Health of Eastern North American Sugar Maple Forests and Factors Affecting Decline

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ABSTRACT: *Sugar maple (*Acer saccharum*) is a keystone species in the forests of the northeastern and
midwestern United States and eastern Canada. Its sustained health is an important issue in both managed and
unmanaged forests. While sugar maple generally is healthy throughout its range, decline disease of sugar maple
has occurred sporadically during the past four decades; thus, it is important to understand the abiotic and biotic
factors contributing to sugar maple health. Soil moisture deficiency or excess, highway deicing salts, and
extreme weather events including late spring frosts, midwinter thaw/freeze cycles, glaze damage, and
atmospheric deposition are the most important abiotic agents. Defoliating insects, sugar maple borer
(*Glycobius speciosus*), Armillaria *root disease, and injury from management activities represent important
biotic factors. Studies of sugar maple declines over the past four decades reveal that nutrient deficiencies of
magnesium, calcium, and potassium; insect defoliation; drought; and* Armillaria *were important predisposing,
inciting, and contributing factors in sugar maple declines. Forestland managers can contribute to sustained
health of sugar maple by choosing appropriate sites for its culture, monitoring stress events, and examining soil
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Sugar maple (*Acer saccharum*) is a keystone species in the forests of the northeastern and midwestern United States and eastern Canada. Often called hard maple or rock maple, its wood is well known as a source of lumber for furniture; its sweet sap is used to produce maple syrup; its flaming orange and yellow fall foliage is a source of enjoyment to everyone; and the stately trees line both rural roads and urban streets (Houston 1999). Because of its economic and social importance, sustained health of sugar maple is an important issue in both managed and unmanaged forests. Surveys conducted since 1989 in the northeastern United States and eastern Canada by the joint United States–Canadian North American Maple Project (NAMP) health monitoring network generally have shown that sugar maple is healthy throughout its range. During the past four decades, sporadic declines of sugar maple have occurred in Ontario and Quebec, Wisconsin, Vermont, New York, and Pennsylvania (Millers et al. 1989, Kolb and McCormick 1993, Long et al. 1997). Declining trees are characterized by a slow loss of crown vigor, dieback of fine twigs, and reduced radial increment over a period of years, frequently ending in death. Each decline event has

been the subject of intense research, but because the declines typically have been ephemeral, it has been difficult to fully understand the causes of sugar maple decline. The most recent decline was in Pennsylvania and was the impetus for a series of research studies to determine the causes of sugar maple decline (Kolb and McCormick 1993, Long et al. 1997, Bailey et al. 1999, Drohan et al. 1999, Wargo 1999, Horsley et al. 2000, Marcais and Wargo 2000).

In this article, we review the range and habitat requirements of sugar maple. We consider the impacts of abiotic and biotic stressors and damaging agents on sugar maple health and summarize research on decline phenomena throughout the eastern United States and Canada. Finally, we consider our own research, offer a working hypothesis for sugar maple decline, and suggest some implications for forest management.

Range and Habitat Requirements

Growing on approximately 31 million ac in the United States, the native range of sugar maple extends from the eastern edge of the prairies in Minnesota, Iowa, Missouri, and Kansas, and eastward across southern Canada to the Maritimes. In the United States, sugar maple is found in all of the New England, middle Atlantic, and midwestern

states and at high elevations in the Appalachian Mountains as far south as Tennessee (Godman et al. 1990). Small outlier communities occur further south and in South Dakota. The species is long-lived; individual trees and stands reach 300 to 400 years of age.

Sugar maple grows best in cool, moist climates. Its presence is limited by low temperature on the northern edge of its range; in the southern portion of its range, sugar maple is found primarily in cool, moist, high elevation areas of the Appalachian Mountains. Sugar maple is sensitive to both drought (Skilling 1964, Westing 1966) and excessive soil moisture (Ward et al. 1966). The species occurs on soils with a range of textures, pH and fertility, though best development occurs on loamy soils with slightly acid to neutral pH (Leak 1978, 1982, Auchmoody 1987, Godman et al. 1990, Whitney 1990, 1999, Nyland 1999).

The ability of sugar maple to complete its life cycle on a wide range of sites is reflected in its presence and abundance in pre-European settlement forests. Analysis of early land survey records shows that although sugar maple was abundant throughout the region, it seldom accounted for more than 15% of witness trees (Whitney 1999). Its greatest abundance probably occurred in hemlock (*Tsuga canadensis*)–northern hardwood [sugar maple–American Beech (*Fagus grandifolia*)–yellow birch (*Betula alleghaniensis*)] forests of northern Wisconsin and Upper Peninsula of Michigan where sugar maple sometimes accounted for more than 50% of the trees. Sugar maple was abundant on alkaline, carbonate containing till soils in northeastern Ohio and on calcareous till soils south of Lake Ontario in New York (Marks and Gardescu 1992, Seischab 1992). Sugar maple was a prominent species across a wide range of soils in the western Adirondack Mountains of New York and in Vermont and New Hampshire (Cogbill 2000). Its greatest abundance in this area was on high carbonate till soils in northern Vermont (Siccama 1971, Cogbill 2000). South of the Wisconsin glacial boundary on the Allegheny Plateau in northwestern Pennsylvania and southwestern New York where residual soils were more acidic and sugar maple typically was less abundant, the species was strongly associated with better drained, coarser textured, sandstone-derived soils and with thick deposits of "non-rubbly sandy loam to silt loam soils" on the plateau top (Goodlett 1954, Whitney 1990). Goodlett (1954) reported the presence of large, old sugar maple in the summit physiographic position on unglaciated plateau sites. Plateau tops/summits are the nutritionally poorest sites in this landscape (Ciolkosz et al. 1989). On the adjacent glaciated Allegheny Plateau in southwestern New York, sugar maple was found on all of the major soils and associated parent materials in the region, including glacial till and outwash, deltaic sands, and glacial lake sediments (Seischab 1992). Further south in the Ridge and Valley Province of central Pennsylvania, sugar maple was associated with alluvial soils of floodplains (Whitney 1982) and calcareous soils on valley floors (Abrams and Ruffner 1995). Thus, factors in addition to nutrition seem to determine the long-term occurrence of sugar maple within its geographic range.

Much of the presettlement forest was cleared by European settlers for agriculture during the eighteenth, nineteenth, and early twentieth centuries, or by industrial loggers for wood products. Subsequent land abandonment usually resulted in recolonization by the same species, though often in different proportions than in the presettlement forest. In postsettlement forests of the northeastern and Great Lakes states, sugar maple abundance typically was similar to or greater than that in presettlement forests (Whitney 1990, 1999, Abrams and Ruffner 1995, Cogbill 2000). In contemporary forests, sugar maple is an important component of six forest cover types: sugar maple–American beech–yellow birch, sugar maple–basswood (*Tilia americana*), sugar maple, black cherry (*Prunus serotina*)–sugar maple, red spruce (*Picea rubens*)–sugar maple–American beech, and American beech–sugar maple; it is an associate in 17 additional cover types (Eyre 1980).

Stressors and Damaging Agents

Sugar maple is affected by a variety of abiotic and biotic agents that cause loss in economic value by reducing tree vigor and causing root, stem, and crown damage, or tree mortality. Individually, most agents have a limited impact on trees in a local area, though under certain circumstances some stressors have the potential to cause health problems over a wider area.

Abiotic Factors

Soil moisture deficiency or excess, highway deicing salts, and extreme weather events including late spring frosts, midwinter thaw/freeze cycles, glaze damage, and atmospheric deposition are the most important abiotic agents affecting sugar maple.

Soil Moisture Deficiency or Excess. — Sugar maple grows poorly on dry, shallow soils and typically is not found on wet sites such as swamps (Godman 1965, Godman et al. 1990). Accounts of unusual sugar maple mortality in the first half of the twentieth century frequently were associated with prolonged drought (Westing 1966, Millers et al. 1989). Severe drought in the late 1950s in Wisconsin (Skilling 1964) and in the mid-1960s in Massachusetts (Mader and Thompson 1969) was one of several factors associated with unusual levels of sugar maple dieback and mortality. In Pennsylvania, Kolb and McCormick (1993) suggested that severe drought in 3 of 5 yr in the mid-1960s may have initiated a decline in sugar maple health that was not evident until the early to mid-1980s. Using tree ring analysis, Payette et al. (1996) showed that drought was one of several factors that could be associated with reduced growth and dieback of sugar maple in southern Quebec in the 1980s. Only a few studies have separated drought effects from those of other factors. In a manipulative study, Skilling (1964) showed that reduction in soil moisture by interception of precipitation from June to August during three consecutive years reduced shoot growth, but had little effect on branch dieback unless more than 50% of the precipitation was withheld. Robitalle et al. (1995) found that superficial winter soil freezing followed by a single summer of drought increased foliage transparency of sugar maple trees, but did not result in crown dieback.

Excess soil moisture also reduces tree vigor. Soil-site conditions that lead to impeded drainage reduced root growth and were correlated with increased incidence of *Fusarium* stem cankers in sugar maple (Ward et al. 1966).

Highway Deicing Salts.—Use of highway deicing salts has been associated with crown dieback and mortality of sugar maple trees along urban streets and rural highways (Westing 1966). Sugar maple is intolerant of heavy salt applications typically used for winter highway deicing in northern areas (Shortle and Rich 1970). Trees within about 9 m of the roadway are most affected and frequently display premature leaf coloration, leaf scorch, crown dieback, and tree mortality (Lacasse and Rich 1964). Trees in these high use corridors often are subject to other types of abuse and damage, as well.

Extreme Weather Events.—Late spring frosts sporadically occur throughout the range of sugar maple and may affect trees in a local area. Young partially expanded leaves are killed, requiring a large expenditure of carbohydrates to refoliate the tree. Thus, frost damage at this time of year has an effect similar to a late spring insect defoliation (Hendershot and Jones 1989). Most trees seem to accommodate a single defoliation of this sort without lasting effects, as long as it is not accompanied by other large carbohydrate-demanding stresses such as insect defoliation of the new leaves (Wargo 1999).

Unseasonal midwinter thaws followed by deep soil freezing (≥40 cm) occasionally have occurred, particularly in the more northern areas of the sugar maple range (Auclair et al. 1997). The most recent incidence of this extreme weather condition occurred in southern Quebec in February 1981. Auclair et al. (1992) suggested that root breakage, xylem cavitation, and subsequent reduced water uptake resulting from deep soil freezing may have caused sugar maple dieback and mortality in this region (Auclair et al. 1992). Indeed, in a manipulative experiment, Robitalle et al. (1995) demonstrated that deep soil freezing (≥40 cm) increased crown transparency and fine twig dieback, while superficial freezing (≤ 20 cm) produced only ephemeral increases in crown transparency. However, all instances of midwinter thaw/freeze cycles have not been accompanied by dieback symptoms (Auclair et al. 1997). Moreover, insect defoliations in the region from 1979–1982 followed by drought in 1983 make it difficult to determine the role of these extreme weather events alone on sugar maple health (Payette et al. 1996).

Ice (or glaze) damage to northeastern forests is more frequent than one might presume. Glaze is the clear layer of ice formed when super-cooled water freezes on the surface of objects (Smith 2000). According to United States Weather Bureau records, from 1900 to 1960 glaze storms occurred at the rate of 2–8 events per decade in northeastern and midwestern states (Smith 2000). The most recent ice storm occurred in January 1998, when nearly 7 million ha of forestland in northern New York, Vermont, New Hampshire, Maine, Ontario, Quebec, and the Canadian Maritimes were damaged. On a local basis (10s of ha), damage varied from little to severe; average crown loss varied from 0 to 64%. Sugar maple was most heavily damaged in Maine and Quebec (Miller-Weeks and Eagar 1999). The degree of injury/damage from ice storms depends on topography, forest composition, tree size and crown position, and meteorological conditions. Sugar maple is less susceptible to glaze damage than some of its northern hardwood associates and has been classified as susceptible to resistant in various studies of ice storm damage; large trees seem to be the most severely damaged by ice (Smith 2000). In the short term, branch breakage stimulates outgrowth of dormant buds to form a new crown and exposed areas of the bole may be killed by sunscald, caused by the increase in intense sunlight and temperature. Though sugar maple is capable of forming a new crown, it is less effective than many of its associates, and it is more sensitive to sunscald (Godman 1965). Experience of land managers suggests that trees which have lost >75% of their crown are not likely to survive; 50–75% crown loss puts trees at risk of mortality from other stressors (Smith 2000). In the longer term, sapwood and heartwood rotting and discoloring fungi introduced where branches have been broken or bark killed may grow slowly for decades (Spaulding and Bratton 1946). Trees weakened by glaze damage also become susceptible to invasion by the *Armillaria* root disease fungus that ultimately can kill the tree (Wargo 1999).

Atmospheric Deposition.—During the 1980s, concern arose that atmospheric deposition, especially acidic deposition of nitrate and sulfate, was causing sugar maple decline in Ontario, Quebec, and Vermont (Vogelmann 1982, McLaughlin et al. 1985, Vogelmann et al. 1985, Carrier 1986). Sugar maple was declining at a number of sites where soils were classified as susceptible to acidification. Examples of such sites included the Muskoka area of southern Ontario, the Bauce region of southern Quebec, and Camel's Hump Mountain in Vermont. Factors such as drought, defoliation, and climatic effects were dismissed, and attention was focused on direct effects of acid deposition. Subsequently, it was realized that decline did not occur as a direct result of acid deposition. In contrast, to the extent that acid deposition plays a role in sugar maple decline, it seems to be through acceleration of base cation loss (Ca, Mg, K) in soils susceptible to acidification in the long term (Manion and Lachance 1992, Houston 1999, Drohan and Sharpe 1999, McLaughlin and Wimmer 1999).

Biotic Factors

Sugar maple is affected by a variety of rots, cankers, wilts, defoliators, borers, sucking insects, scale insects, bud miners, and diseases (Godman et al. 1990).

Foliage Consuming Insects.—Foliage-consuming insects have the greatest potential for negative effects on large trees over a wide geographic area. Loss of foliage early in the growing season has a negative effect on nonstructural carbohydrates, particularly root starch reserves, which play a critical role in tree vigor (Parker and Houston 1971, Wargo et al. 1972, Wargo 1981a, b, c, Gregory and Wargo 1986, Gregory et al. 1986, Renaud and Maufette 1991, Wargo 1999). Root starch reserves are lowest early in the

growing season following leaf expansion. Very early season defoliations (April–May) frequently result in crown refoliation, but because trees still have nearly the whole growing season to photosynthesize, they are able to recover. When defoliations occur between late May and mid-July, the remaining growing season usually is not long enough to replenish starch reserves, thus trees have reduced starch reserves in the dormant season. Trees defoliated late in the growing season, from mid-July to August, are less likely to refoliate and usually are not damaged unless they are defoliated repeatedly for several years. Multiple defoliations from a combination of frost, insects, and fungi (e.g., anthracnose *Discula campestris*) in the same or sequential years have particularly serious effects on carbohydrate reserves and have been associated with both crown dieback and mortality of sugar maple (Hall et al. 1999).

Defoliating insects are the most common insects attacking sugar maple. Though outbreaks of defoliating insects occur infrequently, sustained outbreaks have caused extensive growth loss, crown damage, and mortality to sugar maple trees over large areas of the northeastern and mid-western United States and eastern Canada (Giese and Benjamin 1964, Allen 1987, Kelly 1988, Bernier et al. 1989, Hendershot and Jones 1989, Bauce and Allen 1991, Gross 1991, Allen et al. 1992a, b, Kolb and McCormick 1993, Stout et al. 1995, Payette et al. 1996, Horsley et al. 2000). Forest tent caterpillar (*Malacosoma disstria*) has been associated with large-scale defoliations of sugar maple more than any other defoliator. Defoliations typically occur over a period of about 5 wk early in the growing season. Other early season defoliators associated with large-scale defoliation of sugar maple include: fall cankerworm (*Alsophila pometaria*), elm spanworm (*Ennomos subsignarius*), and Bruce's spanworm (*Operophtora bruceata*). Saddled prominent (*Heterocampa guttivitta*) is an important late season defoliator of sugar maple; in many instances, heavy saddled prominent defoliation (e.g., in July) causes refoliation (Allen 1987).

Pear thrips (*Taeniothrips inconsequens*) is an exotic sucking insect usually considered a pest of fruit trees (Hebert 1992, Kolb et al. 1992). However, during the decade following its positive identification in forest environments of the northeastern United States in 1980, pear thrips caused extensive damage to sugar maple for several years. The insect emerges from the soil early in the spring and attacks leaf and/or flower buds. Symptoms of damage to sugar maple included tattered, chlorotic, undersized leaves. Synchrony between thrips emergence and budburst and temperature conditions during budburst contribute to the severity of thrips damage (Kolb and Teulon 1991, 1992). Even a small number of thrips can cause substantial damage to sugar maple leaves and flowers if thrips emergence and budburst overlap and if temperatures are cool, resulting in an extended period of leaf expansion. In 1988 and 1989 when sugar maple was most seriously affected, more than 400,000 ha were defoliated in Pennsylvania, and there were serious defoliations of sugar maple in Massachusetts and Vermont, as well; defoliations were severe enough to cause sugar maple trees to refoliate, but in many instances the growing season was long enough for trees to recover, and little dieback or decline resulted from these defoliations. In some Pennsylvania stands, however, thrips defoliation was associated with reduced root carbohydrate storage, increased crown transparency and reduced growth rate (Kolb et al. 1992, Kolb and McCormick 1993).

Sugar Maple Borer.—Sugar maple borer (*Glycobius speciosus*) is an important secondary insect that invades the subcortical area on the lower 5 m of the stem of low vigor trees (Talerico 1962, Allen 1987). Attacked trees usually are recognized by transverse areas of raised bark formed by callus tissue around the wounded stem or exposed wood from bark loss with meandering diagonal larval galleries. Larval galleries may extend as much as 10–15 cm into the sapwood (Newton and Allen 1982). While trees usually are not killed, affected trees may have lower sap yields and greater wood defect; borer-damaged trees also are more vulnerable to breakage by wind. The burrowing larvae of the sugar maple borer form transverse, longitudinal, and spiral galleries that partially girdle the tree and may result in loss of a portion of the crown. Moreover, affected stems usually contain decayed, twisted grain associated with wound healing, and mineral stain resulting from the accumulation of antifungal compounds in the vicinity of borer wounds. Borer attacks usually begin in pole-size (15–28 cm dbh) trees. As many as one-quarter of the trees in forest stands and as much as one-third of the trees in sugarbushes may be affected by sugar maple borer in vulnerable stands (Allen 1987). The etiology of sugar maple borer attack presently is not well understood; maintenance of tree growth and vigor seems to be the best measure to reduce tree and stand vulnerability to attack.

Armillaria Root Disease.—Armillaria root disease historically has been considered an opportunistic disease of low vigor trees weakened by some other cause(s), though *Armillaria mellea* is known to attack healthy trees (Wargo and Harrington 1991, Houston 1999). Pathogenicity toward a particular host depends on the species of *Armillaria*. *Armillaria calvescens* frequently has been associated with sugar maple, though other species sometimes are found (e.g., *Armillaria gemina, Armillaria mellea*) (Marcais and Wargo 2000). While the growth requirements of various *Armillaria* species and etiology of disease development are not well understood for individual species, composite information for *Armillaria* spp. gives some insight into its potential effect on sugar maple.

Armillaria species are able to grow on a variety of carbon sources; glucose, for example, from the hydrolysis of starch, is a preferred source (Garraway et al. 1991). Addition of ethanol, a product of anaerobic respiration, to glucose produces prolific mycelial growth. Amino acids are the preferred source of nitrogen. And, like other fungi, *Armillaria* has relatively high requirements for magnesium, phosphorus, potassium, sulfur, and to a lesser extent calcium. Soil pH affects the ability of *Armillaria* to absorb nutrients; both pathogenicity and aggressiveness are greater on low pH soils (Garraway et al. 1991). *Armillaria* growth is inhibited by some phenolic compounds, for example gallic acid (Wargo 1980).

Trees normally defend themselves against attack by potentially pathogenic organisms, though this is energetically expensive. Phenolic compounds and other preformed natural products provide chemical defense against invasion. The outer bark of tree roots apparently is not an important impediment to *Armillaria* species that are aggressive pathogens. Rhizomorphs attach to the surface of the outer bark and grow through it to the inner bark where they colonize and kill inner bark, cambium and outer wood tissue. However, for species of *Armillaria* that are stress-induced pathogens, bark does act as a barrier to infection; colonization rhizomorphs form on the outer bark and mycelium "challenges" the inner bark tissues. In this instance, the mycelium is prevented from colonizing the inner bark and cambium until the host is sufficiently stressed and defenses are weakened (Morrison et al. 1991, Wargo and Harrington 1991).

Both drought and defoliation affect root carbohydrate and nitrogen levels; starch is hydrolyzed to produce reducing sugars, including glucose, and total amino nitrogen levels are increased (Wargo 1972). Moreover, in the presence of increased levels of glucose, the inhibitory activity of phenolic defensive compounds such as gallic acid is reduced (Wargo 1980). If stress continues, *Armillaria* may overwhelm the host's defenses and kill the tree; however, if stress diminishes and overall tree vigor improves, *Armillaria* may again be kept at bay. In a recent study, Marcais and Wargo (2000) showed that the addition of dolomitic limestone to a magnesium and calcium-poor site resulted in increased growth and vigor of both *Armillaria* and sugar maple trees and a decrease in infection of sugar maple roots, presumably due to the greater increase in vigor of sugar maple.

Management Activities.—Management activities may improve, have no effect, or reduce sugar maple health. The NAMP suggested that sugarbush management activities have no effect on health (Allen et al. 1999). Between 1989 and 1997, the NAMP surveyed the health of sugar maple trees annually in sugarbush and nonsugarbush stands in the northeastern and midwestern United States and eastern Canada (ten U.S. states and four Canadian provinces). Trees in both dominant/codominant and intermediate/suppressed crown classes were compared. Background mortality rates for the time period ranged from: 0.1–1.8% yr^{-1} for dominant/codominant trees in sugarbushes, 0.0–0.8% yr^{-1} for dominant/codominant trees in nonsugarbushes, 0.3–3.0% yr^{-1} for intermediate/suppressed trees in sugarbushes, and 0.1–4.7% yr^{-1} for intermediate/suppressed trees in nonsugarbushes. In most states and provinces there was no significant difference between mortality in sugarbushes and nonsugarbushes (Allen et al. 1999).

During a similar time period (1990–1995), Long (unpublished) compared the mortality of dominant/codominant sugar maple on plots in uncut and thinned forest stands in northwestern Pennsylvania installed using NAMP protocols. He found that thinned stands managed for timber production had annual mortality rates 34% below those of uncut stands.

Houston et al. (1989) point out that frequent human activity in sugarbushes may contribute to higher levels of damage and mortality. Soil compaction and stem and root injury due to movement of sap-collecting equipment or animal grazing provides an avenue for entrance of wood discoloring and decay organisms. Overly aggressive tapping, particularly of stressed trees, and improper tapping methods, also can contribute to reduced tree health. Long's (unpublished) study suggests that thinning appears to promote growth and health by removing trees that might otherwise have died and by increasing resources to trees that remain (Smith 1986, Stout et al. 1995, Nowak 1996). Overthinning that results in too much sun exposure to residual stems may result in sunscald and introduction of pathogenic organisms. And as in sugarbushes, stem and root damage and soil compaction caused by movement of heavy equipment on vulnerable soils may allow entrance to wood discoloring and decaying organisms.

Sugar Maple Decline

Dieback, or loss of a portion of the crown, is a general response of trees to stress; trees die back to recover balance between resource requirements of the crown and the ability of the stem and roots to supply those requirements. It is clear from the previous section that some abiotic and biotic factors have the capacity to cause dieback or mortality of sugar maple trees as single agents. For example, if defoliation is severe enough or prolonged enough, some trees will die back and some ultimately will die due to the effect of defoliation alone.

The concept of a *decline* addresses situations where dieback or mortality cannot be attributed to a single agent. Declines are characterized by a gradual loss of tree vigor and eventual death. Manion (1991) defines decline as, "an interaction of interchangeable, specifically ordered abiotic and biotic factors to produce a gradual general deterioration, often ending in death of trees." Several factors may interact to produce the final outcome, and these factors may be different in different situations. Manion (1991) used the terms predisposing, inciting (or triggering), and contributing to describe the factors involved in tree decline. Houston (1992) characterized the decline process as a series of stress and tree response reactions that cause successive alterations in tree tissue. Houston's (1999) conceptual model is based on 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 factors reduces resistance to invasion by opportunistic, secondary-action organisms that result in death of tissues— sometimes of trees."

Houston's (1992) concept of decline arose from an episode of sugar maple decline on about 4,000 ha of commercial forestland in Florence County, Wisconsin. In 1957, foresters reported the sudden deterioration of crowns and death of thousands of sugar maple trees and saplings in mixed northern hardwood stands (Giese et al. 1964). They referred to this phenomenon as "maple blight." An interdisciplinary team of scientists studied the maple blight situation to determine its causes. This was the first comprehensive investigation of a sugar maple decline. Previous declines of sugar maple had

been documented as far back as 1912–1913, but none had received intensive investigation (Westing 1966, Millers et al. 1989). The team found that during the 10 months of 1956–1957 preceding mortality, rainfall had been 21 cm below normal (Skilling 1964). Subsequently, in 1957, affected stands were defoliated by a complex of insects at different periods of the growing season. These included two leaf rollers, *Sparganothus acerivorana* and *Acleris chalybeana*, and the maple webworm (*Tetralopha asperatella*) (Giese and Benjamin 1964). Defoliation was followed by aggressive attack of damaged trees by the opportunist fungus, *Armillaria mellea* (sensu lato) (Houston and Kuntz 1964). Mortality occurred during 1957 and 1958, and then began to subside in 1959 with the collapse of defoliator populations. According to Houston's (1992) model, drought and defoliation stress altered resistance of sugar maple tissue resulting in invasion by the opportunist, *Armillaria mellea*. In later studies (cited above in the section on *Armillaria*), Houston and others confirmed the defoliation stress/*Armillaria* association and clarified the biochemical basis for the lowered resistance of defoliation-affected tissues to attack by *Armillaria*.

Since the Wisconsin maple blight episode, there have been a number of other well-documented sugar maple declines. Sugar maple declines have occurred in: Massachusetts in the 1960s (Mader and Thompson 1969); Ontario in the 1970s (Hendershot and Jones 1989, Gross 1991); Quebec, New York, and Vermont in the 1980s (Bernier and Brazeau 1988a, b, c, Kelly 1988, Bernier et al. 1989, Hendershot and Jones 1989, Bauce and Allen 1992, Cote et al. 1995, Ouimet and Camire 1995, Wilmot et al. 1995); and Pennsylvania in the 1980s and 1990s (Kolb and McCormick 1993, Long et al. 1997, Horsley et al. 2000). While combinations of defoliations, droughts, and extreme weather events were common themes in all of these declines, foliar and soil nutrient sampling in the more recent declines began to reveal additional factors. Nutrient deficiency, particularly of base cations (Ca, Mg, K), seemed to be a common thread. Declines seemed to be more common on base poor soils. The recent decline in Pennsylvania provides a case in point (Horsley et al. 2000).

In the early to mid-1980s, forestland managers in the northwestern and north central Pennsylvania portions of the Allegheny Plateau began to notice unusual levels of crown dieback and mortality of sugar maple in stands on unglaciated sites on upper slopes above about 550 m elevation; stands on lower slopes did not decline. Affected areas lay just south of the terminal moraine of the Wisconsin glacial advances of 12,000 to 21,000 yr ago. Soils at unglaciated sites frequently are highly weathered Ultisols and have low base saturation, whereas soils on glaciated portions of the Plateau are Inceptisols and have higher base saturation. Tree ring analysis on declining and nondeclining sugar maple suggested that basal area increment of trees that declined began to decrease, compared with trees that did not decline, after a 5 yr period in the mid-1960s with 3 yr of severe summer drought (1962, 1963, 1966) and 2 yr of insect defoliation (1964, 1965) (Kolb and McCormick 1993). During the decades of the 1980s and 1990s, there were additional episodes of defoliation, and droughts occurred in 1988 and 1991. For example, detailed

records on the 200,000 ha Allegheny National Forest show that between 1984 and 1996 trees were subjected to 1 to 5 moderate to severe defoliations and severe droughts that occurred in 1988 and 1991. Kolb and McCormick (1993) also found that foliar concentrations of Ca and Mg were well below and Mn was well above those of presumably healthy trees observed by other researchers and reported in the literature.

In a study beginning in 1985 at four high-elevation (677–716 m), unglaciated sites similar to those investigated by Kolb and McCormick (1993), dolomitic limestone was applied to the soil surface at the rate of 22.4 megagrams ha^{-1} (Long et al. 1997). Liming increased soil pH and exchangeable Ca and Mg in the upper horizons, while exchangeable Al and Mn decreased. After a lag of 3–8 yr, there were significant increases in survival, crown vigor, diameter and basal area growth, and flower and seed crop production for sugar maple on limed compared with unlimed areas. None of these benefits occurred for American beech or black cherry trees at the same sites. Increases in levels of Ca and Mg and decreases in Al and Mn also were reflected in the foliar chemistry of sugar maple. Evaluation of carbohydrate status in limed and unlimed plots showed that limed sugar maple trees consistently had higher levels of root storage carbohydrates than unlimed trees (Wargo 1999); moreover, postmortality assessment showed that most recently dead sugar maple had been colonized by *Armillaria* (Marcais and Wargo 2000). Positive responses of sugar maple growth and vigor to base cation additions also have been shown in studies in Vermont (Wilmot et al. 1996) and Quebec (Cote et al. 1993, 1995, Moore et al. 2000).

The dramatic species-specific effects of lime on sugar maple in Pennsylvania prompted further investigation to determine the distribution of Ca, Mg, Al, and Mn in the landscape (Horsley et al. 2000). In 1995 and 1996, 43 stands were located along topographic gradients at 19 sites on glaciated and unglaciated portions of the Allegheny Plateau in northwestern and north central Pennsylvania and southwestern New York. Health of dominant and codominant sugar maple trees, foliar chemistry, defoliation and management history, and stand characteristics were evaluated in each stand. Using percent dead sugar maple basal area as the measure of health, the most important factors associated with sugar maple health were foliar concentration of Mg and Mn and defoliation history. Declining stands had ≤700 mg kg^{-1} Mg, ≥2000 mg kg^{-1} Mn, and ≥2 moderate to severe defoliations in the 10 yr preceding health evaluation. All moderately to severely declining stands were located on the upper slopes of unglaciated sites in summit, shoulder, or upper backslope physiographic positions. The lowest foliar Mg, highest foliar Mn, and the highest number and severity of defoliations were associated with these physiographic positions. Stands on glaciated sites and the lower slopes of unglaciated sites were not declining.

Differences in base cation nutrition may be explained by the following model: due to the age (>500,000 yr) and long-term geologic weathering of these soils, few weatherable minerals are located within the rooting zone on unglaciated

sites (Bailey et al. 1999). Weatherable minerals are present within the soil profile of unglaciated sites, but they are located well below the rooting zone and thus are unavailable to trees growing on the summit or upper slopes. High levels of nitrate and sulfate deposition received in northwestern Pennsylvania (Lynch et al. 1997) contribute to low Mg and Ca availability because they accelerate base cation loss (Knoepp and Swank 1994, Bailey et al. 1996, Likens et al. 1998, Markewitz et al. 1998, Swistock et al. 1999) presumably expanding the area of marginal base cation sites. Trees growing on mid- or lower slopes may receive weathering products such as Mg or Ca via water flowpaths that bring weathering products from the deeper soil layers or bedrock to the rooting zone. By contrast, soils on glaciated sites derived from relatively recent glacial erosion contain weatherable minerals within the rooting zone of both upper and lower slope sites.

Expansion of these studies to an additional 40+ sites in northwestern, central, and eastern New York, Vermont, and northern New Hampshire provided complementary data (Hallett et al. pers. comm.). While all of these additional sites were glaciated, the quality of till materials varied substantially resulting in a spectrum of sites with base cation nutrients similar to those found in northwestern and north central Pennsylvania and southwestern New York. Defoliation stress levels were, however, somewhat lower, and sugar maple health was commensurately higher. Moreover, Ca seemed to be more closely related to sugar maple health than Mg.

Taken together, our work and that of others suggests that sugar maple decline results from an interaction between mineral nutrition and stress. The roles of Mg and Mn nutrition and defoliation (and drought) stress in plant carbohydrate economy suggest that root storage carbohydrates may be reliable indicators of overall tree condition since they serve to integrate the various factors that incite sugar maple decline (Wargo 1999). The roles of Mg and Mn may be linked to their physiological and biochemical functions and to interactions between them. Mg deficiency, due to uptake inhibition by other cations including K, NH_4, Ca, Mn, and H, is well known in agriculture; both Mg deficiency and Mn excess have been associated with reduced leaf chlorophyll, net photosynthesis, and transport of leaf carbohydrates (Maas et al. 1969, Marschner 1995). Field studies of sugar maple trees and seedlings corroborate these results. Trees with low foliar Mg and/or Ca had reduced foliar levels (mass basis) of chlorophyll (Liu et al. 1997) and lower net photosynthetic rate (Ellsworth and Liu 1994; Liu et al. 1997) than trees with higher foliar Ca and Mg. Ultrastructural evaluation of leaves and roots from field and greenhouse-grown seedlings with high foliar Mn showed evidence of chlorosis, foliar accumulation of starch, discrete electron-dense areas in chloroplast thylakoid membranes, and other abnormalities compared with those with low foliar Mn (McQuattie et al. 1999, McQuattie and Schier 2000). All of these effects lead to reduced production and transport of carbohydrates to storage sinks in the roots and elsewhere [for example, as observed by Wargo (1999) in unlimed sugar maple]. Furthermore, there is

abundant evidence that severe or multiple defoliation events that reduce crown area by >50% result in lower root storage carbohydrate levels (Wargo et al. 1972, Wargo 1981a, b, c, Gregory et al. 1986, Renaud and Mauffete 1991, Kolb et al. 1992, Wargo 1999). Defoliations that result in refoliation put an enormous demand on storage carbohydrates (noted earlier in the section on foliage consuming insects) and cause biochemical changes that may lead to invasion by *Armillaria*.

Management Implications

Forestland managers can take positive steps to maintain the health of sugar maple by choosing appropriate sites for its culture, monitoring stress events, and examining soil nutrition.

Choosing Appropriate Sites

Stress events such as droughts and defoliations are inevitable for long-lived species. Culture of sugar maple on the sites that most closely meet its growth requirements and discrimination against it on sites that are not suitable will increase the probability that it will remain healthy. Recent research suggests that sugar maple grows faster, is more resistant to attacks by stress-induced opportunistic organisms such as *Armillaria* (Marcais and Wargo 2000), and is more resilient to defoliation and drought events on mesic, loamy sites with effective rooting depth of 0.6–1 m and adequate nutrition, particularly of magnesium, calcium, and potassium (Auchmoody 1987, Cote et al. 1993, 1995, Ouimet and Camire 1995, Wilmot et al. 1996, Long et al. 1997, Nyland 1999, Horsley et al. 2000, Moore et al. 2000, Long et al. 2001). Thus, sites with soils that are excessively wet or dry, nutrient poor, or shallow are inappropriate for sugar maple. Other species are more suited to these sites and managers should discriminate against sugar maple during thinnings or other activities.

Knowledge of what constitutes optimum nutrition for sugar maple throughout its range presently is not complete. Soils with low calcium and/or magnesium have been reported throughout the northeastern United States and eastern Canada; soils with low potassium have been reported in portions of Ontario and Quebec (Ouimet and Camire 1995). Foliar analysis of presumably healthy dominant and codominant trees near the end of the growing season can provide an integrative index of tree nutritional status and potential for health and growth problems. While we found that foliar nutrient values of magnesium less than about 700 mg kg^{-1} and calcium less than about 5000 mg kg^{-1} were associated with sites containing declining trees (Horsley et al. 2000), others have found substantially higher values associated with sites containing fast growing, healthy sugar maple. Kolb and McCormick (1993) compiled the range of foliar nutrient values associated with presumably healthy sugar maple trees in the literature; potassium ranged from 5500–10,400 mg kg^{-1}, calcium from 5000–21900 mg kg^{-1}, and magnesium from 1100–4000 mg kg^{-1}. Cote et al. (1993) suggested optimum leaf nutrient concentrations of 7700 mg kg^{-1} for potassium, 1100 mg kg^{-1} for calcium, and 1400 mg kg^{-1} for magnesium. Lozano and Huynh (1989) have developed a set of Diagnostic Recom-

mendation Integrated System (DRIS) equations for estimating optimum sugar maple foliar nutrition based on an Ontario dataset.

Some soil series categorized as Ultisols may be marginal for sugar maple culture, and many Inceptisols and Spodosols have base saturation as low as Ultisols, though usually adequate for sugar maple growth. Alfisols represent the best quality soils and generally will produce adequate levels of magnesium, calcium, and potassium in sugar maple foliage. While soil maps produced by the Natural Resources Conservation Service and state geologic survey are useful tools for finding the general location of these soils, the maps are at inappropriate scales for guiding decisions at the stand level. Site-specific information is preferable. Where critical decisions need to be made, site-specific soils mapping and quality testing should be performed. Some efforts have been made to develop the use of herbaceous plants as site-specific indicators of site quality within the range of sugar maple in Canada and the Lake States (Spies and Barnes 1985, Kotar 1988, Ringius and Sims 1997). We are currently working on a system of herbaceous indicators of sugar maple site quality for the northeastern United States.

Monitoring Stress Events and Their Effects

Stresses such as droughts, midwinter thaw/freeze events, ice storms, and late spring frosts are difficult or impossible to forecast, and managers can do little to prevent them. When managers monitor and document stress events, however, they can take preventive stress suppression actions, particularly on soils with suboptimal nutrition, where sugar maple is more susceptible to stress. The effects of stressors on tree health can be determined by carefully observing changes in upper crown condition. Development of small leaves, early fall coloration, and dieback of fine twigs in the upper canopy are indicators of stress. Dieback usually starts at the outer tips of twigs and branches and progresses inward. A small amount of crown dieback, usually less than 10 or 15%, is normal; larger amounts indicate potential problems and should be monitored closely. Large lower branches that die from shading are not an indication of serious problems. By examining changing crown conditions, land managers can assess the severity of stress events.

Stresses, such as those associated with insect defoliation, may be preventable. Forest pest detection surveys conducted by the USDA Forest Service, State and Private Forestry, and forest pest management divisions of state natural resource organizations can give early warning of insect buildups. Managers can then combine this information with stress history and site nutrition information to increase the efficiency and effectiveness of pest suppression activities for sugar maple.

Supplementing Nutrition

During the past few decades, there has been some interest in the use of fertilizers to increase sugar maple growth or correct soil nutrient deficiencies. Much of this effort concentrated on the addition of nitrogen, phosphorus, or potassium fertilizers.

The work reviewed here suggests that from a health perspective, magnesium and calcium may be more important.

Presently, there are insufficient experimental results to recommend fertilization or other nutrient addition practices for sugar maple stands. However, it is useful to consider what has been learned from recent research in order to guide future practices. Information gathered from experimental lime applications reported in the literature suggests that application rates of dolomitic limestone for northeastern forest sites probably should range from 4.5–11 megagrams ha^{-1} (2–5 tons ac^{-1}); Long et al. (1997) observed some over-liming effects with 22.4 megagrams ha^{-1}. Until recently, magnesium and calcium were not recognized as nutrients limiting the health or growth of sugar maple. This probably occurred for several reasons: (1) Magnesium and calcium are not limiting to all northeastern tree species; for example, addition of 22.4 megagrams ha^{-1} (10 tons ac^{-1}) of dolomitic limestone did not influence health or growth of black cherry or American beech, even after 10 yr (Long et al. 1999). (2) The amount of magnesium and calcium applied (usually as dolomitic limestone) was insufficient; prescription of specific amounts of dolomitic limestone to apply must be determined in association with soil sampling and diagnostic foliar analysis. Applying too little lime can result in no detectable tree response, while applying too much lime can result in imbalance of other nutrients; for example, potassium and phosphorus. (3) Responses were evaluated too soon after lime application. When lime is applied to the soil surface, its dissolution and movement into the soil is very slow. Long et al. (1997) observed that while chemical characteristics of the 0–5 cm horizon changed significantly within 1 yr, 3 or more years were required to affect chemical characteristics in horizons >5 cm below the surface. Significant differences in crown vigor and basal area increment did not occur for 3 and 8 yr, respectively, after lime application. Large lime applications are likely to have long-lasting affects; 15 yr after lime application, there is no indication of reduced benefit to sugar maple (Long, pers. comm.). We do not at this time recommend fertilization or liming of sugar maple stands except on an experimental basis.

The information reviewed here coupled with findings from our own research shows that sugar maple decline disease is caused by a complex combination of factors and events which ultimately result in reduced health or even death for stands of trees across the northeastern United States. However, despite this complexity, forestland managers can take positive steps to maintain the health of sugar maple by choosing appropriate sites for its culture, monitoring stress events, and examining soil nutrition.

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