Introduction

The return of plant life to Michigan after final recession of the glaciers encompasses a complex and fascinating sequence of events. Plant species migrated in from various places and at different times. Once established on the landscape, their distributions and abundances were in constant fluctuation in response to variations in climate and ecological processes. This chapter is the story of the in-migration and redistribution of plants during post-glacial times. Only by knowing the forces and factors that have affected plants in Michigan’s past can we understand their current distribution (Chapter 21). Moreover, insights gained from investigations of past biodynamics can be used to predict future changes in the species composition and distribution of Michigan’s ecosystems in response to global warming and other future environmental changes that may occur.

The current landscapes of Michigan hold the keys to unraveling the complex history of plant occupation in our state. Plant fossils preserved in the sediments of lakes and bogs record the details and sequences of vegetation shifts and climate changes in the state since the last glaciation. By retrieving these sediments and examining the fossils they contain, we can obtain a better understanding of the dynamics of current forest systems in Michigan. Specifically, the analysis of past vegetation (paleoecology) provides a long-term (prehistoric) perspective on the plant geography and forest ecology of Michigan.

Paleoecological proxies and research methods

The vegetation history of Michigan can be largely reconstructed through the study of plant fossils, such as seeds, leaves, stems, cones, and pollen grains, most of which are recovered from aquatic sediments. These fossils can be identified to taxa (species, genus or family levels) based on their morphology, i.e., shape and size. Once the fossils are identified, they are correlated to their modern living representatives, which have specific tolerance ranges for temperature, precipitation, and soil type—a concept known as the “modern analog” principle (Overpeck et al. 1985). Fossils of different plants found together, a fossil assemblage, are indicative of a particular vegetation assemblage that may have existed for a time interval in the past. Based on the modern analog principal, shifts in the dominance of different taxa from assemblage to assemblage indicate vegetation change through time, and can be used to infer past climate and landscape changes.

Fossils are preserved when plant remains (pollen, seeds, etc.) are washed or blown into lakes and bogs, accumulate at the bottoms of these basins, and become buried by sediments (Fig. 7.1). Persistent moisture in aquatic sediments, as well as acidic conditions, inhibit decay and allow for the preservation of these plant fossils. The
deposition and preservation of plant fossils may, however, be episodic in bogs and peatlands, because they often undergo periodic drying. Consequently, lakes and ponds are preferred as sites for paleoecological study (Bennett and Willis 2001).

Pollen production rates vary among plant species. Wind-pollinated plants, such as oaks (Quercus) and pines (Pinus), produce large quantities of pollen, which are mixed together by air currents and fall into aquatic environments as “pollen rain” (Davis 1967). Insect-pollinated plants, such as many species of maple (Acer), produce significantly less pollen and thus are under-represented in the pollen rain.

Sediments from the bottoms of lakes and bogs, which contain these plant fossils, are retrieved using a coring device (Figs. 7.1, 7.2). The coring device, operated from the water surface using either a raft or the ice as a platform, collects sediment cores from the bottom of the lake (or pond) basin. Sediment samples are collected at regularly spaced intervals from the cores, and later analyzed for pollen and plant macrofossils (Fig. 7.1). Fossil seeds and other plant macrofossils from certain stratigraphic levels can also be sampled, and their ages assessed using radiocarbon dating. The resulting radiocarbon ages can then be converted to calendar “dates” (Stuiver et al. 1998; Chapter 13).

Pollen samples from the cores are first prepared by removing any sediments (sand, silt, and clay) from the sample to concentrate the pollen, using a series of standard chemical treatments (Faegri and Iversen 1975). A sub-sample of each prepared pollen sample is then viewed under a microscope and individual pollen grains are identified and counted (Bennett and Willis 2001). The resulting pollen data are plotted as abundance in standard pollen diagrams. The pollen diagram shown in Figure 7.3 is based on data obtained from the North American Pollen Database (www.ncdc.noaa.gov/paleo/napd.html)—a repository for pollen data collected by different scientists from sites all over North America. Note that the X (horizontal) axis of these diagrams shows the percentage of total pollen for each taxa (pollen type) and the Y (vertical) axis displays the age of the sediments and their depth of the sediment core. Pollen diagrams are read from the bottom upwards with an eye toward dramatic shifts in the relative abundance of key pollen types or taxa. A shift in the relative abundance of a key pollen type may indicate a change in the surrounding forest, in response to a warming or cooling of

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**FIGURE 7.1** Schematic illustration (not to scale) of pollen and macrofossil deposition in and around a typical lake basin.
the regional climate, or some other environmental change, e.g., fire or precipitation regime. Pollen diagrams may be divided into pollen zones, which are considered to represent fossil assemblages, and hence plant communities, of the past. Shifts in the dominance of different taxa between pollen assemblages indicate large vegetation shifts, and, by inference, are proxies for paleoclimate change. Maps displaying isopolls, lines representing equal pollen percentages for individual taxa, are also useful in interpreting past vegetation shifts through time (Fig. 7.4).
**FIGURE 7.3** Summary of pollen data from Wintergreen Lake, Kalamazoo County. The study was originally conducted by Manny et al. (1978). Pollen data were downloaded from NAPD (2005).

**FIGURE 7.4** Maps of selected species isochrones, for multiple time periods in Michigan’s past: 13,000, 11,000, 10,000, 7,000, 3,000, and 500 years ago. The isochrones represent lines of equal pollen percentage for each taxa in the pollen record at a variety of sites, for spruce (20%), pine (20%), hemlock (3%), birch (10%), elm (10%), ash (5%), maple (2%), beech (2%), and oak (20%). The percentages represent the amount of pollen for each species in a particular lake’s record. After Webb et al. (1983).
The vegetation history of Michigan over the last 17,000 years

In this chapter, we focus on the broad changes in the species composition and distribution of plant communities in Michigan over the past 17,000 years, primarily using data from studies of fossil pollen, augmented by analyses of seeds and other plant macrofossils. The last 17,000 years are referenced in calendar years before present. For a discussion of calendar vs radiocarbon years, see the Focus Box in Chapter 13.

Vegetation changes through time are discussed below in five different intervals of relative forest stability. This reconstruction focuses on the arrival, establishment, and range (distributional) shifts of important tree species and associated forest communities. We also examine the inferred paleoclimate changes that are largely responsible for these vegetation shifts. The paleovegetation changes are summarized in the isopoll maps and charts for important species (Fig. 7.4, and, as reconstructed plant communities, Fig. 7.5). Also, two pollen diagrams from Michigan, one from Wintergreen Lake, which is representative of the southern Lower Peninsula (Fig. 7.3; NAPD 2005) and the other, from Kitchner Lake, which is typical for the Upper Peninsula (Fig. 7.6; NAPD 2005), are provided to illustrate the major paleovegetation changes in the state.

FIGURE 7.5 Summary of the major vegetation changes in Michigan (by sub-region) from 17,000 years ago to present. Solid arrows indicate the persistence of a forest type and dashed arrows indicate fluctuations between types.
Plant colonization: 17,000 to 13,000 years ago

The first plant communities to colonize eastern North America after the recession of the glaciers were mainly comprised of species that exist today in cold, Arctic environments. These and all subsequent plants migrated northward from areas south of the maximum glacial limit after the ice sheet melted. The first of these plants arrived in the southern Lower Peninsula about 17,000 years ago. They did not shift northwards as biomes—where entire collections of tree species migrate together—but rather, they moved in an individualistic manner dependent upon species-specific rates of seed production, dispersal and the availability of suitable micro-sites (Davis 1981, Jackson et al. 2000). The plants colonized an unstable landscape that was undergoing periglacial (intermittently frozen) processes and which had variable amounts of inundation by glacial lakes and meltwater streams (Wright 1976; Chapters 6, 8, 13).

Glacial readvances also affected the timing and pattern of plant colonization and succession. Because the landscapes of Michigan were unstable at this time and some lakes were not yet formed or remained filled with ice blocks, only a few of the plant fossil sites record this initial colonization of arctic plants. For example, this pioneering period of vegetation is not represented in the pollen record of Wintergreen Lake (Fig. 7.3). Available plant fossil data indicate that this early, colonizing vegetation was “tundra-like,” being comprised of mainly non-arboreal (herb) plants, including sedges (species of Cyperaceae), wormwood (Artemisia), and shrubs such as willow (Salix) (Kerfoot 1974). Leaves of arctic tundra plants, such as arctic dryad (Dryas integrifolia) and snowbed willow (Salix herbacea), were recovered along with willow stems that date to 13,950 years ago at the Cheboygan bryophyte bed site in the northern Lower Peninsula (Larson et al. 1994; Chapter 6). This tundra-like phase occurred earlier in areas to the south, e.g., from 20,600 and 18,900 years ago, in northeastern Illinois (Curry and Yansa 2004). Based on the temperature ranges of these arctic-adapted plant species, Baker et al. (1986) estimated that the average summertime temperature in the upper Midwest was about 10°C cooler during at this time than it is today. Soon thereafter, however, the climate began to warm and spruce vegetation invaded, replacing the arctic-adapted plants.

Spruce-sedge parkland: 13,000 to 11,000 years ago

Pollen and plant macrofossil records throughout central and eastern North America all report spruce-dominated vegetation during this period—the transition from the Late Pleistocene to early Holocene. Originally, this vegetation was interpreted as that of a spruce-dominated, or boreal forest (Delcourt and Delcourt 1991). But more recently, this vegetation has been considered to have a more open character, resembling more of a spruce-sedge parkland (Yansa 2006). Ample habitat for sedges and other marsh plants was provided by the high water tables—a result of melting ice blocks and permafrost (Webb et al. 2004). The dominant tree species of this community was white spruce (Picea glauca);
however, black spruce (*P. mariana*) occupied swampy locales (Pregitzer et al. 2000, Webb et al. 2004). Subdominant (secondary) trees included black ash (*Fraxinus nigra*), poplar or aspen (*Populus spp.*) and balsam fir (*Abies balsamea*) (Kapp 1999).

There are numerous reports of now-extinct Pleistocene megafauna associated with the spruce fossils of the Upper Midwest. In Michigan, finds of mastodon (*Mammut americanum*) and less commonly mammoth (*Mammuthus jeffersoni*) skeletons are associated with the spruce phase (Oltz and Kapp 1963, Kapp 1986; see Focus Box below; Chapter 8).

The onset of the spruce phase in Michigan occurred earliest in the southern part of this state and later towards the north. This pattern is expected, because the glaciers retreated in a northwards direction, resulting in a temperature gradient (cooling) from south to north. In the southwestern Lower Peninsula, the spruce phase persisted from about 15,300 to 11,400 years ago in the vicinity of Wintergreen Lake (Fig. 7.3). During the latter part of the spruce phase in this area, deciduous trees, such as poplar, black ash, and ironwood (*Ostrya virginiana*) or bluebeech (*Carpinus caroliniana*), appeared in greater numbers (Kapp 1999).

Meanwhile, to the north, local climatic conditions were affected by cold, dense winds blowing off of the ice sheet (Barnosky et al. 1987, Krist and Schaetzl 2001), accounting for the presence of tundra and boreal species in the pioneering vegetation of northern Michigan (Lawrenz 1975, Pregitzer et al. 2000). Over time, due to the warming climate, the cold-tolerant tundra plants decreased in abundance and eventually died off, while boreal ones remained.

**FOCUS BOX: Mastodon habitat in the Lower Peninsula**

Numerous pollen and plant macrofossil studies conducted by the late Ronald Kapp and his students of Alma College have documented that a spruce-sedge parkland occupied Lower Michigan during the Late Pleistocene (17,000–10,000 years ago). These studies identified an open environment with some trees, mainly white spruce (*Picea glauca*) and ash (*Fraxinus*), and abundant herbs, such as wormwood (*Artemisia*), grasses (*Poaceae*), and sedges (*Cyperaceae*). Several of these studies involved the analysis of plant fossils in direct association with mastodon (*Mammut americanum*) skeletons, e.g., Oltz and Kapp (1963), Held and Kapp (1969), Kapp (1986), Bears and Kapp (1987), and Kapp et al. (1990) (Chapter 8). For example, at the Heisler Mastodon site in Calhoun County, wood in contact with mastodon bones dates to 13,080 years ago (Bears and Kapp 1987). A few of the mastodon skeletons show signs of butchery and post-date the local arrival of Paleoindians (Fisher 1984). The Eldridge Mastodon specimen, for example, has deep cut marks, which indicate the presence of Paleoindians in Montcalm County sometime between 14,120 and 12,000 years ago, based on radiocarbon dates on wood that bracket the skeleton (Kapp et al. 1990). The mastodon habitat reconstructed from these pollen and plant macrofossil studies is depicted in the figure. Refer to the legend of Figure 7.1 to interpret the plant icons.
The boreal spruce phase in the Kitchner Lake area of the Upper Peninsula (Delta County) occurred from 13,000 to 10,300 years ago (Fig. 7.6). Birch (Betula) and pine (Pinus) were present in low abundances in certain areas of the Upper Peninsula during this time, but they became more common after the boreal (spruce) phase (Pregitzer et al. 2000).

The climate changed, warming quickly, during the spruce phase, driven mainly by shifting orbital cycles (variations in the orbit of the earth around the sun) that affected the amount of solar radiation (insolation) received at the earth’s surface (COHMAP 1988). Astronomical calculations and models suggest that, from 12,000 to 9000 years ago, 7% more insolation was received during summers and 7% less during winters, compared to today (COHMAP 1988, Kutzbach et al. 1998). Climate model data also suggest that by about 11,000 years ago, summer temperatures were comparable to or slightly warmer (ca. +1°C) than modern (pre-industrial levels, ca. A.D. 1800), whereas winters were still several degrees cooler (Kutzbach et al. 1998). In response to this warming, several species of pine and birch as well as other deciduous trees became more common, and closed-canopy forests developed (Kapp 1999).

**Early Holocene species diversification: 11,000 to 6800 years ago**

The early Holocene was marked by rapid northward plant migration in response to climate changes, resulting in increased species diversity in the forests of both the Upper and Lower Peninsulas. By this time, the ice front was positioned farther north, primarily in Ontario, and was retreating rapidly, and the waterlogged landscapes of Michigan were starting to dry out. Summers were now slightly warmer (ca. +1°C) than they are today, but winters were still several degrees cooler (Webb et al. 2004).

As summers in Michigan became warmer, more temperate types of conifers and pines displaced spruce northwards. Pine first appeared in the southwestern Lower Peninsula during the spruce phase at 13,000 years ago (Fig. 7.3), and by 11,000 years ago several species of pine dominated many of the forests of the southern Lower Peninsula (Manny et al. 1978, Kapp 1999). Jack and/or red (Pinus banksiana/resinosa) pine arrived first, followed by white pine (Pinus strobus). During this period of pine expansion, several deciduous taxa also increased in abundance, including birch (most likely Betula papyrifera), ironwood (Ostrya or Carpinus), and elm (Ulmus), in response to the warming summers. These trees became significant components of these pine-dominated forests. The resulting community, a mixed conifer-northern hardwood forest, dominated primarily by pine, occupied most of the southern Lower Peninsula. Other deciduous trees, such as oak, walnut (Juglans), hickory (Carya), and basswood (Tilia), also expanded their ranges into the Lower Peninsula after 11,000 years ago, but were probably limited to favorable micro-habitats (Kapp 1999).

Meanwhile, in the northern Lower Peninsula and most of the Upper Peninsula, spruce persisted as the dominant tree until about 10,000 years ago. At this time, the spruce-pine forests in the central Upper Peninsula transitioned to pine-dominated forests that included (as sub-dominants) birch, aspen, hornbeam, juniper/cedar (probably Thuja occidentalis), and elm (Fig. 7.6). The spruce-pine forests in the western Upper Peninsula persisted for several more centuries, until about 10,500 years ago (Booth et al. 2002).

Thus, by 10,000 years ago, two forest ecotones, or boundaries, between major forest types were present in Michigan. The northernmost ecotone resided between the spruce-pine forests in the western Upper Peninsula and the pine-dominated forests in the eastern Upper Peninsula and northern Lower Peninsula (Webb et al. 1983). The second ecotone existed in the center of the Lower Peninsula between the pine-dominated forests (to the north) and the mixed conifer-northern hardwood forests in the southernmost part of the state (Webb et al. 1983).

By 9000 years ago, the ranges of the oak species had expanded dramatically northwards within the southern Lower Peninsula, as pines declined in abundance. The shift from mixed conifer-hardwood forests (dominated by pine) to oak-dominated forests in the southern Lower Peninsula at this time is evident in Figures 7.3 and 7.5. Oaks are well adapted to warm and dry conditions; their increased abundance indicates the development of these climatic conditions (Wolf 2004). Maple (Acer) had also reached the Lower Peninsula by 9000 years ago and had become a component of local deciduous forests. Maple trees require more mesic (moist) conditions for optimal growth than do oak trees, so the presence of maple indicates moister conditions in locales where maple was dominant. Meanwhile, farther north, stands of spruce decreased dramatically in the Upper Peninsula (replaced by pine) as spruce continued its migration northward into Ontario, in response to climatic warming (Liu 1990). For the first time since initial colonization, spruce became a minor component of plant communities through-
out Michigan (spruce pollen abundances are <20% after 9000 years ago; Figs. 7.3, 7.6). Michigan had become a warm environment.

The trend of plant species diversification in local floras, evident in the isopolls from 11,000 to 10,000 years ago (Fig. 7.4), slowed considerably after 9000 years ago. After 9000 years ago, two more species of note, hemlock (Tsuga canadensis) and beech (Fagus grandifolia) migrated into the state. Their late arrival has been mainly attributed to the development of a suitable microclimate for hemlock, and the slow dispersal rate of beech seeds (Davis et al. 1986).

Hemlock, a characteristic species of northern mesic forests, prefers moist, acidic soils, and is relatively shade tolerant. It reached Michigan relatively late, compared to most other northern species such as spruce and pine, entering Michigan from its eastern refugia and arriving in the northern part of the state about 7800 years ago (Davis et al. 1986; Fig. 7.6). It then spread slowly across the northeastern Upper Peninsula and did not become a significant component of the forests there and in the northern Lower Peninsula for at least a thousand years (Davis et al. 1986).

Beech initially reached the Lower Peninsula about 7800 years ago from its refugia in the south, and continued to migrate slowly northward (Figs. 7.3, 7.4; Woods and Davis 1989). Beech, along with other mesic species such as basswood, elm, and ironwood, became a subdominant in the newly formed, maple-dominated forests. These forests were most likely occupied moist, fertile sites in the Lower Peninsula (Kapp 1999). Small pockets of swamp hardwood forests, comprised of species of ash, basswood, maple, and elm, existed in the wettest areas (Bailey and Ahearn 1981).

At this time, the oak- and maple-dominated forests co-existed as a mosaic that covered most of the southern Lower Peninsula. Hickory (Carya spp.) and walnut (Juglans nigra) were components of the oak-dominated forests present on the dry (xeric) sandy sites (Kapp 1999). The prevalence of oak, hickory, and walnut correlates with the climate at the time—with its slightly warmer summers than today (because summertime insolation was still higher than at present), and greater aridity beginning at 8800 years ago, which lasted into the mid-Holocene (Webb et al. 1987, Bartlein et al. 1998, Kutzbach et al. 1998, Booth et al. 2002, Calcote 2003).

**Mid-Holocene climate and vegetation shifts: 6800 to 3200 years ago**

The mid-Holocene is marked by continued variations in climate and corresponding shifts in the distribution and dominance of several tree species. Pollen records from eastern North America document peak warmth and aridity beginning around 6800 years ago; this period is referred to as the Hypsithermal, Altithermal, or mid-Holocene warming (Kutzbach et al. 1998). In some other areas of North America, this warming occurred earlier (Barnosky et al. 1987, Webb et al. 1993, Yansa 2006). By about 6000 years ago, summertime insolation was about 5% greater than it is today; causing temperatures from June to August to be 0.5 to 2°C warmer than at present (Kutzbach et al. 1998). This period of Michigan’s past was not only warm, but also dry. Compared to modern levels, precipitation was approximately 20% less at ca. 6000 years ago, and for a few millennia thereafter (Bartlein et al. 1984, Webb et al. 1993).

In the Upper Peninsula, the mid-Holocene warm/dry interval began at 8800 years ago and lasted until around 6600 years ago (Fig. 7.5). This interval is marked by increase in the abundance of pine species, which are well adapted to this type of climate (Kapp 1999; Booth et al 2002). Thereafter, the climate in the Upper Peninsula shifted. Beginning at about 6600 years ago, there was a slight increase in precipitation and winter temperatures, coupled with a slight decrease in summer temperatures (Booth et al. 2002, Calcote 2003). This slightly cooler/moister trend accounts for the decline of pine populations and the corresponding abundance increase in hemlock (Fig. 7.6). By 6000 years ago, hemlock had spread from the eastern Upper Peninsula in both a westward direction across the Upper Peninsula and in a southwesterly direction into the Lower Peninsula (Davis et al. 1986, Calcote 2003). Other mesic taxa, such as cedar, birch, and maple, likewise expanded their ranges in the Upper Peninsula at this time (Booth et al 2002, Calcote 2003).

As the climate was becoming slightly cooler and moister in the Upper Peninsula by about 6000 years ago, the southern Lower Peninsula, along with much of the southern Great Lakes region, were experiencing peak aridity and warmth. Patches of prairie and oak savanna, driven by fire, were developing on the driest sites in the southwestern Lower Peninsula (Ahearn and Kapp 1990, Kapp 1999). Mixed oak forests (with hickory) dominated much of the rest of the Lower Peninsula. Correspondingly, there were slight decreases in the pollen abundances of the mesic deciduous trees (beech, maple, basswood, and elm), due to the warmth and aridity (Fig. 7.3). The mesic beech-maple,
forests were most likely limited to moist, loamy soils on areas of ground moraine (Kapp 1999). Hardwood swamp forests comprised of elm and ash were probably restricted to wet low-lying sites near lakes, such as the area around Saginaw Bay, and near rivers (Kapp 1999).

The forest tension zone, an ecotone between the deciduous forests (mixed-oak forests and beech-maple forests) of the southern Lower Peninsula and the mixed coniferous-deciduous forests (dominated by pine) of the northern Lower Peninsula, which had formed during the early Holocene, shifted northward during this mid-Holocene interval. The northward shift of the forest tension zone (Curtis 1959; Chapter 21) within the central part of the Lower Peninsula is assumed to have been a vegetative response to the warmer/drier climatic regime (Fig. 7.4). This ecotone reached its furthest northern extent during the entire Holocene, about 6000 years ago (Webb et al. 1983).

Several other vegetation changes are evident during the mid-Holocene. These include a dramatic decrease in hemlock pollen abundances at several sites in the Upper Peninsula and elsewhere in the Great Lakes Region between 5500 and 4000 years ago—attributed primarily to an insect/pathogen outbreak (Davis et al. 1986, Calcote 2003). The range of yellow birch (*Betula alleghaniensis*), a species with similar habitat characteristics as hemlock, expanded significantly, as did its abundance in the Upper Peninsula after 5000 years ago, during the population decline of hemlock (Jackson and Booth 2002). Beech trees reached the Upper Peninsula by 4400 years ago but became only a minor component of local forests (Fig. 7.6). By about 4000 years ago, insolation (sunlight and heat) values throughout the year attained modern levels and thereafter other mechanisms exclusively determined climatic and vegetation patterns (COHMAP 1988).

Late Holocene vegetation dynamics: 3200 years ago to 150 years ago

Climatic reconstructions for much of eastern North America, including the Lower Peninsula, indicate a marked increase in precipitation and an associated temperature decrease starting at about 3200 years ago (Webb et al. 2004). Interestingly, this cool/moist trend began earlier in the Upper Peninsula. Embedded within this overall cool/moist pattern were alternating wet and dry intervals and temperature variations, which caused shifts in the range distributions of various plant communities in Michigan during the late Holocene (Jackson and Booth 2002, Webb et al. 2004).

Of these climatic perturbations, the most significant is the transition from the mid-Holocene warmth and aridity to a cooler and moister regional climate at about 3200 years ago, and persistence of this climate until ~1000 years ago (Bernabo 1981, Jackson and Booth 2002). During this time, extensive bogs, marshes and peatlands formed in much of the central and eastern Upper Peninsula in response to the increased moisture (Kapp 1999) and the rebound of the land mass, which caused many northwardly-draining rivers to flow more sluggishly. Correspondingly, there were expansions in the ranges of several key, mesic species, e.g., beech, birch, and hemlock, within the Upper Peninsula from 3200 to 1000 years ago (Davis et al. 1986, Woods and Davis 1989, Jackson and Booth 2002).

Species diversity also increased in the forests of the Upper Peninsula during the late Holocene. Newly formed hemlock-dominated forests, containing birch, maple, ash, and beech as subdominants, occupied moist, fertile soils throughout the eastern Upper Peninsula (Calcote 2003). Pine forests and mixed pine forests (containing some hardwoods) inhabited the drier, sandier sites (Kapp 1999). In the western Upper Peninsula at this time, northern hardwood forests, comprised of birch, maple, and elm, were more common than pine forests. This trend is evident in the pollen diagram for Kitchner Lake (Fig. 7.6), while at 3200 years ago the pollen abundance of birch is much greater than that of pine, which had reached its lowest level since initial colonization.

Meanwhile, in the Lower Peninsula, the beech-maple forests expanded from their limited locations after 3200 years ago as a result of increased moisture. Correspondingly, the oak-dominated forests, and the prairie/oak savannas in southwestern Lower Michigan, contracted in areal extent (Kapp 1999). In the central Lower Peninsula, the cooling climate encouraged the range expansion of white pine and the mixed pine-hardwood forests.

In response to the cool and wet climate, the tension zone in the Lower Peninsula had shifted south by 3000 years ago. South of the tension zone, expansion of the beech-maple forests is clearly evident in the pollen record (Fig. 7.3), where beech pollen percentages increase dramatically just after 3200 and oak pollen percentages decline.
slightly. Throughout much of the southern Lower Peninsula, oak forests became less common at this time, but they remained a significant forest type in the mosaic dominated by beech-maple forests and, to a lesser extent, by swamp hardwood forests (Kapp 1999; Chapter 21).

Relatively little is known about climate and associated vegetation changes in the Upper Peninsula after 3200 years ago. Available pollen data from the eastern Upper Peninsula indicate the continued expansion of the cool mesic northern hardwood forests (dominated by birch, cedar, hemlock, and beech), after 3000 years ago (Delcourt et al. 2002).

More detailed pollen data are available for the Lower Peninsula (Bernabo 1981, Hupy 2006). Studies have detected vegetation changes in association with two climatic episodes in the late Holocene—the Medieval Warm Period (MWP), from 1000 to 800 years ago, and the Little Ice Age (LIA), from 600 to 150 years ago. Both of these climatic intervals have been recognized throughout much of northern North America, northwestern Europe and at other locales in the middle and high latitudes (Bradley 1999). Compared to today’s climate, the average summertime temperature was probably 0.5 to 0.8°C warmer during the MWP and about 1°C cooler during the LIA (Bradley 1999). Bernabo’s (1981) study of four lakes situated along a 75-km transect in the northern Lower Peninsula (from Charlevoix to Crawford County) detected increases in the pollen abundances of pine and oak, associated with the MWP temperature increases beginning around about 1000 years ago. Pollen data collected from three lakes spanning the forest tension zone in the central Lower Peninsula also detected vegetation responses to climatic variations over the past 2000 years (Hupy 2006). Three major ecotonal shifts were detected, including the range expansion of oak forests northward during the MWP as well as the expansions of both the beech-maple forests and the mixed pine forests during the LIA (see FOCUS BOX below).

Vegetation disturbance caused directly by Native American land use has not yet been identified in the pollen records of Michigan, but undoubtedly occurred, given the archaeological record (Chapter 25). In contrast, pollen records throughout eastern North America and the Midwest indicate dramatic changes in the forest communities associated with Euro-American logging, fire and agriculture (Kapp 1999). The activities of Euro-American settlers are evident in many pollen records for Michigan. For example, the pollen records of both Wintergreen (Fig. 7.3) and Kitchner Lakes (Fig. 7.6) clearly indicate the historic period by the dramatic decline in forest species and concurrent increase in the pollen of ragweed (Ambrosia-type) and Eurasian crop weeds. Pollen records also document the mid- and late-20th century reforestation of Michigan and confirm that the species composition and age structure of these young forests differed significantly from the pre-settlement forests (Scull and Harman 2004, Hupy and WinklerPrins 2005) Discussions of the pre-settlement forests and subsequent changes associated with Euro-American land use are provided in Chapters 21 and 40.

FOCUS BOX: Ecotone dynamics: The last 2,000 years of vegetation change

Fossil pollen data collected from Cowden Lake, Montcalm County, located within the floristic tension zone of the central Lower Peninsula, have documented significant shifts in the dominance of different tree species over the last 2000 years (Hupy 2006). In sum, these data demonstrated that the tension zone—a major vegetation boundary in the state—is dynamic in nature and responds to small-scale oscillations in climate over short time periods. Three separate ecotone shifts, and four different pollen assemblages, were identified, for this time period.

From 2100 to 1650 years ago, oak-dominated forests were prevalent near Cowden Lake, indicating a relatively mild (warm) and dry climate. At about 1700 years ago, the climate became cooler and moister, which caused a substantial decline in populations of oak species and the expansion of beech-maple forests. Oak-dominated forests expanded once again after 1300 years ago, in response to the warmer temperatures associated with the MWP. Forests surrounding Cowden Lake also responded to the LIA, when regional temperatures fell by about 1° C (Bernabo 1981). After about 800 years ago, during the LIA, oak abundance in the local vegetation declined and pine became more common. Beech-Maple forests also expanded at this time, not only in the Cowden Lake area but also at other locales in Michigan (Bernabo 1981, Davis et al. 1986).
Conclusions

Fossil pollen records indicate that the composition and distribution of Michigan’s vegetation have been in slow and constant flux since the last glacial recession. Species migrated northward from refugia to the south and east of the ice sheet, as changing climatic and substrate (soils) conditions allowed. The first arrivals were pioneering arctic tundra-adapted plants that quickly colonized the barren landscape, south to north, between 17,000 and 13,000 years ago. This vegetation was succeeded by a spruce parkland that lasted until about 11,000 years ago. Pine and the majority of deciduous trees arrived in Michigan thereafter. At this point, competition between different species in response to climate changes began in earnest, which resulted in the expansion and contraction of the distribution of different species, each according to their climatic tolerances.

Climatic changes during the Holocene varied across the state, which helps explain why the species composition of forests in the Upper Peninsula differed from those of the Lower Peninsula. Pine forests were dominant in most of the Upper Peninsula for much of the early and mid-Holocene, in response to the prevailing warm/dry climate and the sandy soils that prevail there. Starting at about 6600 years ago, the climate of the Upper Peninsula became cool and moist, which caused greater abundance and range expansion of several mesic taxa. Northern hardwoods forests, dominated by mesic birch, maple, hemlock, and beech trees, occupied the moist fertile sites (only in the eastern half of the Upper Peninsula), while pine-dominated forests were present on the drier sites. In contrast, the mid-Holocene warm/dry interval occurred later, from 6000 to 3200 years ago, in much of the Lower Peninsula, during which oak forests were more dominant. With the onset of a cool and moist climate after 3200 years ago in the Lower Peninsula, oak forests declined in areal extent as the more mesic beech-maple forests expanded. Meanwhile in the Upper Peninsula, the mesic taxa, especially hemlock, continued to increase in abundance.

Detailed vegetation-climate reconstructions based on fossil pollen analyses demonstrate that plants respond to climate changes of varying degrees. Forests respond to long-term (millennial-scale) climate changes associated with variations in insolation. At the same time these plant communities also react to smaller-scale shifts in tem-
perature and precipitation, such as during the Medieval Warm Period and Little Ice Age. Indeed, the vegetation encountered by the first Euro-Americans in Michigan was not the long-term norm, but may have represented a relatively new arrangement of species and forest communities, the geographic ranges of which had only been stable for the past few hundred years.

**Literature Cited**


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Further Readings


