White pine in the transition hardwood forest

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Eastern white pine (*Pinus strobus*) in central New England is found in pure stands and as a component of mixed hardwood – pine stands. In older mixed forests, this pine is emergent over the surrounding hardwood canopy. Owing to the only moderate shade tolerance and initial slow growth rate of pine, there has been frequent speculation about how pine could survive and grow in hardwood forests. Results presented here indicate that successful white pine regeneration is achieved (*i*) by group reproduction in dense hardwood stands (25 $m^2 \cdot ha^{-1}$) where the group acts as a buffer around a central and eventually surviving pine; (*ii*) by single pine seedlings if hardwood competition is not too severe (18 $m^2 \cdot ha^{-1}$); (*iii*) occasionally by advanced regeneration from a previous stand; and, (*iv*) in mature forests, by regeneration in larger canopy gaps.

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Dans le centre de la Nouvelle-Angleterre, le pin blanc (*Pinus strobus*) se rencontre en peuplements purs et dans des peuplements mixtes de bois-francs et pins. Dans les forêts mixtes les plus âgées, le pin blanc émerge au-dessus de la voûte environnante des arbres décidus. Comme le pin ne manifeste qu'une tolérance moyenne à l'ombre et que son taux initial de croissance est lent, on s'est souvent demandé comment il pouvait croître et survivre dans des forêts de bois-francs. Les résultats présentés ici montrent que le pin blanc peut se régénérer avec succès (*i*) par une reproduction en groupes dans des peuplements denses de bois-francs (25 $m^2 \cdot ha^{-1}$), là où le groupe agit comme tampon autour d'un pin central qui finira par survivre, (*ii*) par des plantules isolées de pin si la compétition par les bois-francs n'est pas trop sévère (18 $m^2 \cdot ha^{-1}$), (*iii*) occasionnellement, par une régénération avancée à partir d'un peuplement déjà présent et (*iv*) dans les forêts matures, par la régénération dans de grandes ouvertures de la voûte.

[Traduit par le journal]

The precolonial forest of southern New England was primarily a hardwood forest with a small conifer component. Prior to land clearing by the colonists, the forest cover was nearly continuous and, while uneven-aged in a large sense, was composed of a mosaic of even-aged patches of trees, from young to very old (Cline and Lockard 1925; Bromley 1935). Rarely did it fit the classic notion of the primeval forest, dark with old trees and little undergrowth. The white pine (*Pinus strobus*) component of this forest was particularly striking because the pine was frequently found as an isolated emergent or superdominant tree towering above the surrounding hardwood forest (Cline and Lockard 1925; Bromley 1935; Raup 1966). These pine were so valuable that in 1710 much of the pine was reserved for ship masts for the British Navy.

The origin of this pine in the hardwood forest has been the subject of much speculation and, as more has been learned about the growth characteristics of the species, the origin has become less certain. The rate of height growth of young white pine is much slower than that of associated hardwoods (Cline and Lockard 1925; Anonymous 1965) and can lead to the situation observed by Spurr (1965). He found that among the regeneration following canopy removal by the 1938 hurricane, the white pine was quickly outgrown and so usually found in the understory of the predominantly hardwood forest. When the only moderate shade tolerance of white pine (Anonymous 1965) is also considered, it becomes unclear how these pines might survive, let alone grow to become isolated dominants above the hardwood forest.

To solve this dilemma, Cline and Lockard (1925) presumed that today's dominant white pines represent lone survivors of larger groups of white pine reproduction. The group acted as a buffer against surrounding hardwoods until height growth of the central pines caught up with that of the encroaching hardwoods. They also suggested that the young pines sometimes seen in the understory of the old forests might be released following canopy removal by a wind storm and form part of the next forest. This forest would be two-aged, with hardwoods filling spaces between the older pines. A similar result is seen today where pine in low density colonized old fields and hardwoods later colonized vacant spaces.

A more general review of the natural regeneration of white pine produces three situations in which pine has been found to regenerate.

Following fire

Fire tends to produce large open areas with an ash or mineral seedbed, an ideal situation for the reproduction

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of nearly pure forests of white pine (Anonymous 1965). Severe fire also tends to reduce competition with hardwoods by eliminating the many species that reproduce by advanced reproduction, stump sprouts, and buried seed. This increases early survival of white pine. Examples of pine reproduction following fire have been described in southern Quebec (Maissurow 1935), southern New Hampshire (Henry and Swan 1974), and New England in general (Bromley 1935). The phenomenon of old-field white pine is analogous in many respects.

Following small wind disturbances

Oliver and Stephens (1977) describe a portion of the Harvard Forest, Petersham, MA, which has been repeatedly disturbed by man and wind, creating a stand of even-aged patches in the larger uneven-aged forest. They found no white pine on their study plot but assumed that the pine in the adjacent forest dated to some distant catastrophic disturbance. I have dated some of this pine (basal ring counts) and found that it originated following a relatively recent (about 100 years) intermediate canopy disturbance. These pines are part of small even-aged patches composed mostly of hardwood species.

Following large wind disturbance

Large wind disturbances (e.g., the 1938 hurricane in New England, see Rowlands 1941; Baldwin 1942) remove the forest canopy over extensive areas by both breaking and uprooting trees. Species regenerate in many ways, producing an even-aged forest composed of many tree species, mostly hardwoods (Cline and Lockard 1925; Spurr 1956; D. E. Hibbs, unpublished). Cline and Lockard (1925) discuss in detail the creation of mixed hardwood – pine stands following logging, a process that results in conditions similar in some respects to those produced by large wind disturbances. They note the importance of site parameters and seed source in regulating the relative densities of the species present.

Height-growth studies of white pine and associated hardwoods of the transition hardwood forest zone of south central New England have been done, but only on individuals growing relatively free from interspecific competition, in pure pine or pure hardwood stands. Only Oliver (1978) has looked at development of groups of trees, focusing on red oak (*Quercus rubra*), red maple (*Acer rubrum*), and black birch (*Betula lenta*). Cline and Lockard (1925) studied height growth of white pine and selected hardwoods growing on heavy soils (the mesic or better soils of the region, glacial till with fragipan, (Goodlett 1960)) in northern Massachusetts and southern New Hampshire. They looked only at trees that had always been growing in unsuppressed conditions and found that early height growth of white pine was far less than that of hardwoods, but that, by age 60, the faster growing white pine individuals were taller than the faster growing hardwood individuals. This agrees with the general description of white pine as being a slow starter but later being able to maintain high rates of height growth for many years (Anonymous 1965).

A study of forest succession at the Harvard Forest following the 1938 hurricane (Spurr 1956; D. E. Hibbs, unpublished) describes white pine regeneration as suppressed by the faster growing hardwoods 10 years after the hurricane. By 1978, however, white pine comprised 33% of the codominant canopy positions, although none of the dominant ones. From this study it is not clear if these successful pines represent remnants of groups (e.g., Cline and Lockard 1925) or some other process.

In summary, early white pine growth appears to be slow, relegating the species to the understory of hardwood stands. This pine, however, is frequently found in older hardwood stands in dominant or emergent canopy positions. Several possible solutions to this apparent dilemma have been proposed. In addition, there are several mechanisms available to produce uneven-aged mixed hardwood – pine forests. The objective of this paper is to reconstruct the development of successful white pine trees with respect to their nearest neighbors and describe the conditions that led to this success in the transition hardwood forest.

Study area

Most of this study was done at the Harvard Forest, Petersham, MA. The paired height/age data came from areas within 30 km of the Harvard Forest. The forests of this region have been described as a transition between the Appalachian oak and northern hardwood forests (Kuchler 1964) and as transition hardwood forest (Braun 1950).

The soils of the Harvard Forest are glacial till and glacial outwash of varying depth, with and without fragipans. Much work has been done on species/site/soil relationships at the Forest (reviewed in Goodlett 1960), and the general concensus provides a scheme that divides the soil continuum into three broad classes: heavy (moist tills with a pan), medium (well-drained tills), and light (outwash). Heavy soils tend to support stands of ash (*Fraxinus americana*), red and sugar maple (*A. saccharum*), red oak, and yellow birch (*Betula allegheniensis*), and a scattering of other species. Medium and light soils support red and black oak (*Q. velutina*), white pine, red maple, and paper birch (*B. papyrifera*) with the composition highly variable but medium soils tending to more hardwood and light soils tending to more pine. This study was done on sites with medium and light soils. Nomenclature follows Little (1979).

Methods

Height growth of small clusters of trees which were centered around single dominant or codominant white pine trees was measured by felling the trees, sectioning them into 1.2-m units, and aging each section by ring counts. Six groups in 40-year-old posthurricane stands and five groups in 100+-year-old growth stands were analyzed. Clusters selected for analysis were those that grew on medium or light soils and contained several hardwood species.

Profile diagrams were constructed by mapping stem position and crown projection on 5 × 15 m transects in a 40-year-old posthurricane stand. Only trees whose base was in the transect were included. Tree height and canopy depth were measured with a Haga altimeter. Basal area was measured using a two-factor metric prism with selected pine trees in 40-year-old posthurricane mixed hardwood – pine stands as plot center. These trees could be placed in one of five descriptive classes: dominant or codominant trees that had been completely surrounded by a group of pine reproduction; dominant or codominant trees that had been partially buffered by a larger group of pine reproduction; dominant or codominant trees that had always had hardwoods as nearest neighbors; suppressed, but also 40-year-old trees in the understory of the same stands as the above three catagories; and dominant or codominant trees in pine stands. In the sampled stands, basal area around all trees in the first three classes (unbuffered, partially buffered, and buffered) was measured. Sample size of these three classes, then, reflects their respective relative frequency. Only a small subsample was made of the suppressed pines and pines in pine stands.

Results

E. E. Tarbox and P. M. Reed (Harvard Forest Records, Inactive Research, 1923–file 4) aged by increment cores individuals in small groups of trees in the vicinity of Harvard Forest and found that white pine tended to be the same age or older than associated hardwoods (Table 1). Successful pine regeneration, then, usually precedes or coincides with hardwood regeneration. Pine rarely was found to colonize within established hardwood stands aged 25 to 70 years old.

Cline and Lockard (1925) ascribe great importance to the notion of single pines as having regenerated as part of a larger, buffering group of pines. Figure 1A is a profile diagram of such a group after 40 years of growth. There is one codominant pine, several surviving understory remnants of the group, and many dead pine stems. Figure 1B presents a codominant pine in a contrasting situation. There are many fewer stems and no buffering pines. There is only an isolated codominant pine.

In the survey of basal area around isolated canopy pines in the hardwood forest (Table 2), I found 31 examples (24%) of a group remnant (Fig. 1A), 47 examples (36%) of single pines (Fig. 1B), and 51 examples (40%) which fell somewhere between these two extremes. Many pines in these stands therefore appear not to be regenerating in groups but as isolated individuals surrounded by hardwoods.

A clue to the successful regeneration of these isolated pines is found in the density of stems seen in Figs. 1A and 1B. Stem density around the isolated pine is approximately 1450 live stems·ha^{-1} and approximately 3000 around the group remnant. If stand density is considered to reflect degree of competition, it appears that individual pines can regenerate when hardwood competition is not too severe.

To further document the role of competition in the successful regeneration of white pine, I measured basal area, a measure of stand density, around selected pines in 40-year-old forest stands (Table 2). Pines that were remnants of pine groups, pines that were partially buffered from hardwoods by pines, and pines in the understory (trees that had failed to grow well and that will most likely die in the understory), all grew under conditions of moderate density, 22–25 m^2·ha^{-1}. Pines that were able to survive and grow without the aid of buffering pines grew in low-density stands, about 18 m^2·ha^{-1}. Pure pine stands had a much higher density than mixed hardwood – pine stands (34 m^2·ha^{-1}). Apparently, then, white pine can grow in hardwood stands of low density unaided by a buffering group of pine but, as hardwood competition increases (as it

TABLE 1. Relative age and height of dominant and codominant white pines with paired hardwood, 25–70 years old. Same age equals ±5 years; same height equals ±2 ft (1ft = 0.3048 m) (Tarbox and Reed, Harvard Forest Records, Inactive Research, 1923–file 4)

Sample	N	% of population		
		Older	Same age	Younger
All pairs	73	23*	68	8
		Taller	Same height	Shorter
All pairs	73	36	49	15
Pairs same age	50	32	56	12
Pairs ≥45 years	43	47	44	9

*Example: 23% of the pines were >5 years older than their hardwood neighbor.

TABLE 2. Basal area around dominant and codominant white pines

Isolated pine	Sample size (N)	Basal area ± SE (m^2·ha^{-1})
Group remnant	31	25.13±1.01[a]
Partially buffered	51	22.39±0.90
Always isolated	47	17.79±0.68
Understory pine	64	24.46±0.73[a]
Pine stand	12	33.71±1.45

[a]Not significantly different (p = 0.05), Duncan's new multiple range test (Steel and Torrie 1960).

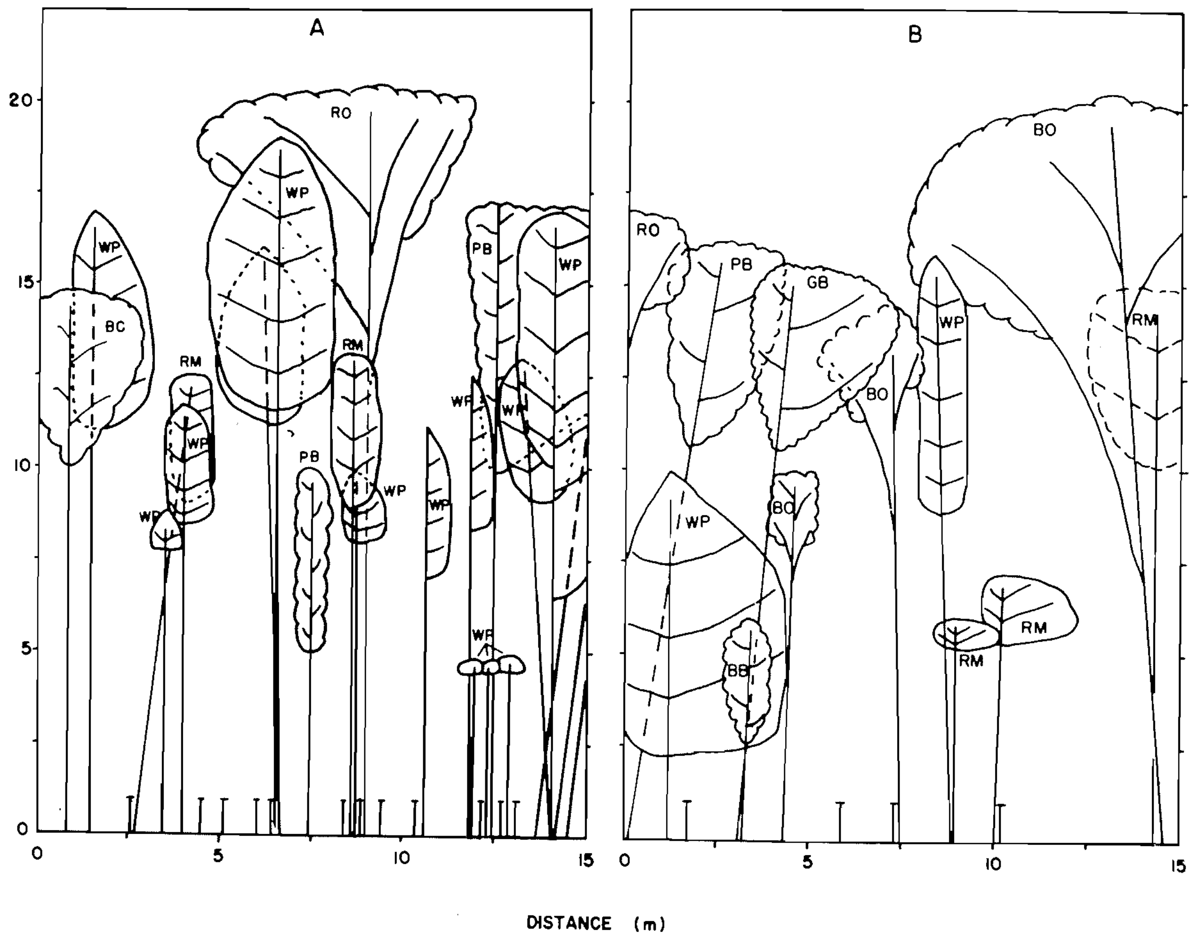

FIG. 1. Canopy profile diagrams from 5 × 15 m transects. BB, black birch; BC, black cherry (*Prunus serotina*); BO, black oak; GB, gray birch; PB, paper birch; RM, red maple; RO, red oak; WP, white pine. Short vertical bars represent dead stems.

could for many reasons, including seed source and increased soil moisture), buffering becomes important. Trees that fail to grow well do so because density, particularly early density, is too great.

The height growth of six small groups of 40-year-old and five groups of trees 100+ years old centered around a dominant or codominant white pine was investigated. The three 40-year-old groups selected for presentation here (Fig. 2) illustrate certain phenomena but are not materially different from the other three groups. In Fig. 2A, the present canopy trees were all growing within 3 years of canopy removal and have grown at a nearly constant rate for 40 years. Hemlock has maintained a slow but constant growth rate and, because of its extreme shade tolerance (Anonymous 1965), can be expected to continue to do so. One white pine germinated 11 years after the hurricane, and it has grown slowly in the understory. Figure 2B repeats the basic pattern of Fig. 2A except that pin-cherry (*Prunus pensylvanica*), which has a life-span of 30 to 40 years, has about ceased height growth. The white pine in this group, although a late colonizer, is maintaining a high growth rate. This is a tree which colonized a site still unoccupied 9 years after the hurricane and so has been able to grow unshaded. Figure 2C contains a cluster of postdisturbance regeneration and two white pines. One is a late colonizer with poor growth. It appears to have grown well for about 15 years and then become overtopped. The other pine appears to be an understory remnant of the previous stand, but even this 20-year head start seems to have conferred little long-term advantage.

While the rate of height growth of most trees appears to have increased for the first 10 years (especially Fig. 2B) as expected in classic sigmoid growth curves, the growth of white pine is not necessarily less than that of hardwoods. This is in contrast with Cline and Lockard (1925) who show 10-year-old white pine on heavy soils

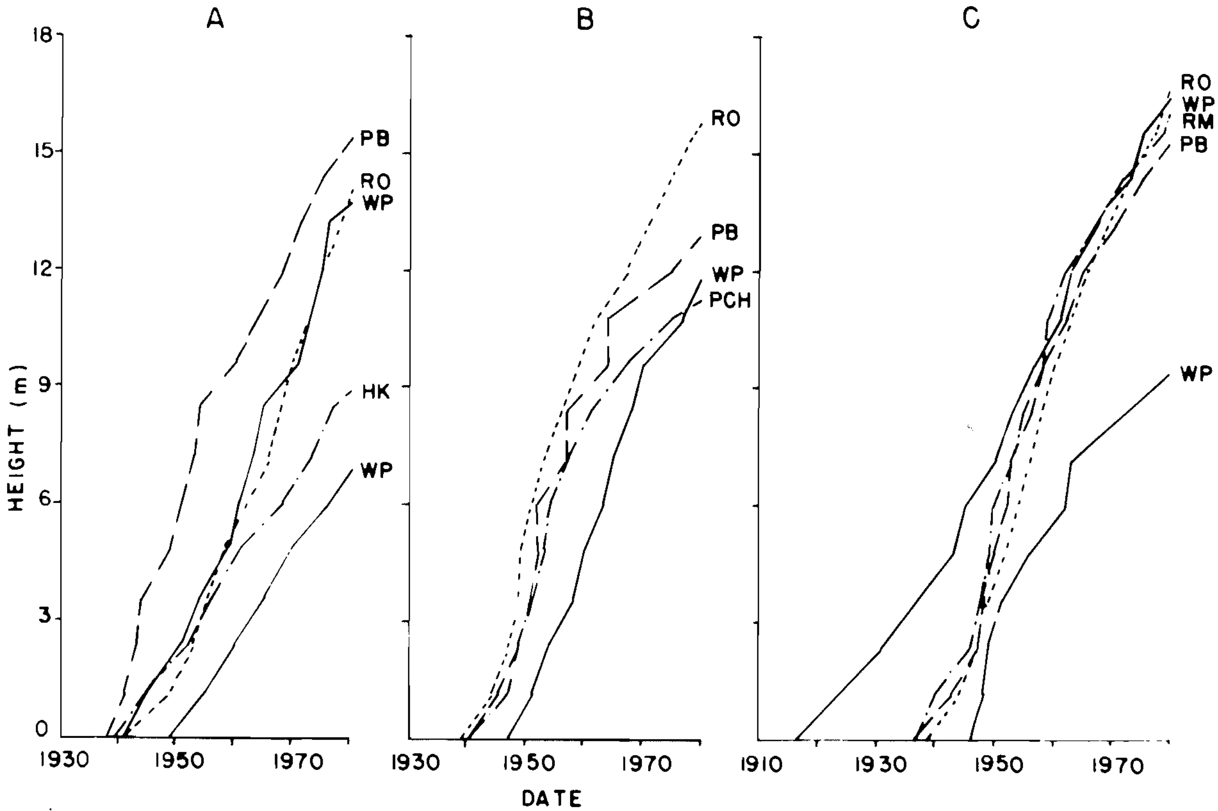

FIG. 2. Height growth of individual trees grouped around a central pine in stands originating following canopy destruction by the 1938 hurricane. HK, hemlock; PB, paper birch; PCH, pin-cherry; RM, red maple; RO, red oak; WP, white pine.

ranging in height from 4 to 9 ft (1.2–2.2 m) and hardwoods ranging from 7 to 17 ft (2.1–5.2 m), although pine has nearly caught up by year 40.

The growth of five groups of trees 100+ years old was also examined. Four groups are presented here (Fig. 3). The fifth closely resembles Fig. 3A. Figure 3A represents an essentially even-aged situation although the pine is 10 years younger than the oldest (103 years) tree. Height growth was relatively constant until about 1920 (40 years). Growth generally slowed until about 1950 when, for unknown reasons, growth again resumed at a high rate. Between 1950 and 1980, the white pine grew from the shortest to the tallest tree of the group. The pine and hemlock of Fig. 3B appear to be understory remnants of an early stand. They were released following canopy removal in about 1895, the year the hardwoods began to grow. Hemlock responded more quickly than white pine to this release. The trees in Fig. 3C are again two-aged, the red oak initially growing well over the suppressed red maple, hemlock, and the older pine. Around 1920, some event, perhaps the chestnut blight, released these trees and provided the growing space for a new white pine. This pine has grown at a high ($0.28\ m^2 \cdot year^{-1}$) and nearly constant rate for 68 years. The group of trees in Fig. 2D contains a remnant hemlock and three younger trees that exhibit little of the fluctuation of growth rate seen in Fig. 3A–3C.

Several generalizations about these growth patterns can be made. Although it was not suspected when they were chosen for study, three of five groups are two-aged. They originated from situations of disturbance, and of gap regeneration in at least some cases. White pine, red oak, and red maple all were found to regenerate in these gaps. Hemlock and black birch are equally, if not more, shade-tolerant than these species and so also presumably regenerate in gaps. It is likely, however, that different size gaps favor regeneration of different species (Hibbs *et al.* 1980). White pine and hemlock also appear to have survived as understory remnants to form part of the canopy of later stands.

White pine, 90 or more years old, generally appears to be taller than similar-aged neighbors (Figs. 3A, 3C, 3D and not shown fifth group). In addition, among similar-aged hardwoods in all five groups, the red oak is always tallest, followed by red maple, and then black birch. The height of hemlock, as a very shade-tolerant tree (Anony-

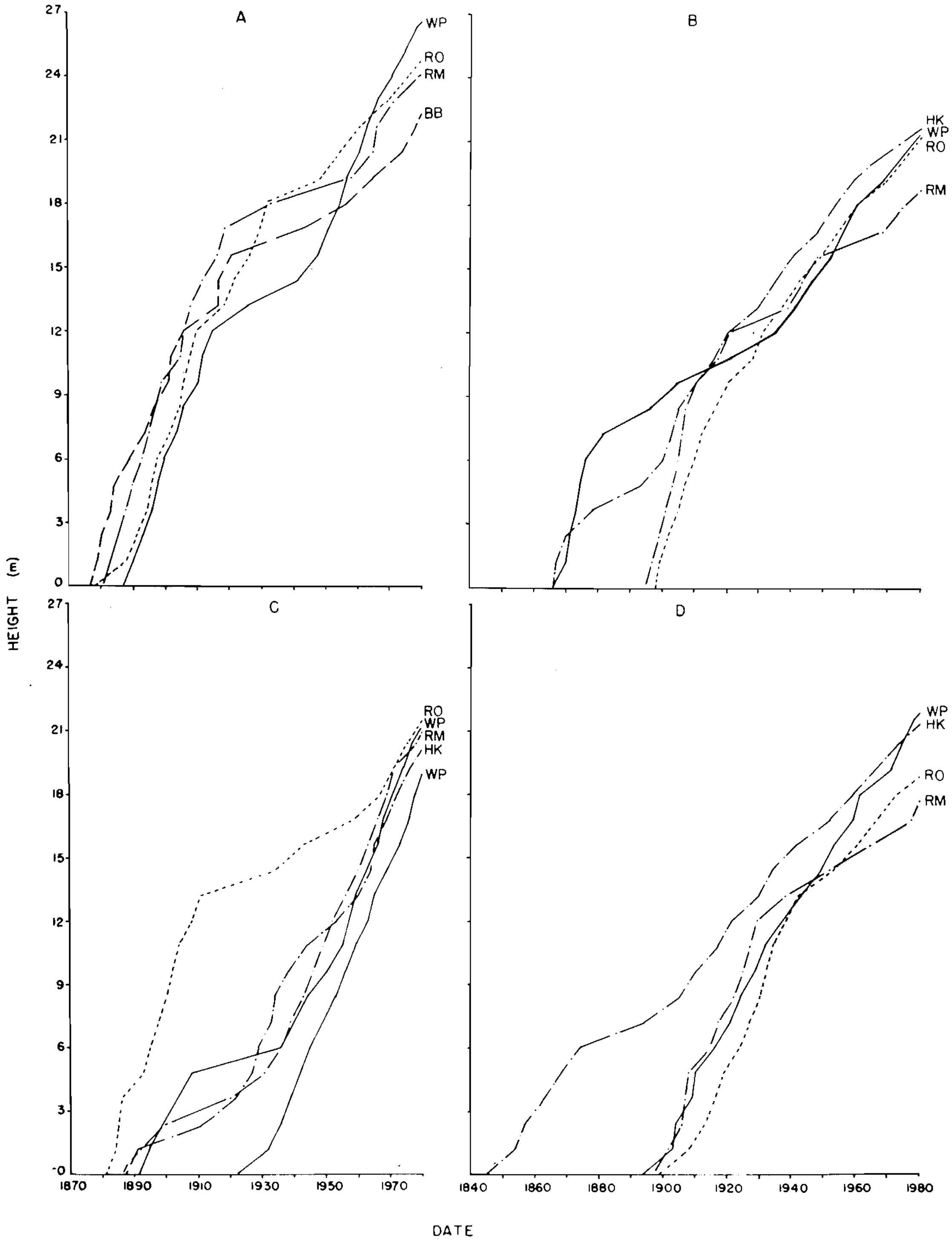

FIG. 3. Height growth of individual trees grouped around a central pine in old (> 100 years) stands. BB, black birch; HK, hemlock; RM, red maple; RO, red oak; WP, white pine.

mous 1965), is a function of age and suppression history. Hemlock appears to respond to release more quickly than other species (Figs. 3B, 3C) but achieves lower maximum growth rates. It therefore has a rather sporadic history of height growth.

Discussion

Origin of white pine

There are several possibilities for regeneration of white pine in a hardwood forest. The importance of each varies with site parameters, seed source, stand age, and disturbance history. (*i*) When hardwood competition is high, pine may regenerate in small groups. (*ii*) When hardwood competiton is not severe, single pines may survive to maturity. (*iii*) Understory pine from a previous stand may survive and grow after canopy removal. (*iv*) Pine may also regenerate in larger canopy openings in older forests.

A small group of pine regeneration can act as a buffer against encroaching hardwoods and allow a central individual to survive to maturity (Cline and Lockard 1925). This process may be more important on better sites (medium and heavy soils (Goodlett 1960)), where hardwood competiton is more severe. In this situation basal area is high (Table 2) and pine trees found in the overstory are frequently (24% of isolated canopy pines in the study area) the product of such a group. Single pine trees in these stands are suppressed because they are quickly overtopped by hardwoods.

On rare occasions, suppressed understory pine in an older stand may survive canopy destruction to form part of the canopy of the new stand. This head start, however, does not appear to give much height advantage to these trees in the long run. Because white pine is only moderately shade-tolerant (Anonymous 1965), successful advanced reproduction (more than about 10 years old) in natural situations is probably rare.

The opposite condition, pine younger than surrounding hardwoods, also is rare, except in old forests. In younger forests (<60 years), pine more than 10 years younger than the hardwoods is rare. The forest is essentially even-aged and any late-coming pines, with few exceptions, are found in the understory. In larger canopy gaps in older forests, pine occasionally reproduces. A sufficiently large opening is necessary, but the lack of the common, competing early successional species, pin-cherry and gray birch (*B. populifolia*), in these openings probably also contributes to the success of pine. In a summary of old-growth stands in southwest New Hampshire, Cline and Spurr (1942) also found pine reproducing after moderately severe canopy disturbances.

Growth of white pine

With rare exceptions, white pine trees found in the forest canopy were trees that had always been part of the canopy. In the cases studied here, the rate of height growth of white pine and the associated hardwoods is surprisingly similar. Growth curves tracked each other through extended linear-growth phases and through periods of decreased growth. Little evidence of the often described (Cline and Lockard 1925; Anonymous 1965) early slow growth rate of pine was found. It may simply be that trees exhibiting this behavior do not survive in mixed hardwood – pine stands.

Textbook growth curves are sigmoidal, but only the pin-cherry curve (Fig. 2B) has this form. Pin-cherry is a short-lived tree dominant in early succession. The remaining growth curves are characterized by phases of linear growth interspersed with phases of erratic, slow growth. Even the growth of young trees bears scant resemblance to the first stages of a sigmoidal curve. Apparently, the many impinging environmental factors are sufficient to obscure this basic form in mixed-species stands.

In older stands, differences in rate of height growth produce an interesting pattern of canopy stratification. Several of the older pines examined were beginning to emerge through the hardwood canopy, and a very distinct stratification was present among the hardwoods. This is similar to Oliver's (1978) description of canopy structure in the hardwood forest of central New England: red oak tending to be taller than and spreading out over red maple and black birch. Oliver found, however, that black birch averaged a little taller than red maple, the opposite of the situation described here.

The contrast between these results and those of Cline and Lockard (1925) are strong. They presumed that pine in hardwood stands came about as a result of group reproduction of pine, or occasionally, from understory remnants of previous stands. These two processes do take place but they are far from the only ones. To this must be added single-tree growth in low-density stands and, in old forests, reproduction in canopy gaps. The reason for this contrast with Cline and Lockard (1925) lies in their having generalized the growth of hardwoods and pine in relative isolation, at least partially, from each other and over a broad area, and having examined only reproduction and growth following logging. Comparing growth within a group of trees alleviates some of the problems of sampling from different sites, and reproduction following canopy destruction by wind probably reduces the amount of sprout reproduction over that found following logging. Cline and Lockard (1925) also focused on trees growing on heavy soils while the stands considered here are on medium and light soils. The competitive advantage shifts from hardwoods to pine through this continuum, from moist (heavy) to dry (light) soils.

So the conclusions of Cline and Lockard (1925), while true, are incomplete. White pine can be found in many situations, in nearly pure pine stands following fire or farm abandonment or on drier sites and in mixed hardwood – pine forests varying in composition from nearly pure pine to rare and scattered pine among numerous hardwoods. It can also be found as a component of regeneration in larger canopy openings in mature forest. White pine can successfully reproduce and grow under all of these conditions. In the hardwood forest, white pine can eventually become an emergent tree over the loosely layered (red oak over red maple and black birch) forest canopy.

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