CHAPTER 6

Long-Term Forest and Landscape Dynamics

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Stand Dynamics in a Cultural Landscape

In the previous chapter, we saw that broad changes in forest composition accompanied the transition from presettlement forests to those dominated by European land use. These regional trends represent the aggregate consequences of the individual decisions of thousands of landowners and the effects of many separate disturbances, which by and large occur at the level of the forest stand. The stand is a coherent unit with a broadly uniform history and underlying environment. It is often the scale at which management takes place, whether in a field or a forest. It is also a scale at which forest dynamics can be mechanistically tied to biological processes such as competition for light and other resources.

The ecological dynamics of disturbance and succession discussed in this chapter drive the composition and structure of forest stands. Whether a disturbance is a natural event, like a windthrow, or a cultural intervention, like a logging operation, the distribution of biological resources (such as water, nutrients, and light) is rearranged, the influence of competitors is altered through selective damage or mortality (each species is more or less susceptible to different types of disturbance), and the physical substrate and environment may be rearranged. As time passes, resource availability continues to change because of the relative abilities of different species to establish or resprout and grow and then utilize these resources, resulting in a successional sere. Traditionally, ecologists and foresters characterize tree species as having an early (for example, paper birch), mid (red oak), or late (hemlock) successional role. In this chapter we will examine how detailed historical records of stand development can add insights to such simple characterizations and to the long-term developmental history of the broader New England landscape.

Early ecologists and foresters at Harvard Forest developed a strong understanding of how the effects of historical land use played out at the

stand level. They characterized the most ubiquitous stand-level compositional trajectory on the landscape in the Fisher Museum's dioramas (Figure 4.17). Through the sequence of historical scenes, we see the pre-European forest transformed by forest clearance and increasingly intensive agriculture, and then we follow the process of forest succession on abandoned farmland leading from white pine to the hardwood forests that currently dominate much of central New England.

This sequence forms the backdrop for the work discussed here. The dominance of the postagricultural signal in regional vegetation history is confirmed by broad consistency between the regional pollen signal discussed in the previous chapter and the Fisher Museum's stand-level dioramas. But the ubiquity of agricultural abandonment in the region presents forest ecologists with a perplexing question: if the bulk of the landscape is shaped by a particular historical process, what kinds of changes occurred in the rest of the landscape, especially the less intensively disturbed areas that remained as forested woodlots? This question has important implications both for basic ecology and for conservation biology because fragments of primary forest that escaped agricultural clearing and have always supported native vegetation are considered to function as more "natural" systems both in the reforested landscape of New England and in parts of the world currently undergoing deforestation. They are thought to provide a link between the cultural present and the presettlement past.

Most of the examples in this chapter come from historical reconstructions of primary forests in and around the Harvard Forest. At the broadest level, we are interested in knowing whether the least-disturbed forests on the modern landscape maintained elements of the composition and dynamics of the presettlement landscape or whether they tracked the cultural transitions of the past 300 years in parallel to the postagricultural landscape in which they are embedded. This general framework leads to specific stand-level questions for presettlement and postsettlement times.

For the pre-European forests and their stand dynamics, we are interested in knowing the following: How common were late-successional communities? Were stand dynamics driven by disturbance or autogenic processes? Was stand composition stable, changing slowly, or in constant flux? When we look to the dynamics of the postsettlement primary forests we ask: To what extent do primary forests retain their presettlement character and species mixtures? Do sites with similar modern composition share similar histories?

Long-term stand-level reconstructions also help us address questions about the ecology of individual species because they tie the population dynamics of those species to local environmental change. In particular we would like to know: Does our understanding of the successional status of a species account for its response to the dynamics

seen in the historical record? What was the successional role of species, such as chestnut, that no longer exist in the canopy of New England's forests?

The Forests and Approaches Used to Unravel Long-Term Forest History

We describe in detail the dynamics of four stands on three different sites (Figure 6.1). Hemlock Hollow is a small, seasonally flooded forest hollow (or vernal pool) in a protected lowland on the Prospect Hill tract that is currently surrounded by an extensive forest dominated by hemlock (Figure 6.2). The stand, which lies at the edge of the Black Gum Swamp, was an active woodlot owned by John Sanderson's family during the nineteenth century. Scattered dead chestnut poles leaning against the large hemlocks indicate that the site had a dynamic past despite the abundance of sizable late-successional trees (Figure 6.3). Chamberlain Swamp is a small wetland basin (40 by 70 meters) on a broad upland ridge adjacent to the Quabbin Reservoir that is completely dominated by oak forests (Figure 6.4). The "oak side" of the swamp, where one sediment core was retrieved, is a stand typical of the vegetation across the ridge, as it is dominated by red oak and other hardwoods. In contrast, there is a small hemlock stand on the "hemlock side" of the wetland basin, where another sediment core was taken. Sediment

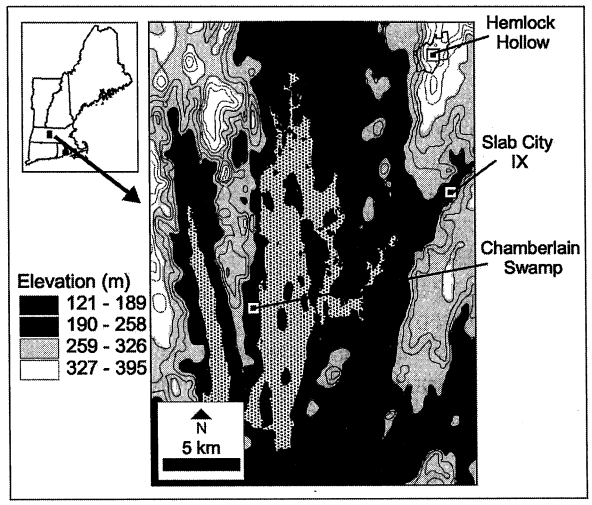


Figure 6.1. Location of Chamberlain Swamp on the Prescott Peninsula in the Quabbin Reservoir watershed, Hemlock Hollow at the Prospect Hill tract, and Slab City IX in the southern part of Petersham. Elevation data from U.S. Geological Survey 1993.

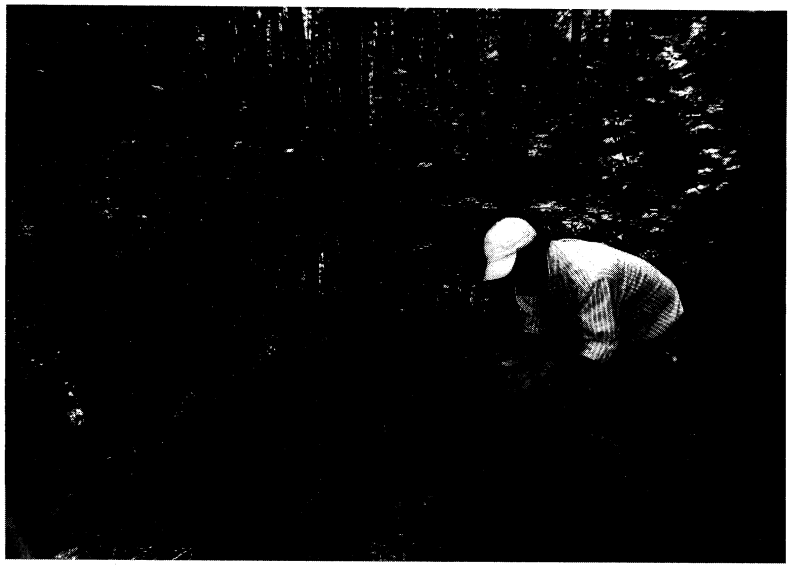


Figure 6.2. Small hollows, vernal pools, and organic soils can provide lengthy and detailed records of local vegetation and environmental change. The closed canopy and small size of the basin and pollen-collecting area mean that most pollen, charcoal, and other material come from the neighboring forest. Hemlock Hollow, pictured here, provided a continuous 9,000-year record of forest dynamics (Foster and Zebryk 1993). Photograph by J. Gipe.

records from these small hollows give long presettlement histories of two contrasting environmental settings: a moist lowland and an exposed ridge top.

In many hemlock-dominated stands, deep accumulations of mor humus preserve pollen as do the sedimentary settings used more typically in paleoecological studies. The final stand we describe, on the Slab City tract south of the center of Petersham, contains such a pollen record extending to presettlement times (Figure 6.5). The surrounding forest is dominated by large old hemlocks and has been the repeated subject of investigation by ecologists such as Steven Spurr and Hugh Raup because it has many of the physical and biological characteristics that forest ecologists associate with late-successional undisturbed forests.

In each study site, local pollen records provide the strongest evidence for long-term compositional change at the stand level. Forest hollows and humus profiles collect most of their pollen from a scale approximating the local stand (for example, an approximate 50-meter radius), in contrast to the lake sediments described in Chapter 5, which collect pollen produced at the landscape or subregional level. Over the past few hundred years, pollen records can be usefully augmented by tree-ring and archival records of forest history, which provide informa-

Figure 6.3. Hemlock stand in the center of the Prospect Hill tract of the Harvard Forest showing the leaning stems of chestnut that formerly dominated the stand but were killed by blight in 1913. Understory hemlock grew rapidly in the open environment to become the major canopy species. The remarkable decay resistance of chestnut wood has enabled these stems to remain standing over the ninety years since their demise. Photograph by D. R. Foster.

tion on disturbance history and structural changes that accompanied the compositional changes observed in the pollen record. Each of the stand histories described here was developed using a combination of reconstructive approaches. We illustrate the strength of this complementary approach in detail for the Slab City hemlock forest.

Presettlement Forest Dynamics

Forests at Hemlock Hollow have been dominated by hemlock since the species' arrival into the landscape about 8,000 years ago (see Figure 4.14). Because of the site's moist, sheltered environment, fire and other disturbances were infrequent, apparently only affecting the stand once every 500 to 2,000 years. For the first 5,000 years of hemlock dominance, succession after fire or other disturbance involved an initial decline in hemlock and increases in oak, pine, and birch. Hemlock eventually resumed its dominance in approximately 500 years after the

Figure 6.4. An extensive oak forest dominates the long ridge containing Chamberlain Swamp. The forest is composed of many multiple-stemmed trees due to the history of logging and fire. Photograph by D. R. Foster.

disturbance, presumably because of its shade tolerance and longevity. The last major change to affect the composition and dynamics of the stand in the presettlement period was the arrival of chestnut around 1,500 to 2,000 years ago (Figure 6.6). An interesting result of the immigration of this new species to the region was that it changed the stand's dynamics following disturbance. After its arrival, chestnut, rather than oak, pine, or birch, increased after fire, illustrating quite clearly that a change in the pool of available species may significantly alter the competitive balance and successional dynamic in the forest.

The ability of chestnut to dominate the stand after disturbance more effectively than other species did not affect hemlock's importance in the absence of disturbance, however. In fact, the continued low frequency of

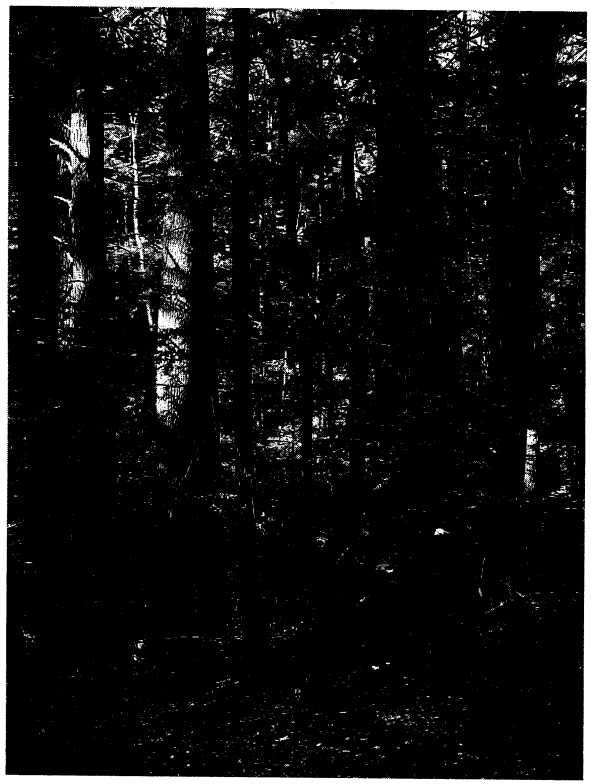
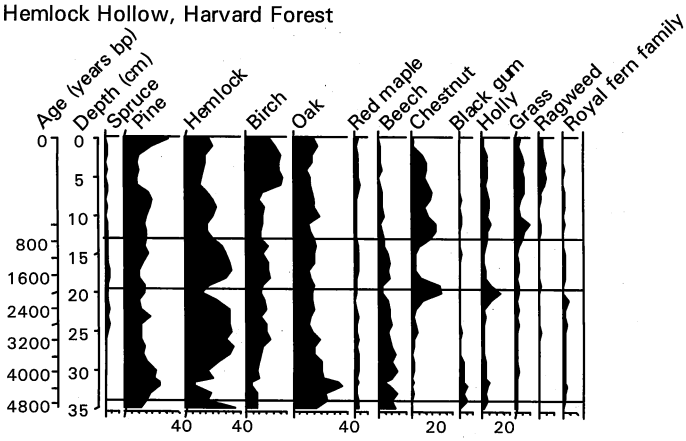


Figure 6.5. Old hemlock forest on the Slab City tract of the Harvard Forest in the southern part of Petersham. On the basis of the size, age, and composition of the trees, Hugh Raup described this stand in the 1930s as the closest to a climax stand that he had seen. Photograph by D. R. Foster.

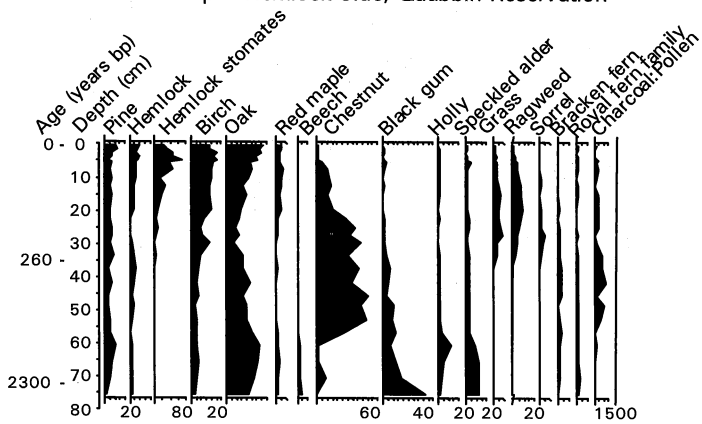
disturbance at this site allowed hemlock to dominate through much of the time preceding the arrival of European settlers 250 years ago. Overall, presettlement forest dynamics at Hemlock Hollow were fairly stable and relatively predictable. Over a 4,000-year period, only minor changes occurred in forest composition as a consequence of long-term climatic change. The low frequency of disturbance persistently favored hemlock as a late-successional species.

In contrast to Hemlock Hollow, uplands on both sides of Chamberlain Swamp were dominated by oak for thousands of years before the arrival of chestnut (Figure 6.6). There is strong evidence for aboriginal populations in the valleys surrounding this ridge, so the association between local aboriginal burning and oak dominance hypothesized more broadly for other parts of the Northeast may hold here. It is also likely that compositional differences between Chamberlain Swamp and Hem-

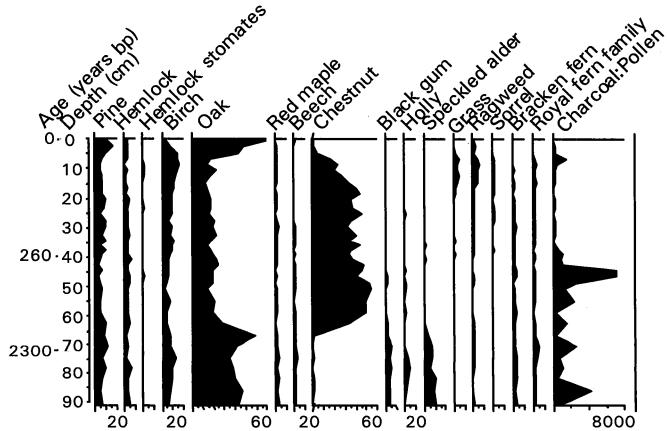
Hemlock Hollow, Harvard Forest



Chamberlain Swamp – Hemlock Side, Quabbin Reservation



Chamberlain Swamp - Oak Side, Quabbin Reservation



lock Hollow reflect differences in soils, hydrology, and exposure to disturbance, including damage from natural fire, wind, and ice. At Chamberlain Swamp, the arrival of chestnut had a very different effect on stand composition than at Hemlock Hollow. During the first 500 years after chestnut's arrival, it was a minor component of the forest. After an apparently abrupt change to a cooler and most likely moister climate approximately 1,500 years ago, chestnut rapidly became the dominant species; chestnut pollen percentages from that time to the twentieth century are among the highest recorded at any paleoecological site. It is interesting to note that at both Hemlock Hollow and Chamberlain Swamp chestnut seems to have taken over the role of oak in responding to disturbance. At the moister and less fire-prone hemlock-dominated site, chestnut had a transient increase after disturbance, whereas on the drier site with more frequent fire, it replaced oak as the dominant species.

The contrast between the two stands in different parts of the landscape allows us to better understand some of the landscape variation in forest pattern and process, including the dynamics of species invasion. Chestnut arrived in New England forests much later than most hardwoods with similar modern distributions. Whether this migration lag was due to dispersal limitation in this large-seeded species or to subtle climatic limitations on its range has been the subject of debate. Our studies show that, once it arrived, chestnut existed in low populations in central Massachusetts for hundreds of years, and its rise to prominence was triggered by changes in environmental factors. At Hemlock Hollow the long periods between disturbances caused its abundance to vary considerably over time, as chestnut functioned as a successional species. At Chamberlain Swamp, a subtle change in site water balance, indicated by changes in the abundance of wetland taxa here and at nearby Lily Pond, allowed chestnut to reach its compositional dominance in the stand, where it was presumably maintained by fire. Interestingly, following these environmental shifts chestnut maintained a consistent though different niche in the two forests.

Figure 6.6. Pollen diagrams from Hemlock Hollow (see Figure 6.2), a low-lying site dominated by hemlock in the Harvard Forest, and from the opposite sides of Chamberlain Swamp, which lies on an oak-dominated ridge near the Quabbin Reservoir (see Figure 6.4). Locally around Chamberlain Swamp there is a small hemlock stand on one side and broad hill of oak on the other. Because of the small size of the sites, each of the diagrams shows local vegetation dynamics and fire history within approximately 50 meters. At each site, there has been considerable vegetation dynamics involving chestnut, oak, and other species, including hemlock, as a result of climate change, fire, insect outbreak, and logging. Modified from Foster and Zebryk 1993, with permission from the Ecological Society of America, and Foster, Clayden et al. 2002.

The Effect of European Land Use

The influence of European land-use practices is first detected at most paleoecological sites by increases in agricultural weed pollen. These first pollen changes generally do not represent actual disturbance or change at the site; rather, they reflect regional changes, including agriculture and deforestation in the earliest settled part of the region, that alter regional pollen signals. Subsequent more-pronounced changes mark direct cutting and disturbance to the local forest. At Hemlock Hollow, this initial episode is marked by a vegetation response qualitatively similar to disturbance response in the pre-European forests. The early period of colonial activity involved intensive forest cutting locally and extensive clearing in surrounding areas. Active cutting of hemlock and pine in the stand around Hemlock Hollow as a source of timber and use of hemlock and chestnut for tanbark and chestnut poles in the nineteenth century resulted in the establishment of a new forest dominated by chestnut (a prolific sprouter) along with increases in birch and red maple (Figure 6.6). The elimination of chestnut from the forest canopy by the chestnut blight in the early twentieth century resulted in the development of the current hemlock stand at the site. It is interesting that after 250 years of anthropogenic fire, logging, and pathogen outbreaks, a stand has developed that is dominated by large hemlocks and is perhaps structurally similar to the presettlement forest at the site. Our knowledge of history and tree-ring records from the stand, however, suggest that an anthropogenic disturbance regime favoring hemlock played as much of a role in the increase of hemlock at the site as the natural process of autogenic succession.

At Chamberlain Swamp, forest cutting resulted in a decrease in chestnut, in contrast to Hemlock Hollow. Birch appears to have increased because of nineteenth-century disturbance (Figure 6.6), and the site is called a "sproutland" in archival records from the 1930s. Through the twentieth century, birch declined and oak increased, as intensive use of the site lessened and as chestnut was eliminated by the blight. Overall, the postsettlement dynamics of this side of Chamberlain Swamp indicate a transition from chestnut dominance to oak dominance as a result of disturbance. The way this transition qualitatively mirrors the displacement of oak by chestnut 3,000 years earlier might suggest that oak is simply regaining its competitive dominance at the site with the elimination of chestnut, but the compositional differences between the two sides of the swamp illustrate how complicated the long-term dynamics of forests can be.

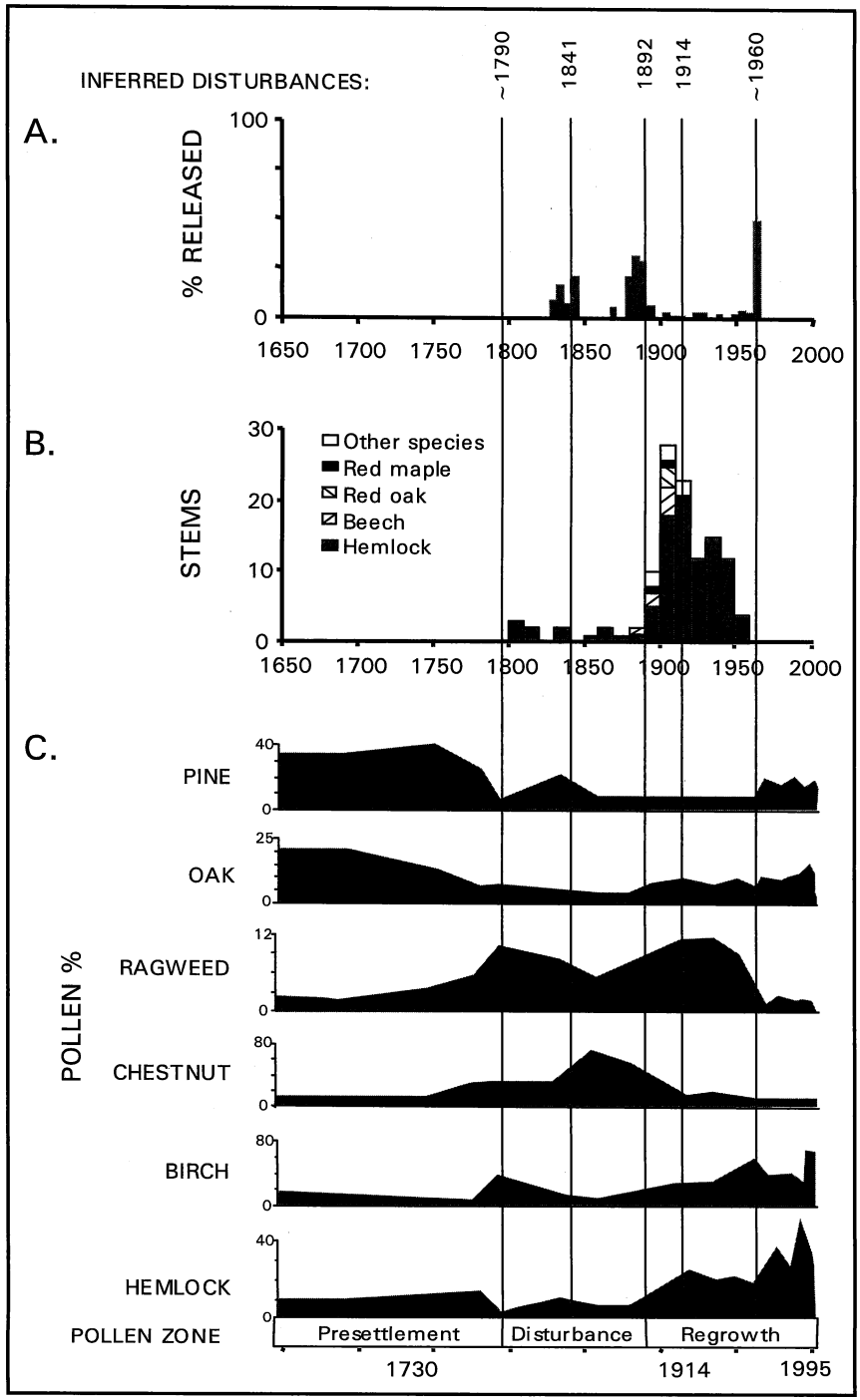
Until European settlement, pollen records from both sides of the swamp showed the same trends, suggesting that no strong underlying environmental difference exists between the sites. The sites begin to strongly differ in composition only after the chestnut blight in the early

twentieth century. At the hemlock side of the swamp, the increase in oak pollen with chestnut decline is also accompanied by increases in red maple and hemlock and the persistence of high birch abundances. Currently, the site is dominated by hemlock and is compositionally more similar to the forest at Hemlock Hollow than to the oak stand at Chamberlain Swamp. The postsettlement forest dynamics at Chamberlain Swamp suggest two important lessons. First, strong differences in the composition of adjacent stands can be predominantly the product of recent human impact; and second, this can be true even for stands dominated by large late-successional trees.

Convergence in Forests Following Different Histories

The contrast in the compositional history between Hemlock Hollow and the hemlock side of Chamberlain Swamp suggests that sites that appear structurally and compositionally similar today may actually be the product of very different histories. We investigated this possibility through detailed reconstructions of the history of Slab City IX and three other primary hemlock stands at the Harvard Forest. Currently, the stands are all quite similar, and their dominance by large late-successional hemlocks suggests that they might be the stable product of autogenic succession. However, the pollen records derived from the humus soils in each stand show that the forests were all different from each other at the time of European settlement, that they all experienced major compositional change in the eighteenth and nineteenth centuries due to forest cutting, and that they converged on their current hemlock-dominated assemblages in the twentieth century.

When we combine tree-ring data, a stand-level pollen record, and the history of known disturbances from archival records, we develop insights into the ecological mechanisms underlying the compositional history of one of these sites. In Figure 6.7A we see that the oldest trees currently in the stand are hemlocks that originated around the turn of the nineteenth century, but that most trees, including all the hardwoods, recruited in the few decades surrounding the turn of the twentieth century. In Figure 6.7B, three growth releases in the nineteenth century confirm archival data suggesting that the stand was repeatedly cut. The last of these cuttings initiated the origin of the modern stand. Although the chestnut blight is not strongly reflected in the tree-ring record, Figure 6.7C shows that the compositional response to nineteenth-century cutting was an abundance of sprout chestnut. As at Hemlock Hollow, the elimination of chestnut by blight after 1913 allowed hemlock, which already was established as advanced regeneration, to dominate the stand. Because of the specific disturbance history of this stand, including forest cutting, wind, and pathogens rather than agricultural clearance and


INFERRED DISTURBANCES:
~1790
1841
1892
1914
~1960
A.
% RELEASED
100
0
1650 1700 1750 1800 1850 1900 1950 2000
B.
STEMS
30
20
10
0
Other species
Red maple
Red oak
Beech
Hemlock
1650 1700 1750 1800 1850 1900 1950 2000
C.
POLLEN %
PINE
OAK
RAGWEED
CHESTNUT
BIRCH
HEMLOCK
POLLEN ZONE
Presettlement
Disturbance
Regrowth
1730
1914
1995

fire, the stand is now dominated by large old hemlocks. It is worth noting that before European settlement the stand was dominated by oak and pine rather than by the late-successional hemlock-hardwood assemblage that occurred at the Hemlock Hollow site. In fact, none of the three other hemlock sites we investigated had the same presettlement assemblages, and none of the trajectories of compositional change shows signs of returning to pre-European composition.

The Ecology of Hemlock and Chestnut

In addition to deepening our understanding of the ecology of forest communities, reconstructing the long-term dynamics of forest stands provides insight into the basic ecology of tree species, whose life-history characteristics often remain poorly understood because of their long generation times. It is a major goal of forest ecology to evaluate the potential response of forest species to accelerating changes in land use, climate, and atmospheric chemistry, but tools such as computer-based forest models must have accurate information about the ecological attributes of these species in order to evaluate their performance effectively. The sites discussed in this chapter provide specific information on the autecology and competitive dynamics of two important eastern tree species: eastern hemlock and American chestnut.

The common perception of the late-successional role of eastern hemlock is well-characterized by its presettlement dynamics at Hemlock Hollow. For thousands of years, hemlock dominated undisturbed late-successional assemblages. It was dramatically reduced after disturbance by fire and took hundreds of years to reassert its former dominance. Postsettlement dynamics of this species at Hemlock Hollow, as well as at the hemlock side of Chamberlain Swamp and at Slab City, present a

Figure 6.7. Stand dynamics at the Slab City IX site. Vertical lines signify disturbances to the site (historically documented logging operations in 1841 and 1892, the chestnut blight of 1913, and disturbances inferred from pollen and tree ring records at approximately 1790 and 1960). (A) Growth releases in hemlock tree rings. Hemlocks in the stand experienced growth releases surrounding the two cutting episodes and after an undocumented disturbance in 1960. (B) Year of recruitment of current stems. A few overstory hemlocks date to the early nineteenth century, but most hemlocks in the stand and all of the hardwoods recruited after the 1892 cutting. The lack of recruitment after 1950 is a methodological artifact (trees of less than 5 centimeters in diameter were not aged). Hemlocks have continued recruiting into the stand until the present. (C) Pollen percentages from soil humus. Presettlement forests were dominated by pine and oak. Regional increases in ragweed pollen indicate the period of regional historical deforestation. At Slab City IX chestnut sprouts followed local cutting. Blight eliminated chestnut in 1913. It was replaced by the hemlocks that now dominate the site. Modified from McLachlan et al. 1999, with permission from the Ecological Society of America.

more obscure aspect of its ecology but one that may be more important in the strongly human-influenced forests of today. At these sites, wind, cutting, and pathogens acted to promote hemlock dominance rather than to reduce it. Instead of characterizing hemlock as a disturbance-sensitive, late-successional species, in New England it is more accurate to consider the specific effects of different disturbance types, intensities, and patterns on a species that has a rather broad successional role.

Chestnut was an important species in the region before it was eliminated from the forest canopy by blight early in the twentieth century. Historical sources give important accounts of the character and distribution of this species, but the details of its role in forest succession before the blight are not well known. Because of this lack of information, evaluating the impact on current forests of the loss of this species is difficult. The records examined in this study highlight the complex response this species had to natural and anthropogenic disturbance. After its arrival in New England, chestnut replaced oak on some sites as the most successful species following fire. The Hemlock Hollow and Chamberlain Swamp records indicate that this was true on both relatively wet sites, where its successional role was only temporary, and on dry sites, where it dominated stand composition for millennia. As we found for hemlock, however, chestnut's predictable response to presettlement environments was not mirrored in its response to the anthropogenic disturbances of the postsettlement period (Figure 6.8). At Hemlock Hollow, chestnut sprouted vigorously after cutting of the original hemlock stand, but at Chamberlain Swamp and Slab City, chestnut's relative abundance actually decreased in response to similar eighteenth- and nineteenth-century disturbance.

A final and unfortunate comparison between hemlock and chestnut is that both species have suffered greatly from introduced organisms. Chestnut has been reduced to an understory shrub for nine decades and, despite ongoing efforts at reducing the effect of the blight or breeding resistance into chestnut, hopes for the tree's imminent recovery are dim. As we have seen in this chapter, the direct impact of the blight on stand-level dynamics is obscured by other twentieth-century phenomena such as land use. Nevertheless, the dynamics of eastern forests in the twentieth century were undoubtedly driven to a large extent by long-term compositional responses to this event. The decline of hemlock populations since the arrival of the hemlock woolly adelgid to southern New England in the 1980s suggests that forest dynamics in the twenty-first century might be characterized by a similar response to major decline of a dominant forest tree. Even if this grim scenario fails to occur, we can be certain that New England's forests face a period of intense and novel dynamics. The historical record provides an important tool for evaluating how they will respond.

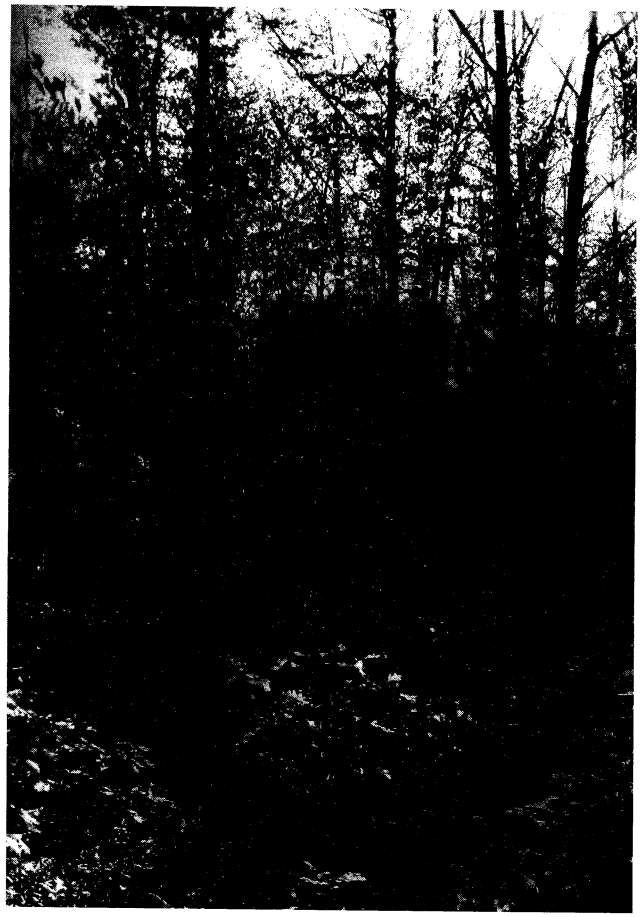


Figure 6.8. Coppice forest of American chestnut in Massachusetts around 1900 showing the open structure of the forest and sprout form of the trees. Reprinted from Paillet 2002, with permission from Blackwell Science Ltd.

Conclusions

A broad examination of forest history underscores the contrasting patterns of forest development on different sites in New England's postagricultural landscape. Perhaps the most common, and certainly the best recognized, pattern is the sequence of changes in forest composition on former agricultural land, as depicted in the Fisher Museum's dioramas. Original transition hardwood–hemlock forests were converted to agricultural land that remained open for a century or more be-

fore being abandoned from active use. Today, most of these sites are forested with mid-successional hardwoods like red oak and red maple that assumed dominance after the initial postagricultural forests of white pine and other early-successional species were cut or blown down. Late-successional species such as hemlock and beech are becoming established only very slowly. On primary forest sites, including the two examined here, the long-term dynamics were nearly as dramatic as those of postagricultural stands. The original chestnut forests of Chamberlain Swamp and the old-growth white pine–oak community of Slab City were repeatedly cut over during the eighteenth and nineteenth centuries, resulting in assemblages of sprout hardwoods. Over the past 100 years, the effect of human activity has grown less apparent, and the stands now are among the oldest in New England.

These historical sequences illustrate some important generalities about the current forests of central New England. First, the regional homogenization of forest types shown in the previous chapter masks a good deal of variability at the stand level. Second, this stand-level variation may have more to do with site history than with the underlying environment. Finally, stands in our landscape that show characteristics of old natural forests are often anthropogenic in origin. This last conclusion does not diminish the value of these forests for conservation purposes, including landscape diversity and wildlife habitat. Indeed, they illustrate the potential of the modern landscape for generating extensive seminatural mature forests, especially on primary forest sites.

Revisiting the questions raised at the beginning of this chapter, we can see that detailed records of forest change from a variety of sites can provide answers to basic questions about long-term stand dynamics. Topographic position created differences in presettlement stand composition and disturbance frequencies across the landscape, but composition at sites as different as Hemlock Hollow and Chamberlain Swamp was fairly stable and presumably in balance with underlying environmental forces. With European settlement, the bulk of the landscape was converted to open pasture or agricultural use, but even the approximately 20 percent of the land that remained forested was subject to substantial structural and compositional change. Forests that appear to be stable and natural on the modern landscape have experienced natural and anthropogenic disturbance approximately every decade and have undergone major compositional changes every century. The complex disturbance regimes of these stands complicate our traditional view of successional dynamics and illustrate the flexibility that tree species have for dealing with novel environmental change.

In Chapter 8, the relative roles of local environment and site history are investigated further using detailed analyses of the correlation be-

tween modern vegetation and site characteristics. In such static studies of the modern landscape, the role of history emerges as an important contributor to the distribution of species, and it is useful to keep in mind the scale and timing of the dynamic processes observed in the historical reconstructions presented here.