



Species composition and dynamics in two hardwood stands in Vermont: a disturbance history

Peter R. Hannah*

University of Vermont School of Natural Resources, Department of Forestry, Aiken Center, Burlington VT 05405-0088, USA

Received 4 February 1998; accepted 19 November 1998

Abstract

Stand composition and structure utilizing stem analysis was studied in two hardwood stands in Vermont. In a mixed hardwood stand with some white pine and hemlock, a major entry of new trees in the main canopy seems associated with harvesting coincident with land exchange. More recent partial cuttings have promoted establishment of new seedlings or development of suppressed advanced-growth shade-tolerant beech, (*Fagus grandifolia*, Ehrh.), hophornbeam (*Ostrya virginiana*, (Mill) K. Koch), and striped maple (*Acer pensylvanicum*, L.). Very few sugar maple and red oak seedlings and saplings are present.

In a northern hardwood stand some red spruce (*Picea rubens*, Sarg.), that were 240 to 306 years old, became established before any known harvest, and exhibited release following harvests of the mid-1800s. This major harvest, coupled with the differential growth between spruce and hardwoods, and seed/seedling availability, resulted in a major change in stand composition. Trees now in the main canopy of sampled stands appear to have either been released or newly established following various harvests. Harvests have been of such frequency that natural disturbances seem insignificant. Many of the competitive understory species have become abundant following harvests of the 1960s and 1980s and may have been present as advanced growth and responded to the release. Following the harvest of 1981–1982, abundant yellow birch became established on skid trails. Elsewhere in the stand, yellow birch seedlings and saplings are only in great abundance in areas that were possibly sizable gaps following earlier harvesting.

The dynamics of tree entry and growth in gaps of small or large size probably occur in a similar way in many other stands of the region. Though the sampling of this study is limited, there is no suggestion of continuous tree establishment at any particular location, the new age classes seem associated with either a gap or stand replacing disturbance attributed to harvesting. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Stand dynamics; Northern hardwoods; Tree height growth

1. Introduction

Forests of the northeastern United States have endured much disturbance since the arrival of Euro-

peans. The agricultural era of the 1800s, and extending into this century, resulted in extensive clearing of forest lands for farming. Vermont was only about 25% forested at the peak of this period. As a result of past land use, much of Vermont's forests are comprised primarily of second-growth stands re-established on abandoned pasture or cultivated land. Although

*Tel: +1-802-656-0682; fax: +1-802-656-8683; e-mail: p.hannah@nature.snrr.uvm.edu

original stands were not entirely removed, most have been modified by various intensities of harvest. Since the natural reforestation following the agricultural era, many of the second-growth stands have had multiple entries for partial harvests. The array of forest stands now on the landscape present a wide variety of age-class structures and species compositions.

An understanding of stand structures and how they develop is essential in devising silvicultural practices that are ecologically compatible with our developing concepts of ecosystem management and maintenance of biological diversity. Much is known about the ecology of the individual species comprising the hardwood forests of the northeast. We know that forests returned following the major disturbance of farming, but there is sketchy information on how stands of varying structures developed over time. In forest stands that were harvested but never completely removed, there is likewise limited information on the dynamics of how the new structures developed to their present state. Watt (1947), was among the first to examine and hypothesize how forests and other plant communities may develop. Watt's introduction of the concept of 'gap phase' in stand development has led to decades of investigating this phenomenon in the study of stand dynamics in forests throughout the world. Oliver and Larson (1996) review much of the more recent literature on forest stand dynamics.

Most studies of forest stand structure and development in the northeast have focused on changes in composition over time, (e.g. see Leak, 1987; Fain et al., 1994), and the effect of gap size on resulting composition (e.g. see McClure and Lee, 1993). Many stand-dynamics studies are based on detailed measures taken during a short time interval, incorporating knowledge of stand history and disturbances. Few studies are based on repeat measures in the same area over a long period (e.g. see Stephens and Ward, 1992). Changes in species composition over time usually show a trend toward domination by late successional species until a major large gap or stand replacement disturbance occurs to potentially initiate an earlier stage. The struggle among trees over time for a position in the main canopy is not revealed in most of these studies. In a recent study of stand development, primarily by analysis of age/size classes in the relatively undisturbed Bowl area of

New Hampshire, Gamboorys (1996) postulates that late succession species, primarily red spruce (*Picea rubens*) and American beech (*Fagus grandifolia*, Ehrh.), in northern hardwood-spruce-fir forests may alternate in dominance and yellow birch (*Betula alleghaniensis*, Britton) may be sparse if no major gaps occur.

The use of stem analysis methods can demonstrate the constant competition among survivor trees for position in the main canopy and the change in stand structure over time. In a study in the northeastern United States, Oliver (1978), while combining stem analysis techniques and stand history, demonstrated the competitive ability of northern red oak (*Quercus rubra* L.) in association with red maple (*Acer rubrum* L.) and black birch (*Betula lenta* L.). He found that oak, often a subordinate in the early stages of an even-aged stand, invariably emerged as a dominant tree in the canopy after ca. 30 years.

Stem analysis has not been widely used to study competitive dynamics among species in northern hardwood stands. This study employed detailed stem sectioning of trees to determine height growth patterns in second-growth northern hardwood stands as they progress toward the mature stage. Use of stem analysis methods should demonstrate how northern hardwood stands dominated by American beech, yellow birch and sugar maple (*Acer saccharum*, Marsh), develop following reinvasion of abandoned farmland, or following partial cutting or clear-cutting of original forests, or maturing second-growth forests.

I hypothesize that since Vermont was judged at only ca. 20% forested in the mid-1300s, virtually all stands seen today are second growth and have been repeatedly entered for partial harvest. These human disturbances along with those that occur naturally, usually as small gap disturbances, would have a primary influence on succeeding composition, structure, and growth rate. Major changes in composition, distribution of age classes and formation of a stratified canopy structure should indicate whether the present stand results from gap or stand replacing disturbances or continued replacement by new or advance regeneration as individual trees die. This study, on two northern hardwood stands, comparing stem analysis, was conducted to assess the influence of human disturbances, primarily harvesting, on stand composition and development.

2. Study area and history

The two study sites are in northwestern Vermont near 44°30' latitude and 72°55' longitude. A mixed northern hardwood stand (Stand 1) dominated by sugar maple, red maple (*Acer rubrum*, L.), northern red oak, and American beech, and numerous understory associates was studied at The University of Vermont Research Forest in Jericho. This stand of ca. 2 ha (5a) in area has apparently been in continuous woodland since settlement in the late 1700s. It was used as a farm woodlot with some cattle grazing until 1917 (Shannon, 1950). The stand is at 700 feet (213 m) elevation on an outwash sandy loam soil over schist bedrock near the eastern edge of the Champlain Valley. Plot 1 is on a rocky, shallow-to-bedrock portion of the area on a hilltop and Plot 2 is on a lower slope near an abandoned road and reforested fields.

There is no known record of forest composition when the land was settled in 1790. In the surrounding area beech, sugar maple, red maple, yellow birch, white birch (*Betula papyrifera*, Marsh.), white pine (*Pinus strobus*, L.), northern red oak, bigtooth aspen (*Populus grandidentata*, Michx.), trembling aspen (*Populus tremuloides*, Michx.), eastern hemlock (*Tsuga canadensis*, (L.) Carr.) and black cherry (*Prunus serotina*, Ehrh.) are found. Pine timber was harvested from the land prior to sale of the farm in 1851. The farm was sold again in 1902.

In 1940, The University of Vermont acquired the 160-acre farm and began establishing conifer plantations on the open fields. Following purchase, there is no record of harvesting activity in the study area until 1956 when an improvement cut was made removing hophornbeam (*Ostrya virginiana*, (Mill) K. Koch) and other poor quality hardwoods. Additional light harvests were made in 1968–1969, and light selection cuts in 1978 and in 1996.

The second stand is in Underhill, on the west slope of Mount Mansfield in the Green Mountains at ca. 450–500 m (1500–1700 feet) elevation. This mature stand is on fairly steep land and has apparently always been in forest cover but harvested at least three times (Cogbill, 1996). Sugar maple, yellow birch, and American beech dominate in the main canopy. Hobblebush (*Viburnum alnifolium* Marsh.), striped maple (*Acer pensylvanicum*, L.),

and American beech dominate the understory, but sugar maple and yellow birch are also present. The silt loam soil at this site is derived from glacial till and usually has a firm horizon within two feet of the surface, resulting in saturated soil conditions during early spring. This soil condition is typical of much of the forested uplands of Vermont. Productivity on these soils is good but can vary with location, being greater on lower slopes and protected coves and on sites with greater depth to the drainage-restricting layer.

Records of harvesting up to the early 1900s suggest the area was heavily cut. Lumbering evidently began in the early 1800s. In 1838, open land was purchased in Underhill and a mill was built by the year 1840 (Cogbill, 1996). H.P. Hickok, a Burlington lumberman, and partner M.L. Stevens established the logging village of Stevensville with two sawmills in 1843 (Cogbill, 1996). In 1849, 300 MBF were milled and in 1856 another 100 MBF/year planned for harvest during four years (Cogbill, 1996). Cogbill defines 1836–1865 as the first major cutting period in the area. Most of the wood cut in the area was evidently red spruce (*Picea rubens*, Sarg.). Harvesting subsided after 1865 and stumps were cleared on the lower slopes for farming. About 1897, harvesting in the area shifted to hardwoods and even 'sugar orchards' were cut (Dwyer, 1976). By the early 1900s, most of the area had been heavily cut and farming expanded. Farming had long been important in the area; in 1840, there were an estimated 3400 sheep on mountainside pastures in Underhill (Dwyer, 1976). After the logging, dairy farming began and expanded until the 1930s and 1940s; thereafter, it began to decline. Today, there is little dairy farming in the area. The Vermont Department of Forests, Parks and Recreation acquired much cutover forest land in this area near the end of the lumbering era and established the Mt. Mansfield State Forest, the first land acquired in 1914 (Vermont State Forest Land Records). Other parcels were obtained in later years. By 1934–35, stands were recovering and an improvement and spruce release cut was made, followed by a selection cut in 1956 and another in some areas in 1966. In 1983–85 a combination of thinnings and shelterwood cuts were made throughout the 200 acres, including the sampled area.

Table 1
Tree density and basal area per hectare by species for trees 10 cm and larger based on 0.04 ha plots for four study sites at Jericho Forest and Mount Mansfield in Vermont

Plot	Species	Trees/ha	Basal area m ² /ha	
1. Jericho	red maple	148.8	3.95	
	red oak	24.7	2.46	
	white ash	24.7	0.46	
	sugar maple	148.2	8.45	
	hopornbeam	49.4	0.41	
	bitroot aspen	24.7	2.46	
	Total	420.5	18.19	
	2. Jericho	red maple	123.5	12.05
		beech	74.1	1.22
		hemlock	74.1	1.38
yellow birch		74.1	1.22	
white pine		24.1	2.46	
black birch		49.4	3.12	
Total		419.9	21.45	
3. Mt. Mansfield		sugar maple	321.0	14.14
		beech	24.7	1.24
		red spruce	49.4	7.28
	yellow birch	24.7	0.21	
	Total	419.8	22.87	
	sugar maple	296	32.59	
	beech	74	3.21	
	Total	370	35.80	
	4. Mt. Mansfield	red maple	123.5	12.05
		beech	74.1	1.22
hemlock		74.1	1.38	
yellow birch		74.1	1.22	
white pine		24.1	2.46	
black birch		49.4	3.12	
Total		419.9	21.45	

3. Methods

In each stand, two 0.04 ha (1/10 acre) circular plots were established. Diameters of all trees 9 cm (3.6") DBH and larger were recorded and stem density and

4. Results

Among the trees presently in the main canopy of these two second-growth hardwood stands, stem analyses indicate they apparently entered the stands during several distinct establishment periods closely

An electronic caliper was used to record in a disk, five-year average radial increments, and dis-compute the number of growth rings counted on each disk, year average radial increments, and disk data were used to plot height growth patterns for each tree using Sasgraph (SAS Institute, 1988). Radical growth data will be used to study volume growth of the sample trees. Because it was evident that composition and age vary within the stand, data for each plot is analyzed and presented separately. An analysis of covariance (ANCOVA) test was made to detect differences between plots within sites and differences between sites.

basal area determined (Table 1). A sample of trees usually representing a large and small diameter tree each species, was then felled for stem analysis. Soil trees were sampled from beyond the plot perimeter to represent the species diversity of the stand. Cross-section disks were removed, usually at stump height at 1.3 m (4.5 feet), thereafter at 2-4 m intervals. Numerous understory trees and shrubs were also sampled on each plot, most with only one disk taker near ground line to determine total age. Density of understory woody vegetation was determined on two randomly located 10-m² plots within each 0.04 ha plot (Table 2).

Table 2
Stem density of seedlings/saplings per hectare 1 m tall to 10 cm DBH for four study sites at Jericho Forest and Mount Mansfield, VT, based on tally of two 10-m² plots in each 0.04-ha sample area. (All species in the stands are not represented in these tallies)

Species	Jericho Plot 1	Jericho Plot 2	Mr. Mansfield Plot 3	Mr. Mansfield Plot 4
Beech	1000	3000	4000	7000
Hobblebush	0	0	0	0
Hopornbeam	3000	1000	0	4500
Striped maple	5000	2500	0	0
Sugar maple	500	2000	0	5500
White ash	500	0	0	500
Yellow birch	0	0	0	0
Total	10000	9000	7000	18000

JERICOHO PLOT 1 -- 1990

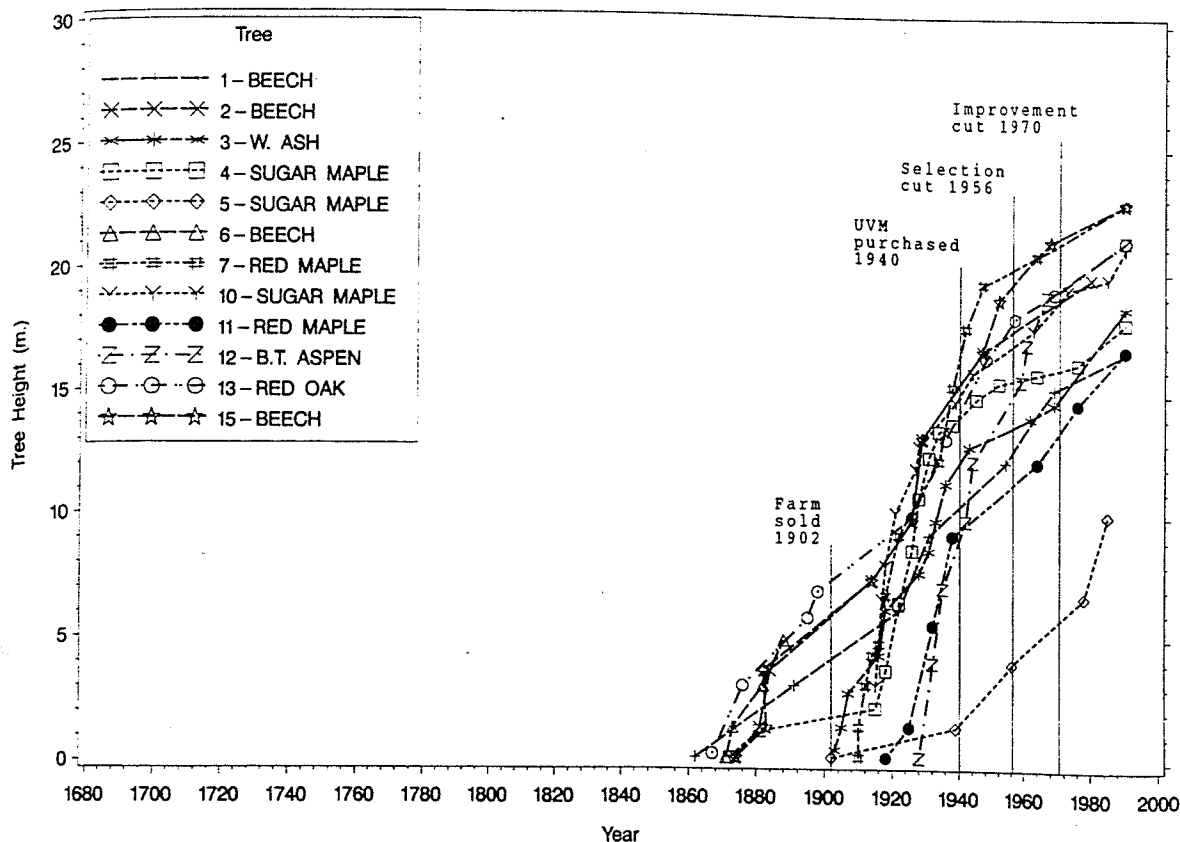


Fig. 1. Height growth of individual hardwood trees determined by stem analysis in a second-growth stand (Plot 1) on stony, sandy soil (Adams-Lyman) in the Champlain Valley, Jericho, VT.

associated with harvesting disturbances. At Jericho, some trees on Plot 1 entered the stand between 1860-1880. Another major establishment period occurred between 1900 to 1930. On Plot 2, some sampled trees became established in the early 1900s and another cohort entered from 1920s to the 1940s (Figs. 1 and 2). These establishment periods closely coincide with ownership changes suggesting that harvesting may have occurred before or after each sale of the land, and thus created openings for new trees to enter.

On Plot 2, at Jericho, the red oak and red maple that established in the early 1900s show a pattern of relatively unsuppressed height growth. Trees established in the period between 1920s and 1940s show patterns of both, suppression and response to release. The yellow birch shows substantial response follow-

ing partial cutting in the late 1970s. Most of the trees in this area probably established since ca. 1900, but a white oak (*Quercus alba*, L.) on a fence line nearby is aged from an increment core at 140 years, thus establishing at ca. 1850, a time of land exchange. This tree had barbed wire in it, possibly erected about 1900. Steepness of height growth curves on Plot 2 suggest trees are growing at a good rate (Fig. 2). This plot is at the base of the slope facing east and on land of higher site quality than Plot 1. The ANCOVA test of growth rate indicates trees on Plot 2 are growing significantly faster ($p < 0.05$) in height than trees on Plot 1.

Ages of most seedlings/saplings sampled in Plot 2, and nearby, indicate they became established or responded as advanced-growth seedlings following

A sample of trees, all diameter tree of stem analysis. Some at the plot perimeter to the stand. Cross at stump height, 2-4 m intervals. Shrubs were also taken at one disk height. Density of trees determined on two disks each 0.04 ha plot

to record in a disk counted on each disk, and disk height data for each tree. Radical growth of the sample plot is analyzed for covariance differences between

main canopy of stands, stem analysis of the stands during periods closely

field, VT, based on

Mansfield Plot 4

000
000
0
00
00
0
00
00

JERICHO PLOT 2 -- 1990

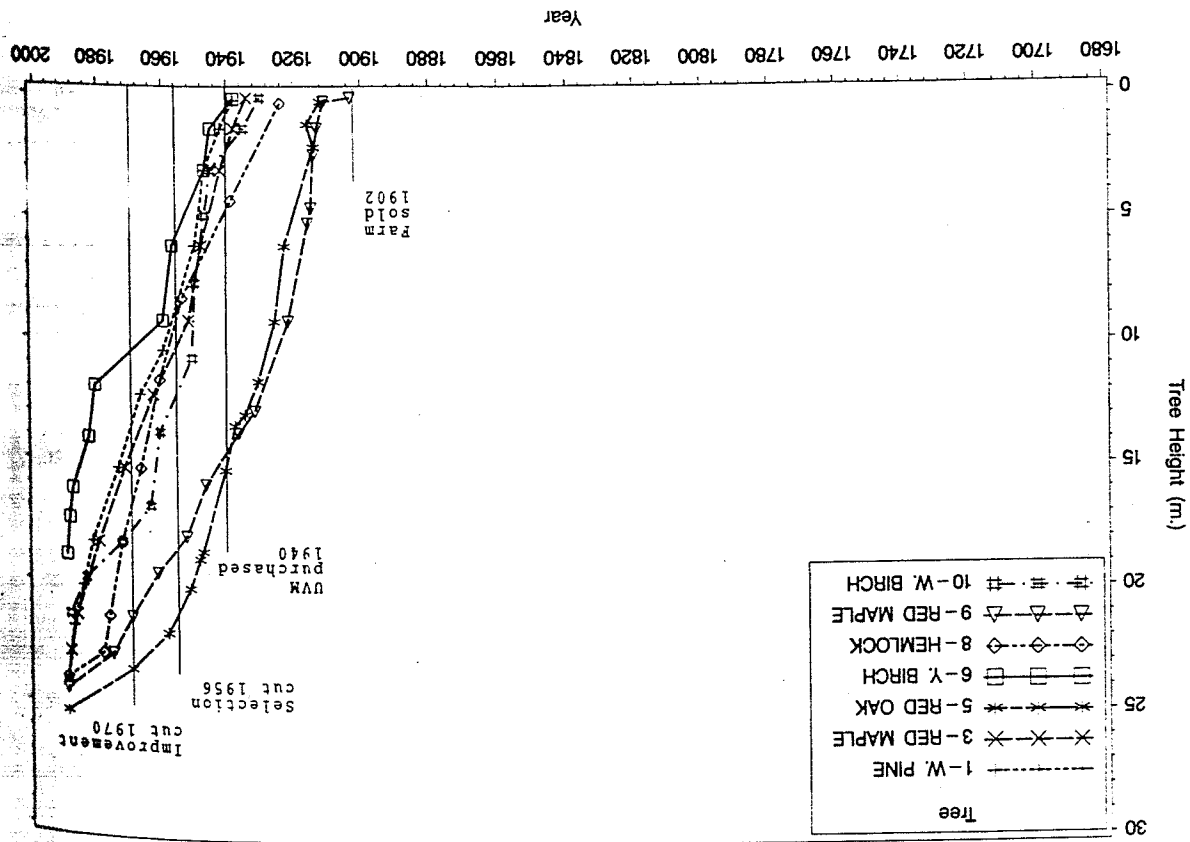


Fig. 2. Height growth of individual hardwood trees determined by stem analysis in a second-growth stand (Plot 2) on sandy soil (Adams Sand) in the Champlain Valley, Jericho, VT.

the harvesting of 1956 and 1968 (Table 3). Beech, red maple, hophornbeam and striped maple are among the more common understory species (Table 2). In the greater stand area beech, red maple, red oak, birch, hemlock and white pine dominate in the main canopy (Table 1). Wildlife is apparently having a major effect on current understory composition in both plots and surrounding areas. Beech and hophornbeam do not appear browsed and are identified by Howard (1979) as not highly preferred deer browse. Observations of deer browsing in this, and other, areas indicate that red oak and sugar maple are highly preferred browse.

The stand on Mt. Mansfield, at an elevation of 1400-1600 feet, can be regarded as typical maturing second-growth northern hardwoods, primarily beech, yellow birch, and sugar maple with some scattered red spruce and other associates. There is no information

on the condition of the forest when it was acquired by the Vermont Forest and Parks Department in 1914, but lumbering activity from ca. 1840 to the early 1900s suggest the areas was heavily cut (Cogbill, 1996). Trees on Plot 3, at ca. 1400 feet elevation, show the greatest variation in age. The oldest sampled tree, a red spruce, was about 30 cm tall in 1685, the other 30 cm tall in ca. 1755, prior to any known harvesting in the area. Both these spruce trees grew very slowly until ca. 1860, the older tree was then ca. 10 m (30 feet) tall, 175 years old, and ca. 15 cm DBH. Until 1850-1860, this spruce was evidently suppressed under a canopy of other spruce or hardwoods, then released (Fig. 3). The history of lumbering in the area suggests that logging occurred in the vicinity of the study plots about that time. Spruce was the principal tree being harvested as evidenced by a photo taken near the



Jams Sand)

quired by 1914, but ly 1900s l, 1996). show the ree, a red er 30 cm ng in the until ca. (eet) tall, 10-1860, a canopy (Fig. 3). ests that dy plots ee being near the

Table 3 Mean age and height of a random sample of understory trees and shrubs sampled in hardwood stands at Jericho and Underhill (Mt. Mansfield) Vermont

Species	Jericho Plot 1			Jericho Plot 2			Mt. Mansfield Plot 3			Mt. Mansfield Plot 4		
	average age	range	average height (m)	average age	range	average height (m)	average age	range	average height (m)	average age	range	average height (m)
Beech	13	9-24	2	17	14-23	8	13	8-15	7	18	17-23	3
Yellow birch				22	21-23	8	13	8-23	4	20		3
Sugar maple				19		6						
Red oak				41	39-44	11						
Hemlock				20		3						
Hophornbeam	26	16-43	6	32		9						
American Hornbeam				35	35-36	10						
(<i>Carpinus caroliniana</i>)							16	9-22	3	16	9-22	3
Striped maple	17	16-29	2	15		8						
Witch hazel				20	13-34	8						
Elderberry							7	6-9	3	9	8-18	2
Hobblebush							10	7-18	2	10		2

MT. MANSFIELD PLOT 3 -- 1992

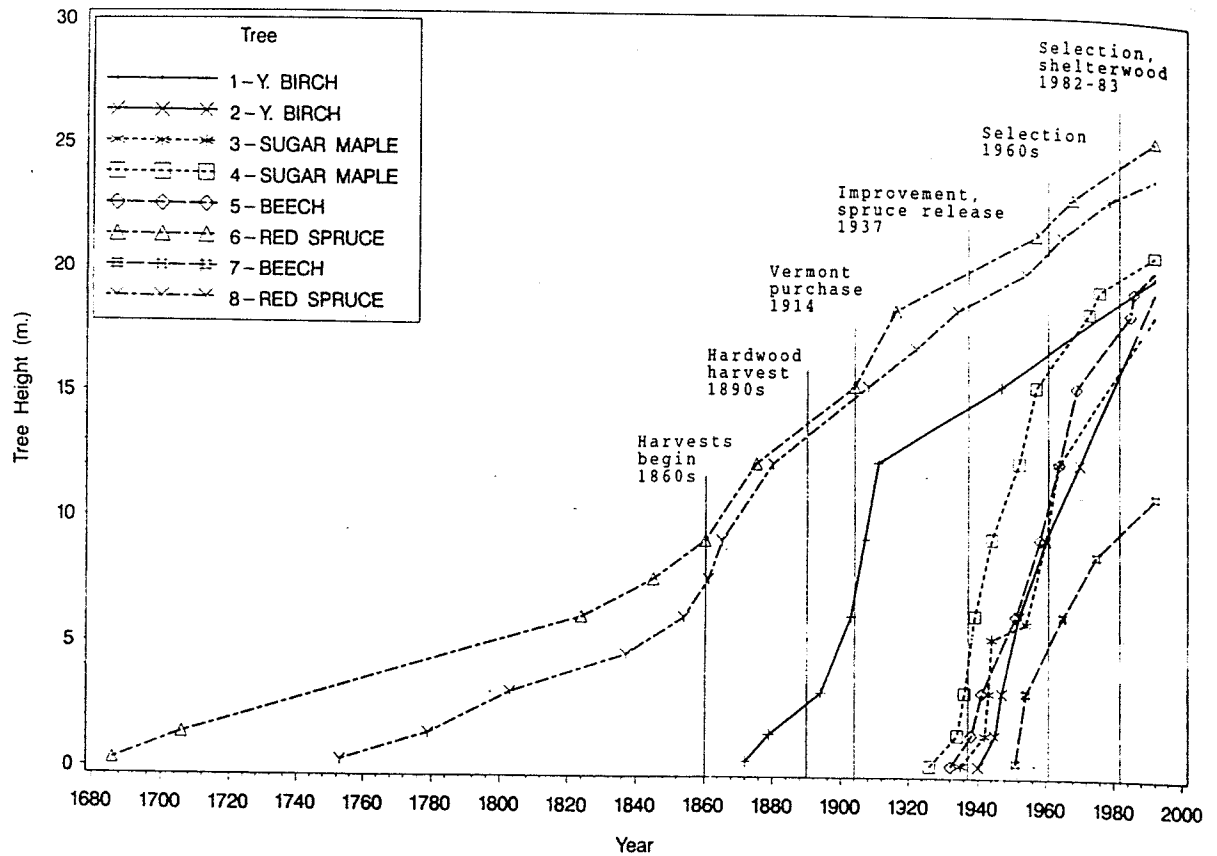


Fig. 3. Height growth of hardwoods and red spruce determined by stem analysis for Plot 3 lower site on Mt. Mansfield, Underhill, VT.

Halfway House Lodge ca. 1850, showing large spruce trees in the surrounding forest. A new house on the same site, photographed in the 1920s or 1930s has a hardwood stand behind it (Hagerman, 1975). Harvesting in the area from about 1860–1900 evidently resulted in conversion of the stand from spruce to northern hardwoods as they now dominate the stand at this elevation. There are no stumps evident, which is indicative of the spruce harvesting.

Among other trees on Plot 3, a yellow birch represents an age class entering in the 1860s, and a third age class of main canopy trees apparently entered the stand during the period 1920–1940. The youngest trees on Plot 3 evidently began after the harvest cuts of 1956, 1966 and 1980–1983. They were either advance seedlings that were released following each

cut or new seedlings that entered after the harvests. Striped maple, beech and yellow birch dominate the regeneration, most of it under 20 feet tall (Table 2). Sugar maple may dominate in localized areas. Yellow birch occurs as scattered individuals or occasionally in small groups. Yellow birch carpets some of the skid trails made during 1982–1984 harvest, but little new birch came in elsewhere at that time (Hannah, 1991).

On Plot 4 at Mansfield, ca. 200 feet higher in elevation, there appears to be two age classes of hardwoods and an older spruce component. A red spruce sampled near the plot evidently became established ca. 1740, and shows an abrupt response to release about 1890 (Fig. 4). Some beech and sugar maple became established between 1840 and 1870 and coincide with the first harvests. Other trees established

MT. MANSFIELD PLOT 4 -- 1992

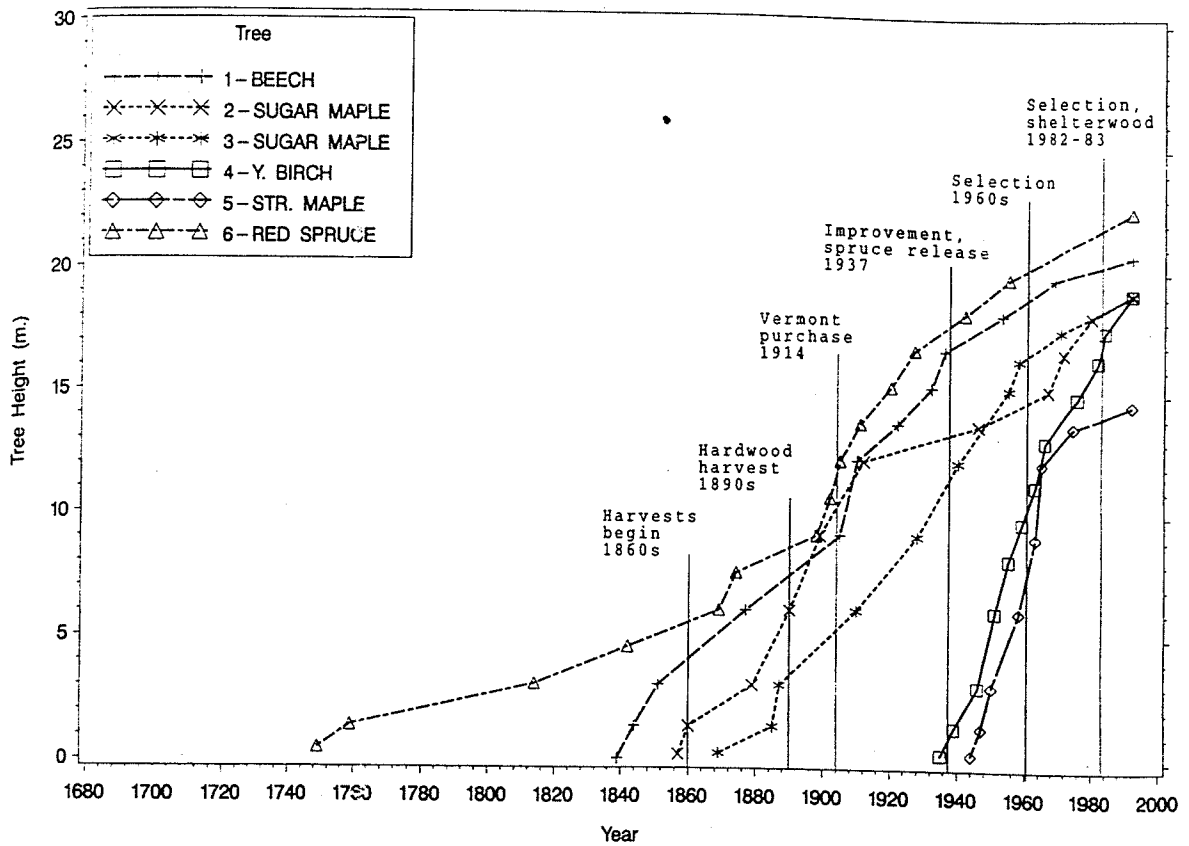


Fig. 4. Height growth of hardwoods and red spruce determined by stem analysis for Plot 4 upper site on Mt. Mansfield, Underhill, VT.

following improvement cuts of the 1930s. It is possible, trees also established in the early 1900s when harvesting ended, but are not represented in this sample. Regeneration in, and near, this plot is dominated by striped maple, beech, and hobblebush (Table 2). The spruce established before 1840 cannot be attributed to any known harvesting but perhaps some other natural disturbance. Analyses of covariance indicate trees on Plot 3 were growing significantly faster ($p < 0.05$) than on Plot 4. The spruce were not included in this test because of their greater age and different growth pattern.

It appears that the major changes that occurred in the Mt. Mansfield stand in the mid-1800s, a reduction in stocking, increased growth of suppressed spruce, and entry of new trees, primarily hardwoods, were the result of harvesting. Pit-mound microtopography is

evident in the area, but it appears much older than many of the existing trees.

Further testing showed that, while there are significant differences in height growth between the two plots within both the Jericho and Mt. Mansfield stands, there is no significant difference ($P > 0.14$) between the Jericho stand and the Mount Mansfield stand when all plots were combined for ANCOVA. Plot 1 at Jericho has height growth similar to Plot 4 at Mt. Mansfield, and Plot 2 at Jericho is similar to Plot 3 at Mt. Mansfield.

5. Discussion

These stand development studies on the Mt. Mansfield and Jericho forest show patterns of tree entry

coincident with harvesting or changes in land ownership that involved harvesting or other possible disturbance before or after the exchange. If natural disturbance, e.g. wind throw, disease or some other agent, was a factor in tree replacement, it is masked by harvesting as the major periodic disturbance. If the harvests are improvement cuts or single tree or group selection cuts, then a process analogous to replacement in small natural gaps is most likely occurring. If the harvest is major, as was evidently the case with spruce removal on Mt. Mansfield in the mid-1800s, then a stand replacement disturbance has occurred, probably with advance seedlings playing the major replacement role. Presumably many other trees, and possibly other species, were in the stand at times before sampling and have naturally died or been harvested. Siccama (1974) indicates beech may have been one of the most common trees in the original forests at lower elevations, but harvesting activities indicate red spruce was a prominent species in the original stands above 1500 feet in elevation in the mid-1800s (Cogbill, 1996). The large quantities of beech now in the understory suggest beech may be the dominant main canopy species in the future.

When the Mansfield stands were cut in the 1850s and 1860s, it is very likely there were some sugar maple, beech and birch seed-producing trees in a predominantly spruce stand. These trees most likely served as a seed source for additional hardwoods that established after spruce was cut. Striped maple and hobblebush were probably also present in the 1860s, but may not have been as abundant as they are today and presumably sugar maple, beech and birch seedlings came through the competition to create a predominantly hardwood stand. By the end of the century there was probably a two-storied stand, the older hardwoods and scattered spruce trees left from the previous harvests because of their small size, and 40-year-old saplings. The older hardwoods were evidently cut in the early 1900s to end the logging era.

When the land was purchased by the Vermont Department of Forests, Parks and Recreation in 1914, the stands evidently had a low level of stocking consisting of large poor quality hardwoods, pole-sized hardwoods and scattered spruce. In 1930, improvement cuts were made in a stand that was evidently ca. 70 years old. More trees apparently entered the stand after this cut. Striped maple and hobblebush may have

been quite abundant at that time but beech, birch, and maple eventually formed the closed high canopy. The harvests of 1956, 1966 and 1982–1983 disturbed the canopy and forest floor sufficiently to release or establish more striped maple, hobblebush, and beech along with some sugar maple and yellow birch, white ash (*Fraxinus americana* L.) and black cherry as minor components (Hannah, 1991). Assuming this stand development sequence, striped maple and hobblebush, where they are major advance growth understory species, can respond to the release and potentially dominate the regeneration for many years following disturbance. If seed sources for beech, yellow birch and maple are present, new seedlings will have an opportunity to enter the regeneration after a disturbance and ultimately become the major components of the main canopy. Following a major disturbance, it may take perhaps 30 or more years for the main canopy species to emerge from the mixed understory, particularly if there is also substantial remaining high shade to hinder their height growth. Howard (1979) indicated a similar time requirement for trees to emerge from the small sapling stage. Hill (1986), on shelterwood study plots in New Hampshire, reported that yellow birch seedlings overtopped by beech suckers may emerge through the competition in 10 to 15 years.

Red spruce can persist a long time as advanced growth in predominantly hardwood stands at elevations above ca. 1500 feet; an advance-growth spruce, only 1 m tall and over 50 years old, was found near the study plots. Occasionally, spruce is quite abundant as an understory species where there is an adequate seed source nearby and could potentially again become dominant in the main canopy following release. With increasing elevation, a transition from northern hardwoods and red spruce to balsam fir (*Abies balsamea* (L.) Mill.), mountain white birch (*Betula cordifolia*) and mountain ash (*Sorbus americana*, Marsh.) usually occurs.

In the stand at Jericho, growing at a lower elevation on sandy soil, red maple, white birch, aspen, white pine and beech will likely dominate the main canopy if major stand-replacement disturbances (harvesting, blowdown, etc.) occur. Striped maple, hophornbeam and beech will likely dominate in the understory and become the advanced regeneration responding to any disturbance. Based on observations in numerous other

stands in Vermont, deer browsing may contribute to dominance of beech, striped maple, hophornbeam, and other less preferred species and potentially result in scanty presence of sugar maple, white ash, yellow birch and red oak. Beech is likely to become more abundant over time, if disturbances that create only small gaps favorable to shade-tolerant species occur and a composition described by Siccama (1974) could potentially re-occur. Red oak is likely to be present only as a scattered tree unless near-ideal regeneration and establishment conditions occur. Deer browsing seems to be a major hindrance to establishment of sugar maple and red oak; many observed seedlings show evidence of deer browsing at Jericho.

6. Conclusion

Much of Vermont was cleared for agriculture and, thus, second growth stands on former farmlands are relatively even-aged. Most of the existing stands have been subjected to further harvest and disturbance since original establishment making their structure more complex. It appears, based on study at Jericho and Mt. Mansfield, that most trees in the main canopy of many northern hardwood forests are aided in gaining a dominant position following some kind of disturbance, often harvesting. Many species, once in the main canopy, could potentially remain there for 200 years or more. Before settlement, wind, ice and snow damage, and disease were probably the main factors that removed individual large trees or groups of trees. Widespread disturbances due to major windstorms or possibly fire, though fire is rare in hardwood forests of New England, occurred with less frequency than in conifer stands (Lorimer, 1977). The effects of pre-settlement disturbances are undoubtedly masked by harvesting during the last century or more. With the advent of harvesting, disturbances ranged from removal of single trees scattered throughout the forest to clearcutting over a sizeable area. With partial harvests, advance regeneration of all species present will respond to the increased sunlight, available soil moisture and nutrients, and thus exhibit gap replacement. New regeneration may claim vacant spaces on the forest floor, the first germinating, fastest growing and most shade-tolerant being most successful on each microsite. Ferns may also dominate for a period of

time but, ultimately, the more shade-tolerant species will dominate in the main canopy – in the northern hardwood type it will likely be beech and sugar maple, with yellow birch succeeding in larger gaps and other species of low shade tolerance (e.g. white ash, paper birch, black cherry, aspens) that establish in larger openings and get the edge on competition. With an abundance of striped maple, hobblebush and other shade-tolerant low-stature species on a site, the main canopy species may be considerably delayed in entering the upper stratum and may only be successful if a canopy gap occurs.

Barring unusual circumstances, the size of a disturbance area, caused by harvesting or natural events, species seed source, advance growth seedlings, and growing space for new seedlings, will be the principal factors influencing composition and structure of future stands. Tree harvesting as a gap or stand replacing disturbance will have a strong influence on future stand composition and structures. With little or no harvesting disturbance at mid- and low elevations in the mountains, shade-tolerant northern hardwoods will potentially dominate in the main canopy with spruce as a possible minor-to-major component. Because of the shade tolerance and longevity of red spruce, it also has the potential to displace hardwoods – this may have been manifested during the 1800s when spruce was abundant on Mt. Mansfield. With increasing elevation, red spruce and balsam fir will probably assume co-dominance in the stands. Above 2500 feet in elevation, spruce will probably give way to balsam fir as the dominant conifer. In the valleys and other sites below about 1500 feet in elevation, except for the spruce–fir region, a wide variety of hardwoods will probably occur along with white pine and hemlock. In most cases, the influence of wildlife should not be dismissed in assessing the composition and development of stands.

Stand composition and development patterns similar to those described in this study may have occurred in much of the northern hardwood forest of the northeast on account of agriculture and repeated partial-to-complete removal harvests. Deer populations have been influenced by these disturbances and, in turn, influenced the forest (Tierson et al., 1966). In northern hardwoods of the Lake States region, red spruce is absent and beech less abundant, thus the composition may differ but gap-and-stand replacement harvest

disturbances are and probably still the principal stand-development influences, wherever harvesting occurs.

Acknowledgements

Alan Howard, University of Vermont Computer Services provided invaluable assistance in constructing figures and with statistical analysis. Claudette Laplume, School of Natural Resources, was instrumental in preparing this manuscript. This study was supported by the McIntire–Stennis Forest Research Program.

References

- Cogbill, Charles V., 1996. Historical Ecology of Upper Stevensville Brook Watershed, Underhill, Vermont. A report for the Vermont Department of Forests, Parks and Recreation and Vermont Monitoring Cooperative, pp. 11 plus maps.
- Dwyer, Loraine S., 1976. History of Underhill, Vermont. Underhill Historical Society.
- Fain, Jay J., Volk, T.A., Fahey, T.J., 1994. Fifty years of change in an upland forest in southern central New York: General patterns. *Bulletin of the Torrey Botanical Club*, 121(2), 130–139.
- Gemborys, Stanley R., 1996. Structure and dynamics in a virgin northern hardwood spruce fir forest, the Bowl, New Hampshire. U.S. Forest Service, Northeastern Forest Experiment Station, Res. Paper NE-740, pp. 15.
- Hannah, Peter R., 1991. Regeneration of northern hardwoods in the northeast with the shelterwood method. *North. J. Appl. For.* 8(3), 99–104.
- Hagerman, Robert L., 1975. Mansfield: The Story of Vermont's Loftiest Mountain. Phoenix Publishing, Canaan, NH, pp. 120.
- Hill, D.B., 1986. Stand dynamics and early growth of yellow birch and associates in the White Mountains. In: *Current Topics in Forest Research, Emphasis on Contributions by Women Scientists*. Proc. Soc. For. Expt. Sta. General Technical Report-SE-46.
- Howard, Lauren David, 1979. Phytosociology and plant succession in the foothills of the Green Mountains, Vermont. Ph.D. Thesis, University of Vermont, pp. 623 plus appendix.
- Leak, William B., 1987. Fifty years of compositional change in deciduous and coniferous forest types in New Hampshire. *Can. J. For. Res.* 17, 388–393.
- Lorimer, C.G., 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology* 58, 139–148.
- McClure, J.W., Lee, T.D., 1993. Small-scale disturbance in a northern hardwoods forest: effects on tree species abundance and distribution. *Can. J. For. Res.*, 23(7).
- Oliver, Chadwick D., 1978. The development of northern red oak in mixed stands in central New England. *Yale Univ. School of Forestry and Environmental Studies. Bull.* 91, pp. 63.
- Oliver, Chadwick D., Larson, Bruce C., 1996. *Forest Stand Dynamics*. McGraw Hill, New York, pp. 520.
- SAS Institute, Inc., 1988. SAS/STAT User's Guide. SAS Inst., Inc., Cary, NC.
- Shannon, R., 1950. The management of a farm woodlot through integrated utilization and marketing. Masters Thesis, University of Vermont, pp. 117.
- Siccama, T.G., 1974. Vegetation, soil, and climate on the Green Mountains of Vermont. *Eco. Monogr.* 44, 325–349.
- Stephens, G.R., Ward, J.S., 1992. Sixty years of natural change in unmanaged mixed hardwood forests. *Conn. Agr. Exp. Sta., New Haven. Bull.* 902, pp. 63.
- Tierson, W.C., Patric, E.F., Behrend, D.F., 1966. Influence of white-tailed deer on the logged northern hardwood forest. *J. For.* 64, 801–805.
- Vermont State Forest Land Records. Department of Forests, Parks and Recreation. On file, Waterbury, VT.
- Watt, A.S., 1947. Pattern and process in the plant community. *J. Ecology* 35, 1–22.