Stand Dynamics and Silviculture of Mixed Conifer-hardwood Stands in Southern New England

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Abstract

The mixed hardwood-conifer forests of southern New England have undergone a series of human impacts that have significantly altered the relative proportions of tree species. Old-growth forests were comprised largely of eastern hemlock (*Tsuga canadensis* [L.] Carr.) and many species of hardwoods, dominated by red oak (*Quercus rubra* L.) and chestnut (*Castanea dentata* [Marsh.] Borkh.), with scattered white pine (*Pinus strobus* L.) occurring as emergents above the level of the main canopy. Most of these forests were cleared for agriculture in the eighteenth century. With the widespread abandonment of agriculture in the nineteenth century, fields regenerated to nearly pure white pine. Silvicultural research in the early twentieth century attempted to design treatments to harvest and regenerate pure pine stands, but these efforts generally failed. The management focus shifted to mixed stands, similar in structure to the original forests, and this focus has been largely maintained to the present time. However, white pine has proven difficult to maintain in mixture with hemlock and hardwoods. The species composition and average canopy position of each species in young, mixed stands is strongly influenced by the density and heights of the advance regeneration initially present. For several of the most important species, the development of large advance regeneration is an important facet of silviculture in this forest type.

Introduction

The forests of southern New England are a complex mixture of conifer and broadleaf tree species that often are composed of 10 or more species per hectare. These forests were among the first in North America to be heavily exploited for timber during the period of European colonization, and were also among the first to experience a succession of other uses. First, widespread deforestation for agricultural development occurred in the eighteenth and early nineteenth centuries, followed by natural reforestation on abandoned farmlands in the late nineteenth century. Then, an industry developed based on harvests of the second-growth stands. Planned silvicultural treatments were subsequently applied, together with associated scientific forestry research in the early twentieth century. These waves of human activity dramatically altered the relative proportions of tree species in the forests, but did not permanently change the overall composition. Because of this relatively long history of exploitation and silvicultural experimentation, lessons may be learned from this region that are of value to forest managers from British Columbia or other regions, where interest exists in managing complex species mixtures.

Regional Forest Description

This discussion focuses on forests covering a large part of the states of Massachusetts, Connecticut, and Rhode Island, and the southern parts of New Hampshire and Maine (Figure 1). The region has been repeatedly glaciated, and is neither truly mountainous nor level, but has a rolling topography with broad flat-topped hills that rise to the same elevation within a locale. The bedrock consists mainly of schist and gneiss, which are both resistant to glacial grinding. Consequently, the parent material for most soils is a thin layer of bouldery glacial till, with water-worked sand, gravel, and clay deposits occurring on a small percentage of the land. Annual precipitation for the region is about 1000 mm, evenly distributed throughout the year. The large number of tree species that coexist in these forests is directly related to the pattern of uniform, abundant precipitation.

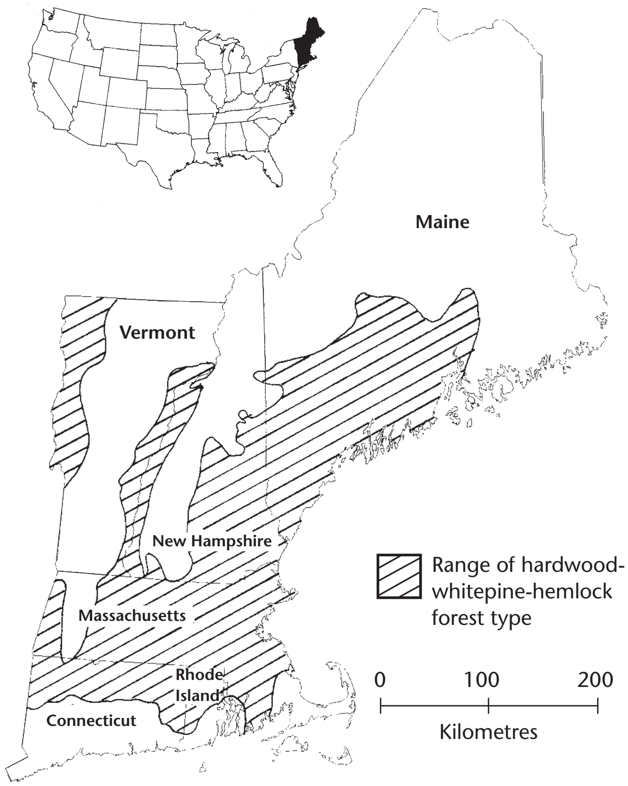

FIGURE 1 *The range of the hardwood-white pine-hemlock forest type in southern New England. This forest type includes both the "transition" and "central" hardwood species (Westveld 1956), in which northern red oak is the most common hardwood species of the main canopy.*

The hardwood species include those of the northern hardwood type, dominated by beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), and sugar maple (*Acer saccharum* Marsh.), and those of the central hardwood type to the south, dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.). Stands composed of mixtures of northern and central species are thus referred to as "transition" hardwoods (Westveld 1956). The most common main canopy hardwood species is northern red oak (*Quercus rubra* L.) in both the transition hardwoods and the northernmost part of the central hardwoods. On most upland sites, eastern hemlock (*Tsuga canadensis* [L.] Carr.) and eastern white pine (*Pinus strobus* L.) are the only conifer species of importance. Thus, the natural forest vegetation is referred to as the "hardwood-hemlock-white pine" forest type, and as discussed here, is comprised of both the "transition hardwoods-white pine-hemlock" and "central hardwoods-hemlock-white pine" types of Westveld (1956).

The principal natural disturbance that affects these forests is wind damage associated with infrequent hurricanes and other more common, but less severe, windstorms. Fires are uncommon in the region except on the droughtiest sites. Major fires can occur on average sites only after catastrophic wind damage or widespread harvesting has left large amounts of woody fuels to dry.

Precolonial Forests and Their Early Exploitation
Only small patches of old-growth forest exist in southern New England today, and these occur mainly on steep inaccessible areas that are not typical of most sites. The last large remnants of the original forest were either harvested or destroyed by windstorms in the early part of the century. However, some of them survived long enough to become the subjects of study by forest ecologists (Nichols 1913; Cline and Spurr 1942). These studies have been combined with reports from early travelers and reconstructions from windthrown stands (Henry and Swan 1974) to give a picture of the original stand structure. Typical old stands were composed of widely scattered emergent white pines above a main canopy of hardwoods (oaks, chestnut [*Castanea dentata* (Marsh.) Borkh.], maples, and others), with hemlock forming an understorey canopy. Stands that had regenerated following overstorey destruction by windstorms would maintain their even-aged character for about 150 years if no additional disturbance occurred. As these stands aged further and the overstorey hardwoods began to die, the shade-tolerant, long-lived hemlock in the lower canopy would be released and fill in the main canopy; hemlocks would also be the main regeneration occurring in small gaps (Figure 2). Thus, hemlock would increasingly become dominant in all canopy strata (except in the emergent position), and the stands would become increasingly uneven-aged. In many stands, the conifers could form 50% or more of the total basal area; of the two, hemlock would dominate in density and basal area, but white pine would dominate in height.

The emergent pines, rising to 45 m or more in height, were the most important timber trees of these forests. They achieved considerable fame because of their value for ship masts during the

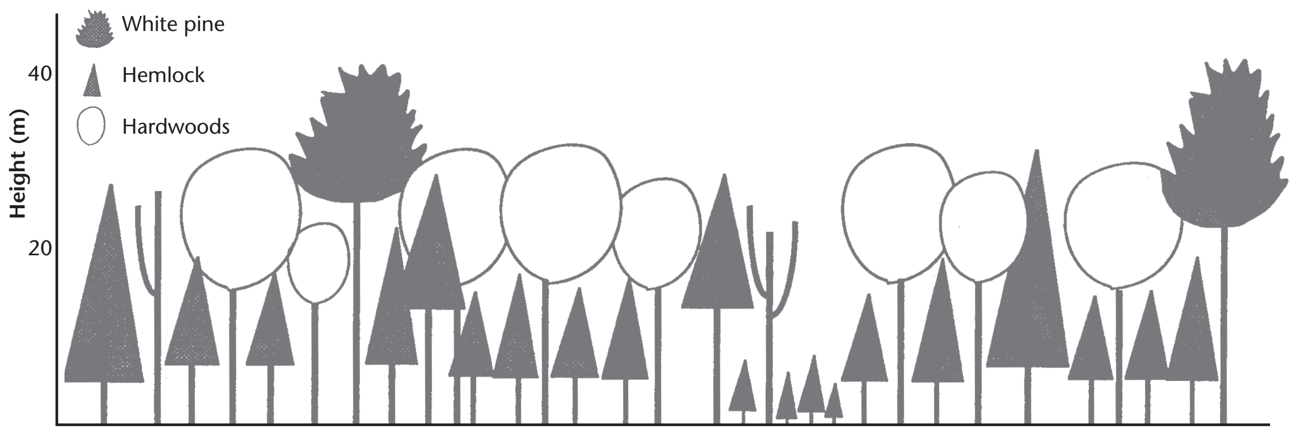

FIGURE 2 *Typical structure of an old hardwood-white pine-hemlock stand. This stand is predominantly even-aged, and is just entering the "transition old-growth stage" as defined by Oliver and Larson (1990).*

colonial period. Disputes over the rights to cutting these trees led to the British Crown reserving all pines growing on unincorporated land in the New England colonies. White pine was also valuable for other less strategic uses in timber-starved England; sawn pine lumber for clapboards was among the first timber exported from New England (Perlin 1989). White pine was then and continues to be highly prized for products requiring soft, easily worked wood.

As settlement of the region continued, hemlock bark became important as a source of tannin for treating leather, with the bark often being more valuable than the wood of this species. As a result, considerable harvesting of hemlock occurred. Oak, chestnut, and other hardwoods were also harvested for various products, but the initial exploitation generally consisted of the removal of the conifer component of the original stands, leaving most of the hardwoods behind. This wave of conifer removal occurred through most of the region and further throughout the northeastern United States. In some cases, the remaining hardwoods expanded to fill the gaps left in the canopy, so that years later, it was not obvious that any species had been removed.

The Era of Agriculture and the Second-growth Pine Industry As the population of the region grew during the eighteenth century, much of the forest land was cleared for agriculture, reducing forests to about 25% of the landscape. Most of the remaining forests were repeatedly cut either as farm woodlots or for industrial charcoal production. Agricultural use continued for 100–150 years on much of the land, but farming was widely abandoned in the latter part of the nineteenth century. This occurred because of the development of transportation from better-quality farmlands further west and the attraction of jobs in the New England cities. The natural reforestation that occurred on abandoned fields was dominated by white pine. This pattern was so widespread that a wooden container industry was established based on the plentiful supply of raw materials. The pines that grew on these old fields were not of the excellent quality found in the virgin forests. This was due partly to the low density at which the pines became established, leading to the development of large branches, and to the effects of the white pine weevil (*Pissodes strobi* Peck), a native insect that kills the terminals of pines. Pine seedlings that grow in shaded conditions are generally not attacked, but the large diameters of the terminal shoots of open-grown trees and the warm temperatures of the shoots in the direct sun create optimum conditions for weevil activity. Thus, old-field pines repeatedly have their terminals killed, with laterals assuming dominance. Although the overall vigour of trees infested by weevils is not affected, multiple-stemmed, crooked trees result. Still, the wood quality met the needs of the packaging industry for producing boxes, barrels, and pails. Knotty wood could be used for many purposes, and clear wood was needed only in short lengths that could be cut from single knot-free internodes. This forest industry flourished from about 1890 to 1930.

In old-field pine stands past the age of 40 years, understoreys composed of most native hardwood species began to develop. Hemlock was generally absent from these understoreys. The reasons for the slow return of hemlock compared to hardwood species have not been clearly documented. Hemlock has small wind-dispersed seeds that require exposed mineral soil or decomposing wood for germination and overstorey shade for early seedling survival. It may be that this combination of conditions were rarely found in the first-generation pine stands. The widespread clearcutting of pine stands for the boxboard industry was largely done without any silvicultural planning. As a result, the harvested pine stands were replaced by a mix of hardwood species either released from the understorey or newly established after the harvest. It soon became evident that the pine resource would be eliminated after the first generation. The desire to maintain pines for this productive industry led to some of the earliest applied silvicultural research in North America, aimed at the regeneration and subsequent management of white pine following the harvest of old-field stands.

Early Silvicultural Research

Some of the early silvicultural research took on many characteristics of "adaptive management" (Baskerville 1985; Walters 1986)—a management style that is currently receiving attention as a highly efficient model for research programs in natural resources. This occurred at the research forests of Yale and Harvard universities (Toumey 1932; Goodlett 1960) and the Massachusetts Agricultural College (now the University of Massachusetts). The commercial harvesting of white pine was an important management component in these forests, but it was done so that each operational-scale application of a silvicultural treatment became an experiment. Hypotheses were formed about the future development of stands following various treatments and these were compared to actual results. The original hypotheses were then modified and subsequent treatments reflected this new knowledge.

By about 1910 it was learned through this research that abundant white pine regeneration could be dependably established by two cutting methods: block clearcutting carried out during a good pine seed year or shelterwood cutting, with overstorey removal occurring about 5 years later. In either case, the forest floor was disturbed during harvesting to expose mineral soil, and hardwood seedlings were cut back to ground level. Shelterwood cutting was found to be the most successful because the young pine seedlings were protected from excessive heating. However it became clear that the initial height growth of the newly established pine seedlings was less than that of the hardwood sprouts and also less than the growth of new seedlings of cherry and birch. The key to successful pine regeneration was not in the cutting method, but in the weedings, which were accomplished by cutting back hardwood sprouts and seedling competitors using machetes. But on a majority of sites, even repeated weedings at about 4-year intervals failed to release pines because of the resprouting of cut hardwoods (Lutz and Cline 1947, 1956).

This early experience identified the importance of matching silvicultural goals and treatments to site conditions. The majority of the region's landscape is covered by thin glacial till deposits containing particles ranging in size from boulders to clays. The common texture of the upper soil horizon is sandy loam, and the moisture-holding capacity of such soils is good enough to allow rapid growth of hardwoods. On these sites, attempts to regenerate white pine stands were generally abandoned entirely, and management shifted to the valuable hardwoods—principally red oak and white ash (*Fraxinus americana* L.). On the droughtier sites underlain by glacial outwash sands and gravels, hardwoods were less dense and had slower height growth, so one weeding was often sufficient to release the young pines. These kinds of sites occupy only about 10% of the landscape on average, and pine management was soon limited to these areas; even here, the objective was generally scaled back to that of creating a mixed pine-hardwood stand (Goodlett 1960).

It is interesting to reflect on the necessity of this course of action in the 1920s. At that time, chemicals that could kill small hardwoods either during site preparation or in release operations did not exist. Also, there was no economical means to remove the hardwood understorey by intensive mechanical site preparation before pine establishment. Conifers are established on good soils in the face of aggressive hardwood competition in many parts of the world today, and much money and effort is spent accomplishing now what could not be accomplished 70 years ago. However, the fact that it now can be done does not necessarily mean that it is always wise to do so.

Current Management in the Region

The early distinction between "hardwood sites" and "pine sites" in southern New England is still recognized today. It is defined in current silvicultural guides by the height growth rate of hardwoods (red oak or sugar maple), with an approximate break point site index of 18.3 m at base age of 50 years (Lancaster and Leak 1978). Nearly all sites will revert to hardwoods following overstorey removal, and nearly all can be made to grow pine with the technology now available. However, because of the high cost of applying intensive treatments to control hardwoods on rich, moist sites, pure pine stands should only be established on sites with an index lower than 18.3 m; sites with an index of 18.3–21.3 m are favourable for mixed pine-hardwood stands, and sites with an index greater than 21.3 m are best managed for hardwoods (Lancaster and Leak 1978).

Most forest land in southern New England is owned by private nonindustrial landowners whose management objectives include a combination of aesthetic, wildlife habitat, and economic concerns. Land in public ownership in this densely populated region is managed for these same objectives, with watershed protection also being an important consideration.

On hardwood sites, red oak has been favoured because of its high timber value. This has steadily increased and the current stumpage price is several times that of white pine per unit volume (although volumes per acre are lower and rotation lengths are longer for oak than for white pine). It is also one of the most important wildlife habitat tree species, because its acorns are a food source for many animal species.

Hemlock is also of interest, even though it has never had high value as a timber species. Its importance comes from its value as winter cover for deer and many other animal species, and for aesthetics and watershed protection. Hemlock also has timber-related value as a trainer tree: the best-quality white pine is grown in mixture with a dense understorey of hemlock, which shades lower branches (Tarbox and Reed 1924). The same is true of red oak and other hardwood species that grow above a dense understorey of hemlock. (This is the stand structure that was carefully developed to produce the famous high-quality oak [*Quercus petraea*] logs in the Spessart region of Germany, in which oak is grown above a dense European beech [*Fagus sylvatica* L.] understorey.)

There is also an interest in maintaining a component of white pine within hardwood or hardwood-hemlock stands. When it is knot-free, white pine has high value for furniture and finishing wood. Although chemicals and mechanical site preparation equipment are now available to control hardwoods, there is little interest in using them to create pine-dominated stands on "hardwood" sites. The "ideal" stand structure closely resembles that of the original forest and does not differ much from the structure desired by forest researchers in the 1920s.

Structure and Dynamics of Young Stands

Although important interactions occur throughout stand development, the most dynamic period is the earliest stage, during which a closed canopy is first formed. This is the "stand initiation" stage of the model described by Oliver and Larson (1990). The structure and composition of the stand at the end of this stage (usually at age 15 to 20 years in this forest type) will determine a good deal about the long-term pattern of development. At age 20, the structure is strongly influenced by the regeneration characteristics that exist just after the overstorey is cut or destroyed. The composition of the regeneration will be affected by such factors as location of seed sources of each species, forest floor conditions relative to germination requirements, and presence of advance regeneration of some species. The development of canopy structure is then controlled by the inherent height growth pattern of each species, the type of regeneration (sprout vs. seedling origin), and the spatial pattern and density of each species, which can affect whether slower-growing species can escape being overtopped by faster-growing ones, simply because of their location (Oliver and Larson 1990).

"Pioneer" and "Gap-phase" Species To discern overall development patterns in complex species mixtures, it is useful to recognize groups (or "guilds") of species that have common characteristics. However, this introduces the danger of oversimplifying species life histories and therefore overlooking distinctions among the species, but is still helpful if used with caution. The most basic classification of species is into two groups (Whitmore 1989):

- "pioneer" species, with low shade tolerance, rapid juvenile height growth, and the ability to become established on exposed sites; and
- "gap-phase" or "advance-regeneration-dependent" species, with intermediate to high levels of shade tolerance, slower juvenile height growth, and the ability to become established beneath an overstorey and advance to an upper canopy position after the overstorey is partially or completely removed or destroyed.

Of the hardwood species in southern New England, the pioneers consist mainly of birch and cherry species. Of these, paper birch (*Betula papyrifera* Marsh.) and gray birch (*Betula populifolia* Marsh.) produce small, wind-dispersed seeds, whereas the seeds of black cherry (*Prunus serotina* Ehrh.) and pin cherry (*Prunus pensylvanica* L.f.) are bird-dispersed, and remain dormant in the forest floor. Quaking aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*Populus grandidentata* Michx.) also fit into this group, but they usually occur only in small numbers in these forests. The most important advance regeneration species include the oaks, maples, hickories, white ash, chestnut, and beech. These have a wide range in shade tolerance, but all survive in the understorey and most can sprout vigorously from stumps (or roots in the case of beech) after stems are cut or broken off. The problems with grouping species are illustrated by the characteristics of black birch (*Betula lenta* L.), which could be appropriately placed in either group; it germinates on exposed sites and grows rapidly in height, but is shade tolerant and regenerates as an understorey seedling as well, and produces sprouts from stumps when young.

Of the two conifer species, hemlock is fairly easy to place within these two groups. It is a very shade-tolerant, long-lived species with slow juvenile height growth and depends on advance regeneration. An understorey hemlock can respond with increased growth when canopy gaps of all sizes are created repeatedly throughout its life (Marshall 1927; Oliver and Stephens 1977). White pine is not as easy to classify, and its place within stand dynamics has been the subject of considerable interest and debate. Because of its prevalence and rapid height growth on exposed sites following farm abandonment, it has sometimes been considered a pioneer. However, seedling growth becomes rapid only after an initial period of slow growth, lasting about 5 years. Germination is best on exposed mineral soil or moss beds, but moderate shade benefits early establishment because of the small size of seedlings during the first years. White pine has an intermediate level of shade tolerance. Understorey pine saplings can survive with slow growth for at least 20 years and still respond quickly to release, but the extent of this species' behaviour as a gap-phase species has not been well documented.

Initial Regeneration Conditions The composition and structure of 20-year-old stands can be affected by different initial conditions of regeneration. Four initial conditions are considered (Figure 3).

Following Severe Fire or on Abandoned Agricultural Land On exposed, severely disturbed sites such as those left after abandonment of agriculture, the colonizing species are limited to the wind-dispersed pioneer hardwoods (mainly gray birch and paper birch), as well as white pine (Figure 3a). These species dominate following major fires as well, but pin cherry and black cherry may also be present, germinating from seed stored in the forest floor. In old-field stands, the presence of faster-growing birch species with their sparsely foliated crowns increases the early survival of pine by moderating microclimatic conditions, without badly suppressing them. Free-ranging livestock selectively browsed on hardwoods in these abandoned pasture lands, thereby increasing the dominance of pine in the young stands; large deer populations can cause the same effect. White pine has a greater average lifespan than the birch or cherry species, so the dominance of pine would continue to increase with age as the other species died. The young stand in Figure 3a is the same as those that dominated the landscape 100 years ago, and developed into the high-volume but poor-quality pine stands that fed the boxboard industry.

Following Cutting, with Small Advance Regeneration Present Stands with greater species diversity develop following strip or patch clearcutting in a mixed-species stand, because a seed source for all species is near and advance regeneration of some species is usually already present. If only very small seedlings are present for species that cannot germinate after the cut, and if sprouting from stumps is eliminated, a highly stratified stand structure develops by age 20 (Figure 3b). These specific conditions may not occur often, either in nature or in managed stands, but they have been incorporated in an experimental design that efficiently examines the relative height growth of species growing in mixtures, with all species starting from essentially an equal level as small seedlings (Smith and Ashton 1993). These conditions produce a stand with an upper canopy composed of pioneer birch and cherry, with advance regeneration species such as red oak, red maple, and beech in a lower stratum. Hemlock and white pine occur in the lower stratum as well, often at the lowest heights. While finer distinctions in the pattern of stratification can be made (Smith and Ashton 1993), the distinction between these two main canopy layers is of greatest importance. The long-term development of stands of this structure is not well understood. As the short-lived gray birch and pin cherry begin to die at about age 20, the lower canopy oak and maple may be released to advance to the main canopy; however, black birch, paper birch, and black cherry are longer lived and may continue to dominate the upper canopy for many decades. Hemlock and beech can tolerate deep shade and will likely persist with little growth for many decades. White pine will not survive nearly as long and many will die by age 20 years; their survival would vary with the density and composition of the overstorey canopy.

Following Cutting, with Large Red Oak and Maple Advance Regeneration Present A more common initial set of conditions is similar to those described for Figure 3b, except that red oak and red maple (and white ash on some sites) occur as large seedling or sapling advance regeneration (Figure 3c). These species can respond quickly following overstorey removal, or can sprout from stumps if the stem has been cut or broken off. The rapid growth of these established hardwood seedlings or sprouts keeps their height equal to that of the pioneer hardwoods. This was the common structure of young stands after the old-field white

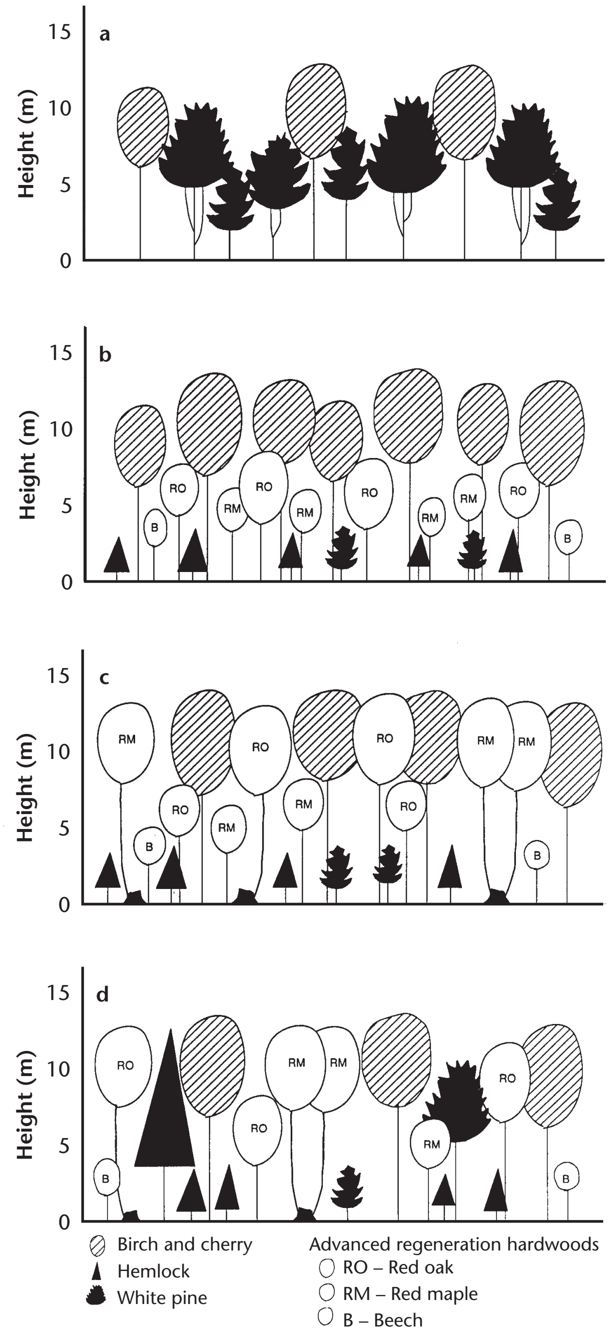

FIGURE 3 *Composition and structure of 20-year-old stands in the hardwood-white pine-hemlock forest type, as influenced by initial regeneration conditions: (a) following severe fire or on abandoned agricultural land; (b) following cutting, with only small advance regeneration present; (c) following cutting, with large advance regeneration of red oak and red maple present; (d) following cutting, with large advance regeneration of red oak, red maple, white pine, and hemlock present.*

pine had been clearcut from 1890 to 1930 (McKinnon et al. 1935), or after the overstorey was destroyed by winds such as the 1938 hurricane, which affected much of the region (Spurr 1956). The long-term development of these stands, which are the most common kind on the landscape today, has been the focus of several studies (Oliver 1978; Hibbs 1982; Kelty 1986). The birch and cherry species (but not the more shade-tolerant black birch) will generally die while still occupying overstorey positions. Red oak will increasingly dominate the overstorey canopy by age 50 and older, with red maple and black birch falling to a subordinate canopy layer. If hemlock is present at all, it will survive well and form the lowest stratum.

Following Cutting, with Large Red Oak and Maple, White Pine, and Hemlock Advance Regeneration Present The initial conditions in this final example differ from the one described for Figure 3c, in that some of the hemlock and white pine advance regeneration occurs as saplings or larger at the time of overstorey removal (Figure 3d). If sufficient in magnitude, this head start in height development will prevent the conifer species from being overtopped by the initial rapid growth of hardwoods. The pine and hemlock often do not keep ahead of the hardwoods, but form part of the main canopy at approximately equal heights (Oliver and Stephens 1977; Hibbs 1982; Kelty 1986; Kelty and Entcheva 1993). The minimum initial size necessary for the conifers to maintain an upper canopy positon will vary with site conditions; hemlock will likely need a greater initial size than white pine because of its slower height growth. These minimum sizes are not known, however. An irregular size structure in conifer advance regeneration that included larger saplings may have been a common situation in old natural stands. It is likely that canopy gaps would allow advance regeneration to develop, and when severe wind disturbances occurred would leave an irregular set of residuals to respond. The larger hemlocks that fill this role may be older than is commonly thought of as advance regeneration; they may be lower canopy trees of the same age as the destroyed overstorey, but because they are still able to respond at advanced ages, they function as advance regeneration.

Silvicultural Concepts about the Regeneration of Mixed Stands

The preceding discussion stressed the importance of the size of advance regeneration in the early development of stand structure in mixed stands. This concept is well accepted for regeneration of oaks; silvicultural guidelines recommend that oak advance regeneration be a minimum of 1.4 m tall before it can be considered safely established and likely to compete well with pioneer species following overstorey removal.

The importance of large advance regeneration has not been stressed in silvicultural recommendations for the conifer species. This is not surprising for hemlock, because it is often considered desirable to maintain hemlock in lower canopy positions. However, there is ample evidence that small hemlock advance regeneration quickly falls to a lower canopy position and that larger residuals can reach the main canopy following overstorey removal (Oliver and Stephens 1977; Hibbs 1982; Kelty 1986). The situation with white pine is not as clear. Maintaining pine in mixture with hardwoods in managed stands posed difficulties and led early researchers to study natural stand structure to infer the developmental patterns. Their methods and ideas have implications for mixed stand silviculture in general, and are thus worthy of further consideration.

After initial attempts at regenerating white pine in the 1910s, researchers were faced with conflicting evidence about the competitive ability of pine on moist sites. The existence of nearly pure pine stands on these sites clearly resulted from the particular condition found in abandoned fields. The next generation of pine seedlings rarely survived and developed on these sites, even with repeated weedings of the hardwood regeneration. However, single large pines existed in or above the main canopy of mature hardwood stands, even on the richest sites. These pines had developed without the benefit of silvicultural treatment. Consideration of the potential developmental pathways for these stands led to the hypothesis of group development of pines in hardwood-dominated stands (Cline and Lockard 1925). Each mature pine was thought to be the survivor of a group of pine seedlings that had initially dominated the regeneration in a small area because of ground cover conditions, soil factors, or light conditions in canopy gaps before overstorey destruction (Figure 4). By this hypothesis, the group buffers the central pine from hardwood competition during early stand development; the outside pines of the group are overtopped by hardwoods and eventually die, but the central one escapes competition and advances to the main canopy. The sustained height growth of pines at older ages would then eventually take them to emergent positions.

New England researchers received support for this hypothesis from "several prominent European foresters" (Cline and Lockard 1925). At that time, European foresters were shifting their focus from Norway spruce (*Picea abies* [L.] Karst.) monocultures to mixtures of spruce with other species, mainly European silver fir (*Abies alba* Mill.) and European beech. The technique widely used to accomplish this, particularly in Germany, was to incorporate fir and beech in groups comprising about 30% of the stand area, with pure spruce accounting for the remainder. Fir and beech had slower juvenile growth than spruce, so those species were overtopped and often eliminated early in development. The group-wise establishment pattern for these species is still used in Germany. This concept was generalized to a certain extent in New England to explain the coexistence of species in mature, unmanaged stands. The conifer plantations established at the Harvard Forest had species confined to monospecific blocks of a carefully calculated size. Each block would then be reduced through successive thinnings to one tree in the mature stand, although this was done only on a limited experimental basis. This concept was more importantly directed to the management of young pine-hardwood stands that developed after the harvest of old-field pines. The regeneration was segregated into groups of pine and hardwoods by weeding hardwoods in patches of about 0.01–0.04 ha only where promising groups of pine seedlings had become established (Cline and Lockard 1925).

The idea of grouping each species in natural stands appears to be a rather artificial construct. Much of the problem of the early suppression and death of one species in a mixture arises when regeneration is established at high densities; the species with faster initial growth will eliminate the slower-growing one, unless the faster-growing one has sparse foliage, as happens with some pioneer species. On the other hand, if the faster-growing species occurs at low density, the other species may be able to survive its period of slow juvenile height growth and either grow for long periods as a lower canopy tree or later advance into the main canopy. This idea has been put forward for spruce-dominated mixtures in Germany. Kenk (1992) suggested that establishing spruce at wider spacing would allow other species to develop without the need to confine them into groups in a carefully designed pattern.

For New England stands, the importance of the outer pines in groups sheltering the central pines from hardwood competition is difficult to understand because hardwoods so quickly grow taller than pines. The important factor appears to be that hardwoods have very low density or are missing entirely from a patch, because of initial soil or ground cover conditions. (Pine seedlings initially grow so slowly that it is unlikely that their presence would prevent the initial establishment of the hardwoods). Thus, the patches represent "uncontested" sites, where a stronger competitor is absent. It is likely that a pine establishing on such a site could advance to the hardwood canopy level, whether the site was occupied by a group of pines or was devoid of other tree regeneration. This does not mean that group regeneration of pines does not occur, but that the absence of high-density hardwood regeneration from a patch by itself is the important factor, rather than the existence of a group of pines.

The hypotheses about white pine establishment and development can be summarized as follows. Pine occurs in nearly pure stands only on sites that are very droughty or that have been severely disturbed by fire or clearing for agriculture. It plays the role of a pioneer species in these situations, even though it does not have all the life history characteristics generally associated with pioneers. Pine becomes established in mixed stands with hardwoods and hemlock after less severe disturbances (windthrow or overstorey cutting) in two ways:

1 Shortly before or after overstorey removal, pine

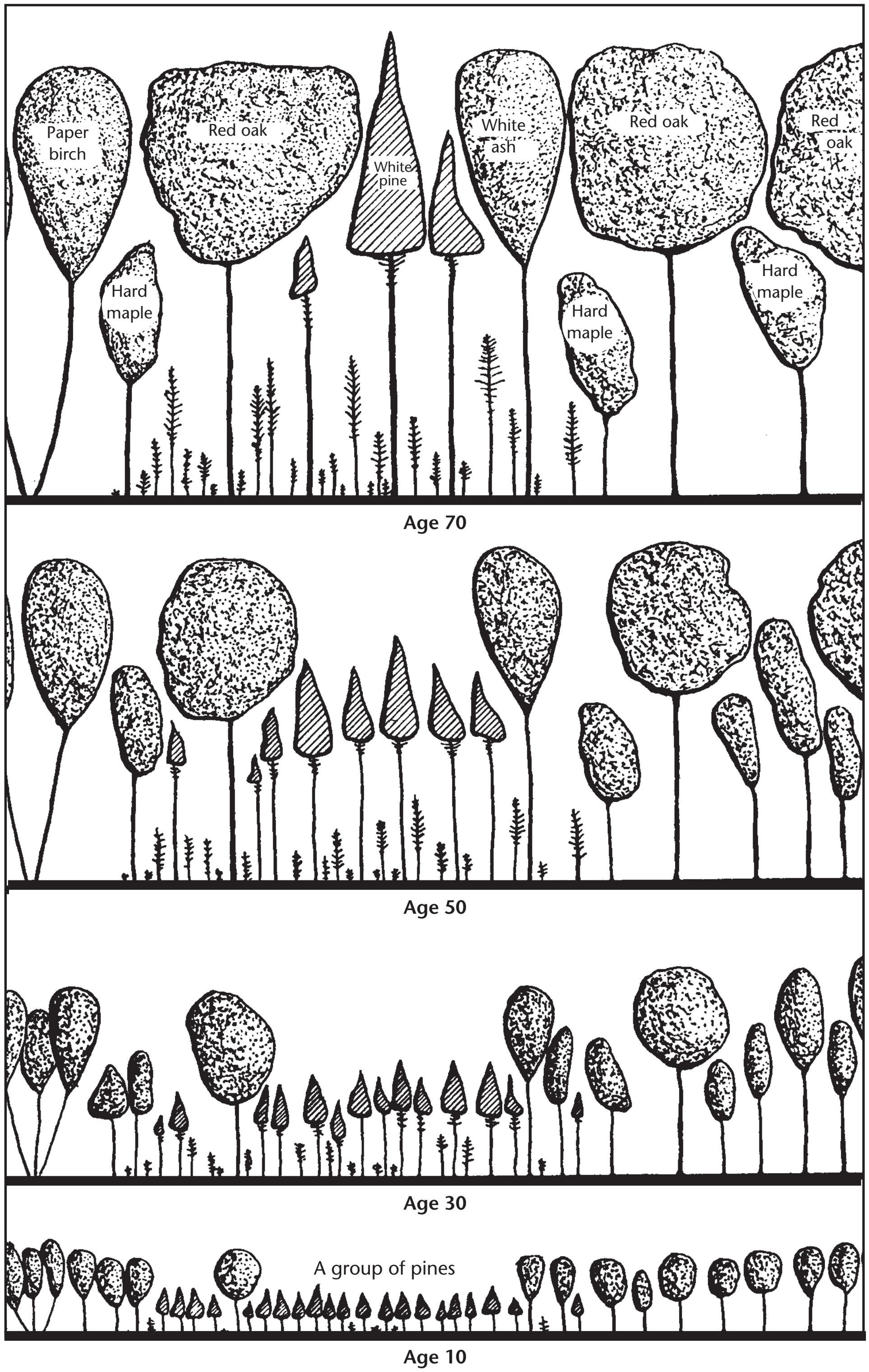

FIGURE 4 *An illustration of the group development of white pine in hardwood stands. (Reprinted with permission from Cline and Lockard [1925].)*

seedlings become established on patches where hardwood regeneration is lacking or occurs at low density (i.e., uncontested sites); the pines may or may not regenerate in groups on these patches.

2 Many years before overstorey removal or destruction, pines become established in the understorey and grow slowly to sapling size; these saplings can then respond to release and grow into overstorey positions.

In natural (unmanaged) stands, uncontested sites are hypothetically more prevalent on drier "pine" sites because of the generally lower density of hardwood establishment there. With higher hardwood density on moister "hardwood" sites, large pine advance regeneration may increase in importance as a means for pine to develop into the main canopy. However, the behaviour of white pine as an understorey species has not been examined in silvicultural experiments, except in a very limited way (Kelty and Entcheva 1993).

Conclusions

Several of the concepts discussed in this review of the management and silvicultural experimentation with the hardwood-white pine-hemlock forests in southern New England have more general application to silviculture in other forest types. First, the study of stand development patterns in unmanaged forests is an important part of silvicultural research. Designing silvicultural treatments that mimic natural processes can lead to efficient management strategies. Second, knowledge of the composition and structure of young stands, of an age just past the development of a closed canopy, can lead to predictions of long-term stand development. Understanding the dynamics that control early composition and structure is therefore very important. Third, some species have considerable flexibility in their characteristics, and may follow different developmental pathways depending on the nature of disturbances, competing species, and site factors. And finally, the role of the size and density of advance regeneration is of great importance in the early development of stands, even for species such as white pine, which may behave as pioneers in some circumstances.

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