Abstract on the Aspen Association of Northern Michigan

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Cover Photograph: Young aspen clones in the eastern Upper Peninsula, Michigan. All photos by Christopher R. Weber unless otherwise noted.

Overview

This document provides a brief discussion of the aspen association of Michigan, detailing this system's landscape and historical context, range, ecological processes, characteristic vegetation and fauna, and threatened and endangered species. In addition, potential options and strategies are suggested for enhancing biodiversity of managed aspen associations and for restoring these systems to later successional forest types.

Introduction

The aspen association occurs throughout the Great Lakes region as a disturbance dependent vegetation assemblage. Aspen clones and stands of aspen are important components of several forested natural communities. The Michigan Natural Features Inventory's (MNFI) classification of natural communities of Michigan (MNFI 2003) does not recognize the aspen assemblage as a separate natural community. MNFI does not track early-successional forested systems. In addition, the focus of MNFI's community classification is on natural communities and the majority of aspen forests that constitute the aspen association have been created and maintained by extensive, anthropogenic disturbance. The aspen association, of which the dominant species include trembling aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandidentata*), and paper birch (*Betula paperifera*), comprises 43% of all pulpwood harvested in the Great Lakes region (4.2 million cords) (Piva 2006). Aspen forests are also important habitat for game species such as deer, turkey, woodcock, and grouse (Gregg and Hale 1977, Kidd and Koelling 1996, McDonald et al. 1998, Nguyen et al. 2004). The demand for aspen forest products and early-successional habitat is increasing (Gustafson et al. 2003), meanwhile aspen associations haves largely replaced later-successional communities in Michigan such as dry-mesic northern forest and old-growth mesic northern forest (Cohen 2000, 2002, and 2005). The increasing demand for aspen and high proportion of Michigan's forested landscape occupied by early successional forest highlights the relevance of a review of the aspen association. This document provides a discussion of the history, range, physiographic context, ecological processes, floristic and faunal composition, and biodiversity management of aspen dominated forests.

Range

Trembling aspen has the most extensive range of any North American tree (Barnes et al. 1998). Its native range covers a large swath from the Atlantic Ocean to the Pacific Ocean, spreading from its southern limit in northern Illinois, Indiana, Ohio, and Pennsylvania north to the Hudson Bay. Trembling aspen's range reaches into the northern and southern Rocky Mountains, and all the way west through Canada and east to Newfoundland and Labrador (Perala 1990). Throughout the south and west Rocky Mountains, trembling aspen is found as a late-successional species, having long-lived clones, sometimes with thousands of stems that expand over large acreages (Barnes et al. 1998). Aspen has been found to compete with prairies in the Canadian west (Bird 1961) and is an integral part of the savanna/forest-prairie transition in Wisconsin and Minnesota (Buell and Buell 1959, Buell and Facey 1960, Cochrane and Iltis 2000). In Michigan, trembling aspen approaches the southern limit of its range, where in undisturbed, old-growth situations it is kept in check by competition in upland, nutrient rich sites and usually relegated to open lowlands such as stream or swamp margins (Barnes and Wagner 2004). Bigtooth aspen's range is more limited and does not extend west of Minnesota and Iowa, but reaches northeast through Nova Scotia and south to Virginia. Northern Lower Michigan is where bigtooth aspen has reached its highest abundance throughout its range (Barnes and Wagner 2004). Both species of aspen are prevalent in areas of recent natural disturbances such as fire or windthrow.

Physiographic Context

Aspen's early-successional life strategy, which includes prompt responses to natural and anthropogenic disturbance, results in a wide physiographic range. Researchers have examined aspen communities with many different climatic and edaphic characteristics. In a comprehensive book on aspen ecology, Graham et al. (1963), discuss the growth and form of aspen growing on various substrates including: sandy outwash plains, eroded outwash/sandy moraines, sandy loams, and seepages. On sandy outwash plains, aspen is in its poorest condition and usually grows in scattered individual clones. There, soil moisture dictates the shift in the balance between jack pine (*Pinus banksiana*) and aspen. Aspen of the highest commercial value is found on the hills and valleys of eroded outwash plains or on similar positions on sandy moraines. Aspen is most productive on well-drained, nutrient rich sandy loams, but in the absence of disturbance, cannot compete with other hardwoods. Aspen found on seepages is usually attributed to an exceptionally hot fire during a dry year that burns most of the large portion of organic soil, leaving the bare mineral soil for aspen regeneration (Graham et al. 1963).

Other studies have examined aspen on excessively-drained outwash sands and well-drained glacial till (Barnes 1966, Wells 1978, Palik and Pregitzer 1992, Palik and Pregitzer 1995, Peterson and Squiers 1995, Roberts and Gilliam 1995, White et al. 2004), on poorly-drained morainal sand with a seasonally-high water table (Roberts and Richardson 1985, Sakai et al. 1985), and on moderately-drained, calcareous till and glacial lake plain (Lee et al. 1997, Edgar and Burk 2001, Hassett and Zak 2005). Aspen also occurs on thin soils overlying bedrock in northeast Lower Michigan and throughout the eastern Upper Peninsula. Aspen can be found on a full range of topographic positions, growing on ridgetops, upper, mid, and lower slopes. Bigtooth aspen is more prevalent on high slope positions, bedrock ridges, and shallow soil, whereas trembling aspen is more prevalent on mid and lower slopes with deeper soils.

Vegetation Description

Aspen is part of several forested systems in Michigan. Because of its diverse array of physiographic contexts, vegetation within the aspen association varies depending on geography, topography, soil texture, soil drainage, and disturbance regime. Aspen forest types are numerous according to NatureServe (2006) and include both upland and wetland types. Upland associations generally occur on deep, well- to rapidly-drained loam soils on a variety of topographic positions with gentle to moderate slope. The canopy is dominated by trembling aspen, white birch, and bigtooth aspen. Canopy associates include sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), beech (*Fagus grandifolia*), basswood (*Tilia americana*), red oak (*Quercus rubra*), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*). The subcanopy often includes serviceberries (*Amelanchier* spp.), striped maple (*Acer pensylvanicum*), and ironwood (*Ostrya virginiana*). Conifers, usually present in the subcanopy and shrub layer, include balsam fir (*Abies balsamifera*) and white spruce (*Picea glauca*). Other common constituents of an aspen understory and ground layer are eastern white pine (*Pinus strobus*) and red pine (*Pinus resinosa*).

Common shrubs include beaked hazelnut (*Corylus cornuta*), bush honeysuckle (*Diervilla lonicera*), American fly honeysuckle (*Lonicera canadensis*), wild rose (*Rosa acicularis*), blackberries and raspberries (*Rubus* spp.), Canada blueberry (*Vaccinium myrtilloides*), blueberry (*Vaccinium angustifolium*), sweet fern (*Comptonia peregrina*), witch-hazel (*Hamamelis virginiana*), and maple-leaved arrow-wood (*Viburnum acerifolium*). The herbaceous layer can include: wild sarsaparilla (*Aralia nudicaulis*), big-leaved aster (*Aster macrophyllus*), maidenhair fern (*Adiantum pedatum*), bluebead-lilly (*Clintonia borealis*), bunchberry (*Cornus canadensis*), wintergreen (*Gaultheria procumbens*), shining club moss (*Lycopodium lucidulum*), twin flower (*Linnaea borealis*), running ground-pine (*Lycopodium clavatum*), ground pine (*Lycopodium obscurum*), Canada mayflower (*Maianthemum canadensis*), Indian cucumber root (*Medeola virginiana*), bracken fern (*Pteridium aquilinum*), starflower (*Trientalis borealis*), partridge berry (*Mitchella repens*), naked miterwort (*Mitella nuda*), pinesap (*Monotropa hypopithys*), fragrant bedstraw (*Galium triflorum*), rough-leaved rice-grass (*Oryzopsis asperifolia*), large-leaved shinleaf (*Pyrola elliptica*), false spikenard (*Smilacina racemosa*), rose twisted stalk (*Streptopus roseus*), common trillium (*Trillium grandiflorum*), wild strawberry (*Fragaria virginiana*), and violets (*Viola* spp).

Lowland aspen communities are found on lower slopes, draws, and occasionally on seepages. Soils are deep, poorly-drained, fine-textured, and usually lacustrine in origin. Dominant trees include trembling aspen and balsam poplar (*Populus balsamifera*). Associates can include balsam fir, paper birch, white spruce, and burr oak (*Quercus macrocarpa*). The shrub and sapling layers are usually quite developed and include: balsam fir, tag alder (*Alnus rugosa*), serviceberries (*Amelanchier* spp.), red-osier dogwood (*Cornus stolonifera*), bunchberry, wild currants (*Ribes* spp.), wild rose, wild red raspberry (*Rubus strigosus*), and dwarf raspberry (*Rubus pubescens*). The herb layer includes: wild sarsaparilla, northern heart-leaved aster (*Aster ciliolatus*), big-leaved aster, wood anemone (*Anemone quinquefolia*), blue-joint grass (*Calamagrostis canadensis*), sedges (*Carex* spp.), blue-bead lily, spinulose woodfern (*Dryopteris spinulosa*), horsetails (*Equisetum* spp.), fragrant bedstraw, Canada mayflower, northern bluebell (*Mertensia paniculata*), and naked miterwort. The following rare plants can be found within the aspen association: fairy bells (*Disporum hookeri*, state endangered), heart-leaved arnica (*Arnica cordifolia*, state endangered), sweet cicely (*Osmorhiza *depauperata*, state threatened), and rayless mountain ragwort (*Senecio indecorous*, state threatened). (The above species lists were compiled from Gates 1930, Kittredge 1938, Westell 1960, Wells 1978, Robertson and Richardson 1985, Sakai and Sulak 1985, Comer et al. 1995, Palik and Pregitzer 1995, Peterson and Squiers 1995, NatureServe 2006, and Michigan Natural Features Inventory Biotics database).

Natural Processes

Aspen's natural function in forest ecosystem dynamics is that of a pioneer species and as such plays a key role in natural forest succession. Flourishing after a disturbance, shade-intolerant aspen proliferates through rapid establishment and growth and by out-competing slower growing, shade-tolerant tree species in the short term. A hormonal imbalance within the roots of aspen after a disturbance triggers the sprouting of suckers (Schier 1973). The growth of aspen suckers is enhanced by elevated post-disturbance light levels and resulting increased soil temperature (Maini and Horton 1966, Prevost and Pothier 2002). Aspen suckers usually have very large leaves and can grow up to eight feet tall in the first year (Graham et al. 1963). As an aspen stand matures, a self-thinning process occurs where the multiple aspen clones begin to senesce, leaving fewer, larger mature trees (Pollard 1971).

Aspen stands can deteriorate rapidly. Not only are aspen trees short-lived, but some clones are more susceptible to diseases and fungi such as hypoxylon canker (Anderson et al. 1997). Healthy stands of mature aspen can be reduced to a few dying stems in just three to six years (Shields and Bockheim 1981). The remaining trees are subject to increased wind exposure and evaporative stress, which tends to accelerate decline (Peterson and Peterson 1992). The result of this rapid decline for the aspen stand is an essential ecological process, that of coarse woody debris production. Standing dead trees (snags) are utilized as foraging sites, nesting sites, and roosts for a number of birds and mammals. Dead and downed coarse woody debris fosters a variety of fungi, mosses, lichens, herbaceous and woody vascular plants as it decays on the forest floor (Harmon 1986). Aspen logs also provide a substrate for conifer and hardwood seedling establishment. Under a natural fire regime in aspen-dominated boreal forests of Alberta, coarse woody debris can persist for as long as 50-65 years after stand initiation (Lee et al. 1997) with most snags falling 10-20 years after disturbance (Lee 1998). Persistence of aspen coarse woody debris is thought to be shorter in Michigan (i.e., 10-45 years, depending on site conditions) (Burton Barnes, Dan Kashian, and Ronald Murray, personal communication). Coarse woody debris left by deteriorating aspen stands is also a critical component of soil nutrient cycling (Harmon 1986, Hafner and Groffman 2005). Along with the coarse woody debris, shed leaves of the dominant aspen trees are very rich in calcium, and decay quickly adding essential nutrients to the forest floor. The nutrients from leaves and coarse woody debris are then utilized by later-successional species.

Prior to senescence (Photograph 1), the structure of the aspen canopy plays a role in successional capacity and understory composition. Mature aspen canopies are usually open, with crowns that block much less light than in mature northern hardwood forests (Photograph 2). This excess light allows an extensive shrub and forb layer to develop. The early-successional aspen community is quite diverse, as many shade-intolerant species take advantage of the available light. The light allowed through the canopy also supports advance regeneration of more tolerant species, such as hardwoods or conifers, whether by low stand density on xeric sites (Roberts and Richardson 1985) or by thin aspen crowns on more productive sites (Goff and West 1975). As the aspen stand ages, the understory vegetation may compete for resources and reduce soil temperature through increased shading, which contributes to the decline of aspen and further development of canopy gaps (Frey et al. 2004). The later-successional species are then poised to replace the mature aspen as disturbances create gaps in the aspen canopy.

Photograph 1. Mature aspen on the brink of senescence. (Photo by Michael R. Penskar)

Photograph 2. The relatively open canopy of a sixty-year-old aspen stand allows for the development of dense and diverse shrub and forb layer.

Canopy deterioration and gap creation is a vital occurrence in aspen stand development (Hill 2005). The nature of the disturbance, whether it is fire, windthrow, insect outbreaks, or wood decay pathogens, in turn determines the characteristics of the canopy gap (Frey et al. 2004). Gap size, which is dependent on the severity of the disturbance, will dictate the successional pathway of the individual aspen stand. Large canopy gaps tend to foster regeneration of intolerant species, essentially aspen replacing itself (Prévost and Pothier 2003). Smaller gaps lead to less understory microclimatic fluctuation and allow more shade-tolerant species to exist (Hill 2005). In forests governed by natural disturbance regimes where succession is allowed to run its course, the patches of aspen exist as a shifting mosaic within later-successional communities. Here, natural disturbance creates gaps and fosters the development of uneven-aged forests (Zhang et al. 1999).

Natural development of aspen stands is disturbance based. In Michigan, historic natural disturbances were quite common; however the scale and severity of the disturbance was fundamental to the prevalence of aspen on the landscape. In northern hardwood forests of Michigan, for example, the primary manner of disturbance was that of minor episodes of wind-throw which promoted gap phase dynamics that maintained shade-tolerant species composition. About 60% of the trees in the northern hardwood stands entered the canopy as a result of these minor episodes of light disturbance and gap creation (Frelich and Lorimer 1991). Episodes of 20% to 50% canopy removal could be expected once or twice during the life span of a cohort of trees (Frelich and Lorimer 1991). Large stands of aspen were not usually promoted by small, gap-phase dynamics of mature hardwood forests.

Photograph 3. Large-scale disturbance gaps generated by windthrow promote regenerating aspen suckers.

Pockets of early-successional habitat, such as aspen forests, typically required major, catastrophic disturbances such as fire, massive wind-throw, insect epidemics, or flooding (Photograph 3). These disturbances varied by region and local conditions and where aspen occurred initially in sparse numbers, these larger scale disturbances resulted in rapid colonization by aspen because of its ability for suckering and rapid growth. In northern hardwood forests, 3% to 15% of the landscape over a 15 year period would have been affected by disturbances of at least moderate intensity (Lorimer and White 2003). Moderate- and large scale disturbance events resulted in a heterogeneous mixture of species and age classes in which aspen clones colonized many of the most recently disturbed locations within a shifting mosaic of forest cover.

Dominance on the Landscape

Many studies have examined the composition of circa 1800 forests of Michigan (Whitney 1986, Whitney 1987, Palik and Pregitzer 1992, Comer et al. 1995, Van Deleen et al. 1996, Zhang et al. 2000, Leahy and Pregitzer 2003). The prevailing view is that aspen played a reduced role in circa 1800 forests, compared to current forests of Michigan. Aspen was not absent from the circa 1800 landscape, but rather was a minor component, relegated to isolated areas of natural disturbance and stream and swamp margins (Graham et al. 1963, Whitney 1987, Frelich 2002). Near the University of Michigan Biological Station in the northern Lower Peninsula, 87% of bearing and line trees recorded by the original surveyors were hemlock, beech, or white pine (Palik and Pregitzer 1992). In contrast, present day relative basal areas for bigtooth aspen in the same area was 74% (Palik and Pregitzer 1992). Another study in northeastern Lower Michigan shows a shift in acreage of the aspen association land cover type from 0% circa 1800 to 17.2% present day (Leahy and Pregitzer 2003). Comer et al. (1995) estimated circa 1800 aspen cover for the whole state to occupy 326,769 acres, 0.87 % of the state and 0.99% of forested landcover. Aspen cover for the entire state was calculated from IFMAP (Integrated Forest Monitoring, Assessment, and Prescription) landcover data from the year 2000 to be 2,548,842 acres (7%), which is approximately 14% of total forested landcover for the state (Michigan DNR 2000, 2001a, 2001b). According to analysis of FIA data in the Great Lakes, aspen-birch forest has declined since its recorded peak in the 1930s by 24%, with the acreage decreasing in Michigan by 37% from 1935 to 1993. Despite the trend of decline from the 1930s, the current extent of the aspen association is likely an order of magnitude greater today than in the circa 1800 forests of Michigan (Cleland et al. 2001).

Aspen's current prevalence within Michigan's landscape mosaic of early-successional forest is tied to cataclysmic and unprecedented anthropogenic disturbances of the past (Host et al. 1987, Palik and Pregitzer 1992, Zhang et al. 2000, Lorimer 2001, White et al. 2004) and more recent management activities (Karamanski 1989). In the late nineteenth and early twentieth century, nearly all of Michigan's primary white pines, eastern hemlocks, and northern hardwoods were removed by extensive logging (Whitney 1987). The vast slash barrens left from ubiquitous logging provided fuel for catastrophic fires that dominated much of the post-logging era (Graham 1963, Karamanski 1989). Most of the competing hardwoods were eliminated by the slash fires and the mineral seed bed was perfectly prepared for pine regeneration (Whitney 1987). However, although the original white pines on the drought prone, coarse-textured soils of northern Lower Michigan were themselves a product of earlier wildfires, the pine seed source had been removed through extensive logging (Whitney 1987). After logging removed the conifer seed source and the frequent and devastating fires that followed the logging boom eliminated the advance regeneration of prevalent hardwood deciduous species (Palik and Pregitzer 1992), the stage was set for aspen dominance.

Slash fires facilitated aspen dominance in multiple ways. Aspen seedlings are very susceptible to ground competition, therefore seedling establishment requires minimal ground vegetation (Barnes 1966). Fire reduces ground layer competition by killing or top-killing woody seedlings and also provides an environment of largely bare mineral soil for seedling establishment. In addition, a single, top-killed aspen stem resulting from fire can produce many suckers all capable of growing into an adult tree. The dominance of aspen today is thought to be more the result of suckering and sprouting in response to fire, rather than from seedling establishment (Barnes 1966).

Current forest and wildlife management practices often maintain and expand early-successional forest systems such as the aspen association through repeated, short-rotation harvest regimes. In many areas, aspen stands that replaced dry-mesic northern forests and mesic northern forests have been maintained and even expanded by silviculture and wildlife management geared toward promoting pulp production and providing favorable habitat for game species of early-successional forests (particularly white tailed deer, turkey, woodcock, and grouse) (Photograph 4).

Wildlife

The aspen association provides habitat to a wide array of wildlife and various successional stages of aspen foster specialized types of organisms. As noted above, some of the game species that utilize the aspen association include deer, turkey, woodcock, and grouse. In addition, the aspen association provides important habitat for numerous non-game animals, including several rare species.

Aspen stands are an important food source for white-tailed deer (*Odecoilus virginiana*). Deer heavily browse aspen sprouts, which are not the most preferred food for these ungulates. Deer browse in areas of high deer density may actually impede aspen regeneration after final harvest (Westell 1960, Graham et al. 1963). Aspen's relatively open canopy allows light to penetrate to the shrub and herbaceous layers, thus stimulating lush vegetation for deer browse. The mature forests of northern Michigan and throughout the Great Lakes, prior to turn of the century logging, were sparsely populated by deer (Alverson et al. 1988, Langenau 1994). The current, widespread, early-successional habitat that has been maintained through forest and wildlife management practices has helped maintain high deer densities in many locations. This management has had many repercussions throughout other forest communities in Michigan by increasing deer browse pressure, specifically impacting diversity of northern hardwoods and cedar swamps, and limiting conifer and oak regeneration (Alverson et al. 1988, Van Deelen et al 1996, Augustine and Frelich 1998, Rooney and Waller 2003, Kraft et al. 2004).

Aspen staminate flower buds are a primary source of food for ruffed grouse (*Bonasa umbellus*) in winter (Jakubas et al. 1989, Jakubas and Gullion 1991). Grouse density has been highly correlated to use of trembling aspen as a dominant food supply (Jakubas and Gullion 1991). Ruffed grouse tend to feed on older trees that are in poor health (Svoboda and Gullion 1972), partly due to the decreased chemical defense ability in older aspen clones (Jakubas and Gullion 1991). Small staged clear-cuts in aspen tend to increase grouse populations by adding a diversity of age classes and habitat conditions within aspen stands (McDonald et al. 1998). High stem densities of young aspen stands protect grouse and American woodcock (*Scolopax minor*) from predators (Dessecker and McAuley 2001). Woodcock often nest in young aspen stands and utilize moist early-successional forest for foraging (Gregg and Hale 1977, Dessecker and McAuley 2001). Aspen is also considered high-quality habitat for wild turkey (*Meleagris gallopavo silvestris*) (Nguyen et al. 2004).

Photograph 4. A twenty-year-old stand of aspen, considered high-quality deer, turkey, and grouse habitat.

Aspen is habitat for numerous non-game mammals. Small mammals such as the red-backed vole (*Clethrionomys gapperi*) have been found to prefer recently clear-cut aspen stands, due to the amount of slash, which maintains the vole's moisture and temperature requirements during foraging. Alternately, logging slash was found to physically impede foraging in leaf litter for some small mammals, such as the masked shrew (*Sorex cinereus*) (Yahner 2006). Aspen snags that have decayed heartwood, yet maintain relatively sound sapwood structure have been found to serve as roosts for big brown bats (*Eptesicus fuscus*), which will return to the same snag in subsequent years (Willis et al. 2003). Other bats such as the little brown bat (*Myotis lucifugus*) or the silver-haired bat (*Lasionycteris noctivagans*) were also found to utilize aspen stands that were past the mature stage, preferring tall, near-dead or newly-dead trees with low leaf cover (Crampton and Barclay 1998).

Large, mature aspen trees are selected as nest trees by some raptors. Red-shouldered hawks (*Buteo lineatus*, state threatened) will choose dominant, mature aspen trees with suitable structure to build stick nests (Cooper 1999). Northern Goshawks (*Accipiter gentiles*, state special concern) have also been observed utilizing aspen habitat. Forest song bird species diversity is enhanced within aspen stands through the practice of leaving small (0.5 acre to 2.0 acre) uncut patches within aspen clear-cuts that ranged in size from 5 acres to 40 acres respectively (Merrill et al. 1998). Aspen associated with riparian areas provide preferred foraging habitat for beaver (*Castor canadensis*). Aspen is a favored food of beaver and a high proportion of aspen cover in the landscape can contribute to high beaver populations (Wisconsin Department of Natural Resources 2001)

Biodiversity Management Considerations

This section details opportunities for enhancing biodiversity of managed and unmanaged aspen associations at multiple scales and discusses strategies for restoring these systems to later successional forest types.

From a small-scale biodiversity perspective, aspen stands provide species-rich groundcover and habitat that is important for numerous wildlife species. However, the issue becomes more complex when one considers ecological diversity and landscape integrity. Logging-induced shifts toward greater dominance of aspen may enhance stand-scale diversity while simultaneously reducing landscape-scale diversity (Reich et al. 2001). Increasing landscape-level biodiversity and ecological function would dictate shifting emphasis towards regenerating more shade-tolerant species and away from maintaining large aspen clones (Palik et al. 2003). Presently, the ecological processes of natural succession are often missing from managed landscapes (Niemelä 1999). Aspen stands that are succeeding to later-successional forest types such as pine or northern hardwoods are often harvested to maintain the aspen cover type. In this way, silvicultural practices tend to impose a stagnant pattern on landscapes (Cohen 2005). Forest rotations under 110 years have no natural precedent and can create an artificial, homogenized landscape with single cohort stands occupying over 15-25% of the landscape (Seymour et al. 2002). In addition, the placement of aspen stands on the landscape can contribute to forest fragmentation and excessively high deer browse pressure in adjacent sites managed for biodiversity. Where reducing forest fragmentation and increasing landscape-level biodiversity and ecological integrity are goals, aspen stands can be allowed to succeed to dry-mesic or mesic northern forests. Similarly, where protection and management of high-quality natural communities or ecological reference areas is a primary management objective, overbrowsing by deer may be reduced by allowing nearby aspen stands to succeed to late-succesional forests. Mature upland forests provide deer less suitable spring and summer habitat than early successional forest. Over time, natural plant succession of early-successional habitat to more mature forest can lead to the development of lower quality and quantity of spring and summer deer food and as trees reach maturity, deer utilize these upland habitats less frequently (Verme 1969, Kohn and Mooty 1971, Felix et al. 2004).

Current forestry research is emphasizing the importance of mimicking natural disturbances that promote more dynamic patterns of vegetation types and differing age classes (Zhang et al. 1999, Seymour et al. 2002) and many ecologists believe that the conservation of biological diversity depends on this approach (Lorimer 2001). Historically, the natural disturbance regime of upland forests created a shifting mosaic pattern of vegetation across the landscape (Zhang et al. 1999). Frequent small disturbances resulted in a diverse stand age structure within large blocks of uneven-aged and even-aged forest. Infrequent catastrophic windthrow and fire created patches of early-successional forest that moved across the historical landscape over time. Foresters are now realizing the importance of allowing natural senescence and succession to take place.

Sustainability of forest resources may depend on allowing natural succession to play a role in maintaining ecological processes that will ensure long term forest productivity. Aspen is known to be a very calcium-demanding species (Paré et al. 1993) that stores high concentrations of nutrients in perennial tissues (Pastor and Bockheim 1984, Yu and Sucoff 2001). Following clear-cutting in aspen stands in Michigan, Richardson and Lund (1975) documented nutrient losses, especially of Calcium and Magnesium, on nutrient-rich soils (i.e., loamy sands). Scientists across the Great Lakes region (e.g., from Wisconsin [Boyle et al. 1973] and Minnesota [Silworth and Grigal 1982]) and in the southern boreal region of Canada (Bergeron and Harvey 1997) speculate that with constant regeneration of single cohort aspen stands in the same location, soil calcium could be depleted, altering long-term nutrient cycling. In addition, short-rotation aspen management in the northern Lower Peninsula and in the western Upper Peninsula of Michigan has been found to reduce microbial biomass and activity, thus possibly further limiting the future productivity of these ecosystems (Hassett and Zak 2005). In the western Upper Peninsula, the northern Lower Peninsula, and northern Minnesota, repeated total tree harvesting on sandy soils was found to reduce aspen growth and productivity (Stone 2001, Stone 2002). In addition, compaction of the soil resulting from harvest roads and skid trails in northern Minnesota impacts understory vegetation (Berger et al. 2004). Studies in the western Upper Peninsula, the northern Lower Peninsula, and northern Minnesota revealed that soil compaction on fine-textured soils can reduce aspen sucker density, diameter and height growth, and biomass production (Stone and Elioff 2000, Stone 2001, Stone 2002).

Study of the boreal aspen forests of Canada have illuminated some pertinent conclusions as to the management of single cohort aspen stands. Researchers suggest the importance of maintaining forested patches within managed landscapes and managing towards more diverse mixed wood stands that reflect natural disturbance regimes. Some argue for silvicultural practices to be perceived as disturbance and mimic more closely those of natural origin. By favoring species replacement and allowing a stand to transition from one type to another, forests will be more diverse, and therefore more resistant to diseases and exotic insect outbreaks (Bergeron and Harvey 1997). A shift to partial cutting could better mimic the natural senescence of aspen and generation of canopy openings. Residual networks of remnant forest patches left during partial cutting can help ensure the survival of interior understory species and species sensitive to complete canopy removal (Berger et al. 2004, Moses and Boutin 2001). Clear-cuts successfully repeat those stand-replacing anthropogenic disturbances of the early 1900s that led to the initial shift in importance towards early-successional forests. However, landscape-level, stand-replacing disturbances are considered to be much rarer than small within-stand patches of disturbance (Seymour et al. 1999). Canopy gaps in trembling aspen boreal forests are frequent occurrences and present as early as 60 years following stand origin (Hill et al. 2005). Gaps in shorter living aspen stands in Michigan can form within 40 years (Frey et al. 2003). Partial cutting could slowly give way to smaller clear-cuts, as the portions of intolerant aspen regeneration increase within these gaps (Bergeron and Harvey 1997). These practices resemble natural disturbances such as budworm outbreaks and minor windthrow occurrences (Bergeron and Harvey 1997). Partial cuts in aspen stands do carry with them a trade-off in terms of production potential. Studies in riparian aspen stands in northern Minnesota indicate that leaving some canopy in order to maintain riparian ecological function, decreases the density and biomass of the aspen production (Palik et al. 2003).

Research in boreal aspen forests has also compared regeneration of aspen after wildfire, a natural disturbance, with the regeneration after a clear- or partial-cut. Although the soil properties were affected differently with the two methods, productivity of aspen did not differ (Pare et al. 2001). The major difference between fire and partial or clear-cutting was structural, in that fire left many more dead standing trees (Pedlar et al. 2002, Haeussler and Bergeron 2004). Standing dead trees or snags have a great deal of ecological value and are important components of healthy forest ecosystems (Harmon et al. 1986). A crucial step in mimicking natural disturbances in aspen clear-cuts is to leave some mature live and dead stems (Lee et al. 1997, Haeussler and Bergeron 2004).

In many areas, aspen forests that replaced dry-mesic northern forests and mesic northern forests have been maintained and often expanded by short-rotation silviculture and wildlife management (Cohen 2005). Self-replacement of aspen in large gaps, either of natural or clear-cut origin, has delayed some succession to conifers (Cumming et al. 2000). Some researchers feel restoring white pine where it has been replaced in the landscape by aspen will be difficult due to competing aspen roots and white pine blister rust (Whitney 1987, Peterson and Squiers 1995). However, other research suggests that early-successional forest, especially aspen stands, can function as nurse crops for the rehabilitation of late-successional forests (Curtis 1959, Mosseler et al. 2003) (Photographs 5 and 6). A positive relationship has been observed between white pine growth rate and local aspen abundance as aspen stands age (Peterson and Squiers 1995). In addition, white pine is the most dominant species of advance regeneration under some big-toothed aspen stands and does not necessarily require a canopy gap for successful establishment and growth (Palik and Pregitzer 1995).

Photographs 5 and 6. Aspen stands can function as nurse crops for conifer regeneration. (Photograph 6 by Joshua G. Cohen)

Allowing early-successional stands of aspen and paper birch to revert back to late-successional forest would require the employment of the management tool of patience (Cohen 2005). By allowing aspen stands, old fields, and wildlife openings to succeed to white pine, managers can re-establish the prevalence of the white pine seed source throughout the landscape and develop sites for eventual mature forest re-establishment. Forests of the Great Lakes are becoming increasingly fragmented (Mladenoff et al. 1993, Heilman et al. 2002, Bresse et al. 2004), and forestry and wildlife management practices that focus on species- and stand-based management have directly and indirectly promoted landscape fragmentation and exacerbated edge effects (Bresse et al. 2004). Allowing early-successional aspen forest to succeed to late-successional dry-mesic northern forest and mesic northern forest will not only increase uncommon forest types in the Great Lakes landscape, it can also help dampen the effects of forest fragmentation.

Research Needs

Demand for aspen products (e.g., paper, lumber, wood composite building material, and biofuel) and aspen as wildlife habitat is increasing at the same time there are increasing pressures to enhance the non-commodity, non-game benefits of aspen forests. Aspen management involves a delicate balance between economic, social, and ecological values. One method of mitigating the strain on this resource is to research where aspen is grown in relation to where it would have the greatest growth potential (Gustafson et al. 2003). Perhaps the total acreage of aspen could decline if stands managed for aspen were more productive. However, the most productive aspen stands may also be high-quality sites for diverse late-successional forest. This idea raises important questions: How can resource practitioners make aspen production and management more compatible with ecological goals? Where are aspen stands in relation to 1) areas of high site index, 2) areas of limited forest fragmentation, and 3) areas of high biodiversity? Aspen management is thought to increase deer populations which, in turn, have many deleterious effects on adjacent native communities because of increased deer browse pressure (Westell 1960, Alverson et al. 1988, Van Deelen et al 1996, Augustine and Frelich 1998, Wisconsin Department of Natural Resources 2001, Horsley et al. 2003, Rooney and Waller 2003, Kraft et al. 2004). Will high-production aspen sites be located near ecological reference sites, specifically large tracts of congruent high-quality natural areas? Can fragmentation of natural forested areas be limited by allowing lower productivity aspen stands to succeed into mature forests? An investigation into location, productivity, and ecological setting of areas of aspen management could lead to more effective balancing of the economical, social, and ecological uses of this resource.

Additional research could examine the intensity with which aspen is harvested. How does repeated, short-rotation management, which has no natural disturbance precedent in terms of intensity and return interval, affect nutrient dynamics, floristic and faunal composition, site potential, and late-successional seed sources at multiple scales? What are the landscape-level effects of current management practices that utilize stand-replacing procedures? Research aimed at these and similar questions will contribute to sustainable forest management practices and the long-term viability of Michigan forests.

Other Classifications:

Michigan Natural Features Inventory (MNFI): Mesic northern forest, dry-mesic northern forest, dry northern forest

Michigan Natural Features Inventory Circa 1800 Vegetation: Aspen-Birch Forest (413).

Michigan Department of Natural Resources (MDNR): A-Aspen

Michigan Resource Information Systems (MIRIS): 410 (Broadleaved Forest/Upland Deciduous Forest), 4131 (Aspen/Birch), 4132 (Bigtooth Aspen), 4133 (Trembling Aspen), 4134 (Undifferentiated Aspen/White Birch), 414 (Wetland Deciduous/ Lowland Forest), and 4142 (Aspen)

Integrated Forest Monitoring, Assessment, and Prescription (IFMAP): Aspen Association

NatureServe/Nature Conservancy National Classification:
CODE; ALLIANCE; ASSOCIATION; COMMON NAME

I.B.2.N.b; *Populus tremuloides - Betula papyrifera* Forest Alliance; *Populus tremuloides - Betula papyrifera* / (*Abies balsamea*, *Picea glauca*) Forest; Aspen - Birch / Boreal Conifer Forest

I.B.2.N.b; *Populus tremuloides - Betula papyrifera* Forest Alliance; *Populus tremuloides - Betula papyrifera* - (*Acer rubrum*, *Populus grandidentata*) Forest; Aspen - Birch - Red Maple Forest

I.B.2.N.b; *Populus tremuloides - Betula papyrifera* Forest Alliance; *Populus tremuloides - Betula papyrifera* / *Acer saccharum* - Mixed Hardwoods Forest; Aspen - Birch / Sugar Maple - Mixed Hardwoods Forest

I.B.2.N.d; *Populus tremuloides* Temporarily Flooded Forest Alliance; *Populus tremuloides - Populus balsamifera* - Mixed Hardwoods Lowland Forest; Aspen - Balsam Poplar Lowland Forest

I.C.3.N.a *Picea glauca - Abies balsamea – Populus* spp. Forest Alliance; *Picea glauca - Abies balsamea - Populus tremuloides* / Mixed Herbs Forest; Spruce - Fir - Aspen Forest

I.C.3.N.a *Pinus strobus* - (*Pinus resinosa*) - *Populus tremuloides* Forest Alliance; *Pinus strobus* - *Populus tremuloides* / *Corylus cornuta* Forest; White Pine - Aspen - Birch Forest

II.B.2.N.a; *Populus tremuloides* Woodland Alliance; *Populus tremuloides* - (*Populus grandidentata*) Rocky Woodland; Mixed Aspen Rocky Woodland

Related Abstracts: Red-shouldered hawk, northern goshawk, mesic northern forest, dry-mesic northern forest, dry northern forest

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