Hardwood Regeneration Failure in the Adirondacks

Preliminary Studies of Incidence and Severity

BY JERRY JENKINS

Cover Photo
Jerry Jenkins/ Sugar Maple Sapling

Foreword

The Autumn of 1997 was one of the most beautiful in recent memory across the northeastern U.S. In New York's vast Adirondack Park, mild temperatures and sunny skies combined to highlight the annual riot of colors, as the brilliant golds, reds, and oranges of the forested canopy held their peak intensities for an exceptionally long period. Even at its most ephemeral, the region's Fall foliage is one of Earth's great natural spectacles. Yet, far below the canopy, a transformation has begun which may greatly diminish this display, and undermine far more fundamental values of the Northern Forest.

Hardwood Regeneration Failure in the Adirondacks addresses a concern identified over the past ten years by an increasing number of foresters and private landowners. The shared experiences of these individuals included a perceived lack of regeneration following logging activities on their lands. Among key hardwood species most dramatically affected was the traditionally abundant and commercially valuable sugar maple. As awareness of the problem spread, so did the perception that it was most extreme in the western half of the Adirondacks. Causes and solutions, however, remained elusive.

In the following study, Wildlife Conservation Society (WCS) researcher Jerry Jenkins builds on his own extensive field work to confirm the phenomenon of hardwood regeneration failure in the western Adirondacks. Among his most striking findings is that while sugar maple, red maple, black cherry, and hemlock show normal distributions among mature species found in the canopy, they are virtually absent in the seedling and sapling layers of the same forest stands. This is in sharp contrast to the situation in most of the eastern Adirondacks and neighboring Vermont, where understory distributions are comparable to those in the canopy. Furthermore, Jenkins contends that this failure has been occurring for much longer than suspected and is evident in unlogged as well as active commercial forests. Among several interrelated causal factors, the strongest evidence suggests that decades of acid rain have seriously depleted calcium from the region's soils, thereby lowering their capacity to support certain species.

The implications of *Hardwood Regeneration Failure in the Adirondacks* are enormous. The dramatic shift in forest composition now underway could generate cascading effects throughout the ecosystem. Certain wildlife species dependent on particular habitat types or food resources could be displaced or perhaps even disappear from the region. The impact is likely to be most immediate on the many Adirondack residents whose livelihood still depends on the "working forest" or a viable commercial forestry sector. There is much talk these days of sustainable forestry: the exploitation of natural forests in a manner and at a rate which produces a steady stream of commercial benefits without causing significant ecological degradation or loss of species diversity. A hardwood forest which cannot regenerate itself cannot satisfy any of these conditions.

The Wildlife Conservation Society plays a leadership role in understanding and resolving conservation problems through more than 250 projects in 53 countries around the world. Through its cooperative, information-based approach, WCS works to save endangered species, protect critical habitats, promote sound stewardship of private lands, and involve local communities in the conservation process. For the past several years, we have applied this approach to the Adirondack Park, where public and private lands co-exist in a complex mosaic covering 10,000 mi² of mountain forests and wetlands. It is our hope that this study will contribute to our understanding of the Adirondack ecosystem and the role that human activities continue to play in the transformation of the Northern Forest.

Bill Weber
Director, North America Program

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HARDWOOD REGENERATION FAILURE IN THE ADIRONDACKS: PRELIMINARY STUDIES OF INCIDENCE AND SEVERITY

A research report, prepared for the Wildlife Conservation Society by:

Jerry Jenkins
White Creek Field School
White Creek, New York 12057 5186867208

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Abstract

In 1996-1997 the author and his associates carried out a study of hardwood regeneration in the Adirondacks. The study, which was sponsored by the Wildlife Conservation Society, was designed to investigate reports that hardwoods other than beech were regenerating poorly in the western Adirondacks.

Adirondack forests are currently over 90% hardwoods. Sugar maple and beech are the most important hardwood species, followed by yellow birch, red maple, and black cherry. About 60% of the forest lands are privately owned and 40% owned by New York State. Most of the private lands are used for commercial timber production. The state lands are part of the New York State Forest Preserve, and, by Article 14 of the New York State Constitution, can not be logged.

Large areas of the west Adirondacks regenerated well after heavy cutting and extensive fires early in this century. Thus regeneration problems, if they exist at all, have developed within the last 50 years.

Our study measured canopy composition and regeneration density on 407 plots at 46 sites. The plots were all in upland forests with over 50% hardwoods, at points where there was at least 50% canopy cover. They thus provide a sample of regeneration in forest interiors and small or partly reforested gaps, but not in large, long-persistent gaps.

We found few saplings of any species except beech and red spruce. Beech saplings were abundant, averaging 5055 stems between 0.5 cm and 10 cm basal diameter per hectare in the west Adirondacks and 1696 stems per hectare in the east Adirondacks. Red spruce saplings averaged 700 per hectare in the west Adirondacks, suggesting that spruce was reproducing about 60% as well as beech relative to its canopy abundance. Sugar maple saplings were 63 times less abundant than beech in the west Adirondacks, averaging 80 stems per hectare. They were more abundant (430 stems per hectare) in the east Adirondacks but still four times less abundant than beech, even though sugar maple was three to four times more abundant than beech in the canopy. Other hardwood species had similarly low or lower numbers of saplings.

The low sapling densities of yellow birch, red maple, and black cherry, species which reproduce poorly in forest interiors, are not surprising. The low values for sugar maple, a shade-tolerant species that commonly regenerates from sapling banks in forest interiors, definitely are. Data from the literature and from plots on Mt. Equinox, Vt., suggest that sapling densities of 1000 stems per hectare are common in sugar maple stands outside the Adirondacks, and that on fertile sites sugar maple sapling densities are often between 2000 and 3000 stems per acre. Thus west Adirondack sugar maple regeneration densities are 10 to 30 times lower than those seen elsewhere, and east Adirondack densities two to seven times lower. We conclude that Adirondack sugar maples are showing a *regeneration deficit* relative to their abundance elsewhere and to their abundance in Adirondack canopies.

The regeneration deficit is largely restricted to small saplings under 5 cm. basal diameter. Demographic curves (plots of abundance versus diameter) show that while the numbers of canopy trees and large saplings are similar in the Adirondacks and on Mt. Equinox, the numbers of small saplings differ greatly. Further, sugar maple productivity (number of small saplings per unit basal area of sugar maple in the canopy) was three times lower in the west Adirondacks than in the east Adirondacks (17.4 versus 52.6) and 20 times lower higher in the west Adirondacks than on Mt. Equinox (17.4 to 353). The west Adirondack sites actually have fewer small sapling maples than large saplings or canopy trees and so have *reversed demographic curves*. Such curves seem highly anomalous and have not been encountered elsewhere.

Comparisons of old-growth, commercial, and ex-commercial (formerly logged, now protected) forests in the west Adirondacks found small differences in canopy composition but no significant differences in sugar maple regeneration. All the stands we examined, regardless of their history, showed reversed demographic curves and deficits of small saplings.

Several different mechanisms could be generating the regeneration deficits. The deficits of yellow birch, black cherry and red maple could be the result of episodic reproduction since these are early successional

species that may need large gaps or soil disturbance to regenerate. The sugar maple deficits are unlikely to be of this origin. They might be the result of a sharply size-dependent shade mortality curve that insured that small saplings that were not in gaps were very likely to die. The resulting demographic curves would be stable and would not lead to changes in canopy composition. But they would be inconsistent with the normal behavior of sugar maples elsewhere and unlikely to produce the uniformly high canopy and subcanopy abundances and uniformly low regeneration densities that we observed.

Since neither episodic reproduction nor size-specific mortality seem consistent with the uniformity of the deficits we have observed, we conclude tentatively that the sugar maple deficits in the Adirondacks are mostly likely the result of a regeneration failure of recent onset that has thus far only affected the numbers of small saplings. If this is correct, the demographic curves we have observed are unstable, and we expect that over the next few decades the number of large sugar maple saplings, subcanopy trees, and canopy trees will gradually decline.

Our prediction of the progressive depletion of canopy sugar maples is supported by observations of gap regeneration in the west Adirondacks, which, driven by high beech to sugar maple ratios, is entirely dominated by beech. Sapling beech to sugar maple ratios in the west Adirondacks are about 60 to 1; in the east Adirondacks they are 4:1 and in northern New York as a whole about 1:1.

The traditional explanations for Adirondack regeneration failures are logging practices, deer, and competition from beech. All of these may be contributing to what we are seeing today, but none seem an adequate explanation for the region-wide failure we have observed. Regeneration deficits are as severe on unlogged as on logged lands. Deer densities are believed to be below the threshold known to cause regeneration failures and, in any case, have decreased during the period when regeneration problems have apparently increased. And beech densities, while high at some sites, are not exceptionally high and do not correlate with low sugar maple sapling densities.

We consider it possible that the west Adirondack regeneration deficits result from a depletion of soil calcium caused by acid rain. This hypothesis is not as yet substantiated by direct measurements but is biologically and geochemically consistent with many known facts. West Adirondack soils are poorly buffered and low in mineral calcium and so sensitive to acid rain. Watershed-scale observations elsewhere in the northeast have suggested that northern forest soils have lost large amounts of calcium over the last 50 years, and that the calcium losses have not been reversed by atmospheric or bedrock inputs as the acidity of precipitation has decreased. Calcium is known to be physiologically critical in many tree species, and mortality rates of shaded sugar maple saplings seem to increase as soil calcium decreases. And finally, calcium depletion has exactly the right temporal and spatial signature to produce the regeneration deficits. No other suggested mechanism we have investigated does.

The current hardwood regeneration deficits, combined with almost universal abundance of beech in forest understories, make it likely that hardwoods other than beech will be progressively dominated from west Adirondack forest canopies, and that within fifty years many of these canopies will contain mostly beech. Since beech is suffering from a bark disease and tends to die before maturing, the current reproductive failures have the potential to make great changes in the age, height, and diversity of west Adirondacks forests, and to have substantial economic, social, and ecological effects. The rapid increase in the abundance and dominance of immature beech could, in time, eliminate mixed-age old-growth forests, decrease the variety of habitats and foods available to animals, simplify food chains, and drastically limit the ability of the forest to produce hardwood timber. The consequences can not be predicted; it is certainly possible that forests will loose structural diversity and animal and plant species, that land values and ownerships will be destabilized, and that sustainable forestry, which is widely regarded as the key to the economic future of the Northern Forest Region, will be unachievable.

Currently we are undertaking comparative sampling in areas with high and low sapling densities. Our goal is to determine when Adirondack regeneration deficits first developed and look for a correlation between sugar maple regeneration and soil calcium. We invite comments, suggestions or criticisms from anyone interested in the problem and would welcome the chance to collaborate with other researchers.

CONTENTS

Tables

Figures

1. Introduction and Definitions

This report contains the preliminary findings of a study of hardwood regeneration in the Adirondacks. The study began in 1996 and is expected to continue for several years.

The project was supported by the Wildlife Conservation Society's North America Program. The White Creek Field School supported the data analysis and supplied facilities and field equipment. My thanks to Bill Weber, Director of the North American Program, and Cheryl Fimbel, Rob Firnbel, and Angie Hodgdon of WCS for direction, help and encouragement; to Sally Bogdanovitch, Larry Denis, Joe Hanley, Greg Frohn, Don Potter and Ken Super for access to private lands and invaluable discussions of Adirondack forestry; to Charley Canham, Charley Cogbill, Jeff Hughes, Dick Sage, and Kerry Woods for ecological data, ideas, and advice; to Mark David, Charley Driscoll, Greg Lawrence and Peter Murdoch for discussions and help with the geochemical literature; and most particularly to Anna Kehler, Alex Morton, Mike Papaik, Daphne Ross, and Lynda Vaeth, who collaborated in the field work.

This is the fourth in a series of reports on conservation-related issues in the Adirondacks produced by the Wildlife Conservation Society. Like my previous report on the 1995 west Adirondack blowdown, it is intended for a general audience and contains more background information than would be included in a research report. Readers wishing to focus on the scientific essentials will find a discussion of comparable results from other sources in Section 4, methods in Section 6 and Appendix 1, the central results in Sections 8-11, and our interpretations of the results in Sections 12 and 13.

Units & Definitions Metric units are used throughout; Appendix 1 gives conversion factors to the English units commonly used in forestry. Table 1 defines the four diameter classes C layers') which we will refer to throughout the report.

Table 1. Diameter classes used in this report

Layer 1 (Canopy)	>= 20 cm dbh
Layer 2 (Subcanopy)	10 - 19 cm dbh
Layer 3 (Understory, Large Sapling)	5 bd - 9.9 cm dbh
Layer 4 (Understory, Small Saplings)	0.5 - 4.9 cm bd

Abbreviations: bd = basal diameter; dbh = diameter at breast height

Readers not familiar with forestry practice may want to note that canopy tree diameters are universally measured at 1.6 meters above the ground and reported as diameter at breast height (dbh). No standard way of measuring saplings and small trees exists; we measure their diameter 20 centimeters above the ground and report the results as basal diameters (bd). The *density* of a stand means the number of plants per unit area, reported here in stems per hectare. The *basal area* means the aggregate cross-sectional area of all the stems, measured at breast height and reported as square meters per hectare.[1]

Following common usage, by the *Adirondacks or Adirondack Park* we mean the 24,000 km² region of northern New York surrounded by the 'Blue Line', a statutory boundary, and administered by the Adirondack Park Agency. The *Forest Preserve* is the 9,800 sq. km. ensemble of state lands within the Park. The *west Adirondacks* are the relatively flat and wet plateau region west of Saranac Lake, the *east Adirondacks* the dryer and more Tugged eastern part. A *commercial* forest is one that is currently used for timber production; an *ex-commercial* forest one that was used for timber production in the past but has not been harvested for 50 years or more; an *old-growth* forest one that has never been harvested and, in addition, has at least some canopy trees over 150 years old. *Clearcuts* remove all the canopy trees, while *thinning cuts* remove some limited portion (usually less than 50%) of the canopy. *Shelterwood cuts* are two-stage clearcuts, in which an initial thinning cut is followed by a final clearcut. *High-grading* is a

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[1] Informally some ecologists call a basal area of one square meter per hectare a Curtis and one of one square foot per acre a *Pinchot*. These eponyms, though convenient, have as yet no formal status.

damaging form of thinning that removes all the desirable trees, leaving the canopy depleted of seed trees and healthy growing stock. The *advance regeneration* is the ensemble of saplings found in a forest interior before a natural or artificial gap forms. The *subsequent regeneration* is the ensemble of saplings that germinate or sprout after the gap forms.

Following technical usage, a *demographic curve* is a plot of the abundance of trees versus their size or age. (In this phase of the study we work entirely with size.) Since demographic curves normally slope from left to right (fewer large trees than small), a *reversed demographic curve* is one with a portion that slopes the other way (fewer small trees than large). A *stable curve* doesn't change over time; an *unstable* one does. A *shade-tolerant* species is one whose saplings can survive but not necessarily grow in moderate shade; an *intolerant* species will neither survive nor grow in moderate shade. A *cohort* is a group of plants of similar age. A *histogram* is a way of visualizing the distribution of a sample: in our case (p. 29) it shows the number of sample plots with a specified density of maple or beech saplings.

2. Background

Adirondack Forests and Forest Products Adirondack upland forests are currently 80 to 90% hardwoods. Sugar maple is the dominant species overall, followed by beech, then black cherry, yellow birch, and red maple. Red spruce and balsam fir are currently the only important softwoods. Black spruce and tamarack occur in small quantities in wetlands. Hemlock and white pine were formerly important but were heavily cut in the 19th century and today are mostly represented by relic stands that are not reproducing.

Currently much hardwood is used for veneer and fuel, and both hardwoods and softwoods are extensively cut for lumber and pulp. David Smith estimated in the mid-1980's that while hardwood lumber production in northern New York only slightly exceeded softwood sawlog production (132 million board feet or roughly 0.37 million cubic meters vs. 127 million board feet or roughly 0.33 million cubic meters), the total harvest of hardwoods (lumber, pulp and fuelwood) exceeded that of softwoods by about 50% (1.9 million cubic meters to 1.3 million cubic meters). Sugar maple was the most important single hardwood species, making up 27% of the hardwood harvest and 16% of the total harvest.

History of Regeneration Problems Problems with Adirondack hardwood regeneration are not new. In the 1950's many Adirondack forests were recovering from 40 years or more of heavy cutting. Deer were relatively abundant, both on commercial lands and in the Forest Preserve, and reached densities of 10 or more per square kilometer in favorable areas. Sugar maple had apparently been depleted from some forest canopies by unsustainable harvesting and, at least locally, from the regeneration layer by high deer populations. Beech, a species of low commercial value, was abundant in many forest understories, and foresters at Huntington Forest found they had to kill understory beech with herbicides before they could get sugar maple to regenerate[2].

In the last 40 years deer populations are believed to have dropped substantially[3] (Section 16), but there is no evidence that hardwood regeneration has improved. In the 1970's, foresters for International Paper

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[2] Sam Parmalee, who managed the seventy-five thousand acre Draper tract of land in the northwest Adirondacks in the 1950's and 1960's said that Draper wanted sugar maple to sell to bobbin mills and that he was given ten cents per acre per year to spend on timber stand improvement work to accomplish this. He used the money to cut and poison beech, and instructed his men to shoot an the deer they could eat, and 'not just the ones with antlers.' His tactics succeeded: forty years later we found a higher percentage of 10-20 cm maples on his lands than anywhere else we sampled. Foresters at the Huntington Forest central east Adirondacks were using the similar techniques on experimental plots in the late 1960's. Before doing shelterwood cuts they cut all the beech, applied a paste herbicide to kill their roots, applied a mist-blown herbicide to kill any remaining undergrowth, and hunted the deer until they had reduced the population from an estimated 10 animals per sq. km. to about 5 per sq. km.

[3] Sadly, there are no widespread annual censuses of deer in the Adirondacks, and so no estimates, current or historical, Of absolute deer densities in the regions we are interested in. Records of deer killed by county are available, but since most Adirondack counties include substantial amounts of land outside the park (on which deer densities are generally higher), these are not very informative.

Company did some experimental cuts in Edinburg in which they tried a mixture of thinning and row cuts designed to give sugar maple an advantage over beech. While this seemed to work at first, eventually the better-established beech outgrew the sugar maple, and at present the whole area is covered by a dense, single-species canopy of young beech. IP concluded that hardwood regeneration would not succeed on many of their Adirondack lands unless they first controlled beech. Since controlling beech is both expensive and, because it involves herbicides, politically controversial, they have since de-emphasized long-term hardwood production and tried to convert forests to softwoods when possible.

I suspect that the conclusions of the IP foresters were broadly shared by many Adirondack foresters in the 1970's and 1980's. Everyone knew of lands with poor hardwood regeneration, but the general feeling was that the problems were local and resulted from some combination of former high-grading, too many deer, and too much beech. If beech and deer were controlled, the thinking ran, and if cuts were designed to create the sort of openings that the other hardwoods liked to grow in, then good hardwood reproduction would be achieved. Sustainable hardwood production was possible but would take planning and effort.

To my knowledge, no one in the Adirondacks in the 1970's and 1980's was wondering why hardwood regeneration, which had happened more or less automatically for centuries, now required planning and effort. Adirondack forests had regenerated successfully, essentially without any attention, after having been more or less butchered and burned in the early part of this century. Why were the much more carefully managed forests of the 70's and 80's so reluctant to produce young maples and birches? If deer and beech were really the major problems, had they somehow become worse after 1950, or was something new exacerbating their effects? Were there really too many beech, or was there a maple problem independent of beech?

By the 1990's enough examples of west Adirondack regeneration failure were available to suggest that even deliberate effort, however well-intentioned, might not be enough. In the Grass River drainage there were extensive grass- and fern-dominated "cherry orchards" where there was no hardwood regeneration at all. In the heavily cut lands in Whitney Park, which unintentionally had recreated the high-graded landscapes common in many Adirondack forests earlier in this century, there was surprisingly little hardwood regeneration. At sites in Piercefield where foresters had attempted to restore a severely high-graded forest by removing the remaining trees there were large brushy thickets with very few saplings of any commercial species.

By 1995, a number of foresters had come to believe that the 'regeneration problem' was more widespread than they had previously assumed. At a west Adirondack conservation roundtable hosted by the Wildlife Conservation Society a number of land owners spoke of regeneration problems that were not responding to traditional silvacultural techniques. Ken Super of Wagner Woodlands said that some of his forest models for west Adirondacks timberlands showed the recruitment of economically desirable hardwoods to the canopy stopping in the next 40 years. Sally Bogdanovitch said that at Paul Smith's College (north-east Adirondacks) they had been able to get maple to reproduce in experimental plots near the college, but only with intensive site preparation.

The WCS Study Our conclusion from the roundtable discussions was that we needed to study the regeneration problem over a wide area and determine its history and severity. Accordingly, we began this study in April 1996. The first phase (April - June 1996) involved visits to commercial and protected forests in the company of owners and foresters. The second phase (July 1996 - May 1997) involved quantitative reconnaissance-level surveys. The third phase, currently under way, will extend the reconnaissance survey, try to determine when the declines in hardwood reproduction began and what phases in the regeneration process they are affecting, and look for relations between soil calcium and regeneration success.

This report presents the findings of the first and second phases of this study. Its central conclusion is that the foresters were right that there is a widespread problem with Adirondack hardwood regeneration but underestimated its extent and so may have mis-diagnosed its causes. The problem is not limited to commercial lands, or to sites where there are large numbers of deer, or interfering grasses and ferns, or a history of high-grading. It is as severe or more severe in old-growth than on commercial lands and is apparently independent of the abundance of beech. Its clearest and most dramatic expression is a deficit in

the number of small sugar maple saplings, which appear to be 10 to 100 times rarer in the Adirondacks than in equivalent forests elsewhere. The deficit is largely confined to small saplings. This suggests that the regeneration problem has only developed recently and that there has been a widespread change in either the production or mortality of maple seedlings within the last 50 years.

Summary: Foresters were aware of problems with sugar maple regeneration in the west Adirondacks over 40 years ago but tended to blame them on high deer populations and excesses of canopy beech left behind by former high-grading. In the intervening years, during which deer populations have dropped and much beech has died or been removed in timber stand improvement operations, the problems have remained or intensified. At present many foresters believe that hardwood regeneration problems are ubiquitous in the west Adirondacks and that no routine silvacultural techniques will regenerate sugar maple there. Our study, initiated in 1996, has confirmed the picture of a region-wide hardwood regeneration problem and found that it is present in old-growth as well as commercial forests.

3. Outline

The report begins with a brief review of normal regeneration in northern hardwood forests elsewhere (Sections 4,5). We then introduce two quantitative indices - productivity and relative abundance - that are useful for comparing understory and canopy compositions (Section 6). Section 7 describes the methods and design of the study, and Section 8 the history and landscape of the five study areas. The results occupy Sections 9-11. We present the main quantitative geographical comparisons in Section 9, the comparisons between sites of different histories in Section 10, and contains qualitative observations related to seedlings, edge reproduction, gaps, and deer in Section 11. The remainder of the paper is devoted to discussions. In Section 12 we consider several possible mechanisms that could cause reversed demographic curves and argue that it is unlikely that the present demography is stable. In Section 13 we examine the traditional explanations for regeneration deficits. In Section 14 we discuss acid rain and soil calcium depletion and note that a connection between calcium depletion and regeneration deficits in sugar maple would explain the geographic and temporal patterns we have observed. We conclude with a brief discussion of the possible ecological and social consequence of continuing hardwood regeneration failure (Section 15) and a description of the work we are doing in the 1997-1998 phase of the project (Section 16).

4. Regeneration in Other Forests 1: Standard Models for Hardwood Reproduction

In order to detect a reproductive failure we have to know when and where trees reproduce and how much reproduction to expect. If Adirondack hardwoods don't reproduce within forest interiors, our failure to find them doing it is not very important.

At present there is broad agreement among foresters and ecologists about how regeneration works in northern hardwood forests. The principles are that:

> The seed production, new-seedling mortality, and numbers of small seedlings of shade- tolerant species fluctuate greatly from year to year.

> The shade-tolerant seedlings that do survive the first few years are accumulated into a slowly-growing *seedling bank* that contains a number of different cohorts (age-classes) and so averages out the year-to-year variations in reproduction.

> The competitive ability of a seedling is determined both by its ability to survive in the shade (its mortality rate under stress) and its ability to respond rapidly to light and nutrients (its maximum growth rate.)

> Since even shade-tolerant species do most of their growing in gaps, the rate at which seedlings become saplings or subcanopy trees depends on the rate of gap formation.

Small gaps are created continuously by the death of canopy trees, which averages somewhere around 1% per year in old, unmanaged forests. They close by the lateral expansion of adjacent crown trees and so are short-lived.

Larger gaps are created, very unpredictably by windstorms or fires. They are more long- lived than small gaps and eventually fill from the vertical growth of the saplings within them. Logging can create either small or large gaps, depending on the silvacultural system.

Seedlings in small gaps grow vertically when the gap forms, cease vertical growth when the canopy closes, and resume it when a new gap forms. Usually several growth episodes are required for a seedling to reach the canopy. Seedlings in large gaps may reach the canopy in a single growth episode.

Because small gaps are commoner than large ones in many northern forests, most shade- tolerant saplings go through several episodes of suppression and release before they reach the canopy. The suppressed saplings waiting for the next gap are called the *advance regeneration*.

Small gaps are usually dominated by the advance regeneration that was established before the gap formed. Often the advance regenerants in a gap are dense enough to suppress the growth of seedlings below them, and the gap becomes dominated by a *cohort* of saplings of roughly uniform size and height.

Because existing sprouts and saplings can usually suppress new seedlings, the species with the largest numbers of large saplings in the advance regeneration are the most likely to succeed in small gaps.

Larger gaps are dominated by a mix of advance regeneration, shrubs, sprouts, and new seedlings, which may be shade-tolerant or intolerant species. The latter often require soil disturbance, which is created by tip-over mounds, fire, or logging. Which species eventually dominate a large gap depends on how much advance regeneration is present, what seeds are available in the first few years after the gap forms, and whether stumps or fallen trees in the gap are able to sprout.

These principles apply equally to natural and commercial forests. What is important is how big a gap is and how much advance regeneration it contains. Silvaculture changes the frequency and sizes of gaps and the amount of soil disturbance but not the basic mechanics of regeneration within them[4].

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[4] Thinning cuts, which are common in the Adirondacks, create small gaps which depend almost entirely on advance regeneration by shade-tolerant species. Shelterwood cuts and clear-cuts create big, long-lived gaps, which take advantage of advanced regeneration when it is there but are designed to encourage subsequent regeneration by sprouts and seedlings as well.
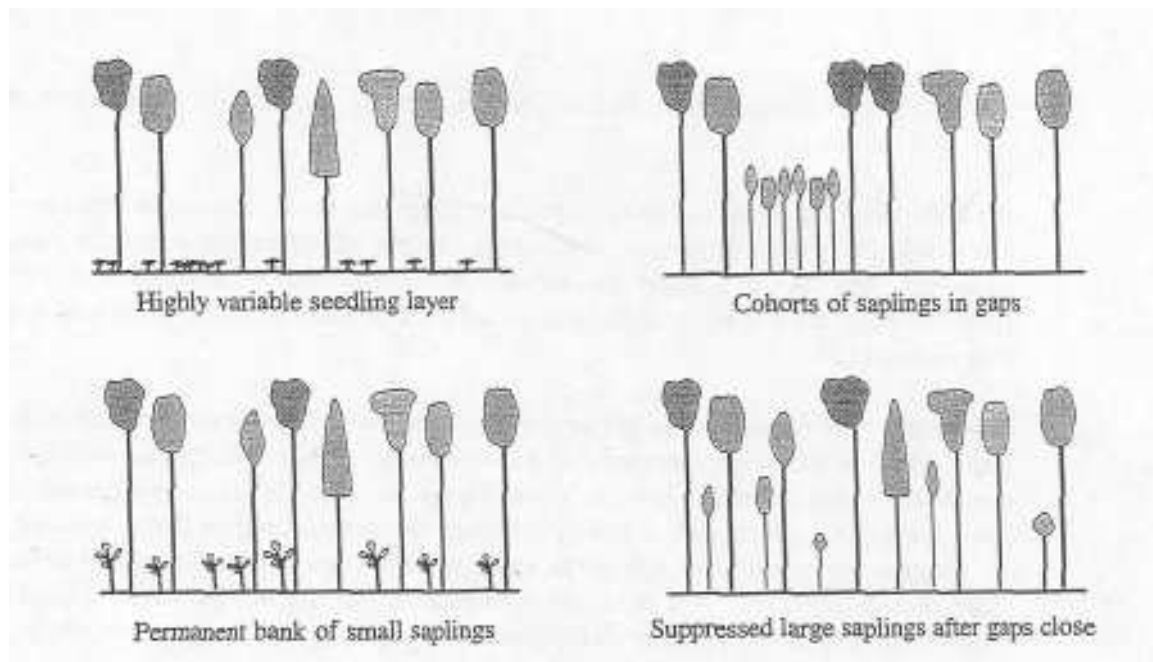
Figure 1. Predictions of the standard model of forest interior reproduction

The importance of this picture of hardwood regeneration is that it makes simple predictions about how much regeneration we should find in the forest interior (Figure 1). In particular:

The numbers of new seedlings (germinants) will fluctuate greatly depending on seed output and seedbed conditions.

Shade-tolerant species will commonly have a well-established seedling bank.

The number of seedlings in the bank will depend on the amount of light on the forest floor.

Suppressed saplings of shade-tolerant species will be found throughout the forest. They will be most common where there have been recent gaps.

The average number of suppressed saplings within a forest will depend on how big (and hence long-lasting) the gaps are and how fast the saplings in them can grow. If gaps are big enough for saplings to move all the way from the seedling pool to the canopy in one or two release periods, the pools of suppressed saplings of intermediate sizes will be fairly small. If the gaps are smaller and the saplings only advance by one or two size classes when a gap forms, the intermediate size classes will be well populated.

At any given point the saplings are likely to form a cohort of stems of similar size and age that have been released and suppressed together. But because gaps form randomly, the cohorts in different gaps are of different sizes and ages and the advance regeneration in the forest as a whole will contain a wide mixture of sizes and ages.

Shade-intolerant species will not be found in substantial numbers in forest interiors or small cuts or gaps. They constitute the subsequent regeneration that germinates or sprouts after a gap forms. They will only be found in larger gaps or areas that have recently had a large gap. Their canopy populations will have a demographic cutoff - trees under a certain age will be missing.

I call the situation described above - persistent seedling bank, suppressed saplings of a variety. of sizes, episodic growth of saplings alternating with periods of suppression - the standard model of the demographics of a shade-tolerant species. Considerable evidence in the ecological literature suggests that both natural and periodically thinned stands of sugar maple and beech fit this model well.

Summary: The regeneration of trees in forest interiors depends on the size and frequency of gaps. Shade-tolerant species establish banks of suppressed seedlings and saplings which dominate the regeneration process in small gaps. Locally, on scales of a few meters, the advance regeneration tends to form even-sized cohorts of saplings that originated together in single gaps. Averaged over a forest in which gaps or harvests have occurred randomly, all sizes should be present. For shade-tolerant species, the size and density of a species of advance regeneration relative to that of its competitors is a good predictor of its success in gaps.

5. Regeneration in Other Forests II: How Many Sugar Maple Saplings Should We Expect Within a Sugar Maple Forest?

In this section and much of what follows we focus on sugar maple. It is a classical example of a shade-tolerant species, and the most abundant Adirondack hardwood. Since it is uniformly well represented in the canopies and subcanopies of both commercial and old-growth forests, it has apparently reproduced successfully in the Adirondacks within perhaps fifty years of the present. If it is not currently reproducing in the Adirondacks, we have *prima facie* evidence that there has been a major, recent change in the ecology of Adirondack hardwood forests.

There are several ways that regeneration can be described. The commonest way is to give the sapling density, which is the total number of saplings in some specified size range per unit area. But since small saplings can be thousands of times more common than somewhat larger ones simple densities can be misleading: a small number of large saplings may be much more important than a large number of small ones.

A much better way to characterize regeneration is to present a *demographic curve* showing the density of saplings as a function of their size. Since the regeneration in small areas will often be dominated by a single cohort (Section 4), to obtain a demographic curve that contains a number of different cohorts and is representative of the whole forest we should sample a number of points and pool the results to obtain an average curve.[5]

Full Demographic Curves We have recent demographic data for beech and sugar maple from 30 plots in an area of several square kilometers on the east slope of Mt. Equinox, a limestone mountain with rich hardwood forests in southwestern Vermont. The study area has been logged in the past, but not for 30 years or more. Figure 2 shows the demographic curve and Table 2 gives the data. In these and all subsequent tables each size class is labeled by its lower limit: thus the 1-cm class extends from 1.0 to 2.4 cm. Classes below 10 cm are basal diameters, classes 10 cm and up are diameters at breast height.

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[5] Full demographic curves are surprisingly rare in the forest literature. Most studies either sample relatively few size classes or a relatively few plots and do not contain enough information to construct the average demographic curve for a study area of significant size.
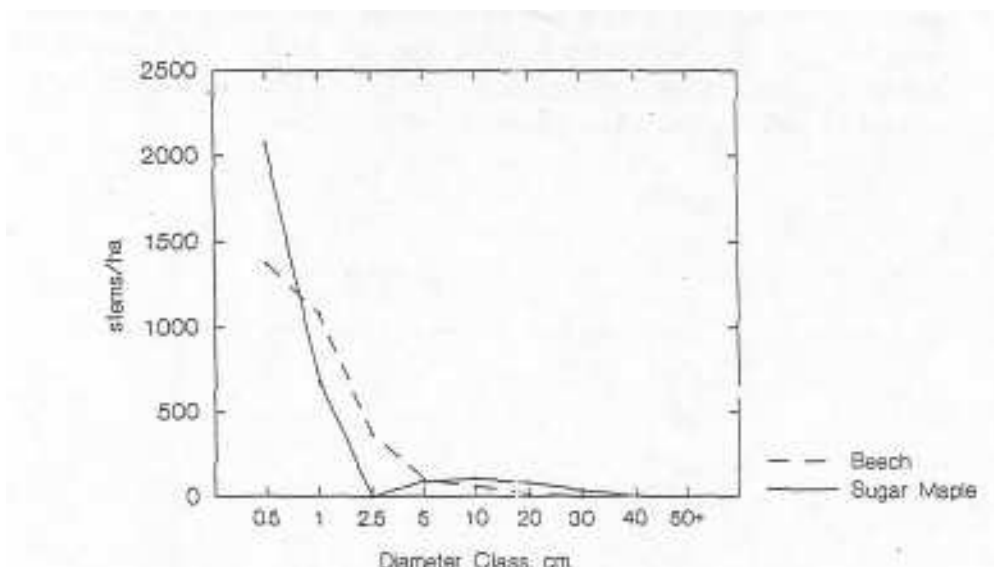
Figure 2. Demographic curves for sucrar maple and beech on Mt. Equinox, Manchester, Vt.

Table 2. Densities of sugar maple and beech saplings on Mt. Equinox

	Layer 4			Layer 3	Layer 2		Layer 1		
Size Class, cm	0.5	1	2.5	5	10	20	30	40	50+
Sugar Maple, stems/ha	2067	684	0	89	105	82	37	4	0.35
Beech, stems/ha	1375	1081	356	102	60	17	2.4	0.6	0.1

Data from 30 circular plots, Feb. 1997. Size-classes extend from the diameter given to the next largest (the 0.5-cm class contains saplings from 0.5 cm to 0.9 cm, etc.)

Note that all size classes of sugar maples are represented, and that the smallest classes are the most numerous. The stand contains a total of some 3068 stems per hectare of sugar maple and 2994 stems per hectare of beech, giving a total sapling density of 6062 stems per hectare or 0.6 stems per square meter. Some 2751 stems of sugar maple per hectare (90%) are in Layer 4 and 89 stems per hectare (3%) are in Layer 3. The absence of trees in the 2.5-cm class is interesting. It could be a statistical fluctuation, an artifact of how we grouped the observations into size classes, or a real effect indicating that the saplings in that size class have higher growth rates or experience higher mortality.[6] The curve for beech is generally similar but does not show a dip in the 2-cm class.

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[6] Similar dips occur in the Adirondack data and remain after the size classes are rescaled to give stems per hectare per centimeter of diameter, suggesting that they are not an artifact. See Section 10 for further discussion.

Figure 3, from data collected by Kerry Woods and his associates on permanent plots in an old- growth forest in northern Michigan, gives demographic curves for sugar and red maples. The sugar maple curve is generally similar to that from Mt. Equinox and has similar absolute densities of small saplings. Red maple, which is less tolerant of shade, has a demographic curve the same general shape but with three to four times fewer canopy trees and 10 to 20 times fewer saplings. Its total canopy basal area here has changed little since 1974 and its demographic curve may be stable, in spite of its low sapling abundance. This is what you would expect of a species known to reproduce well in gaps and on tip-over mounds.
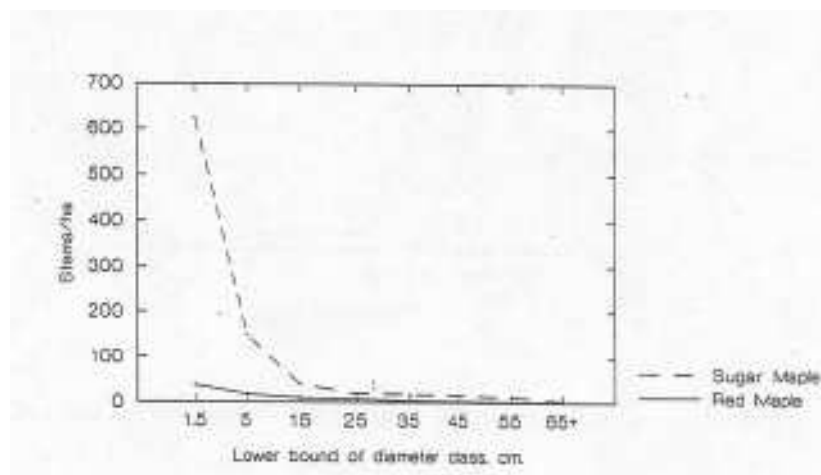
Figure 3. Demographic curves for sugar and red maples in Dukes Research Natural Area, Michigan. Unpublished data from Kerry Woods.

Other Sapling Data Other studies suggest that the regeneration densities found at Mt. Equinox and in northern Michigan are broadly representative of sugar maple densities on good sites:

> *Rich Woods, Goshen, Vt.* Charley Cogbill and his associates, working at the Cape, a Research Natural Area in the Green Mountain National Forest, found 964 sugar maple stems per hectare in Layer 4 and 137 stems per hectare in Layer 3.

> *High Elevations, Northern Green Mountains* Jeff Hughes and Walter Poleman found roughly 1000 saplings per hectare between 1 m tall and 2 cm dbh[7] in transects 100 m below the upper elevation limits of sugar maple on five west-facing mountain slopes in the northern Green Mountains. The number declined dramatically as the elevation limits of sugar maple were approached.

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[7] This size range is roughly equivalent to our 0.5 mm and I cm classes combined, and so is a little smaller than what we call Layer 4.

New York State In the *Forest Statistics For New York* (1995), Alerich & Drake estimate that New York, excluding the Forest Preserve, has 5,244 million sapling maples on the 3.31 million hectares of forest land with trees of saw-timber size, giving 1544 saplings per hectare.[8]

The density estimate derived from the New York statistics is a minimum, since the 3.3 million hectares of saw-timber include much conifer and oak forest. Alerich and Drake estimate that New York contains 1.8 million hectares of northern hardwood saw-timber. If we assume, conservatively, that 80% of the sapling maples in the state are in northern hardwood forests, the average sapling density in northern hardwood forest would be roughly 5200*0.8/1.8 = 2300 saplings per hectare.

Table 3. Average densities of sugar maple saplings in different regions in New York State

Region	Saw Timber Area (million ha.)	Maple Saplings (millions)	Maple Saplings (number per ha.)
Capital District	0.315	419	1330
Catskill & Hudson	0.542	276	509
E. Adirondack	0.312	379	1215
N. Lake Plain	0.457	951	2081
South Central	0.546	666	1220
Southwest	0.340	378	1112
St. Lawrence	0.437	1270	2906
W. Adirondack	0.356	906	2545
All N.Y.S.	3.31	5244	1584

Data from Alerich & Drake, 1995, for lands stocked with trees of saw-timber size. State lands in the Adirondacks are not included. The Saint Lawrence, E. Adirondack and W. Adirondack regions mix private lands within the Adirondacks with private and public lands outside the Adirondacks.

Sugar maple sapling densities should vary with forest type and with soil fertility. Table 3, also based on the *Forest Statistics For New York* (Alerich & Drake, 1995), shows that this is roughly true. Maple sapling densities are lower within the regions that have substantial amounts of pine or oak-hickory forests (Catskill, Capital District, South Central, Southwest) and higher in regions with mostly northern hardwoods. They are highest in the Lake Plain, St. Lawrence and 'West Adirondacle regions, all of which include large areas of fertile alluvial plains.[9]

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[8] Their sapling class is defined as anything over 1 foot tall and less than 4.9 in. dbh. Since saplings 1 foot tall are usually slightly less than 5 mm at 20 cm above the ground, and 4.9 in. dbh = 12.3 cm dbh, their sapling class is a little larger than our Layers 3-4 (0.5 mm to 10 cm) put together.

[9] Note that what Alerich and Drake call the East and West Adirondack Regions contain substantial amounts of land outside the Adirondack Park and omit the Forest Preserve lands which constitute about 40% of the park. They are thus statistically more representative of lands near the Adirondacks than of the Adirondacks themselves.

Taken together, the various studies quoted above suggest that sugar maple saplings - here broadly defined as plants between 5 mm basal diameter and 10 cm dbh - occur at densities of 1000 stems per hectare or more in many sugar maple stands and may occur at densities of over 2000 stems per hectare on productive sites. This corresponds well with current forestry practice, which suggests that a regeneration density of somewhere around 2500 stems per hectare after a cut guarantees successful sugar maple reproduction.

Seedlings The densities of seedlings are less well reported than those of saplings but can be much higher than those of saplings. In a peak year a sugar maple stand can produce several million seeds per hectare, and over a million of these may germinate and produce seedlings the following year. Relatively few of the germinants - typically a few percent at most - will survive. Causes of mortality vary, but drought, insects, shading, and fungi are all important. Because the input of seeds can vary by as much as 1000 times between good and bad seed years, and because juvenile mortality is high and variable, the numbers of small seedlings can vary from almost none to hundreds of thousands per hectare.

The mortality of large seedlings is substantially less than that of small seedlings, and many maple forests develop a conspicuous seedling bank of plants 20 to 50 cm tall and anywhere from three to more than 20 years old. The seedling bank smooths the year-to-year fluctuations in seed output and germination and allows small maple saplings to be a permanent feature of the understories of many forests.

Many of the study areas mentioned above have conspicuous seedling banks. On Mt. Equinox, small maples in the 20 to 50 cm range covered about 5 % of the forest floor and were the most important ground-layer species. At the Cape their cover was 4.4%. In the Five-Ponds Wilderness (west Adirondacks), on 33 plots which had sugar maple basal areas of three square meters per hectare or more, the median cover of sugar maple in the middle 1970's was 1.8%.

The absolute seedling densities are not known for any of these sites. On the conservative assumption that the mean area per seedling is less that 0.05 square meter, a stand with 5% cover of seedlings would have a density of over 10,000 seedlings per hectare. This is consistent with results from a study of regeneration in Vermont sugarbushes by Jeff Hughes and Tim Wilmot. They found that densities of sugar maples one year old but less than 2 cm dbh ranged from a few hundred to over 100,000 per hectare, with median values somewhere near 10,000 stems per acre.

Summary: Many sugar maple stands have 1000 or more saplings per hectare in the 0.5 cm bd to 10 cm dbh range. Seedling numbers are often much higher, at least on fertile sites. In such cases, the demographic curves of Figures 2 and 3 would continue to rise as the small seedlings in the seedling bank were included and then begin to fluctuate when they reached the region dominated by variable seed input and high seedling mortality.

6. Measuring Regeneration Relative to Canopy Composition

Because we don't expect many saplings where there are not many parent trees, it is often useful to have an index of sapling, abundance relative to the abundance of parent trees in the canopy. Two ways to measure this are a) to take the ratio of the percentage of a species in understory to the percentage in the canopy or b) to take the ratio of the density of the saplings in the understory to the basal area of the parent species in the canopy. I call the first ratio the *relative abundance* and the second the *productivity*.

The relative abundance is dimensionless and measures how well a species is succeeding relative to its competitors in the stand. It depends on the abundance of competing species, and, like any competition index, can not distinguish between deficits of the species in question and excesses of its competitors.

The productivity is the number of saplings produced per square meter of canopy basal area. It measures how well the parent trees are doing at producing saplings, irrespective of their absolute abundance in the stand. Unlike the relative abundance it contains no information about percentage composition and is insensitive to fluctuations in the abundance of other species. Thus, were the saplings of a competitor to die off suddenly, the density and hence the productivity of the remaining species would be unchanged but their relative abundance would increase.

Two examples will show the kind of numbers involved:

> *Mt. Equinox* The canopy basal area of sugar maple averaged 10.2 square meters per hectare and was 48.3% of the total canopy basal area. The understory contained an average of 2844 sugar maple stems per hectare, which were 33.9% of all the understory stems. The relative abundance of sugar maple in the understory was 33.9/48.3 or 70.2%, and the productivity 2844 stems / 10.2 square meter or 279 stems per square meter of basal area.

> *New York State* From the Forest Statistics, sugar maple makes up 5.5 1 % of the understories and 12.2% of the canopies of the forests in the state as a whole, giving a relative abundance of 45%. It is estimated to have produced 5.2 billion saplings from 11,800 square kilometers of canopy basal area, giving an average productivity of 443 stems per square meter of basal area.

Note that in both indices the abundance of maple in the canopy is computed from basal area per hectare rather than stems per hectare, since basal area correlates with crown size and seed production much better than the number of canopy stems per hectare does. Also remember that ratios, however interesting, have vicious and unreliable statistical properties. They are generally noisy, have large variances, and are very sensitive to small denominators. The latter property means that, unless the datasets are massaged in some fairly brazen ways, averages of ratios may be dominated by plots where the species is rare. This is exactly what you don't want in a biologically meaningful measure. Thus we should be somewhat suspicious of what the abundance and productivity indices ten us, and always ask whether the absolute measurements say the same thing as the ratios.

In the sections that follow we will say that a species has an absolute regeneration deficit when the absolute densities of its seedlings and saplings fall substantially below what is seen in stands believed to be regenerating normally and a relative regeneration deficit when the relative abundance or productivity falls substantially below what is seen in stands believed to be normal. In these terms, the factual argument of this paper is that the density, relative abundance, and productivity of young sugar maples in forest interiors in the west Adirondacks are an order of magnitude or more below what we see in maple forests elsewhere, and so there are significant sugar maple regeneration deficits, both absolute and relative to the canopy.

Summary: The abundance of the saplings of a given species can be measured relative to that species' abundance in the canopy by either of two ratios, the productivity and relative abundance. The productivity gives the sapling density per unit canopy basal area. The abundance measures whether a species makes up a larger or smaller fraction of the understory than it does the canopy. Productivities of sugar maple at Mt. Equinox and New York as a whole were 229 and 443 understory stems per square meter of canopy basal area; relative abundances were 70% and 45%. These indices are useful to compare sapling abundances in situations where canopy abundances differ but have some statistical biases and should be used with care.

7. Methods

Our work in 1996 was a reconnaissance-level study concentrating on advance regeneration in forest interiors and small gaps. We choose sample areas in upland hardwood forests and in each sample area took 10 individual samples at points spaced 100 in. apart. We rejected sample points that fell in openings, wood roads, or wetlands, or at points where there was less than 50% canopy or less than 50% hardwoods in the canopy. At each sample point we measured canopy tree basal area by a prism, estimated canopy diameters by eye (often verifying these with calipers), and measured understory diameters and densities within nested two- and five-meter radius circular plots. Canopy densities were obtained by dividing the tally for each diameter class by the area of the circle within which a prism samples trees whose diameters equal the

midpoint of the diameter class.[10] Figure 4 shows the sampling design, and Appendix 2 gives the details of the field and computational methods.

Three features of the sampling - the focus on forest interior reproduction, the use of prism samples, and the use of nested sapling plots - require brief explanations.

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[10] A tree with a diameter of d cm will be tallied by a "1-factor" metric prism if it is within $d/2$ meters of the sample point. If N trees are tallied in a diameter class with a midpoint d cm, the estimated density of that diameter class is just $4N/3.14d^2$.

1. Individual Plots
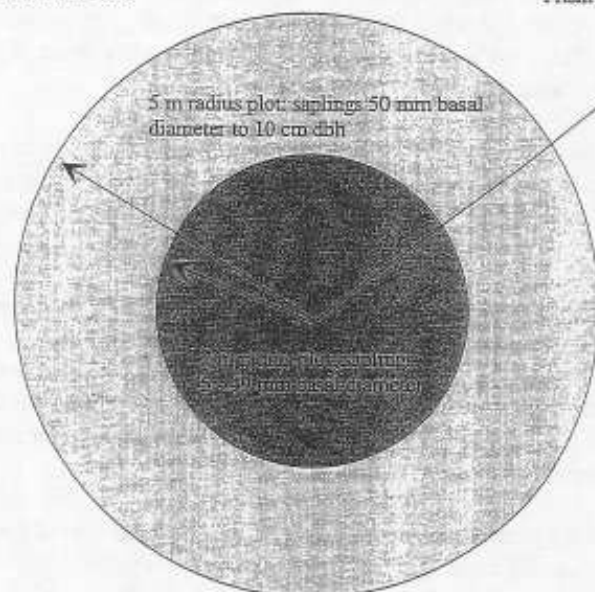
Prism Sample: Trees >= 10 cm dbh

5 m radius plot: saplings 50 mm basal diameter to 10 cm dbh

Canopy diameters estimated visually to nearest 10 cm.

Understory diameters (at 20 cm above base) measured with gauge.

Slope, aspect, elevation, dominant species by layer recorded

Plots not sampled if :
    a: canopy cover less than 50%
    b: plot fell in a wetland
    c: plot more than 50% exposed bedrock

2. Study Areas (Groups of 7-10 Plots)

Plots in groups of 10 where possible.

Usually on moderate slopes and varying 200-500 feet in elevation.

In upland deciduous or mixed woods where substantial amounts of sugar maple are present.

Usually beginning 30-100 m from a road.
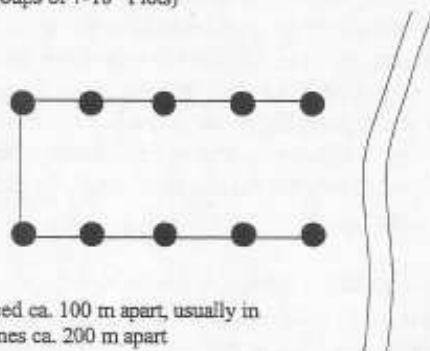
Plots spaced ca. 100 m apart, usually in parallel lines ca. 200 m apart

3. Size Categories

Layer 1 (Large Canopy):   over 20 cm dbh

Layer 2 (Subcanopy & Small Canopy): 10-19 cm dbh

Layer 3 (Large Regeneration):   5 cm basal diam. to 9 cm dbh

Layer 4 (Small Regeneration):   0.5 mm - 4.9 cm basal diameter

dbh (1.6 m)

basal diam. (20 cm)

Figure 4. Sampling design used in 1996.

Advance Reproduction Because we were interested in the relation between regeneration and canopy composition, we chose to work in forest interiors and small gaps where there was at least a partial canopy. This also allowed us to compare old growth forests, where there were no large gaps, to commercial lands where there were.

The disadvantage of not sampling within current gaps is that in many forests the most rapid sapling, growth occur in gaps. By choosing to work in forest interiors we were, in effect, overlooking the places where regeneration was most active and ignoring the species that only reproduce in gaps.

This restriction is not as bad as it might at first seem. As noted in Section 6, the literature suggests that for shade-tolerant species the advance regeneration in the forest interior is a good predictor of what species will eventually dominate a subsequent gap. And further, because small gaps are relatively common and because we sampled any point with 50% canopy or more, a number of our sample points were actually either in or near small gaps, or in areas that had gaps in the recent past.[11]

Prism Samples Prisms count big trees at some distance from you but small trees only when they are close. In our case this meant that the small canopy trees were being tallied within a radius of roughly 5 meters, and large ones within a radius of roughly 30 meters. (See Note 11.) This has the advantage that it is a fast way of sampling and so appropriate for the kind of survey we were doing. It also provides a more accurate estimate of the density of big trees - which contribute disproportionately to the seed rain - than is possible with a fixed plot of reasonable size. Its disadvantages are that it is somewhat less accurate overall than sampling a plot of fixed size, and that it yields estimates of basal area rather than stem density. We did not need highly accurate information about canopy composition and were able to derive density estimates from basal areas and diameters. These densities would probably not have been accurate enough for a detailed study of canopy demography but were adequate for our purposes.

Nested Understory Plots Because small saplings of beech and striped maple were often much more abundant than larger ones, we measured saplings under 5 cm, basal diameter in a two-meter radius plot and those over 5 cm in a five-meter radius plot. This gave us comparable samples of large and small saplings, increased the accuracy of our density estimates for large saplings, and incidentally saved a lot of meaningless counting of small beeches and striped maples.

Summary: The study compared overstories and understories of evenly-spaced plots in forest interiors and small gaps. Canopy basal areas were measured with a prism and converted into density estimates for each diameter class. Understory densities were measured in nested circular plots. Samples were restricted to upland forests with 50% or more canopy; wetlands, edges, and large gaps were not sampled.

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[11] Since the death of canopy trees averages somewhere around I% per year in old unmanaged forests, about 20% of the points in such a forest will have been in a gap in the last 20 years, and almost all of them near a gap in the last 20 years.

8. Study Areas

Thus far the study has measured 294 plots at 30 sampling areas in the west Adirondacks, 113 plots at 12 sampling areas in the east Adirondacks, and 30 plots in three sampling areas on Mt. Equinox in southwest Vermont. The west Adirondack sites had similar forests but different histories and were chosen to test for relations between regeneration and land use history. The east Adirondack sites were more diverse ecologically but had similar histories. They were included so that we could study the geographic and ecological variation of regeneration over a large area. The sites on Mt. Equinox were uniform geographically and historically, and were chosen to provide 'outgroup' comparisons at a site where sugar maples were reproducing well that was ecologically different from the Adirondacks.

West Adirondack Vegetation and History The 30 west Adirondack sample areas were clustered in three study areas (Figure 5): commercial timberlands in the Grass River Basin, former commercial lands in the Cranberry Lake Wild Forest, and old-growth forests near Stillwater Reservoir. The last two are both part of the Forest Preserve. All are mid-elevation (300 to 600 m) lands of moderate relief with sandy to rocky, highly acid soils. They have northern hardwood forests on the uplands and conifer forests in the lowlands. The sites are all located in the northwestern Adirondacks and form a rectangle about 30 kilometers wide and 60 kilometers high that is roughly centered on Cranberry Lake.

The composition of these forests is very uniform. The commonest hardwoods are beech, sugar maple, yellow birch and red maple. Black cherry is locally abundant on the commercial lands and scarce on the state lands. Small amounts of big-tooth aspen and ash also occur on the commercial lands. Red spruce is present throughout but usually makes up less than 10% of the canopy. Only small amounts of hemlock are present, mostly on steep slopes and at the edges of lakes and wetlands. Forest understories are largely dominated by beech; red spruce is also common in the understory but rarely dominant. Hobblebush and striped maple are locally abundant in some areas and absent in others. Herb floras are typically simple: evergreen woodfern is a ubiquitous dominant, hayscented fem is locally abundant where there have been gaps and soil disturbance, and shining clubmoss and wood sorrel are locally abundant where the forest floor is moist. Raspberries are extremely common in gaps throughout.

Structurally these forests are all heterogeneous. The older ones have suffered much recent mortality of large trees (especially of beech but also of yellow birch, spruce, and sugar maple) and are often two-tiered, with an incomplete overstory and a dense subcanopy or understory. Gaps of all sizes, both natural and man-made, are common. Some appear to persist for several decades or more, but most rapidly fill with dense thickets of young beech or with mixtures of beech and striped maple.

The land-use histories of the three west Adirondack study areas differ greatly, and are typical of what we call the commercial, ex-commercial, and old-growth landscapes. The commercial lands were logged for softwoods in the early 19th century and may have produced hemlock bark for several large tanneries as well (Appendix 3).
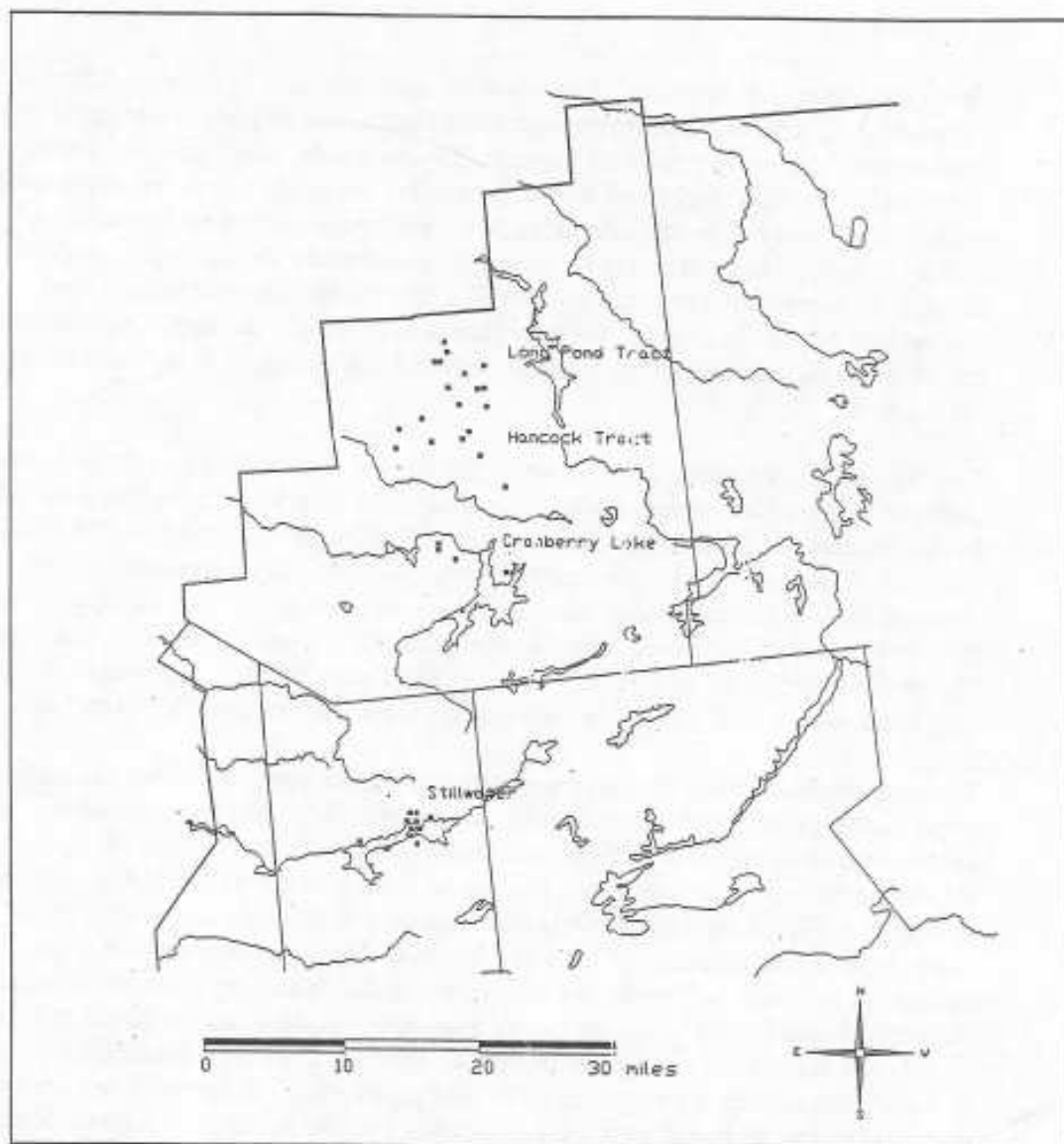
Figure 5. Northwest Adirondacks, showing areas sampled in August and September 1996. Each square represents 8-10 sample plots, spaced 100 meters apart on one or two parallel transects.

Extensive hardwood logging by Emporium Forestry, a large company whose principal product was hardwood flooring, began after 1915. Logs were shipped by a network of railroads to mills at Conifer and Cranberry Lake. By the 1940's the company was importing logs from outside the Adirondacks, suggesting that local supplies of timber had been depleted. Much of Emporium's land was sold in the 1940's. It remained in commercial use through several changes of ownership, and was logged fairly heavily through the 1970's. At present the forestry on the commercial tracts is conservative, aiming at long-term gains in forest quality and sawlog volume. As markets for hardwood pulp have become available, considerable efforts have been made to remove low-value trees and improve stand quality.

Current management plans emphasize thinning cuts at intervals of about 15 to 20 years and normally leave 30 to 50% of the canopy in place after each cut.[12]

The *ex-commercial* forest on Forest Preserve lands near Cranberry Lake was cut heavily for softwood pulp by International Paper early in this century and then selectively for hardwoods by either Emporium or possibly the Rich Lumber Company. Beech are extremely common on these lands, probably because of the selective removal of other hardwoods. Most of the large beech here have died in the last 20 years, leaving a patchy canopy and dense thickets of beech saplings.

The *old-growth* study area is part of a 20,000 hectare tract of old-growth forest within the Five Ponds Wilderness of the New York State Forest Preserve. All our study areas were adjacent to the Stillwater reservoir. The lands north of the reservoir were acquired by the state from W, S. Webb in 1895, and, according to depositions in a court case that preceded their acquisition, have never been logged. The lands immediately south of the reservoir also belonged, at least in part, to Webb and were part of the corridor for his Mohawk and Malone Railroad, built in 1891-92.[13] They are said to be second-growth and are near both the Flow Road and the railroad itself, making it quite likely that timber was removed at some time. But they still have many large trees and in many ways look quite similar to the virgin forests north of the reservoir.

West-Adirondack Disturbance History It is likely that some parts of all three west Adirondacks; sites burned in the early 1900's, when post-logging fires were common in the northern Adirondacks. Maps of the 1903 and 1908 fires show major fires southwest of Cranberry Lake on Forest Preserve lands that were not included in this study, and smaller fires along the south shore of Stillwater reservoir and scattered in commercial lands. We presume that the lands around Burnt Pond on the north shore of Stillwater burned at some time, but as yet don't know when.

In the last 30 years all west Adirondack forests have been affected by the beech-bark disease (a scale insect-*Nectria* fungus complex). The disease has almost affected all the adult trees and killed a large number of them: at present almost all beeches over 40 cm dbh are dead or dying, and most beeches 20 to 40 cm dbh show the characteristic swelling and cracking caused by the disease. Dying trees commonly produce abundant root sprouts, and gaps produced by the death of older beeches commonly fill with dense thickets of beech sprouts.

Mortality of older trees of other species was also noted but was much more local. We saw areas where there were many dead maples, birches, or spruce, but also areas where there were relatively few dead trees.

None of our study areas was seriously affected by the blowdown of July 15, 1995, though several are adjacent to areas that were. Historical maps suggest that the old-growth forests immediately north of the Stillwater Reservoir were affected by the blowdown of November, 1950, but we found no clear evidence for this in the areas we visited.

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[12] Cutting is locally heavier in areas where the canopy trees are diseased, but even so most recent openings are less than a hectare

[13] This was the first railroad to cross the Adirondacks and a major force in the industrial and recreational development of the region.
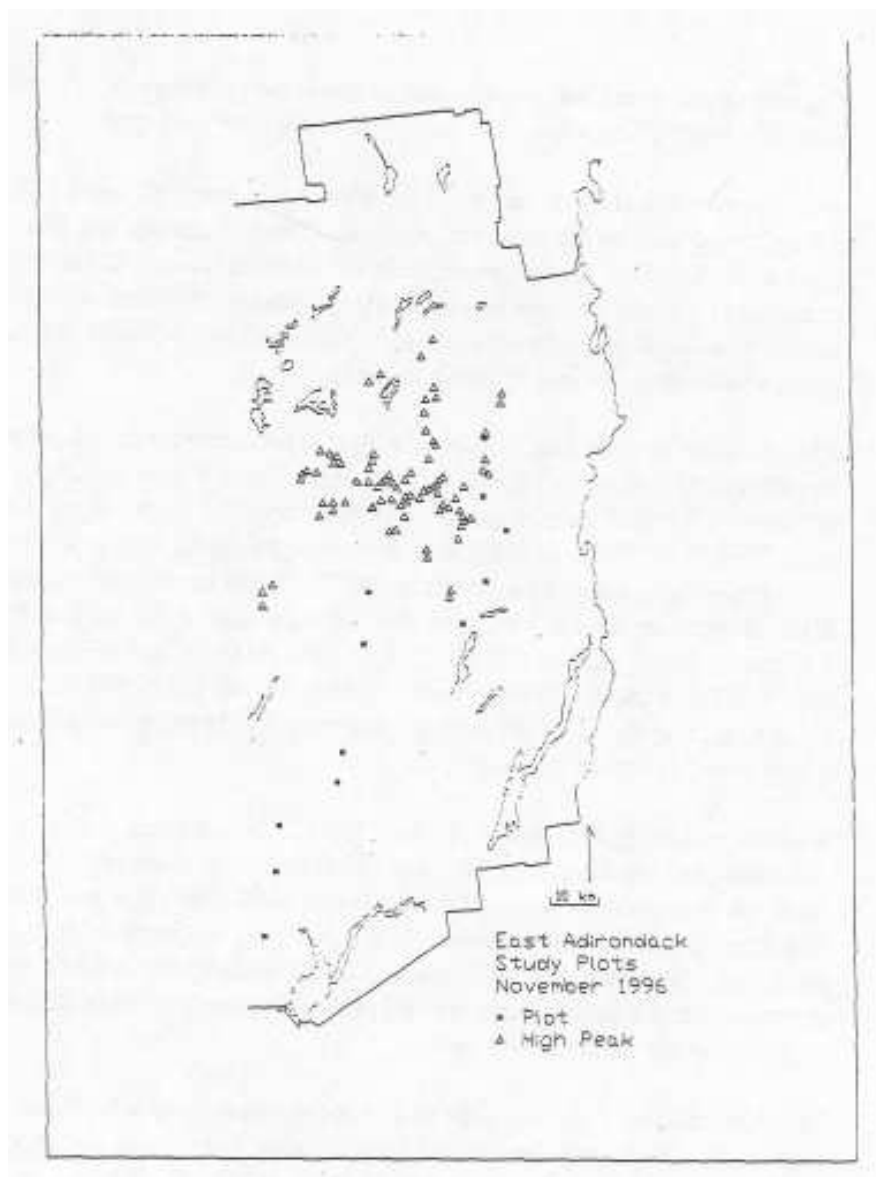
Figure 6. East Adirondacks, showing areas sampled in November 1996. Each circle represent 7-10 plots.

East Adirondacks The 12 sample areas in the East Adirondacks are scattered along an irregular line about 120 km long running east of the High Peaks region (Figure 6). They are all on ex-commercial lands that are now in the Forest Preserve. The altitudes were generally similar to those of the west Adirondack sites, but the slopes were often steeper and the sites somewhat warmer and with less acid soils. Herbs and shrubs indicating high- calcium soils occurred at some of the sampling sites. The forests were more diverse overall than those in the west Adirondacks and, in some cases, had substantial amounts of red oak, white ash, basswood, and bigtooth aspen, trees that are rare or absent in the west.

None of the east Adirondack sample areas had been cut recently, and some of them may not have been cut in this century. Their ownership and land-use histories have not been investigated.

Mt. Equinox The three sample areas on Mt. Equinox are all on the east side of the mountain. The elevations are comparable to those of the Adirondack sites. The bedrock here is a calcareous marble, and the forests quite productive and diverse. Sugar maple and red oak are the commonest forest trees. The sample areas have been logged commercially several times in this century but not within the last twenty years. The lands are currently an ecological reserve managed by the Equinox Preservation Trust.

Summary: The west Adirondack sites included commercial timberlands, ex-commercial timberlands, and old growth. All are in maple- and beech-dominated northern hardwood forests on acid, infertile soils. The east Adirondack sites were mostly ex- commercial lands now in the state forest preserve. They are strongly sugar maple- dominated but have more diverse canopies and, at least in some places, more fertile soils than the west Adirondack sites. The Mt. Equinox site is an ex-commercial sugar maple- red oak forest on highly fertile soils derived from marble bedrock.

9. Quantitative Results 1: Geographic Variation in Forest Composition

Figures 7-9 show the forest composition for each of the three areas studied. There is a page of graphs for each study area. Each individual graph within a column gives composition of a single layer, with the canopy (Layer 1) at the top of the page and small saplings (Layer 4) at the bottom. For species abbreviations see Table 4. The left hand graphs give absolute measurements and the right hand ones percentages. Canopy abundances are measured in basal area per hectare and sapling abundances in stems per hectare. Standard errors are typically 5 to 10% for the Adirondack data and 10 to 25% for the Mt. Equinox data (which had many fewer plots), with the regeneration layers often more variable than the canopy.

Table 4. Abbreviations used in graphs

BE	Beech	BW	Basswood	SM	Sugar Maple
BB	Black Birch	HE	Hemlock	STM	Striped Maple
BC	Black Cherry	HH	Hop Hornbeam	YB	Yellow Birch
BF	Balsam Fir	RM	Red Maple	WA	White Ash
BNH	Butternut Hickory	RO	Red Oak	WB	White Birch
BTA	Bigtooth Aspen	RS	Red Spruce		

West Adirondacks West Adirondack canopies (Figure 7, first graph) are fairly diverse, with four main species and three other significant ones. Sugar maple is the most abundant species. Subcanopies (second graph) are less diverse and tend to be dominated by beech but still contain significant amounts of sugar maple. The regeneration layers are nearly
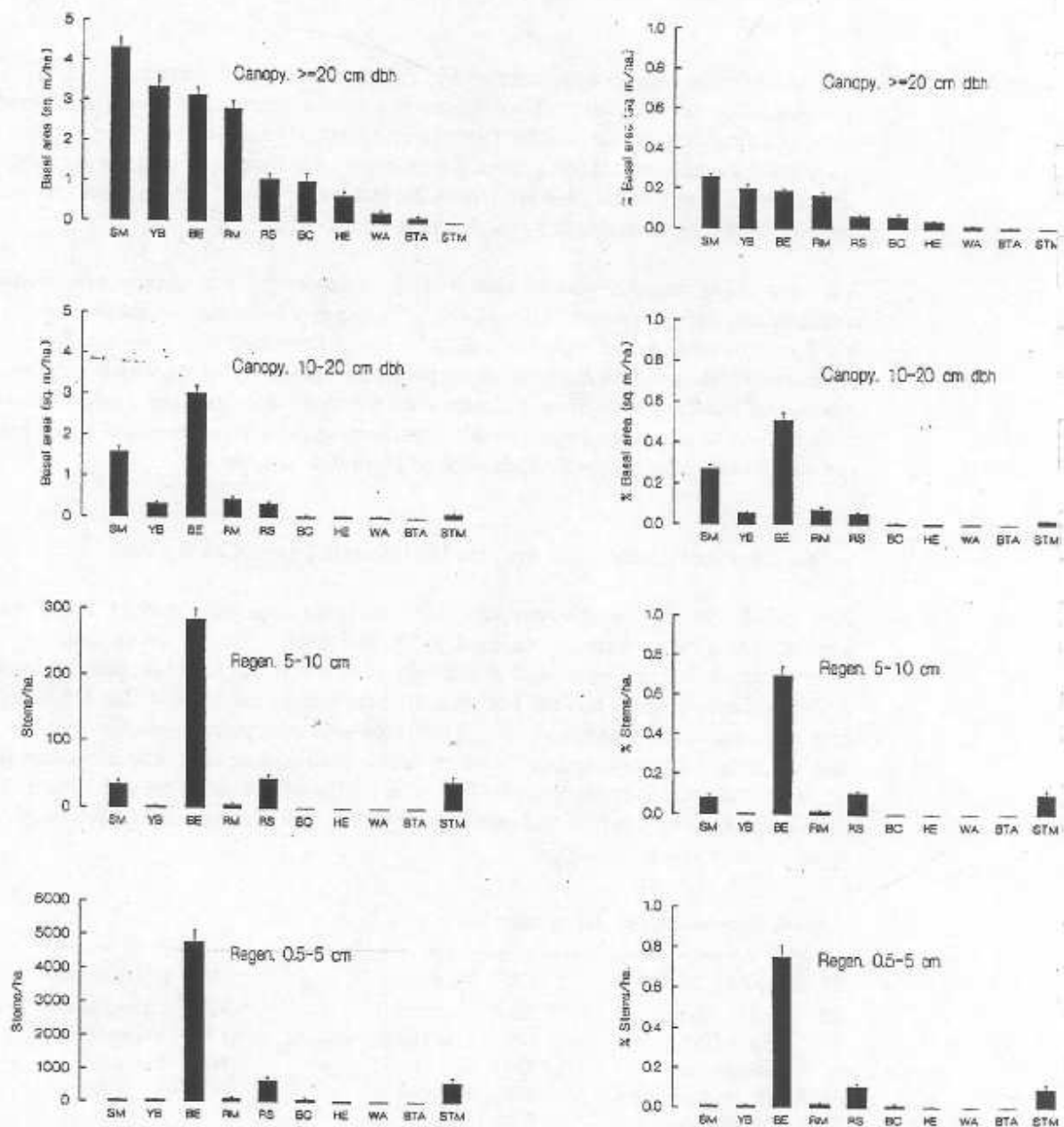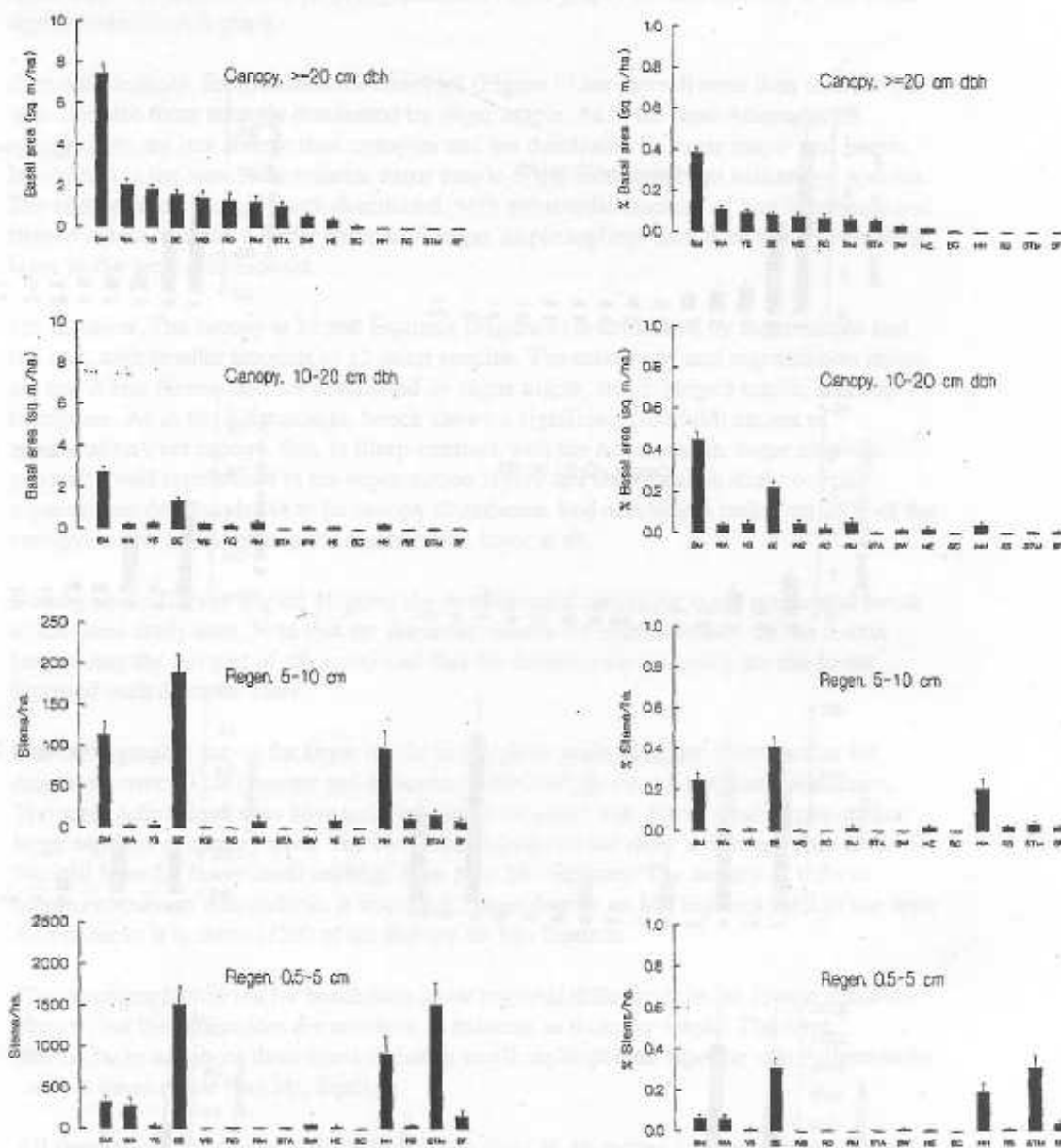
Figure 7. Composition of west Adirondack forests

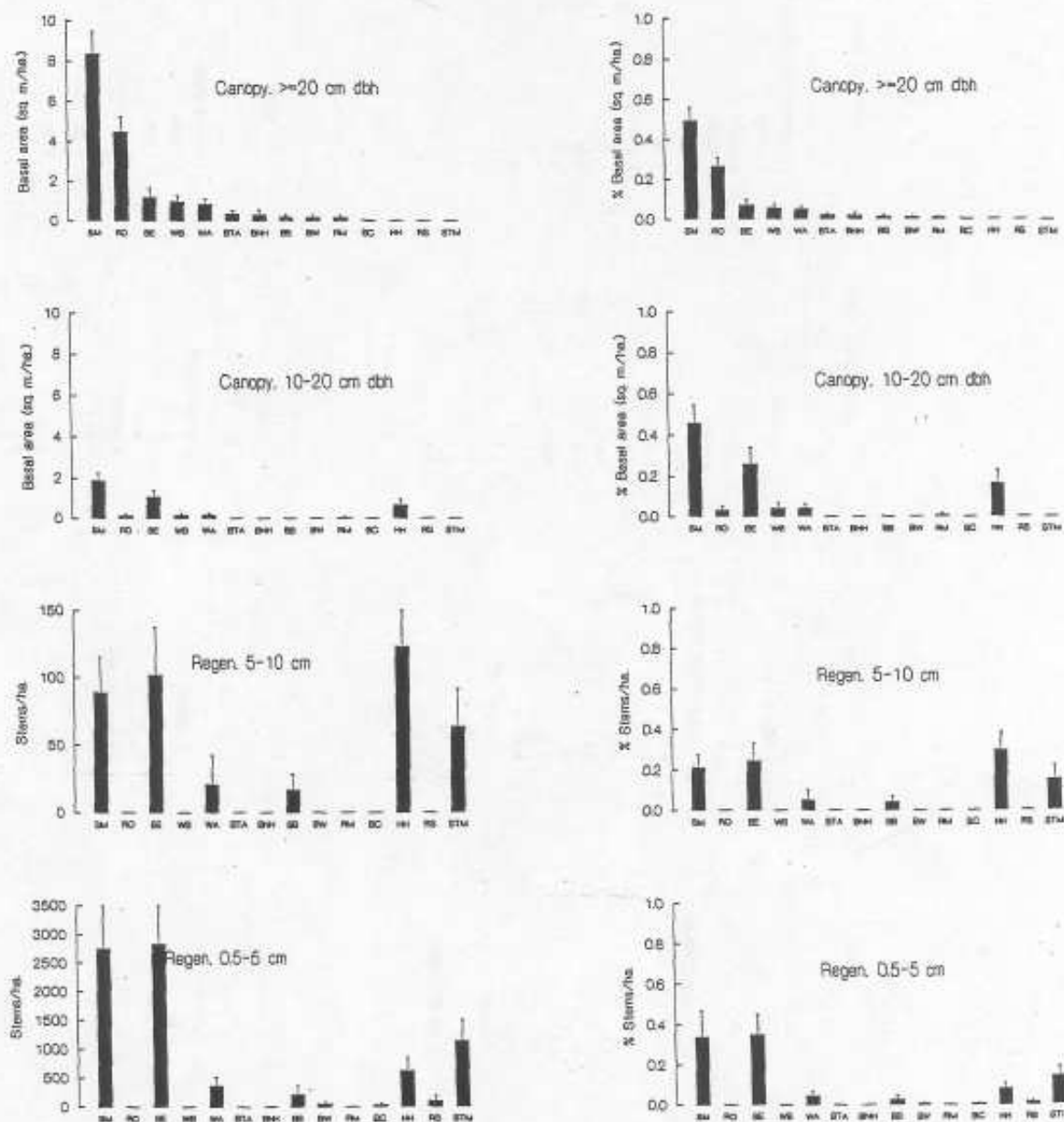Figure 8. Composition of east Adirondack forests

Figure 9. Composition of forests on Mt. Equinox

70% beech, with small but significant amounts of red spruce and striped maple. About 8% sugar maple is present in the large regeneration (third graph) but almost none in the small regeneration (fourth graph).

East Adirondacks East Adirondack canopies (Figure 8) are more diverse than those in the west but also more strongly dominated by sugar maple. As in the west Adirondacks, subcanopies are less diverse than canopies and are dominated by sugar maple and beech. In contrast to the west Adirondacks, sugar maple is the most important subcanopy species. The regeneration layer is beech-dominated, with substantial amounts of hop hornbearn and striped maple, and has a larger number of sugar maple saplings than does the regeneration layer in the west Adirondacks.

Mt. Equinox The canopy at Mount Equinox (Figure 9) is dominated by sugar maple and red oak, with smaller amounts of 12 other species. The subcanopy and regeneration layers are much less diverse and are dominated by sugar maple, beech, striped maple, and hop hombeam. As in the Adirondacks, beech shows a significant (fivefold) excess of regeneration over canopy. But, in sharp contrast with the Adirondacks, sugar maple is generally well represented in the regeneration layers and shows only a slight overall regeneration deficit relative to its canopy abundance. Red oak, which makes up 26% of the canopy, is not represented in the regeneration layer at all.

Demographic Curves Figure 10 gives the demographic curves for sugar maple and beech at the three study sites. Note that the diameter classes are spaced equally on the x-axis (expanding the left part of the scale) and that the numbers on the x-axis are the lower limits of each diameter class.

The demographic curves for sugar maple in the three study areas are quite similar for diameters over 10 cm (canopy and subcanopy) but diverge strongly at small diameters. The west Adirondack sites have a *demographic reversal*, with fewer small saplings than large saplings or canopy trees. The east Adirondacks do not show a demographic reversal but still have far fewer small saplings than does Mt. Equinox. The density of 0.5-cm maples in the east Adirondacks is about 1/25 their density on Mt. Equinox; and in the west Adirondacks it is about 1/250 of the density on Mt. Equinox.

The demographic curves for beech also show regional differences in the lowest diameter classes, but the differences are nowhere as extreme as those for maple. The west Adirondacks are about three times richer in small sapling beech than the east Adirondacks and 1.3 times richer than Mt. Equinox.

All three study areas have a dip at the 2.5-cm class in the curves for sugar maple (Figure 10). No similar dip occurs in the beech curves. As noted above (p. 9), the dip could be a real feature or an artifact of the way we have divided the size classes. If it is real, it could either be a transient feature resulting from a recent fluctuation in the numbers of seedlings or a permanent feature indicating that the average growth rate of the 2.5-cm class is higher than that of the 5-cm class, so the saplings race through the 2.5-cm class and pile up in 5-cm class. Either interpretation would be biologically interesting.
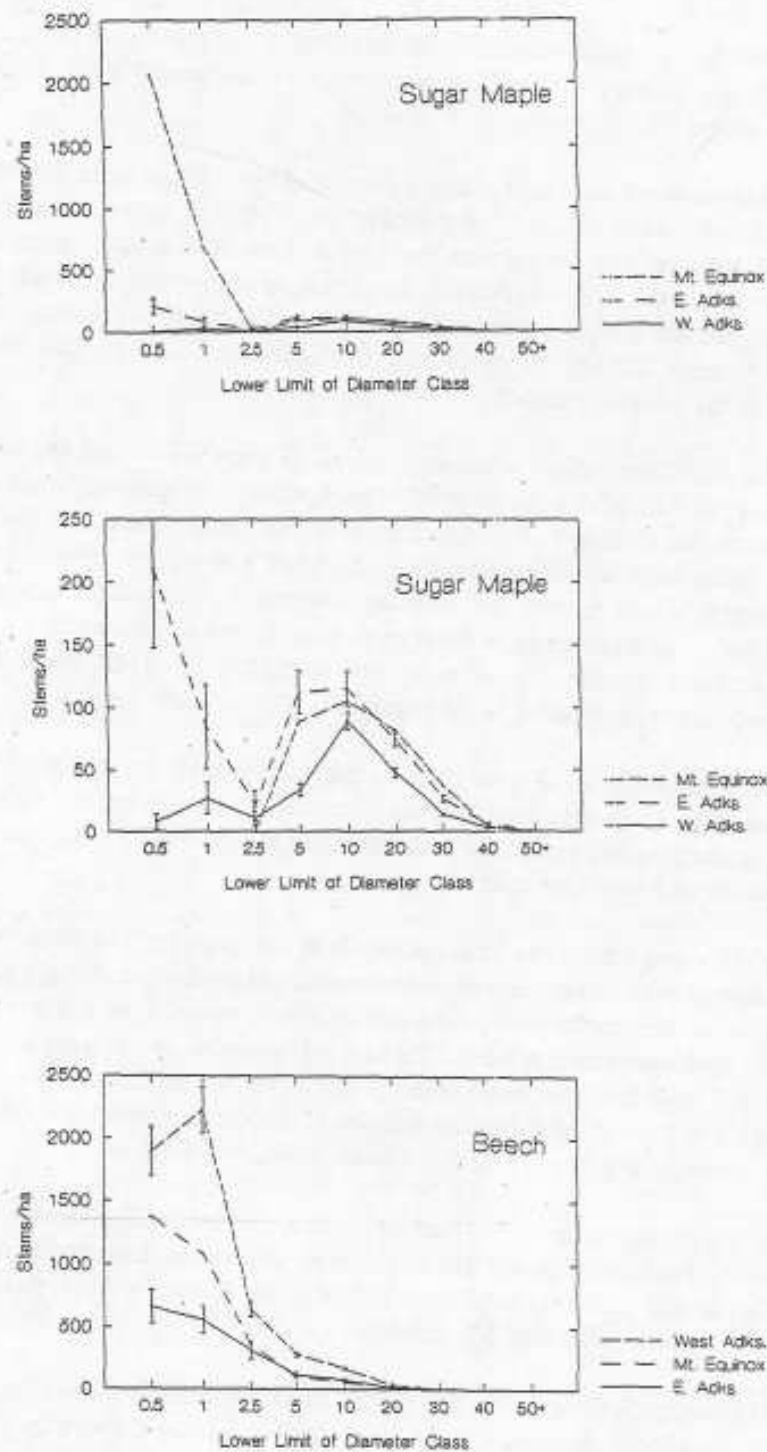
Figure 10. Demographic curves for sugar maple and beech. Top graph: demographic curves for sugar maple at the three study areas. Middle graph; same as top but with a l0x expansion of the Y- axis. 0.5-cm and 1-cm, values for Mt. Equinox are off-scale.

To test whether the dips at 2.5 cm are produced by the way we have grouped the diameters into size classes, we can rescale Figure 10 by dividing the densities size class by the width of the size class, producing graphs of stems per hectare per centimeter of diameter. Figure 11 shows that the dips persist when the graphs are rescaled in this way, suggesting that they are a real feature.
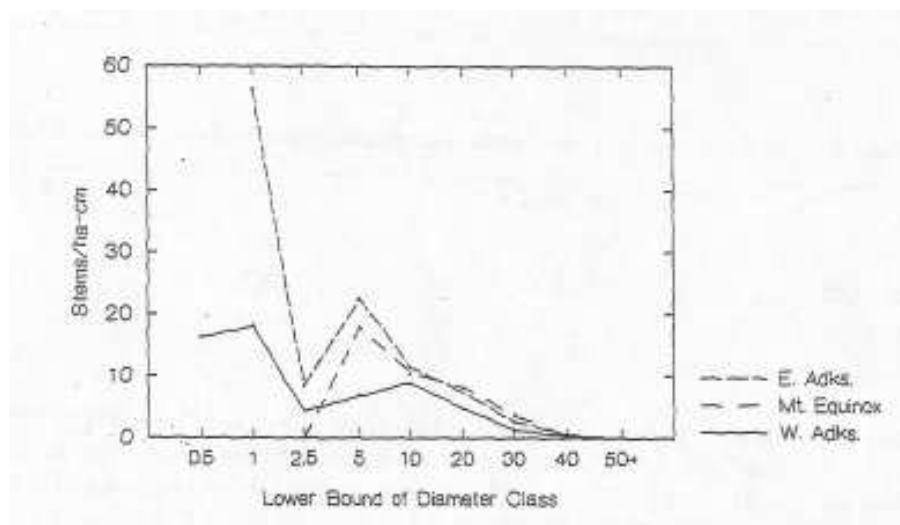
Figure 11. Density of sugar maple per centimeter of diameter. Y-values are estimated stems per hectare per 1-cm diameter increment.

Sapling Densities Table 5 gives the total densities of sugar maple and beech saplings in Layers 3 and 4. The low sugar maple densities in the west Adirondacks are striking. There is a sevenfold difference in the numbers of small sugar maple saplings (SM4) between east and west Adirondacks and a fifty-fold difference between Mt. Equinox and the west Adirondacks. Densities of large sugar maple saplings (SM3) vary about threefold; the east Adirondacks have significantly more large saplings than the west Adirondacks. Mt. Equinox is intermediate and, given the standard errors, not strongly distinguishable from either. The numbers of small beech saplings (B4) also differ about threefold, with high numbers in the west Adirondacks and Mt. Equinox and the lowest numbers in the east Adirondacks. Here again the variance is high, and the differences are not as strong as they look. The numbers of large beech saplings (B4) differ twofold; the west Adirondacks are highest, Mt. Equinox and the east Adirondacks comparable.

Table 6 compares the total sapling densities (Layers 3 + 4) from our study to the average densities for northern New York computed from the *Forest Statistics For New York* (Alerich & Drake, 1995). It also computes the ratio of beech saplings to sugar maple saplings (BSM ratio).

Table: 5. Densities of sugar maple & beech saplings in various forests by layer

	SM(4)		SM(3)		B(4)		B(3)	
West Adk.	46.0	(15.3)	34.2	(5.2)	4749	(358)	286.7	(20.0)
East Adk.	316.9	(73.9)	112.6	(16.9)	1507	(220)	189.2	(21.9)
Mt. Equinox	2440.5	(992.0)	63.6	(25.0)	3853	(1059)	147.4	(52.7

Data from this study, 1996-1997. Values are stems per hectare. SM(3) = sugar maples in Layer 3, B(3) = beech in Layer 3, etc. Standard errors are in parentheses.

Table: 6. Total sugar maple & beech sapling densities and BSM ratios in various forests

	SM(3+4)	B(3+4)	B(3+4)/SM(3+4)
West Adk.	80	5055	63.2
East Adk.	429	1696	4.0
Mt. Equinox	2504	4000	1.6
Northern N.Y.	2187	2142	0.97

Data from this study (Adirondacks, Mt. Equinox) and Alerich and Drake, 1995 (Northern New York). AU densities in stems per hectare. SM(3+4), B(344): total sugar maple and beech sapling densities, Layers 3 and 4. B(3+4)/SM(3+4)= ratio of total beech sapling density to total sugar maple sapling density (BSM ratio). See Section 4 for notes on the N.Y.S. data, and recall that their saplings are defined slightly more broadly than our Layers 3+4 combined, and so their sapling density should exceed our Layer 3+4 density if measured at an equivalent site.

Total densities of maple saplings in the Adirondacks are strikingly lower (five to twenty- seven times lower) than the northern New York average, while those of beech are slightly higher (0.8 to 2.4 times). BSM ratios are near unity for Mt. Equinox and northern New York as a whole but rise to four in the east Adirondacks; and 63 in the west Adirondacks.

Plot-to-Plot Variation in Sapling Density Figure 12 contains histograms showing the number and proportion of plots with different densities of sugar maple and beech. West Adirondack sugar maple reproduction is uniformly low: over 80% of the 294 samples had no sugar maples in Layer 3 and 96% had no sugar maples in Layer 4. In contrast, beech regeneration is not only higher than sugar maple regeneration on average but more variable. Over 10% of the plots had densities of 12,000 stems per hectare or more of sapling beech, while 30% of the plots had no beech regeneration at all,

Beech-to-Sugar-Maple Ratios for Different Size Classes Regeneration success often depends on which species is most abundant locally: a shade-tolerant species like sugar maple whose saplings are uncommon overall might persist in the forest if there were particular places where it was the most common sapling. Thus we need to examine both the average value of the BSM ratio and its plot-to-plot variance.
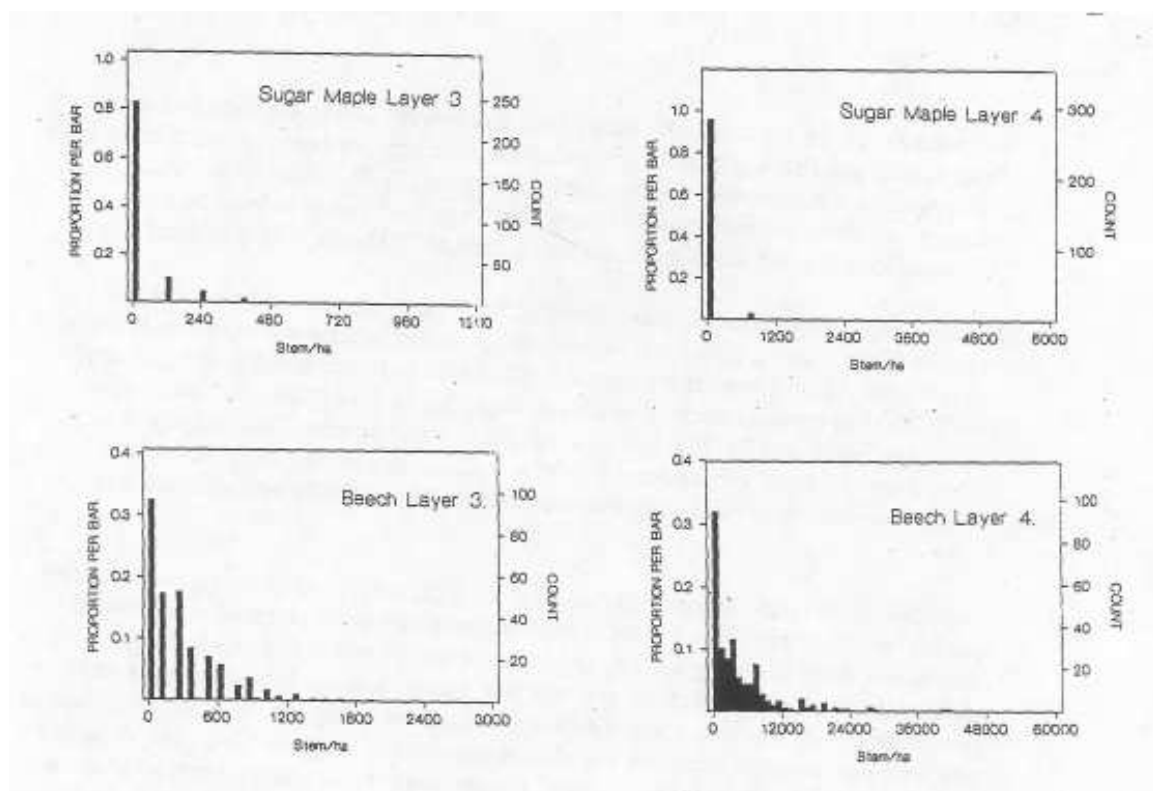
Figure 12. Histograms of sugar maple and beech sapling, densities in the west Adirondacks. Bars give the number of plots (and proportion of the 294 plots) with a given density of saplings.
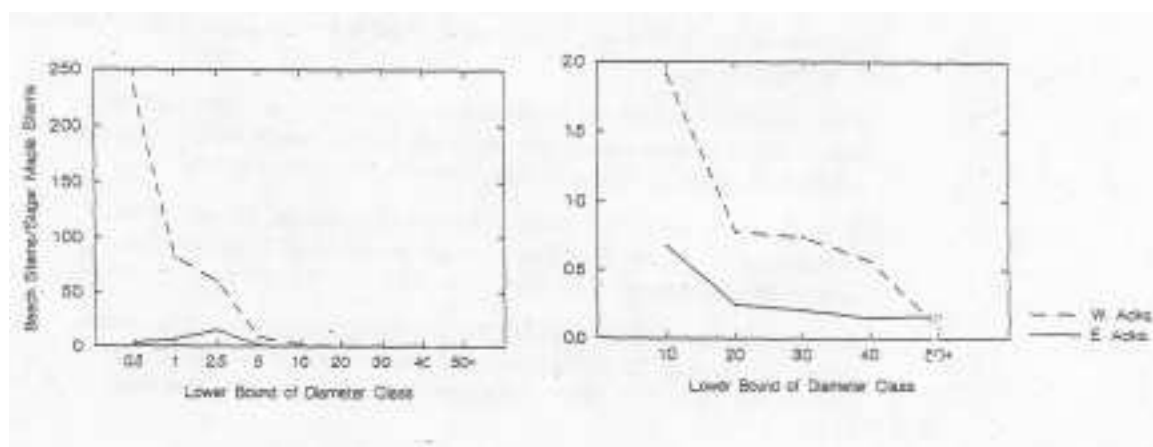

Figure 13. Beech-to-sugar maple ratios for the east and west Adirondacks. The right figure is an enlargement of the right-hand portion of the left.

As noted above, the average BSM ratios (Table 6) observed on Mt. Equinox and calculated from Alerich and Drake (1995) for northern New York are near one. The ratios in the East Adirondacks are higher but not enormously so (Figure 13). The ratios in the west Adirondacks differ dramatically from the regional averages and even from the east Adirondacks: in the 0.5 to 0.9 cm class there are about 230 beeches for every sugar maple.

Because sugar maple densities are uniformly low (Figure 12), there is little inter-plot variance in these ratios. Beech was numerically dominant at almost everywhere in the west Adirondacks: of the 294 plots we sampled, 263 (89%) had more beech than sugar maple, two (0.7%) had equal numbers of beech and sugar maple, four (1.8%) had more sugar maple than beech, and 25 (9%) had no seedlings of either species. This suggests that, unless there is a large compensating excess in the mortality rate of young beech, the canopy composition of the next forest generation will be radically different than it is today.

Correlations Between Densities Figure 14 plots sugar maple and beech sapling densities against canopy composition and each other. If canopies were depleted of mature sugar maples and the seed supply was limiting regeneration we would expect sugar maple sapling densities to depend on the abundance of canopy maples. If beech sprouts were suppressing sugar maple, we would expect the sugar maple sapling densities to increase as beech sapling densities increased. Our data shows neither. Sugar maple sapling densities are not correlated with either the amount of sugar maple in the canopy, or with the number of beech saplings in the plot with them. In contrast, beech regeneration shows a weak but significant relation to the number of beech in the canopy.

Productivity and Relative Abundance Table 7 gives the productivity and relative abundance of sugar maple and beech at the three sites. (See Section 6 for a discussion of these indices.) The principal results are that:

> The productivity and relative abundance of sugar maples in Layer 3 don't differ much at the three sites.

> The productivity and relative abundance of sugar maples in Layer 4 differ substantially: the west Adirondack values are three to six times below the east Adirondack values and 10 to 20 times below those for Mt. Equinox.

> Beech is two to seven times enriched relative to its canopy abundance in the understories of all three sites. The variances are large and there are no strong differences between any of the three sites or between Layers 3 and 4 at any given site.

> Beech productivities differ significantly between the sites, but the maximum differences are only 2.2-fold and do not show a consistent geographic pattern: Mt. Equinox has the highest Layer 4 productivity and lowest Layer 3 productivity of any site.
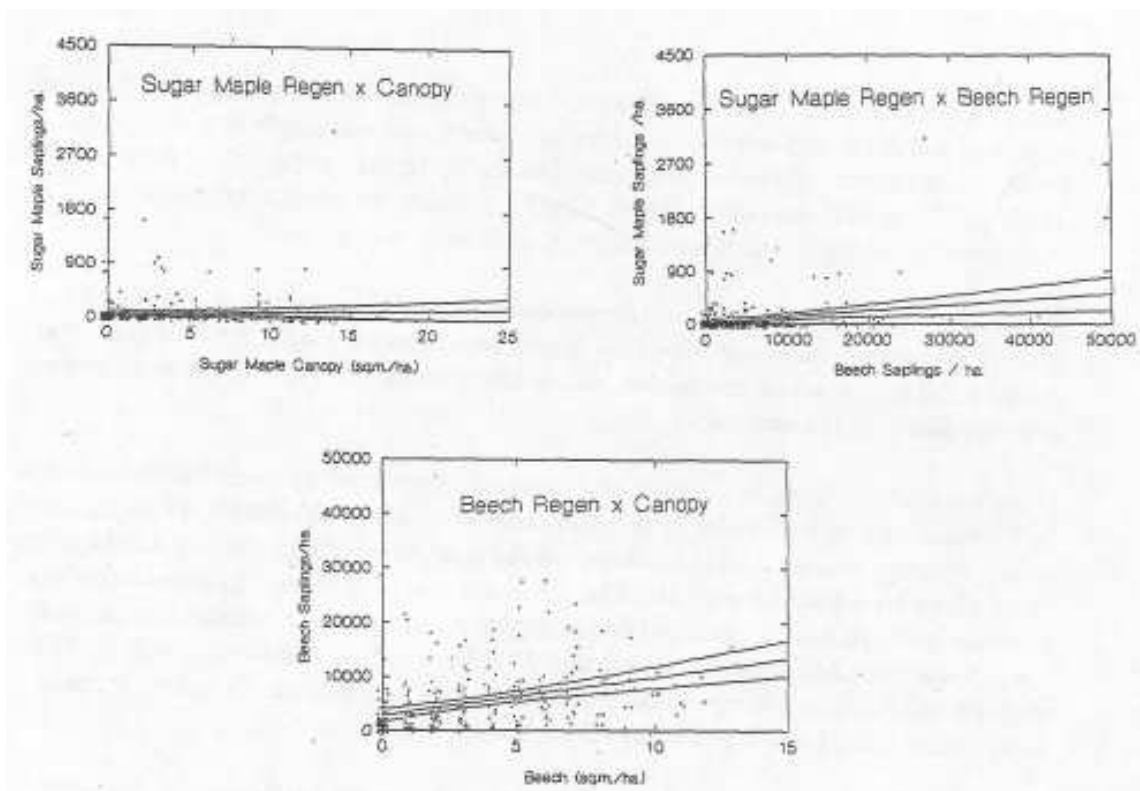
Figure 14. Correlations between sapling densities. Values are 'jittered' (perturbed slightly) before plotting to show individual data points. The straight line is the best linear fit, the curved lines the
95% confidence interval for that fit. Only the third graph shows a significant (slope clear different from 0) correlation.

Table 7. Relative Abundance and Productivity of Sugar Maple and Beech at Three Study Areas

Relative Abundance

	SM (4)		SM (3)		B (4)		B (3)	
W. Adk.	0.06	(0.03)	0.34	(0.03)	3.7	(0.3)	7.2	(3.4)
E. Adk	0.41	(0.23)	0.87	(0.17)	5.1	(1.9)	4.5	(0.6)
Mt. Eq	0.67	(0.23)	0.62	(0.23)	3.5	(1.1)	2.2	(1.1)

Relative Productivity

	SM (4)		SM (3)		B (4)		B (3)	
W. Adk.	17.4	(8.3)	6.2	(1.3)	1048	(111)	72.0	(8.5)
E. Adk	52.6	(17.4)	14.1	(2.6)	648	(113)	77.9	(13.0)
Mt. Eq	353.3	(198.0)	8.4	(3.9)	1461	(541)	35.6	(16.7)

Data from this study, 1996-7. Abbreviations as in Table 6. Productivity = density stenis/ha of the given species in a given layer per square meter of canopy basal area of that species. Relative abundance = (stems of that species in layer / all stems in layer) / (basal area of that species in canopy/all canopy basal area). Standard errors are in parentheses.

The productivity and relative abundance data corroborate the data on absolute densities (Table 5) and suggest that the unusual ratios of beech to sugar maple in Adirondacks understories are not caused by an excess of beech but rather by a deficit of sugar maple saplings. The deficit is most evident in Layer 4. Deficits are present throughout the Adirondacks, but far worse in the west Adirondacks than in the east.

Summary: Adirondack hardwood forests have fairly diverse canopies, but much less diverse understories and regeneration layers. Beech, sugar maple, and red spruce are found in all layers, while red maple, yellow birch, black cheF7Y, red oak and hemlock are only found in the canopy.

Densities and demographic curves of canopy and large sapling sugar maples are similar in Vermont and on both sides of the Adirondacks. Average densities of small sugar maple saplings are 30 to 50 times lower in the west Adirondacks than on Mt. Equinox or in northern New York as a whole. The extremely low west Adirondack small sapling densities are reflected in reversed demographic curves, relative abundances six to ten times lower than Mt. Equinox or average New York values, productivities 20 to 25 lower than Mt. Equinox or average New York values, and beech-to-maple ratios 60 times higher than Mt. Equinox or average New York values.

Sugar maple sapling densities in the west Adirondacks are uniformly low, with little variance. Beech was more numerous than sugar maple at 89% of the plots sampled, while sugar maple exceeded beech at only 1.4% of the plots sampled. The high absolute densities of beech and substantial excesses of beech over sugar maple make it likely that beech will dominate almost all the hardwood regeneration in small gaps.

Sugar maple regeneration in the east Adirondacks is intermediate between that in the west Adirondacks and that outside the Adirondack Park. Demographic curves are flat, with only a slight excess of saplings over canopy. Sapling densities are five to seven times lower than the corresponding regional values and productivity about five to seven times below regional values. Relative abundances and beech-to-maple ratios are close to regional values.

Demographic curves for beech in both the west and east Adirondacks generally resemble those for Vermont and do not show large excesses of beech of any size. Absolute and relative abundances of beech saplings vary by factors of 1.5 to 3 between the study sites, with the west Adirondacks tending to have more beech and more dominance of beech than other sites. Compared to the great variation in sugar maple demographics, the range over which the beech demographics vary is not great.

Since all indices of sapling sugar maple abundance vary much more between the sites than those for beech abundance, the high west Adirondack beech-to-sugar maple ratios are largely the result of low sugar maple abundance rather than high beech abundance.

10. Quantitative Results II: The Effects of Forest History on Canopy Composition and Regeneration

If the regeneration deficits are in some way related to forest history - perhaps because some species regenerate well after heavy cutting or because high-grading has depleted seed trees of certain species from the canopies - then the demographic curves and canopy composition should depend on the forest history.

When the west Adirondack data is divided by land-use history (Figures , 15-19 Tables 8-9), the three types of sites appear to have similar forests with only moderate differences in canopy composition and no major differences in regeneration deficits.

Table 8. Canopy Basal Areas in Three West Adirondack Forest Types

	Tot. Basal A. (sq.m./ha)	Sugar M. (sq.mJha.)	Beech (sq.nVha.)
All (n=294)	22.6 (0.4)	5.9 (0.35)	6.2 (0.3)
Old-growth (n=100)	26.5 (0.5)	5.1 (0.6)	6.0 (0.4)
Ex-Commercial (n=46)	17.5 (0.6)	6.0 (0.5)	7.2 (0.5)
Commercial (n=146)	21.7 (0.5)	6.4 (0.55)	6.0 (0.4)

Data from this study, 1996-1997. Standard errors are in parentheses.

Basal Areas The canopy basal areas of sugar maple and beech in the three forest types are similar (Table 8); total canopy basal areas are about 20% greater in the old-growth than in the commercial stands and about 20% less in the ex-commercial stands (where many large beeches have recently died) than in the commercial.

Canopy composition The overall canopy composition (Figure 15) is broadly similar in the three types. The old-growth has much more yellow birch and significantly more spruce than the commercial and ex-commercial lands. Both these species were heavily cut on commercial lands in the first half of this century. The commercial forests have more red maple and cherry (both shade-intolerant species that do well in openings) than the others. The ex-commercial forests, which were probably high-graded in the first half of this century, have the largest amounts of beech. All these differences are consistent with the different histories.

Demographic Curves Figures 16 and 16a show the diameter distributions of the major species in more detail. Note the differences in vertical scale between the figures. Noteworthy features are:

The general absence of hardwood regeneration other than beech.

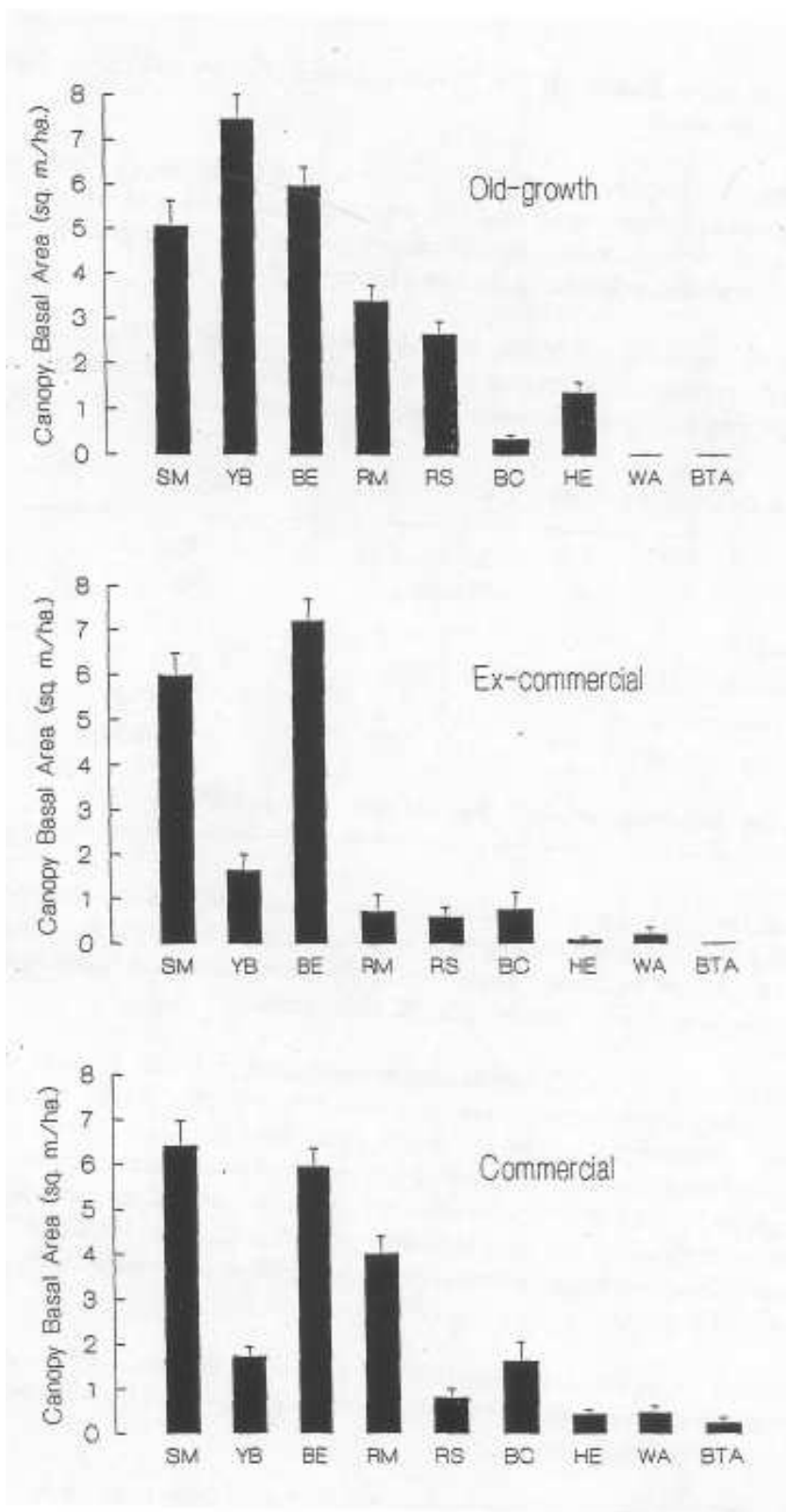The significant amount of red spruce regeneration in the old-growth.

Figure 15. Canopy composition of west Adirondack forests with three different histories. Y-values are total basal area of trees 10 cm dbh and over.

The abundance of yellow birch in the old-growth canopy and preponderance of large trees in the diameter distribution.

The concentration of canopy black cherry in the commercial lands.

The figures suggest that the overall demographics of the three types of lands are more similar than different. Beech reproduction is highest in the ex-commercial woods and lowest in the old-growth. But despite these differences, young beech are abundant throughout and dominate all other regeneration. Red spruce, though not abundant, is reproducing well.[14] The old-growth stands have more canopy yellow birch and red spruce than do the commercial and ex-commercial lands, and there is a distinct suggestion that the larger canopy yellow birches in the old-growth represent a maturing cohort that is not being, replaced.

Figure 17 shows the demographic curves for sugar maple in the three land types. The three curves are similar overall. The density of Layer 4 maples is apparently high in the ex-commercial forests, but the variance is also high and the difference may not mean much. All three types of forests show reversed demographic curves with fewer small saplings than large.

Figure 18 shows the demographic curves for beech in the three land types. The curves for canopy beech are the same in all three forest types. The sapling curves differ significantly. The ex-commercial stands have the lowest density of 10 cm beech and the greatest density of 0.5-cm and 1-cm beech. This may well reflect differences in the incidence and timing of the beech bark disease in the three areas.

Table: 9. Sugar Maple & Beech Sapling Densities in West Adirondack Forests of Different Histories

	SM(3)	SM(4)	B(3)	B(4)
Old-growth	30.5 (8.3)	15.9 (11.2)	350.0 (34.5)	2498 (316)
Ex-commercial	59.8 (.15.4)	129.9 (70.9)	475.5 (55.0)	9067(1069)
Commercial	28.1 (7.2)	38.4 (17.9)	179.3 (22.1)	4884 (535)

All densities are stems per hectare. Data from this study, 1996-1997. Abbreviations as in Table 6. Standard errors are in parentheses.

Sapling Densities Table 9 gives the densities of sapling sugar maples and beech in the three land types. The ex-commercial lands, which have many recent gaps, have significantly higher amounts of beech and marginally higher amounts of sugar maples. Otherwise there are no consistent differences between the three forests. Except for the numbers of small sugar maples (which have large variances and aren't reliable), the range

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[14] Relative to its canopy abundance, red spruce has a productivity of 432 stems in Layers 344 per square meter of canopy basal area, 39% of the corresponding productivity of beech and 18 times higher than sugar maple. Spruce regeneration is better in the old-growth than in the commercial stands, but this may simply reflect the greater proportion of mature red spruces in the old-growth canopies.
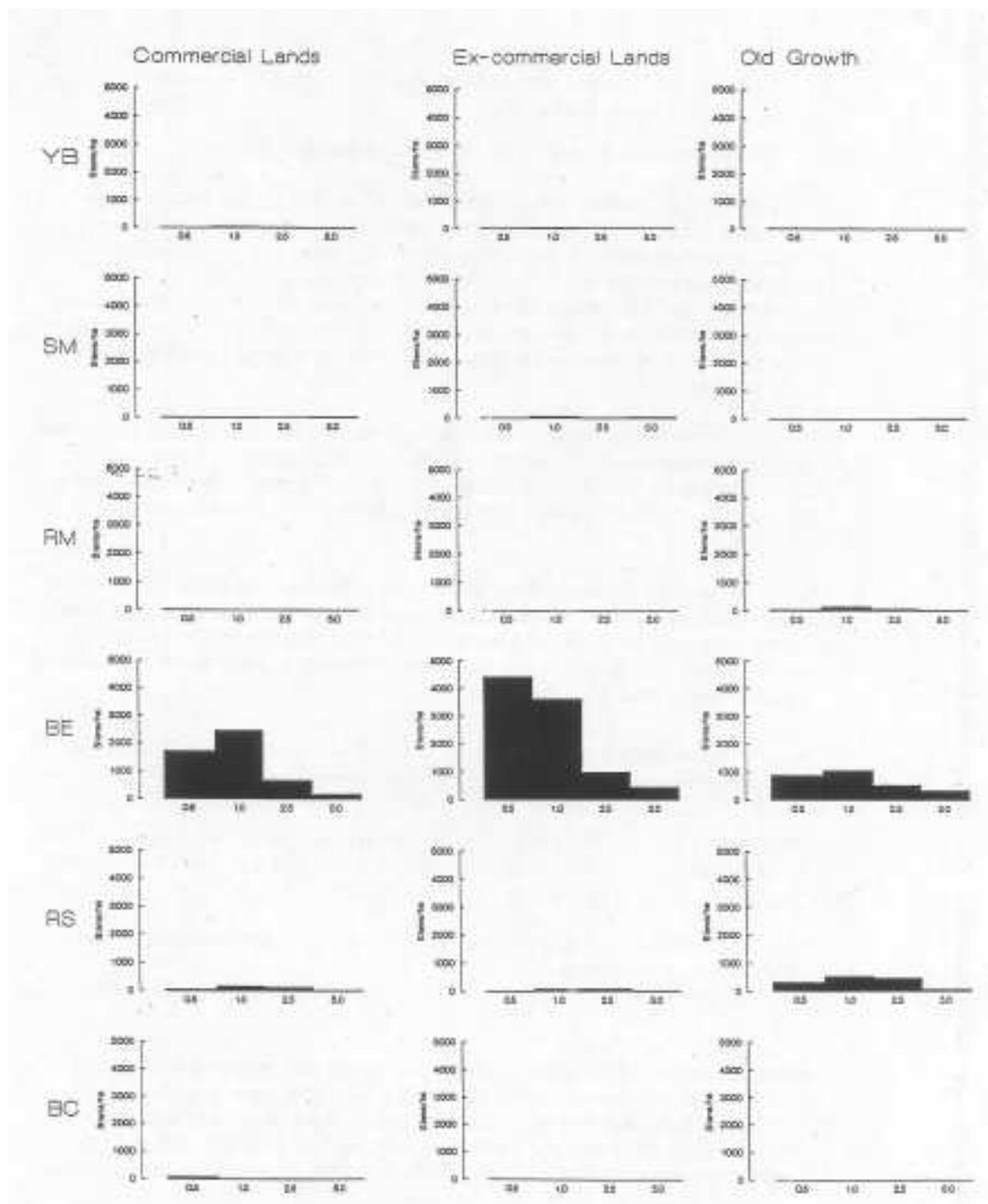
Figure 16. Demographics of saplings in west Adirondack forests of three different histories. Each row of graphs is one species; for abbreviations see Table 4, p. 21. X-values are diameter classes in centimeters, measured 20 cm above the base.
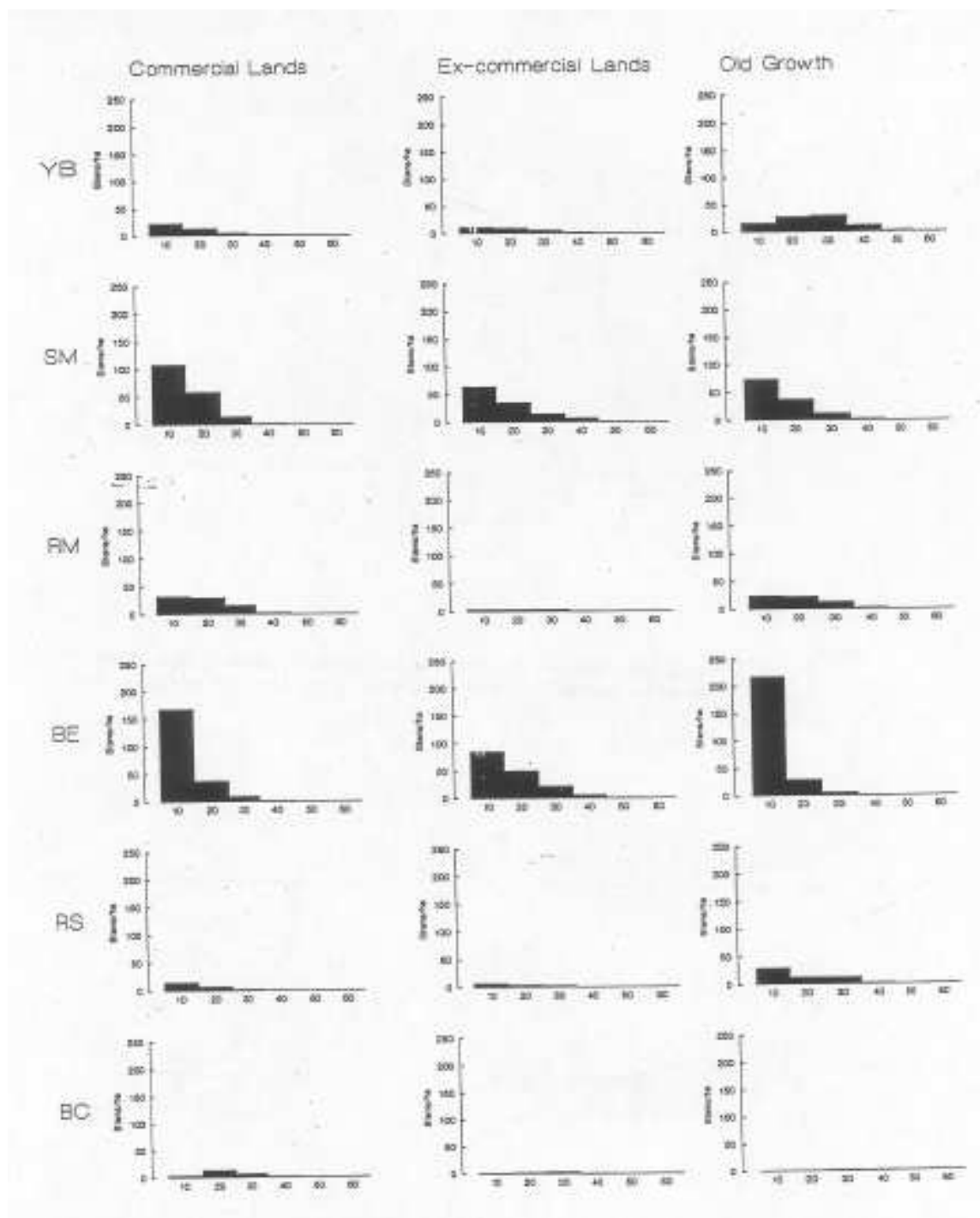
Figure 16a. Demographics of canopy and subcanopy trees in west Adirondack forests of three different histories. Each row of graphs is one species; for abbreviations see Table 4, p. 21. X-values are diameter classes in centimeters, measured at breast height.

Figure 17. Demographic curves for sugar maple in west Adirondack forests of three different histories. Error bars give standard errors. Sapling maples are scarcer than larger trees in all three forests.
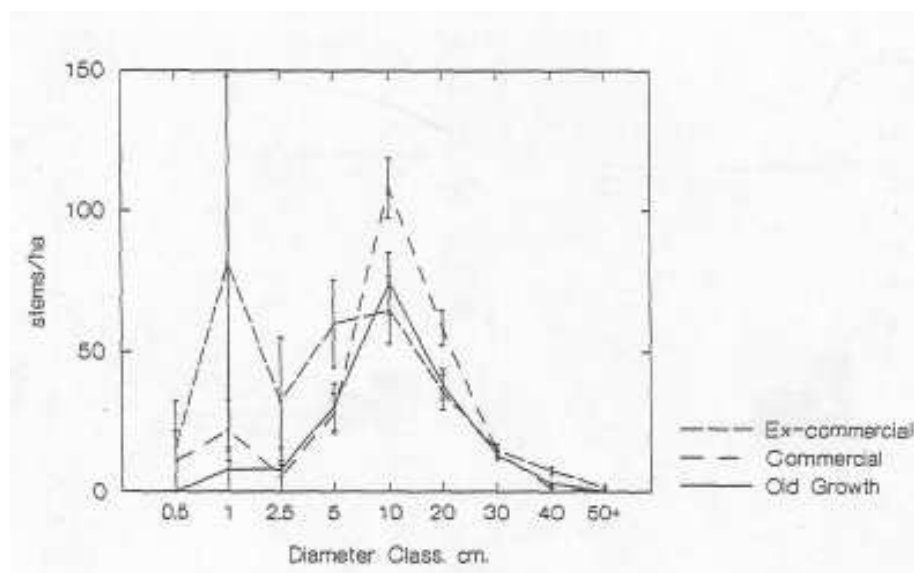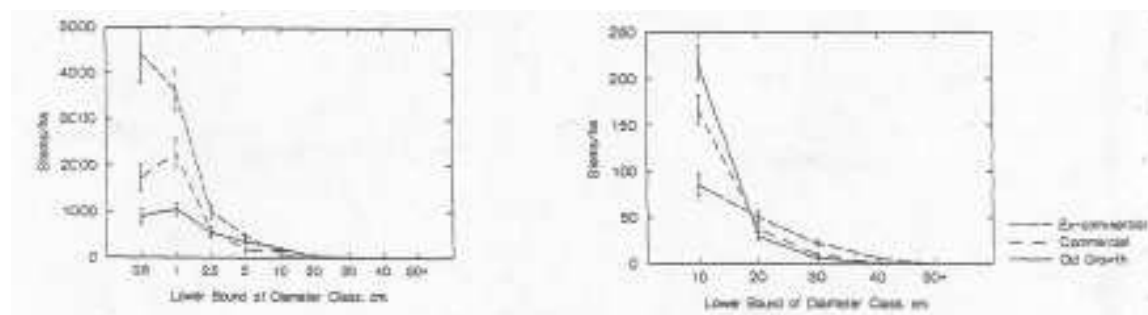

Figure 18. Demographic curves for beech in west Adirondack forests of three different histories. Error bars bars give standard errors. The right figure is an enlargement of the right-hand portion of the left. Note that the Y-axis scale of the left figure is 33 times greater than that of Figure 17.

of variation in all these values is two to three times, an order of magnitude less than the range of variation in sapling densities between Adirondack and non-Adirondack sites (Tables 5,6).

Summary: Although there are a number of significant differences between the three forest types (more spruce and yellow birch in old-growth, higher basal area in commercial, lowest beech regeneration in old-growth), the overall composition of the three types offorest is generally similar. The regeneration in all of them is heavily dominated by beech. In all three forests there are fewer small sugar maple saplings than large sugar maple saplings or canopy sugar maples. There are no significant differences in sugar maple sapling densities between old-growth and commercial lands and at most slight differences between the ex-commercial lands and the others.

11. Results III: Miscellaneous Qualitative Observations on West Adirondack Sugar Maple Regeneration

Here we mention some qualitative observations on the local success and failure of regeneration.

Regeneration at the Edges of Forests In contrast to their rarity in forest interiors, sugar maple, red maple, and yellow birch saplings are locally plentiful at forest edges, especially near roads, permanent clearings, and shores. The common features of these areas seem to be that a) they have moderately high levels of light, b) the high light levels are semi-permanent, and c) some factor (human use, local absence of adult beech, edges of a waterbody) limits competition from beech sprouts and shrubs. This *edge regeneration* is truly limited to edges; it is not found in open gaps (where there is often intense competition from sprouts and raspberries) and rarely extends even a few meters into the forest interior.

Hardwood Regeneration in Small Gaps The situation in gaps is surprisingly different from that along edges. Our observations of many small gaps suggest that none of the hardwoods except beech is doing any better in small gaps than it is in the forest understory.

Seedling Banks As noted in Section 3, many sugar maple forests elsewhere have a more- or-less permanent bank of small seedlings, which may cover 5% or more of the forest floor. Such seedling banks were common in rich woods in Vermont but uncommon in the Adirondacks. They occurred at one or more sample points at about a third of the sites we sampled in the east Adirondacks but were not seen at all in the west Adirondacks.

Local Pockets of Successful Maple Regeneration Thus far only two areas have been found in the west Adirondacks where sugar maples are reproducing plentifully away from an forest edge. The first was a young thicket of perhaps 1 hectare in commercial forests near Blue Pond. The second was an area of continuous canopy woods of at least 10 hectares in the Forest Preserve south of Marble Mt. Here beech was largely absent, and small sugar maples and black cherries of all sizes were plentiful. Neither area was in one of our study sites and so neither is represented in the data presented here.[15]

Effects of Deer Signs of browsing were seen throughout. Intensely browsed areas with abundant scat were found in a few places, mostly near camps where deer were fed or near softwood stands that may have been used as wintering areas. Most of our study sites were much less intensely browsed and had relatively little scat.

Places Without Any Regeneration Small-scale failures of regeneration in patches of 0. 1 hectare or so occur throughout the Adirondacks; about 10% of our 2-meter radius plots had no saplings at all. Such failures most often occur when a recent gap has filled with a dense cohort of understory young beech or striped maple, and consequently the forest floor is quite dark.

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[15] In 1997 we located 5 other areas in the west Adirondacks where sugar maple regeneration was locally successful. Five had indicator species suggesting calcareous soil.

In some areas in the northwest Adirondacks there are larger areas, usually dominated by grasses and ferns, in which there is no hardwood regeneration at all. These *fern-glades* range from a few tenths of a hectare to five hectares or more in size. They may be completely open or have a hardwood or hardwood-spruce canopy of moderate density. Some have no tree regeneration at all, while others have substantial numbers of red spruce saplings. Most of them are on light sandy soils in areas that were heavily cut early in this century and had an extensive network of logging railroads.[16] Many have been open as long as anyone can remember and are widely believed to have originated from fires in former cuts. The common dominants are two patch-forming ferns (hayscented fern, New York fern), the grass *Brachyeletrurn erectum*, and several sedges, most commonly *Carex debilis*. Deer graze heavily in these glades, and it seems quite likely that tree regeneration is being suppressed by some combination of grazing, competition, and allelopathy.

These glades are currently limited to commercial lands and are likely to be artifacts of site history rather than a regular feature of Adirondack biology. Grasses and patch-forming fems are relatively rare elsewhere in west Adirondack forests and can not be a regional cause of regeneration failure. Clump-forming ferns (particularly evergreen woodfern) are common throughout the Adirondacks, but there appear to be no significant differences in regeneration between plots with abundant clump-forming ferns and plots with none. Furthermore, as was the case with beech, clump-forming ferns are also common at sites in Vermont and the east Adirondacks where there is abundant sugar maple regeneration.

Summary: In many places in the west Adirondacks sugar maples are regenerating locally on roads and edges where there are higher light levels and less competition but not in natural or artificial gaps. In addition there appear to be a few areas, all small where forest-interior regeneration is abundant. As yet we do not know how these areas differ from the rest of the forest. Many individual plots showed no regeneration of any species. These were usually in deep shade, and often had a dense subcanopy of young beech. Larger, well-lit, glade-like forests occur in the northwest part of the study area, most commonly near old logging-railroad rights-of-way in the Grass River Basin. They lack hardwood regeneration and have dense ground layers of grass and fern. They may have originated in fires and are probably maintained by some combination of competition, allelopathy, and browsing.

Signs of deer browsing are common throughout all the study areas but only abundant in a few places.

12. Discussion 1: Origin and Stability of Regeneration Deficits

Relative to the adjacent regions, the west Adirondacks lack small sugar maples and have anomalous demographic curves. In this section we consider two questions: a) whether these features have existed for a long time and so are in some sense normal and b) whether they will ultimately lead to significant changes in canopy composition. The first is a question of when and how reproductive deficits have originated and the second a question about whether the distinctive reverse-demographic curves that result from them are stable or unstable.[17]

General Comments on Regeneration Deficits A regeneration deficit is essentially a hole in a demographic curve - a size-class that is smaller than we think it should be. A *stable* hole is one that just stays where it is and does not affect other size classes. An *unstable* hole is one that, in time, propagates to the right and leads to holes in the size classes adjacent it in the demographic curve.

> Some straight-forward reasoning about the dynamics of size-classes (Appendix 3) leads to three useful principles:

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[16] The rail network, the North Tram, was built by the Emporium Lumber Company. It connected Cranberry Lake and Claire, and totaled about 100 miles of track.

[17] Note that proving that sugar maples aren't reproducing inside Adirondacks forests is, of course, not the same as proving that they are not reproducing in the Adirondacks at all. It is possible that sugar maples have never reproduced in forest interiors in the Adirondacks (even though they apparently do so freely everywhere else), and that Adirondack regeneration has always been limited to edges or gaps.

Holes in demographic curves can be generated either by a) a decrease in the number of plants entering a size class per unit time, b) an increase in the mortality rate for plants in that class, or c) an increase in the average growth rate (and hence a decrease in the average residence time) for that size class.

Holes caused by a) or b) are not stable: they will move to the right and the demographic curve will change until a stable curve results. The stable curve that eventually results may have a step, but will not have a hole.

Holes caused by c) are stable and will not cause progressive changes in the demographic curve.

These principles suggest several possible answers to our question about the origin and stability of Adirondack regeneration deficits.

a) *Naturally Episodic Reproduction* The deficits could result from natural long-term fluctuations in reproductive success (seed production or seedling or sapling mortality). Such fluctuations would create unstable holes that would eventually affect the canopy.

b) *Race-Across-the-Gaps Strategy* The deficits could result from some natural mechanism that accelerated the average growth rates of small saplings relative to those of larger saplings. This would create an odd but stable demographic curve that would not propagate to the right and would not affect the canopy.

c) *Anomalous Recent Reproductive Failure* The deficits could result from a recent decrease in seed production or increase in seedling mortality. This would create an abnormal (historically novel) deficit that would create unstable holes that would eventually change the canopy.

All three possibilities are biologically plausible and may apply to some species in some parts of the Adirondacks. Only c) seems consistent with our observations that sugar maples are uniformly abundant in west Adirondack forest canopies and uniformly absent from forest understories, regardless of forest history.

Episodic Reproduction Intermittent reproduction is well known and biologically plausible. Successional species may reproduce episodically following rare disturbances like windstorms or fires; range-limit species may require climatic conditions that are only occasionally available. Two common demographic features of episodic reproducers are 'senescent' canopies with more large canopy trees than small, and canopy and understory abundances that vary greatly from place to place and depend strongly on stand history.

Yellow birch, which seems to require large gaps with substantial amounts of soil disturbance, is clearly an early successional species that is an episodic reproducer. So is white pine, which rarely reproduces in the Adirondacks at present and is strongly associated with old fires. Red maple and black cherry, early or mid-succession species that established after fires and heavy cuts early in this century, may be episodic but the case is less clear. Both red maple and black cherry have substantial numbers of 10 to 20 cm canopy trees, which suggests at least limited small-gap reproduction in the recent past, rather than episodic reproduction at long intervals.

Sugar maple is almost certainly not an episodic reproducer. The critical evidence is that:

It does not have a senescent canopy size distribution and in fact has substantial populations of subcanopy and understory trees (Figure 15).

It is uniformly represented in canopies of lands with different histories (Tables 5, 6).

It has been shown to reproduce fairly continuously in Adirondack old-growth.

And it has never been shown to reproduce episodically anywhere else.

Race-across-the-gaps Strategy If all sugar maples grow substantially faster in a certain size class *i* than they do in adjacent size classes, the average time they spend in that size class will be smaller and the demographic curve will have a stable hole. Such a *size-dependent growth rate* could be caused either by a genetically programmed growth increase, or, somewhat paradoxically, by heavy mortality that was restricted to a particular size class. The first seems unlikely, both because growth rates need to respond flexibly to the availability of resources and because a programmed growth spurt has never been noticed, despite many studies of sapling growth rates.

A mortality-controlled growth rate is more plausible. From the arguments in Section 4, at any given moment each size class contains fast-growing maples in gaps and slow growing maples in shade. If the mortality in class *i* is higher than in adjacent classes, this will tend to eliminate the slow-growing saplings of that class, either because the slower growing ones have fewer reserves to deal with disease and herbivory, or because they spend longer in a high-risk class. With the slow-growing saplings preferentially eliminated, the average growth rate for that size class will be greater than for adjacent size classes, and there will be a stable hole. Thus a strongly size-dependent mortality curve biased against slow- growing or shaded saplings could produce a size-dependent growth rate and a reversed but stable demographic curve.

I call this a race-across-the-gaps (RAG) model because the only way a sapling has much chance of surviving the high mortality size class is to grow fast and the only place it can do this is in a gap. The above argument is really a complicated way of stating a simple possibility: if shade-tolerance is size-dependent, then most of the seedlings of the intolerant size class will be in gaps, and our demographic curves for forest-interior plants will have holes.

While theoretically possible, the RAG hypothesis has enough contrived, not to say bizarre, features to warrant our suspicions. First, to account for reversed demographic curves, the sapling mortality rates have to be size-dependent enough to eliminate almost any sapling under 5-7 cm growing in the shade. In effect, sugar maples must be strongly shade-tolerant down to some diameter and strongly shade-intolerant below that diameter. Second, to account for uniformly low sapling densities in different forest types, the elimination of saplings in the shade has to function at uniform efficiency in landscapes with different histories and rates of gap formation. And third, if small sugar maple saplings really circumvent high shade mortality by growing in gaps, they will need some mechanism to out-compete the larger and more numerous beech saplings they will inevitably meet there.

The RAG model makes a number of testable predictions. If small sugar maples are rewarded for growing, in gaps, we should observe them there. Further, since the young maples in a gap don't die instantly when the gap closes, a few will persist in recently closed gaps. This should be reflected, at the very least, by a higher variance of sapling densities in landscapes with more recent gaps. And finally, since sugar maples will only succeed in gaps when the gaps are not preempted by beech, the beech-sugar maple ratio be low.

Our data are simply not consistent with these predictions. We saw almost no sugar maple saplings in gaps, even though we examined many recent gaps and sampled many partial and recently-closed ones. Variances of sapling densities were uniformly low in all landscapes, regardless of the rate of gap formation. And finally, ESM ratios were very high: in the west Adirondacks; there are six beech saplings over 5 cm for every sapling sugar maple under 5 cm. With these kinds of inequities in both density and size, it seems extremely unlikely that small sugar maple saplings are in fact behaving as a shade- intolerant species and colonizing gaps successfully.

Anomalous Regeneration Failure A recent, widespread regeneration failure, probably resulting from some change in environment, would be unusual but not implausible. In particular, it is consistent with what we know about the relations between acid rain, nutrient depletion, and the mortality of seedlings under stress (Section 14). Furthermore, the observed facts about the regeneration deficits in sugar maple -- that they are widespread, independent of site history, most intense on nutrient-poor soils, and affect mostly small saplings - are consistent with the hypothesis that an environmental stress has caused recent decline in the sugar maple seed output or a recent increase in seedling or small sapling mortality.

The clearest way to prove the regeneration failure hypothesis would be to show that Adirondack sugar maples formerly regenerated more prolifically in forest interiors and gaps than they do now. Thus far we have not found any quantitative data that clearly support or refute this. An interesting qualitative observation comes from Gifford Pinchot, who said in the 1890's that in Nehasne Park *The hard maple reproduces prolifically and is tolerant of heavy shade both in youth and later life. When the hardwood forest is thinned dense thickets of hard maple come up, often to the exclusion of other species.* In the 100 old-growth plots we examined in the Five Ponds Wilderness, just west of Nehasne Park, we found a total of two sugar maple saplings between 0.5 and 5 cm basal diameter.

The only quantitative historical data we have found thus far comes from a thesis by John Roman, who sampled 70 old-growth plots the Five Ponds Wilderness in the middle 1970's. He tallied saplings that were at least breast height and less than 10.2 cm dbh in a 50 square-meter section of each plot. Thirty of his plots had over three square-meters per hectare basal area of sugar maple and are comparable to our Five Ponds plots. Table 7 compares our old-growth data to his. It assumes that his sapling class corresponds to our combined 1-cm, 2.5-cm, and 5-cm classes,

Roman's work was done before the beech-bark disease had become acute and used deliberately selected plots thought to exemplify the major old-growth forest types. Perhaps for this reason, his plots have substantially larger canopy basal areas of both beech and sugar maple than ours. Overall, our beech sapling density and productivity are about two times his, our sugar maple sapling density a fifth of his, and our sugar maple productivity about a third of his. The data suggest that a change may have taken place, but, given his small sample size and deliberate selection of sample points, are not fully convincing.

Table 10. Canopy Abundances and Productivities of Maple and Beech in the Five Ponds Wilderness

	Canopy Basal Area (Sq. m. / ha.)	Regeneration Density (Stems / ha.)	Regeneration Productivity (Stems / sq. m.)
Beech			
Roman	10.8	1662	153.9 (23.3)
This Study	6.0	2346	460.5 (97.9)
Sugar Maple			
Roman	10.5	211	20.1 (6.3)
This Study	5.1	40	7.8 (2.8)

Data from Roman, 1980, based on 30 plots taken ca. 1975 with basal areas of sugar maple over 3 sq. m./ha. Data from this study based on 100 plots taken in 1996. Romans regeneration data includes all stems at least 1.6 m high and under 10.5 cm dbh. Our regeneration data includes all stems 1 cm basal diameter to 9.9 cm dbh. Productivity (stems per hectare of regeneration)/(canopy basal area). Standard errors in parentheses.

Summary: The observed west Adirondack regeneration deficits may be either normal or anomalous, and stable (not leading to canopy change) or unstable. Deficits arising from episodic reproduction would be normal and unstable; those arising from recent regeneration failure would by abnormal and unstable; and those arising from a strongly size-dependent mortality curve (race-across-the-gaps strategy) would be normal and stable.

The regeneration deficit for yellow birch, white pine, and perhaps red maple and black cherry may well be unstable deficits arising from episodic reproduction. The sugar maple deficits can not be. At present the most likely hypothesis is that the sugar maple deficits are the result of a recent, anomalous reproductive failure which has resulted in unstable demographic curves. The unstable demography will eventually lead to decreases in the amount of sugar maple in the canopy. Alternate hypotheses, (episodic

reproduction, the race-across-the-gaps model) still need to be considered but tend to have fairly contrived demographic conditions. Thus far we have not found an alternative model that is consistent with: a) the uniformly low densities of small maple saplings, b) the substantially higher densities of larger saplings and small canopy trees, c) the high beech-to-sugar maple ratios and the apparent absence of sugar maple in current and recently closed gaps, and d) the presence of similar regeneration deficits and demographic curves at sites with different histories.

13. Discussion II: Possible Roles of Logging, Competition, and Deer

What could cause a recent, widespread regeneration failure? The commonly suggested causes for regeneration failures - logging, beech, and deer - tend act locally and be spatially variable. In this section we argue that while all of them may be important for some species in some places, none seem adequate for the uniform west Adirondack regeneration failure we are observing.

Too Much Logging Heavy cutting or high-grading might have depleted canopy seed trees or altered soil nutrients seedbed conditions. But substantial regeneration deficits occur at sites that have never been logged (Figure 17). And even on commercial lands regeneration deficits often occur in plots where the parent species are abundant in the canopy (Figures 17). This is particularly true for sugar maple and is evidenced by the large differences in regeneration per unit canopy basal area between the Adirondacks and adjoining regions (Table. 7). Equal basal areas of canopy sugar maple produce one seventh as many small saplings in the east Adirondacks as at Mt. Equinox. Equal basal areas in the west Adirondacks produce one twentieth as many. Furthermore (Figure 14), sugar maple sapling abundances at Adirondack sites do not correlate with canopy basal areas, suggesting that the supply of seed trees is not limiting.

Too Little Logging Early and mid-successional species may require large openings and substantial amounts of soil disturbance to regenerate. As noted in Section 12, regeneration deficits for white pine and yellow birch are probably successional, and those for black cherry and red maple may or may not be. But this can not be true for sugar maple, which is abundant in the subcanopy and large sapling layers of the relatively undisturbed west Adirondack old-growth forests, and which behaves as late-succession dominant elsewhere.

Competition With Beech Beech saplings have been abundant in Adirondack forest understories for at least 50 years, and probably increased in abundance after the onset of the beech bark disease, since dying trees sprout profusely. In many places the young beech have filled the gaps created by logging and natural canopy mortality, and now make a dense subcanopy that casts a deep shade which supresses herb and sapling growth near the forest floor. Is it possible that the new cohorts of young beech sapling have become so numerous that they are completely stopping sugar maple regeneration?

There is no question that locally high densities of sapling or subcanopy beech can limit the growth of young sugar maples. Experiments at Huntington Forest in which herbicide treatments were followed by shelterwood cuts resulted in abundant sugar maple and yellow birch regeneration, and clearly established that these species can reproduce well at high light levels if beech are eliminated. This establishes, as does the edge reproduction observed in unmanaged forests, that Adirondack sugar maples will still regenerate when given enough sun. But it does not establish that the additional shade cast by beech is the reason why sugar maple, reputedly a shade tolerant species, now refuses to reproduce in the shade at all.

The problem with models of maple decline based solely on competition with beech is that the density of sugar maple seedlings is low everywhere, not just in areas where beech saplings are abundant. If beeches are excluding maples, sugar maple sapling density should be inversely correlated with beech sapling density, and beech density should be substantially higher than in other places where sugar maples are regenerating. Figure 14 shows that the sapling densities of sugar maple and beech are not correlated, and Table 6 shows that while the west Adirondack beech sapling density is only about 2.4 times the northern New York average sugar maple sapling density is 27 times below the regional average. In fact, the highest sugar maple sapling densities that we have thus far observed were at a Vermont site with 1400 beech saplings per hectare (Figure 2), which is close to the average density of small beech saplings in the west Adirondacks (1800 per hectare) and well above the average density of small beech saplings in the east

Adirondacks (600 per hectare). Either sugar maple saplings are very sensitive to small excesses in the number of beech saplings, or beech sapling abundance is not the sole cause of regeneration failure.

Competition with Grasses, Sedges, and Ferns Hardwood regeneration is completely absent from the fern glades mentioned in Section 12, and it is likely that it is being suppressed by some combination of direct competition, allelopathy, and browsing. These glades are currently limited to commercial lands within the former corridor of the Grass River Railroad and are, so far as I know, not found on ex-commercial lands or old-growth. Our observations show that sugar maple regeneration is independent of the abundance of ferns in much of the Adirondacks, and regeneration failures occur on many plots where there are few competitors of any kind.

Browsing by Deer Deer are clearly responsible for hardwood regeneration failures elsewhere and are known to browse selectively on small maples in the size range for which we see the most pronounced deficits. But this does not mean that deer are the principal cause of the regeneration deficits, or that if there were less deer there would be more maples.[18] The critical questions are how many deer there are and whether deer densities have increased or decreased in the period in which regeneration deficits seem to have developed.

No regular deer surveys are done in the Adirondacks, and so the geography and density of Adirondack deer are mostly a matter of inference. The commonly accepted picure, which is consistent with Adirondack forest and social history, is that west Adirondack deer densities were very low a hundred and twenty years ago when most of the Adirondacks were continuously forested and hunting was relatively unrestrained. They then rose in the period when hunting was regulated and many of the forests were heavily cut, peaking roughly fifty years ago. In the 1950's deer were more numerous in the interior of the park than on the more intensely hunted agricultural periphery. In the last 50 years the forests have recovered, especially in the interior of the park. Deer populations decreased in the forested center and increased on the agricultural periphery, where there was more logging and an extended period of post-war agricultural abandonment.

Dick Sage of Huntington Forest, the researcher most familiar with the history of deer in the Adirondacks, believes that deer were abundant in the park in the 1950's and reached densities of 10 or more per square kilometer in the most favorable areas on commercial lands. He thinks that deer decreased following a series of severe winters beginning in 1969, continued to decline with subsequent reforestation, and now average about two deer or fewer per square kilometer on most Forest Preserve lands. Densities may reach three deer per square kilometer at Huntington Forest, and four per square kilometer on some commercial timberlands.

These densities are substantially below those believed to cause major regeneration problems. The U.S. Forest service estimates that problems with hardwood regeneration start when deer densities exceed five per square kilometer and become acute when, as in Pennsylvania, they reach ten per square kilometer or more.

If these estimates are even approximately correct it is unlikely that deer are the main cause of a widespread and site-independent regeneration failure over much of the west Adirondacks. They are very likely contributing to regeneration problems, especially in areas where densities are locally high. But it is unlikely that they are the whole cause, simply because that deer densities are neither a) particularly high, b) substantially higher than they were before there was a regeneration problem, nor c) substantially higher than they are in places where there is no regeneration problem.[19]

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[18] Exclosures at Huntington Forest have shown that sugar maple will regenerate in full sun when deer are present, and apparently will not regenerate in the shade even when deer are excluded.

[19] Chris Anderson, who worked with us in the surruner of 1997, has suggested that high deer densities in the 1950's and 1960's could have reduced sugar maple sapling abundance to the point where it could not recover when the deer densities declined, both because beech abundance was increasing and because the amount of grazing per maple sapling would increase as maple density decreased. This is an interesting point, and will be dealt with in our paper reporting on the 1997 field work. My current thought is that it might account for the absence of large maple saplings, but does not account for the almost complete absence of sugar maple saplings under 20 cm, which we will document in the next paper.

Summary: logging, competition with beech and understory plants, and browsing by deer all have the potential to cause regeneration deficits, but seem unlikely, by themselves, to have caused the widespread, uniform deficits that currently occur in the west Adirondacks. Logging can not be involved in deficits in the old-growth forests; competitive effects should result in variable, rather than uniformly low, hardwood regeneration; and deer densities are not believed to be exceptionally high, and seem to have decreased, rather than increased, in the period when regeneration deficits were developing.

14. Discussion III: Possible Roles of Acid Rain & Calcium Depletion

The regeneration deficits have a distinctive geographic and historical signature: they have apparently developed in the last 50 years, are worse in the Adirondacks than in adjacent regions, and are worse in the west Adirondacks than in the east. None of the causes considered in the previous section has that signature and so none is, by itself, an adequate explanation. Acid rain does have this signature and so must be regarded as a possible cause of the Adirondack regeneration deficits.

At present we do not have field data that show a direct association between acid rain and regeneration failure. But we can argue that a) a known mechanism, soil calcium depletion, could link acid rain and regeneration failure and b) this mechanism is an attractive hypothesis for future investigation because it predicts the geographic and historical signature that we have observed.

Background Acid rain contains sulfuric and nitric acids, mostly from fossil-fueled generating plants and industrial sources in the midwest. The Adirondacks are one of the most heavily affected regions in the U.S. Currently the average pH of Adirondack rain is about 4.3. Past pH's are not well known; if they parallel those measured elsewhere, they were probably significantly acidified in the 1950's, reached their maximum acidities near pH 4.0 in the 1960's, and have become 0.2 to 0.3 pH units less acid since 1970's, largely because of reductions in sulfur emissions. Under the most recent federal emission standards there are expected to be only modest future reductions in sulfur emissions, and so little change in the acidity of Adirondack rainfall in the near future.[20]

Most discussion of the possible effects of acid rain on hardwood forests has focused on soil chemistry changes. Acid rain has three main effects on soil. It makes soil solutions more acid, mobilizes and leads to the loss of calcium and other positive ions which are bound to soil ion-exchange sites, and mobilizes aluminum, again through ion exchange.[21] The increased acidity can have direct effects on root growth and function. The loss of calcium, an important nutrient, can alter many physiological processes (photosynthesis, growth, shade tolerance, etc.). The free aluminum is toxic at high concentrations and at lower concentrations can prevent trees from taking up calcium and other positive ions.

Acidification of Soil Solutions Changes in the overall acidity of soils has thus far not been shown to be a biological problem in northern forests. In many forest soils the upper layers are naturally quite acid, and several chemical processes (anion shifts, buffering by aluminum compounds) set lirnits on how much additional acidification can occur.

Aluminum Toxicity Direct aluminum toxicity has not thus far been shown to be a major problem in forest soils. Aluminum can only reach toxic concentrations in extremely acid soils. Most forest soils, and especially those in hardwood forests at moderate elevations, probably never become this acid. Indirect aluminum effects (sub-toxic levels of aluminum are interfering with the uptake of other ions) can occur in less acid soils. They have only been discovered recently, and thus far their incidence and severity are not known.

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[20] New York and several New England States have recently petitioned for changes in the current federal emissions standards on the grounds that they do not meet the stated goals of the Clean Air Act. If this suit prevails, or if we get a Congress and administration generally committed to doing something about fossil fuel consumption and acid emissions, we could see substantial reductions in emissions in the next two decades.

[21] An equilibrium process called the salt effect also contributes to the mobilization of aluminum.

Loss of Soil Calcium The 'ion imbalance problem' (the loss of calcium and other nutrients from the soil caused by added hydrogen and sulfate ions) is potentially much more serious. It is a cumulative effect which can occur even in naturally acid soils and is hard to detect because it is not reflected in pH changes. There is good evidence that calcium is in fairly short supply in many northern forests, and that, under normal conditions, these forests recycle many nutrients very efficiently rather that lose them. This suggests that any process that causes substantial nutrient losses may have a substantial biological effect.

The effects of acid rain on soil chemistry depend strongly on whether the soil contains carbonate minerals like calcite and dolomite that can neutralize the acid. Soils with such minerals are said to be buffered. Many soils in lowland Vermont and the northern lake plains of New York are derived from limestones and marbles and so are well buffered. Most west Adirondack soils are derived from granites and quartzites and are poorly buffered. East Adirondack soils, which are generally granitic but may contain marble or calcium-rich igneous rocks, vary: some are poorly buffered, some relatively well buffered.

The differences in natural buffering have created a strong regional pattern of differences in vulnerability to acid rain. The west Adirondacks are highly vulnerable: 95% of the highly acidified (pH<=5.5) lakes in the Adirondacks are in the west half of the park. The east Adirondacks are less vulnerable, and lowland Vermont and parts of New York adjacent to the Adirondacks hardly vulnerable at all. A suggestive feature of the regeneration problem is that the pattern of regeneration deficits corresponds well to the pattern of regional vulnerability.

Has acid rain reduced the availability of calcium in northern forests? Watershed studies have shown that acid rain has increased calcium losses from northern forests, and that more calcium has been leaving the test watersheds than has come in from precipitation and dry deposition. What is not clear is whether the calcium exported represents a net loss from the soil calcium pool or whether the pool has been replenished by an accelerated release of calcium from the weathering of bedrock. The matter is complicated since weathering rates can not be measured directly. In addition, atmospheric calcium inputs have dropped recently, and the natural maturation of forests can sequester calcium and deplete the available calcium in forest soils, quite independent of acid rain.

None the less, several recent papers have concluded that acid rain has caused cumulative losses of calcium from northern forest soils. The evidence is inferential, but seems, in aggregate, fairly strong. The chief arguments are that:

> Watershed studies and nutrient cycling budgets suggest that calcium losses from experimental watersheds have exceeded inputs for at least 30 years.

> Calculations and experimental measurements of weathering rates suggest that the release of calcium from rocks is not compensating for the losses.

> Experimental measurements of soil in test bags show that variations in calcium losses correspond to variations in acid rain inputs, suggesting that there is no significant calcium release mechanism buffering the effects of acid rain.

> The acid-neutralizing capacities of stream water, a measure of the overall acid-base balance of the watershed, have not increased as acid rain inputs have decreased, suggesting that the pools of soil calcium available to neutralize acid rain have been depleted.

Thus it currently appears likely, though not yet firmly established, that acid rain has depleted soil calcium pools in forests with calcium-poor bedrock.

Could calcium depletion cause regeneration failures? There is both direct and indirect evidence that suggests that cumulative calcium loss could have substantial effects on forests. Calcium is the fifth most abundant element in trees and, after nitrogen, the second most abundant mineral element. It is involved in the functioning of ion channels and so is a critical component in all cell membranes. It is required for all

growth processes and is important for many other physiological processes. Specific results that suggest that calcium deficits could be affecting the overall performance of forest trees are that:

Calcium-deficient red spruces have increased dark respiration and so grow less efficiently in shade. They also have reduced radial growth rates and reduced cold tolerance.

Calcium concentrations in trees on elevational gradients decrease with decreasing soil calcium concentrations and increasing soil aluminum concentrations. Tree growth often decreases along the same gradients, suggesting that calcium may be a limiting nutrient.

Mortality of sugar maple saplings in shade seems to increase as soil calcium decreases.

Fertilization experiments in Vermont have shown that the condition of sugar maples improves after calcium is added to the soils.

Summary: At present we have a plausible story connecting acid rain with regeneration deficits but no direct evidence to prove the connection. The story is that:

a) Acid rain creates ion imbalances that mobilize calcium bound in soils and increase the rate of calcium loss for the ecosystem.

b) Although some of the losses are offset by weathering of soil minerals and by atmospheric inputs, overall losses exceed gains and surface soils are progressively depleted of calcium.

c) This decreases the availability of calcium to trees, especially at higher elevations or in extremely acid soils where free aluminum may block calcium uptake.

d) As trees become deficient in calcium their growth rates decline, possibly (if sugar maple behaves similarly to red spruce) as a result of increased dark respiration. They may become less hardy, suffer more dieback in hard winters and have fewer good seed years and a lower average seed output.

e) In addition the mortality of their seedlings increases and the ability of their seedlings to tolerate shade and browsing decreases.

f) Whether because of reduced seed output or increased seedling mortality, seedling and sapling populations decline, and individual saplings are less able to compete with other species, especially in the shade.

g) The declines are worst at higher elevations and on shallow, poorly buffered granitic soils; they are mitigated by the greater calcium reserves of deeper soils and soils derived from calcareous bedrock

If true, this story could provide a consistent explanation of the observed patterns of Adirondack regeneration failure. But it is far from established. At present there is good evidence for a-c and some evidence for d and e. Neither f nor g, which are crucial for connecting calcium losses to west Adirondack regeneration deficits, have as yet been studied. Our current project is designed to investigate this connection.

15. Biological and Economic Significance of Regeneration Deficits

Until we know why regeneration deficits have arisen and how long they may persist we will not be able to discuss their effects in detail. But it still is important to realize that they have the potential to cause major changes in forest structure and ecology and so may have consequential biological and economic effects.

If the arguments of Section 13 are correct, the current regeneration deficits will lead to the replacement of the current mixed-species canopies with ones heavily dominated by beech. On Forest Preserve lands, with

average canopy mortality rates of somewhere around 1% per year, this could be largely complete in 30 to 70 years. On commercial lands, where harvesting accelerates the replacement of canopy trees with understory ones, the turnover could happen faster, and we could see beech-dominated canopies in 20 to 50 years.

Since most beech over 20 cm dbh are infected with the beech bark disease and most over 30 cm dead or dying, the future beech-dominated forests are likely to contain large numbers of small trees, and to be lower and more like thickets than the present forest canopies.

If forest canopy composition does change in this way there may be substantial ecological and economic results. Biologically it will mean the end of the tall mixed-species old- growth forests as we currently know them. The younger, smaller, less diverse forests that result may well have lower bird and insect diversity. If sugar maple is eliminated and beech dies before maturity, it is likely that overall tree seed crops will decrease substantially. Since these seeds are one of the major paths for plant-vertebrate energy transfers, this will directly affect the resources available to mammals and birds and indirectly affect the resources available to their predators.

Economically the changes will mean that forests currently producing hardwood lumber and veneer will be replaced by forests producing hardwood pulp, making sustainable hardwood timber production unachievable. The worst-case results could be that forest managers will have high-grade to meet economic goals, that local forest-based industries will not have a dependable supply of sawlogs, and that large tracts of privately owned lands will be stripped of their timber and thrown on the market for speculation and development.

The seriousness of these possible changes is best appreciated by contrasting the forests that may result from continued regeneration failures to the forests of 150 years ago. The pre-European Adirondack forests contained two or three major conifers (red spruce, hemlock, sometimes white pine) and three major hardwoods (beech, sugar maple, yellow birch). Red maple and black cherry were probably minor components. A hundred and fifty years of cutting have essentially eliminated pine and hemlock as major species, reduced yellow birch and red spruce to a third or less of their former abundance, and increased the abundance of black cherry and red maple. If the current regeneration problem depletes sugar maple from west Adirondack canopies, and if the mortality of adult beeches from beech-bark disease remains high, we will have Adirondack forests in which beech and red spruce are the only pre-European dominants still present in significant numbers, and in which no important hardwood species of the original forests regularly reaches maturity.

Our qualitative observations on recent gaps suggest that the switch to beech-dominated canopies is already happening, and surprisingly rapidly. At all of the west Adirondacks sites we studied, most of the recent canopy gaps that have filled by promoting trees from the sapling pool are now filled either by thickets of young beeches or by a mixture of beech and striped maple.

16. 1997-1998 Research

In July 1997 we began the third phase of the regeneration research project. This is a joint undertaking of the Wildlife Conservation Society, the Institute for Ecosystem Studies, and the White Creek Field School. Our goals are to determine:

> Whether seed production and germination are normal.

> Whether sapling densities and sapling mortality vary with soil calcium.

> Whether the recruitment of small saplings to the large sapling or subcanopy pools slowed at a particular time in the past.

> Whether maple regeneration failure is restricted to areas with exceptionally low light levels.

The preliminary results from this student have proven quite interesting. They show that sugar maple seedlings are often abundant in areas where older saplings are absent; that second-year and older seedlings are absent over large areas, showing that the holes in the demographic curves may be caused by high mortality of seedlings that have not yet entered the sapling bank; that the areas that have abundant maple sapling banks often, but not always, have associated indicator species suggesting a calareous soil; and that in the areas where calcareous indicators are present beech sprouts are uncommon, even though dying adult beeches may be present.

Some of this confirms our expectations, and some suggests that forests are, as always, more complex than we had expected or hoped. We will be analyzing soil samples, canopy photos, and tree cores this fall, and expect to issue a second report on our results this winter.

The problem is a large and complicated one, and, we think, important. We would welcome ideas, suggestions, comparable data sets from elsewhere, and, especially, collaboration.

APPENDICES

1. Metric to English Conversions

Length
1 meter = 39.37 inches = 3.2808 feet
1 kilometer = 1000 meters = 0.6213 miles

Area
1 square meter = 10.764 sq. feet
1 hectare = 10,000 sq. m. = 2.471 acre
100 hectares = 1 square kilometer = 0.3860 square miles

Stem Density
1000 stems/hectare = 405 stems/acre

Basal Area
1 square meter/hectare = 4.356 square feet/acre.

Deer Density
10 deer/square kilometer = 25 whole deer plus 1 fractional (0.9 1) deer/sq. mile

2. Details of Methods

Study sites were selected in more-or-less continuous, upland, hardwood-dominated forests at elevations between 300 and 700 meters. Study sites were typically spaced between 2 and 15 Ian apart depending on the overall size of the area being sampled.

Seven to ten points were spaced at 100 m intervals along 1 - 2 parallel straight-line transects within each study site. If a potential sample point fell a) in a gap with less than 50% canopy, b) in a wetland or an area with more than 50% exposed bedrock, c) in a stand with over 50% conifers, or d) in or immediately adjacent to a road or recently disturbed area, then that sample point was rejected and a series of potential sample points at 10 m intervals was inspected until a satisfactory one was found.

At each sample point we recorded slope, elevation, aspect, dominant species in canopy, subcanopy, understory and groundlayer, and approximate canopy and groundlayer cover.
A l-x metric prism was used to tally living trees over 10 cm. dbh. The diameter of each tree

tallied was estimated to the nearest 10 cm by eye; diameters of borderline trees up to 40 cm dbh were verified with calipers.

Basal diameters of saplings under 10 cm dbh were measured 20 cm above the ground with a gauge that assigned them to one of four diameter classes (0.5 cm to 0.9 cm; 1.0 cm to 2.4 cm; 2.5 cm to 4.9 cm; and 5.0 cm basal diameter to 10 cm dbh). Saplings 0.5 cm to 4.9 cm were measured in a 2 m radius circle (0.00126 ha). Saplings 5 cm basal diameter to 10 cm dbh were measure in a 5 m radius circle (0.00785 ha). Saplings less than 0.5 cm basal
diameter were not counted.

The sapling counts included all woody species capable of growing 2 m high or more. Witch hazel, striped maple and mountain maple were tallied as saplings, but hazelnut, leatherwood, and hobblebush were not.

No attempt was made to distinguish root sprouts from seedlings.

A stem was considered living if it had any green leaves or living buds. Stems that forked below the measurement height (20 cm for saplings, breast height for trees) were tallied separately. Small sprouts from the bases of living parent trees were not counted as saplings.

Field data was entered into database files and manipulated using FieldData software written by the author.

Observed numbers of saplings were converted to estimated densities in stems per hectare by dividing by the plot area. An estimate of N saplings in a plot of radius R gives an estimated density of $10,000N/3.14(R)^2$ saplings per hectare, and the resulting conversion factors are:

Diameter Class being sampled	Radius of Plot	Multiply Tally by
0.5 cm	2 m circle	795.7
1.0 cm	2 m circle	795.7
2.5 cm	2 m circle	795.7
5 cm	5 m circle	127.3

Prism count tallies were converted to densities by using the midpoints of the diameter classes to get an approximate sample area. (A 1X metric prism will count trees of radius R cm within a circle of radius R meters. If you tally *N* trees of diameter *D* cm, the estimated area that you have sampled is *$3.14(R/2)^2$* square meters, and the estimated density of trees in this size class is *$N/3.14(R/2)^2$* stems/ha.. The resulting conversion factors are:

Estimated Diameter	Multiply Prism Tally by
10-20 cm	56.6
20-30 cm	20.4
30-40 cm	10.4
40-50 cm	6.3
50+ cm	3.5

Statistical analysis and graphing was done using Systat.

3. Additional Historical Notes

Northwest Adirondacks There were substantial sawmill complexes on the lower Grass River in Canton and the adjacent Oswegatchie in Rensellaer Falls by 1810. The Grass River was declared a public highway for the transport of logs in 1824 and the Oswegatchie in 1816. One of the largest tanneries in the Adirondacks

(Hull Tannery, later St. Lawrence Tannery) operated in Colton between 1856 and ca. 1897, and at its height used 5000 cords of hemlock bark (or roughly the hemlock on 1000 acres) annually. Two other large tanneries were in operation in the 1880's and may well have bought bark from the Grass River watershed.

The Emporium Lumber Co. began purchasing land in 1905 and eventually owned 125,000 acres, including much or all of the Hancock and Long Pond tracts. Emporium opened a sawmill at Conifer (east of Cranberry Lake) in 1911, and from 1915 on developed a system of small-gauge logging railroads extending from Cranberry Lake to the North Branch of the Grass River in Claire. The company's principal product was hardwood flooring, but they also sold softwoods and, until 1917, hemlock bark. The railroad operated until about 1941, by which time the company had sold most of its lands. Emporium is said to have taken 1.1 billion board feet of lumber in its 35 years of operation. If most of this was from its own lands this would be over 8000 board feet of lumber per acre per 35 years, representing quite intense production.

Stillwater Reservoir The lands immediately north of the reservoir were apparently owned by the Adirondack Company, part of W. W. Durant's Adirondack empire of the 1880's. They were first sold to Mary Lyons Fisher (who may have owned them when the Beaver River was dammed to produce Stillwater Reservoir in 1886) and then to W. S. Webb as part of the corridor for his Mohawk and Malone Railroad, which was finally built south of Stillwater in 1892.

The lands immediately south of the reservoir also belonged to Mary Lyons Fisher and then were sold, at least in part, to Webb.

4. Demographic Holes

A reversed demographic curve has a hole somewhere on the left side where we expect to see a peak. We wish to know what can generate holes in demographic curves, and what the holes do after they are generated.


A. Demographic curve with hole
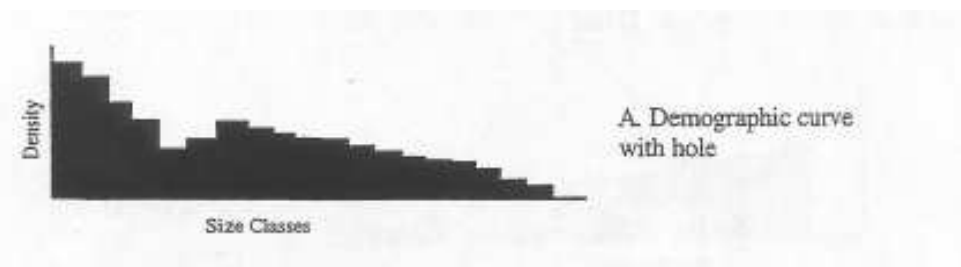
A demographic curve is a snapshot of a growing population. Trees move through each diameter class, exactly like vehicles moving through a segment of road. On a road, the average number of vehicles in a segment depends on the length of the segment, the number entering it each second, and the average time they take to cross it. Trees are similar, but some die along the way. If N_i is the number in the ith diameter class, and if growth and mortality have been constant for some time, we can write

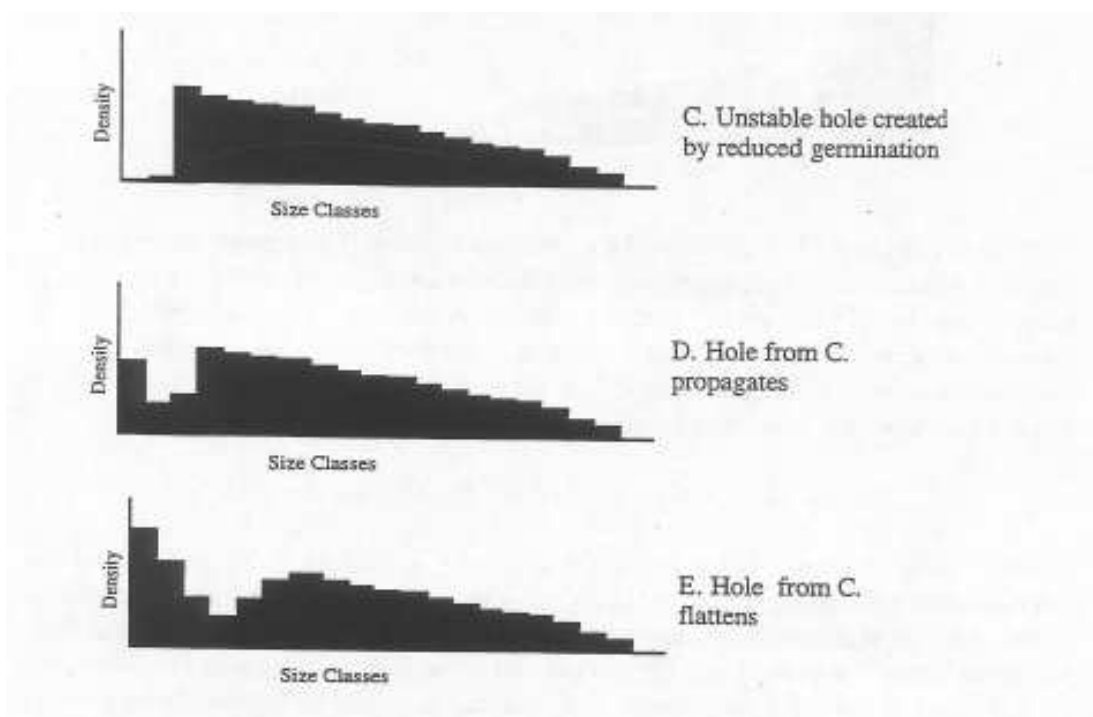$$N_i = (E_i - M_i)T_i \ (1) \qquad E_{i+1} = E_i - M_i \ (2)$$

where E_i is the number of plants per unit time entering the size class, M_i the mortality rate per unit time while in the size class, and T_i the average time a plant spends in this size class. The first says that the number in a size class depends on input, mortality and residence time. The second says that the number of saplings entering a size class per unit time is number that enter the previous size class minus the mortality while in the previous class.

If the size classes are chosen so that the amount of time spent in each one of them is equal to or shorter than the one to its left, and if mortality is greater than 0, then the density of each diameter class will be equal or

less than that of the one to its right (because the output from each size class, $E_i - M_i$, is less than the input to that class) and the demographic curve will slope to the right, like B. We call this a normal demographic curve.
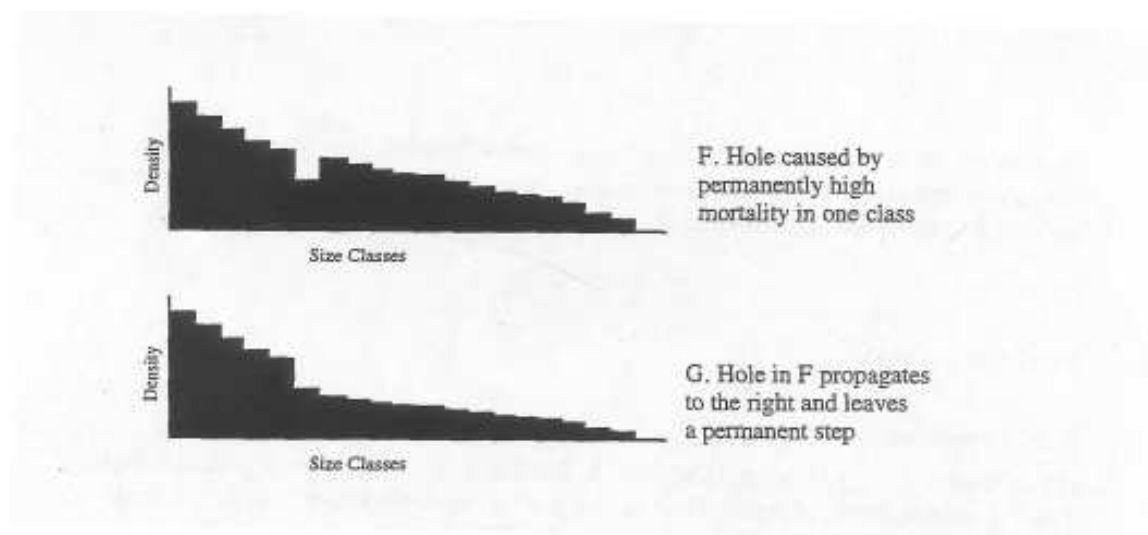

B. Normal demographic curve
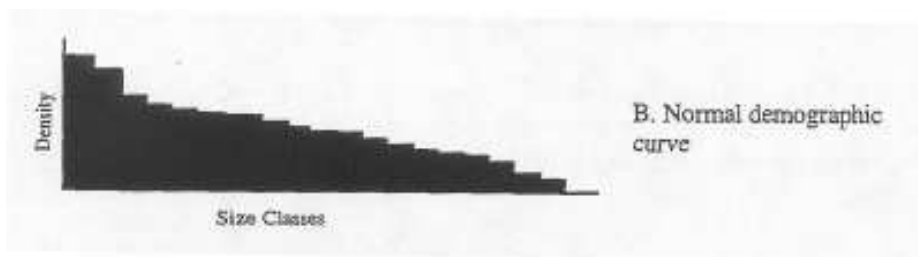
Now imagine that we either decrease the seed production or turn up the seedling mortality for a period of a decade or so, and then let it return to normal. The result will be a curve like C, with a hole in the smallest size classes. This hole will gradually fill after mortality and reproduction have returned to normal, but in the meantime it decreases the number of plants entering, the size classes to its right, and so decreases the height of those classes. Effectively it propagates to the right, flattening as it does so because of the variation in growth rates, as in D and E.

C. Unstable hole created by reduced germination

D. Hole from C. propagates

E. Hole from C. flattens

Next imagine we turn the mortality for some particular intermediate diameter class i up, as in F, but this time we keep it turned up. Once again there is a hole in the ith diameter class and the holes moves to the right, and eventually the demographic curve stabilizes. But since the mortality in the ith class is now permanently high, it will be lower than it was before, and the final demographic curve will have a step, as in Figure G.

These two examples show that holes caused by input or mortality fluctuations eventually move to the right and alter the whole demographic curve. If the mortality remains high the curves that result may show a step, but will not show a hole.

This principle has a useful corollary: since holes generated by mortality do not persist, any hole known to be generated by mortality must have developed recently, an fact must have developed within a period of time equal to the average age of the size class in which it currently occurs.

F. Hole caused by permanently high mortality in one class

G. Hole in F propagates to the right and leaves a permanent step

What about stable holes? If we relax the above assumption that the time spent in each class is equal or less than that spent in the preceding class, then Equation (1) shows us that any size class i that trees move through rapidly and so has a small Ti can have a small Ni. Since the small Ni is generated by a small Ti rather than a small Ei - Mi, it will not affect the input to the next size class and the hole will not propagate. Thus fluctuations in the length of time spent in a given size class relative to the time spent in its neighbors, or, what is the same thing, fluctuations in the average size-specific growth rate, can create stable holes that do not propagate. These holes will not affect densities of canopy trees.

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The numbers in the references refer to entries in the bibliography, which begins on page 60. Not all the items in the bibliography are cited here.

Section 2: Adirondack forests, 6,9; *regeneration problems*, 24,25, plus conversations with foresters.

Section 3: Standard model of regeneration, 55-74

Section 4: Cogbill and Woods data, personal communications; *Hughes data*, 95, 96; *NYS Forest Statistics*, 40.

Section 5: NYS Forest Statistics, 40.

Section 8: West Adirondack history, 5-7, 10; *Beech disease*, 9.

Section 12: the discussion of demographic holes, the RAG model, and the theoretical exposition in Appendix 4, are original; *episodic reproduction of yellow birch*, from discussions with Kerry Woods and others; *Pinchot*, 7; *Roman's data,* 8.

Section 13: much information and ideas from conversations with Carl Anderson, Charley Canham, Charley Cogbill, Sam Parmalee, Dick Sage, and Kerry Woods.

Section 14: much information and ideas from Charley Driscoll, Pete Murdoch, Greg Lawrence, and Mark David; extensive reliance on the acid rain, spruce and maple decline, and calcium depletion literature, as given under those headings in the bibliography.

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