identified 5 dominant or co-dominant sugar maple trees that were judged to be healthy by lack of crown dieback. These trees were used for mid-crown foliage collection during the last 2 weeks in August. Foliar levels of N, P, K, Ca, Mg, Al and Mn were determined for each tree, then averaged for each stand. The foliage sample trees became the locus for plots to evaluate other site and stand characteristics.

Health of all trees including sugar maple was measured in mid- to late July on three 400 m^2 plots in each stand using North American Maple Project protocols (Cooke et al. 1996). Four parameters were calculated for sugar maple which gave an estimate of sugar maple health over different time scales: % Dead sugar maple basal area (PDEADSM), crown vigor index (SMVIG), crown dieback (SMDIE) and crown transparency (PTRANS). Cluster analysis was used to determine which health variable best discriminated healthy from unhealthy stands. PDEADSM, the best health measure, separated the 43 stands into a healthy group of 37 stands with 0 - 11% dead sugar maple basal area and an unhealthy group of 6 stands with 21 - 56% dead sugar maple basal area.

Stand species composition, structure and density were calculated from data obtained on the three 400 m^2 plots. Species composition was evaluated as the percent of the total basal area that was sugar maple and the percent of the total basal area that was black cherry. Relative sugar maple diameter was the measure of stand structure and expresses the relative position of sugar maple in the diameter distribution of the stand. Relative density was used as the measure of stand density.

At each site, aspect was estimated with a compass and elevation was determined from 7.5 minute topographic maps after geolocating the sites with a GPS unit.

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Information on disturbance histories was determined from two sources: 1) annual layers of digitized defoliation sketch maps were queried to determine the timing, severity and agent of defoliation, and 2) land managers who were responsible for each stand were contacted and queried concerning stand management history and additional information on stand defoliation history.

Results

Thirty-three of the 43 stands were on north and east facing slopes; 4 (12%) were unhealthy. The remaining 10 stands were on south and west facing slopes; 2 (20%) were unhealthy. All of the unhealthy stands were at elevations >500 m, but there was not a precise relationship between sugar maple health and elevation.

Health of sugar maple varied with glacial history and topographic position. Sugar maple were uniformly healthy and there were no trends with topographic position on glaciated sites. But on unglaciated sites, PDEADSM was higher on upper than lower topographic positions. Health on the lower slopes of unglaciated sites was indistinguishable from that on glaciated sites. Each stand was categorized according to its physiographic position. Summits, shoulders and upper backslopes represent the positions in the landscape where the soils are most leached and the driest; mid- and lower backslopes have moderate leaching potential and higher moisture. Foot and toe slopes and enriched sites such as those with concave microtopography, benches or seeps have the least potential for leaching; soil moisture is variable depending upon position in the landscape and the nature of enrichment. On unglaciated sites, stands with unhealthy sugar maple were located on summits, shoulders and upper backslopes. But, all stands in these physiographic positions were not unhealthy. Stands on mid- and lower backslopes, on foot or toe slopes or on enriched sites remained healthy.

Among the stand variables, competitive effects of black cherry, which forced sugar maple into a lower crown position and a lower relative diameter, seem to be the most important. The proportion of sugar maple in the stand and the stand relative density had little relationship with sugar maple health. Overall, the effects of stand parameters on sugar maple health were relatively small.

Disturbances caused by stand management activities also had little effect on sugar maple health. Thinning was the only management activity at the study sites over the past 20 years. Eleven of the 43 stands were thinned from 4 - 20 years previously. The remaining 32 stands had no management activity in the past 20 years. Thinning did not predispose or protect sugar maple from decline in the long term. Two thinned and four unthinned stands were among the six stands with unhealthy sugar maple.

Defoliation disturbance played a key role in determining which stands were unhealthy. We evaluated the number of defoliation events and defoliation severity for the 10 and 20 year period prior to overstory health evaluation. A defoliation severity index was constructed by assigning a value of 3 to a heavy defoliation where >60% of the foliage was lost, a 2 to moderate defoliations where 30 - 60% of the foliage was lost and a 1 to a light defoliation where <30% of the foliage was lost. These values were summed over the 10 or 20 year period prior to health evaluation. The most recent 10 year period proved to be the most important. The upper slopes of unglaciated sites were defoliated more often and more severely than the lower slopes of unglaciated sites or any topographic position on glaciated sites. Both the number and severity of defoliation events had an effect on sugar maple health. Stands with unhealthy sugar maple were those defoliated 2 or more times during the past 10 years with a defoliation severity index of 4 or more, representing two moderate defoliations. However, all stands with these defoliation history characteristics did not have unhealthy sugar maple, suggesting that there must be something which makes trees in some stands more resilient to repeated defoliation.

There were important relationships between foliar levels of Ca, Mg, Al and Mn and glacial history, topographic position, physiographic position and sugar maple health. Foliar chemistry data were expressed on concentration, content and leaf area bases. There were no differences in interpretation of the results among these expressions. There also were no relationships between foliar N, P and K and sugar maple health.

Comparison of the foliage chemistry of healthy sugar maple on glaciated and unglaciated sites showed that trees on glaciated sites had more Ca and Mg and higher molar ratios of Ca:Al, Ca:Mn and Mg:Mn, similar amounts of Al and less Mn than trees on unglaciated sites. There were few differences in foliar values between upper and lower slopes of glaciated sites; trees in upper slope stands had similar levels of Ca, Mg, and Al and molar ratios of Ca:Al, Ca:Mn, and Mg:Mn and more Mn than trees in lower slope stands. On unglaciated sites, there were important differences. Foliage from trees in upper slope stands had less Ca and Mg, lower molar ratios of Ca:Al, Ca:Mn, and Mg:Mn and more Al and Mn than foliage from trees in lower slope stands. Similar trends in foliar nutrition were found when each stand was assigned to a physiographic position.

Foliar nutrition was correlated with sugar maple health and with defoliation disturbance history. Foliar Mg, Mn and the Mg:Mn molar ratio were significantly correlated with PDEADSM and the Ca:Al molar ratio was marginally correlated with PDEADSM. Foliar Mg content showed a strong relationship with PDEADSM. Stands with less than threshold amounts of foliar Mg became unhealthy, if the stands had had ^{3}2 moderate or severe defoliations (defoliation severity index ^{3}4) during the past 10 years. Stands with greater than threshold levels of foliar Mg could withstand greater numbers and severity of defoliation and still remain healthy. Foliar Mn alone could not be used to distinguish healthy from unhealthy sites. All stands which became unhealthy had relatively high foliar Mn content, but in some stands, trees with foliar Mn as high or higher than those which became unhealthy remained healthy; these trees had greater than threshold amounts of Mg. The molar ratio of Mg:Mn did not distinguish healthy from unhealthy stands as well as foliar Mg alone.

Discussion

Our work confirms the observations of practicing foresters that sugar maple is healthy on glaciated sites and the lower slopes of unglaciated sites. Unhealthy sugar maple was found on unglaciated upper slopes in the summit, shoulder and upper backslope physiographic positions. These sites had the lowest foliar Ca and Mg, the highest Al and Mn, and were defoliated more often and more severely than any other landscape position. Poor base cation status of upper slope sites probably is the result of long-term weathering of initially base-poor substrates, which may be aggravated by acid deposition. Flowpaths of water which is in contact with Ca and Mg-containing bedrock may explain the higher base cation status of lower slope unglaciated sites (Bailey et al. this volume).

Foliar Mg was the key ion associated with sugar maple health. Healthy trees had greater than threshold amounts of foliar Mg. Mg interacted with defoliation stress. Unhealthy trees were those with low Mg AND two or more moderate or severe defoliations in 10 years. Sugar maple remained healthy on low Mg sites if defoliation stress was low. This is corroborated by the fact that sugar maple with low foliar Ca and Mg and low stress in New England remained healthy (Hallett et al. this volume). Furthermore, trees with greater than threshold foliar levels of Mg were more resilient to stress, withstanding greater numbers and severity of defoliation. Foliar levels of Mn seem to be important only when there is inadequate Mg; at present, the role of Mn in sugar maple decline is unclear.

The decline of sugar maple fits the definition of a decline-disease: a syndrome of canopy-dominant trees characterized by gradual deterioration in health and vigor which leads to death (Manion 1991; Houston 1992). Decline-diseases seem to result from complex interactions of factors that predispose or weaken trees, followed by inciting or triggering events that result in dieback and mortality. Our study suggests that sugar maple decline occurs as a result of an interaction between imbalanced Mg nutrition and excessive defoliation stress. Sugar maple with low foliar levels of Mg (and Ca) photosynthesize at a lower rate than those with higher levels of these cations (Liu et al. 1997). The level of storage carbohydrates accumulated by trees growing on base cation-poor sites likely is less than those growing on base cation-rich sites. Thus, trees growing on base cation-poor sites are predisposed to be less resilient to stress because they have less carbohydrate reserves to maintain living tissue and repair damaged tissue. Stresses such as defoliation, particularly those that are severe enough to cause refoliation, and to a lessor extent drought, trigger or incite decline because they result in a substantial drain on storage carbohydrates (Wargo this volume). Under these circumstances, trees first dieback, reducing the amount of living tissue that is supported by storage carbohydrates. If stress continues trees often die, either as a result of carbohydrate starvation or from the action of secondary organisms such as *Armillaria*, which invade the weakened trees (Wargo and Harrington 1991).

For land managers, the implication of our study is that unglaciated upper slope sites in northwestern and north central Pennsylvania are sensitive sites where sugar maple and other high base cation-demanding species may be at risk during stress events such as insect defoliations. They are areas where land managers should focus insect monitoring and suppression activities and consider management activities that favor species with lower base cation requirements.

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Influence of Geologic and Pedologic Factors on Health of Sugar Maple on the Allegheny Plateau

Scott W. Bailey, Stephen B. Horsley, Robert P. Long and Richard A. Hallett[1]

Popular Summary

Decline of sugar maple (*Acer saccharum* Marsh.) has been a problem on the Allegheny Plateau of Pennsylvania since the mid-1980's (Kolb and McCormick 1993; McWilliams et al. 1996). Horsley et al. (this volume) found that declining stands were distinguished from non-declining stands by a combination of repeated insect defoliation and low foliar calcium and magnesium concentrations. Stands that exhibited only one of these two conditions remained healthy. Information is needed (1) to determine whether low foliar nutrient concentrations are related to soil quality, (2) to determine key parameters and threshold values that describe soil conditions which might predispose a stand to decline, and (3) to develop methods to predict the distribution of susceptible sites across the landscape. Furthermore, information about the role of acid deposition in inducing soil fertility problems remains elusive.

The present study was initiated to examine soil factors leading to sugar maple decline on the Allegheny Plateau. Soil description and sampling were conducted at a number of plots, spanning the geographic range of the Plateau in northwestern and north-central Pennsylvania and adjacent southwestern New York. Plots include a range of stand heath conditions, landscape positions, and bedrock and glacial geologic influences.

Methods

Study plots were established at 19 sites described by Horsley et al. (this volume) across the Allegheny Plateau from Chautauqua County, New York in the west to Tioga County, Pennsylvania in the east. Study plots span a wide range of soil parent materials and geologic influences found on the Allegheny Plateau. At each site, two or three plots were established to span the elevational distribution of sugar maple. County soil surveys and reconnaissance observations were used to locate one representative sampling pit per plot. Pedon description, according to National Resource Conservation Service methods, was conducted to a depth of at least 130cm, unless bedrock was encountered at a shallower depth. Samples for chemical analysis were collected by genetic horizon. Additional forest floor samples (O and A horizons) were collected by the pin-block technique (Federer 1984) at three locations in each plot. This provided information on spatial variability in surficial horizons as well as the ability to express nutrient levels on a landscape area basis. Soil samples were analyzed for pH, extractable cations and organic matter content generally following the methods of Robarge and Fernandez (1987). Forest composition and health measurements are described in Horsley et al. (this volume).

Results

Surveyed sugar maple stands were located on all physiographic positions from summit to footslope, on soils that ranged from moderately deep to very deep, well drained to poorly drained, and included soils of four orders (Inceptisols, Spodosols, Alfisols, and Ultisols). All declining stands were located on summit, shoulder or upper backslope physiographic positions on Ultisols. Declining stands had lower extractable calcium and magnesium and higher exchangeable aluminum than non-declining stands. Subsoil horizon chemistry was a better predictor of decline than chemistry of the forest floor or upper mineral horizons.

Overall, a great variety of nutrient conditions was measured. For example, extractable concentrations of calcium, magnesium and aluminum each ranged over a factor of 250. Further analysis is planned to determine which chemical parameters for which horizon or sequence of horizons best correlates with foliar chemistry and health parameters.

Soils in unglaciated upper landscape positions contained lower concentrations of extractable nutrient base cations compared with other landscape positions. Soils on upper and lower landscape positions of glaciated sites and in lower landscape positions on unglaciated sites had similar moderate to high base cation content. Mineralogy also played a role in site nutrient status. Plots influenced by calcareous bedrock, such as the Oswayo and Huntley Mountain Formations, contained the highest concentrations of soil extractable base cations. Some plots at mid to lower physiographic positions contained seeps. Chemistry of seep water corroborated site nutrient status indicated by soil extractable cations. No declining stands were located on plots containing seeps; seeps did not occur in landscape positions where decline was observed.

Discussion

Nutrition appears to be a predisposing factor in sugar maple decline on the Allegheny Plateau. Declining stands are marked by low foliar calcium and magnesium concentrations, which follow low concentrations of extractable pools of these elements in the soil. The variation in site quality across the Plateau might be explained by a model that considers the location of weathering reactions and the effect of landscape position on delivery of weathering products to the rooting zone.

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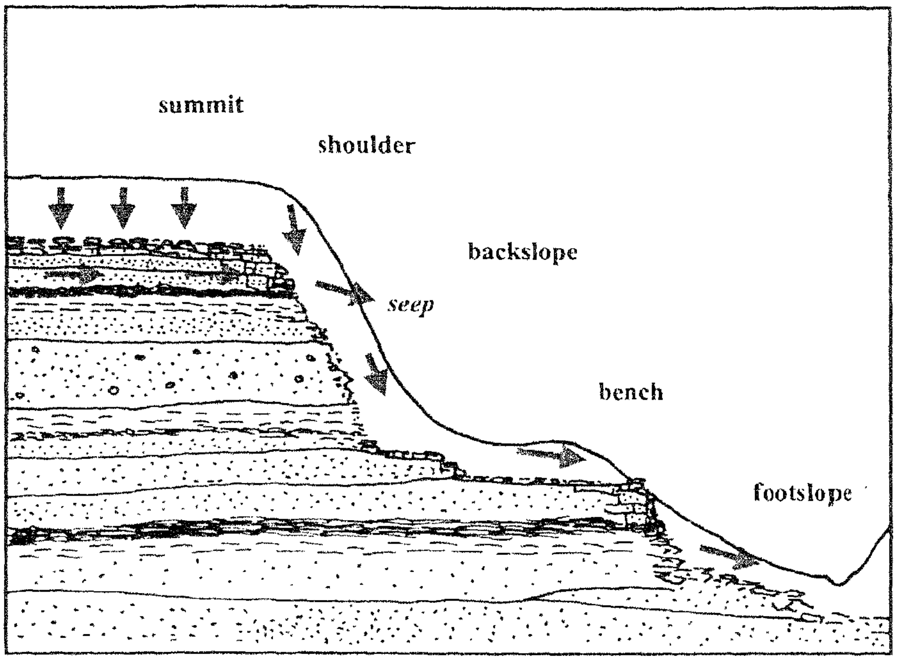

Figure 1.—Schematic cross section of the unglaciated portion of the Allegheny Plateau. Patterned areas represent interbedded sandstone, siltstone and shale bedrock. Soils are developed in relatively thick, weathered residuum, colluvium and alluvium shown as the unpatterned area above the bedrock. General locations of physiographic positions where sugar maple plots occurred are labeled. Arrows indicate generalized hydrologic flowpaths.

Mineralogy of unglaciated soils is dominated by primary minerals such as quartz and muscovite, which are resistant to weathering, and secondary minerals such as kaolinite and illite, which are stable in the soil environment. Weatherable minerals are confined to lower portions of the regolith well below the rooting zone or within bedrock. Thus the delivery of weathering products, such as calcium or magnesium ions, to the rooting zone is limited to portions of the landscape where water flowpaths bring ions released from bedrock or deeper regolith to the soil (Figure 1). Such locations may be those where water that has percolated into the bedrock is forced laterally back into the regolith by a strata of low permeability, thereby influencing soil chemistry and in some cases creating seeps. On other portions of the landscape, particularly unglaciated summits, shoulders and upper backslopes, nutrient inputs are confined to atmospheric inputs; nutrient conservation by biomass cycling is particularly important on these sites.

In contrast, on glaciated portions of the Plateau, much of the weathered regolith was removed by glacial erosion. Soils are developed in glacial till (Figure 2), which incorporates relatively unweathered material freshly exposed by glacial erosion. Thus, weathering reactions occur within the rooting zone, creating less contrast in weathering inputs by landscape position. However, even on glaciated sites weathering in the rooting zone may be limited where glacial till is largely derived from bedrock units with few weatherable minerals.

Although none of the soils investigated contained carbonate minerals, weathering of carbonate-bearing bedrock may contribute to soil fertility at both unglaciated and glaciated sites in mid to lower landscape positions on certain bedrock formations. Some of the highest concentrations of base cations in soil and seep water occur in this situation. These sites may be best suited to management of relatively high nutrient-demanding species such as sugar maple and white ash. Further analysis is planned to develop predictive tools for identifying site quality.

The role of acid deposition in contributing to sugar maple decline remains unclear. Acid deposition has been shown to reduce extractable base cations in soil based on theoretical grounds and in laboratory studies (Lawrence et al. this volume). Long-term depletion of exchange pools has been documented by retrospective studies (Shortle and Bondietti 1992; Lawrence et al. this volume) and in field-based mass balance studies (Bailey et al. 1996; Likens et al. 1998). However in the present study, the base cation-poor sites where sugar maple decline has occurred are located in landscape positions and on bedrock formations that one would expect to have the lowest nutrient levels, based on

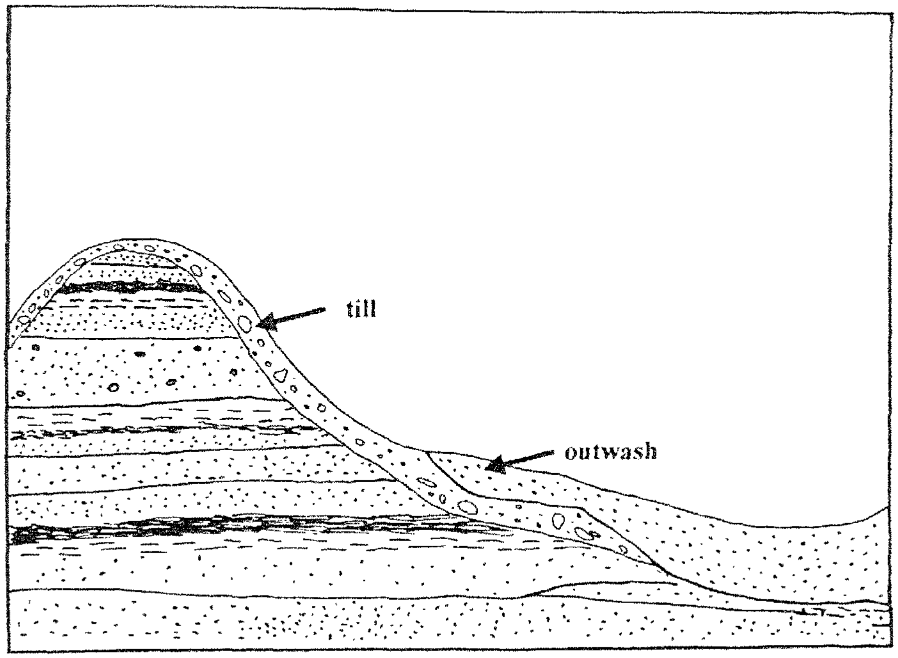

Figure 2.—Schematic cross section of the glaciated portion of the Allegheny Plateau. Soils on glaciated portions have developed in relatively thin glacial till on upper portions of the landscape and in glaciofluvial deposits (e.g. outwash) in lower valleys.

lack of weatherable minerals in the rooting zone and lack of hydrologic pathways to deliver weathering products from deeper sources. Given the available evidence, one would reasonably hypothesize that nutrient depletion due to acid deposition has increased the portion of the landscape with nutrient values below a critical, but as yet undetermined, threshold. However, in light of the great variety of nutrient concentrations attributable to landscape position, mineralogy and soil development, the extent that sugar maple decline is due to acid deposition remains speculative.

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Foliar Chemistry of Sugar Maple: A Regional View

Richard A. Hallett, Stephen B. Horsley, Robert P. Long, Scott W. Bailey, and Thomas J. Hall[1]

Abstract

Forest health and monitoring issues have become major focus of scientists and research institutions in Europe and North America during the last decade because of widespread forest decline symptoms in Europe, high elevation spruce/fir decline in eastern North America and sugar maple (*Acer saccharum* Marsh.) decline in Quebec, and the United States. Foliar concentrations of Ca, Al, K, Mg, N, and P are highly correlated with tree growth, health, and physiological function for a wide range of species. Other studies have shown that foliar Ca and Ca:Al ratios are correlated with dark respiration rates and basal area increment on sites that are affected by acid deposition or are susceptible to cation depletion. Further work in Pennsylvania and New York has linked decline of overstory sugar maple trees to multiple insect defoliations in stands with low foliar nutrient status. These results have implications for forest management agencies across the northeastern United States.

In order to understand sugar maple productivity and health at a regional scale, 75 plots representing a wide range of soil types, spanning the northeastern United States have been established. A suite of soil chemical and physical variables will be measured along with health and productivity. Results from the chemical analysis of sun leaves from 3 to 5 healthy, dominant or co-dominant sugar maple trees per plot are presented here. Foliar Ca fell below putative minimum values (5000 ppm) on 24% of the plots region wide. Foliar Mg fell below putative minimum values (700 ppm) on 22% of the plots region wide. Low Ca and Mg values can indicate deficiencies of these elements. Maximum Mn values were 3740 ppm, much higher than the putative maximum of 1630 ppm reported in the literature. High foliar Mn may indicate toxicity in sugar maple. Other elements (Al, P, K and N) were not at levels that could be considered deficient or toxic. Sugar maple decline symptoms exist in PA and NY but are not widespread in NH and VT. However, foliar chemistry data show that many stands in NH and VT are at least as nutrient poor as affected stands in PA and NY. This data set in conjunction with other data collected on these plots will allow us to understand the linkages between soil chemistry, foliar nutrition, and sugar maple health at a regional scale. In addition this study will allow us to provide tools for forest managers that can be used to identify sugar maple stands that may be vulnerable to decline.

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Nutritional Factors Associated with Decline in Canada

Benoît Côté[1]

Abstract

Forest decline in eastern Canada was particularly severe in the early 1980's and is still prevalent in some areas (Bowers and Hopkin 1997). Early public and scientific opinions on the causes of forest decline were often not based on sound scientific knowledge. Factors such as acidic precipitation and ozone were most often mentioned as direct causes of forest decline in the early stages. Although standards of nutrition for sugar maple (*Acer saccharum* Marsh.) were not known at the time, some common nutrient deficiencies were identified: K in the Eastern Townships, Mg on some sandy soils, and P on some sites with mull humus. More than 10 years after the onset of decline, we now have a better understanding of the nutritional problems associated with forest decline. The problem was complex as many combinations of nutrients were found to be deficient. Most common combinations of deficient nutrients were in descending order of importance: K+Ca (31%), K+N (23%), K+Ca+N (11%), K (9%), P (8%), and K+Ca+Mg+N (3%).

Nutrient deficiencies were corrected through diagnostic fertilization. Diagnoses were usually made using DRIS indices. Typical application rates ranged from 400 to 800 kg ha^{-1}. Fertilizers were applied manually or by air. Terrestrial applications were slightly more efficient. Fertilization was found to have long-term effects (> 5 years) in many instances. The use of diagnostic fertilization rather than the use of general fertilizer guidelines should be favored in declining stands as nutrient imbalances can easily be exacerbated with an inappropriate fertilizer mixture.

As mentioned before, the forest is still declining in some areas. Based on nutrient status, our results suggest that many forest stands are "walking on a tight rope" in that most of their nutrients are at critical levels. Any perturbation of the nutrient cycle in these stands is likely to trigger nutrient imbalances and deficiencies in one or more nutrients. This is in agreement with the recent publication of the critical loads for eastern Canada (Bowers and Hopkin 1997) which suggests that large tracts of forest have soils that are susceptible to nutrient leaching and soil acidification via acidic deposition.

Forest management can also lead to soil acidification. Some species are known to improve soil fertility. Birch (*Betula* spp.) and basswood (*Tilia americana* L.) are well known as soil improvers. Sugar maple, which has been favored in most sugar bushes to the detriment of other hardwoods, has leaf litter characteristics that suggest a strong potential for soil acidification (Côté and Ouimet 1996). Among all common hardwoods of eastern Canada, red and sugar maple have the most acidic leaf litters and their C:N ratios are high. Leaf litter N concentrations are low in maples and other nutrients are generally lower than in basswood. Clear evidence of soil acidification under maple was provided by comparing soil acidity under 27 year-old plantations of white pine (*Pinus strobus* L.), white spruce (*Picea glauca* (Moench) Voss), yellow birch (*Betula alleghenìensis* Brit. and maple(*Acer* spp.) (France et al. 1989).

Although forest decline does not make the news anymore in Canada, it is still present and many sites are in a precarious state with regard to nutrient status. Some ecosystems may require a bit of help to fully recover and become more resilient to natural and anthropogenic stress factors. Diagnostic fertilization and sound management of forest composition may be what is required.

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Trends in Growth Rates of Vermont Sugar Maples from 1953-1992 in Relation to Stand Nutrition

Timothy R. Wilmot[1]

Abstract

Growth of sugar maple (*Acer saccharum* Marsh.) in 7 northern Vermont stands managed for sap production and 22 unmanaged stands distributed around the state was studied for the period 1953-1992 in relation to stand nutrition and other site factors. In 4 managed stands where at least 25% of the trees had 10% or greater crown dieback, average annual basal area increment (BAI) for 1953-1992 in codominant trees averaged 17.5 cm^2 compared to 32.3 cm^2 in 3 managed stands where less than 10% of the trees had 10% or greater crown dieback. Soil surface horizons of slower growing stands were characterized by significantly lower pH and Ca, ($p < 0.05$) marginally lower Mg and marginally higher Al than faster growing stands, while soil P and K were not different. Foliar Ca was lower ($p < 0.01$) in slower growing stands (6,400 $mg\ kg^{-1}$) than faster growing stands (12,200 $mg\ kg^{-1}$) but other foliar nutrients did not differ significantly. No other stand characteristics, including age, basal area, stem density, elevation or aspect were apparently related to differences in growth rates and crown condition between these two groups. A 49% decline in BAI of the faster growing trees from the mid-1970's to 1992 was noted, but the small sample size precluded interpreting this as a region-wide growth decline.

In a second study, 22 hardwood stands composed of at least 1/3 sugar maple, and not thinned since 1943 were identified on state and federal lands in the Green Mountains and the Vermont Piedmont east of the mountains. Twelve sugar maples per stand 27 cm in diameter or greater were cored in 1993, and surface soil horizons were sampled around each tree. Average annual stand BAI for the period 1953-1992 ranged from 8.9 cm^2 to 26.9 cm^2. Stand growth rates were not correlated with stand basal area (range = 20.7 - 28.3 $m^2\ ha^{-1}$), tree density (range = 197 - 388 stems > 15 cm dbh ha^{-1}) , slope (range = 5 - 69%) or elevation (range = 195 - 807 m). There was a negative correlation between soil pH and average stand dieback ($p < 0.01$), but, unlike the managed stands in northern Vermont, base cation availability and soil pH in soil upper horizons were not well correlated with growth rates on either a stand or tree basis, although soil P was negatively correlated with stand growth ($p < .05$). Other site factors that were not examined, such as soil depth, water-holding capacity, and soil nutrient pools in deeper horizons may have had an overriding influence on stand growth rates.

A moderate growth decline over the period 1979-1992 was observed across most of the 22 unmanaged stands. Average annual BAI for trees that were canopy codominants in 1953 (30-46 cm DBH) was approximately 22 cm^2 between 1953 and 1977, but declined to 15.6 cm^2 by 1992. A period of defoliation by forest tent caterpillar (*Malacosoma disstria* Hubner) over much of the state from 1978-1982 was a likely inciting factor in this decline, as was an outbreak of pear thrips (*Taeniothrips inconsequens* Uzel) in 1988. Records from Vermont weather stations did not indicate long-term changes in growing season precipitation between 1953-1992. Continued monitoring is needed to determine whether this change in growth rate was due to stand closure or other factors, and if growth rates will recover to previous levels. It is notable that the average annual BAI of nearly 15 cm^2 in 1992 for all trees at all sites was near or above the average growth rate for sugar maple reported from other parts of its range.

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Foliar Nutrient Analysis of Sugar Maple Decline: Retrospective Vector Diagnosis

Victor R. Timmer and Yuanixin Teng[1]

Abstract

Accuracy of traditional foliar analysis of nutrient disorders in sugar maple (*Acer saccharum* Marsh) is limited by lack of validation and confounding by nutrient interactions. Vector nutrient diagnosis is relatively free of these problems. The technique is demonstrated retrospectively on four case studies. Diagnostic interpretations consistently suggest that decline incidence involves Ca and Mg deficiency induced by toxic accumulation of Mn.

Introduction

The evaluation of nutrient sufficiency in trees is complex because there are many nutrients considered essential for vigorous tree growth. These nutrients are usually required in different amounts and balanced proportions, and their availability to trees may be affected by interactions occurring between different nutrients and also between nutrients and other elements in the soil or plant system. The interactions are difficult to detect and quantify, thus confounding interpretations of simple measures of deficiency and excess of nutrient supply. These problems are particularly pertinent to diagnosing nutritional symptoms of maple decline because of the widespread belief that multiple rather than single factors of stress may be contributing to the incidence of disorders (Cote and Oimet 1996). Thus reliable diagnostic techniques must have the capacity to cope effectively with multiple nutrients and their complex interactions.

Under such circumstances, foliar analysis rather than soil chemical analyses is the preferred method of assessing tree nutrient status since elemental composition of the leaf is considered a more direct index of nutrient availability to trees compared to measures of soil nutrient supply. It is also simpler to screen multiple element status (such as both macro- and micronutrients) by foliar analyses rather than by soil analysis because fewer and less complex laboratory procedures are involved. Traditionally, three major interpretive techniques have been applied to assess leaf chemistry of sugar maple: the critical concentration concept, the nutrient ratio approach and the DRIS norm system. Each technique has inherent limitations in terms of interpretive accuracy and reliability (Timmer 1991). This paper will introduce a fourth approach to foliar analysis interpretation, called vector nutrient diagnosis that has not been previously applied to sugar maple decline disorders. The technique is more comprehensive than the others, and has the potential to improve diagnostic power.

Current Approaches

We reviewed recent studies relating sugar maple leaf chemistry to decline ratings or dieback symptoms in a range of stand conditions in eastern Canada and the United States (Bernier and Brazeau 1988; Bernier and Brazeau 1988; Cote and Camire 1995; Cote et al 1995; Cote and Ouimet 1996; Fyles et al 1994; Heisey 1995; Kolb and McCormick 1993; Liu et al 1997; Mader and Thompson 1969; McLaughlin 1992; Ouimet et al 1995; Ouimet et al 1996; Ouimet and Fortin 1992; Wilmot et al 1995; Wilmot et al 1996) to determine the most popular diagnostic technique used. We noted a clear reliance on pre-established "critical" or "threshold" concentrations of elements as indicators of nutrient sufficiency. Although simple in application, the diagnostic reliability and sensitivity of the critical level approach must be questioned. Published critical concentrations for mature sugar maple are highly variable and poorly defined (Kolb and McCormick 1993; van den Burg 1985), they are seldom verified and validated by controlled fertilization experiments (Timmer 1991), and may not account for nutrient interactions. Interpretations can be confounded by inconsistencies of leaf tissue concentration with age, season and development stage, and by possible dilution and accumulation effects when comparing plants or plant components of unequal size (Timmer 1991).

In general, diagnoses offered in these studies tended to be qualitative rather than quantitative, focusing more on nutrient deficiency rather than toxicity because of the lack of published critical toxicity levels, and the difficulty in distinguishing between luxury consumption and toxic uptake above sufficiency concentrations. All studies screened macronutrient status, only a few included micronutrients, which implies that the role of micronutrients and their interactions were not considered crucial in diagnosing this disorder. In three studies (Cote and Camire 1995; Cote et al 1995; Long et al 1997), diagnostic interpretations were supplemented by comparing leaf nutrient status of healthy and unhealthy trees, and using optimum nutrient ratios or DRIS norms to assess nutrient balance. This approach is more inclusive than that based solely on critical levels, but reliability suffers from similar problems of weak definition, calibration and validation. Vector diagnosis may avoid the interpretive problems associated with traditional foliar analyses because its application is independent on pre-established critical levels, nutrient ratios or DRIS indices, and the technique has been calibrated and validated by fertilization trials. We have applied this approach retrospectively to foliar chemistry data published in these studies to demonstrate its potential in evaluating nutritional problems associated with maple decline.

Vector Diagnosis

Graphical vector diagnosis is explained in detail (Timmer 1991), and has been reviewed by Weetman 1989 and Haase

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and Rose 1995, thus it will only be briefly described here. Initially developed by Timmer and Stone 1978, the technique has undergone periodic refinements to enhance reliability and flexibility. Interpretations of complex multi-vector responses were simplified by normalization procedures (Timmer and Morrow 1984). Identifying nutrient interactions was improved by comparing multiple nutrients in similar space (Teng and Timmer 1990a; Teng and Timmer 1990b; Timmer and Teng 1990). Concepts of steady-state nutrition were introduced by integrating dynamic or temporal parameters in the system (Imo and Timmer 1997). Recently, interspecific nutrient competition between species was identified by adopting a two-crop format of the technique (Imo and Timmer 1997).

Its application recognizes the biological principle that growth of plants is dependent on nutrient uptake, hence the nutrient concentration in the plant is a function of two fundamental processes: nutrient uptake and biomass accumulation. This relationship is examined by comparing growth and nutrient status of trees, or tree components, differing in health and/or productivity in a nomogram that plots biomass (accumulation) on the upper horizontal axis, nutrient (uptake or) content on the lower horizontal axes, and corresponding nutrient concentration (nutrient content divided by component biomass)on the vertical axis (Figure 1). When normalized to a specified reference sample (usually the control set to 100), differences are depicted as vectors because of shifts in both direction and magnitude. Diagnosis is based on vector direction of individual nutrients, identifying occurrence of deficiency (C), sufficiency (B), luxury consumption (D), toxicity (E), antagonism (F) and dilution (A). Each configuration corresponds to a specific phase in dose response curves relating changes [increasing (+), decreasing (-), or none (0)] in plant growth, nutrient content and nutrient concentration to increasing soil nutrient supply (Timmer 1991). Vector magnitude reflects the extent or severity of specific diagnoses, and facilitates relative ranking and prioritizing.

When only part of the tree is sampled (usually the case with large trees, not seedlings), the presumption is that biomass changes in plant components (such as shoots or foliage) accurately reflect growth changes of the sample trees (Timmer and Morrow 1984). In this exercise, it was assumed that routine measures of maple decline in stands, such as crown transparency, branch defoliation, canopy dieback, growth decline, etc. are closely correlated with tree productivity. Hence these measures served as surrogate estimates of foliar biomass in the nomograms. Accordingly, the upper and lower horizontal axes in Figures 2, 3 and 5 were labeled as indices of foliar biomass and nutrient content.

Case Studies

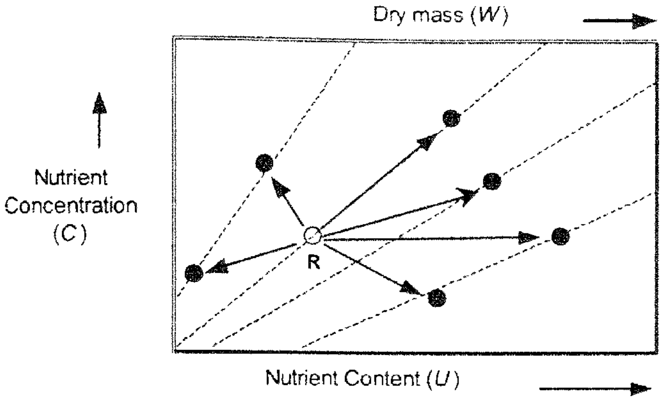
We present here data from studies that monitored both macronutrients and micronutrients in foliage in relation to a range of maple decline. The nomograms (Figure 2 and 3) show a common pattern of the largest downward, left-pointing vectors associated with Ca and Mg (Shift F, antagonism in Figure 1), and the largest, upward left-pointing vectors associated with Mn (Shift E, toxicity in Figure 1). Vector length increased with reduced foliar biomass or the severity of decline. Since the Mn vectors were larger than corresponding Ca or Mg vectors, diagnosis suggest that the disorder involved a toxic build up of Mn that inhibited uptake of Ca and Mg uptake, i.e., a case of Mn-induced Ca and Mg deficiency. Thus, as decline ratings increased, uptake (content) of base cations (mainly Ca and Mg) in foliage was severely depressed, while uptake (content) of Mn was slightly reduced in highly affected trees, or increased in less affected trees.

The mechanism could be explained by soil acidification increasing exchangeable Mn levels in the soil, which resulted in excess or toxic build up of this ion in trees (Marschner 1995). High levels of soluble Mn may in turn displace exchangeable Ca, Mg or K on the soil exchange complex inducing deficiencies of these nutrients for the trees. It is also well known in agriculture that within the plant high supplies of Mn may inhibit transport of Ca and Mg into fast growing tissues (Graham et al 1988).

Our diagnosis was supported indirectly by growth and nutritional responses of trees in independent fertilization experiments testing soil base status and liming treatments. Response patterns of sugar maple seedlings raised on a gradient of soil base saturation and pH under greenhouse conditions (Figure 4) were similar to those of Figure 2 and 3. Biomass and uptake of Ca and Mg in foliage was markedly reduced (Shift F) as base saturation of the soil decreased (Figure 4). Since Mn uptake was little changed, and concentration increased appreciably (Shift E), interpretations suggest growth inhibition due to Mn-induced Ca and Mg deficiency. Logically, the problem could be alleviated by effective liming to increase pH and base status of the soil. Liming of mature sugar maple affected by decline raised soil pH and stimulated tree growth, while reducing crown dieback symptoms (Figure 5). The response was accompanied by increased uptake of Ca and Mg (Shift C, deficiency in Figure 1) and decreased uptake of Mn (Shift F) in foliage. Apparently, applications of dolomitic limestone corrected a deficiency of Ca and Mg, and antagonistically reduced Mn uptake thus counteracting possible Mn toxicity.

Conclusion

We have limited our demonstration of retrospective vector nutrient diagnoses to four studies. Vector nomograms (not shown here) of other studies (Cote and Camire 1995; Liu et al 1997; Ouiumet et al 1995; Ouiumet and Fortin 1992; Wilmot et al 1995; Wilmot et al 1996) that monitored mostly macronutrient status in foliage, revealed similar patterns of reduced uptake of Ca and Mg (or K on some Quebec sites) in declining trees, supporting the diagnosis that base cation limitation may be associated with maple dieback. However, interactions with Mn could not be confirmed because of the lack of Mn data. We surmise from our combined results that sugar maple decline may be linked to induced base cation deficiency that is caused by toxic Mn accumulation in the rooting zone of soils. This preliminary diagnosis needs to be confirmed by field trials testing controlled additions of Mn to the soil in problem stands.



Vector shift	Change in relative W	Change in relative U	Change in relative C	Nutritional effect	Nutrient status	Diagnosis
A	+	+	-	Dilution	Non-limiting	Growth dilution
B	+	+	0	Accumulation	Non-limiting	Sufficiency, steady-state
C	+	+	+	Accumulation	Limiting	Deficiency response
D	0	+	+	Accumulation	Non-limiting	Luxury consumption
E	-	-, +	+	Concentration	Excess	Toxic accumulation
F	-	-	-	Antagonism	Limiting	Induced deficiency by E

Figure 1.—Interpretation of directional changes in relative dry mass and nutrient status of plants (or plant components) contrasting in growth and/or health. The reference condition (R) is usually normalized to 100. Diagnosis (A to F) is based on shifts (increase [+], decrease [-] or no change [0]) of individual nutrient characterized in dose response curves relating plant growth, nutrient concentration, and nutrient content to increasing soil nutrient supply. Vector magnitude reflects extend or severity of the diagnosis identified (modified from Timmer 1991). Note that results in this paper involve mostly vectors E and F, suggesting that the toxic accumulation of nutrient E antagonistically induced a deficiency of nutrient F.

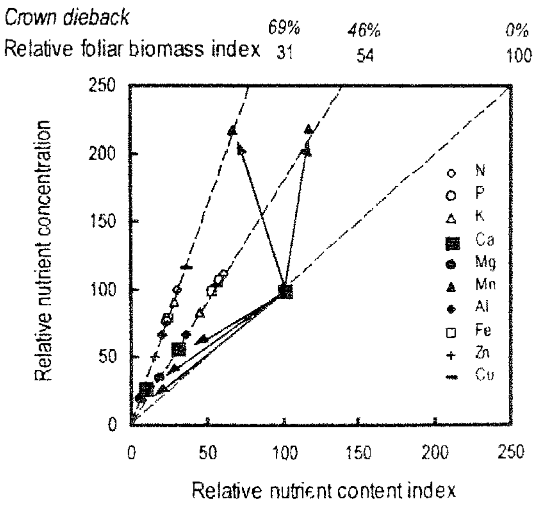


Figure 2.—Relative biomass index, nutrient concentration and nutrient content index of foliage of sugar maple stands of various degrees of crown dieback severity in Pennsylvania (Kolb and McCormick 1993). Crown dieback was defined as the proportion (percentage) of total crown volume containing dead branches with tips less than 2.5 cm in diameter. Rating was visually scored using the North American Maple Decline Project system. Relative foliar biomass index was calculated as 100 minus crown dieback rating. Foliar nutrient content index was the product of relative nutrient concentration and relative biomass index. Status of the healthy stand (with 0 to 5% crown dieback) was normalized to 100. Note that dieback severity increased with higher Mn uptake and lower Mg and Ca uptakes, suggesting a diagnosis of Ca and Mg deficiency induced by Mn toxicity.

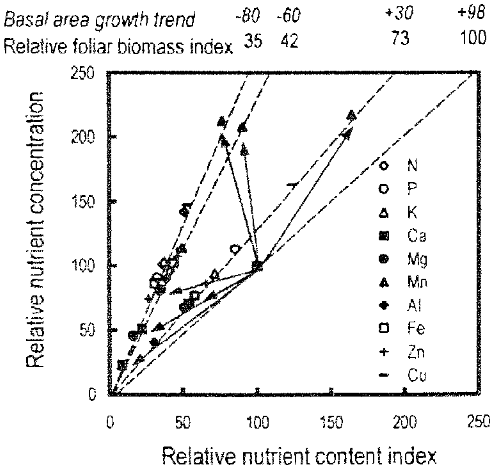


Figure 3.—Relative foliar biomass index, nutrient concentration and nutrient content index of sugar maple stands of similar age, but varying in relative basal area growth (RAG) compared to a 60-yr growth period (1928-1987) in Pennsylvania (Heisey 1995). The trend is positive if RAG increased and negative if it declined. Relative foliar biomass index was estimated as a linear function of RAG for the 1978-87 period. Foliar nutrient content index was the product of nutrient concentration and biomass index. Nutrient status of the stand with the highest RAG difference (+98) was normalized to 100. Note that basal area growth trends decreased with higher Mn uptake and lower Mg and Ca uptake, suggesting Ca and Mg deficiency induced by Mn toxicity.

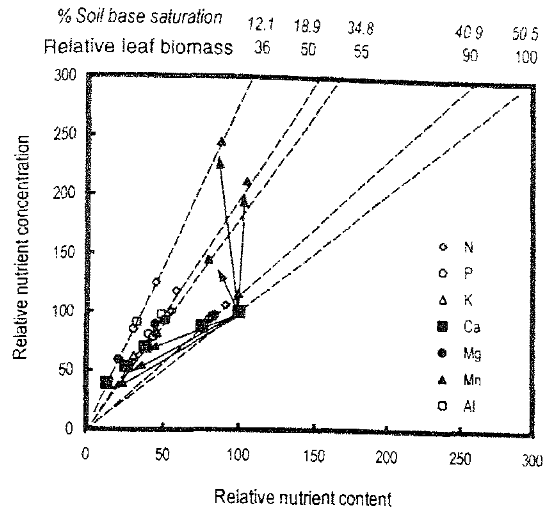


Figure 4.—Effect of soil base saturation on relative leaf biomass, nutrient concentration, and nutrient content of sugar maple seedling in a greenhouse pot trial in Quebec (Ouimet et al. 1996). The soil was a strongly acidic (pH = 4.1) sandy loam podzol with low base saturation (5%). A gradient of increasing soil base saturation was created by adding base cation solutions. The seedlings were transplanted to the pots at cotyledon stage and grown for three months. Note that low soil base saturation inhibited leaf biomass and depressed uptake of Ca and Mg most, and Mn least.

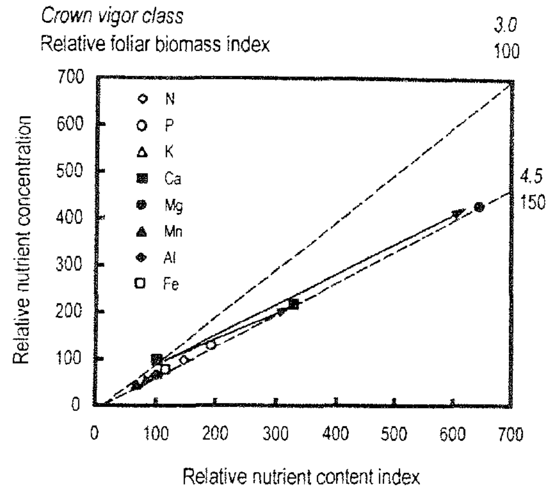


Figure 5.—Response of declining maple trees to liming in Pennsylvania (Long et al. 1997). The liming treatment was a single application of commercial pulverized dolomitic limestone (Ca = 21%, Mg = 12%, CaO equivalent = 58.8) at 22.4 Mg.ha⁻¹. Foliar biomass index was estimated as a linear function of total basal area. Nutrient status of the unlimed plots was normalized to 100. Foliar nutrient content index was the product of nutrient concentration and biomass index. Note that the positive biomass response was associated with depressed Mn uptake (-65%), and enhanced Ca (+330%) and Mg (+640%) uptake, suggesting that liming alleviated Ca and Mg deficiency, and countered Mn toxicity by reducing Mn availability.

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Root Dynamics and Nutrient Allocation in Sugar Maple

Ronald L. Hendrick[1]

Abstract

My colleagues, Kurt Pregitzer and Andy Burton, and I have been studying root dynamics in sugar maple forests in Michigan for the past 10 years. We have used a combination of traditional soil cores, minirhizotron video images and physiological techniques in an effort to understand patterns of carbon and nutrient allocation to roots, particularly the ephemeral, small diameter roots.

With respect to the role of roots in ecosystem annual net primary production (NPP), roots <2.0 mm in diameter account for about 60% of ecosystem NPP. These same roots account for about 50 – 60% of the total amount of N returned through above and below ground litterfall. Foliage production and litterfall account for about 1/3 of NPP and N returns, respectively. About 85% (numbers) of the roots are less than 0.50 mm in diameter (70% of biomass and 80% of length), and less than 2% exceed 1.0 mm. The average diameter of sugar maple fine roots is about 0.35 – 0.37 mm. In addition to their overall importance to the C and N economy of sugar maple forests, we have measured a substantial degree of simultaneity in root production and mortality throughout the year. Traditional approaches that rely on measurements of temporal biomass changes to quantify root production and mortality would yield estimates about 50% too low in these forests. Combined with the tendency to use a relatively coarse (1.0 – 2.0 mm) screen through which to wash and recover roots, we believe that the importance of very fine roots has been underestimated in at least some previous root studies.

We have used minirhizotrons to follow the appearance and fate of individual roots as a measure of root longevity. In sugar maple forests, about 40% of all annual root production occurs prior to and coincident with canopy expansion. Most mortality occurs after leaf fall and over winter. Root mortality rates for any time period during the year are the same for all roots produced that year, regardless of when they first appeared. However, mortality rates drop dramatically over winter, and remain low for roots surviving into their second growing season. However, roots produced the subsequent year die off at the same, higher mortality rates as did roots produced the previous year.

Based upon the above data, it appears that changing environmental conditions during the growing season do not affect mortality rates. However, we have measured substantial differences among sites arrayed along a north-south gradient of about 400 km. In earlier studies we observed that root mortality rates were highest at our warmest, most southern site, suggesting that higher rates of root respiration might be associated with shorter root life spans. However, we subsequently measured equally high root mortality rates at the coolest, most northern site. Root chemistry assays and soil nutrient dynamics data revealed that root nitrogen content, and ultimately root nitrogen supply potential, explain the differences. Contrary to observations from other forests, high levels of soil N increase sugar maple root lifespan, regardless of soil temperature regime. Greater tissue N concentrations were associated with higher respiration rates at all temperatures, but high rates of respiration do not appear to be shortening root lifespans.

Further studies of the relationship between root dynamics and soil temperature, matric potential and site water balance showed that there are no strong effects of the soil environment on the dynamics of fine roots at our sites. There is some tendency for periods of abundant water to be associated with lower mortality and higher production rates, but the relationship is weak. There does appear to be a temporal correspondence between the onset of periods of high, midsummer water demand and the production of deep (80 – 100 cm) roots, and between autumn leaf fall and the death of the deep roots, but it is highly variable spatially.

Our current efforts are focused upon better understanding the role that soil N, mycorrhizae, and root physiology play in regulating root dynamics, and how controls over root dynamics in sugar maple forests compare with a variety of coniferous and deciduous forests across North America.

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Mechanisms of Base-cation Depletion by Acid Deposition in Forest Soils of the Northeastern U.S.

Gregory B. Lawrence, Mark B. David, Walter C. Shortle, Scott W. Bailey, and Gary M. Lovett[1]

Abstract

Several studies have indicated a long-term decrease in exchangeable Ca in forest soils within the northeastern United States, but the regional extent of these decreases and the importance of acid deposition as a cause has not been fully resolved. Results, from two recently completed studies have provided the opportunity to further investigate the role of acid deposition in depletion of base cations in northeastern forest soils. These two studies entailed 1) a survey of soils in northeastern red spruce (*Picea rubens* Sarg.) stands, which were selected to encompass the range of environmental conditions to which this species is subjected, and 2) a study of base-cation leaching in soils of a hardwood watershed in the Catskill Mountains of New York.

Results from the survey of spruce stands indicated that exchangeable Ca concentrations varied considerably in the Northeast as a result of differences in parent material mineralogy. A stronger relationship between relative weathering potential of parent material and exchangeable Ca concentrations was observed in the Oa horizon than in the B horizon of soils at these sites. Concentrations of exchangeable Ca in the B horizon may have decreased to a level at which further decreases are buffered by high concentrations of exchangeable Al.

An upslope increase in atmospheric deposition of SO_4^{2-} corresponded to an upslope increase in the leaching of base cations, and an upslope decrease in acid-neutralizing capacity of stream water in the Catskill Mountain watershed. Upslope gradients in natural factors that could increase base-cation leaching were not detected. Decreases in concentrations of exchangeable base cations were approximately balanced by increases in concentrations of exchangeable Al. Greater Al mobilization in the mineral soil by acid deposition at upper elevations than at lower elevations was the most probable explanation for the upslope increase in leaching of base cations and stream water acidity.

Low Ca to Al ratios in mineral soil solution were found to be related to high levels of Al saturation in the forest floor in the survey of spruce stands. Mobilization of Al in the mineral soil tends to increase Al saturation in the forest floor by making Al available for upward transport by biocycling and water movement. Reversal of past decreases in exchangeable Ca concentrations will be hindered by 1) continued inputs of mobile anions that facilitate leaching, 2) high Al saturation in the mineral soil that will interfere with uptake of Ca by roots, 3) increasing Al saturation in the forest floor, and 4) decreasing trends of atmospheric deposition of Ca..

Introduction

The possibility that acid deposition could deplete base cations in soils was acknowledged in the early stages of acid rain research in the 1970's (Cowling and Dochinger 1980). The effect of acid deposition on forest soils remained unresolved at the close of the National Acid Precipitation Program (NAPAP) in 1990, however, because (1) there was no historical soil data to show that changes in soil Ca concentrations had actually occurred, either through natural processes or acid deposition, 2) release of bases through weathering could possibly compensate for losses from leaching, and 3) the importance of natural sources of acidity relative to acid deposition was unknown. A comprehensive literature review by Shortle and Bondietti (1992) provided the first indication that exchangeable base concentrations may have decreased in the second half of the 20th century. This paper showed that, before 1950, concentrations of exchangeable Ca plus Mg in the soils of coniferous forests in the Northeast were generally about twice that of concentrations measured after 1970. The first study to directly compare Ca concentrations measured early in the century with those measured after the discovery of acid deposition in the 1970's showed that extractable Ca concentrations were significantly lower in 1984 than in 1930-32; a result attributed to forest aggradation in this study (Johnson et al. 1994a). Detailed Ca budgets developed on Whiteface Mountain, NY, indicated that the exchangeable Ca pool in the forest floor of this site declined from 1986 to 1990 (Johnson et al. 1994b) at a rate greater than that found in in the study of Johnson et al. (1994a). In this study, a long-term decreasing rate of atmospheric deposition of Ca, identified by Hedin et al. (1994), was cited as a possible cause for the decrease in the 80's (Johnson et al. (1994b). The development of ecosystem Ca budgets through the use of stable isotopes of Sr (a biogeochemical analog of Ca) at Whiteface Mountain, NY (Miller et al. 1993), and Cone Pond, NH (Bailey et al.1996) provided additional evidence of decreasing pools of exchangeable Ca in the Northeast.

The results of these studies indicate that decreases in exchangeable soil-base concentrations have occurred at several locations within the Northeast, but the regional extent of these changes, and the importance of acid deposition as their cause was not fully resolved. Results from two recently completed studies have provided the opportunity to further investigate the role of acid deposition in depletion of base cations in northeastern soils. In the first of these projects, soil and soil solution samples were collected from 12 red spruce stands (*Picea rubens* Sarg.) in New York, Vermont, New Hampshire and Maine (Figure 1), which were chosen to encompass the range of environmental conditions and stand health experienced by

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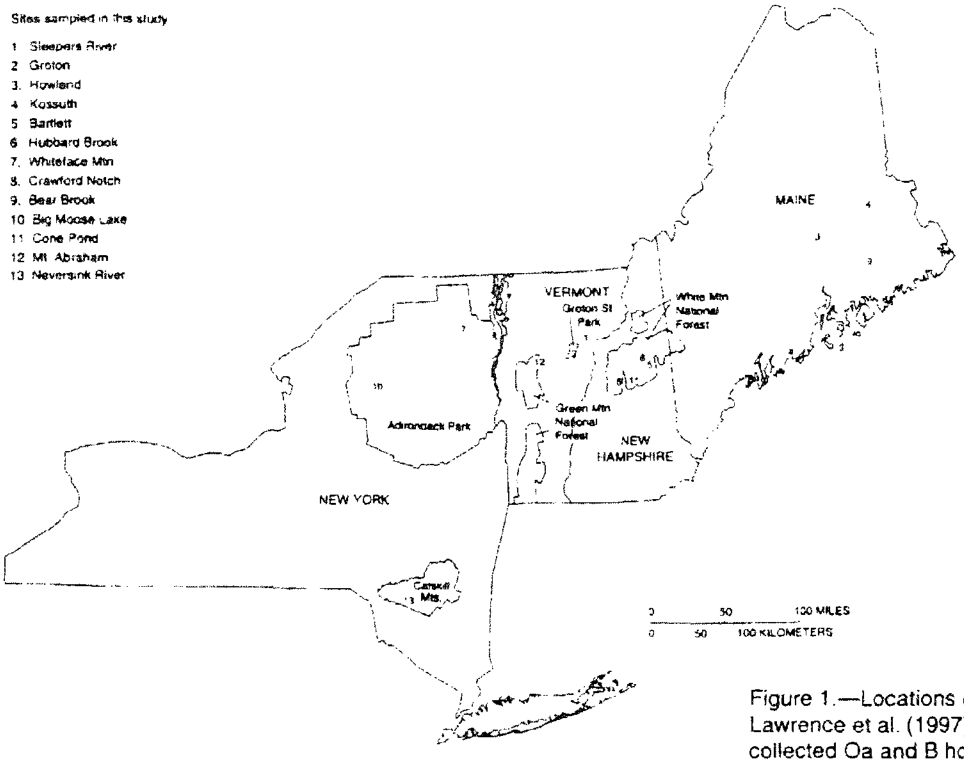


Figure 1.—Locations of red spruce stands where Lawrence et al. (1997) and Lawrence et al (in press) collected Oa and B horizon soil samples.

red spruce in this region. In the second project, soil-base leaching was studied over an elevational gradient in a hardwood forested watershed in the Catskill Mountains of southeastern New York (Figure 1). The purpose of this report is to integrate the published results of these two studies to summarize the mechanisms through which acid deposition affects the availability of base cations in the forest soils Northeast.

Methods

Survey of Soil Chemistry in Northeastern Red Spruce Stands

Red spruce was the predominant species in each of the 12 stands, although other coniferous and deciduous species were common. Increment cores indicated that the average age of canopy spruce at each site ranged from 96 to 175 years. Apparent stand health varied from good to poor where extensive dieback had occurred. Stand elevations ranged from 80 m at Howland ME to 975 m on Whiteface Mountain, NY. Wet deposition of SO_4 at six of the sites, was determined from on-site monitoring; at the remaining six sites, wet deposition was estimated from the nearest monitored site. Details of how wet deposition estimates were derived are available in Lawrence et al. (1997). Wet-only atmospheric deposition of SO_4 ranged from 12.7 mmol m^{-2} yr^{-1} at 150 m elevation at Kossuth, ME to 28.8 mmol m^{-2} yr^{-1} at 810 m elevation in Crawford Notch, NH.

A relative value of calcium weathering potential was assigned on the basis of general mineralogy, determined from bedrock maps and a till-source model that identified rock types that could be present in non-local till (Bailey and Hornbeck, 1992). Relative weathering potential varied from 1 at sites underlain by metapelite and quartzite, to 3 at sites influenced by calcareous schist. Further details about these sites including ratings of relative Ca weathering potential are available in Lawrence et al. (1997). Soils at all sites were classified as Spodosols.

Soil samples were collected from the faces of nine individual soil pits at each site (grouped in three plots, each with three pits). Eight of the 12 sites were sampled in mid-June and late September or early October of 1992 and 1993; four of the 12 sites were only sampled once (early summer or early fall) in each of the two years. In each pit, a sample was collected from the middle of the Oa horizon and from the top 10 cm of the B horizon. This sampling design was chosen to compliment assessments of red spruce tree condition conducted in conjunction with the soils investigation. Sampling in the early summer and early fall was timed to coincide with the periods when nutrient concentrations in foliage were both high and low for purpose of biochemical studies of foliage processes. The three individual soil samples from each horizon, in each plot, were combined into one sample and thoroughly mixed before chemical analysis to yield one sample from each horizon in each plot. All samples were analyzed for exchangeable cations (Ca, Mg, Na and K) by extraction with 1*M* NH_4Cl (Blume et al.

1990) and exchangeable acidity (Al, H) by extraction with 1*M* KCl (Thomas 1982). Samples from Oa horizons collected on two dates at each site were analyzed for acid-extractable-Ca concentrations (Friedland et al. 1984), and Oa-horizon samples collected on one date were analyzed for total Ca concentrations by neutron activation (Parry 1991). Mineral Ca concentrations were calculated by subtracting concentrations of acid-extractable Ca from concentrations of total Ca; reactive nonexchangeable Ca concentrations were calculated by subtracting concentrations of exchangeable Ca from acid-extractable Ca concentrations. Exchangeable Ca is probably the most representative form of plant-available Ca.

The study of Johnson et al. (1994a), in which Ca concentrations in Adirondack Mountain soils in 1930-32 were compared to values in 1984, followed the methods of Heimburger (1934), which were not directly comparable to the method of Friedland et al. (1984); a commonly used method for determination of extractable Ca concentrations in the 1980's and 1990's. Methods tests by Lawrence et al. (1997) showed that the data from the studies of Johnson et al. (1994a) and Heimburger (1934) yielded concentrations about 25% higher than the Friedland et al. (1984) method. This factor was applied to the data of Johnson et al. (1994a) and Heimburger (1934) to allow comparisons with data from other studies.

Soil solutions were collected from all soil samples by expulsion (described and evaluated in Lawrence and David 1996). The procedure entails 1) manually packing field moist soil in a PVC cylinder to reduce porosity, 2) adding simulated throughfall solution to saturate the soil column, 3), discarding solution that drains off by gravity, and 4) applying air pressure (172 kPa for Oa horizon samples; 138 kPa for B horizon samples) to force out the solution that is collected for analysis of total Al, total monomeric Al and organic monomeric Al by methods in Lawrence et al. (1995). Concentrations of polymeric Al were determined by subtracting total monomeric Al concentrations from total Al concentrations; inorganic monomeric Al concentrations were determined by subtracting organic monomeric Al concentrations from total monomeric Al concentrations.

As part of the regional survey of spruce stands, soil chemistry also was evaluated in spruce stands of two adjacent watersheds in eastern Maine. Through the EPA-sponsored Watershed Manipulation Project 1800 equiv ha^{-1} yr^{-1} of $(NH_4)_2SO_4$ was applied to one of these watersheds between 1989 and 1995 (Norton et al. 1994). This treatment resulted in significantly higher concentrations of NO_3 in stream water of the treated watershed than the reference watershed, in response to elevated nitrification rates in soil. The effects of increased nitrification rates and associated acidity on Al mobilization were evaluated by determining pH and concentrations of total Al, total monomeric Al and organic monomeric Al in soil solutions collected by expulsion, as described above. To further investigate possible changes in soil Al concentrations associated with changes in soil acidity, archived Oa horizon soil collected in spruce stands in the Hubbard Brook Experimental Forest, NH, in 1969-1970, 1987 and 1992, were analyzed for concentrations of exchangeable and acid-extractable Ca and Al, by the methods given above.

Soil-Base Leaching in Hardwood Forested Watershed

The effects of acid deposition on base leaching were studied over an elevational gradient (approximately 800 m to 1230 m) in Winnisook watershed, a subbasin of the Neversink River, in the Catskill Mountains of NY. Atmospheric deposition was measured along the gradient at 14 stations from 799 m to 1234 m near the summit of the watershed. At each station, four 20-cm diameter funnels collected throughfall solutions that were combined by station for analysis. During November through April, the funnels were replaced with galvanized cylinders lined with plastic bags, to collect frozen precipitation. Throughfall measurements have been shown to be a reliable method for estimating total atmospheric S deposition (Lindberg and Garten, 1988; Lindberg and Lovett, 1992, Lawrence and Fernandez, 1993). Throughfall collections also were used to estimate water input to the watershed.

This watershed is forested primarily by *Acer saccharum*, *Betula alleghaniensis*, and *Fagus grandifolia*, but stands of *Abies balsamea* are common along upper elevation ridges. Soils are classified as Inceptisols. Soil samples were collected from the B horizon at 48 locations along the elevational gradient, by taking equal volumes of soil from each 10 cm increment of the mineral profile, which were mixed before analysis to yield one B horizon sample from each location. Exchangeable cation concentrations were determined by methods used in the survey of northeastern spruce stands. Mineral soil was also collected from a single pit downslope of Winnisook watershed at 570 m elevation where soil-base saturation was higher than within Winnisook watershed. This soil (the 0-10 cm layer below the O horizon) was thoroughly mixed and put in nylon mesh bags, which were then placed beneath the Oa horizon at 35 locations along the elevational gradient. The approach followed the buried bag method described in David et al. (1990). Bags were removed and chemically analyzed after one year by the methods used in the survey of spruce stands.

Relations among acid deposition, soil base saturation and base leaching were further evaluated by leaching solutions of H_2SO_4, HNO_3, CaCl and NaCl through B horizon soil of three different base saturation values. Ionic strength (0.32 to 0.52 mM_c L^{-1}) and pH (3.7 to 4.8) of the added solutions were similar to mean values measured in Oa horizon soil solutions in the Neversink watershed (D.A. Burns, USGS, unpublished data). Soil samples used for the buried bag experiment were also used for the leaching study; samples with the highest base saturation (14.4%) had not been placed in the soil profile in Winnisook watershed, whereas the other samples (base saturation 9.6% and 4.5%) had been in the soil profile of Winnisook watershed for one year. Solutions were extracted from the soil samples with a mechanical vacuum extractor (Blume et al. 1990). Duplicate extractions were done for each treatment. Concentrations of base cations (Ca, Mg, Na and K) and acid anions (SO_4, Cl, and NO_3) were measured in leachates, as described in Lawrence et al. (1995).

Table 1.—Exchangeable Ca concentrations as $cmol_c kg^{-1}$ and as a percentage of cation exchange capacity (Ca saturation) for the Oa and B horizons of 12 red spruce stands and 2 hardwood stands in the Northeast. Samples were collected from the upper 10 cm of the B horizon in the spruce stands, from the Bh horizon at Hubbard Brook. In Winnisook Watershed equal volume samples were collected at 10 cm depth increments through the entire B horizon, then mixed before analysis.

	Oa Horizon		B Horizon	
SITE	($cmol_c kg^{-1}$)	(($cmol_c kg^{-1}$) CEC^{-1})100	($cmol_c kg^{-1}$)	(($cmol_c kg^{-1}$) CEC^{-1})100
SPRUCE STANDS				
Sleepers River, VT [1]	22	51	0.68	6.9
Groton, VT [1]	14	41	0.32	13
Howland, ME [1]	11	34	0.19	3.8
Kossuth, ME [1]	6.3	24	0.19	2.6
Bartlett, NH [1]	11	31	0.18	3.4
Hubbard Brook, NH [1]	7.9	25	not sampled	not sampled
Whiteface Mt., NY [1]	6.3	26	0.57	7.3
Crawford Notch, NH [1]	6.8	21	0.30	3.1
Bear Brook, ME [1]	5.3	21	0.32	4.1
Big Moose Lake, NY [1]	6.4	20	0.37	3.1
Cone Pond, NH [1]	3.5	10	0.11	1.6
Mt. Abraham, NY [1]	2.1	9.1	0.41	4.0
HARDWOOD STANDS				
Hubbard Brook, NH [2]	6.75	38.5	0.63	8.4
Winnisook Watershed, NY [3]	2.31	13.4	0.16	2.7

[1] From Lawrence et al. (1997)
[2] From Johnson et al. (1991)
[3] Previously unpublished data, G.B. Lawrence, U.S. Geological Survey

Stream water samples were collected weekly at the base of Winnisook watershed and approximately monthly at seven upstream sites from May 1991 through September 1994. These samples were analyzed for Ca, Mg, Na, K, SO_4, Cl, NO_3, total monomeric Al, and organic monomeric Al (methods described in Lawrence et al. 1995). To evaluate elevational trends in stream chemistry that were most influenced by soils (and least influenced by ground water), only samples collected on dates with the highest 20% of stream flows were included.

Results and Discussion

Current Status of Soil Calcium

Concentrations of exchangeable Ca, the predominant base cation in northeastern forest soils, varied by a factor of 10 in the Oa horizon of the 12 red spruce sites (Table 1). There were no geographical patterns other than high concentrations in eastern Vermont; the concentrations at the Big Moose Lake site were similar to those measured in Maine, and the concentration at the Bartlett, NH site, in the central White Mountains, was three times that of Cone Pond, in the southern White Mountains of New Hampshire. Exchangeable Ca concentrations expressed as Ca saturation (Ca as a percentage of total cation-exchange capacity) varied by a factor of 5. Exchangeable Ca concentrations in the upper 10 cm of the B horizon at these sites were less varied than in the Oa horizon, and 1 to 2 orders of magnitude lower (Table 1). Geographic patterns of B horizon concentrations also differed somewhat from the Oa horizon; Whiteface Mountain, NY and Mt. Abraham, VT had relatively high concentrations in the B horizon, but these sites had concentrations in the Oa horizon that were among the lowest. Although soils in hardwood stands are generally considered less acidic than soils in conifer stands, exchangeable Ca concentrations in the Oa and B horizons in Winnisook watershed were in the lower range of the spruce stands, and the average value reported for a hardwood watershed at Hubbard Brook was slightly less than that measured in the spruce stands at Hubbard Brook (Table 1).

Exchangeable Ca was the largest Ca fraction in the Oa horizon of all spruce sites except those with a mineral-matter content greater than 30 percent (Whiteface, NY, Bear Brook, ME, and Mt. Abraham, VT), where mineral-bound Ca was the largest fraction (Figure 2). Reactive-nonexchangeable Ca was generally a minor component. Averaged for the 12 sites, acid-extractable Ca was comprised of 92 percent exchangeable Ca and 8 percent reactive-nonexchangeable Ca.

Concentrations of acid-extractable Ca measured in the spruce survey ranged from 13.9 mmol kg^{-1} to 103 mmol kg^{-1} (Figure 3). This range encompassed values determined by McNulty et al. (1991) for 11 red spruce stands, also in New York, Vermont, New Hampshire and Maine. The average of samples collected in 59 red spruce stands throughout the Adirondack Mountains of New York by Johnson et al. (1994a) fell in the middle of the range of the spruce survey data of Lawrence et al. (1997), but the average value

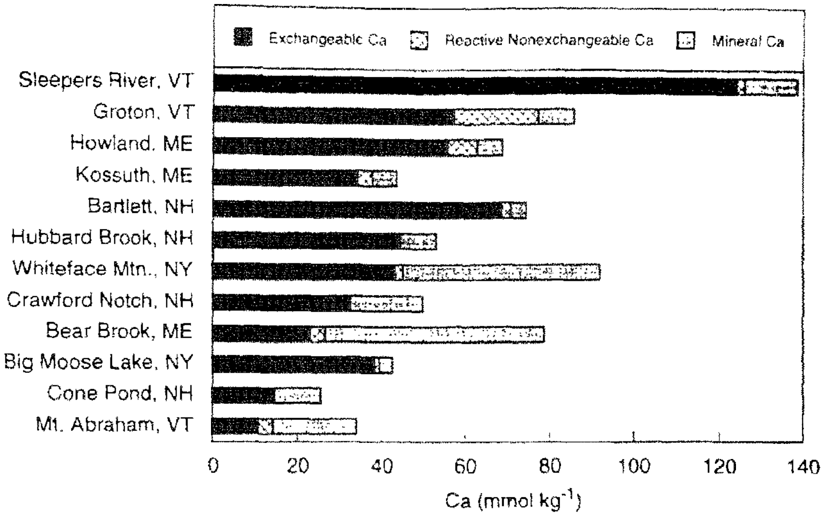


Figure 2.—Mean concentrations of exchangeable Ca, reactive nonexchangeable Ca (acid-extractable Ca concentrations minus exchangeable-Ca concentrations) and mineral Ca (total Ca concentrations minus acid-extractable Ca concentrations) in the Oa horizon of 12 northeastern red spruce stands. Reprinted with kind permission from Kluwer Academic Publishers (Biogeochemistry, vol. 38, 1997, Assessment of soil calcium in red srpuce forests in the northeastern United States, Lawrence, G.B., David, M.B., Bailey, S.W., and Shortle, W.C., figure 4, p. 30, copyright 1997).

obtained for the same sites by Heimburger in 1930-34 was approximately 30 mmol kg^{-1} higher, and in the upper quarter of the range determined in the spruce survey of Lawrence et al. (1997).

Causes of Regional Variability

The considerable variability observed in exchangeable Ca concentrations in the spruce survey of Lawrence et al. (1997) could be a result of spatial variations in (1) net Ca uptake by trees, (2) atmospheric deposition of Ca, (3) acid deposition, or (4) mineralogy of parent material. Analysis of increment cores of 54-108 live trees at each site indicated that all of the red spruce stands averaged approximately 100 years in age or older and had been experiencing similar rates of declining growth since 1965. The extent of mortality was highly variable from site-to-site, however, which suggested that net uptake of Ca may also have varied from site-to-site. Variations in net Ca uptake could therefore not be ruled out as a factor in the observed spatial variability, although neither stand health nor stand age were related to exchangeable Ca concentrations. Atmospheric deposition of Ca was also unlikely to be the primary cause of variability in exchangeable Ca concentrations among the spruce sites because deposition of Ca decreases consistently from west to east (Table 2), whereas soil Ca concentrations did not show a spatial pattern.

Table 2.—Atmospheric wet deposition of Ca (kg ha^{-1} yr^{-1}) in the northeastern United States, measured by the NADP/NTN network (http://nadp.sws.uiuc.edu/).

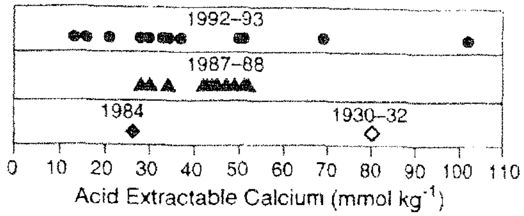
	1985	1995
Bennett Bridge, NY	1.95	1.60
Huntington Forest, NY	1.03	0.68
Underhill, VT	1.09	0.70
Hubbard Brook, NH	0.69	0.53
Greenville, ME	0.63	0.42

Calcium saturation was weakly related to wet deposition of SO_4 in the Oa horizon and unrelated to wet deposition of SO_4 in the B horizon (Figure 4), but was highly correlated with relative weathering potential in the Oa horizon. A weaker relation between Ca saturation and relative weathering potential was observed in the B horizon than the Oa horizon, despite the greater abundance of parent material in the mineral soil (Figure 4).

This relation suggests that acid deposition was unlikely to be the primary cause of variation in exchangeable Ca concentrations among sites, however enhanced leaching by acid deposition in the mineral soil can explain why Ca saturation is more strongly related to relative weathering potential in the Oa horizon than the B horizon. If base saturation is less than 20%, solute concentrations, and therefore cation leaching, are strongly controlled by exchangeable Al, which results in high rates of Al leaching and low rates of Ca leaching (Reuss, 1983). For example, in soil with a base saturation of 4.5%, only 0.11 meq L^{-1} of Ca are released per meq L^{-1} of added acid anion (Figure 5). The base saturation of the B horizon at all 12 spruce stands was less than 14% (Figure 6), whereas base saturation in the Oa horizon was greater than 20% at 10 stands, and greater than 16% at all 12 stands. Acidic deposition may have lowered base saturation in the B horizon to levels where further changes in base saturation were buffered by Al, which obscured the effect of differences in parent material Parent material was more clearly expressed in the Oa horizon where vegetative recycling reduces loss of Ca to leaching.

Acid Deposition and Ca Leaching

Additional information on leaching of Ca from soil was obtained in Winnisook watershed in the recent study by Lawrence et al. (in press). Within this watershed, atmospheric deposition of SO_4^{2-} increased by a factor of 2 from the lowest to the highest elevations in the watershed



EXPLANATION

- ● Mean concentrations of calcium in soils of individual sites in New York, Vermont, New Hampshire and Maine sampled by Lawrence and others (1997) in 1992–3.
- ▲ Mean concentrations of calcium in soils of individual sites in New York, Vermont, New Hampshire and Maine sampled by McNulty and others (1991) in 1987–88.
- ◇ Mean concentrations of calcium in soil of 38 samples collected by Heimburger (1934) throughout the Adirondack Mountains of New York in 1930–32.
- ◆ Mean concentrations of calcium in soil of 59 samples collected by Johnson and others (1994a) throughout the Adirondack Mountains of New York in 1984.

Figure 3.—Acid-extractable Ca concentrations in Oa horizons of red spruce stands in the northeastern US measured in this study and the studies of McNulty et al (1991), Johnson et al (1994a), and Heimburger (1934). Values from this study and the study of McNulty et al (1991) represent means of individual sites; the values from Johnson et al (1994a) represents the mean of 59 samples collected throughout the Adirondack Mountains of New York; the values from Heimburger (1934) represent the mean of 38 samples collected throughout the Adirondack Mountains of New York. Values reported by Johnson et al (1994a) and Heimburger (1934) have been adjusted for method bias. To express Ca concentrations on a soil mass basis loss-on ignition values of 0.90 were assumed for the data from the McNulty et al study and the Johnson et al study.

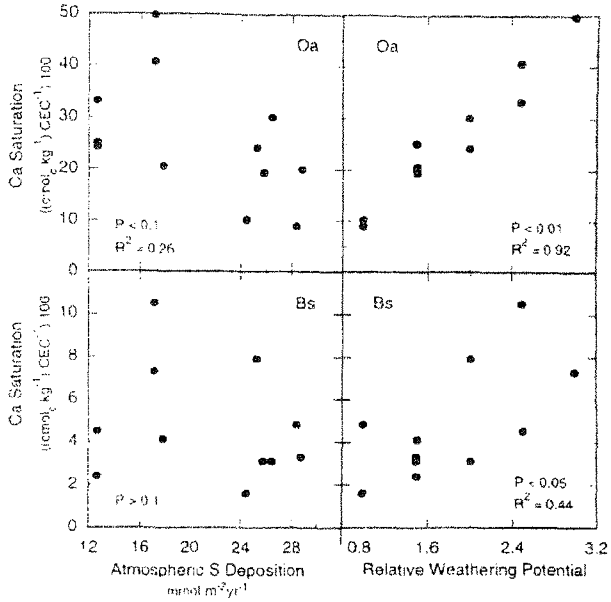


Figure 4.—Ca saturation as a function of atmospheric deposition and relative weathering potential in Oa and Bs horizons. Reprinted with kind permission from Kluwer Academic Publishers (Biogeochemistry, vol. 38, 1997, Assessment of soil calcium in red srpuce forests in the northeastern United States, Lawrence, G.B., David, M.B., Bailey, S.W., and Shortle, W.C., figure 5, p. 31, copyright 1997).

(fig. 7a), whereas the concentrations of exchangeable base cations in both undisturbed soil and soil bags, and the ratio of base cations to acid anions in stream water, decreased from the lowest to the highest elevations (fig. 7b,c,d). The decrease in exchangeable base cation concentrations in the soil bags was approximately balanced by an increase in exchangeable Al concentrations (Lawrence et al. in press).

Effects of the spatial trend in SO_4^{2-} deposition may be analogous to the effects of past temporal trends in acidic deposition through a space-for-time substitution. This approach assumes that the elevational gradient of SO_4^{2} deposition in Winnisook watershed has been maintained during past decades when acidic deposition rates both increased and decreased. Natural acidification processes may cause elevational gradients in the chemistry of soils and stream water, however (Lawrence et al., 1986). An elevational increase in net uptake of Ca by vegetation could contribute to an elevational trend in exchangeable base-cation concentrations in soil, as could decreased temperatures and increased abundance of conifers at upper elevations that would lead to a greater accumulation of organic acids and higher leaching rates than at lower elevations. Upslope increases in precipitation, decreases in evapotranspiration (ET), or decreases in soil depth would cause an elevational gradient in soil-water flux per volume of soil, which could also result in an elevational gradient in soil chemistry. Lastly, spatial variations in the mineral composition of parent material could result in an elevational gradient in base-cation concentrations in soil.

Winnisook watershed had been selectively cut up to about 900 m elevation before 1950, but we found no physical or historical evidence that the watershed was ever cleared or burned (Kudish, 1985). The cutting that had been done would most likely cause a decrease rather than an increase in exchangeable base-cation concentrations at low elevations by increasing aggradation rates. Spatial variations in tree species could not explain these spatial trends because all soil investigations (sampling and soil bag incubations) were done in similar stands of yellow birch (*Betula alleghaniensis* Britton), beech (*Fagus grandifolia* Ehrh.), and sugar maple (*Acer saccharum* Marsh). Vegetation uptake also did not explain the upslope decrease in exchangeable base-cation concentrations because decreased temperatures would tend to shorten the growing

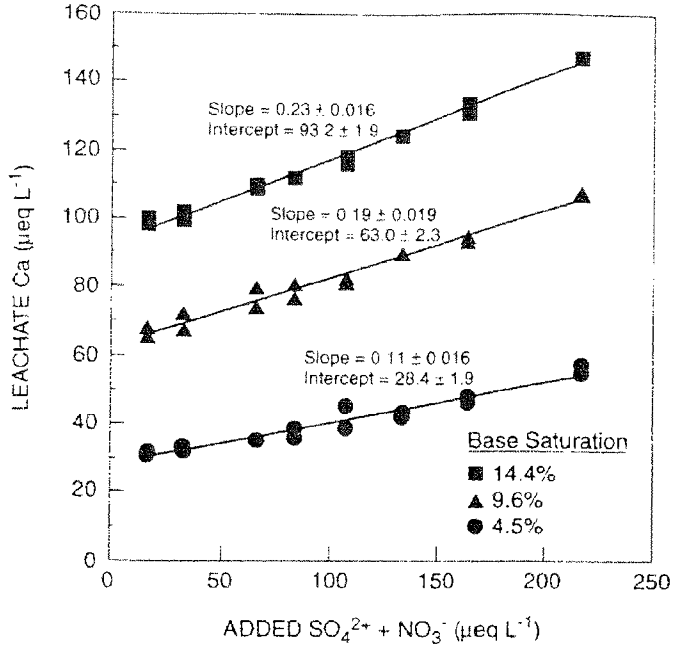


Figure 5. Concentrations of Ca in solutions leached through mineral soil with a vacuum extractor, as a function of SO_4 plus NO_3 concentrations in the added solution. Results of duplicate leachings are shown. Slope and intercepts of linear best-fit lines are given ± 95% confidence intervals (two-sided test). Soils with initial base saturations of 14.4%, 9.6% and 4.5 % were used in the experiment. Reprinted with permission from the Ecological Society of America (Ecological Applications, in press. Soil calcium status and the response of stream chemistry to changing acidic deposition rates in the Catskill Mountains, New York, Lawrence, G.B., David, M.B., Lovett, G. M., et al., figure 8, copyright 1999).

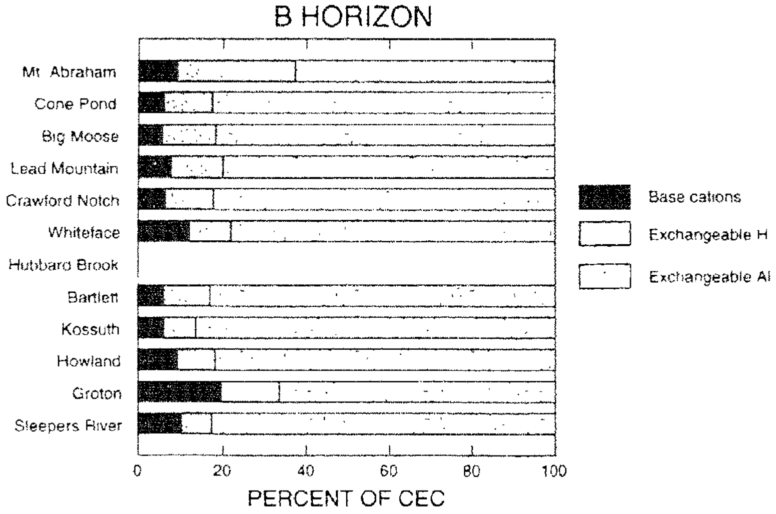


Figure 6.—Concentrations of exchangeable base cations, H and Al expressed as a percent of cation-exchange capacity for B horizons of the 12 northeastern red spruce stands. Reprinted with permission from Williams & Wilkins, (Soil Science, vol. 161, 1996, Soil and soil solution chemistry under red spruce stands across the northeastern United States, David, M.B., Lawrence, G.B., modified from figure 2, p. 320), copyright 1996).

season and decrease net uptake of Ca at upper elevations. A spatial trend in the intensity of podzolization from greater accumulation of organic acids at upper elevations than lower elevations was ruled out as a cause of the gradient in exchangeable base-cation concentrations because no spatial trends were observed in 1) organic carbon concentration in mineral soil, 2) cation exchange capacity of the mineral soil, or 3) pH of the Oa horizon.

Evidence of substantially higher soil water flux at upper elevations was also not apparent. Two years of throughfall measurements did not indicate an increase in precipitation with increasing elevation within the watershed, and no trend in soil depth was detected from the 48 soil pits. Annual ET, estimated by application of the adiabatic lapse rate (Anthes et al. 1975), resulted in an increase in soil-water flux of 14.5% from base to summit. The upslope increase in soil-water flux over the elevation range where soil bags were incubated was less than half this value, but nevertheless, a distinct gradient in base-cation concentrations developed within 1 year in soil of uniform parent material. Futher details of the gradient analysis in this watershed are given in Lawrence et al. (in press).

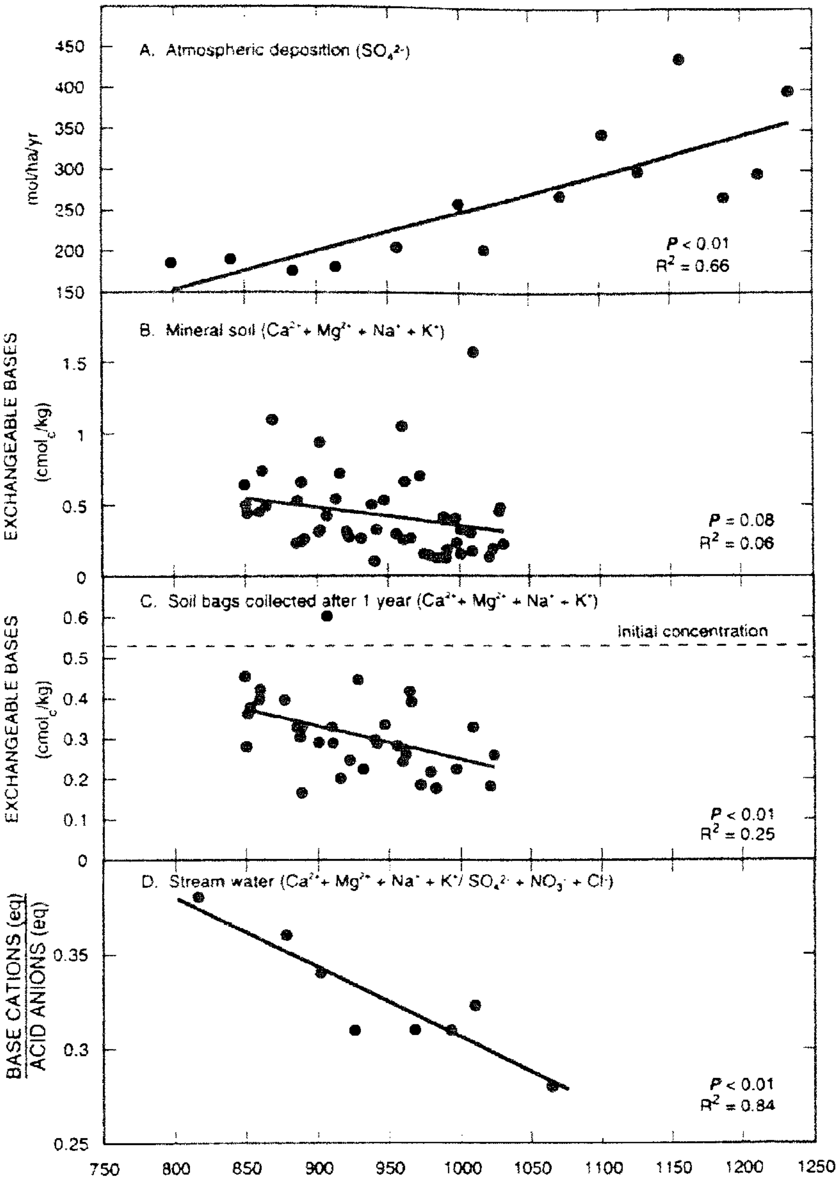


Figure 7.—Elevational gradients of selected chemical constituents in Winnisook watershed: A) annual mean SO_4 deposition measured in throughfall, June 1993 through May 1995, B) exchangeable base-cation concentrations (Ca, Mg, Na and K) in mineral soil samples collected in 1994, C) exchangeable base-cation concentrations in mineral soil samples buried in the mineral profile in mesh bags for one year, and D) the ratio of base-cation concentrations to acid-anion concentrations (SO_4, NO_3 and Cl) in stream-water samples collected during the highest 20% of stream flows from during May 1991 through April 1997. Reprinted with permission from EOS, Transactions, American Geophysical Union, v. 79, No. 16, 1998, p. 200.

In the absence of acidic deposition it is possible that natural acidification processes would cause elevational gradients in soil-base saturation and stream chemistry in Winnisook watershed, but an inability to detect significant gradients in any acidifying factors other than acidic deposition suggests that the effects of these factors were subtle relative to the gradient in atmospheric deposition of SO_4^{2-}, which doubled from the base to the summit of the watershed.

Aluminum Mobilization

B Horizon

Further indication that acid deposition has altered soil chemistry is evident from investigations of episodic acidification of streams in western Pennsylvania, in the Adirondack Mountains, and in Biscuit Brook, a tributary of the Neversink River, approximately 10 km from Winnisook watershed (Wigington et al., 1996). As streamflow increases during episodic periods of precipitation or melting snow, concentrations of inorganic monomeric Al can increase to levels that are toxic to fish (Baker et al. 1996). Concentrations of Al increase with increasing flow because a greater amount of water discharges directly from the soil into the stream channel than during baseflow (Chen et al. 1984; Lawrence et al., 1988; Potter, 1988). Water that has passed through the subsoil before discharging to the stream channel has had a greater opportunity for neutralization and immobilization of Al. Analysis of ionic controls of inorganic

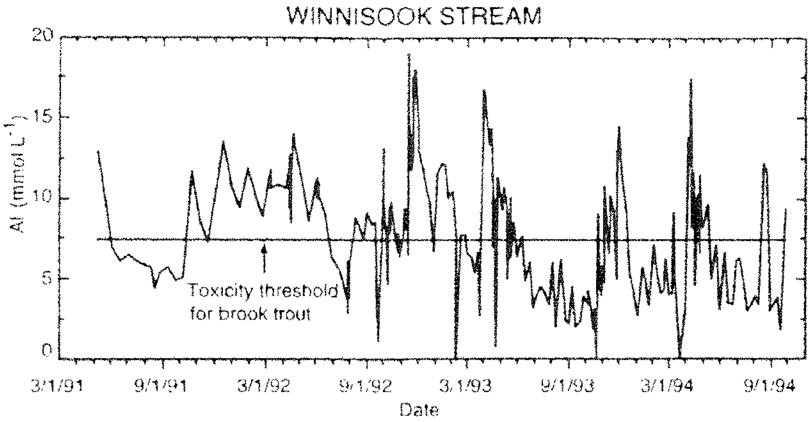


Figure 8.—Concentrations of inorganic monomeric Al in stream water at the base of Winnisook watershed from May 1991 through September 1994.

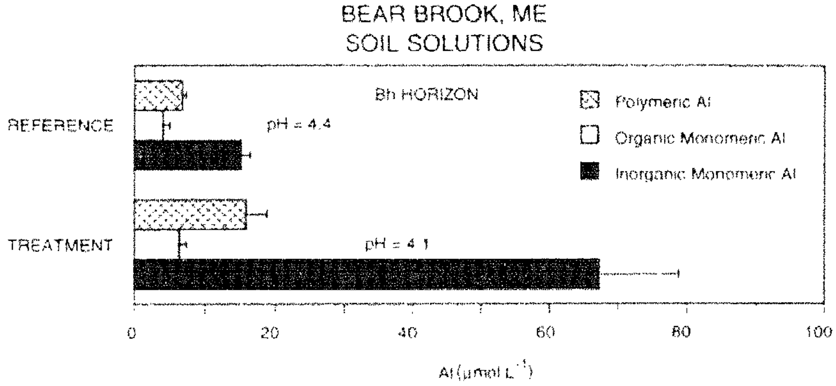


Figure 9.—Concentrations of inorganic monomeric Al (total monomeric Al minus organic monomeric Al), organic monomeric Al and polymeric Al (total Al minus total monomeric Al), in soil solutions of B horizons in treated (additions of $((NH4)_2)SO_4$) and reference stands of Bear Brook watershed, Maine. Each bar represents the mean of 45 samples that were combined into 15 samples for analysis, except for poylmeric Al, which represents 33 samples combined into 11 samples. Standard errors are indicated by horizontal lines. Mean pH for reference and treatment stands is also given. Reprinted with permission from the American Chemical Society (Environmental Science and Technology, vol. 31, 1997, Response of aluminum solubility to elevated nitrification in soil of a red spruce stand in eastern Maine, Lawrence, G.B., David, M. B., modified from figure 1, p. 827, copyright 1997).

monomeric Al concentrations in stream water showed that increased concentrations during high flows were associated with increased concentrations of SO_4^{2-} and NO_3 (Wigington et al., 1996). Naturally occurring organic acids can also mobilize Al and increase concentrations in stream water, but this process forms organically complexed Al, which is not toxic to fish (Driscoll et al., 1980). Concentrations of inorganic monomeric Al measured in the stream of Winnisook watershed from 1991-93 frequently exceeded the toxicity threshold for brook trout (Figure 8), and recent fish surveys indicated that the stream in Winnisook watershed does not support fish because of toxic concentrations of inorganic monomeric Al (Barry Baldigo and Lawrence, in press). Landowners of Winnisook watershed have reported, however, that a population of brook trout (*Salvelinus fontinalis*) previously existed in the stream (Royal Whiting, personal communication). High inorganic Al concentrations and the loss of a previously existing fish population suggests that an increase in inorganic monomeric Al concentrations occurred in this stream sometime in the past. An increase such as this would not occur without an increase of inorganic acidity in the mineral soil. An example of the effect of increased inorganic acidity on Al mobility is shown in Figure 9. Addition of $(NH_4)_2SO_4$ to the treated watershed at Bear Brook Maine increased nitrification rates, lowered pH, and increased concentrations of inorganic monomeric Al in the mineral soil solution (Lawrence and David 1997).

Results of the soil survey of spruce stands showed that Al dominated exchange chemistry in all samples of mineral soil; a factor that is also reflected in Ca to Al ratios in these soils that are well below 1.0 in both soil solution and on exchange sites (Figure 10). Inorganic acids (H_2SO_4 and HNO_3) introduced by acid deposition are the most probable

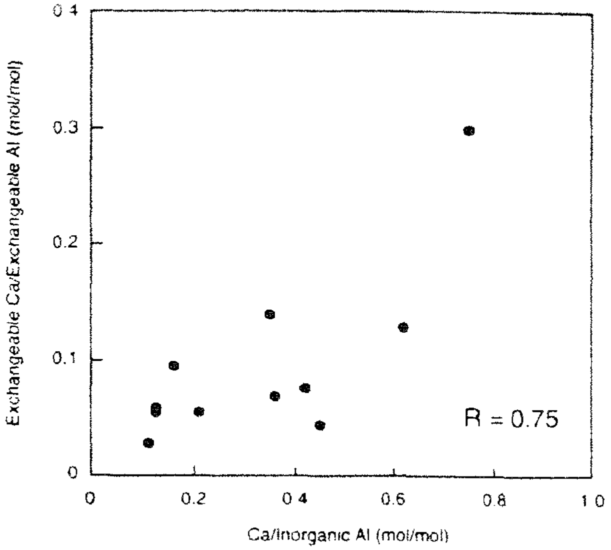


Figure 10.—Ratios of exchangeable Ca to exchangeable Al as a function of ratios of Ca to inorganic Al in soil solution of B horizons in the 12 northeastern red spruce stands. Insufficient mineral soil was available for sampling in the spruce stand at Hubbard Brook. Reprinted with permission from Williams & Wilkins, (Soil Science, vol. 161, 1996, Soil and soil solution chemistry under red spruce stands across the northeastern United States, David, M.B., Lawrence, G.B., modified from figure 6, p. 326), copyright 1996).

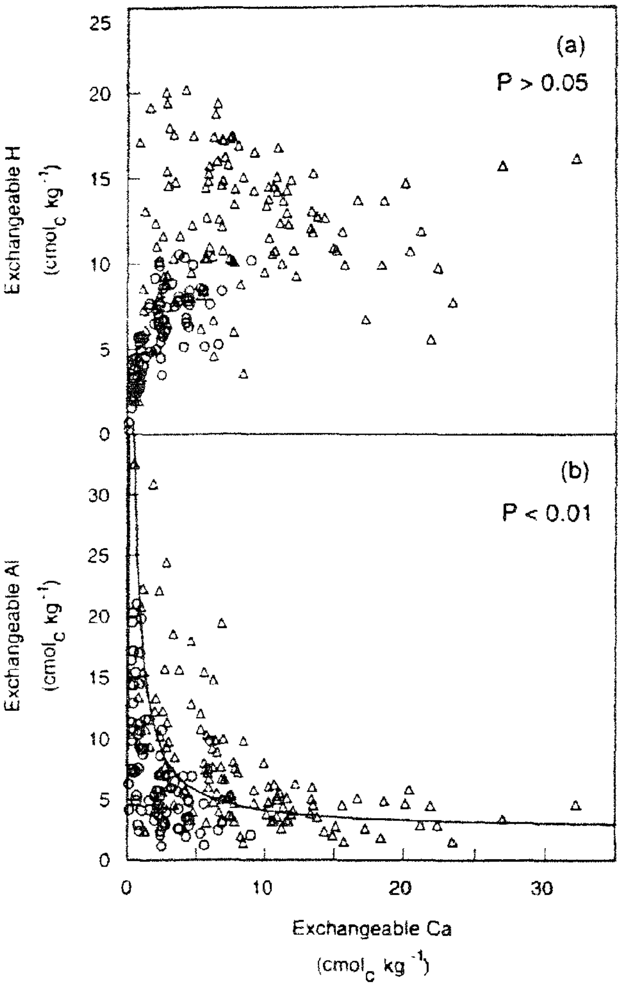


Figure 11.—Concentrations of (a) exchangeable H, and (b) exchangeable Al, as a function of exchangeable-Ca concentrations in the Oa horizon of stands of the 12 northeastern red spruce sites (triangles) and mixed hardwoods in Winnisook watershed (circles). Each triangle represents the value of three samples that were combined before analysis. Hardwood data are based on 68 individual samples. Reprinted by permission from Nature (vol. 378, 9 November 1995, p.163), copyright 1995, MacMillan Magazines Ltd.

cause of high concentrations of inorganic Al in solution and on exchange sites in the mineral soil. Organic acids that are leached from the forest floor also acidify the mineral soil and mobilize Al, but this process is limited by the tendency of organic acids to be removed from solution by adsorption to mineral particle surfaces (DeConinck, 1980). As a result, the mineral soil generally has a higher pH than the forest floor where the organic acidity originates. The high mobility of H_2SO_4 and HNO_3 in the mineral soil, however, makes these acids more effective than organic acids at decreasing the solution pH, leaching cations and increasing inorganic monomeric Al concentrations in soil solutions and stream waters.

Oa Horizon

Although acid deposition is likely to have decreased solution pH (and increased Al mobility) in the mineral soil, acid deposition is unlikely to have caused a decrease in pH in the naturally acidic forest floor. Production of organic acids through decomposition caused soil solution pH values to range from 3.3 to 3.8 in the Oa horizon of the 12 spruce stands (Lawrence et al. 1995). These values are below the pH of precipitation in this region, which averages about 4.4 and is seldom less than 4.0 (NADP/NTN, 1993). There is no established mechanism to explain how addition of precipitation above pH 4.0 could increase mobilization of Al within forest floors that have solution pH values normally less than 4.0. Although the low pH of these Oa horizons suggests that Ca availability is controlled by H, concentrations of exchangeable Ca in the Oa horizon were unrelated to exchangeable H concentrations in the 12 spruce stands and in Winnisook watershed, but inversely related to exchangeable Al concentrations (Figure 11).

The lack of a mechanism to explain mobilization of Al within the forest floor suggests that there is an outside source of Al to this horizon. Mixing with the mineral soil when trees become uprooted provides a mechanism for introducing mineral forms of Al into the forest floor. Analysis of Al chemistry in the forest floor indicate that mineral content was not a strong controlling factor of exchangeable Al concentrations, however; dissolved Al concentrations in the Oa horizon were highly undersaturated with respect to Al bearing minerals, exchangeable Al concentrations were uncorrelated with mineral Al concentrations, and dissolved Al concentrations were unrelated to pH (Lawrence et al., 1995).

TABLE 3.—Concentrations in the Oa horizon of spruce-fir stands at the Hubbard Brook Experimental Forest, New Hampshire, USA. Samples collected in 1969 and 1970 were averaged together, as were those collected in 1987 and 1992. Values are means based on 9-14 samples. Statistically significant differences (P<0.05) between sampling periods, determined by the Wilcoxon nonparametric test, are indicated by superscripts with different letters. Standard deviations are given in parentheses.

Sampling period	Exchangeable ($cmol_c kg^{-1}$)		Acid-extractable ($cmol_c kg^{-1}$)	
	Al	Ca	Al	Ca
1969-70	2.5^a (1.1)	8.3^a (4.4)	19.3^a (10.2)	9.9^a (6.4)
1987, 1992	3.7^a (2.9)	3.5^b (2.1)	37.0^b (21.6)	4.6^b (2.9)

Alternatively, inorganic Al mobilized in the mineral soil by acidic deposition may be transported into the forest floor, where it outcompetes Ca (and other base cations) for exchange sites due to the high affinity of Al for the functional groups of organic matter (DeConinck 1980). Rustad and Cronan (1995) found that biocycling (uptake of Al by roots that is transported upward through the tree then returned to the soil in leaves and branches) plus atmospheric deposition of Al, was roughly 60% of forest-floor leaching losses in a red spruce stand in Maine. Biocycling of Al in the mineral soil is likely at all of the northeastern red spruce stands because ratios of Ca to inorganic Al in soil solutions are considerably less than 1.0, the value defined by Cronan and Grigal (1995) below which Al competes effectively with Ca for uptake by roots. Ratios of exchangeable Ca to Al in Winnisook watershed (0.04 mol mol^{-1}) suggest that ratios in soil solution would also be less than 1.0 (Figure 10).

A rising water table provides an additional way to increase the reactive Al concentrations in organic surface horizons, as does upward movement of water through capillary action from drying of the forest floor by evapotranspiration (Lawrence et al., 1995). When mineral-soil solution, enriched in Al relative to Ca, moves into the forest floor, Al is more effectively retained so that the Ca to Al ratio in solution draining back into the mineral soil has increased, but the ratio of exchangeable Ca to exchangeable Al in the Oa horizon has decreased. A positive correlation between exchangeable Al content of the forest floor and the ratio of inorganic Al concentrations to Ca concentrations in the mineral soil solution supports this interpretation (Figure 12). Analysis of a limited number of archived soil samples collected in 1969-1970, 1987 and 1992, also show an increase in exchangeable and extractable forms of Al and a decrease in these forms of Ca (Table 3).

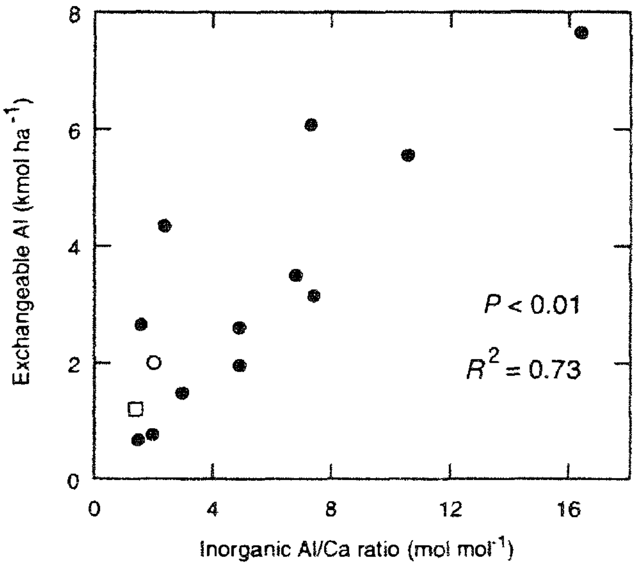


Figure 12.—Exchangeable Al content of Oa horizons of the 12 red spruce stands as a function of the molar concentration ratio of inorganic Al to Ca in B-horizon soil solution. Exchangeable Al was expressed as content to normalize the data for varying forest-floor thicknesses. Each filled circle represents the mean of 18-36 soil and soil solution samples (combined into 6-12 samples for analysis) collected at each of the 12 sites. Data from both the reference and treatment watersheds at Bear Brook Maine are included. The open circle represents the mean of 68 soil samples and 31 seep-water samples, collected in Winnisook watershed. The open square represents soil and seep-water concentrations measured at Tunk Mountain, ME, by Rustad (1988). Reprinted by permission from Nature (vol. 378, 9 November 1995, p.163), copyright 1995, MacMillan Magazines Ltd.

Potential decreases in the availability of Ca in the forest floor are particularly significant in light of the low Ca to Al ratios measured in the mineral soil. Although the forest floor is the primary horizon for nutrient uptake, the original source of mineral nutrients has generally been considered to be weathering in the mineral soil. Two recent studies have indicated, however, that 30 to 50% of available Ca in the forest floor originates from atmospheric deposition (Miller et al. 1993, Bailey et al. 1996), a source of Ca which has been steadily declining in recent decades (Hedin et al., 1994). Decreasing levels of atmospheric Ca deposition and low Ca to Al ratios in the mineral soil will both tend to impede the reversal of Al accumulation in the forest floor.

Summary and Conclusion

Significant progress has been made during the 1990's towards establishing the past and current status of base cation concentrations in forest soils of the Northeast. The studies of Shortle and Bondietti (1992), Johnson et al. (1994a), and Lawrence et al. (1995) presented historical data that indicated long-term decreases at sites in the Adirondack Mountains and northern New England. The survey of soils in northeastern red spruce forests by Lawrence et al. (1997) identified considerable variability in exchangeable Ca concentrations, but an analysis of the methodological bias of the previous studies showed that these data did not alter the conclusion that long-term decreases are common in this region.

Elevated concentrations of inorganic Al in surface waters, also common in this region, suggest that acid deposition has contributed to the decrease in base-cation concentrations in soils. Elevated concentrations of inorganic Al in surface waters is the result of mobilization of inorganic Al in the mineral soil, which, in turn, is the probable result of decreased pH from inorganic acids deposited from the atmosphere. Naturally derived organic acids also mobilize Al, but the high affinity of Al for organic functional groups favors the formation of dissolved organic Al over dissolved inorganic Al. The mobilization of Al in the mineral soil increases concentrations of exchangeable Al by displacing adsorbed Ca, which is then free to be leached with mobile inorganic anions.

The importance of acid deposition as a cause in the decrease of base-cation concentrations in forest soils has been further suggested by results of the survey of soils in northeastern spruce stands (Lawrence et al. 1995, Lawrence et al. 1997), and the analysis of base-cation leaching in the Catskill Mountains (Lawrence et al. in press). The strong relation between relative weathering potential and Ca saturation in the Oa horizon but not in the B horizon, observed in the survey of spruce stands, indicates that base saturation in the mineral soil has been reduced to levels at which Al dominates exchange chemistry and inorganic Al concentrations in soil solution become much greater than Ca concentrations. Data from the survey of spruce stands also indicate that exchangeable Al concentrations are likely to be increasing in the forest floor as a result of Al mobilization in the mineral soil. Lastly, an elevational gradient in base-cation leaching in a Catskill Mountain watershed that could not be explained with any factors, other than an elevational gradient in acid deposition, demonstrates the effect that acid deposition can have on base-cation leaching.

The information summarized in this paper suggests that reversal of past decreases in exchangeable Ca concentrations will be hindered by 1) continued inputs of mobile anions that facilitate leaching, 2) high Al saturation in the mineral soil that will interfere with uptake of Ca by roots, 3) increasing Al saturation in the forest floor, and 4) continued decreasing trends of atmospheric deposition of Ca.

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Changes in Base Cations in Forest Floors

Ruth D. Yanai, Thomas G. Siccama, Mary A. Arthur, C. Anthony Federer, and Andrew J. Friedland[1]

Abstract

Cation loss from forest soils may be a contributing factor in some cases of sugar maple decline. We undertook three studies examining changes in base cations in forest floors. First, we described the pattern of change in forest floor calcium and magnesium in an intensively studied site at the Hubbard Brook Experimental Forest in New Hampshire. We analyzed samples collected at eight different times between 1970 and 1997. Concentrations and contents of Ca were higher in forest floor samples collected in 1970 than in those collected from 1976 to 1997. Changes over time were not significant between 1976 and 1997 for either Ca or Mg . Second, we questioned whether losses of base cations from the forest floor were regionally important. We analyzed samples collected from 28 mature stands of a variety of forest types in the northeastern United States. About half of the stands lost Ca and Mg from the forest floor between 1980 and 1990, but the other half showed gains. The average change in cation content or concentration during this period was not significant. Third, we hypothesized that cation loss from the forest floor might be associated with forest regrowth following logging. We sampled forest floors in a successional sequence of 13 northern hardwood stands in the White Mountains over a 15-year interval. Contrary to our prediction, young stands gained Ca, Mg, and K relative to forest floor amounts measured 15 years previously. Middle-aged stands, harvested between 1930 and 1960, were most likely to show losses of base cations from the forest floor between 1979-80 and 1994-95. None of our studies rules out the possibility of important cation losses from forest floors before the late 1970s. However, the forest floor appears to aggrade, along with living biomass, early in stand development, and may not be a good indicator of changes in mineral soil fertility.

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Response of Northern Hardwood Forests to Nutrient Perturbation

Christopher Eagar[1], *Scott Bailey*[2], and *Amey Bailey*[2]

Abstract

Substantial amounts of calcium have been depleted from the soils of northern hardwood forests in northern New England over the past 50 years. Portions of this depleted calcium have been incorporated into the biomass of the aggrading forests; however, significant amounts have been leached into drainage waters and lost from the ecosystem. The depletion of base cations from the soil exchange pool combined with the acidic conditions of most northern hardwood soils results in increased levels of exchangeable Al. Elevated levels of Al can inhibit the uptake of Ca by sugar maple (*Acer saccharum* Marsh.) and may adversely affect the health of other species. The objectives of this field experiment are to: 1) determine if sugar maple productivity is limited by the declines in calcium pools, 2) evaluate the response of sugar maple to changes in soil Ca:Al ratios, and 3) determine the effect of changes in Ca and Al availability on nutrient cycling. Twelve 45m x 45m plots were established in an 80 year old sugar maple dominated stand located at an elevation of about 750m at Hubbard Brook Experimental Forest (HBEF) in New Hampshire. Four plots received a total of 10 g m^{-2} Ca applied as $CaCl_2$, 4 plots received a total of 4.5 g m^{-2} of Al applied as $AlCl_3$, and the remaining 4 plots were untreated controls. Treatments began in October 1995, with additional applications in May 1996, November 1996 and May 1997. The following attributes are being measured: tree growth, tree health, sugar maple wood chemistry, sugar maple foliar nutrient content, concentration and mass, litterfall amount and chemistry, soil chemistry, soil solution chemistry, and throughfall chemistry.

Table 1.—Average soil solution concentrations and the Ca:Al*i* ratio for the 1997 growing season at three depths

Treatment	Depth	Ca	Mg	Al*i*	Cl	Ca:Al*i*
		- - - - - - - -(μmolL^{-1}) - - - - - - - -				
Calcium	O	135.8	32.6	25.9	371.0	4.3
	25cm	43.0	13.1	19.4	132.3	2.3
	50cm	43.2	14.1	15.1	113.6	3.1
Aluminum	O	103.4	27.2	89.6	492.7	1.4
	25cm	48.0	16.0	40.0	218.7	1.3
	50cm	39.4	13.7	18.8	112.7	2.5
Control	O	23.0	6.8	15.0	25.1	1.5
	25cm	15.0	4.7	13.6	12.6	1.1
	50cm	17.4	5.8	8.5	11.3	2.1

Prior to treatment the soils at the site had low exchangeable base cations (A horizon Ca = 0.68 cmol x kg^{-1} and Mg=0.17 cmol x kg^{-1}) and high exchangeable Al (A horizon Al=5.82 cmol x kg^{-1} from 1M NH_4Cl extraction). These values are similar to other sites at HBEF and are some of the more base-poor values found in the White Mountains. Soil water is collected from three nests of 3 tension lysimeters on each plot. At each nest, lysimeters are located beneath the organic horizon, and at 25 cm and 50 cm below the top of the forest floor. A goal of the study is to increase the concentration of inorganic monomeric Al (Al*i*) in soil solution in the upper soil horizons to at least 100 μmol L^{-1}, a concentration that inhibits the uptake of Ca by sugar maple. Table 1 shows the average soil solution concentrations for Ca, Mg , Al*i*, and Cl and the average Ca:Al*i* ratio for the 1997 growing season. The calcium treatment increased the concentration of Ca at all depths. Other cations, including Al, were elevated relative to the control plots, but not to the degree of Ca. The Ca:Al*i* ratio was increased to a level well out of the range that would be potentially harmful to sensitive plants. The aluminum treatment increased Al concentration to near the target level in the organic horizon and to almost 50% of the target level for the B horizon (25 cm depth). The aluminum treatment also substantially increased the concentration of Ca at all depths; consequently, there was only a minimal change in the Ca:Al*i* ratio compared to the control plots. Multi-cation response suggests that changes in soil water chemistry are due to both added cations as well as native cations contributed from soil exchange sites. Foliar samples for chemical analysis were collected in August of each year from sapling and overstory sugar maple, hobble bush (*Viburnum alnifolium* Marsh.), and wood fern (*Dryopteris spinulosa* (Muhl.) Underw.). There has not been a significant response of foliar concentrations of Ca in sugar maple saplings or overstory trees; however, the trends are in the expected directions with higher concentrations of Ca in the calcium treatment plots and lower in the aluminum treatment plots relative to the control. Wood fern showed the most dramatic response to treatments with the foliar concentration of Ca doubling in the calcium treatments compared to controls and a trend toward reduced Ca in the aluminum treatments.

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Soil Water and Xylem Chemistry in Declining Sugar Maple Stands in Pennsylvania

David R. DeWalle, Bryan R. Swistock and William E. Sharpe[1]

Abstract

Evidence is accumulating that decline of sugar maple, *Acer saccharum* Marsh., in northern Pennsylvania may be related to overall site fertility as reflected in the chemistry of soil water and bolewood xylem. In this paper we discuss factors related to varying site fertility, including effects of soil liming, past glaciation, topographic position and soil acidification. Soil liming experiments at Cherry Springs and Black Diamond sites in northcentral PA have shown a dramatic growth response of sugar maple to improved soil Ca and Mg supplies (Long et al. 1997). Soil water chemistry at 30-cm depth at Cherry Springs and Black Diamond showed significantly higher Ca and Mg and significantly lower Al and Mn concentrations on treated than control plots in 1995-96, over ten years after liming. Ca/Al molar ratios < 1 in soil water on unlimed plots at Cherry Springs suggest that growth stress may be occurring due to nutritional disorders. Sugar maple xylem chemistry at Cherry Springs also showed significantly higher Ca and Mg and significantly lower Mn concentrations on limed than on unlimed plots. Although Al concentrations were undetectable in sugar maple bolewood, Mg/Mn or Ca/Mn molar ratios in xylem were signficantly higher on limed than unlimed plots at Cherry Springs. Similar soil water and bolewood xylem chemistry differences were generally, but not always, found between stands on glaciated and unglaciated sugar maple sites in northern Pennsylvania. Generally, forest stands on glaciated sites showed higher soil water Ca/Al ratios and bolewood xylem Mg/Mn ratios than unglaciated sites. Topographic position (upper, mid, lower slopes) did not consistently correlate with occurrence of high or low Ca/Al and Mg/Mn ratios in soil water and bolewood xylem, respectively, due to the effects of underlying geology and subsurface drainage patterns. Further sampling in 15 sugar maple stands in northern Pennsylvania also showed a positive relationship between radial growth rates and the Mg/Mn ratios in bolewood xylem, suggesting a link between site fertility and growth[2]. Soil acidification experiments at Fernow Experimental Forest in West Virginia and Bear Brook in Maine, which were conducted to test effects of accelerated rates of atmospheric deposition simulated with additions of N and S as ammonium sulfate, have shown rapid leaching of base cations from the soil leading to reduced bolewood xylem Mg/Mn molar ratios (DeWalle et al. in press).

Overall, these studies suggest that wide variations exist in forest site fertility, as reflected by soil water and xylem chemistry, due to complex interactions of glaciation history, topography, and possible accelerated leaching of soil base cations due to atmospheric deposition. Understanding the factors causing such variations in site fertility and their effects on health of sugar maple may provide better management methods for declining sugar maple stands.

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Role of Climate in the Dieback of Northern Hardwoods

Allan N.D. Auclair[1]

Abstract

The incidence of freezing and drought stresses, reconstructed from daily minimum/maximum temperature and precipitation records in areas of severe, recurrent dieback on sugar maple, was not happenstance but clustered at intervals of 8 to 12 years over the 1910 to 1995 period. Initial episodes of severe dieback on sugar maple (*Acer saccharum* Marsh.), as well as ash (*Fraxinus* spp.), white/yellow birch (*Betula papyrifera* Marsh. and *B. alleghenienesis* Brit.), and red spruce (*Picea rubens* Sarg.) occurred within five years of rotation age and coincided with extreme winter thaw followed by sudden freezing. Regional thaw-freeze events correlated significantly with high El Nino-low Southern Oscillation index, and hence with elements of change in global climate. New insights on biome-wide and century-long patterns of dieback and on climate mechanisms are being applied to innovative management approaches including early warning of risk and optimization of stand resistance to dieback.

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The Effects of Defoliation and Thinning on the Dieback, Mortality, and Growth of Sugar Maple in the Tug Hill Region of New York

Robert A. Wink and Douglas C. Allen[1]

Abstract

Some recent literature suggests that thinning should not be conducted immediately prior to, during, or immediately following an outbreak of defoliating insects. Although the individual effects of both defoliation and thinning are well documented in the literature, no study has assessed the combined effect of these two stressors. An outbreak of forest tent caterpillar, *Malacosoma disstria* Hbn., in the Tug Hill region of New York from 1990 to 1993 afforded the opportunity to assess the combined effects using a 2X2 factorial design. The two factors were recent defoliation and recent thinning. The two levels of defoliation were undefoliated and severely defoliated. Stands defined as severely defoliated were those in which a majority of the sugar maple (*Acer saccharum* Marsh.) had a midsummer reflush of foliage for two consecutive years. The two levels of recent thinning were unthinned and thinned. Thinned stands were those that had been treated between fall 1989 and fall 1992. Five defoliated and thinned, eight defoliated and unthinned, five undefoliated and thinned, and six undefoliated and unthinned stands were selected. Five 0.02 hectare (0.05 acre) plots per stand were established to determine the extent of mortality and to assess crown condition. Crown dieback was estimated in 1995 and again in 1997 on 250 dominant and codominant (DC), 112 intermediate (INT), and 260 suppressed (SUP) sugar maple using North American Maple Project (NAMP) protocol. Growth analyses were conducted on 220 DC sugar maple in 1995.

In both 1995 and 1997, DC sugar maple in defoliated stands had significantly greater average dieback (22 percent and 26 percent) than did DC sugar maple in undefoliated stands (9 percent and 11 percent). In both 1995 and 1997, the percent mortality of DC sugar maple was significantly higher in the defoliated stands (10 percent and 22 percent) than in the undefoliated stands (1 percent and 1 percent) Also, DC sugar maple in defoliated stands had significantly reduced growth in 1992, 1993, and 1994 when compared to trees from undefoliated stands during the same years. In

1995, INT sugar maple in defoliated stands had significantly greater average dieback (19 percent) than did INT sugar maple in undefoliated stands (7 percent). Also, in 1995, the percent mortality of INT sugar maple was significantly greater in defoliated stands (14 percent) than in undefoliated stands (1 percent). In 1995, SUP sugar maple in thinned stands had significantly greater average dieback (21 percent) than SUP sugar maple in unthinned stands (13 percent). In 1997, the percent mortality of SUP sugar maple was significantly greater in thinned stands (30.0 percent) than in unthinned stands (10 percent). No defoliation by thinning interactions were detected indicating that during the most recent outbreak of *M. disstria* in the Tug Hill region of New York State, thinning did not exacerbate the effects of defoliation.

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Relationship Between Foliar Chemistry and Insect Performance: the Forest Tent Caterpillar

François Lorenzetti, Yves Mauffette, and Éric Bauce[1]

Popular Summary

Forest tent caterpillar (FTC) feeds on several species of deciduous trees (Stehr and Cook 1968). In northeastern North America, quaking aspen is the preferred host of this spring-feeding insect. FTC commonly defoliates several thousands of hectares of aspen stands each year in Québec (Bordeleau 1990), although its secondary hosts seldom are attacked. Between 1979 and 1982, large outbreaks of FTC occurred in both aspen and sugar maple stands of the southern region of Québec (Bauce et al. 1990). These outbreaks coincided with an episode of crown dieback which affected many broadleaf species. The symptoms were particularly apparent in sugar maple, but aspen was completely unaffected. Although herbivory by FTC was not a major factor explaining sugar maple crown dieback in Québec (Bauce et al. 1990), physical and physiological changes in foliage associated with decline (Houston 1981; Klein and Perkins 1988) are likely to affect foliage quality for herbivorous insects. Despite that forest decline and insect outbreaks often coincide and that foliar chemistry of declining trees is likely to change in ways relevant to insect performance, the response of herbivorous insects to these changes seldom has been investigated (but see Landsberg 1990 *a b c*). Here, we present results of a study in which the performance of FTC larvae on aspen, and healthy and declining maples was compared; we also report leaf chemistry and compare insect performance to these data.

Material and Methods

Sampling of Foliage

Foliage of quaking aspen was collected on trees (n=5) in a stand in Ste-Foy, Québec (46°47' N, 71°21' W). The foliage of sugar maple was sampled from trees in a stand in the southern part of Québec (46°10' N, 71°42' W). Condition of sugar maple trees was evaluated following the classification of Bauce and Allen (1991). Trees with less than 15 percent of the foliage missing from the crown were classified as healthy. Those with more than 50 percent missing foliage were classified having severe dieback. Three (1989) and five (1990) maple trees in each of these two classes were randomly selected for insect rearing and chemical analyses. Foliage of both species was collected early in the morning every 2 to 3 days from the top third of the crown. Leaves for chemical analyses were removed immediately from the twigs and placed on ice in a cooler until they were stored at -80 °C. Foliage for insect rearing was left on the twigs and brought in a cooler to the laboratory where it was placed in distilled water.

Constituents of Foliage

Variables measured were water content (1990 only), total micro-Kjeldahl nitrogen (1990 only) (Allen 1974), free soluble sugars (Renaud and Mauffette 1991), total phenolics (Swain and Hillis 1959), and condensed tannins (Govindarajan and Mathew 1965). Free soluble sugars, total phenolics, and condensed tannins were not measured on aspen in 1989.

Insect Rearing

Egg masses of the FTC were provided by G. Bonneau (Ministry of Natural Resources) and were collected during Marsh from one location in 1989 and from two locations in 1990. At both locations, populations of the FTC were established on aspen. Egg masses were kept at 4 °C until rearing started. Rearing started within 3 to 4 days following budburst in the maple stand and was conducted in growth chambers (22 °C, 80 percent relative humidity, and 16 hr photoperiod). Newly hatched larvae from several egg masses were randomly assigned to feed on the foliage of aspen or on healthy or on declining maples until they reached pupation. Individual leaves were offered to the larvae in Petri dishes. A vial of distilled water was glued to the side of the dish and the leaf petiole was inserted in the vial to maintain turgor. Pupal weight and time to pupation were recorded. Because of the gregarious life-style of FTC, five larvae were reared per Petri dish. To avoid pseudoreplication (Hurlbert 1984), performance data used in statistical analyses were mean pupal weight and mean development time per dish. Alpha=0.05 was the nominal indicator of significance.

Results and Discussion

Foliar Chemistry

Water content decreased in foliage of all species as the season advanced, but the rate of decrease was faster in aspen than in either healthy or declining maples (Fig. 1); a test for the homogeneity of slopes had significant foliage by day interaction term (test performed on $\log_{10}$-transformed data to linearize; $F_{2,110} = 4.00$, $p = 0.0210$). The total nitrogen content decreased at the same rate in foliage of all species as the season advanced ($\log_{10}$-transformed data, F-value for the foliage by day interaction term = 2.73, *d.f.* = 2, 63, $p = 0.0730$). The mean nitrogen content was lower in declining maple than in either healthy maple or aspen (Fig. 1; adjusted least-square means, $p < 0.05$). Multivariate analysis of variance (MANOVA) for repeated measures was used to compare soluble sugar (SS) content among the three foliage

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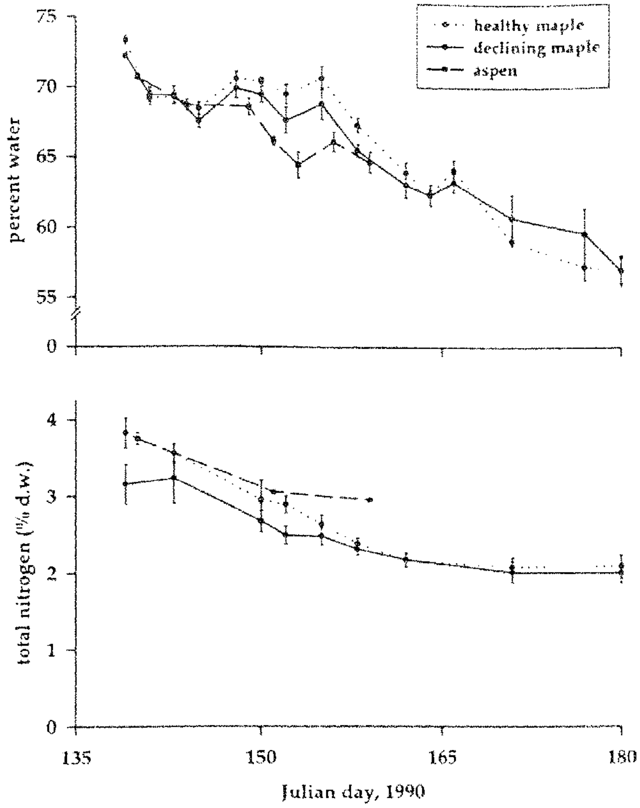

Figure 1.—Water and total nitrogen content of hosts.

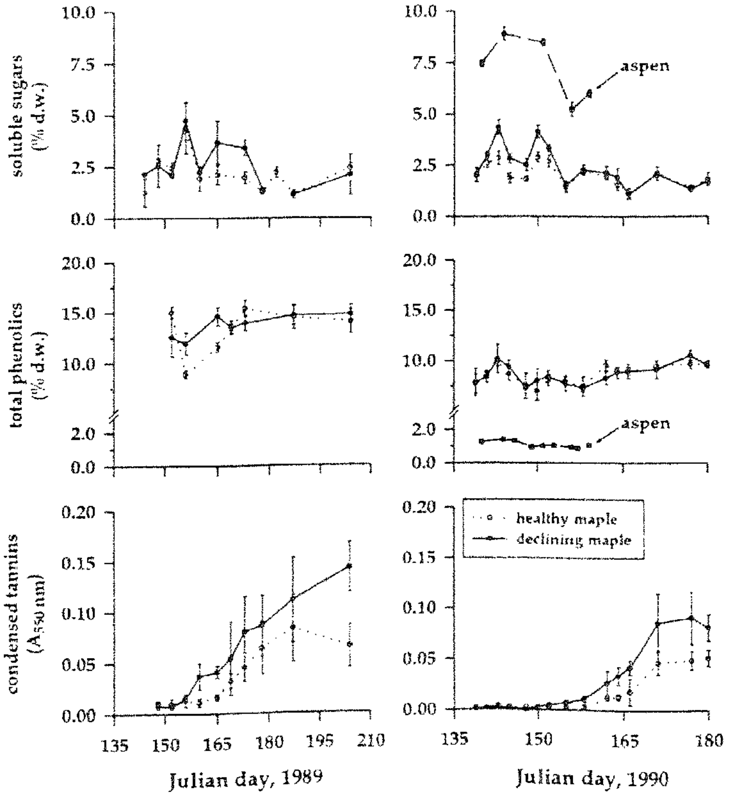

Figure 2.—Total soluble sugar, total phenolic, and condensed tannin content of hosts.

sources. Data included in the analyses were determined by inspecting plots of SS content versus Julian day (Fig. 2). For example, a visual inspection of such plots suggested that the SS content of declining maple foliage was higher than in healthy maple foliage between Julian days 160 and 178 for 1989, and between Julian days 139 and 155 of 1990. Results indicated that there was indeed more SS in the foliage of declining trees for 1990 ($F_{1,7}$ = 15.01, p = 0.0061), whereas no significant difference was found between healthy and declining trees in 1989 ($F_{1,4}$ = 5.76, p = 0.0743). Data for aspen were not included in the analysis because the SS content of aspen foliage was more than twice that in maples (Fig. 2). Interestingly, both species showed the same variation with respect to Julian day, despite the fact that the maple and the aspen stands were separated by 80 kilometers. The mean total phenolics (TP) content in maples was more than 50 percent higher in 1989 (13.5 percent dry weight [d.w.]) than in 1990 (8.6 percent d.w.) (Fig. 2). There was no significant linear trend in either year, as determined by a repeated measures MANOVA (1989: Wilk's Lambda = 0.0027, p = 0.0780; 1990: Wilk's Lambda = 0.0111, p = 0.2127). No significant difference was found between healthy and declining trees (1989: $F_{1,4}$ = 1.10, p = 0.3544; 1990: $F_{1,7}$ = 1.10, p = 0.7898). The TP content was nearly eight times less in aspen than in the maples (Fig. 2). Condensed tannins (CT) started to accumulate in the leaves of maples after Julian day 152 in 1989 and after Julian day 150 in 1990 (Fig. 2), though no significant linear trend was detected by the repeated measures MANOVA (1989: Wilk's Lambda = 0.0342, p = 0.2742; 1990: Wilk's Lambda = 0.7442 , p = 0.0555). This may be due to the large variation among trees, but also to variation between sampling dates within the same tree. Baldwin et al. (1987) reported a similar pattern in their study of leaf tannin variation in sugar maple and yellow birch. In 1990, however, the mean CT content was significantly higher for declining compared to healthy trees ($F_{1,7}$ = 6.33, p = 0.0400). In 1989, the mean CT content tended to be higher in declining trees (Figure 2), but not significantly so ($F_{1,4}$ = 1.93, p = 0.2370). CT were practically absent in aspen (A_{550nm} < 0.008, all dates).

Insect Performance

In both years and in both sexes, FTC larvae developed significantly faster on aspen than on maple (Fig. 3; 1989, males: $F_{2,12}$ = 16.16, p = 0.0004; 1989, females: $F_{2,12}$ = 26.83, p = 0.0001; 1990, males: $F_{2,25}$ = 57.25, p < 0.0001; 1990, females: $F_{2,25}$ = 93.47, p < 0.0001). Development time was not significantly different between healthy and declining maples in either year or in either sex (Fig. 3; Waller-Duncan test at p = 0.05). In 1989, differences in pupal weight were marginally significant in males (Fig. 3; $F_{2,12}$ = 3.72, p = 0.0554), whereas differences were highly significant in females (Fig. 3; $F_{2,12}$ = 23.18, p = 0.0001). In 1990, differences in pupal weight were highly significant in both sexes (Fig. 3; males: $F_{2,25}$ = 100.12, p < 0.0001; females: $F_{2,25}$ = 220.22, p < 0.0001). Both male and female FTC pupae were significantly heavier on declining maple than on healthy maple in 1990 (Fig. 3; Waller-Duncan test at p = 0.05), but not in 1989. FTC pupae were significantly heavier on aspen than on maple, but not in males in 1989 (Fig. 3; Waller-Duncan test at p = 0.05). In both years and in both sexes, ranking of pupal weight was, however, consistent (healthy maple < declining maple < aspen; Fig. 3).

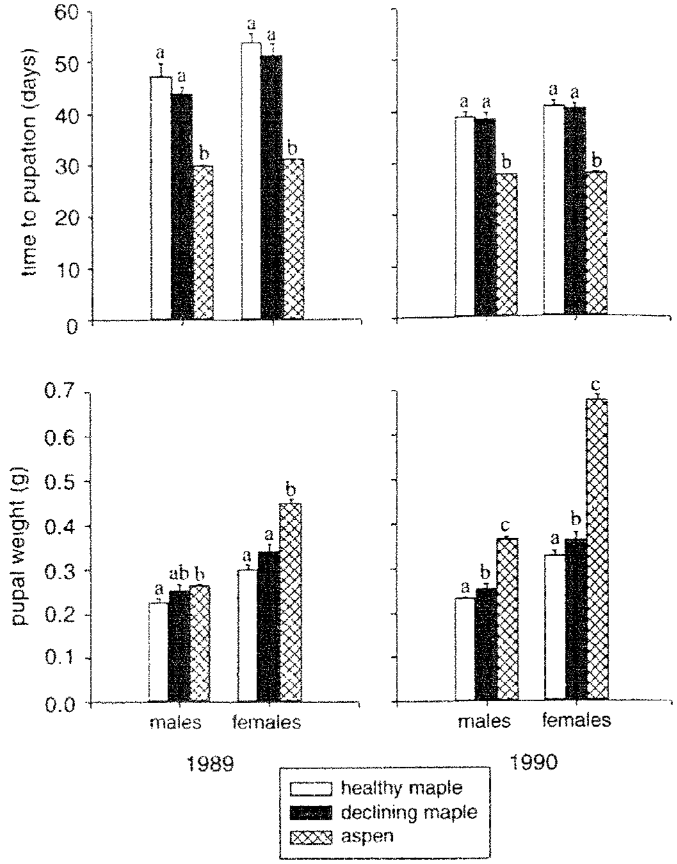

Figure 3.—Time to pupation and pupal weight of Forest Tent Caterpillar on hosts. Different letters above the bars indicate significant differences among hosts within sexes (Waller-Duncan, p = 0.05).

Insect Performance *vs* Leaf Chemistry

High water and nitrogen contents are predicted to increase insect performance (Scriber and Slansky Jr. 1981). Here, variations in water and nitrogen contents among hosts observed in 1990, and the associated response of FTC larvae are inconsistent with this prediction. In aspen, water content was lower than in maples, yet FTC pupae were significantly heavier on aspen than on maples. Declining maple had a lower nitrogen content than healthy maple, yet FTC pupae were heavier on declining maple. Defensive compounds such as soluble phenolics and condensed tannins are generally detrimental to herbivores (Feeny 1968). Here, condensed tannins tended to be higher (1989), or were significantly higher (1990), in declining than in healthy maple, yet FTC pupae were heavier on declining maple. The only consistent relationship between host chemistry and FTC performance that emerges from the results obtained here is between pupal weight and the soluble sugar content of the hosts. In fact, it is possible to correlate pupal weight with the soluble sugar content on a per tree basis, across hosts and across years (Fig. 4). Female pupal weight increased exponentially with increasing soluble sugar content ($y = a\,e^{bx}$; $a = 0.239 \pm 0.008$, $b = 0.137 \pm 0.006$, $R^2_{adj} = 0.97$, $p < 0.0001$), while the relation was linear for males ($y = ax + b$; $a = 0.025 \pm 0.002$, $b = 0.179 \pm 0.007$, $R^2_{adj} = 0.94$, $p < 0.0001$). The exponential relationship for females can be explained by the allometric relationship between pupal weight and the number of eggs at adult emergence (data not shown). When the number of eggs is used, female performance is linearly related to the soluble sugar content of the foliage (Fig. 4; $y = ax + b$; $a = 26.9 \pm 2.1$, $b = 55.8 \pm 10.4$, $R^2_{adj} = 0.93$, $p < 0.0001$). Although the very high proportion of the variation in insect performance explained by these models can be due to the gap in the data set at intermediate values of sugar content, it can be seen that the scatter around the predicted values is in general very small (Fig. 4). The results presented here do not necessarily mean that other constituents of leaves have no effect on the performance of the FTC. For example, FTC larvae took longer to develop on maples in 1989 than in 1990 (Fig. 3), and the total phenolics content of maples were higher in 1989 than in 1990, a pattern consistent with the general mode of action of these defensive compounds. The results do, however, indicate the overriding importance of soluble sugars in the diet of the FTC, especially when fecundity is concerned. Only a few other studies have reported increased insect performance with increasing sugar content in the diet (Chippendale and Reddy 1974; Harvey 1974; Valentine et al. 1983).

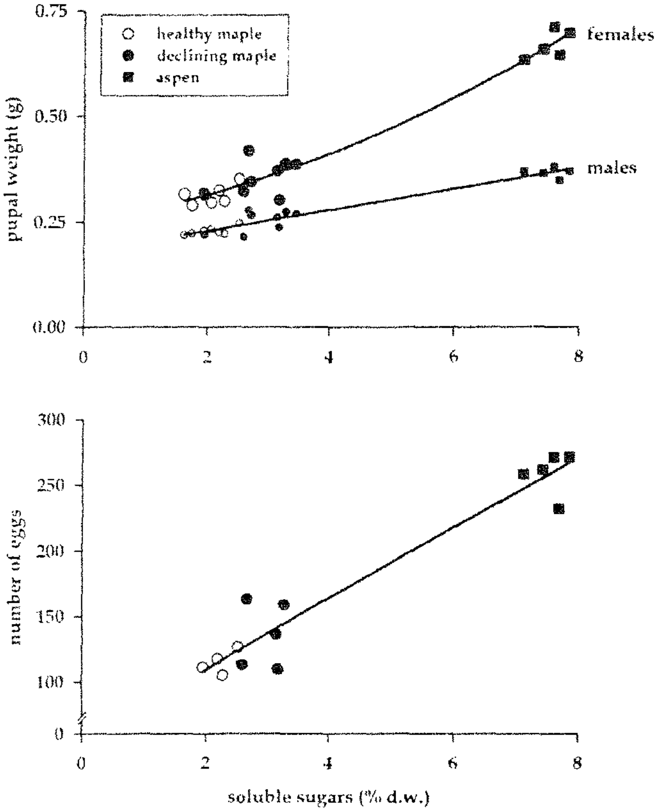

Figure 4.—Mean pupal weight and mean number of eggs per tree in relation to the soluble sugar content of foliage.

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Nitrogen addition affects leaf nutrition and photosynthesis in sugar maple in a nutrient-poor northern Vermont forest

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Abstract

Sugar maple-dominated forest ecosystems in the northeastern U.S. have been receiving precipitation nitrogen (N) inputs of 15-20 kg N ha^{-1} $year^{-1}$ since at least the mid 1980's. Sustained chronic N inputs of this magnitude into nutrient-poor forest ecosystems may cause eutrophication and affect ecosystem functioning as well as the nutritional balance of mineral elements in the tree crown. Canopy responses to N addition at a low rate (30 kg N ha^{-1} $year^{-1}$) over two years were studied in a sugar maple stand on a highly organic, acid soil in northern Vermont to understand the potential effects of N loading on crown nutrition and photosynthesis. In each year, NO_3-N was added just prior to budbreak at a rate of 30 kg ha^{-1} which was approximately 2× the atmospheric wet deposition rate measured at nearby sites. In late July and early August, fully-expanded canopy leaves were collected for measurements of foliar nutrition and leaf photosynthetic measurements under optimal field conditions. Foliar N increased by an average of approximately 4 mg g^{-1} or 28% each year in response to N addition, and maximum leaf photosynthetic rate rose 35% with N fertilization. Changes in leaf N concentration and content were consistent with the interpretation that N was limiting leaf biomass production in the stand. Although stand growth and photosynthetic function appear to be strongly limited by N, there is evidence of other limitations to photosynthesis and/or nutritional imbalances in the stand. However, there was no evidence that N addition at the rate used exacerbated other nutrient limitations in the first two years following fertilization. Thus, the sugar maple forest appears to have the potential to continue to store carbon as photosynthate as a result of continuing N deposition to the region.

Introduction

In northern temperate forests, nitrogen (N) is frequently considered to be the nutrient most commonly limiting net primary productivity (Mitchell and Chandler 1939, Vitousek and Howarth 1991). However, forest ecosystems in the northeastern U.S. currently receive 5-15 kg ha^{-1} of nitrogen annually in the form of wet and dry atmospheric deposition, primarily NO_3 and HNO_3 (Lovett and Lindberg 1993, Townsend et al. 1996, Holland et al. 1997). These anthropogenic inputs of N over many years have the potential to alter tree nutrient balance, internal physiological processes such as leaf carbon fixation, and carbon allocation patterns which ultimately may influence plant responses to other environmental factors such as ozone or elevated CO_2 (Taylor et al. 1994, Magill et al. 1997, Vitousek et al. 1997). It has been suggested that elevated atmospheric N inputs into forest ecosystems may lead to growth dilution of other nutrients, causing nutrient deficiency (Nihlgård 1985, Ågren and Bosatta 1988) although this hypothesis has rarely been tested (but see Lea et al. 1980).

To test for possible effects of increased soil N supply on mineral nutrition and physiological function in sugar maple (*Acer saccharum* Marsh.), individual trees in a nutrient-poor forest in northern Vermont were fertilized with NO_3-N at a low addition rate, equivalent to 2× the current rate of N deposition in the region. The site was typical of sugar maple forests on acidic soils in low-elevation stands in the region which are frequently low in base cations, particularly potassium and calcium (K and Ca; Wilmot et al. 1995). Base cation limitations have been implicated in recent reductions in growth and crown condition in sugar maples throughout the northeastern U.S. (Kolb and McCormick 1993, Wilmot et al. 1995, Wilmot et al. 1996, Long et al. 1997). It was hypothesized that additions of NO_3-N to an acidic soil in a nutrient-poor sugar maple stand would 1) alter tree nutrient balance and internal partitioning of N among photosynthetic processes, and 2) exacerbate leaf K and Ca deficiencies already identified within the stand (Ellsworth and Liu 1994). As a result, both effects would contribute to a relatively minor or negligible photosynthetic response of sugar maple to N addition. Therefore, I asked the following questions: Does increased N input lead to development of other mineral nutrient limitations to tree crown physiology? Does enhanced N supply have a significant effect on tree processes when other nutrients are in short supply? To help answer these questions, a nutrient-poor stand of sugar maple showing evidence of recent crown dieback was selected as a case where marginal nutrient levels would be most likely to interact with N addition in the manner hypothesized above. Leaf nutrients and maximum photosynthesis were monitored for two growing seasons following N addition to the sugar maple forest in northern Vermont.

Materials and Methods

The study was conducted in a stand in Lamoille County in rural northern Vermont (44° 32'N, 72° 34'W). The stand is located at 240 m elevation in the foothills east of the Green Mountains and is found on an acidic soil with pH of soil A horizon < 4.0. The soil is a Salmon coarse silty loam in the Haplorthod group, derived from schistic parent material and low in base cation availability (18 cmol kg^{-1} cation exchange capacity, T. Wilmot, unpubl. data). When the study was initiated in 1991, extractable soil Ca in the O + A horizons was 529 ± 57 μg g^{-1} and extractable Al was 44 ± 16 μg g^{-1}, following techniques described in Wilmot et al. (1995). The 80 to 100-year old stand was comprised of pole to sawlog-sized trees of sugar maple, with minor components of red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga*

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canadensis L. [Carr.]), ash (*Fraxinus americana* L.) and balsam fir (*Abies balsamea* L. [Mill]). The ground flora was comprised largely of ferns, particularly *Dennstaedtia punctilobula* (Michx.) Moore and *Dryopteris* spp. The stand had been unmanaged for 15 years at the time of the study, but had been briefly managed as a sugarbush and had also undergone some timber removal in 1978 to reduce stand basal area. A partial defoliation in the stand by forest tent caterpillar (*Malacosoma disstria* Hubner) was noted in 1982-83. Mean annual rainfall <5 km from the site is 970 mm and NO_3^- and SO_4^{2-} deposition at a similar sugar maple site 20 km to the west (Table 1) were 15.9 kg ha^{-1} and 23.1 kg ha^{-1}, respectively for the years 1982-1992 (National Atmospheric Deposition Program [NADP] 1993).

Table 1.—Description of growing-season rainfall (mm) and mean daily temperature (°C) for the study years compared to the 8-year mean as measured at the Proctor Maple Center, a similar site in the Green Mountains in northern Vermont. Data for the Proctor Maple Center, Underhill VT were provided courtesy of the Vermont Monitoring Cooperative. The site is 20 km from the main study site in an adjacent county.

Parameter (mm rainfall or °C temperature)	1991	1992	1993	Mean (1988-1995)
Rainfall (May-Sept.)	503	407	582	548
June temperature	17.1	16.0	15.8	16.7
July temperature	17.8	16.5	19.3	19.0
August temperature	18.6	17.3	18.7	17.6

Sixteen individual dominant sugar maple trees in the stand were selected for the study. Trees were 25-40 cm in diameter at breast height and were separated from one another by at least 15m to minimize contamination. All trees were rated with some degree of previous crown dieback present according to the protocol given in Wilmot et al. (1995) and following the North American Maple Project (Millers et al. 1991). The average crown dieback rating of the trees at the start of the study was 20 ± 2% (mean ± s.e. for n=30 trees in the stand) and did not appreciably change during the study (data not shown). This indicates that the crown dieback that was initiated in 1988-90 (according to observations of VT Division of Forests and Parks personnel, pers. comm.) was no longer progressing in the stand. Eight randomly-selected trees were fertilized with an application of $NaNO_3$ at a rate of 30 kg N ha^{-1} by hand-broadcasting the fertilizer within a 5m-radius of the designated study trees. The application rate was selected to be equivalent to approximately 2´ the present rate of ambient NO_3^- wet deposition in the region (see NADP 1993). N addition was carried out in a single application before budbreak in both 1992 and 1993. The N addition treatment was not specifically designed to mimic elevated N deposition to forests, which typically occurs as a variety of N species deposited continuously over the season. Rather, N addition was used to test the effects of increased N supply in soil on leaf physiological processes and nutrient dynamics, and determine if the forest was approaching critical N loads as have been hypothesized for other forests (Nihlgård 1985, McNulty et al. 1996, Fenn et al. 1998). The experiment was originally designed as a N × Ca factorial experiment with a Ca application (40 kg ha^{-1}) or N and Ca to a separate set of trees. However, there was no significant effect of Ca addition on leaf Ca ($P > 0.10$; data not shown) and the Ca addition rate was judged too low for the acid soil to increase Ca availability to the trees by at least an order of magnitude (see Wilmot et al. 1995). Thus Ca-amended trees were not included in the present analysis.

Pretreatment leaf macronutrient concentrations were measured on 16 study trees (8 each for the N addition and control treatments). Green foliage was sampled in August in the three years of this study (two treatment years), before the onset of senescence. In each year, two minor branches were harvested from the upper portion of the tree crown using a shotgun and a subset of healthy leaves was collected for analysis of nutrient content. Leaves were oven-dried, ground and homogenized, and analyzed for total N content on a CHN analyzer (CEC-440 Analyzer, Leeman Labs, Lowell, MA) at the University of Vermont Plant and Soil Analysis Laboratory. Single leaf samples measured for photosynthesis were generally not large enough for determining concentrations of multiple nutrient elements, so a pooled sample of adjacent leaves on the same branch was submitted to the University of Vermont Plant and Soil Analysis Laboratory for determinations of leaf macronutrient content using plasma-emission spectrometry (Plasma emission spectrometer, Leeman Labs, Lowell, MA) following digestion.

Measurements of net CO_2 assimilation (A_{net}) were made on leaves from rehydrated upper crown branches from treatment and control trees in late July through mid- August according to methods described in Ellsworth and Liu (1994). The leaves were harvested from near the top of the crown usually concurrent with leaf nutrient sampling described above, and exhibited typical 'sun' leaf characteristics. Immediately upon collection the branches were placed in a bucket of water and recut under water to rehydrate leaves. The leaf CO_2 exchange measurements were made in the field with a portable photosynthesis system (LCA-3, Analytical Development Corp., Hoddesdon, Herts. U.K.) at light saturation achieved with a metal halide lamp (photon flux densities > 1000 $\mu mol\ m^{-2}\ s^{-1}$). Other measurement conditions were near-ambient CO_2 concentrations (340 mmol mol^{-1} at site elevation) and temperatures (22-27°C) The measurements were made for at least two replicate leaves per tree following the protocol used in a related study, and represented maximum values at the physiological measurement conditions (Ellsworth and Liu 1994). Measurement leaves were selected to represent those in the upper crown of the sample trees and appeared healthy with the exception of minor cases of pear thrips (*Taeniothrips inconsequens* Uzel) feeding or mite-induced gall formation. Ellsworth et al. (1994) found that pear thrips feeding has

Table 2.—Results from repeated measures ANOVA for different leaf nutrients with two years of N addition in a nutrient-poor sugar maple stand northern Vermont. Results are for the main effect (Treatment) and interaction (Treatment x Year). Replicates are seven dominant sugar maple trees for which data are available in all three years (one year pre-treatment and two years of N addition). In cases where P > 0.10, the effect was considered not significant (n.s.).

	Main effect			Interaction		
Parameter	F	MSE	P-value	F	MSE	P-value
N	12.83	0.734	0.0072	3.40	0.194	0.0856
K	4.33	0.0247	0.0710	1.54	0.0088	n.s.
Ca	0.58	0.007	n.s.	2.78	0.0344	n.s.
Mg	1.30	0.0004	n.s.	1.83	0.0005	n.s.

minimal effects on area-based rates of photosynthesis and instead principally affects leaf size.

While within-crown variation can be an important factor causing variability in leaf nutrient concentrations and physiology, upper crown branches facing four cardinal directions did not differ in foliar nutrition, and repeat measurements made on different crown branches collected from the same tree on different days had similar photosynthetic rates and nutrient concentrations (data not shown). Previous studies with sugar maple have shown that differences between sun and shade leaves are responsible for most within-crown variability (Ellsworth and Reich 1993). All leaves used in gas exchange measurements were collected and total lamina area and dry mass were determined prior to analysis of leaf chemical content. Leaf punches were taken from the leaf opposite to that used in photosynthesis measurements for measurement of total chlorophyll content (chlorophyll *a* + *b*) using the dimethyl sulfoxide extraction technique as described previously (Ellsworth and Liu 1994).

Data Analyses

One tree in each treatment had to be omitted from the analysis due to missing data in one of the years. Leaf nutrient content over the three years of the study was analyzed using repeated measures analyses of variance (SAS Institute Inc. 1990) for those trees measured in all three years (n=7 trees per treatment). Differences between fertilized and control trees were tested using variation among trees as the error term. The significance associated with the differences between yearly means of the treatments was evaluated using the replicates within each treatment with the tree by year interaction as the error term (Sokal and Rohlf 1995). Orthogonal polynomials were used to partition the trend over time and its interaction with tree and treatment into linear or nonlinear components. The leaf photosynthesis data were analyzed using ANOVA and linear regression models of area- and mass-based leaf photosynthesis on leaf nutrients across both treatment years. A graphical analysis of leaf nutrients based on the trajectory of leaf nutrient concentration and content from pre-treatment to the end of the treatment period was also employed, as described by Timmer and Stone (1978), to help interpret foliar nutrient limitations. This analysis was only conducted on three trees due to missing data.

Results and Discussion

Pretreatment leaf N, P, K, and Mg concentrations of upper crown leaves were 17.6 ± 0.5 mg g-1, 2.3 ± 0.1 mg g-1, 4.7 ± 0.3 mg g-1, and 1.3 ± 0.1 mg g-1, respectively. Leaf calcium (Ca) concentration was 6.3 ± 0.4 mg g-1, among the lowest values reported in the literature for sugar maple (see Kolb and McCormick 1993, Wilmot et al. 1995, Long et al. 1997). There was significant year-to-year variation in leaf N in control trees ($P < 0.001$; Fig. 1), which may have been caused by low leaf N related to a mast-seeding event of sugar maples in spring, or a cool summer in 1992 (year 1 of study; Table 1). It is likely that the observed year-to-year differences in leaf N cannot be ascribed to random sampling variability since I did not observe significant differences in leaf nutrients among sampling dates in the same year or with crown aspect (see Methods). Fyles et al. (1994) noted that such year-year variability necessitates multi-year studies in order to draw conclusions regarding fertilization effects on leaf nutrients and tree vigor, along with pre-treatment data. In the two years of N addition, leaf N was significantly enhanced by the treatment ($P < 0.007$; Fig. 1 and Table 2) with an enhancement of approximately 4 mg g-1 in both fertilization years. Hence leaf N was increased by 28% over the two years in treatment compared to control trees. Given the year-to-year variability in leaf N in control trees, it is unclear if there was diminishing N uptake and allocation into foliage through time although year x treatment was marginally significant for N (Table 2).

In addition to N, there were significant effects of sampling year on leaf P ($P < 0.0017$) and K concentrations ($P < 0.0036$) but not other macronutrients (Fig. 1). There were no significant treatment effects on leaf macronutrients besides N ($P > 0.10$), and no apparent statistical effect of N addition

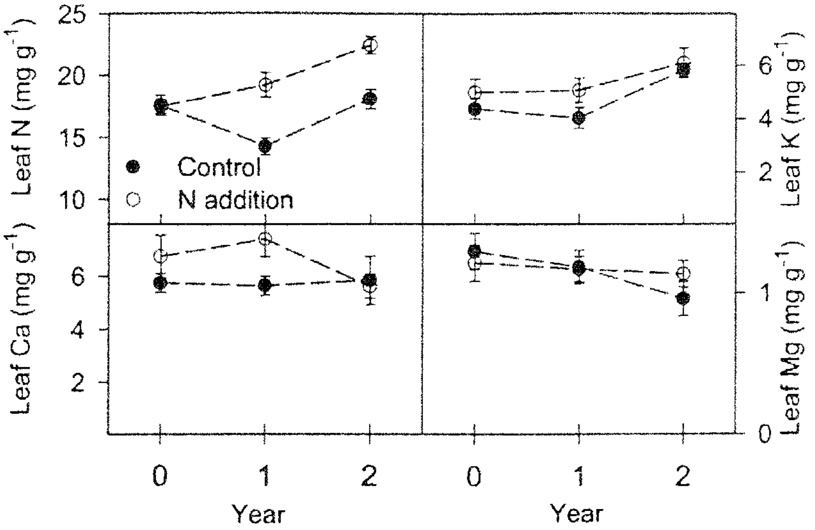

Figure 1.—Leaf nutrient levels in sugar maple foliage in the study stand during pretreatment and the subsequent two years of N addition for treatment (open circles) and control trees (closed circles). Data shown are for N, K, Ca and Mg. Error bars indicate ± 1 s.e. ANOVA results on this data are summarized in Table 2.

on leaf K, Ca or Mg concentrations (Fig. 1; Table 2). When pre-treatment and 2 year-treatment nutrient concentration and content data were plotted as vector diagrams (Timmer and Stone 1978), the trajectories of N upon fertilization showed that unit leaf mass, N concentration and N content all increased from year 0 to year 2 (Fig. 2A), although trees varied in the magnitude of this response. The increases in leaf size and leaf N content shown for all three trees are consistent with the interpretation that the stand was N limited (c.f. Timmer and Stone 1978). The vector diagram for leaf K yielded similar results suggesting that this element also may have been limiting in the stand (Fig. 2B). However, increases in leaf Ca concentration and Ca content followed the unit leaf mass isoline (Fig. 2C), suggesting that leaf Ca was accumulated in proportion to the leaf biomass response to N in Fig. 2A. It is important to note that bulk leaf Ca pools may not adequately assess the physiologically-relevant Ca in leaves since a large proportion of the Ca pool in leaves can occur as inert oxalate crystals. Moreover, it is possible that the addition of nitrate-N may have had 'hidden effects' in altering soil chemistry and Ca availability (Johnson et al. 1996).

Leaf maximum CO_2 assimilation rate was significantly related to leaf N (r^2=0.57, $P < 0.0001$; Fig. 3). Since leaves were sampled as 'sun' leaves near the top of the tree crown, mass and area-based photosynthesis and N can be considered roughly equivalent in this situation. The slope of this relationship was similar to those published previously for sugar maple in Vermont (Ellsworth and Liu 1994) and Wisconsin (Reich et al. 1991), and was not significantly different between control and N treatment trees ($P > 0.10$). On average, A_{net} was 91 ± 6 nmol CO_2 g^{-1} s^{-1} for N treatment trees vs. 60 ± 6 nmol CO_2 g^{-1} s^{-1} for control trees, with a leaf mass to area ratio of 75 ± 1 g m^{-2} for both groups pooled. Overall, mass-based photosynthesis was enhanced by an average of 34% across the two years. Leaf chlorophyll per unit area was also significantly correlated with leaf N (r^2=0.38, $P < 0.0001$; Fig. 3B), and showed enhancement for N treatment trees compared to control trees. Thus both CO_2 assimilation and light energy capture were significantly increased with increases in leaf N due to N addition.

There was a significant but weak correlation between photosynthesis and leaf Ca concentration (r^2=0.27, $P < 0.013$; Fig. 4). As I found previously (Ellsworth and Liu 1994), there was a significant correlation (r^2=0.18, $P < 0.01$) between leaf Ca and N concentrations (data not shown). Thus it is difficult to ascribe a strictly functional relationship between photosynthesis and leaf Ca that is unique from that of N. Instead, since Ca is deposited in leaf tissue in the transpiration stream and both leaf photosynthesis (Fig. 3a) and stomatal conductance to water vapor (not shown) are correlated with leaf N, it is likely that more Ca is deposited in leaf tissue when leaf N is higher as a result of N effects on gas exchange that produce a greater cumulative transpiration (over the season) with higher leaf N. This argument is consistent with the observation of possible Ca 'luxury consumption' in leaves with N addition (Fig. 2C). Together the available evidence indicates that even though leaf Ca concentrations were low in the stand, Ca was likely not limiting to physiological processes responsible for tree growth via mechanisms involving carbohydrate production in leaves. In fact, root biomass and turnover may be more sensitive to soil Ca than any leaf processes (Liu and Tyree 1997).

The data presented here indicate that this sugar maple stand responds strongly to N addition despite its low cation status. Generally, N fertilization on N-limited sites can be expected to increase stand net primary production relative to the control as a result of 1) enhanced photosynthesis per unit leaf area or leaf mass, 2) more or larger leaves per tree, 3) increased leaf duration and/or 4) more relative

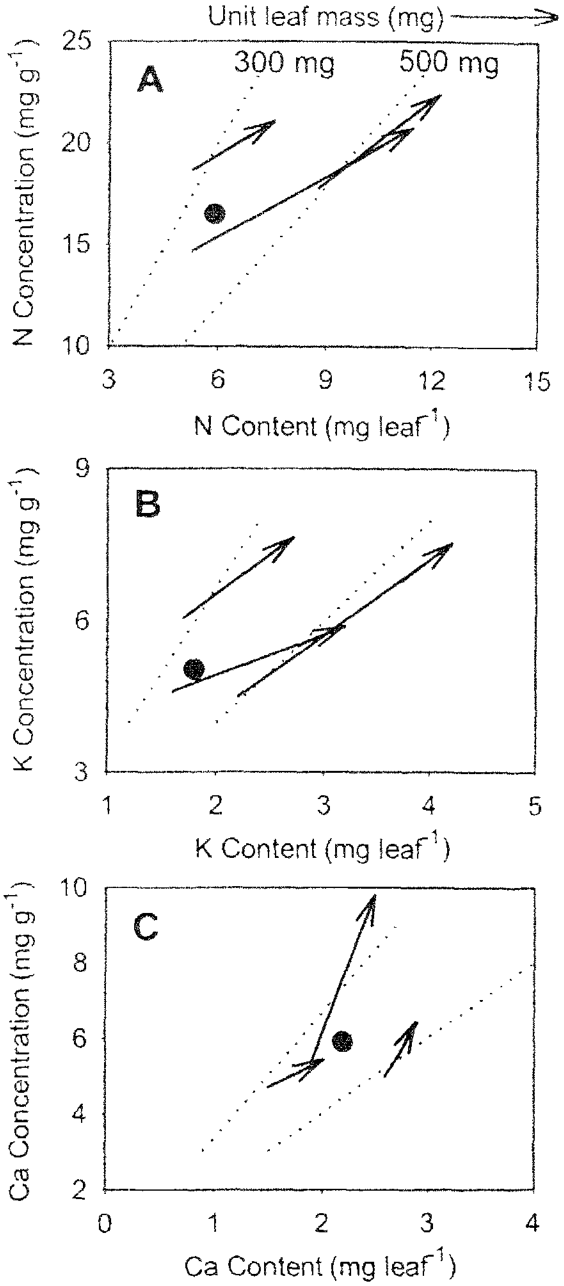

Figure 2.—A. Trajectory of changes in leaf N concentration and N content with two years of fertilization at 30 kg N ha^{-1} shown using a vector diagram (after Timmer and Stone 1978). Arrowed lines each indicate a single tree followed from pre-treatment to two years of N fertilization (year 0 → year 2). Dashed lines indicate the unit leaf mass isolines for 300 and 500 mg per leaf. The dot denotes mean N concentration and N content of control trees in year 2 of the study B. Vector diagram of changes in leaf K concentration and K content with N fertilization. Symbols are as in A. C. Vector diagram of changes in leaf Ca concentration and Ca content with N fertilization. Changes in Ca generally follow leaf mass isolines. Symbols are as in A.

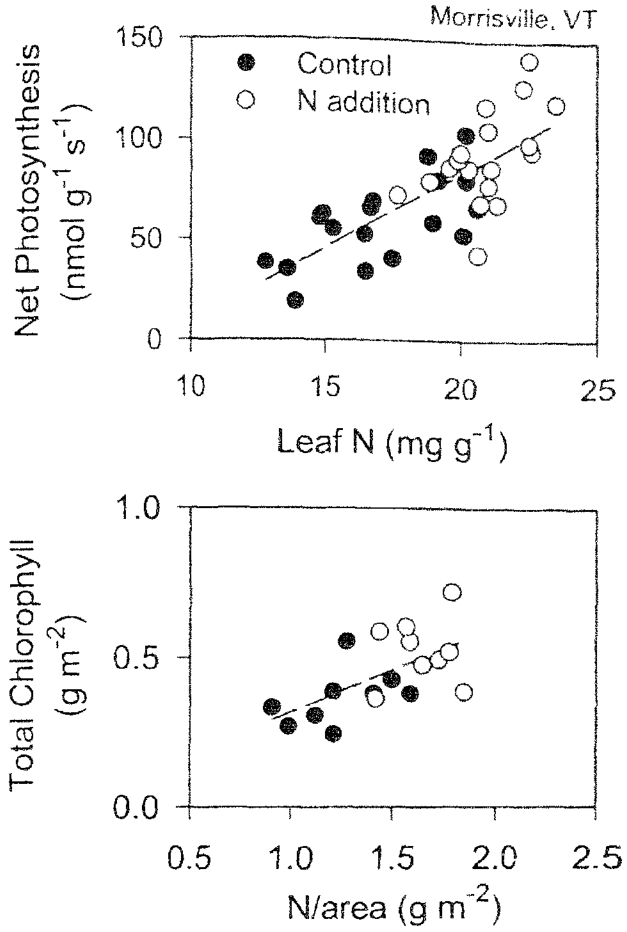

Figure 3— A. Relationship between photosynthesis and leaf N (mass-based) in upper crown *Acer saccharum* leaves for control trees (closed circles) and trees with N added (open circles). Data are pooled between two years as there was no significant effect of year on the relationship ($P > 0.10$). The regression model shown is $Y = -67.1 + 7.53^{*}X$, $r^2 = 0.57$. B. Relationship between leaf chlorophyll and leaf N (area-based) in *Acer saccharum*. The regression model shown is $Y = 0.08 + 0.283^{*}X$, $r^2 = 0.38$.

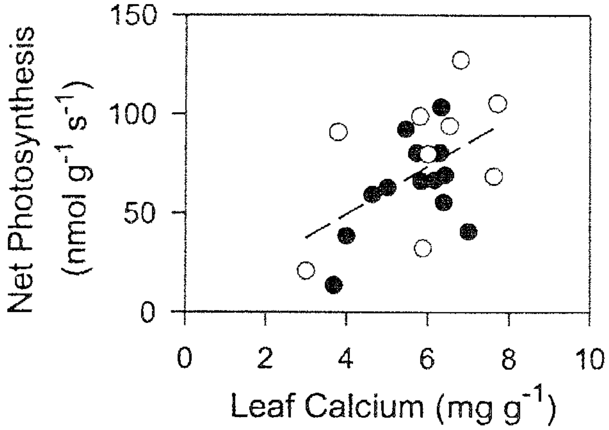

Figure 4.—Photosynthesis in relation to leaf Ca concentration for *Acer saccharum* leaves. Open circles indicated trees with N addition, and closed circles indicate control trees. The regression model shown is $Y = 1.1 + 12.09^{*}X$, $r^2 = 0.27$. There was no difference in the relationship with respect to N treatment ($P > 0.10$).

carbon allocation to the tree crown versus roots. The current study showed that photosynthesis per unit leaf mass (A_{net}) was indeed greatly enhanced by N addition. While leaf mass in the upper crown also increased with N addition (Fig. 2A), a related plot-level N addition experiment on the same site did not significantly increase total leaf area index of trees (Ellsworth, unpubl. data). Observations at the site also indicated that there was no obvious difference in leaf duration in sugar maple with N addition vs. control trees. Thus the main contributor to increased productivity with N addition at this site was likely the enhancement in leaf photosynthesis with N addition. The increased leaf-level photosynthesis was likely due to greater photosynthetic machinery in N fertilized leaves as a result of increases in the carboxylation enzyme Rubisco (Evans 1989).

The available evidence suggests that the sugar maple forest in this study has a strong potential to respond to increasing N with increased productivity in terms of carbon assimilation in the canopy. Sugar maple responses to N addition were also demonstrated by Mitchell and Chandler (1939), Lea et al. (1980), and Stanturf et al. (1989) in New York, Fahey et al. (1998) in New Hampshire, and Carmean and Watt (1975) in Wisconsin. Magill et al. (1997) also observed increases in leaf N and stand productivity in red maple at Harvard Forest, Massachussetts. These results reinforce the conclusion that sugar maple and related hardwood forests in the northeastern U.S. may respond positively to anthropogenic N addition, at least in the near-term (see Magill et al. 1997 and Fenn et al. 1998). However, in some cases these responses diminished in subsequent years of fertilization (Carmean and Watt 1975, Lea et al. 1980, Magill et al. 1997). Moreover, the fact that similar stands also respond to liming which alters soil chemistry in a number of ways that can also impact the N cycle (Fyles et al. 1994, Wilmot et al. 1996, Long et al. 1996) suggests that sugar maple stands on poor sites are likely co-limited by multiple nutrient elements. From the results here and in nearby sugar maple stands in Wilmot et al. (1996), N and Ca and possibly K together limit tree growth on sites in northern Vermont. Such multiple limitations may arise as a result of differential sensitivity of tree organs to different mineral nutrients, e.g. sensitivity of canopy processes to N while root processes are sensitive to Ca. As such, caution is warranted when comparing canopy response results such as those shown here with studies that evaluate nutrient responses in terms of wood or root growth.

From a management perspective, N addition to forest stands is costly and may have negative impacts on water quality (Ågren and Bosatta 1988, Fenn et al. 1998) and therefore cannot necessarily be recommended for large-scale use. However, it is also clear that in a stand expected to be K and Ca-limited on the basis of leaf nutrient concentrations and regional liming of similar stands on closely related soils (Wilmot et al. 1995, Wilmot et al. 1996), large nutritional and physiological responses of tree crowns to N addition are possible although it is unclear how long these responses may be sustained. It can be concluded from this two-year study that there is no evidence to suggest that N deposition at the present rate or even 1.5* current deposition will have significant effects on leaf nutrient concentrations or cause increases in Ca deficiencies, although N addition to the stand did have marginal effects on foliar K (Table 2). These results also suggest that longer-term experimentation (> 5 years) of this type is needed in a range of sugar maple stands in order to draw firm conclusions that are more widely applicable, and more relevant to projections for continuing N deposition in the region into the future.

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Markers of Environmental Stress in Forest Trees.

Rakesh Minocha[1]

Abstract

Gradual long-term changes in soil and environmental factors due to human activity, may affect forest trees and lead to loss of forest productivity. In most cases, the symptoms of stress appear too late for their effects to be reversed through management and/or treatment. The availability of early biochemical indicators/markers that can assess the current status of stress in visually healthy trees in a forest is crucial for planning a potential treatment or management practice for either alleviating the deleterious effects of the stress or removing the cause of stress. Recently, considerable attention has been paid to the study of changes in polyamine metabolism in plants subjected to various kinds of environmental stress. Polyamines (putrescine, spermidine, and spermine) are open-chain polycations of low molecular weight found in all organisms. They play an important role in the growth and development of plants. Abiotic stress conditions such as low pH, atmospheric SO_2, high salinity, osmotic shock, nutrient stress such as K or Ca deficiency, low temperature, ozone, and Al stress all lead to an increase in cellular putrescine levels within hours to days. Polyamine concentrations are inversely related to concentrations of cellular ions such as Ca, Mg, Mn, and K in response to Al treatment. The present studies were aimed at studying the relationship between soil nutrients and foliar putrescine in trees growing under varying soil conditions. We have evaluated the use of polyamines as "early markers/indicators" of stress in "visually asymptomatic trees". Trees growing in soils having variable soil Al:Ca ratios or trees growing in soils treated with chronic nitrogen additions, liming, herbicide, or ozone were analyzed for foliar polyamine levels. The results showed a strong correlation between soil nutrient deficiencies (e.g. Ca and/or Mg) and increased foliar putrescine. Our data support the hypothesis that in conjunction with soil chemistry, foliar putrescine can be used as a marker of general stress in visually healthy trees.

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Integrating the Role of Stressors Through Carbohydrate Dynamics

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Popular Summary

Introduction

Stress Definition

Biological stress is defined as any environmental factor (stressors) capable of inducing a potentially injurious strain in living organisms (Levitt 1972). Organisms respond to these stresses physiologically or developmentally, and depending on the duration and severity of the stress, may or may not be injured. Injury may occur directly from the stress, or indirectly when a stress reduces the capacity of organisms to resist additional or associated stresses. Injury occurs when the stress creates strain that exceeds the ability of organisms to resist the stress either by avoiding or tolerating it.

Stressor/Host/Pathogen Interactions: Decline Disease

Because trees are long-lived perennial-growing plants, they are exposed to numerous biotic and abiotic stressors (agents that cause stress) during their life time. The longevity of trees is testimony to their capacity to resist stress and their resilience to recover from injury when stressed beyond their capacity to resist. However, sometimes stress results in the premature death of a portion or all of a tree.

Decline diseases of forest trees are excellent examples of this deleterious stressor/host interaction and result in excessive and pre-mature mortality of canopy trees. Manion (1991) proposes that trees are predisposed by relatively static factors to inciting stressors that induce attack and colonization by contributing biotic factors which ultimately result in tree mortality. Houston (1992) proposed a similar but simpler model in which trees are predisposed by stressors to secondary pathogens (insects and disease organisms) that colonize and kill stress-weakened trees. The decline syndrome of dieback and progressive deterioration of the crown and eventual mortality illustrates the direct effects of stress and injury (dieback), and the indirect effects wherein the tree becomes susceptible and vulnerable to other stressors, i.e. secondary pathogens that cause additional and sometimes fatal injurious strain.

The effects of stress depend on the tree's genetic capacity (vigor) to resist the stress, the health or vitality of the tree when stressed, and the severity (e.g. % defoliation, millibars of moisture tension), duration or frequency (e.g. successive years of defoliation, length of drought), timing (when in the growing or dormant season), interacting or concert stressors (e.g. defoliation and drought, winter injury and drought), and the presence and aggressiveness of opportunistic pathogens (Wargo 1977, 1978, 1981a; Wargo and Auclair 1999).

These relationships are illustrated in Figure 1. Depending on their health or vitality class - here depicted as crown condition - trees in good, fair, or poor condition respond differently to different levels of stress (S1 < S2 < S3). The time relationship shows that trees change in health status more or less rapidly depending on the severity of the stress, and also that some trees can recover, the time of recovery dependent on initial tree health, and severity of stress. Also the figure illustrates that there is a threshold range where stress reduces the capacity of the tree to defend itself against secondary pathogenic organisms, and trees succumb to their attack and die. Interactions of health, stress level, and time are also illustrated in this threshold relationship.

Carbon Allocation

The threshold level of vulnerability of trees to attack by opportunistic secondary pathogens is a function of the abundance and aggressiveness of the secondary organism and the abundance of carbon allocated, or available to be allocated to defense in the case of organism attack, whether it be inhibitory compounds in tissues attacked by fungi or rapid growth to resist physical damage from insect infestations.

Source-sink Relationships

A simple model of carbohydrate allocation is given in Physiology of Woody Plants (Kramer and Kozlowski 1979):

income = carbohydrates manufactured by photosynthesis (source)

expenditures = carbohydrates used in assimilation and respiration (sinks)

balance = carbohydrates accumulated (sinks)

Although a simple model, it nicely illustrates the major uses of carbohydrates in forest trees and indicates where and how stressors can influence carbon allocation. Stressors can affect the carbon budget by directly affecting the source and reducing photosynthesis and carbohydrate production. Defoliating insects, fungi, and frost and drought can cause reductions in photosynthesis. Other stressors can affect the sinks for carbon allocation by accelerating the use of carbohydrates in assimilation or in increased respiration or both. Drought for example can result in an increase in fine root production which increases the amount of carbon needed for production and growth of the root system (Sharp and Davies 1979; Turner 1986). Reduced calcium in the

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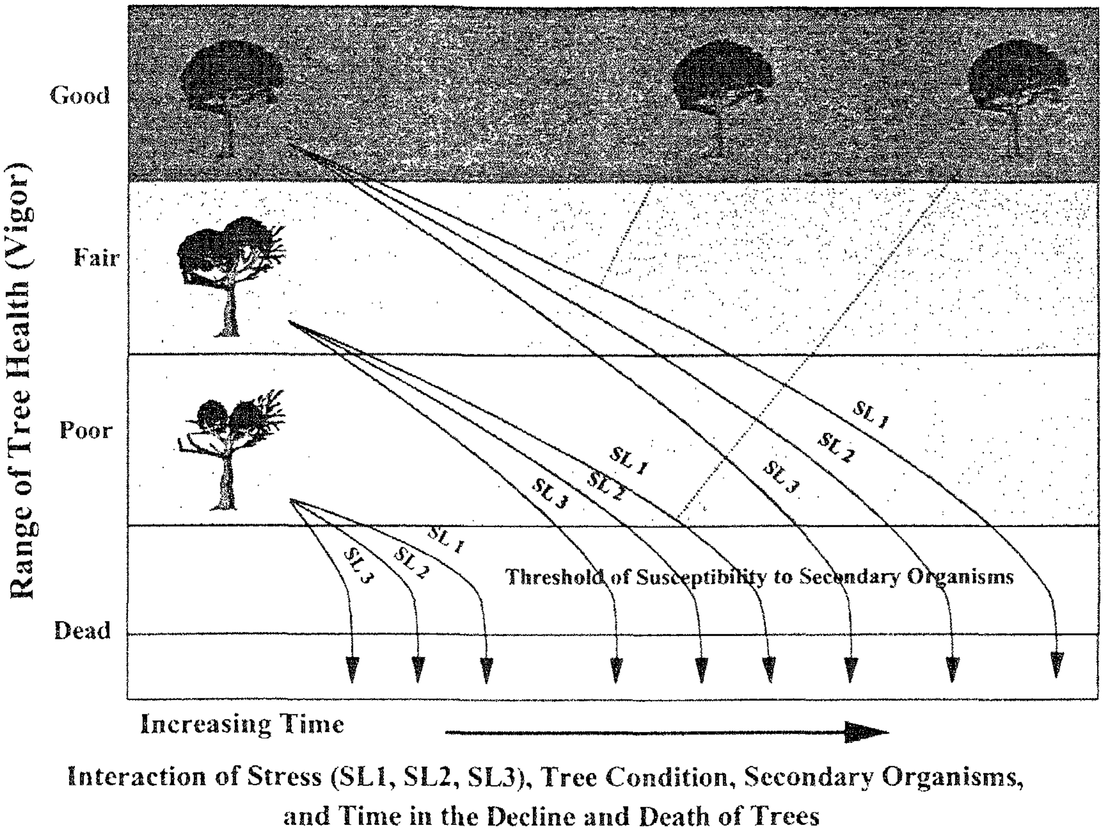

Figure 1.—An illustration of the relationships and interactions of tree health, stress severity (levels S1 < S2 < S3), secondary organisms, and time in the dieback, decline, recovery, or death of trees.

foliage because of aluminum-induced calcium depletion or reduced uptake can increase dark period respiration and increase the carbohydrates used in respiration (McLaughlin et al. 1991).

Both the direct effects of stressors on photosynthesis and carbohydrate production and the increased use of carbon for assimilation and respiration can have effects on the third part of the budget, carbohydrate accumulation. Stresses such as defoliation can result in reduced carbohydrate storage by reducing the total amount of photosynthate available for storage, and by triggering the conversion of stored carbohydrate to assimilitable or respirable soluble carbohydrates during the stress period. The effects would depend on the severity, frequency, and timing of the stress event.

Stressors In Northeastern Forests

Lists of abiotic and biotic environmental factors, that can act as primary stressors in northeastern forests are found in Houston (1987), Manion (1991), and Millers et al (1989). Drought and defoliation are listed as the most common stressors, but sucking insects, such as the beech scale and hemlock woolly adelgid, and defoliation from late spring frosts or fungal pathogens are also prevalent. The most recent and widespread ice storm in the Northeast in January of 1998 has emphasized that ice injury also is a common stressor in our northeastern forests.

Stressors will continue to play a large role in forest health issues in northeastern forests partly because this region has experienced more change in climate, air chemistry, land use, site alterations and other human impacts than any other region in the United States (Wargo and Auclair, in press) and partly because more non-indigenous pests have been introduced and have become established in northeastern forests (Mattson et al. 1993; Liebhold et al. 1995). These "exotic" pests have caused significant damage (mortality) and have resulted in large changes in forest composition, structure, and function throughout the Northeast.

Measuring the Effects of Stressors

Carbohydrate Dynamics and Defoliation

Carbohydrate content, especially reserves stored as starch, has been used as a monitor or indicator of the effects of stressors on hosts, especially the effects of defoliating insects. In work on sugar maple, *Acer saccharum* Marsh. (Parker and Houston 1971; Wargo 1971, 1972; Wargo et al. 1972) starch content of the roots was an excellent indicator of tree response to defoliation. In stands of sugar maple defoliated by the saddled prominent, *Heterocampa guttivita* (Webr.) starch content of the roots not only reflected the severity of defoliation, but also the frequency (Wargo et al. 1972).

Artificial defoliation experiments on sugar maple saplings illucidated the timing and magnitude of change in carbohydrate levels in response to normal seasonal cycles and to defoliation (Wargo 1971, 1972). These studies indicated that changes caused by defoliation were far greater than those occurring because of normal seasonal change in production and use of carbohydrates. These studies also showed that the effects of defoliation depended on when in the growing season trees were defoliated. Effects depended mainly on whether the trees refoliated in response to defoliation and the length of the remaining growing season after refoliation. However, there was a strong interaction with carbohydrate status (starch) at the time of defoliation. Trees with low starch reserves were more likely to die than those with higher reserves, which in general increased as the season progressed. Starch reserves were also important to how these saplings responded to wounding. Wound areas were larger on defoliated trees and were highly and negatively correlated with starch content of the trees (Wargo 1977).

In field studies from 1972 to 1975 on mature oaks, (*Quercus alba* L., *Q. coccinea* Muench, *Q. prinus* L., *Q. rubra* L., and *Q. velutina* Lamarck) defoliated by the gypsy moth, *Lymantria dispar* L., starch content of the roots not only showed the effects of defoliation levels measured in 1972-75 but also revealed that trees had been defoliated prior to 1972 (Wargo 1981c). Although this defoliation was not severe enough to be recorded in earlier years, it still had a significant physiological consequence on the trees. Starch content in these trees was monitored after defoliation ceased and had not recovered to predefoliation levels even after two years of no or very low defoliation (Wargo 1981c).

Starch content in roots of oaks also indicated their vulnerability to mortality associated with defoliation (Wargo 1981c). Trees in the red or white oak groups were assigned a risk of mortality based on root starch content and then monitored for two years after a single heavy defoliation. Mortality was consistently higher in the low starch-high risk trees in both oak groups. Starch was a better indicator of risk of mortality than crown condition.

This relationship of low starch to high risk of mortality was demonstrated experimentally (Wargo 1981b). In these studies, starch content in maple and oak saplings at the time of defoliation determined their response to defoliation. Trees with lower initial starch contents died first after 1 or 2 years of defoliation, while trees with higher initial contents after 3 years of defoliation died later, and trees with still higher starch levels survived the ordeal entirely.

Starch and soluble carbohydrate status in the root system has also been related to crown dieback, rate of crown deterioration and growth loss, in declining mature sugar maple in Canada (Renaud and Muaffette 1991).

Consequences of Altered Carbohydrate Dynamics

Corresponding to decreases in starch content as a result of stress, are substantial increases in reducing sugars, especially in the root system. These increases can be four to five times higher than in unstressed trees at the same time of year and also than the normal seasonal high that occurs in spring when carbohydrates are mobilized for growth (Wargo 1971, 1972). Coupled with changes in nitrogen metabolism, these carbohydrate levels are important to opportunistic organisms, particularly species of *Armillaria.*which can attack and kill stressed trees (Wargo and Houston 1974). Reducing sugars, especially glucose, not only stimulates the growth of this fungus, but also enables it to grow in the presence of inhibitory phenols such as gallic acid (Wargo 1972, 1980, 1981d).

Winter starch reserves in roots of white oak were related to susceptibility and vulnerability to attack by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Dunn et al. 1987). White oaks with low starch reserves attracted more beetles than moderate or high starch trees. And only trees that had extremely low root starch were heavily attacked by the beetle and subsequently died.

Even susceptibility to aggressive primary pathogens have relationships with carbohydrate dynamics. Time of highest susceptibility of American elm, Ulmus americana L. to colonization by Ophiostoma ulmi (Ceratocystis), the Dutch elm disease fungus, is during leaf expansion when starch reserves in the growth rings were lowest (Shigo et al. 1986). In addition, infected trees stored less starch than healthy trees making them even more vulnerable to death after additional infections.

Carbohydrate Status in Declining Sugar Maple - Allegheny Plateau

Carbohydrate status of healthy and declining sugar maple on the Allegheny Plateau in northcentral Pennsylvania were assessed in a series of lime fertilizaiton treatment plots established in 1985 (Auchmoody 1985, Long et al. 1997). Samples were collected in autumn 1997 after leaf drop. Second order woody roots were collected from each of three sugar maples trees within each treatment plot within each block. Approximately 45 cm of root 1 to 2.5 cm in diameter was collected for a series of carbohydrate and phenol analyses. Roots were frozen on dry ice in the field and placed in freezers upon return to the laboratory. A small portion (2 to 3 cm long) was cut from a section of harvested root and used for a visual determination of starch content in the roots of each tree (Wargo 1975, 1978).

Root pieces were thawed quickly in tap water, washed, and trimmed for sectioning and staining as described by Wargo (1975). Root sections were then rated for starch content as very high, high, moderate, low or none based on the density

Table 1.—Visual ratings for starch content in roots of sugar maple trees in a series of lime-treated plots on the Susquehannock State Forest on the Allegheny Plateau in northcentral Pennsylvania

	Blocks[a]				
Treatments[b]	BD1	BD2	CS3	CS4	Average
Control	3.0	3.3	2.7	3.3	3.1
Control Fence	4.7	4.3	4.0	4.3	4.3
Herbicide	2.7	4.3	3.3	3.7	3.5
Herbicide Fence	3.3	4.0	4.7	3.7	3.9
	3.4	4.0	3.7	3.7	3.7
Limed	4.0	4.3	4.7	4.7	4.4
Limed Fence	4.0	4.7	5.0	3.7	4.3
Limed Herbicide	4.3	4.0	4.7	4.7	4.4
Lime Herbicide Fence	3.7	4.0	5.0	4.0	4.2
	4.0	4.2	4.8	4.3	4.3

[a]Blocks were located in 2 sections of the Susquehannock State Forest, Pennsylvania, Black Diamond Road (BD and BD2) and Cherry Springs (CS3 and CS4).

[b]Treatments were arranged in a split-plot design with deer fencing (fence, no fence) as the whole-plot treatment and four sub-plots treatments (herbicide, dolomitic lime, herbicide + dolomitic lime, and no herbicide or lime) within each whole plot (Auchmoody 1985, Long et al. 1997).

[c]Starch rating scale: 1=none, 2=low, 3=moderate, 4=high, 5=very high.

Table 2.—Starch ratings and vigor class of sugar maple trees in the lime treated series of plots in northcentral Pennsylvania

	Vigor of living trees[1]				
Starch ratings	1	2	3	4	Total
Very high	20	2	10	5	37
High	17	3	7	4	31
Moderate	8	0	8	4	20
Low	1	0	0	7	8
None	0	0	0	0	0
Total	46	5	25	20	96

[1]Mader-Thompson System (Mader and Thompson 1969)

of purple-black staining in the ray and xylem parenchyma. A descending numerical value of 5 for very high to 1 for none was assigned each rating and an average for each treatment was determined.

Preliminary results indicated that on average all limed treated plots had high starch contents (Table 1). Lowest starch levels were in untreated control plots. Cherry trees were sampled in only the fenced portion of block CS4. Three trees were sampled per plot. All cherry trees were rated very high or high. The average starch content for cherry was 5.0 for control plot, 4.3 for the herbicide plot, 4.3 for the limed plot and 4.7 for the limed herbicide plot.

Most trees rated as low in starch were in vigor class 4 or greater (vigor 1=healthy, 2=light decline, 3=moderate declin 4=severe decline, 5=dead; Mader and Thompson 1969); however not all poor vigor trees had low starch contents (Table 2). Seven of the 8 low starch trees were from unlimec plots and all were in class 4 vigor.

Conclusions

Carbohydrate status, especially storage carbohydrates primarily starch, integrates the effects of stress on trees vitality and largely determine their ultimate response to stress. Energy reserves are necessary for mobilization to support respiration and assimilation prior to new leaf production at the beginning of the growing season. They are also necessary to support these processes during times of stress. Inadequate carbohydrate reserves predisposes trees to injury from the stress itself but also and especially from opportunistic organisms that are ubiquitous in the environment and depend on stress weakened trees as energy sources.

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Widespread Sugar Maple Decline and Regeneration Failure in the Adirondacks

Jerry C. Jenkins, Elizabeth Moffett, and Daphne Ross[1]

Poster Abstract

Over large areas of the Adirondacks, hardwood stands whose canopies are dominated by or contain abundant mature sugar maple (*Acer saccharum* Marsh.) have almost no sugar maple saplings or seedlings in the understory. Coring shows that most (>80%) of these stands reproduced well in the first half of this century but have added few or no trees to the canopy or subcanopy since 1950. Such forests contrast sharply with maple stands elsewhere in the state and the northeast, which typically have a persistent bank of suppressed seedlings, abundant maple saplings in small gaps, and continuing recruitment of young maples to the canopy and subcanopy. Our research has been designed to assess the incidence, chronology, and ecological correlates of this problem. We find that sugar maple regeneration failure is a) widespread in the east Adirondacks and almost ubiquitous in the western Adirondacks; b) equally common in commercial, ex-commercial, and old-growth forests; c) characterized by the early death of seedlings and hence by sparse seedling banks; d) commonly associated with an abundance of young beech but not restricted to points at which beech is locally abundant; e) found across a range of light levels and not restricted to extremely dark forests; and f) most likely to occur on soils with low (<300 ppm) amounts of exchangeable calcium and least likely to occur on soils with high (>700 ppm) amounts of exchangeable calcium. Our results are consistent with studies from Pennsylvania showing high sugar maple seedling mortality on soils with depleted calcium pools. We suggest that the remarkably uniform occurrence of regeneration failure is ecologically and economically alarming and that our results are consistent with, but do not establish, a central role for soil cation changes, possibly caused by acid rain.

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Relationships Between Stream Acid Anion-Base Cation Chemistry and Watershed Soil Types on the Allegheny High Plateau

Gregory P. Lewis[1]

Poster Abstract

The leaching of calcium and magnesium from forests by atmospherically-deposited strong acid anions (sulfate and nitrate) is evidenced in some watersheds by the positive correlation in stream water between concentrations of these base cations and acid anions. However, in other watersheds, stream concentrations of base cations and acid anions are negatively correlated, even where acidic deposition is high. The goal of this study was to determine if base cation-acid anion relations in headwater streams were related to proportions of soils with shallow perched water tables (SWT) and soils without perched water tables in a watershed. I sampled stream water from 18 forested watersheds in the Allegheny National Forest, Pennsylvania, between August 1996 and June 1997. I placed each watershed into one of three groups according to the base cation-acid anion relationships of its primary stream: (1) positive correlation between base cations and acid anions ($p \leq 0.05$; $n=10$), (2) negative correlations between base cations and acid anions ($n=4$), or (3) either a combination of positive and negative correlations or no significant relationship between base cations and acid anions($n=4$). Percentages of watershed area covered by soils with shallow perched water tables (%SWT) differed significantly (ANOVA, $p=0.01$) among the three groups of watersheds. The percent of the watershed covered with SWT for positively correlated cation-anion relationships was significantly greater ($p<0.05$, Scheffe test) than the percent of the watershed area with SWT for negatively correlated cation-anion relationships, and was marginally ($p=0.055$) greater than the percent of watershed area covered by soils with SWT for mixed or non-significant cation-anion relationships. In two watersheds covered mostly (80-90%) by soils with shallow perched water tables, the streams were flashy (*i.e.*, streams rose quickly in response to precipitation inputs) and calcium, magnesium, and sulfate concentrations all increased similarly with increasing discharge. In contrast, at a watershed with < 32% of its area covered by soils with shallow perched water tables, the stream was less flashy, and base cation concentrations declined sharply with increasing discharge, even though sulfate concentrations increased and nitrate concentrations remained essentially unchanged. These results suggest that flowpaths of groundwater that contribute to stream water are influenced by physical properties of soils in the watershed: where an impermeable layer (e.g., a fragipan) supports a perched water table, most stream water might originate from soil horizons above the impermeable layer. However, where impermeable layers are less extensive, stream water might originate mostly from deeper (more base-rich) groundwater at low flow and shallower (more acidic, base-dilute) groundwater at high flow (e.g., after storms).

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Effects of $CaCl_2$ and $AlCl_3$ Additions on Sugar Maple Fine Roots and Exchangeable Ions in Rhizosphere and Bulk Soils of a Northern Hardwood Forest

Richard P. Phillips and Ruth D. Yanai[1]

Poster Abstract

Increased mobilization of aluminum and accelerated leaching of calcium and magnesium from the rooting zone have been linked to strong acidic inputs to northern hardwood forests. Changes in soil chemistry have been hypothesized to adversely affect Ca and Mg uptake and stress tolerance of sugar maple (*Acer saccharum* Marsh.) on base-poor soils. From 1995 to 1997, three experimental treatments were applied to four replicate northern hardwood plots: $CaCl_2$ (10 g/m^2), $AlCl_3$ (4.5 g/m^2) and control (no chemical additions). We sampled bulk soil, rhizosphere soil and fine roots from four overstory sugar maples in each plot. The $AlCl_3$ treatment resulted in 68% lower (Ca+Mg)/Al molar ratios in bulk soils and 63% lower ratios in rhizosphere soils. Other differences in Al, Ca and Mg concentrations between treatments were too small to be significant. We found the rhizosphere to be depleted in exchangeable and organically-bound Al and enriched in Ca and Mg relative to bulk soil. Fine root concentrations of Al were significantly greater (64%) in $AlCl_3$ treated plots than controls. These results suggest increased mobilization of Al due to decreases in the (Ca+Mg)/Al molar ratios in bulk and rhizosphere soils may lead to preferential adsorption of Al on root exchange sites. Interference of Ca and Mg uptake may have long-term implications for sugar maple nutrition in base-poor soils.

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