by W. B. Leak

Relation of Tolerant Species to Habitat in the White Mountains of New Hampshire

USDA FOREST SERVICE RESEARCH PAPER NE-351
1976

NORTHEASTERN FOREST EXPERIMENT STATION
FOREST SERVICE, U.S. DEPARTMENT OF AGRICULTURE
6816 MARKET STREET, UPPER DARBY, PA. 19082

The Author

WILLIAM B. LEAK joined the Northeastern Forest Experiment Station in 1956, and now is engaged in silvicultural research at the Station's Forestry Sciences Laboratory at Durham, New Hampshire.

MANUSCRIPT RECEIVED FOR PUBLICATION 2 DECEMBER 1975

Relation of Tolerant Species to Habitat in the White Mountains of New Hampshire

Abstract

The occurrence of red spruce, hemlock, beech, and sugar maple stands was related to habitat classified by substratum (generally C horizon or parent material), drainage, aspect, and elevation. Softwoods were found on rocky, outwashed, compacted, and poorly drained substrata; hardwoods were common on open glacial tills. Species was related to climate and apparent resistance of the substratum to weathering.

FOREST SITE or habitat classification in northern hardwoods and associated types in New England is not well advanced. We need an accurate system for classifying forest land for inventory, management, and reporting research results. Certain types of information are already available: yields of even-aged northern hardwoods have been related to site index *(Curtis and Post 1964)*; site index and diameter growth of yellow birch have been found higher on moist soils than on dry, apparently because of higher nutrient concentrations *(Post et al. 1969, Hoyle 1965a)*; the physical-chemical status of certain soils and the associated species mixes have been reported for the Bartlett Experimental Forest, Bartlett, New Hampshire *(Hoyle 1973)*; and a program of broad habitat classification has recently been initiated by Alvis and Lanier[1] of the White Mountain National Forest. They have related current species to broad geologic classes that can be recognized on aerial photographs. This classification works well, but more refinement from on-site measurements would be helpful for certain silvicultural applications.

Hoyle *(1965b)* recognized the relationship of species to forest soil type in the White Mountains, and described the following habitat classification:

Forest soil	*Species*
Rock outcrop soils	spruce-fir
Shallow organic soils over bedrock	spruce-fir, birch
Colluvial soils (talus)	—
Peat soils	spruce, fir, pine, larch, red maple, paper birch, black cherry
Outwash	oak and pine
Till:	
Low elevations:	
south aspect	oak and pine
north aspect	beech, birch, maple, hemlock
Middle elevations	mixed wood[2]
Higher elevations	spruce-fir

[1] Proc. Region 9 Land Systems Conference, White Mountain National Forest, October 15-17, 1974. Unpublished report, 76 p.

[2] Mixed wood is a local designation for a mixture of softwoods and northern hardwoods in which neither makes up 75 percent of the stand.

However, this classification requires additional specification and definition of the forest soil classes, ignores successional position of the species, and does not accord well with the site/species correlations used by the White Mountain National Forest for till and outwash.

To provide some additional information on the relationship of habitat to species composition, successional trend, and productivity, I started a study in the southern half of the White Mountains during the summer of 1974.

RATIONALE

Efforts to relate species and productivity to habitat in New England have not been very successful, possibly because of the complex relationship between soils and species in this glaciated region. Standard soils classifications do not seem to provide a strong basis for relating soils to current species composition *(Pilgrim et al. 1968)*. A new approach seemed necessary.

The competitive exclusion principle *(e.g. Ayala 1972)* indicates that in a given habitat, composition should tend toward the one species (or small number of species) best adapted to that particular habitat. It follows that important differences in habitat should be reflected in differences in species composition, provided that sampling is restricted to old stands of tolerant species where most of the effects of disturbance and chance regeneration have been erased. On this premise, I sampled stands containing trees at least 150 years old (occasionally down to 100), composed mostly of one or two tolerant species, and regenerating to these same species.

Past work, previously cited, had indicated that soil drainage class and geologic history (geomorphic class) may be important in defining site classes. So in taking site measurements I concentrated on the substratum (generally the C horizon or parent material) and drainage class. It is true that tree growth should be directly related to physical and chemical conditions in the upper horizons, but in old stands we might confuse cause and effect in dealing with upper horizons. For example, humus depth and thickness of the A_2 horizon tend to be greater under old softwoods than hardwoods. But these features tend to be a result rather than a cause of the presence of softwoods. Furthermore, upper-horizon conditions should be a product of substratum, drainage, climate, and the resulting vegetative history with one important exception: where a site has been noticeably enriched by the downhill movement of materials. Because of their relationship to landform, certain substrate conditions can be mapped fairly well from aerial photos or on the site.

In summary, then, my approach was to relate the tolerant species in a stand to habitat, classified primarily by substratum and drainage. The first phase is described here. After this preliminary classification is developed, the next steps are to relate succession and silvicultural response to habitat and, of course, to revise and extend the original classification.

METHODS

A total of 84 plots were established in old stands, primarily of red spruce, red spruce-hemlock, hemlock, beech, beech-sugar maple, and pure sugar maple. Most stands were uneven-aged, and they were free from apparent cutting or windthrow in the area sampled. All sites were below 2,500 feet elevation. Most of these stands were several acres in size, although some of the pure sugar maple stands were only about an acre. I made a visual check to be sure that the regeneration was generally the same species as the overstory, and that intolerant species were uncommon in the area.

At each location, a 3-m^2-factor prism sample was taken by species of all trees in the overstory 125 mm (5 inches) dbh and larger. The two or three most common woody species in the regeneration were noted and ranked by abundance. The predominant herb species also were listed. The diameter (just above root collar) and, where possible, the height and age of the largest tree on the plot were determined.

A pit was dug to a depth of at least 1 meter (where feasible) at the center of the plot. Where obstructions were encountered, a second pit was dug. The substratum was classified as open (noncompacted) till, compacted till, boulder till, grus (weathered fragments of granite), bedrock, outwash sands, or gravel. All of these substrate materials are predominantly of granitic origin in this section of the White Mountains. How to recognize these classes is described later. Horizon thicknesses were measured, as well as depths to mottled or compacted layers; texture at the top of the C horizon was classified by hand into sandy (sands, loamy sands) or loamy (sandy loams, loams); and notes were made of elevation (from U.S.G.S. maps), aspect, slope, and general surface conditions.

The first step in the analysis was to discard those plots where vegetation or site could not be classified accurately. Seven plots were dropped because the trees were less than 100 years old or too mixed in species, i.e., no one or two tolerant species dominated. Nine plots were dropped because the site classifications were not clear; the main problem appeared to be mixed classes, e.g., outwash or grus that seemed to have been compacted, or tills that apparently had been partially compacted. Thus, 68 plots remained for analysis.

The overstory and understory on each plot were classified as pure red spruce (RS), red spruce with more or less hemlock (RS / Hem or Hem / RS), pure hemlock (Hem), pure beech (Be), beech with less sugar maple (Be/SM), and pure sugar maple or sugar maple predominating over beech (SM or SM/Be). Plots were sorted by substratum, drainage class, aspect, and elevation. These site factors were then combined into a smaller number of habitat classes that corresponded to apparent differences in vegetation.

HABITAT CLASSES

Habitat classes based on substratum and drainage conditions together with certain features of elevation and aspect separated both overstory and understory species composition (table 1). Softwoods occupied the rocky, outwashed, compacted, and poorly drained habitats. Red spruce predominated on the higher, cooler areas; hemlock was more abundant at lower elevations and on south or west exposures. Hardwoods occupied the open (noncompacted) till soils. Sugar maple predominated over beech where soil texture was finer or more moisture was available.

Red maple was the most common associate in softwood stands, regardless of whether the habitat was dry (rock, outwash) or wet (poorly drained); yellow birch was second in importance. Yellow birch was the only important associate on the hardwood plots. In this study, herbs did not appear closely related to habitat, although blueberry, wintergreen, or bracken fern often were found on dry areas (shallow bedrock, outwash) while violets and asters often were found on the better hardwood sites.

The most important feature of any habitat-classification scheme is careful definition of the categories, so the seven substrate or drainage categories in table 2 and their associated features are described in the sections that follow.

Rock

This category includes three distinct substrate conditions. First, it includes those plots underlain with tight, smooth bedrock at depths of 11 to 55 cm below the top of the mineral soil (i.e., excluding the L, F, and H layers). Bedrock sites usually are evident from areas of exposed bedrock, or bedrock in nearby trails. There may be no surface rocks; if there are any, they have sharp angles that have not been worn down by the glacier.

In the second condition soils are underlain at depths from a few centimeters up to 65 cm below the top of mineral soil with a matrix of either sharp-angled or, occasionally, somewhat rounded boulders. The sharp-

Table 1.—Numbers of overstories and understories (in parentheses) in each species group in plots of each habitat class

Substratum	Drainage	Elevation	Aspect	Number of overstories (understories) in species group					
				RS	RS/Hem Hem/RS	Hem	Be	Be/SM	SM/Be or SM
		Ft.							
Rock	Well-drained	1,000-1,500	S-W		2 (2)				
		1,500+	Any	9 (11)	2				
Outwash sands and gravels	Well-drained, occasionally moderately well-drained	1,000-1,500	S-W		1 (1)	1 (1)			
			Other	1 (1)	1 (1)				
		1,500-2,000	Any	1 (3)	2				
Compact coarse till	Well-to somewhat poorly drained	0-1,000	Any		(3)	4 (1)			
		1,000-2,000		(1)	5 (5)	1			
Open coarse till	Well-drained	0-2,000	Any				3 (4)	1	
Open fine till	Well-drained	1,500-2,000	Any				1 (2)	3 (2)	1 (1)
Enriched till	Well-to somewhat poorly drained	1,000+	Any					5 (12)	19 (12)
Any	Poorly drained	0-1,000	Any		(1)	1			
		1,000-1,500		(2)	3 (1)				
		2,000+		1 (1)					

Table 2.—Average horizon thicknesses, depths, and maximum tree height for each habitat class

Habitat	Horizon thickness			Depth from top of mineral to:			Maximum tree height	
	Organic	A_2	B	Compact layer	Mottling or water	Rock or grus	Average of plots	Range
	cm						*m*	
Rock	16	9	25	—	—	32	20	14-28
Outwash sands and gravels	25	13	37	—	—	—	25	22-29
Compact coarse till	22	12	43	49	Variable[a]	—	24	20-28
Open coarse till	6	4	42	—	—	over 65	23	19-29
Open fine till	7	5	43	—	—	—	24	23-24
Enriched till	12	4[b]	55	—	32[a]	—	28	22-30
Poorly drained	24	6[a]		—	0-15	—	23	21-25

[a] If applicable.
[b] Often absent.

angled boulders are often associated with shallow bedrock; the boulders have been produced by frost churning with little subsequent glacial abrasion; surface rocks usually are readily visible. Rounded boulders are sometimes found in drainage bottoms; apparently the glacial water has rinsed away the finer materials, leaving a matrix of adjacent (touching), rounded boulders; surface boulders may or may not be evident.

A third condition, again often associated with shallow bedrock, is where the substratum is almost pure coarse fragments of weathered granite (grus).

The rock habitats encountered in this study were occupied primarily by red spruce at elevations above 1,500 feet, and by red spruce and hemlock mixtures at lower elevations or on south to west exposures. In some areas, oak occupies a successional role on shallow, tight bedrock — or on interspersed pockets of deeper material — especially on south to west exposures. And scattered white pine also may be found on rock habitats. Some of the poorest sites occur in this category, especially on shallow, tight bedrock where maximum tree heights may be as low as 14 meters.

No fine-textured, shallow-to-rock habitats were encountered in this study. However, observations indicate that beech and sugar maple are more common on rock habitats with finer texture.

Rock habitats are generally found at the beginning of the spruce-fir cap found on the taller mountains. Siccama *(1974)* suggested that this boreal cap on one mountain in Vermont was due to the climate at 2,500 to 2,600 feet, rather than to soil conditions. However, climate does not seem to determine the position of the boreal cap in the White Mountains since it appears in association with rock habitats at anywhere from 1,800 feet to over 2,600 feet elevation. And red spruce mixed with hemlock occurs lower.

Outwash Sands and Gravels

These are materials that have been partly to well sorted and deposited by glacial water. These deposits occur as mounds, level slopes, or flats with few if any surface stones. Outwash substrata usually are loose and single-grained in structure, although B horizons may have iron cementation. Stones, if any, near the bottom of the B horizon generally are rounded and do not have the silt caps found on soils classed as tills. Well-sorted, uniform substrata with few fragments larger than 2 mm were classed as sands. Less well-sorted substrata with stones and fragments larger than 2 mm were called gravels. The outwash habitats supported red spruce and hemlock, with hemlock often more abundant in lower or warmer areas. Some of the best white pine also were found on outwash habitats, and possibilities for white

Figure 1.—Outwash sand supporting red spruce with some white pine and hemlock. Note level to rolling topography and absence of surface stones.

pine management appear to be best on this class *(Hoyle 1965b)*. Maximum tree (softwood) heights ranged from 22 to 29 meters (fig. 1).

Compact Coarse Till

Glacial till soils are characterized by a complete mixture of particle sizes from large boulders down through silts and clays. The compact tills — sometimes called basal till, indurated till, hardpan, or platy tills — are those that apparently have been plastered down by the glacier. Horizons are well defined; the A_2 is distinct. The C horizon is a hard, gray, abrupt layer that is somewhat mottled at the surface. Under this category, I include only the coarse compact tills in which the C horizon usually contains lenses of coarse sand; but a few softwood-dominated plots (not included in the analysis) had very compact C horizon containing a high proportion (over 50 percent) of coarse rotten fragments. The compact C horizon began at 15 to 80 (average = 49) cm below the top of the mineral soil. Most of these habitats were well drained (no evidence of mottling in the B horizon), but a few were moderately to somewhat poorly drained (mottling part way to throughout the B horizon). The degree of compaction on these areas varies, so identification is not always made with confidence. I think that the important criterion is whether the compact surface acts as a barrier to downward water movement. Some of the well-drained habitats had iron-cemented B horizons above the compact C horizon.

Surface boulders often are present on compact tills, but may be alined or pressed into the ground by glacial action. Although pits and mounds may be present, local relief often is subdued even though slopes may range from flat to quite steep. The general area occupied by compact tills usually shows evidence of seeps and meandering intermittent streams. Such areas sometimes contain a great variety of species because of the range in drainage conditions and the presence of pockets of loose till, outwash, and enriched materials.

The compact tills supported hemlock at the lower elevations, and hemlock mixed with red spruce at elevations above 1,000 feet. However, the general area usually appears to be mixed wood.[2] Maximum tree heights ranged from 20 to 28 meters (fig. 2).

Open Coarse Till

These are well-drained coarse-textured tills that have not been compacted. The surface looks like an assortment of boulders, smaller stones, and finer material that has been dumped in place. Topography and local relief are irregular. The soil presents a typical podzol profile: an organic layer about 6 cm thick, a distinct white A_2 horizon about 4 cm thick, and a well-colored yellowish B horizon between 30 and 50 cm thick, grading quite distinctly into a lighter colored C horizon. Stones occur throughout the profile. C horizon textures are coarse (sands and

Figure 2.—Nearly pure hemlock on compact till. Note level terrain. Stones are common but buried.

loamy sands). These habitats run heavily to beech, with a slight admixture of sugar maple. Maximum tree heights ranged from 19 to 29 meters (fig. 3 A-C).

Open Fine Till

These also are typical podzol soils with distinct A, A_2, B, and C horizons. The textures in the upper C horizon are noticeably finer than in the coarse tills. The B horizon often is less brightly colored, and the C horizon firmer, than in the coarse tills. These finer textured tills support a greater proportion of sugar maple than the coarse tills, but beech still is abundant.

In some areas, fine-textured soils are underlain with fine-textured compacted C horizons. I found no old stands of tolerant species on such sites. However, I would expect that well-drained sites of this type would support vegetation similar to that on the fine open tills. The moderately drained sites are similar to the enriched tills described in the next section.

Enriched Till

This category covers those till soils that are enriched by water or materials moving down from above. Most of these sites are on benches, coves, or slope bottoms in areas with open till or occasionally compact till soils. The A_2 horizon frequently is missing or indistinct; the horizons generally are indistinct, apparently because of the lateral movement of water and materials.

The class includes moderately to somewhat poorly drained tills, which have mottling or moving water up into the B horizon. Occasionally, these moist habitats have coarse, sandy or gravelly B or C horizons; tree growth apparently is maintained by flowing nutrient-rich water. Other areas have moist, humus-rich surface layers. Although any of these moist habitats may occur in areas in-

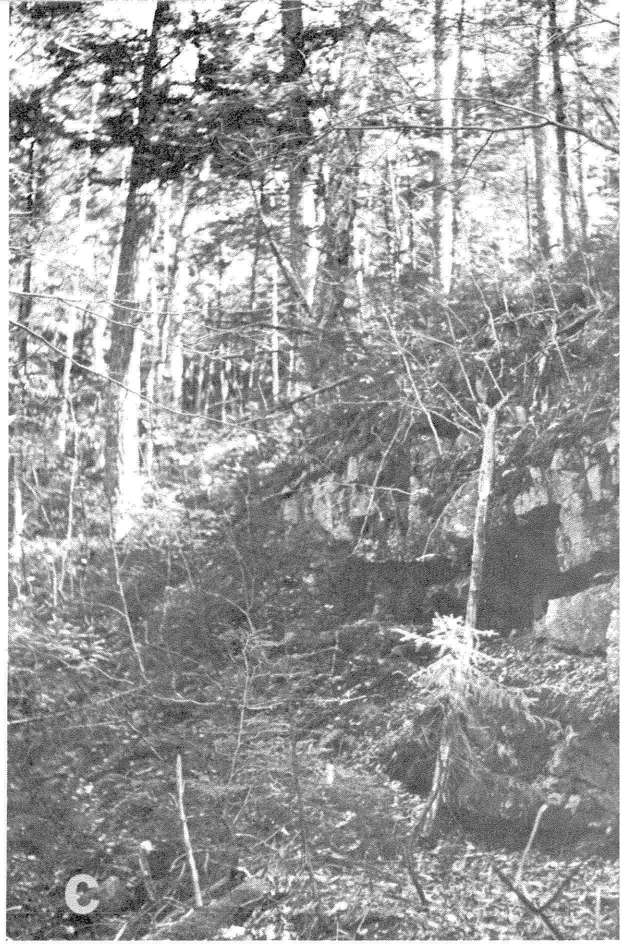

Figure 3.—A. Standing in pure softwoods (red spruce and hemlock) on west-facing streambank, looking toward pure hardwoods on east-facing bank. B. Hardwoods are growing in open till, mostly coarse till. Note surface rocks and topography. C. Prominent bedrock in streambank provides initial evidence that softwoods are growing on a rock substratum. Farther uphill, softwoods are growing on smooth, steep slope with only 30 to 35 cm of mineral soil over rotten granitic fragments.

fluenced by a compact layer, softwood-dominated compact tills previously described have a typical podzol profile coupled with a gray, mottled compact layer at the top of the C horizon.

This category also includes well-drained soils where buried A_2 and humus layers, deep uniform B horizons, markedly different C horizons, or generally poor differentiation of horizons indicate that fine-textured or humus-rich materials have moved in from above.

Enriched tills were dominated by sugar maple in combination with beech. Apparently, these are some of the better sites in the White Mountains, although they frequently occur in small, scattered units. Maximum tree heights ranged up to 30 meters, and averaged 28 meters.

Poorly Drained

This category includes those flat areas of at least a few acres where the soils consist of an organic layer over gray mottled subsoil. Standing water sometimes is visible; water often is present in shallow dug holes. These areas are dominated by hemlock and red spruce mixtures, with greater proportions of spruce as the elevation increases. Maximum tree heights of 21 to 25 meters were measured.

CLIMATIC AND WEATHERING GRADIENTS

Pollen profiles from New England indicate that softwoods preceded hardwoods in the recolonization that followed the retreat of the glacier over 10,000 years ago *(Davis 1969)*. From the peaks of the pollen influx, the trend in certain major species was about as follows:

Spruce
  Pine
    Hemlock
      Beech and sugar maple

Hemlock did not precede beech and sugar maple by very much, but it began to decline much earlier. The driving force behind this recolonization usually is considered to be climate, acting upon reproductive characteristics of the species *(Fuller and Conard 1932)*. A climatic gradient still is evident in the species/site relationships shown in table 1. Note that hemlock tends to be more abundant than spruce on lower or warmer sites. Also, it is well known that beech and sugar maple do not reach as high an elevation as red spruce. Differences between hemlock and the hardwoods are not obvious.

Differences in vegetation among the substrata might be broadly interpreted as a gradient in degree of weathering or soil maturity. Weathering processes include the mechanical disintegration of soil materials and their chemical decomposition. The two types of processes tend to move together: "Vigorous chemical changes will accompany disintegration, and the result will be shown in the greater fineness of the product" *(Lyon and Buckman 1950)*. Organic matter also accumulates. Thus, greater weathering or soil maturity is reflected in a greater departure from the original character of the soil, finer soil texture, increased solum depth, and many associated chemical changes.[3]

If we rank the substrata according to increasing degree of physical disintegration or increased susceptibility to chemical weathering, the order appears to be similar to that of the first five or six entries in table 1:

Rock
  Outwash and compact till
    Coarse till
      Fine till
        Enriched till (position questionable)
          Poorly drained (position unknown)

I place the compact tills before the open tills in the sequence because, although the materials are similar, the compact tills must weather more slowly because they are quite impervious to water, gases, and root penetration. The relative positions of outwash and compact till are not clear. Outwash, especially gravel, apparently is quite resistant to weathering because it contains much coarse material; it also is possible that less

[3] Johnson et al. (1968) describe the fragmentation of rock and increasing solum depth that accompanies chemical weathering of silicate minerals in New Hampshire; they also mention that chemical weathering proceeds more rapidly in finer materials such as till than in consolidated material such as bedrock.

resistant materials have been washed away. Compact till is physically much firmer than outwash, but it contains more fine material. Also, some compact tills probably had an initial surface layer of loose till.

Notice that the sequence of species in table 1 goes from softwoods to hardwoods, corresponding to the weathering sequence given above. Furthermore, the species sequence in table 1 resembles the recolonization sequence given at the beginning of this section. Perhaps recolonization after the glacier can be interpreted as a response to climate and weathering combined.

Apparently, the site/species relationships that now exist in the White Mountains can be broadly correlated with two gradients: a climatic gradient along which species change with elevation or aspect, and a degree-of-weathering gradient along which species change with habitat class. This interpretation provides some basis for predicting how the major tolerant species might change with changes in climate or with increased weathering.

SUCCESSIONAL AND SILVICULTURAL IMPLICATIONS

Successional trends and silvicultural responses on these habitats will be worked out by future studies. However, certain general statements can be made now. Light silvicultural treatments, such as single-tree selection, will tend to maintain the tolerant types identified in this study. However, any cutting or other distrubance in softwood stands tends to increase the proportion of successional hardwoods (such as the birches) and sometimes tolerant hardwoods (such as beech) as well. Disturbance in hardwood stands tends to increase the proportion of successional hardwoods, but it does not generally result in an increase in softwoods. Softwood sites probably average poorer for tree growth than hardwood sites, although this could be changed by culture measures such as fertilization, irrigation, or drainage.

Cover-type changes (changes in the predominant tolerant species) probably can occur and have occurred on some habitats, often following a disturbance. They could happen on those habitats that are marginal between two classes, such as bedrock habitats where the bedrock is 55 cm or more below the surface of the mineral soil, or on partially compacted tills, or on compact tills where the compacted layer is deep. On such habitats, the trend in cover-type changes should be from softwoods toward hardwoods such as beech together with red maple and successional hardwoods. In similar fashion, the time required for the original tolerant species to return following disturbance probably is related to whether the habitat is marginal between two classes or not: e.g., the greater the depth to bedrock or compact C horizon, the slower the return to softwood species, if it ever occurs.

The habitat classes recognized in this study may help provide a basis for classifying forest land into meaningful management units, and should also help provide some basis for laying out and reporting field research. This classification system appears to fit — in habitat definitions and species relationships — the broader system being used on the White Mountain National Forest. Some units of 50 acres or more could be of a single habitat class. Other areas — such as certain ones influenced by compact tills — have a mixed array of habitat classes and a corresponding array of species. Some areas are hard to categorize. The influence of habitat on species composition is more pronounced on larger areas of a single site type, except perhaps for enriched sites, which are usually small. For example, small pockets of compact till or outwash within a general area of open till may not influence vegetation very much.

Classifications like these require modification if they are extended very far outside the area in which they were developed, because the competitive position of the species will change. However, the approach followed in this study may prove useful in other regions.

LITERATURE CITED

Ayala, F. J.
1972. Competition between species. Am. Sci. 70(3):348-357.

Curtis, R. O., and B. W. Post.
1964. Basal area, volume, and diameter related to site index and age in unmanaged, even-aged northern hardwoods in the Green Mountains. J. For. 62(12):864-870.

Davis, M. G.
1969. Climate changes in southern Connecticut recorded by pollen deposition at Rogers Lake. Ecology 50(3):410-422.

Fuller, G. D. and H. S. Conard.
1932. Plant sociology. Translation of Pflanzensoziologie by J. Braun-Blanquet. 439 p.

Hoyle, M. C.
1965a. Variation in foliage composition and diameter growth of yellow birch with season, soil, and tree size. Soil Sci. Soc. Am. Proc. 29(4):475-480.

Hoyle, M. C.
1965b. Forest soils in the White Mountains. What are forest soils? N. H. For. Notes 86:3-8.

Hoyle, M. C.
1973. Nature and properties of some forest soils in the White Mountains of New Hampshire. USDA For. Serv. Res. Pap. NE-260, 18 p.

Johnson, N. M., G. E. Likens, F. H. Bormann, and R. S. Pierce.
1968. Rate of chemical weathering of silicate minerals in New Hampshire. Geochim. Cosmochim. Acta 32:531-545.

Lyon, T. L., and H. O. Buckman.
1950. The nature and properties of soils. 4th ed. MacMillan, New York. 499 p.

Pilgrim, S. A. L., A. B. Prince, and N. K. Peterson.
1968. New Hampshire soils and their interpretations for various uses. N. H. Agric. Exp. Stn. Res. Pap. No. 3, 70 p.

Post, B. W., W. H. Carmean, and R. O. Curtis.
1969. Birch soil-site requirements. *In* Birch Symp. Proc. U. S. Dep. Agric. For. Serv. Northeast. For. Exp. Stn. p. 95-101.

Siccama, T. G.
1974. Vegetation, soil, and climate on the Green Mountains of Vermont. Ecol. Monogr. 44:325-349.