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Suppression and release during canopy recruitment in *Acer saccharum*[1]

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CANHAM, C.D. (Institute of Ecosystem Studies, Cary Arboretum, Box AB, Millbrook, New York 12545). Suppression and release during canopy recruitment in *Acer saccharum*. Bull. Torrey Bot. Club. 112: 134–145. 1985.—Patterns of radial growth were used to reconstruct the history of suppression and release during canopy recruitment of *Acer saccharum* Marsh. in old–growth northern hardwood forests of the Adirondack Mountains of New York. In a stand that had been selectively logged 60–80 years ago, only 20 per cent of canopy trees between 20–40 cm DBH had undergone periods of suppression prior to canopy recruitment. However, in 2 unlogged stands, all of the sampled trees had undergone from 1 to 5 definable episodes of suppression prior to eventual recruitment at an average age of 110–126 years. The mean lengths of periods of suppression (22–28 years in the two unlogged stands), combined with the mean numbers of periods of suppression in each core (2.9–3.1 per tree) indicate that saplings of *Acer saccharum* responded to canopy openings created by the death of neighboring trees before eventually replacing an individual directly overhead. The ability to withstand suppression appears to be an essential trait for a life history that allows *Acer saccharum* to exploit the relatively short–lived pulses of resources created by small canopy openings.

Key words: *Acer saccharum*, canopy disturbance, radial growth, release in canopy gaps, suppression

It is possible to recognize several distinct patterns of growth by which individuals of shade–tolerant tree species reach canopy height. At one extreme is the hypothetical ability of shade–tolerant trees to slowly grow into the canopy in the absence of any form of canopy disturbance. A second mode of recruitment depends on the recognized ability of shade–tolerant species to persist as suppressed saplings beneath a closed canopy and respond to periodic openings in the canopy created by the death of overstory trees. Saplings that do not reach the canopy during an initial period of release may eventually reach the canopy after two or more periods of suppression. There are two major alternatives to this process of successive periods of suppression followed by release in small gaps. Recent studies of gap disturbance regimes in temperate and tropical forests suggest that small canopy gaps are often expanded by successive mortality of trees bordering the gap (Runkle 1984). Runkle (1984) suggests that this process is frequent enough that saplings growing in small gaps frequently reach the canopy without experiencing actual suppression. The other alternative is that much of the actual recruitment by even shade–tolerant tree species occurs in a single period of rapid growth following periodic and extensive canopy disturbance (e.g., Canham and Loucks 1984; Henry and Swan 1974; Oliver and Stephens 1977).

There is surprisingly little information on the relative importance of these different modes of canopy recruitment for the shade–tolerant trees of old–growth northern hardwood forests of eastern North America. The few detailed studies of the frequency of catastrophic disturbances in mesic forests of the northeastern and north-central U.S. (Bormann and Likens 1979; Canham and Loucks 1984; Lorimer 1977) suggest that the average interval between successive catastrophic disturbances in mesic forests is at least several times longer than the lifespans of even the long–lived, shade–tolerant species. The studies of Henry and Swan (1974) and Oliver and Stephens (1977) have indicated the importance of periodic but non–catastrophic natural disturbances for patterns of recruitment in forests of

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southern New England, but both studies reflected the effects of both logging and natural disturbances. The more recent studies of gap disturbance regimes (Runkle 1979, 1981, 1982, Barden 1979, 1980, 1981) provide extensive information on the distribution of gap sizes and composition of regeneration within gaps in comparable forests in the southeastern United States. However, it is not possible from these studies to evaluate the frequency with which suppressed saplings successfully respond to canopy openings.

Acer saccharum Marsh. is one of the dominant shade–tolerant tree species in old–growth northern hardwood and mixed conifer–hardwood forests at elevations between 350 and 950 m in the Adirondack Mountains of New York (Heimburger 1934; Holway and Scott 1969; Roman 1980; Young 1934). Net height growth rates of saplings of *Acer saccharum* beneath the closed canopies of old growth stands are too low (<3 cm/yr) to allow individuals to reach even the bottom of the canopy layer in the absence of some degree of release by nearby canopy gaps (Canham 1984). However, saplings of *Acer saccharum* respond to even small canopy openings (15–75 m^2) with significant increases in overall growth rates (Canham 1984). In particular, net height growth rates of saplings in even small canopy openings are an order of magnitude greater than net height growth rates in the understory. However, height growth rates in canopy openings are still relatively low, averaging less than 30 cm/yr regardless of gap size. At this rate, a sapling would require 50 years to grow from the seedling layer to the bottom of the canopy layer (at approximately 15 m above the ground in the stands I have studied) (Canham 1984). Given the ability of adjacent canopy trees to grow laterally into a gap (Trimble & Tryon 1966; Runkle 1979; Hibbs 1982), and the presence of advance regeneration of several shade–tolerant tree species in the understories of northern hardwood forests, it seems unlikely that individuals routinely grow from the seedling layer to the canopy in single periods of release created by the death of a single dominant canopy tree.

The principal objective of this study was to determine the frequencies of distinct periods of suppression and release during canopy recruitment of *Acer saccharum* in old growth northern hardwood forests of the Adirondack Mountains. Measurements of radial growth rates indicated that ring widths of saplings were significantly narrower beneath closed canopies than in even small canopy openings (Canham 1984). Thus, an analysis of radial increments in canopy trees was used to reconstruct the duration and frequency of both suppression and release during recruitment.

Materials and Methods. The study was conducted in three old–growth northern hardwood forests (Table 1) in the central Adirondack Mountains of New York. All of the sites were located within the Huntington Wildlife Research Forest near Newcomb, New York (Fig. 1). All 3 stands had canopies dominated by *Acer saccharum* and *Fagus grandifolia* (Ehrh.). In both the Arbutus Lake and Wolf Lake stands, individuals of *Fagus grandifolia* ranged from 15 to 35 cm DBH, while *Acer saccharum* was present as large canopy trees between 30 and 80 cm DBH. Both stands had an essentially monospecific layer of *Fagus grandifolia* as understory and subcanopy trees > 10 cm DBH. The sapling layer (stems >1.0 m tall and less than 10 cm DBH) in both stands was also dominated by *Fagus grandifolia.* The stand along Little Sucker Brook had a more diverse canopy, including individuals of *Tsuga canadensis* (L.) Carr., *Fraxinus americana* L. and *Tilia americana* L. *Acer saccharum* was also a major component of the sapling layer at Little Sucker Brook.

The stand along Little Sucker Brook was selectively logged sometime during the first two decades of this century (R. Sage, personal communication). Cutting was apparently limited to softwood species (*Picea rubens* Sarg. and *Tsuga canadensis*). The two other stands at Wolf Lake and Arbutus Lake had no recorded history of logging.

Within each stand, a rectangular plot 75 × 100 m (75 × 150 m at Arbutus Lake) was laid out across the slope. All stems of *Acer saccharum* between 15 and 40 cm DBH that were not overtopped (for at least half of their crowns) by adjacent canopy trees were tagged and numbered. A random sample of 10 trees in each stand was then chosen for coring. In the several cases where trees had hollow cores, they were replaced by additional, randomly chosen trees. Sampling was limited to relatively small canopy

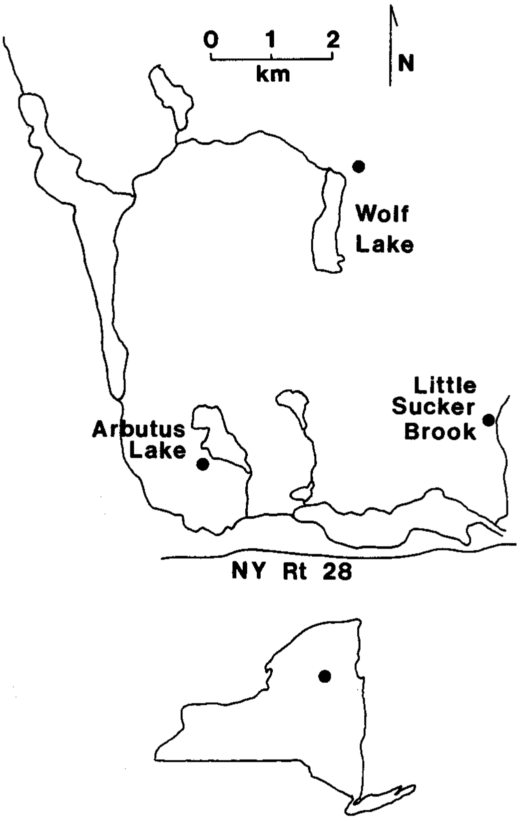

Fig. 1. Locations of the Little Sucker Brook, Wolf Lake and Arbutus Lake stands within the Huntington Wildlife Research Forest in Essex County, New York.

trees for several reasons. First, no attempt was made to distinguish between stands in which the largest canopy trees were even or all-aged. Thus, the largest canopy trees in each of the stands could conceivably have become established in response to catastrophic disturbances several hundred years ago. By coring the smaller canopy trees, sampling was limited to trees that had reached canopy size following small-scale disturbances that did not completely eliminate the overstory of the stand. Coring smaller trees also reduced problems with heart rot and hollow cores.

The trees were cored at 1.0 m above the ground. If a core missed the center of the trunk by more than approximately 1 cm, additional cores were taken until the center (within 1 cm) was included in the core. Trunk diameter at 1.0 m height, DBH and tree height were also recorded. The samples in the 3 stands ranged from 17 to 25 m tall, and from 16 to 38 cm DBH.

Ring widths were recorded to the nearest 0.01 mm using a movable stage and microscope. The screw thread of the stage was connected to an optical encoder that generated 100 pulses per millimeter of movement of the stage (i.e. 100 pulses per revolution of a lead screw with a 1 mm pitch). The pulses were then counted and recorded by a microcomputer (Apple II+, Apple Inc.). The stage was tested against a micrometer, and had no measurable error at 0.01 mm resolution.

There are, however, several sources of potential error in the use of ring widths to estimate radial growth rates. Examination of basal disks of saplings of *Acer saccharum* collected from the Little Sucker Brook stand indicated that some rings were only visible for part of the circumference of a tree. These partial rings were not limited to periods of strong suppression. While partial rings make it difficult to establish precise chronologies for a given tree without some form of reliable cross-dating, they should not significantly affect the calculations of the number and duration of periods of suppression during the growth of a tree because they are relatively uncommon. The basal disks also showed considerable eccentricity in radial growth patterns. However, differences in the width of a ring around the circumference of a disk were most pronounced during years with vigorous growth, rather than in periods of suppression. Thus, single cores may not provide particularly precise estimates of the cross-sectional area of wood produced in any year, but they do provide a reasonably reliable index of relative growth rates over time. The final potential source of error in the use of ring widths depends on the distinctiveness of the boundary between annual growth increments. The cores had distinct boundaries of cells between rings even during the strongest periods of suppression. For the narrowest rings, thin sections of wood were removed and examined against a light background for greater accuracy.

In a related study, radial growth rates of saplings of *Acer saccharum* collected from beneath closed canopies were found to be distinctively and significantly lower than radial growth rates of saplings in a wide range of sizes of canopy openings (Canham 1984). Mean radial growth rates (of the last

Table 1. Descriptions of the three study sites. %D = relative density, %BA = relative basal area of canopy trees. Canopy trees were defined as all stems >10 cm DBH that had at least part of their crowns exposed to the sky.

	Little Sucker Brook		Arbutus Lake		Wolf Lake	
	%D	%BA	%D	%BA	%D	%BA
Acer saccharum	60.9	49.8	52.9	78.1	66.7	78.3
Fagus grandifolia	12.5	8.9	38.2	12.1	27.7	6.1
Betula lutea	14.1	25.2	5.9	8.8	5.6	15.6
Picea rubens			2.9	1.0		
Fraxinus americana	10.9	15.8				
Abies balsamea	1.6	0.3				
Elevation (m)		560		525		580
Slope (°)		15–20		10–15		15
Aspect (°)		140		60		260
Mean canopy DBH (cm)		34.4		44.4		37.9
Total canopy basal area (m^2/ha)		38		31		26
Total density of canopy trees (ha^{-1})		320		170		180

3 years of growth, measured along one radius) of 25 understory saplings from beneath closed canopies ranged from 0.05 mm/yr to 0.51 mm/yr, with an average radial growth rate of 0.22 mm/yr. In contrast, saplings in even the smallest canopy openings sampled (15–75 m^2, covering less than 2% of the sky hemisphere on average) had significantly higher radial growth rates. For seven saplings collected from these small gaps (gaps in which the saplings received no full sun via the gap) radial growth rates ranged from 0.45 to 1.01 mm/yr, with a mean of 0.69 mm/yr. This sharp difference between the growth rates of saplings in the understory and saplings in even very small canopy openings is characteristic of the release of *Acer saccharum* in canopy gaps (Canham 1984).

On the basis of these measurements, a growth rate of 0.50 mm/yr was chosen as a threshold indicating release. Periods of suppression were defined as intervals in which there were 4 or more years of growth below 0.5 mm/yr during which there were no periods of 3 or more years of consecutive growth greater than 0.5 mm/yr. The requirement for 4 years of consecutive growth below 0.5 mm/yr was chosen so that low growth rates due to short–term climatic effects or reductions in growth following reproduction would not be counted as periods of suppression. In order to test the sensitivity of the results to the choice of at least 4 years of low growth without 3 or more consecutive years of intervening high growth rates, results were also calculated for periods of suppression defined by combinations of 2 to 4 years of low growth without 2 to 4 years of high growth rates. Reducing the length of either interval increased the number of distinct periods of suppression and release observed in a core, but did not significantly alter the length of the longest period of suppression, the per cent of years spent suppressed or released, or the size and age at which saplings began the period of release during which they reached the canopy. In general, there were relatively few instances of only 2 or 3 years of growth below 0.5 mm/yr in any of the cores (the mean number of periods of only 2 or 3 years of consecutive growth less than 0.5 mm/yr ranged from 0.8 per core at Little Sucker Brook to 5.2 per core at Arbutus Lake).

For the purposes of this study, canopy recruitment was defined as the year in which an individual began the period of release during which it grew to its current position in the canopy. Thus, for small saplings responding to large disturbances that allowed growth to the canopy in one long period of release, the date of canopy recruitment was defined as the first year of the release, even though the saplings would

Table 2. Aspects of the history of suppression and release prior to recruitment of *Acer saccharum* in three old-growth northern hardwood forests. Canopy recruitment was defined as the point at which saplings began the period of release during which they reached canopy size.

		Little Sucker Brook[a]	Arbutus Lake	Wolf Lake
Percent of cores with periods of suppression		20%	100%	100%
Number of periods of suppression per core	x	2.5	2.9	3.1
	s.d.	(0.71)	(1.29)	(1.37)
	range	2–3	1–5	1–5
Lengths of episodes of suppression (yr)	x	14.6	28.5	22.0
	s.d.	(4.61)	(27.3)	(16.5)
	range	7–19	4–104	5–61
Lengths of longest suppressions (yr)	x	17.5	53.9	39.2
	s.d.	(2.12)	(30.4)	(15.6)
	range	16–19	9–104	9–61
Lengths of episodes of release[b] (yr)	x	11.5	24.0	14.6
	s.d.	(6.76)	(18.9)	(12.3)
	range	4–20	3–66	3–48
Total length of suppression (yr)	x	36.5	79.9	68.3
	s.d.	(0.71)	(39.4)	(29.9)
	range	36–37	29–159	15–105
Age at recruitment (yr)	x	60.5	126.4	109.6
	s.d.	(20.5)	(53.0)	(41.4)
	range	46–75	33–213	37–176
Size at recruitment (cm diameter at 1.0 m height)	x	1.25	11.8	9.8
	s.d.	(2.88)	(4.96)	(4.90)
	range	4.0–8.8	2.3–17.5	1.4–15.2

[a] Results presented for only those trees with definable periods of suppression (2 of 10 trees).

[b] For periods of release followed by suppression.

have been considerably smaller than canopy size at that time.

Results. Only 2 of the 10 trees cored in the selectively logged stand at Little Sucker Brook showed periods of suppression during growth to canopy height, but all of the cores from the unlogged stands at Arbutus Lake and Wolf Lake showed from one to five definable periods of suppression (Table 2). Patterns of suppression and release at Arbutus Lake and Wolf Lake were generally quite similar. Trees in both stands had an average of approximately 3 periods of suppression prior to recruitment. Nine of the ten trees from each stand at Arbutus Lake and Wolf Lake had periods of suppression following early release (rather than a single long period of early suppression followed by canopy recruitment). Trees in the two stands showed an average of 68 or 80 years of suppression prior to final release at an average age of 110 or 126 years. The mean lengths of periods of suppression ranged from 22 years at Wolf Lake to 28 years at Arbutus Lake, while the mean lengths of periods of release ranged from 14 years at Wolf Lake to 24 years at Arbutus Lake. Mean diameters at (1.0 m ht.) at the beginning of final release were 9.8 cm at Wolf Lake and 11.8 cm at Arbutus Lake (Table 2).

The years in which the trees from each stand began their final period of release are shown in Figure 2. The trees with no history of suppression at Little Sucker Brook ranged from 49 to 94 years old at 1.0 m above the ground. The actual years during which the stand was logged are uncertain, but the non-suppressed trees show a fairly wide range of release dates (from 1890 to

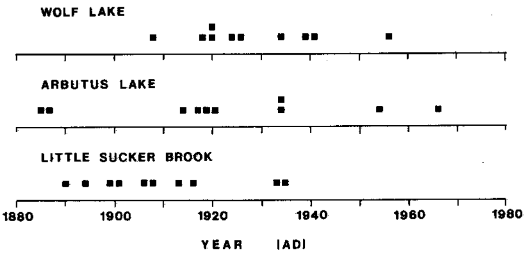

Fig. 2. Dates of final release of the 10 trees in each stand.

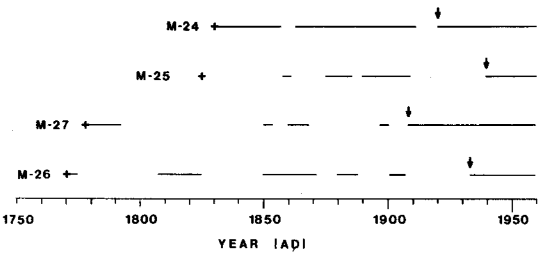

Fig. 3. Periods of release during recruitment of 4 adjacent trees in the Wolf Lake stand. Periods of release are indicated by solid lines. The dates of final release (defined as the point of canopy recruitment in this study) are indicated by arrows. The crosses indicate the oldest rings in each core.

1935). The fairly wide range of release dates suggests that selective logging (presumably high–grading for large conifers) may have occurred several times. In addition, the logging may have affected not only seedlings but also saplings previously released in openings created by either earlier logging or natural disturbances.

The release dates of trees in the unlogged stands (Arbutus Lake and Wolf Lake) should reflect the history of gap formation from natural causes. Release dates in these two stands were examined for evidence of clustering of release in distinct intervals in response to major windstorms or other forms of widespread but non–catastrophic disturbance. In general, there was only slight synchrony in the times of release of trees in the two stands. At Arbutus Lake, 4 trees were released during the period from 1914 to 1920, while 5 trees at Wolf Lake were released during the period from 1918 to 1926. A second minor concentration occurred in 1934 (3 trees from the 2 stands) and 1939–41 (2 trees at Wolf Lake). Only one tree from each stand had a final release date in the years immediately following a major storm in the Adirondacks during November of 1951.

In all cases, the clusters of release dates reflected the release of non–adjacent trees, rather than the release of several trees in a single large gap. Four of the trees cored at Wolf Lake were adjacent to one another, and their patterns of suppression and release (Fig. 3) illustrate the differences in the means by which adjacent saplings eventually reach the canopy. The four trees ranged in age from 153 to 213 years, and had final release dates ranging from 1908 to 1941. The oldest tree (M-26) dated from prior to 1770, and showed 5 relatively brief periods of release during the 164 years prior to final release in 1934. The youngest tree (M-24) was approximately 60 years younger than M-26, but reached the canopy 14 years before M-26, after just two brief periods of suppression lasting a total of 15 years. However, it took 75 years of release in two openings before sapling M-24 reached an opening in which it could continue growth to full canopy height. In contrast, the first tree of the group to actually reach final release (M-27) did so after only a total of 30 years of release during the previous 130 years. Radial growth during periods of release of M-27 contributed only 36% of total radius prior to final release (in 23% of the time prior to final release). However, estimates of height growth rates for saplings of *Acer saccharum* (Canham 1984) suggest that a much greater fraction of total height growth occurred during the 4 brief periods of release prior to final release in 1908. Height growth rates of saplings in even small openings averaged 28.7 cm/yr, while understory saplings averaged just 2.8 cm of net height growth per year (Canham 1984). Thus, even 30 years of release could conceivably contribute over 8 meters of total height, while 100 years of suppression would be expected to result in less than 3 meters of total height growth.

There was very little evidence of synchrony in the times of release of the 4 trees, even though they were separated from their nearest neighbor in the group by only 5–7 meters. The differences in the timing of suppression and release could have resulted from a combination of both highly local variation in the geometry of gaps visible above each sapling, and competitive interactions among the four individuals.

There was considerable year–to–year variation in the ring widths of trees during periods of both suppression and release. Figures 4–7 depict the actual growth rates of 4 cores chosen to represent different general patterns of growth. Dashed lines indicate periods of release; arrows indicate date of canopy recruitment.

Figure 4 shows the growth rates of one of the trees (M-1 at Little Sucker Brook) that had no distinct periods of suppression.

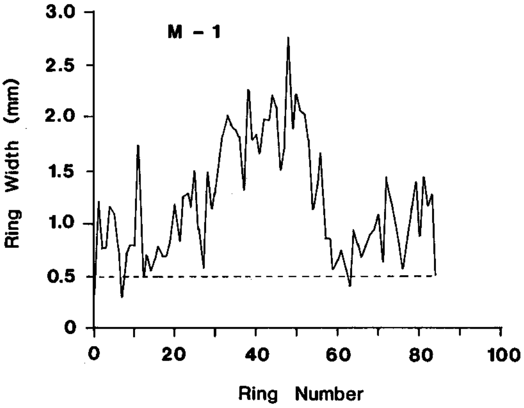

Fig. 4. Pattern of radial growth with no definable periods of suppression in tree M-1 at Little Sucker Brook. Ring #1 is the innermost ring, dashed line indicates period of release.

Nonetheless, there was both considerable short-term fluctuation in yearly growth rates, and evidence of longer-term trends in mean growth rates. While the pattern of a period of increasing average growth rate followed by a general decline in growth rates was common to all of the unsuppressed trees cored at Little Sucker Brook, there was little actual synchrony among the trees in the times at which maximum and minimum average growth rates occurred. Growth rates in these trees may reflect varying degrees and times of crown closure by lateral growth of neighboring and taller trees.

Figure 5 shows a pattern of relatively long, early release followed by suppression, in a core from Wolf Lake (M-21). The earliest rings indicated a 6 year period of suppression, followed by 45 years of release, with growth rates during release ranging from 0.55 mm/yr to 1.59 mm/yr. This was followed by 33 years of suppression with growth rates ranging from 0.10 to 0.62 mm/yr. The second period of release then lasted 28 years, and was separated from the final release by a short, 4 year period of suppressed growth rates.

Figure 6 illustrates an example of a long, well-defined period of suppression (tree M-16 at Arbutus Lake). There was evidence of a brief release from ages 20 to 25, but this was followed by 74 years of uninterrupted suppression. The sapling was then abruptly released at age 105. Growth rates subsequently declined over the next 30 years. The peak at around age 140 may represent an expansion of the opening created 30 years earlier; however, this was followed by a brief (14 year) period of suppressed growth rates. Final release came at ring #166, signaling a period of highly variable but high average radial growth rates.

The core from tree M-26 at Wolf Lake

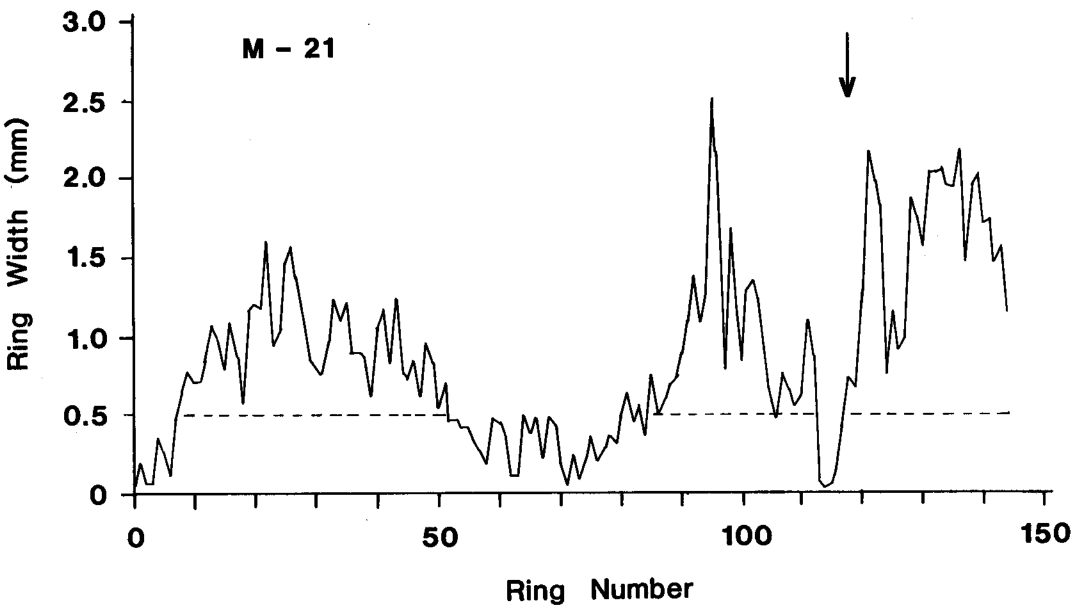

Fig. 5. Long period of release followed by suppression prior to recruitment of tree M-21 at Wolf Lake.

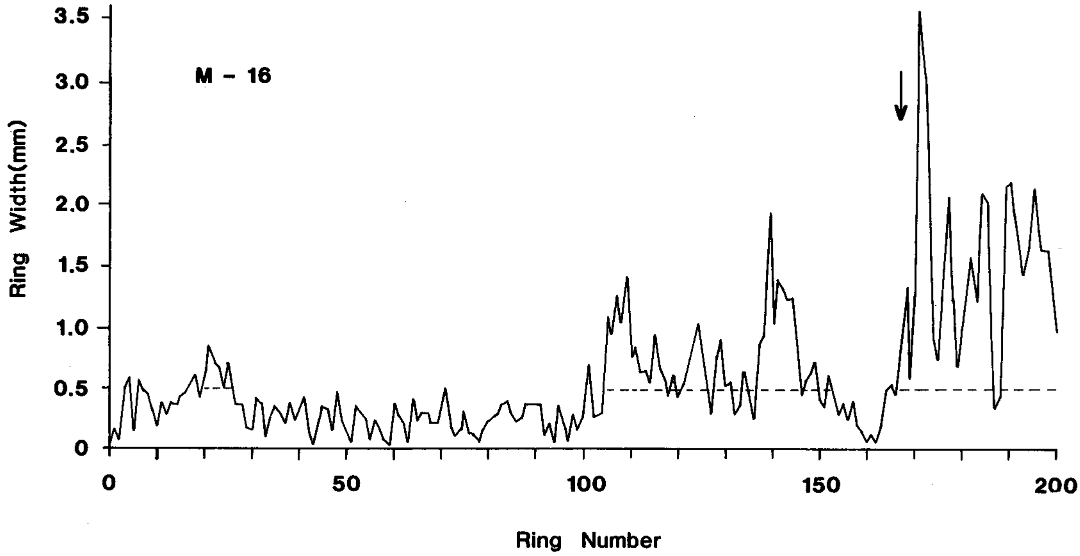

Fig. 6. Pattern of radial growth with a 74 year period of suppression in tree M-16 at Arbutus Lake. The most recent 16 years of growth as a canopy tree (growth rates ranging from 0.34 to 3.43 mm/yr) are not shown.

(Fig. 7) showed 5 distinct periods of release followed by suppression, prior to eventual recruitment at ring #164 (diameter 15.2 cm at 1.0 m height). The 5 periods of suppression ranged from 9 to 32 years in length with a mean length of 21 years. The 5 periods of release ranged from 3 to 19 years in length, with a mean length of 11.6 years. Of the 163 years of growth (above 1.0 m height) prior to recruitment, 105 years were spent in periods of suppression.

The cores from Wolf Lake and Arbutus Lake were also examined to determine the abruptness of the transitions between suppression and release. For all transitions (either suppression to release or release to suppression), where both periods were at least 7 years in length, the magnitudes and directions of the annual changes in absolute radial growth for the 5 years immediately preceding and following the transition were calculated. These rates of change

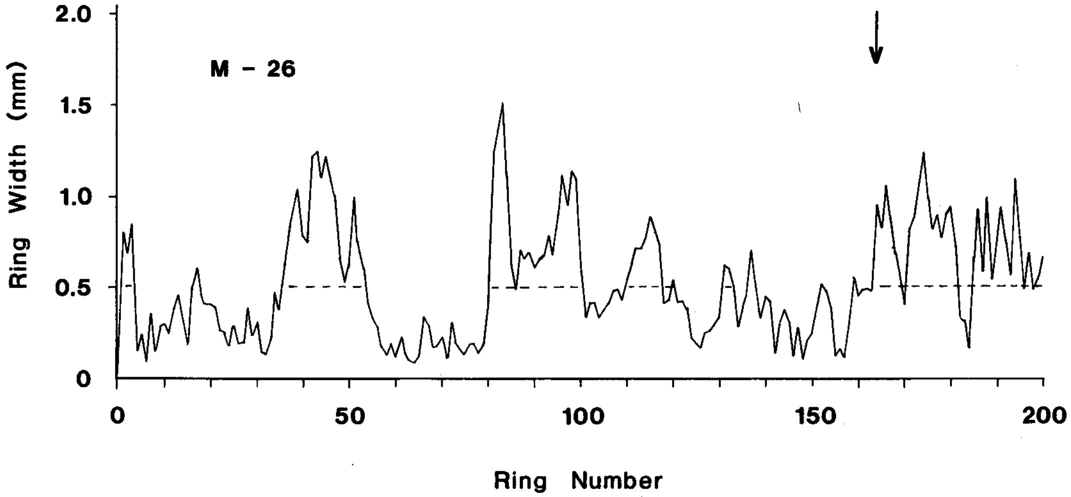

Fig. 7. Successive episodes of suppression and release prior to recruitment of tree M-26 at Wolf Lake. The most recent 13 years of growth as a canopy tree (growth rates ranging from 0.31 to 1.33 mm/yr) are not shown.

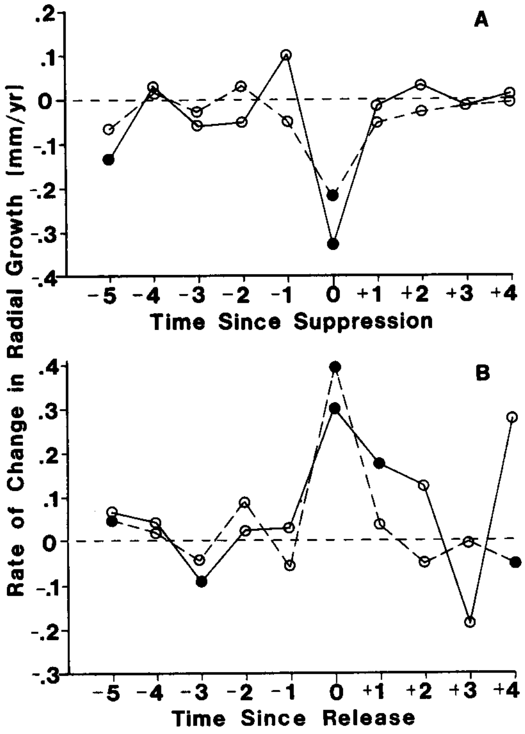

Fig. 8. Mean rates of change in radial growth for the 5 years immediately before and after the beginning of a period of suppression (A) and release (B). Rates of change for years with open circles were not significantly different than zero. Solid lines = Arbutus Lake, Dashed lines = Wolf Lake.

were then averaged for each of the years preceding and following the transition between suppression and release. This procedure acts to average out the effects of yearly oscillations in growth and indicate any general trends that are predictable functions of changes in forest microclimate or changes in biomass allocation in saplings during the years immediately preceding and following the years identified as the start of a period of suppression or release.

If the transition from release to suppression is generally characterized by a gradual decline in growth during the 5 years prior to the start of a period of suppression, then the mean change in growth during that period (averaged over all of the transitions from release to suppression in a given stand) should be negative. For the transitions from release to suppression at Wolf Lake (n = 14) and Arbutus Lake (n = 13), only 1 of the 5 years prior to suppression (year −5) in one of the stands (Arbutus Lake) showed a mean change in growth that was significantly less than zero (Figure 8A). In both stands, the years identified as the start of a period of suppression were characterized by a mean reduction in growth of from 0.22 to 0.33 mm/yr. However, during the 5 years prior to the identified initiation of suppression, the increases in growth from year to year balanced the declines, resulting in no significant trend. Moreover, beginning with the second year following suppression, the mean rates of change were again not significantly different than zero. These results indicate that the transitions from release to suppression recognized by the definition of suppression used in this study (i.e., 4 or more years of growth <0.5 mm/yr without 3 or more years of consecutive growth >0.5 mm/yr) were sharply distinct, with little evidence of gradual declines in growth during the 5 years immediately prior to suppression or the 4 years following the first year of suppression.

The patterns of growth preceding and following the beginning of a period of release showed a similarly abrupt transition (Fig. 8B). For one of the 5 years preceding release in each stand, the average, yearly rate of change in growth was significantly different than zero. However, the year defined as the initiation of release was characterized by a mean increase in growth of from 0.30 to 0.40 mm/yr. At Arbutus Lake, the second year of the release was also significantly greater than zero, indicating a continuation of increasing growth rates into at least the second year of the release. However, at Wolf Lake, the rates of change in growth for three years following release were all not significantly different than zero, indicating that the transition from suppressed to released growth rates occurred in one year, with no evidence of a longer trend of increasing average growth during the years immediately preceding and following release.

Discussion. The results indicate that the ability to withstand suppression is an important component of the process of canopy recruitment by *Acer saccharum* in old–growth forests of the Adirondacks. Selective logging over 60 years ago in the Little Sucker Brook stand was apparently extensive enough to allow many saplings of *Acer saccharum* to reach the canopy in a single period of release. However, in the stands at Arbutus Lake and Wolf Lake with no known history of logging, all of the 20 trees showed signs of at least one period of suppression prior to eventual canopy recruitment.

Several different scales of disturbance to the canopies of an old growth forest can be recognized. Studies of the frequency of catastrophic windstorms in presettlement forests of Maine (Lorimer 1977) and Wisconsin (Canham and Loucks 1984) suggest that the average return time for catastrophic disturbance by severe winds exceeds 1000 years in forests of the northeastern and northcentral United States. At more frequent intervals, severe but not catastrophic storms produce widespread small–scale disturbance to old–growth mesic forests of the northeast (Spurr 1956). In the Adirondacks, such storms can originate in either temperate latitudes as severe low pressure systems (extra-tropical cyclones) or in tropical regions as hurricanes. The most recent storm of this magnitude in the Adirondacks was a severe low pressure system in November of 1951 (Miller 1951, Roman 1980). Such storms appear to provide the major source for the large canopy openings needed for the recruitment of gap–phase species such as *Betula lutea* Michx. In the years between major storms, canopy mortality in old–growth northern hardwood forests of the Adirondacks is largely restricted to isolated individuals or groups of trees (personal observations).

Estimates of the regional frequency of severe wind storms and other forms of large canopy disturbances in the central Adirondacks are not available. Much of the region was affected by the storm in November of 1951 (Miller 1951, Roman 1980). Evidence of the storm in the form of well–rotted logs and clusters of large saplings of *Betula lutea* is common in the old–growth forests of the Adirondacks. However, most of the trees cored for this study had already reached the canopy by 1951. In contrast to other reconstructions of canopy dynamics in forests of the northeastern U.S. (e.g., Henry and Swan 1974; Oliver and Stephens 1977), the relatively small degree of synchrony in the dates of final release for trees in the Arbutus Lake and Wolf Lake stands suggests that major windstorms or other forms of widespread disturbance were not a significant factor in the actual recruitment of *Acer saccharum* in these stands during the period from 1880 to 1950.

The patterns of suppression and release observed in cores from all three of the stands reflect the particular patterns of canopy disturbance that have occurred in the past 200 years. The results of this study do not imply that seedlings of *Acer saccharum* rarely reach canopy size in single episodes of release following major storms. However, that mode of canopy recruitment was not a significant factor for trees that had reached the canopies of these stands during the past century.

While studies of gap disturbance regimes have indicated that many canopy openings are periodically enlarged by the death of trees bordering a gap (Runkle 1984), the patterns of suppression in trees cored at Arbutus Lake and Wolf Lake indicate that the process of sequential mortality of trees bordering small gaps did not create conditions suitable for the recruitment of *Acer saccharum* in single long periods of release.

The results of this study indicate that canopy recruitment by *Acer saccharum* is often a long process. There was considerable variation in the age and size of saplings at the time of their final release, but the mean age of trees in the two stands at the end of the last period of suppression was 110 or 126 years. The trees cored at Wolf Lake and Arbutus Lake spent an average of 68 or 80 of those years in periods of suppression. Barden (1983) reports a comparable mean understory residence time of 114 years (range: 29–230 years) for canopy trees of *Acer saccharum* in an old–growth cove hardwood forest in Great Smoky Mountains National Park, Tennessee.

The analysis of patterns of growth in the years immediately preceding and following the transitions between suppression and release indicates that the transitions are relatively abrupt, without significant trends either before or after the year in which suppressed or released episodes of growth begin. Despite the abruptness of the transitions, it is not possible to establish exact dates for any particular disturbance from the results of this study without independent observations of whether there is a lag between the year in which a disturbance occurs and the onset of released growth rates. The lack of a general decline in growth during the years immediately preceding the initiation of suppressed growth rates may be due to the insensitivity of growth rates in *Acer saccharum* to gap size (Canham 1984).

It is not possible to reconstruct the actual sequence of gap formation that allowed any of the trees to eventually reach canopy size. However, several lines of evidence suggest that the observed patterns of suppression and release were strongly influenced by the penetration of light through an opening into the understory beneath the canopy adjacent to a gap. If saplings only responded to openings directly overhead, then the length of suppression would be determined by the intervals between successive disturbances directly above a point in the understory. Studies of gap disturbance regimes in a wide range of temperate and tropical old growth forests (Brokaw 1984, Runkle 1982, 1984) indicate that residence times for trees in the canopy generally exceed 100 years. While the longest periods of suppression observed in the present study exceeded 100 years, the mean lengths of periods of suppression were much lower (22–28 years in the two unlogged stands). Measurements and simulations of gap light regimes (Canham 1984) indicate that there can be significant increases in seasonal total photosynthetically active radiation at the forest floor as far as 5–10 m away from the edge of a small gap (particularly for locations north of a gap). This effect is more pronounced at high latitudes, where maximum daily solar elevations are lower than at lower latitudes. Thus, even small, single–tree gaps can have a significant effect on growth rates of saplings of *Acer saccharum* in a relatively large area of the understory. Therefore, studies of gap disturbance regimes based on the vertical projection of canopy openings provide estimates of the rate of turnover of canopy trees, but underestimate the frequency with which understory saplings may be released by openings other than directly overhead. However, as saplings get taller, the effects of adjacent gaps should diminish, simply due to the geometry of penetration of light through gaps (Canham 1984). This factor, coupled with potential physical constraints on the ability of a sapling to grow up through the canopy of an overtopping tree, suggests that canopy recruitment eventually does depend on openings directly above a sapling. These considerations suggest that the most likely scenario for successful recruitment of *Acer saccharum* in small gaps involves several periods of release as a small sapling in response to mortality of nearby canopy trees, followed by the eventual replacement of the canopy tree directly overhead.

The mean lengths of periods of release in the two unlogged stands are relatively short (15–24) years, and are consistent with other studies of the rates of closure of small canopy disturbances (e.g., Runkle 1979, 1982). While saplings of *Acer saccharum* respond to even small gaps with significant increases in radial and height growth, the absolute magnitude of growth is still low (<30 cm/yr height growth) (Canham 1984). Thus, the ability to withstand suppression beneath a closed canopy appears to be an essential trait for a life history capable of exploiting these small disturbances that are short–lived relative to the length of time required for growth to canopy size.

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