2001

Ecology and management of aspen: a Lake States perspective

D.T. Cleland

L.A. Leefers

D.I. Dickmann

L.G. Eskew

Recommended Citation

Cleland, DT, Leefers, LA, Dickmann, DI. 2001. Ecology and management of aspen: a lake states perspective. WD Shepperd et al (compilers). Sustaining Aspen in Western Landscapes: Symposium Proceedings. Proceedings RMRS-P-18. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, CO.

Ecology and Management of Aspen: A Lake States Perspective

David T. Cleland[1], Larry A. Leefers[2], and Donald I. Dickmann[2]

Abstract—*Aspen has been an ecologically important, though relatively minor, component of the Lake States (Michigan, Wisconsin, and Minnesota) forests for millennia. General Land Office records from the 1800s indicate that aspen comprised a small fraction of the region's eastern forests, but was more extensive on the western edge. Then Euro-American settlement in the 1800s brought land clearing, timber harvesting, and subsequent widespread wildfires that increased aspen-birch acreages considerably. Although aspen-birch acreage has declined since the 1930s, it remains the region's second most prevalent forest type. Aspen management is probably the most contentious issue confronting forest managers in the Lake States.*

Concerns regarding the status of early successional forest communities have emerged nationally. Across the United States, many disturbance-dependent ecosystems including prairies, savannahs, barrens, and early successional forests have declined in recent decades. These declines are due in part to nearly a century of fire suppression, as well as land conversion, rural development, and grazing. However, loss of late successional communities is also of national concern. Thus, both ends of the successional spectrum, young early successional forests and old late successional forests, have declined due to human activities.

Quaking aspen (*Populus tremuloides*) and bigtooth aspen (*Populus grandidentata*) are among the premier early successional species in the United States. Quaking aspen is the most widely distributed tree in North America (figure 1), whereas the distribution of bigtooth aspen is confined primarily to the northeastern United States and the Great Lakes Region (figure 2). These two species, and their less common eastern associates, paper and gray birch (*Betula papyrifera* and *B. populifolia*), are often characterized as the aspen-birch forest type.

Aspen and aspen-birch forests occur in 27 states within the United States, extending from Alaska to New Mexico in the west and from Maine to West Virginia in the east. The greatest acreage occurs in the eastern states of Minnesota, Wisconsin, Michigan, and Maine, and in the intermountain and mountain states of Utah and Colorado. Combined, these six states have 86% of the aspen and aspen-birch acreage in the lower 48 states. Based on the most recent Forest Inventory and Analysis (FIA) inventories, there are approximately 20.3 million acres of aspen and aspen-birch forest types (predominantly aspen) in the lower 48 states. These types comprise 7% of the nation's forest lands (298.1 million acres of land stocked at least ⅙ with trees) and 10% of the nation's timberland (198.1 million acres of more productive forest land; Powell et al. 1993). The Lake States (Michigan, Wisconsin, and Minnesota) are notably the stronghold of the aspen-birch forest type, with 12.9 million acres, or 63%, of the total acreage, in the lower 48 states.

Within the Lake States, there are 51.9 million acres of forest lands, of which 49.0 million acres are considered timberland. Recent FIA data indicate that the aspen-birch forest type covers 6.3 million, 3.4 million, and 3.2 million acres of

[1]North Central Research Station, Forestry Sciences Laboratory, USDA Forest Service, Rhinelander, WI.
[2]Michigan State University, Department of Forestry, East Lansing, MI.

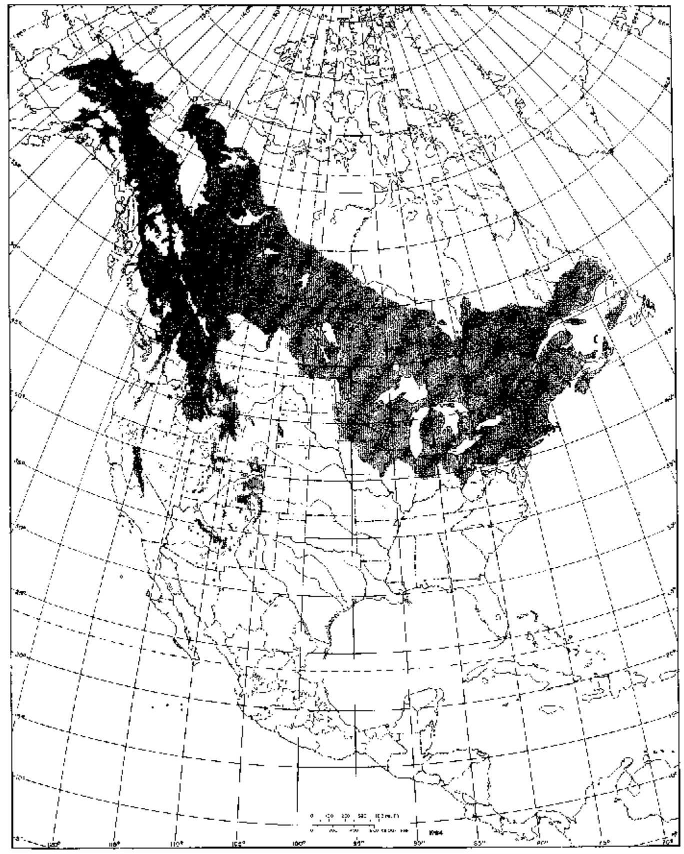

Figure 1—Range map for quaking aspen (*Populus tremuloides*) (source: Burns and Honkala 1990).

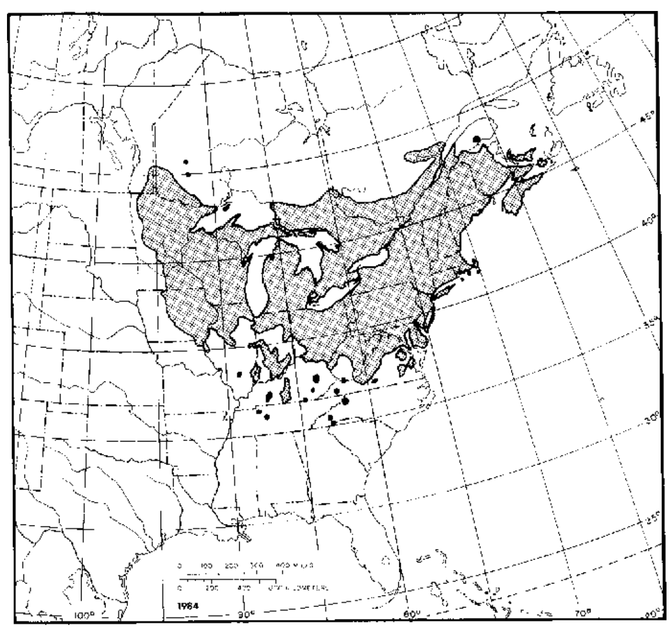

Figure 2—Range map for bigtooth aspen (*Populus grandidentata*) (source: Burns and Honkala 1990).)

Minnesota, Wisconsin, and Michigan, respectively (Leatherberry and Spencer 1996; Miles et al. 1995; Schmidt 1997). The extent of forests is important, but ownership patterns are as well—ownership provides insights regarding management options. In the Lake States, 62% of the timberlands are in private ownership, dominated by nonindustrial private landowners.

Public ownership is also important across the region, and each state's public ownership has evolved differently since the turn of the 20th century. "The lands nobody wanted" 100 years ago became the extensive Lake States public lands, intermixed with private lands (Shands and Healy 1977). Minnesota's public lands are, in descending order of magnitude, state forests, county and municipal forests, and national forests. Wisconsin's public lands are mostly county and municipal forests followed by national and state forests. In Michigan, state forests and national forests are the principal public ownerships; there are few county forests.

The purpose of this paper is to present a Lake States' perspective on aspen ecology and management, thereby providing a broader comparative context for conditions in the western United States. To this end, we describe the historical evolution of the aspen forests in the Lake States, contemporary aspen trends, and management options for aspen in a multiownership/multiobjective environment.

Historical Role of Aspen in the Lake States

Today's acreage of aspen in the Lake States is largely due to the extensive disturbance rendered by turn-of-the-century logging and fires, which greatly favored disturbance-dependent species. Understanding the ecological and social importance of aspen in the Lake States therefore requires a historical perspective.

Ecological Change

During the early part of the Holocene (ca. 10,000 YBP, years before present), following the last series of glacial advances and retreats, the forests of the Lake States underwent dynamic transformations in response to climate change and biological processes, including species migration and forest succession. Broad-scale changes occurred over thousands of years due to the long-term response of vegetation to variations in temperature, moisture, and air mass patterns (Webb et al. 1993). Most of the taxa present in the Lake States today had migrated into the region by 6,000 YBP, with virtually all taxa except hemlock established by 3,000 YBP (Brubaker 1975; Davis 1981; Davis et al. 1993; Frelich 1995; and Webb et al. 1993).

Although the migration of species into the region stabilized at least 3,000 years ago, species' distributions have continued to shift when viewed at a landscape scale (measured in tens of thousands of acres). The nature and rate of these changes have been regulated by interactions of minor climatic fluctuations like the Little Ice Age (600–150 YBP), natural disturbance regimes, insect and disease outbreaks, landform-controlled soil, topographic and hydrologic conditions (Host et al. 1987), and species-specific reproductive strategies and life expectancy.

Mesophilic, wind-driven ecosystems primarily supporting long-lived tree species (e.g., sugar maple, yellow birch, hemlock) historically changed slowly over centuries due to fine-scale blow-downs and relatively rare broad-scale catastrophic storms [Canham and Loucks 1984; Frelich and Lorimer 1991; Runkle 1982]). These "asbestos" forests seldom burned, and exhibited a repeating yet shifting steady state of fine-scaled mosaics of species whose overall proportions remained essentially constant (Borman and Likens 1979). These unevenaged, mesic forests were characterized by supercanopies of trees that were centuries old.

The age and landscape structure of mesophylic forests contrasted with fire-dependent ecosystems, such as spruce-fir, aspen-birch, and red or jack pine forests. These pyrophilic ecosystems were typically evenaged, and were composed of both long-lived tree species (e.g., white and red pine) and short-lived species (e.g., jack pine, aspen, white birch). Locations and sizes of forest patches changed over time due to disturbances from wildfire and burning by indigenous people; changes were more frequent and dramatic than in the mesic hemlock-hardwood forests. Cover types were replaced in patches of hundreds to thousands of acres within several decades to a century or more. Vegetation types were variously savannas, barrens, or dense coniferous forest, depending on fire frequency and extent. Thus, age classes and patch configurations of mesophilic and pyrophilic forests generally followed an ecosystem-dependent periodicity and spatial pattern associated with particular natural disturbance regimes.

While it is commonly accepted that wind and fire disturbance altered local and landscape ecosystems, minor climatic fluctuations did not result in major changes at any scale (Frelich 1995). Pielou (1991) explains this relative stability in the face of climate change with the concept of ecological inertia. She defined ecological inertia as the lag in forest change due to plant persistence, with established communities physically preventing encroachment by invading species that were better adapted to changed climatic conditions—species simply would not have time to migrate. This delayed response of vegetation to short-term climatic change may explain why the biogeography of forest trees changed steadily following Pleistocene glaciation, without any reversals in the direction of the change. She noted that, in addition to ecological inertia, natural selection for progeny adapted to changed conditions also resulted in stability.

Early Human Influences

Understanding the cause and rate of natural change that formerly influenced and distinguished the landscape and local ecosystems of the Lake States, technically termed the dynamics of homeorhetic stability (O'Neill et al. 1986; Reice 1994), requires consideration of biological processes, the physical environment, and disturbance regimes. Human influences have long been integral to these processes, although the extent of early influences remains a matter of debate.

Hunter (1996) makes the point that although the "overall ecological impact of Native Americans was much less than that of Europeans, it was significant in certain times and places." We know that pre-European contact indigenous populations in North America were a very small fraction of modern human populations. Denevan (1992) estimated there were 53.9 million Native Americans in the "New World" in 1492, with 3.8 million in North America. He asserted that "the Indian impact was neither benign nor localized." All ecosystems in the Lake States were not equally susceptible to fire, and burning by indigenous people would have primarily affected systems prone to burn, such as barrens, savannas, upland mixed conifer and oak forests, and other fire-dependent systems. Thus, the overall impact within pyrophilic ecosystems would have been large. This was not the case, however, in fire-intolerant, mesic hardwood forests that occurred throughout much of the Lake States at the time of European settlement.

Stearns (1949) noted that "in the virgin hardwood timber, fire is in the opinion of the writer rarely of much importance as the initial agent of catastrophe although it often follows windfall." He observed that "hot slash fires have burned on the cutover hardwood land. Although these fires burned to the edge of the virgin stand they did not penetrate into it more than a few rods." Even the sweeping wildfires that occurred following the turn-of-the-century logging did not fully consume the advanced regeneration of fire-intolerant hardwood species such as sugar maple in the moraines, loamy glacial lakebeds, and other mesic landforms of the Lake States. The flora of the "asbestos" forests in many cases simply would not burn, probably due to the high moisture content and low fine-fuel loading of the forest floor, and the "inability of the vegetation comprising the understory or residual tree sapling and pole strata to carry fire" (Whitney 1986, 1987). Hence, fire seldom affected mesic hardwood ecosystems, and burning by indigenous people would likely have had minimal impact on them.

Early Records of Lake States Forest Conditions

The original land survey by the General Land Office (GLO) is the earliest systematically recorded information on forest composition in the Lake States. The GLO surveys began in 1826 in Michigan, 1832 in Wisconsin, and 1847 in Minnesota (Stearns 1995). GLO surveyors noted tree species and their diameters along section lines, providing a grid of transects approximately 1 mile apart. Locations of recently burned areas, windthrows, beaver impoundments, rivers and streams, wetlands, existing settlements, trails and roads, and agricultural potential of soils were recorded, and generalized maps of timber types and soil quality were prepared. Pre-European settlement forest land conditions have been mapped by scientists using land survey notes in each of the three Lake States (Comer et al. 1995; Finley 1976; Marschner 1974). All of these maps were developed subjectively to some degree.

General Land Office data and related maps provide insights regarding the pre-European extent of aspen, which was probably an order of magnitude less in the historic forests in Michigan and Wisconsin than today. In northern Minnesota, 13% of all bearing trees recorded by the surveyors were aspen (Almendinger 1997), and nearly 30% of the forest land was composed of mixed communities that included aspen as a component. The situation then (and to a lesser degree now) was that extensive areas of mixed conifer-aspen, aspen-birch, and aspen-oak forests were present in Minnesota, each typified by high densities of aspen stems. Northern Wisconsin and northern Michigan had much smaller aspen components—approximately 300,000 acres in each (Comer et al. 1995; Finley 1976).

Ostensibly, maps generated from GLO notes only provide a single measurement of forest conditions during the early to mid-nineteenth century. As noted, climate change, disturbance regimes, and physical substrates must be considered when interpreting the meaning and utility of maps of historic forests relative to changes in forest ecosystems. Contemporary forests, where aspen is much more prevalent, have undergone tremendous change when compared to these earlier forests. And people set the stage.

The Root of the Aspen Boom

Although aspen had played a significant though minor role in the pre-European settlement forest of the northern Lake States, that situation began to change during the mid-19th century. At that time, prime timber in the northeastern United States was nearly gone. Furthermore, good farmland was scarce for young people starting out on their own and for immigrants just off the boat from Europe. So naturally eyes began to turn toward the virgin pinelands of the Great Lakes—"The West," as it was then known. The timber was magnificent, land was cheap, and state and federal governments vigorously promoted settlement. Furthermore, the then guiding principle of Manifest Destiny deemed that the wilderness had to be tamed so people could settle and farm the land. What happened in the next 80 years was indeed settlement on a grand scale, but it also turned into a rampant human-caused disaster and an ecological disruption seldom rivaled. It couldn't have been better for aspen.

Beginning in about 1850 in the Saginaw River Valley of Michigan, then spreading north and west through the Lower and Upper Peninsulas of Michigan, Wisconsin, and Minnesota, the timber barons and their legions of shanty boys went to work on the timber. Pine was on the top of their priority list, but hemlock, cedar, and hardwoods were exploited when the pine was gone. By 1930 most of the virgin timber in the Lake States had been felled. Today, remnant old-growth forests are virtually nonexistent in Michigan and Wisconsin, although some large tracts still exist in extreme northern Minnesota, principally in the Boundary Waters Canoe Area. What amounted to the clearcut of three states would have bode well enough for the future of aspen, but what usually followed logging suited this "Phoenix tree" even better (Graham et al. 1963).

Disastrous wildfires regularly ripped through the cut-over forest lands, usually in late summer or autumn following periods of extreme drought (Haines and Sando 1969). Consuming both people and pine reproduction without partiality, these fires created in their aftermath ideal conditions for aspen regeneration. The deadliest fires have become part of the lore of American forestry (Holbrook 1944). October 8, 1871, for example, was the worst day of wildfire in recorded history. The Peshtigo and Great Michigan Fires roared through Wisconsin and Michigan, killing nearly 1,500 people and blackening well over 3 million acres. On that same day The Great Chicago Fire burned most of that city to the ground, and thousands of acres of midwestern prairies were ablaze. Other wildfires achieved great notoriety: the 1881 Thumb and 1908 Metz Fires in Michigan; the 1894 fires that consumed much of northwest Wisconsin; and the 1894 Hinckley, 1910 Baudette, and 1918 Cloquet Fires in Minnesota. These fires often reburned land that had previously been scorched, creating an ecologically ideal situation for aspen by diminishing tree competition, creating an optimal seedbed, and stimulating sucker regrowth.

Michigan provides the extreme case study of wildfire's effect on aspen—of the three northern Great Lakes States, none was hit harder by 19th and early 20th century wildfires. Extensive areas were converted from pine to aspen. The area burned during the 60-year period beginning in 1871 is staggering—nearly 11 million acres, most in the northern part of the state (Mitchell and Robson 1950) (figure 3). Three caveats regarding these data, however, need to be emphasized. First, prior to 1930 the perimeters of large fires rarely were carefully measured, so their areas are only rough estimates. An exception was the disastrous 1881 Thumb Fire, the extent of which was carefully documented by Sgt. William O. Bailey of the U.S. Signal Service (Bailey 1882). Second, many smaller fires were not reported, much less known about, so yearly areas actually burned prior to 1930 probably exceed the recorded estimates, in some case by a considerable extent. Third, wildfires frequently reburned areas consumed in previous conflagrations, often repeatedly. Thus, the yearly burn estimates cannot be viewed as a continually expanding cumulative area of the state.

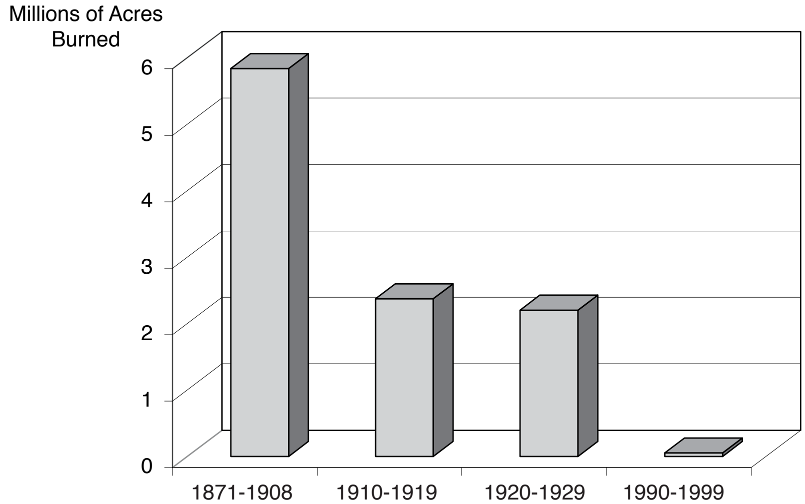

Figure 3—Estimated areas burned by wildfires during three early periods of Michigan history and the last decade of the 20th century. Areas are likely to be underestimated prior to 1930 (sources: Mitchell and Robson 1950; U.S. Forest Service; Michigan Department of Natural Resources).

Due to the combined effects of logging and wildfires, between a fifth and a quarter of northern Michigan was transformed into conditions favoring the establishment of aspen. Similar situations occurred in Wisconsin and Minnesota. This was a monumental ecological event and led to what is probably the largest human-caused forest type conversion in history. The irony of these profound events is that while their intent was to clear the land for the establishment of a vast agricultural enterprise, they instead led to a 20th century timber boom that mirrored the shanty boys' efforts from the previous century. However, the latter-day boom fed on aspen fiber, rather than pine lumber.

In contrast to the pre-1930s situation, wildfire currently plays a minor role in the regeneration ecology of aspen. Fire prevention and suppression efforts have reduced the millions of acres burned before and after the turn of the 20th century to a negligible amount—e.g., 51,630 acres in Michigan in the decade from 1990 to 1999. Wisconsin and Minnesota experienced similar success in taming wildfire. Thus, aspen's future in the northern Lake States depends on continued harvesting of mature stands to promote sucker regrowth and silvicultural practices aimed at natural seed regeneration or planting on carefully prepared sites. Notwithstanding these efforts, the over 17 million acres of aspen that once occupied the cut-over, burned-over lands of these three states will likely never be seen again, or at least never on such a grand scale. The relevant followup question, then, becomes—Why is this a problem?

FIA Records of Change: From the 1930s to Present

The aftermath of logging and burning had social as well as ecological impacts. The rotating ownership of denuded lands eventually gave way to a pattern of private and public ownership across the three-state region. Fire control became commonplace. And slowly, the forests grew, increasing in quality and extent.

Cunningham and Moser (1938a) noted that "…forests originally occupied 80% of all the land in the three States…", and in the 1930s that there was "…a large volume of wood of inferior quality and inferior species available for immediate use…". Over 11 million acres of previous forest land was still deforested in the mid-1930s—a target for planting by the Civilian Conservation Corps.

Although sample methods and definitions have evolved over the 60+ years of FIA inventories, these data provide the best measures we have of forest changes over the Lake States region. Since its recorded peak in the Lake States in the 1930s, aspen-birch acreage has decreased by 24% based on five FIA forest surveys/cycles (Chase et al. 1970; Cunningham et al. 1958; Cunningham and Moser 1938a,b; Findell et al. 1960; Guilkey et al. 1954; Jakes 1980; Lake States Forest Experiment Station 1936; Leatherberry and Spencer 1996; Miles et al. 1995; Raille 1985; Raile and Smith 1983; Schmidt 1997; Spencer and Thorne 1972; Stone 1966; Stone and Thorne 1961). The absolute acreage and rate of decline has varied by state, however (figure 4). Over a 58-year period in Michigan (1935 to 1993) and a 61-year period in Wisconsin (1935 to 1996), aspen-birch acreage declined by 37 and 36%, respectively. Over a 55-year period in Minnesota (1935 to 1990), aspen-birch acreage declined by only 6%.

The decrease in aspen-birch acreage in Wisconsin was relatively constant over this 61-year period, ranging from 0.6 to 0.9% per year. In Michigan, the decrease between 1935 and 1966 was also relatively constant, about 0.2% per year. Between 1966 and 1980, this rate increased seven-fold to 1.4% per year, dropping to 1.0% per year between 1980 and 1993. In Minnesota, a different trend has occurred. Aspen-birch declined initially, but then expanded modestly. The area of aspen-birch declined between 1977 and 1990 by 6%, or 0.4% per year. The end result of these declines creates a greatly reduced aspen-birch resource in Michigan and Wisconsin, and a slightly reduced area in Minnesota, where aspen-birch management has been more intensive.

Contemporary Aspen Trends in the Lake States

While acreages have declined since the 1930s, aspen-birch remains the second most prevalent forest type in the Lake States, representing 26% of the region's 49.0 million acres of timberland and 25% of the region's 51.9 million acres of forest lands. Only northern hardwoods (maple-beech-birch) have a greater acreage, comprising 28% of the region's timberlands and 27% of the forest lands.

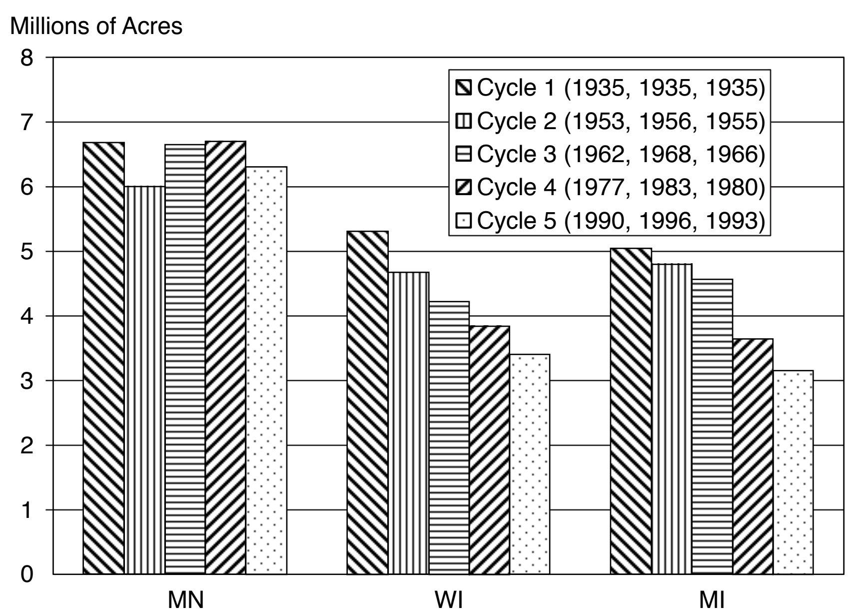

Figure 4—Area of aspen-birch in the Lake States over the five FIA forest survey cycles (cycle year in parentheses for Minnesota, Wisconsin, and Michigan, respectively (source: USDA Forest Service Lake States Forest Experiment Station and North Central Forest Experiment Station).

As we see in the long-term trends, intensive management/disturbance will be required to maintain or expand aspen area. Otherwise, the regional decline in the aspen-birch forest type will continue (e.g., there was a 1.3 million acre decline between the most recent forest inventory cycles). Indications that contemporary management is intensifying are reflected in (1) changes in aspen size classes, (2) forest type transitions identified in recent FIA surveys, and (3) reported production, sales, and stumpage prices.

The last two FIA survey cycles (4 and 5) spanned 13 years for Minnesota (1977, 1990), Wisconsin (1983, 1996), and Michigan (1980, 1993) (Jakes 1980; Leatherberry and Spencer 1996; Miles et al. 1995; Raille 1985; Raile and Smith 1983; Schmidt 1997). During this time, aspen (rather than aspen-birch) area declined by 5, 11, and 21% in Minnesota, Wisconsin, and Michigan, respectively (figure 5). However, several patterns indicating intensive management have appeared. In Wisconsin and Minnesota, acreage of aspen seedling-sapling increased from 39 to 55% and 28 to 34%, respectively, of the total acreage in this forest type. In Michigan, total acres of aspen seedling-sapling decreased, but the proportions remained relatively constant (40–41%). Across the three-state region, the area of aspen seedling-sapling increased from 34 to 41% of the total acreage in this forest type. In Minnesota, seedling-sapling and sawtimber area increased, but there was a substantial decline in poletimber (1.2 million acres). Wisconsin had declines in area of poletimber and sawtimber stands. Michigan's poletimber area declined, too, but the sawtimber area increased.

Ingrowth and conversions into and out of aspen also influence the long-term composition of the Lake States forests. Remeasured FIA plots were examined to identify transitions from aspen to other types between cycle 4 and 5 (figure 6). In Minnesota, a high percentage of plots that were aspen in cycle 4 remained as aspen in cycle 5. This percentage declined to the east. The increasing transition from aspen to maple-beech-birch is evident from west to east. Of course, there also are transitions into aspen—the major source of new aspen acreage is from various softwood forest types. But overall, more land is converting from aspen to more tolerant species than to aspen.

Estimates of current net annual growth versus current annual removals provide another indication of intensity of aspen harvest. Based on the most recent FIA reports, removals exceed net growth by 8% in Minnesota and 45%

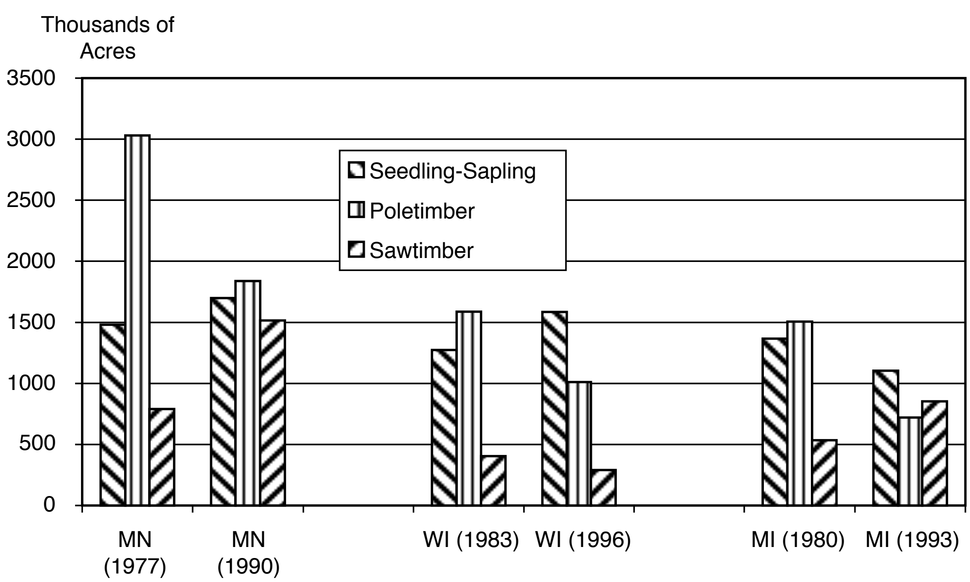

Figure 5—Size class distribution for aspen forest type over last two survey cycles (4 and 5) for Minnesota (1977, 1990), Wisconsin (1983, 1996), and Michigan (1980, 1993) (source: USDA Forest Service North Central Forest Experiment Station).

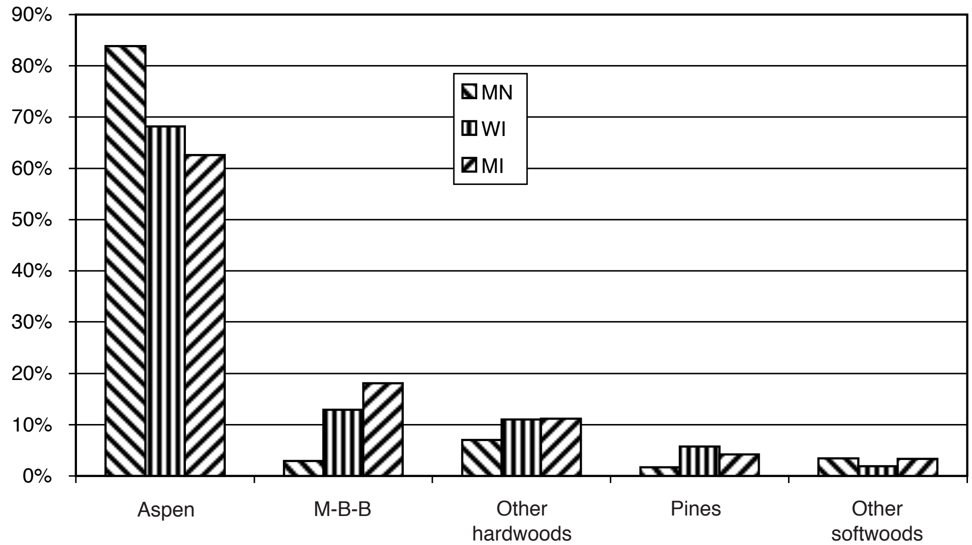

Figure 6—Percentage of area based on remeasured FIA plots that were aspen in cycle 4, and aspen and other types in cycle 5 (source: USDA Forest Service Eastwide Forest Inventory Data Base).

in Wisconsin. Removals are slightly less than net growth (98%) in Michigan. This is an indication of very intensive harvesting, particularly considering the questionable availability of private nonindustrial lands for timber production and the declining availability of federal lands.

Aspen has not always been a popular commodity. Holcomb and Jones (1938) wrote:

> As the supply of other material becomes scarcer and the aspen reached favorable size, several industries began to use it. Many thousands of cords are now consumed annually for excelsior, paper, box shooks, fuel wood, and even fence posts.
>
> It must be remembered, though, that aspen is serving as a nurse crop on depleted soil and much of it will give way to better soil demanding and more permanent species as the soil regains its former productivity.

Later, Spencer and Thorne (1972) emphasized that "[a]spen, one of the postfire species, was especially prolific and was considered a virtually useless weed species by many until recently."

It is no longer a weed tree. The level of aspen pulpwood production has increased substantially in the past 20 years, with Minnesota responsible for most of the growth (figure 7)—this mirrors the higher level of aspen area retention

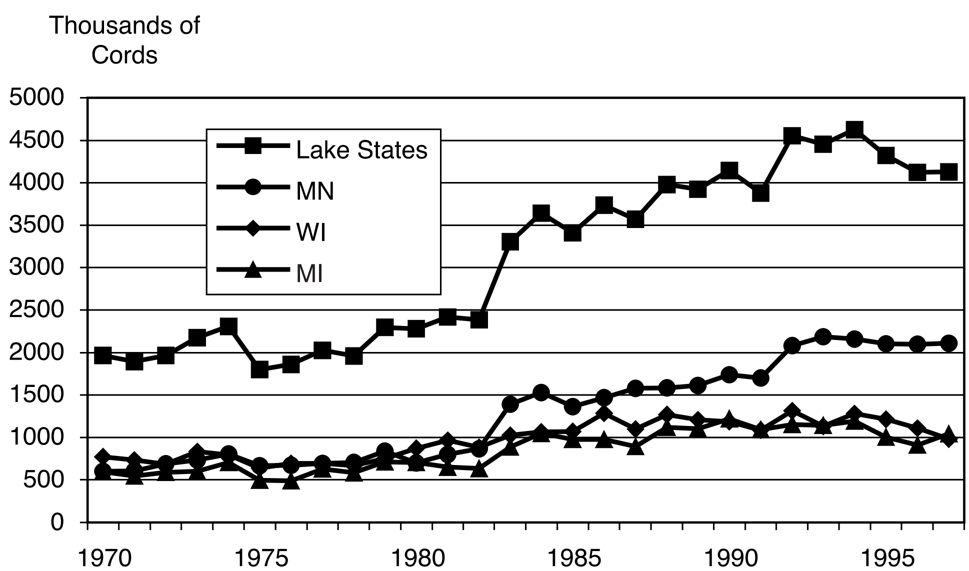

Figure 7—Aspen pulpwood production in the Lake States, 1970-1997 (source: USDA Forest Service North Central Forest Experiment Station).

in Minnesota. While overall aspen production is up, the role of the national forests has diminished (figure 8). Increasing prices for aspen stumpage provide an incentive for many landowners to harvest their timber.

In addition to its role in the timber market economy, the aspen forest type is synonymous with two popular game species in the Lake States—white-tailed deer and ruffed grouse. Hundreds of thousands of hunters wander the north woods with hopes of a successful encounter with these species. But there is much more to aspen in terms of habitat than simply white-tailed deer and ruffed grouse. Beyer (1983), for example, identified 60 bird species and 111 species of vegetation on his aspen study sites—all associated with timber harvesting. Older aspen can provide essential cavities for birds, and decaying aspen contributes to the dynamics of forest death and rebirth.

Based on indicators of changes in acres in aspen size classes and percent of growth harvested, aspen is being managed intensively in the Lake States. So the question again—Why is this a problem?

Management Options for Aspen

The Lake States, like most regions, has many people with different views on the appropriate use of forest lands. Some would have the forest protected from harvest, perceived as exploitation. Others would have them managed even more intensively. Many fall somewhere between the extremes—this creates the root of the problem, what to do with the aspen forests?

Aspen management has given rise to a number of contentious issues. Perhaps foremost are concerns regarding biodiversity, and the effects of aspen management on forest fragmentation and loss of interior habitats needed for area-sensitive species. And although aspen provides critical habitat for many species such as the ruffed grouse, it also helps support enormous deer populations. Overpopulation by deer has led to tens of thousands of car-deer collisions annually in each of the Lake States, has resulted in excessive browsing of tree seedlings and ground flora in general, and according to the National Center for Infectious Diseases in Atlanta, Georgia, has contributed to Wisconsin and Minnesota ranking seventh and tenth in incidence of lyme disease per capita in

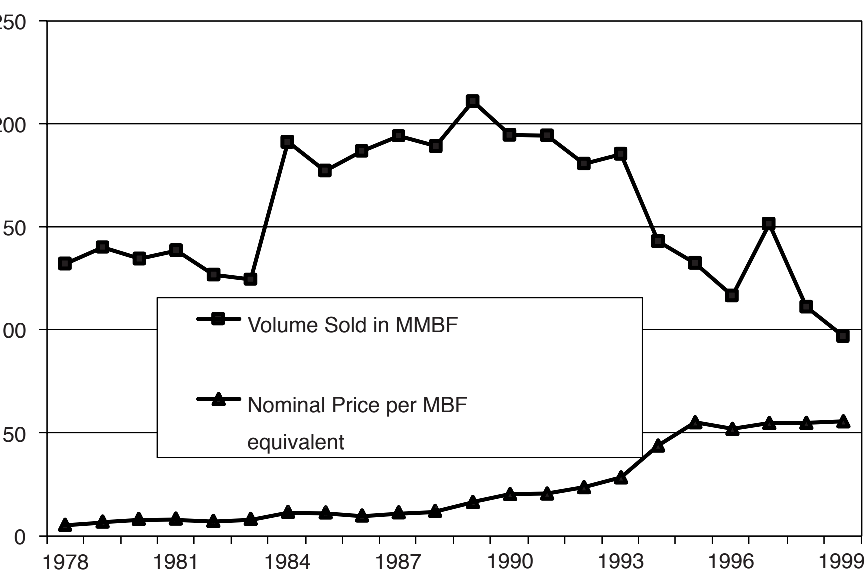

Figure 8—Aspen volume sold and nominal price per MBF equivalent from the Lake States National Forests, 1978-1999 (source: USDA Forest Service; Cut & Sold Reports).

the United States. Thus, management options for aspen are influenced by both social and ecological considerations. Rather than prescribe a social fix, we present a number of options for managing a resilient aspen resource.

The silvicultural prescription for aspen retention on a site has been traditionally viewed by Great Lakes foresters in a rather simplistic way—clearcut a mature stand, stand back and let suckers retake the site, wait, and then clearcut again when the stand matures. No site preparation, no cleaning, no thinning, no pest control, little thinking. Whereas this prescription has worked well in many situations and represents a viable silvicultural option for aspen, the more complex objectives of modern forest management dictate that additional pages be added to the active prescription manual for aspen (Perala 1977). This need is particularly acute for managers of public lands. The traditional approach also does not take into account ecological situations that might call for promoting succession out of aspen, or deterring aspen suckering, e.g., a dense understory of desirable trees and shrubs. Table 1 summarizes the palate of silvicultural options that are available to managers, depending on their management objectives. Our table extends the decision tree for management of mature Lake States aspen proposed by Stone (1997).

Management for timber represents the most straightforward approach to aspen silviculture, especially on forest industry lands. In this case the overriding objective is to maintain a continual supply of aspen raw material to the mill, so rapid growth, yield per acre, wood uniformity, and sustainability are paramount concerns. For pulpwood, oriented strandboard, or solid wood products, the conventional clearcut-coppice prescription works fine in most situations, with rotation length determined by culmination of mean annual increment or a diminishing economic rate of return. But other options are available, e.g., selective or strip thinning of sapling through pole-size stands (Brinkman and Roe 1975). Thinning has been demonstrated to reduce the length of pulpwood rotations (Jones et al. 1990), increase net volume increment (Weingartner and Doucet 1990), and increase sawtimber output up to 40% and veneer output up to 140% (Perala 1977). Thinning also can be an effective means of eliminating poor clones from a stand, provided residual densities are heavy enough to retard suckering. Blandin Paper Company in Grand Rapids, Minnesota, has mechanically thinned about 6,500 ha in the past decade. Their prescription for 8- to 10-year-old aspen sapling stands calls for flattening 2 to 2.5 m wide strips at a spacing of 2 to 3 m (Zasada et al. 2000).

An argument against thinning has been that low stand densities promote infection by *Hypoxylon mammatum* (Anderson and Martin 1981), especially in the very susceptible quaking aspen. Because considerable interclonal variation in canker incidence exists in quaking aspen (Ostry and Anderson 1990), thinning can be a viable option if it is restricted to the most resistant clones. Another option would be to delay thinning of dense stands until the lower branches have naturally pruned, since branches are a major entry point of *Hypoxylon* infection.

On the other end of the scale of management complexity from forest industry are public land agencies—in particular the USDA Forest Service and the state Departments of Natural Resources. Here, timber is just one of many management objectives (table 1), and in some cases a minor one. Aspen's vital role as habitat for game and nongame wildlife, its role as a component of old-growth systems or landscape diversity, and its aesthetic appeal presents a spectrum of management options for public land managers (Brinkman and Roe 1975). Therefore, silvicultural prescriptions—in addition to the traditional clearcut-coppice approach—could be designed to develop a multiage-class

Table 1—Alternative silvicultural approaches to management of Lake States aspen. In all cases the main objective is the retention of aspen as a component of the stand.

Stand silviculture	Management objective				
	Timber	Wildlife habitat	Old growth or aesthetics	Diversity	Conversion to aspen
Harvest	Clearcut commercially mature stands	Clearcut or variable retention of other desirable species	None[a], variable aspen retention, clearcut, or burn as stand breaks up	Clearcut or burn as necessary to maintain aspen type	Clearcut existing stand—hardwood or conifer
Size of harvest units	Generally large (40+ acres) or entire stand	10-100+ acres depending on habitat objectives	<5 acres to entire stand	Extremely variable	ca. 40 acres maximum for seed regeneration[b]
Rotation or cutting cycle	30-70 years[c], depending on site and clone	20-80+ years depending on area age class distribution	60-120+ years	35-70+ years	Variable depending on existing forest type
Site preparation	None[d], except where a dense understory of tolerant trees requires cutting, burning, or herbicide treatment	None[d]	None[d]	None[d]	Burn, scarify, herbicides, or a combination to reduce competition and create a seedbed
Tending	Precommercial or commercial thinning optional for dense stands or to expand desirable clones	Generally none	Optional; thinning will produce large-diameter trees more quickly	Generally none	Cleaning may be necessary in the first or second year after establishment of aspen regeneration
Overstory composition	Pure stands preferred	Pure or mixed species, multistoried stands depending on habitat objectives	Pure or mixed species, multistoried stands	Both pure and mixed stands	Pure or mixed stands; subsequent clearcut harvests can increase aspen component

[a]No harvest or disturbance means succession to a vegetation type devoid of aspen.
[b]Mature aspen seed trees must be upwind of harvest unit; larger sites may be planted.
[c]Very short rotations (<20 years) may lead to deterioration of aspen root systems.
[d]Provided adequate potential for sucker reproduction exists.

distribution across a local administrative district or area; promote mixed, vertically stratified stands with aspen as a major or minor component; grow large-diameter old-growth trees; produce standing or down dead aspen stems; and create vistas where the beauty of aspen and other forest types can be viewed by the public. To meet these objectives, creative application of clearcuts of varying size, thinnings from above or below, dispersed or aggregated partial harvest cuttings, and prescribed burning can be employed (Perala 1977; Weingartner and Doucet 1990).

Retention of aspen or other species on a harvest unit offers a range of creative options to produce stands that meet multiple objectives. Dispersed retention of trees, however, reduces sucker density and growth compared to a complete clearcut, especially if the residuals are aspen (Perala 1977). Nonetheless, residual basal areas as high as 14 m^2 per ha still can produce adequate aspen stocking, although the resulting regeneration will likely be mixed in composition (Doucet 1989). Recent work in the southeastern and western boreal forest has shown that quaking aspen will reproduce in gaps of various sizes that develop in a mature overstory (Cumming et al. 2000; Kneeshaw and Bergeron 1998). Thus, pure or mixed aspen stands could even be managed under an uneven-aged system, at least until tolerant species begin to dominate the understory. Retention of pines, spruces, oaks, black cherry, and other desirable species on harvest units can produce mixed aspen stands with improved wildlife habitat, diversity, or visual qualities. Aggregated retention provides another means to a similar end, without the penalty of reduced aspen stocking on the harvested areas. Groups from <1 ha to several ha in size of mature aspen or associated species can be left on an otherwise clearcut harvest unit to create patches of old growth or for other values.

Burning is another silvicultural approach that could be employed on a wider scale by public land managers in the Lake States. In this case the prescription would be to let fire be the selective agent, creating an unpredictable but nonetheless very natural mosaic within the burn unit. Aspen is uniquely adapted ecologically to recapture a site following fire (Perala 1995). Fire also can increase understory diversity and biomass in stands of sucker regeneration (Brown and DeByle 1989). Burning could be especially useful in the management of wilderness areas where timber harvesting is prohibited or in old-growth units. Private organizations like The Nature Conservancy also could utilize more fully the use of fire in managing aspen on their lands.

Other ownership categories fall somewhere between timber industry and public land agencies in the range of silvicultural options of choice. Organizations that promote game habitat—like the Ruffed Grouse Society or hunting clubs—may have habitat enhancement and diversity as their overriding objectives. In many cases dispersal of small clearcuts across their ownership provides the diversity of age classes needed to support high animal densities. In some cases partial cuttings or fire also may be employed. Still other land managers may choose to reduce aspen clearcutting to reduce fragmentation. One means would be to aggregate compatible land uses, concentrate aspen management in large blocks where possible, and avoid management in areas adjacent to continuous forest lands. Another means would be to selectively thin aspen, leaving residual trees and advanced regeneration composed of later successional species. Retention of some aspen trees may reduce sucker density because sprouting is hormonally controlled, and is suppressed by auxin transported from the stem to the roots (Schier et al. 1985).

In any discussion of ownership management options, the nonindustrial private forest land (NIPF) owners are the wild card. Ranging from complete unawareness of or disinterest in management in any form to sophisticated tree farm operations, the pervasive NIPFs could choose any or all of the options presented in table 1. Education always is of paramount importance when dealing with NIPFs, and in the context of this discussion perhaps the major task facing extension or service foresters is to convince NIPFs that doing nothing means the eventual loss of aspen. This fact has and will continue to come as an unpleasant surprise for many of these owners, especially if their prize aspen stand already has gone around the bend and broken up. On the other hand, the revelation that mature aspen can be sold at an excellent price, with little danger of regeneration failure, may strike other owners as a deal too good to pass up.

A final topic needs particular emphasis—aspen can be regenerated by seed (Zasada et al. 2000). Death and breakup of existing stands, therefore, does not necessarily mean inevitable reduction of the aspen component in a particular landscape. Three factors must come together, however, to get an adequate catch of aspen seedlings on a clearcut or shelterwood harvest area (Brinkman and Roe 1975). First, an adequate rain of seed must occur, which will occur in most years, particularly if aspen seed trees border the harvest unit. Second, a receptive seedbed must be prepared, either by scarification to expose mineral soil or by a hot fire. Third, seedfall must be followed by cool, moist conditions until seedlings are well established. While the last factor is not controllable by silviculturists, proper attention to the first two will produce a likelihood of success that does not differ appreciably from natural regeneration of most Lake States tree species.

Conclusions

Aspen has declined in the Lake States over the past 70 years, although the baseline for these losses was established immediately following a time and a human-caused series of disturbances with no historical precedent. The species and its minor associates remain the second most dominant forest type in the region, and increases in market prices and harvest intensity suggest that aggressive management will continue. As Hunter (1999) pointed out, “Aspen forests in the Lake States, which originated after severe, repeated fires following logging of the old-growth pine, are now valuable enough that foresters consciously perpetuate a severe disturbance regime that was quite uncommon before exploitation.” It appears that the aspen forest type is secure for now in the Lake States, although additional loss of acreage, particularly from unmanaged private lands, is almost certain in some areas.

Questions of balance remain, however. Simultaneously meeting production and conservation goals of sustainable forest management remains an unmet national and international challenge. Blending aspen management with other ecosystem and species maintenance and restoration needs is probably the greatest challenge confronting forest managers in the Lake States. A potential exists to increase aspen productivity through even more intensive management. There is also considerable potential to supplement current supply by increasing the use of fast-growing hybrid aspens or poplars in reforesting poorly stocked forest lands and abandoned agricultural lands. The potential also exists to reduce adverse effects of aspen management by assessing resource conditions and trends across broad geographic areas, identifying opportunities and limitations for multiple-use management that features both conservation and production emphases, and engaging in collaborative resource education, planning, management, and monitoring. In other words, engaging in a voluntary multiownership adaptive management strategy that accommodates desired outcomes among cooperating parties. Under this scenario, the rights and choices of private citizens and landowners, goals of industrial interests, and mandates of government agencies might all be honored while resource production and conservation are achieved.

By acknowledging feasible options and mimicking natural disturbances while maintaining or restoring forest composition and age-class structures at landscape and local levels, we believe conservation goals can be achieved. In cases where we choose to depart from natural conditions and processes (e.g., high levels of aspen and plantation management), aggregating compatible uses to minimize adverse effects is warranted.

References

Almendinger, J.C. 1997. Minnesota Bearing Tree Data Base. Minnesota Department of Natural Resources Biological Report No. 56.

Anderson, G.W. and Martin, M.P. 1981. Factors related to incidence of Hypoxylon cankers in aspen and survival of cankered trees. Forest Science 27:461-476.

Bailey, W.O. 1882. Report on the Michigan forest fires of 1881. Signal Service Notes No.1. Washington, DC: U.S. War Department. 16 p.

Beyer, D.E. 1983. Wildlife response to whole tree harvesting of aspen. M.S. Thesis, Department of Fisheries and Wildlife, Michigan State University. 76 p.

Borman, F.H. and Likens, G.E. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York. 253 p.

Brinkman, K.A. and Roe, E.I. 1975. Quaking aspen: silvics and management in the Lake States. Agr. Handbook No. 486. Washington, DC: U.S. Department of Agriculture, Forest Service. 52 p.

Brown, J.K. and DeByle, N.V. 1989. Effects of prescribed fire on biomass and plant succession in western aspen. Res. Pap. INT 412. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 16 p.

Brubaker, L.B. 1975. Postglacial forest patterns associated with till and outwash in northcentral upper Michigan. Quaternary Research 5: 499-527.

Burns, R.M. and Honkala, B.H. (tech. coords.). 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. Washington, DC: U.S. Department of Agriculture, Forest Service. 2 vol. 877 p.

Canham, C.D. and Loucks, O.L. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65(3):803-809.

Chase,C.D.; Pfeifer, R.E.; and Spencer, J.S., Jr. 1970. The growing timber resource of Michigan, 1966. Resource Bulletin NC-9. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station. 62 p.

Comer, P.J.; Albert, D.A.; Wells, H.A.; Hart, B.L.; Raab, J.B.; Price, D.L.; Kashian, D.M.; Corner, R.A.; Schuen, D.W. 1995. Michigan's native landscape, as interpreted from the General Land Office Surveys 1816-1856. Lansing, MI: Michigan Natural Features Inventory. 78 p. + digital map.

Cumming, S.G.; Schmiegelow, F.K.A.; and Burton, P.J. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecol. Appl. 10:744-759.

Cunningham, R.N. and Moser, H.C. 1938a. Forest areas and timber volumes in the Lake States. A Progress Report on the Forest Survey of the Lake States. Economic Notes No. 10. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station, University Farm. 84 p.

Cunningham, R.N. and Moser, H.C. 1938b. The forests of Minnesota. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station, University Farm. 123 p.

Cunningham, R.N., H.C. Horn, and D.N. Quinney. 1958. Minnesota's forest resources. Forest Resource Report No. 13. Washington, DC: USDA Forest Service. 53 p.

Davis, M.B. 1981. Quaternary history and the stability of forest communities. Pp. 132-153. In: West, D.C.,H.H. Shugart, and D.B. Botkin, eds. Forest Succession: Concepts and Application. New York: Springer-Verlag.

Davis, M.B.; Sugita, S.; Calcote, R.R.; Ferrari, J.B.; and Frelich, L.E. 1993. Historical development of alternate communities in a hemlock-hardwood forest in northern Michigan, U.S.A. Pp. 19-39. In: P. J. Edwards, R. M. May, and N. R. Webb, editors. Large Scale Ecology and Conservation Biology: The 35th Symposium of the British Ecological Society with the Society for Conservation Biology. University of Southampton. Boston, MA: Blackwell Scientific Publications.

Denevan, W.M. 1992. The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers 82(3): 369-385.

Doucet, R. 1989. Regeneration silviculture of aspen. Forestry Chronicle 65:23-27.

Findell, V.E.; Pfeifer, R.E.; Horn, A.G.; and Tubbs C.H. 1960. Michigan's forest resources. Station Paper 82. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station, University Farm. 45 p.

Finley, R.W. 1976. Map. Original vegetation cover of Wisconsin, compiled from U.S. General Land Office notes. Madison, WI: University of Wisconsin Extension. map (1:500,000).

Frelich, L.E. 1995. Old forest in the Lake States today and before European settlement. Natural Areas Journal 15:157-167.

Frelich, L.E. and Lorimer C.G. 1991. Natural disturbance regimes in hemlock-hardwood forests of the Upper Great Lakes Region. Ecological Monographs 61(2):159-162.

Graham, S.A.; Harrison R.P., Jr.; and Westell, C.E., Jr. 1963. Aspens: Phoenix Trees of the Great Lakes Region. Ann Arbor: The University of Michigan Press. 272 p.

Guilkey, P.C.; Granum, B.M.; and Cunningham, R.N. 1954. Forest statistics for Minnesota, 1953. Station Paper No. 31. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station, University Farm. 36 p.

Haines, D.A. and Sando, R.W. 1969. Climatic conditions preceding historically great fires in the North Central Region. Res. Pap. NC-34. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 19 p.

Holbrook, S.H. 1944. Burning an Empire. New York: The MacMillan Company. 229 p.

Holcomb, C.J. and Jones, R.D. 1938. The Antrim area: a study of farm woodland conditions on a cut-over area of lower Michigan. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station, University Farm. 42 p.

Host, G.E.; Pregitzer, K.S; Ramm, C.W.; Hart, J.B.; Cleland, D.T. 1987. Landform mediated differences in successional pathways among upland forest ecosystems in northwestern Lower Michigan. Forest Science 33:445-457.

Hunter, M.L., Jr. 1996. Benchmarks for managing ecosystems: are human activities natural? Conservation Biology 10(3):695-697.

Hunter, M.L. Jr. (ed.). 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, England. 695 p.

Jakes, P.J. 1980. Minnesota forest statisitics, 1977. Resource Bulletin NC-53. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 85 p.

Jones, B.S.; Berguson, W.E.; and Vogel, J.J. 1990. Aspen thinning as a viable cultural tool. In Aspen Symposium '89 Proceedings. Gen. Tech. Rep. NC-140. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 205-210.

Kneeshaw, D.D. and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79:783-794.

Lake States Forest Experiment Station. 1936 (June). Forest areas and timber volumes in Michigan. A Progress Report on the Forest Survey of the Lake States. Economic Notes No.

5. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station, University Farm. 40 p.

Leatherberry, E.C. and Spencer, J.S., Jr. 1996. Michigan forest statistics, 1993. Resource Bulletin NC-170. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 144 p.

Marschner, F.J. 1974. The Original Vegetation of Minnesota, a map compiled in 1930 by F.J. Marschner under the direction of M.L. Heinselman of the U.S. Forest Service. St. Paul, MN: Cartography Laboratory of the Department of Geography, University of Minnesota. map (1:500,000).

Miles, P.D.; Chen, C.M.; and Leatherberry, E.C. 1995. Minnesota forest statistics, 1990, revised. Resource Bulletin NC-158. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 138 p.

Mitchell, J.A. and Robson, D. 1950. Forest fires and forest fire control in Michigan. Lansing, MI: Michigan Department of Conservation, and St. Paul, MN: U.S. Department of Agriculture, Forest Service, Lake States Forest Experiment Station. 82 p.

O'Neill, R.V.; DeAngelis, D.L.; Waide, J.B.; and Allen, T.F.H. 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, NJ.

Ostry, M.E. and Anderson, N.A. 1990. Disease resistance in a wild system: Hypoxylon canker of aspen. In Aspen Symposium '89 Proceedings. Gen. Tech. Rep. NC-140. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 237-241.

Perala, D.A. 1977. Manager's handbook for aspen in the North Central States. Gen. Tech. Rep. NC-36. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 30 p.

Perala, D.A. 1995. Quaking aspen productivity recovers after repeated prescribed fire. Res. Pap. NC-324. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 11 p.

Pielou, E.C. 1991. After the Ice Age: the Return of Life to Glaciated North America. The University of Chicago Press.

Powell, D. S.; Faulkner, J.L.; Darr, D.; Zhu, Z; MacCleery, D.W. 1994. Forest Resources of the United States, 1992. Gen. Tech. Report RM 234 (revised). Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Raile, G.K. 1985. Wisconsin forest statistics, 1983. Resource Bulletin NC-94. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 113 p.

Raile, G.K. and Smith, W.B. 1983. Michigan forest statistics, 1980. Resource Bulletin NC-67. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 101 p.

Reice, S.R. 1994. Nonequilibira determinants of biological community structure. American Scientist 82: 424-435.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63(5):1533-1546.

Schmidt, T.L. 1997. Wisconsin forest statistics, 1996. Resource Bulletin NC-183. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 150 p.

Spencer, J.S., Jr. and Thorne, H.W. 1972. Wisconsin's 1968 timber resource. Resource Bulletin NC-15. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 80 p.

Stearns, F. 1995. History of Wisconsin's northern forests and the pine barrens. In: E.A. Borgerding, G.A. Bartelt, and W.M. McCown, eds. The Future of Pine Barrens in Northwest Wisconsin: A Workshop Summary: proceedings of the workshop; 1993 September 21-23; Solon Springs, WI. PUBL-RS-913-94. Madison, WI: Wisconsin Department of Natural Resources. 4-6.

Stearns, F.W. 1949. Ninety years of change in the northern hardwoods forest in Wisconsin. Ecology 30: 350-358.

Stone, D.M. 1997. A decision tree to evaluate silvicultural alternatives for mature aspen in the northern Lake States. North. J. Appl. For. 14:95-98.

Stone, R.N. 1966. A third look at Minnesota's timber. Resource Bulletin NC-1. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 64 p.

Stone, R.N. and Thorne, H.W. 1961. Wisconsin's forest resource. Station Paper No. 90. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station, University Farm. 52 p.

Webb, T., III; Bartlein, P.J.; Harrison, S.P.; Anderson, K.H. 1993. Vegetation, lake levels, and climate in eastern North America for the past 18,000 years. In: Wright, H.E, Jr.; Kutzbach, J.E.; Webb, T., III; Ruddiman, W.F.; Street, Perrot, F.A.; Bartlein, P.J., eds. Global Climates since the Last Glacial Maximum. Minneapolis, MN: University of Minnesota Press. 415-467.

Weingartner, D.H. and Doucet, R. 1990. The quest for aspen management in eastern Canada. In Aspen Symposium '89 Proceedings. Gen. Tech. Rep. NC-140. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 61-71.

Whitney, G. G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. Ecology 67(6):1548-1559.

Whitney, G. G. 1987. An ecological history of the Great Lakes forest of Michigan. Journal of Ecology 75: 667-684.

Zasada, J.C.; David A.J.; Gilmore D.W.; and Landhäusser S.M. [In press]. Ecology and silviculture of natural stands of Populus species. In Poplar Culture in North America. Ottawa, Ontario: National Research Council Press.