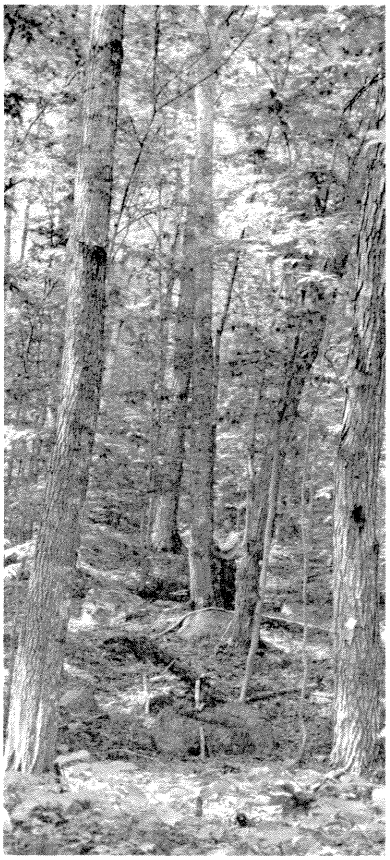

Effects of HABITAT on Stand Productivity in the WHITE MOUNTAINS of New Hampshire

by William B. Leak

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Abstract

Mean annual biomass production of sapling stands was higher on washed tills, which have a hardwood climax, than on habitats having a softwood climax. However, biomass production of pole-timber stands did not differ significantly among habitats. Apparently, differences among habitats in characteristics species composition tends to mask differences in biomass productivity. Demanding species growing on a good site will produce about the same biomass as less demanding species growing on a medium site. Mean diameter growth of sugar maple and yellow birch was much better on fine till and enriched habitats than on the other habitats covered by the study; and preliminary results from older stands indicate that board-foot production is much higher on the better habitats. In conducting intensive silvicultural operations, it is important to favor species well adapted to habitat.

DURING THE LAST FEW YEARS, there has been an appreciable amount of work on land types or habitat classification of New England forests. Ecologic land types are being defined and mapped on the White Mountain and Green Mountain National Forests. These types are defined by correlated features of glacial history or land form, soil materials, and forest vegetation. Supplementary research has shown that species composition of the climax and successional vegetation is related to habitats defined by soil material or type of glacial deposit, and mineralogy (Leak 1978a; 1978b).

However, the relationship of land type or habitat to forest productivity is not clear. Sometimes, land type apparently is indicative of total productivity in volume per acre (Damman 1964). Often, land type is related to the productivity of a particular species such as pine or spruce (Horton and Bedell 1967; Hills and Pierpoint 1960; Mueller-Dombois 1965). Ray's (1956) work indicated that lands with high site index, supporting high proportions of hardwoods, did not necessarily produce the highest volume growth per acre. He found that total volume growth, and volume growth in softwoods, tended to be highest on the poorer sites—those with lower site indexes.

In the White Mountains of New Hampshire, we probably can assume that productivity varies among land types or habitats that are extremely different from one another. High-elevation forests containing stunted trees growing on shallow soils no doubt are much less productive than the taller forests growing on the deeper soils at lower elevations. But productivity differences among lower-elevation forests, which appear potentially suitable for intensive management, are not yet apparent. Past research has shown that certain species, such as sugar maple and white ash, vary appreciably in site index among habitats. But other species, such as red maple, show little consistent change in site index from one habitat to another (Leak 1978a). Available yield information indicates that white pine growing on excessively drained outwash may produce far more volume than hardwoods growing on the best sites. Thus, it seemed quite possible that differences in typical species composition among land types or habitats might minimize differences in productivity.

Because productivity is an important criterion in determining forest land use or management intensity, a study of stand productivity related to habitat was conducted in 1977 through 1979 in areas of granitic drift on the White Mountain National Forest.

METHODS

The general approach was to establish temporary plots in well-stocked, uncut even-aged stands; to carefully age the stands; and then to express stand or species productivity in mean annual growth. Two main series of plots were established: one in sapling stands that averaged about 7 to 14 years of age, the other in poletimber stands that averaged 60 to 70 years.

Thirteen sapling stands were sampled and analyzed. In each stand, eight to ten 54 ft^2 (5 m^2), closely spaced, circular plots were established. On each plot, diameter at breast height (dbh) (if available), height (with a measuring pole), and species of all stems 1 foot tall and taller were recorded. Two trees per stand per species were cut at ground level, and a disc was taken back to the lab for age counts. Because the stands were young, and because sampling was done throughout the growing season, stand ages were estimated to the nearest ¼ year based on (1) sampling date during the growing season, and (2) width of the new or current annual ring. In the midst of each plot cluster, a pit was dug to a depth of about 3 ft and the habitat was classified according to criteria previously described (Leak 1978a) (Fig. 1). Previous re-

Figure 1.—Examples of two habitats in granitic drift. (A) An enriched habitat supporting an abundance of sugar maple sawtimber; (B) A wet compact till supporting a successional stand of red maple and paper birch with some softwoods in the understory.

search indicates that the washed tills, fine till, and enriched habitats have a hardwood climax, while the rock, poorly drained, outwash, wet and dry compact till, and sediment habitats have a softwood climax (Leak 1978a).

Twelve poletimber stands were sampled and analyzed. In each stand, two clusters of four plots each were taken; the two clusters were separated by a distance of up to about 100 feet. Two clusters were used because in these older stands, which have wide-spreading root systems, I wished to make sure that the habitat was uniform over a sizeable area. The four plots within each cluster were 538 ft^2 (50 m^2) closely spaced, circular plots. On each plot, stems 4.5 ft tall or taller were recorded by dbh and species. The largest stem of each species, if a dominant or codominant, was bored at the top of the butt swell (approx. 1 foot above ground) for an age count, and the height was measured with a clinometer. In the middle of each of the two clusters per stand, a pit was dug and the habitat was classified as before. Results from the two clusters per stand (a total of eight plots) were combined into one average in the analysis.

Differences in growth characteristics of sapling and poletimber stands were tested by single-classification analysis of variance, except where data were limited. In making these tests, two habitats sometimes were combined into a single group, e.g., rock and outwash, or fine till and enriched.

In addition to the plots described above, several 10-factor prism plots were taken in stands about 100 years old on the Bartlett Experimental Forest to check on possible differences among habitats in board-foot production. These stands were aged approximately with increment borings; due to varied past histories, these older stands exhibited much more variation in age than the younger poletimber and sapling stands. Board-foot volumes, on these prism plots were estimated with local volume tables.

All stands in this study were well stocked with no evident openings in the canopy. Poorly stocked or open areas, which sometimes are on rock habitats or in young stands on wet compact tills, were avoided. The rock habitats were primarily on old streambeds; these have a matrix of rounded rocks in the substrate, sometimes mixed with outwash. None of the rock habitats consisted of very shallow bedrock often encountered at high elevations. All of the stands were at or below 2,000 ft elevation.

BIOMASS ESTIMATION

Because many plots were not accessible by road, and because some of the trees were large in the poletimber stands, biomass was estimated from published regressions and tables. First, comparisons were made of the several available estimators that have potential application to the study area (Goldsmith and Hocker, 1978; Kinerson and Bartholomew, 1977; MacLean and Wein, 1976; Ribe, 1973; Whittaker et al., 1974; Young and Altenberger, 1964; Young and Carpenter, 1967).

In poletimber stands, the Whittaker et al. (1974) equations for aboveground biomass have provided good estimates (a little high) of amounts actually harvested by chipping operations.[1] So we have some confidence in the Whittaker equations for the study area, although their accuracy in sapling stands has not been verified.

I used the Whittaker equations for the poletimber stands, using his red spruce equations for all softwoods and proportionally reducing his sugar maple estimates to calculate the biomass of lower-density hardwoods:

Species	*Specific gravity*	*Proportion*
Sugar maple	.595	1.0
Paper birch	.515	.87
Red maple	.515	.87
White ash	.575	.97
Aspen	.365	.61

[1]Personal communication from J. Hornbeck, Forestry Sciences Laboratory, Durham, N.H.

Dry weights were estimated separately for stems and branch wood plus bark; the total aboveground equations were not used because apparently they contain errors.

For sapling stands, I used the Goldsmith-Hocker (1978) regressions, using separate equations for stems (based on dbh and height) and branches (based on dbh). The Goldsmith-Hocker estimates apparently are more applicable to small trees than the Whittaker estimates.

RESULTS

Species composition

Sapling stands. Species composition of the sapling stands (Table 1) varied appreciably, and was inconsistent with previous research on the relationships of species to habitat (Leak 1978a). Few softwoods were present, even on habitats such as rock, outwash, and wet compact tills where softwoods usually are quite aggressive. The lack of softwoods probably is the result of complete clearcutting, which left little advance regeneration.

Paper birch was quite abundant in all stands except the one growing on the rock habitat. Past research indicates that paper birch may be as common or more common on rock habitats as on any other. Yellow birch was very abundant on outwash; older stands on outwash seldom contain this much yellow birch. The abundance of red maple on the compact tills is reasonable but I would expect red maple to be equally abundant on the rock and outwash habitats. Beech was most abundant on the rock and outwash sites; past research indicates that the washed tills will gradually develop the strongest beech component. Sugar maple was present in noticeable amounts on the wet compact till, however, older stands on this habitat seldom contain much sugar maple. The sapling stands also varied considerably in amounts of pin cherry, striped maple, and other species (chiefly willow and witch hobble).

In general, species composition of the sapling stands appeared to reflect chance events, seed source, or sprouting ability rather than the long-term suitability of species to habitat.

Poletimber stands. Species composition of

Table 1.—Species composition of sapling and poletimber stands, in percent of basal area, and stand characteristics, by habitat of the study areas

Habitat	No. of areas	Mean age	No. stems	Mean dbh	Eastern hemlock	Red spruce	Balsam fir	Paper birch	Yellow birch	Red maple	Aspen	Beech	Sugar maple	White ash	Pin cherry	Striped maple	Other
		years		inches	percent												
SAPLING STANDS																	
Rock	1	11.5	20,414[a]	.85	—	.6	—	.6	—	5.0	—	53.6	—	—	24.6	15.5	.1
Outwash	2	7.1	43,577	.50	—	.4	—	15.0	42.8	—	.6	30.6	—	—	10.6	—	—
Wet compact till	2	9.6	30,919	.74	—	—	—	15.3	2.2	33.4	8.3	4.0	5.1	1.6	5.4	6.8	17.9
Dry compact till	3	13.7	17,321	1.14	—	1.1	—	12.5	4.3	19.0	.1	10.8	—	—	50.4	—	1.8
Washed till	5	8.4	25,934	.78	—	—	—	36.3	5.1	.6	1.7	21.1	.4	—	27.5	7.3	—
POLETIMBER STANDS																	
Rock	4	69	1,034[b]	5.73	15.9	14.0	5.8	18.7	8.1	15.9	10.5	10.2	—	—	.2	.7	—
Dry compact till	4	62	1,318	4.54	—	—	—	47.6	10.6	23.5	2.0	14.8	.2	—	—	1.1	.2
Washed till	1	64	1,032	4.70	—	—	—	38.3	5.4	23.2	14.2	18.2	.1	—	—	.6	—
Fine till	2	62	607	5.99	—	—	—	—	31.0	4.5	—	4.8	59.7	—	—	—	—
Enriched	1	65	961	5.75	—	—	—	4.1	3.4	16.6	8.5	1.0	55.2	11.2	—	—	—

[a]Stems per acre 1 ft tall or taller.
[b]Stems per acre 4.5 ft tall or taller.

the poletimber stands was much more in line with expectations (Leak 1978a). The rock habitat supported an admixture of softwoods, although these softwoods tended to be concentrated in certain stands. Yellow birch was distributed over all habitats and was most abundant on fine till, a result that was in accord with previous findings. Red maple was moderately abundant on rock, compact tills, and washed tills. Sugar maple was abundant only on fine tills and enriched habitats, a very consistent finding in previous work. And, white ash was abundant only on the enriched sites. Paper birch was more common on rock sites in the poletimber stands than in the saplings, but the proportions still are somewhat variable.

In general, the poletimber stands had developed a species composition that was quite typical of the habitat conditions. The rock habitat supported mixed wood. The dry compact and washed tills supported a beech/red maple/birch association. The fine till had sugar maple/yellow birch (beech usually is a more common component on this habitat). The enriched habitats had sugar maple/ash with miscellaneous other species.

Stand productivity

Sapling stands. Mean biomass production per acre per year was about 25 to 65 percent greater on the washed tills than on the other habitats studied in the sapling stands (Table 2). The washed tills have a hardwood climax (beech primarily) while the other habitats have a softwood climax in areas where the drift is derived from granite. The washed tills have a high proportion of paper birch, which could account for the high biomass production. However, the dry compact till had a very high proportion of pin cherry, which is considered a fast, early producer (Marks 1971); biomass production on this habitat was third highest. Rock, the second highest biomass producer, supported only a moderate amount of pin cherry and a very low proportion of paper birch. It is difficult to see any clear and logical relationships between species composition and biomass production in the sapling stands.

These biomass estimates are similar to Mark's (1971) figures for 4- to 14-year-old

Table 2.—Mean annual growth in biomass per acre, basal area per acre, dbh, and height, by habitat for sapling and poletimber stands

Habitat	Biomass[a]	Basal area[a]	Dbh[a]	Height[b]
	lb	*ft²*	*in*	*ft*
		SAPLING STANDS		
Rock	3,491	6.49	.07	1.07
Outwash	2,821	6.51	.07	1.10
Wet compact till	2,664	6.01	.08	.84
Dry compact till	2,931	5.66	.08	.75
Washed till	4,398	8.76	.09	1.25
	(*)	(**)	(NS)	(**)
		POLETIMBER STANDS		
Rock	2,129	2.54	.08	.96[c]
Dry compact till	2,263	2.31	.07	1.06
Washed till	2,198	2.31	.07	.94
Fine till	2,162	1.77	.10	1.06
Enriched	2,916	2.67	.09	1.11
	(NS)	(NS)	(*)	(NS)

*Means significant at 0.05 level; **means significant at 0.01 level; NS means not significant.
[a]All stems 4.5 ft tall or taller.
[b]All stems 1 ft tall or taller.
[c]A sample of the largest dominant and codominant trees.

hardwood stands (primarily pin cherry) in New Hampshire which show mean annual aboveground production rates (stems plus branches) of about 3,500 to 4,200 lb per acre. Safford and Filip's (1974) estimates for mixed 4-year-old northern hardwoods are equivalent to about 1,300 lb per acre (stems plus branches). Young's (1967) estimates of mean annual biomass production (stems plus branches) for various hardwood stands in Maine range from about 1,200 to 3,500 lb per acre.

Mean annual basal area and height growth of the sapling stands also varied among habitats in a somewhat similar fashion to biomass production (Table 2). Differences in mean annual diameter growth were not significant, although the trend is toward increasing growth from the rock and outwash habitats to the washed tills. Note the high mean annual basal area growth rates of up to 8.76 ft^2 as compared to the usual rates of about 2 to 3 ft^2 in older stands.

Poletimber stands. In poletimber stands, there were no significant differences in biomass production among habitats (Table 2). The one stand on an enriched habitat had a mean annual biomass production somewhat higher than those of the other habitats; however, examination of this figure as a possible outlier (an observation from another population, Dixon and Massey 1957) did not indicate that it was significantly different. Mean annual diameter growth was about one-third greater on the fine till and enriched habitats than on the other habitats, which indicates that these habitats produce somewhat larger trees although total biomass production is not greater.

Mean annual biomass production tends to be somewhat higher for the sapling stands than the poletimber stands, particularly on the washed tills where biomass production up to sapling size (based on five stands) was about double the production up to poletimber size (based on one stand).

Because diameter growth patterns varied somewhat among habitats, I examined merchantable growth relationships among habitats in the poletimber stands to see whether these differed from trends in biomass production. Based on local volume tables, mean annual growth in cubic feet (4-inch diameter inside bark (dib), top) varied little among habitats; it ranged from about 40 ft^3 per acre on the combined fine till and enriched habitats to about 44 ft^3 on the rock habitats. Mean annual growth in board feet. (Int. ¼-inch rule; trees 11.0 inches and over) in 60- to 65-year-old poletimber stands (ignoring one older stand on the rock habitat) ranged from 55 board feet on the combined fine till and enriched habitats to about 30 to 35 board feet on the other habitats. This difference reflects the ability of the better sites to produce somewhat larger trees.

The influence of habitat on board-foot production is more evident in the data from a few older stands on the Bartlett Experimental Forest (Table 3). These stands are essentially even-aged, although there is some variation in age distribution and past history. Mean annual board-foot production on the enriched habitat was about 60 percent higher than on the silty sediments; both of these habitats supported well-stocked, nearly pure hardwood stands of 130 to 140 ft^2 of basal area per acre. Mean annual production on the enriched habitat was over two times that found on the dry compact till; this latter stand had 135 ft^2 of basal area. Mean annual board-foot production on the enriched habitat was about 25 and 100 percent better than on the wet compact till and poorly drained habitats, respectively. These latter two stands had somewhat variable age distributions. Both supported a high percentage of softwoods, probably because the cutting that created these stands left a residual understory. Probably the softwood component on these two

Table 3.—Approximate board-foot volume per acre,[a] mean annual board-foot growth, and stand characteristics by habitat for old stands

Habitat	Forest type	Volume	Stand age	Mean annual growth	No. 10-factor prism plots
		fbm	*yr*	*fbm*	
Poorly drained	Spruce-fir	4,760	70[b]	68 (following release)	5
Wet compact till	Mixed wood	11,300	100	113	
Dry compact till	Beech/red maple/birch	5,490	90	61	4
Silty sediments	Beech/red maple/birch	8,747	100	87	5
Enriched	White ash/sugar maple	14,200	100	142	3

[a]Trees over 11.0 inches diameter to an 8.0-inch dib for all species. Approximate figures based on local volume tables, International ¼-inch rule.
[b]Total age of this stand is approximately 115 years; the stand apparently was released about 70 years ago.

Table 4.—Mean annual growth in dbh and height in sapling and poletimber stands, by species and habitat

Habitat	Dbh				Height[a]			
	Sugar maple	Yellow birch	Red maple	Paper birch	Sugar maple	Yellow birch	Red maple	Paper birch
	in				*ft*			
SAPLING STANDS								
Rock	—	—	.08	.04	—	—	1.23	.99
Outwash	—	.07	—	.07	—	1.16	—	1.20
Wet compact till	—	.06	.08	.10	—	.82	1.12	1.54
Dry compact till	—	.07	.06	.10	—	.80	.72	1.36
Washed till	—	.04 (NS)	.05 (NS)	.11 (NS)	—	1.06 (NS)	.60 (NS)	1.71 (NS)
POLETIMBER STANDS								
Rock	—	.07	.14	.12	—	—	1.05	.97
Dry compact till	.03	.05	.09	.14	—	.88	1.03	1.10
Washed till	—	.03	.09	.13	—	—	.97	.96
Fine till	.11	.11	.12	—	1.11	1.04	.98	—
Enriched	.08 (no test)	.10 (**)	.12 (*)	— (no test)	1.14 (no test)	—	1.09	1.09)

[a]Mean height of all stems 1 ft tall or taller in sapling stands; mean height of the largest dominant or codominant stem per species in the poletimber stands.

habitats accounts for the relatively high board-foot production, since softwoods are well adapted to these sites.

Productivity by species

In the sapling stands, there were no significant differences among habitats in mean annual diameter or height growth of any species analyzed (Table 4). Although there appear to be trends—moving in opposing directions—in both diameter and height growth for paper birch and red maple, the trends are not significant because of great variation and overlap in the individual observations.

In the poletimber stands, which represent a greater range in habitat than the sapling stands, mean annual diameter growth of yellow birch was roughly 50 to 100 percent better on the fine tills and enriched habitats than on the other habitats, a result that was highly significant. A similar trend is evident for sugar maple. Differences in diameter growth of red maple among habitats were significant; the rock habitat had higher rates than the fine till and enriched habitat, which in turn, were higher than the dry compact and washed tills. Note that diameter growth of paper birch on rock, dry compact till, and the washed tills was among the highest of any species on any habitat. No tests of height growth in poletimber were made because of limited data; height growth differences tended to parallel differences in diameter growth.

SUMMARY AND DISCUSSION

The main findings of productivity related to habitat were:

1. The relationship of habitat to species composition was clearly reflected in poletimber stands; but species composition varied inconsistently in sapling stands apparently because initial species composition may be caused by many factors other than site. The implications are that species composition may change materially over time when species are reproduced on sites that they are not well adapted to.

2. Mean annual biomass production of sapling stands was significantly better on washed tills (4,398 lb per acre) than on rock, outwash, or compact tills (2,664 to 3,491 lb per acre). Mean annual biomass production of poletimber stands varied from 2,916 lb per acre on one enriched site to between 2,162 and 2,263 lb per acre on fine tills, washed tills, dry compact tills and rock; the differences were not significant although it is possible that additional plots on enriched habitats would substantiate a real difference. In well-stocked stands that do not represent extreme site conditions, demanding species such as sugar maple growing on a good site apparently will produce about as much biomass as less-demanding species (red maple, paper birch, softwoods) growing on less fertile sites. Possibly the differences among habitats in biomass production of sapling stands came about because many of these young stands were undergoing changes in species composition—moving toward associations better adapted to the habitat.

3. Mean annual growth in diameter of poletimber stands was best on enriched habitats and fine tills. The differences were not great, but the results indicate some advantage on the best sites for producing large-size trees. Preliminary plot work in 100-year-old stands indicates that board-foot production is much greater on the better habitats due to the development of large-size trees.

4. Diameter growth patterns in poletimber varied considerably by species. Mean annual diameter growth of yellow birch and sugar maple was much better on enriched habitats and fine tills than on other habitats. Red maple and paper birch, on the other hand, often exhibited good growth rates over a range of habitats. These variable growth patterns help explain why less-demanding species on a mediocre site produce about as much biomass as demanding species on a good site. However, keep in mind that species growth patterns probably are conditioned by competitive effects from other species. It is still quite possible that paper birch, red maple, and softwoods would grow best on the fine tills and enriched habitats if they were free from competitive stress from other species.

The implications are that although long-term production of biomass does not vary greatly over a range of habitats, production by species will vary considerably. And, the better habitats (fine tills, enriched habitats) tend to produce larger-size trees and higher board-foot growth. In conducting intensive silvicultural operations—including weedings, thinning, prunings, and reproductive efforts—the demanding species such as sugar maple, white ash, and yellow birch should be favored on those habitats where they are well adapted. This seems particularly important when establishing or treating young stands; due to early biological events, these stands may acquire or contain species that are not well suited to habitat over the long run.

Several additional types of productivity research are needed; in particular, the effects of habitat on (1) direct measurements of biomass productivity, which would account for differences among habitats in specific gravity and tree form, (2) the growth responses of managed stands, (3) the productivity of stands of a single species, and (4) the board-foot and quality production of older stands.

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