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# Suppression and release during canopy recruitment in *Fagus grandifolia*[1]

**Charles D. Canham**

New York Botanical Garden, Institute of Ecosystem Studies,
Mary Flagler Cary Arboretum, Box AB, Millbrook, New York 12545

ABSTRACT

CANHAM, C. D. (Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545). Suppression and release during canopy recruitment in *Fagus grandifolia.* Bull. Torrey Bot. Club. 117: 1–7. 1990.—Stem radial growth patterns were used to reconstruct the history of suppression and release during canopy recruitment of *Fagus grandifolia* Ehrh. (beech) in three old-growth northern hardwood forests. Overall, eighty percent of the cores showed periods of suppression prior to recruitment. The average number of periods of suppression in the 3 stands ranged from 1.9–2.4, and the average total length of suppression ranged from 45–52 years. At recruitment, trees averaged 66–80 years old with diameters of 5.1–7.4 cm at 1 m height. In comparison with *Acer saccharum* Marsh. (sugar maple) in the same stands, beech trees reached final release after fewer and shorter total length of suppression, and at much smaller sizes. Calculations using average height growth rates for suppressed and released saplings of both species suggest that beech saplings achieve half of their height at final release while suppressed, while growth of sugar maple saplings during suppression accounts for only 15% of their height at final release. The frequency and duration of periods of release in beech indicate that canopy gaps were short-lived relative to the time required for canopy recruitment in this shade-tolerant species, and that saplings responded to gaps created by the deaths of nearby canopy trees before replacing the canopy tree directly overhead.

Key words: *Fagus grandifolia,* canopy recruitment, canopy gaps, radial growth, suppression, release, northern hardwood forests.

The ability of shade-tolerant tree species to withstand suppression allows qualitatively different responses to gap disturbance regimes than those observed in shade-intolerant species (Canham 1989). Shade-intolerant species require relatively large gaps because of their need for gaps that neither close laterally nor through growth by advance regeneration of shade-tolerant species, rather than simply because of a physiological requirement for relatively high illumination per se. In contrast, combinations of physiological and morphological traits allow shade-tolerant tree species to respond to even slight increases in understory light levels produced by the penetration of diffuse radiation through small, short-lived openings anywhere in the canopy (e.g., Platt and Hermann 1986; Canham 1988a). Thus, the fate of saplings of shade-tolerant species may depend more strongly on the frequency of disturbance and the duration of periods of suppression and release than on gap size or actual gap light levels (Canham 1989).

Turnover times for canopy trees in a wide range of temperate and tropical forests are often in the range of 100–200 years (Brokaw 1985; Runkle 1985); however, the penetration of light into the understory adjacent to a gap (Canham 1988b) should result in releases of shade-tolerant saplings much more frequently than once every 100–200 years. Saplings of *Acer saccharum* (Marsh.) (sugar maple) experienced an average of three distinct periods of suppression before finally reaching a position (at an age of over 100 years) that allowed unimpeded growth to canopy height in two old growth northern hardwood stands in the central Adirondack Mountains of New York (Canham 1985). However, given the pronounced spatial variation in understory light levels present in and around gaps (Canham 1988b), shade tolerant species requiring different minimum light levels for release may experience very different frequencies of release under any given disturbance regime.

*Fagus grandifolia* Ehrh. (beech) is the most

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abundant shade-tolerant tree species in old-growth northern hardwood and mixed conifer-hardwood forests of mid-elevations in the Adirondack Mountains of New York (Heimburger 1934; Roman 1980), although populations are declining throughout the region due to mortality from a bark-canker disease (*Nectria* spp.). Height growth rates of saplings beneath a closed canopy are very low (approximately 5 cm/yr), but increase significantly when saplings are exposed to an additional 1–4% of full sunlight in small canopy gaps (Canham 1988a). In contrast with sugar maple, the other dominant shade-tolerant hardwood in these forests, beech saplings show greater height growth beneath a closed canopy and a smaller magnitude of response to gaps (Canham 1988a).

The objectives of this study were (1) to determine the patterns of suppression and release during canopy recruitment by beech saplings in old growth northern hardwood forests, and (2) to compare canopy recruitment in beech with patterns of suppression and release documented in a previously published study of sugar maple (Canham 1985).

**Materials and Methods.** The study was conducted in three old-growth northern hardwood forests located within the Huntington Wildlife Research Forest in the central Adirondack Mountains of New York. The study was done concurrently with a study of suppression and release in sugar maple (Canham 1985), and used the same research sites and methods [see Canham (1985) for a more detailed description of the study sites and basic methods]. Sugar maple and beech were canopy co-dominants in each of the three stands, while beech was generally predominant in subcanopy and understory layers (Canham 1985).

Within each stand, a random sample of 10 beech trees was selected from the population of canopy trees that were between 15 and 40 cm DBH. The trees were cored at 1.0 m above the ground, and ring widths were recorded to the nearest 0.01 mm using a microscope and a moveable stage connected to a microcomputer (Apple IIe, Apple Inc.). No attempt was made to cross-date the cores, since the analysis did not require precise chronologies. It is likely that some rings were missed due to partial or completely missing rings; however the analyses were not particularly sensitive to the absence of a few rings in any core. The various forms of standardization used in traditional dendrochronological studies were not necessary for the much simpler analysis of patterns of suppression and release used in the present study (Canham 1985).

As is the case for sugar maple, radial growth rates of beech saplings beneath closed canopies are significantly lower than radial growth rates of saplings in even very small gaps (Canham 1984, 1985). Beech saplings have average radial growth rates of 0.29 mm/yr (95% C.I. = ±0.17 mm/yr) beneath closed canopies and growth rates of 0.62 mm/yr (95% C.I. = ±0.11 mm/yr) in small gaps (Canham 1984). Radial growth rates of saplings in gaps are weakly but positively correlated with gap light levels. There is, however, no correlation between radial growth and stem diameter, suggesting a relatively constant absolute radial growth rate in any given light regime (Canham 1984). On the basis of these measurements, a growth rate of 0.5 mm/yr was chosen as a threshold indicating release. As in the previous study of sugar maple, 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. This definition greatly reduced the sensitivity of the results to short-term fluctuations in growth due to climatic effects. 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 (Canham 1985).

Estimates of height growth achieved during periods of suppression and release for both species were computed by multiplying the duration of suppression and release for each core by height growth rates of suppressed and released saplings measured in a concurrent study (Canham 1988a). Net height growth was not correlated with sapling height in either species (Canham 1984). Saplings of both species respond to even very small gaps with significant increases in height growth rates (Canham 1988a). However, height growth rates in both species are not correlated with additional increases in light levels from larger gaps (Canham 1988a). In effect, height growth in both species can be modeled as a simple step function (suppressed versus released) regardless of sapling height.

Cores from all three stands were examined to determine the abruptness of transitions between suppression and release (and vice versa) in beech. Rates of change in radial growth for the 4 years immediately preceding and following the transitions were calculated for all transitions where both the suppression and release were at least 7

Table 1. Aspects of the history of suppression and release prior to recruitment of *Fagus grandifolia* in three old-growth northern hardwood forests. The results were computed for only those cores with definable periods of suppression in each stand. Canopy recruitment was defined as the point at which saplings began the period of release during which they reached current canopy size. F statistics from one-way ANOVA models showed no significant differences among the 3 stands for any of the parameters in the table.

| | | Little Sucker Brook | Arbutus Lake | Wolf Lake |
|---|---|---|---|---|
| Percent of cores with periods of suppression | | 70% | 100% | 70% |
| Number of periods of suppression per core | $\bar{x}$ | 2.3 | 1.9 | 2.4 |
| | SD | (1.4) | (0.7) | (1.0) |
| | range | 1–4 | 1–3 | 1–4 |
| Lengths of episodes of suppression (yr) | $\bar{x}$ | 22.6 | 23.4 | 18.9 |
| | SD | (15.0) | (18.7) | (17.9) |
| | range | 5–64 | 4–75 | 4–77 |
| Lengths of longest suppression (yr) | $\bar{x}$ | 32.9 | 34.3 | 28.7 |
| | SD | (16.6) | (19.0) | (23.5) |
| | range | 17–64 | 13–75 | 4–77 |
| Total length of suppression (yr) | $\bar{x}$ | 51.7 | 44.6 | 45.9 |
| | SD | (39.3) | (24.5) | (32.3) |
| | range | 17–120 | 13–104 | 4–108 |
| Lengths of episodes of release[a] (yr) | $\bar{x}$ | 15.3 | 17.8 | 11.6 |
| | SD | (11.6) | (25.7) | (9.4) |
| | range | 3–39 | 3–72 | 3–38 |
| Total length of release prior to recruitment (yr) | $\bar{x}$ | 26.1 | 19.6 | 18.3 |
| | SD | (22.7) | (27.3) | (14.5) |
| | range | 0–63 | 0–72 | 3–47 |
| Age at recruitment (yr) | $\bar{x}$ | 79.6 | 65.5 | 65.9 |
| | SD | (56.6) | (47.3) | (37.5) |
| | range | 25–161 | 14–172 | 18–132 |
| Size at recruitment (cm diameter at 1.0 m height) | $\bar{x}$ | 7.41 | 5.73 | 5.14 |
| | SD | (6.24) | (6.09) | (2.65) |
| | range | 0.8–17.5 | 0.9–18.2 | 1.8–9.7 |

[a] For periods of release followed by suppression.

years in length. This procedure is identical to doing a first-difference standardization (Fritts 1976), with values being averaged on the basis of time since suppression or release, rather than for calendar years. The procedure allows detection of consistent positive or negative trends in radial growth as a function of time since suppression or release.

**Results.** Eighty percent of the beech trees cored in the three stands showed distinct periods of suppression prior to canopy recruitment, and the patterns of suppression and release were very similar among the three stands (Table 1). For the 24 trees showing at least one period of suppression, individual trees experienced an average of 1.9–2.4 periods of suppression lasting a total of 45–52 years before eventual recruitment at an average age of 66–80 years and a stem diameter of 5.1–7.4 cm (at 1 m height) (Table 1).

These results for beech can be compared with comparable measurements for sugar maple in the three stands (although the number of maple cores showing suppression and release in the Little Sucker Brook stands is too small for meaningful statistical comparisons) (Table 2). In general, beech saplings reached final release after fewer periods and lower total length of suppression, and at a much younger age and smaller size than sugar maple stems in the same stands (Table 2). The results suggest that beech and maple both achieve roughly 2 m of height growth while suppressed (Table 2), although the beech saplings require much less time because of higher growth rates while suppressed (i.e., 5.2 cm/yr vs. 2.8 cm/yr, Canham 1988a). In contrast, the two species differ greatly in the amount of height growth in gaps prior to final release (2.3–3.3 m for beech vs. 6.6–13.1 m height growth for maple) (Table 2).

It is possible to define three modes of canopy recruitment in these two shade-tolerant species: (A) growth to canopy size without any intervening suppression, (B) an initial, single period of suppression as a small sapling, followed by release in a gap that allows continuous growth to

Table 2. Comparison of suppression and release patterns in sugar maple and beech cores from each of the three stands. Asterisks give the significance of *t*-tests for differences between maple and beech cores in each stand (*: $P < 0.05$, **: $P < 0.01$). Data for maple are from Canham (1985) and additional analyses done for the present study.

| | Little Sucker Brook | | Arbutus Lake | | Wolf Lake | |
|---|---|---|---|---|---|---|
| | Maple | Beech | Maple | Beech | Maple | Beech |
| Number of cores with periods of suppression (N) | 2 | 7 | 10 | 10 | 10 | 7 |
| Number of periods of suppression | 2.5 | 2.3 | 2.8 | 1.9* | 3.0 | 2.4 |
| Length of longest suppression | 15.5 | 32.9 | 53.9 | 34.3 | 39.2 | 28.7 |
| Total length of suppression | 36.5 | 51.7 | 79.1 | 44.6* | 68.3 | 45.9 |
| Total length of release | 23.0 | 26.1 | 45.8 | 19.6 | 38.6 | 18.3 |
| Estimated height growth during suppression (m) | 1.0 | 2.7 | 2.2 | 2.3 | 1.9 | 2.4 |
| Height growth during release prior to recruitment (m) | 6.6 | 3.3 | 13.1 | 2.5** | 11.1 | 2.3** |
| Age at recruitment | 60.5 | 79.6 | 127.8 | 65.6* | 109.5 | 65.9* |
| Stem diameter at recruitment | 6.3 | 7.4 | 11.8 | 5.7* | 9.8 | 5.1* |

canopy height, and (C) multiple periods of suppression prior to final release. The results show that, despite differences in the frequency and duration of suppression between the two species, the pattern of multiple periods of suppression and release was still the predominant mode of canopy recruitment for both species (Fig. 1). These results are in agreement with calculations by Runkle and Yetter (1987) using measurements of sapling height growth and gap closure. Even when gaps were relatively large (i.e., 400 $m^2$), they predicted that two or more gap events were required for canopy recruitment of a wide range of species in old-growth forests of the Great Smoky Mountains.

Specific examples of the three modes of canopy recruitment are given in Fig. 2. The core from tree B-23 at Wolf Lake (Fig. 2A) illustrates growth to canopy size without any intervening suppression. As was the case for sugar maple cores showing the same mode of recruitment (Canham 1985), there is substantial year-to-year variation as well as evidence of longer-term trends in growth. The core from tree B-18 at Arbutus Lake (Fig. 2B) shows 57 years of early suppression, followed by release in 1921. Although the sapling was only 2.1 cm in diameter at that time, it grew without further suppression to its current canopy position (and a diameter of 17.8 cm in 1983). The core from tree B-30 at Wolf Lake (Fig. 2C) shows a 29-year period of initial suppression, followed by a 12-year period of release. The sapling was suppressed for the next 30 years, although growth rates in several isolated years exceeded 0.5 mm/yr. Canopy recruitment occurred in 1935 when the sapling was 4.5 cm in diameter. The cores from B-18 and B-30 both show periods of relatively low radial growth during parts of the past 20–30 years. Many of the beech trees in the tree stands show cankers from beech bark disease, and the timing of the decline is consistent with the spread of the disease into the Adirondacks (Houston et al. 1979). The higher growth rates in cores B-18 and B-30 in the late 1970's may reflect release of these canopy trees due to death of adjacent trees.

The approximate dates of canopy recruitment for the sampled beech trees ranged from 1867 to 1980 (Fig. 3). However the majority of recruitment dates for both species were clustered between 1900 and 1940. Although the sample does not provide a complete chronology of recruitment dates for the 3 stands, the results indicate a pulse of canopy recruitment by both species prior to 1940, with a subsequent hiatus during the past forty years. The pulse of recruitment resulted in a significant number of relatively young and small canopy trees in all 3 stands. This may have acted to both reduce the subsequent rate of canopy tree mortality, and increase the rate of gap closure as these new canopy trees actively expanded to fill adjacent gaps.

Transitions from suppression to release were characterized by an average increase in radial growth rate of 0.37 mm/yr (from 0.34 mm/yr in the year prior to release, to an average growth rate of 0.71 mm/yr in the year of release). However, for the 4 years preceding and following release, only one year showed a significant change in rate of growth (Fig. 4). This result is compa-

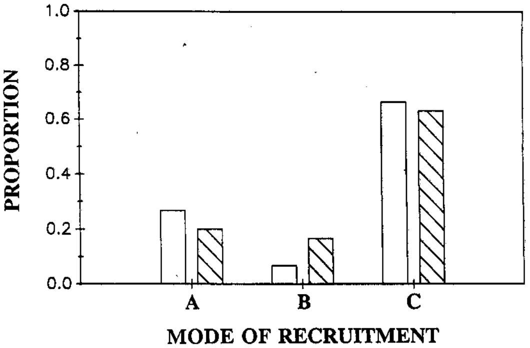


Fig. 1. Proportions of current canopy trees (15–40 cm DBH) that reached the canopy through three different modes of recruitment: (A) growth to canopy size without any periods of suppression, (B) an initial, single period of suppression as a small sapling, followed by release in a gap that allowed continuous growth to canopy size, and (C) multiple periods of suppression prior to final release. Beech = striped bars, maple = clear bars. The data are averaged over all three stands. Data for maple are from Canham (1985) for comparison.

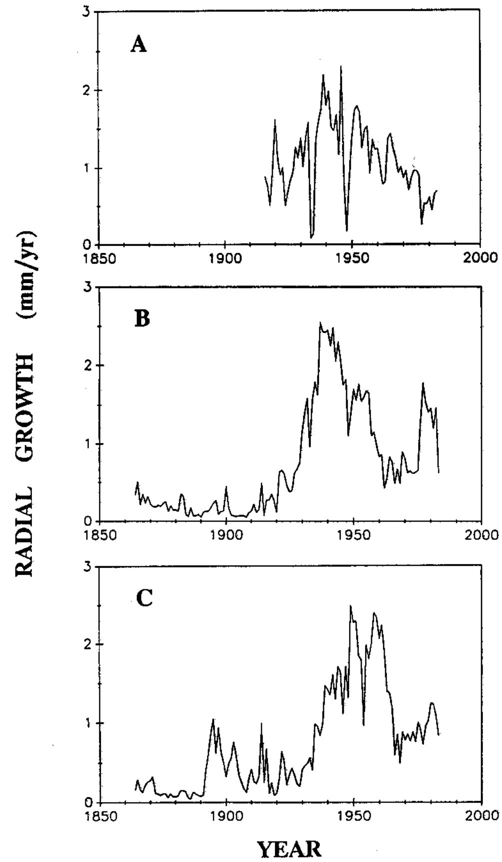


Fig. 2. Representative radial growth patterns from three beech trees. (A) A core from the Wolf Lake site showing no suppression. (B) A core from Arbutus Lake showing a 57-year period of suppression prior to canopy recruitment in 1921. (C) A core from Wolf Lake showing a 29-year period of suppression, 12 years of release, and then 30 more years of suppression prior to canopy recruitment in 1935.

rable to the pattern observed in sugar maple (Canham 1985) and indicates that the transition from suppression to release occurs within one year, with no subsequent general trend in growth during the following 4 years.

Transitions from release to suppression mirrored the pattern described above. The year identified as the start of suppression was characterized by a drop in radial growth rate of 0.33 mm/yr (from an average growth rate of 0.64 mm/yr in the year prior to suppression to 0.31 mm/yr in the first year of suppression). However, only one of the 4 years immediately preceding or following the start of suppression showed a significantly non-zero rate of change in growth (Fig. 4). It should be noted that without independent dating of gap formation and closure, it is not possible to determine whether the observed changes in radial growth occurred immediately following gap formation or closure, or were delayed by some period of years.

**Discussion.** The average durations of individual periods of suppression are similar for both beech and sugar maple (15–29 years), and are much shorter than the expected return time for a canopy disturbance directly above any point in the understory. However, even small canopy gaps allow significant penetration of light into the understory adjacent to a gap (Canham 1988b). Thus, saplings of both species appear to be successively released by the deaths of nearby canopy trees, allowing saplings to reach subcanopy size and eventually replace the canopy tree directly overhead.

The most striking differences between the patterns of suppression and release in the two species are the size and age of stems at recruitment (Table 2). Previous results showing higher growth rates by beech saplings beneath a closed canopy (Canham 1988a) suggest that beech may have a lower threshold of light required for release than sugar maple. It is possible that ambient light levels above 5 m height (the average height of final release in beech) are sufficiently high that beech saplings are effectively released in most locations even though there are no distinct gaps overhead. Terborgh (1985) has suggested that light levels reach a local maximum at an intermediate height

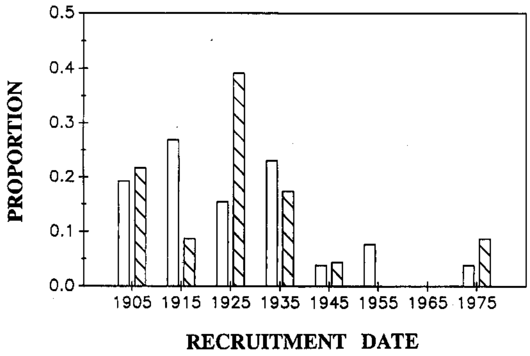


Fig. 3. Proportions of current canopy trees with recruitment dates in the 8 decades between 1900–1980. Beech = striped bars, maple = clear bars. The data for each species are averaged over all three stands. Data for maple are from Canham (1985).

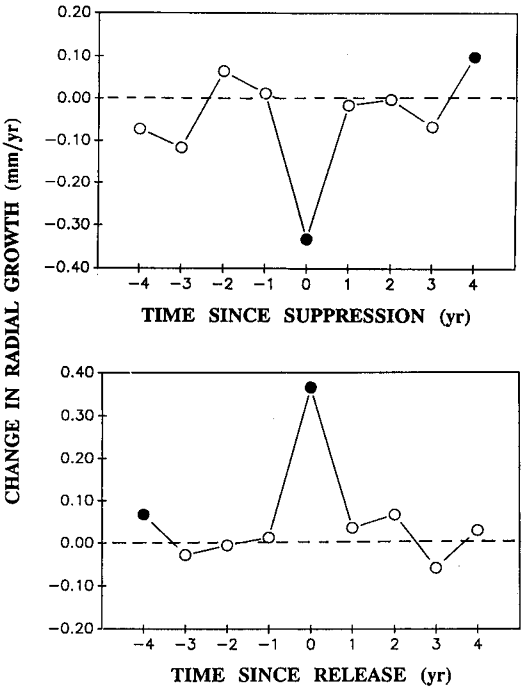


Fig. 4. Mean rates of change in radial growth for the 4 years preceding and following the beginning of periods of suppression or release in beech. Rates of change with open circles were not significantly different than zero (using a two-tailed *t*-test).

above the forest floor, and then a minimum at a height just beneath the crowns of canopy trees. However, there is currently too little data on vertical gradients of light in northern hardwood forests to support any specific predictions. Given the relatively low height growth rates of beech saplings even when released (i.e. <15 cm/yr, Canham 1988a), a 5 m tall sapling located beneath an intact canopy tree would require at least 67 years of release to reach 15 m height (the average height of the base of the crowns of large canopy trees in the study areas, personal observation). This period of time is long enough that there is a reasonable probability of mortality to the canopy tree overhead. There were beech cores in my samples that showed suppression of large saplings. However, under this scenario, most saplings would be expected to grow continuously once they reached roughly 5 m height, with death of the canopy tree directly overhead occurring before the sapling was either physically suppressed by mechanical abrasion (Kelty 1986) or physiologically suppressed by low light levels.

There is a gradient in the degree to which shade-tolerant species respond to the pulses of light and other resources created by canopy disturbance. At one extreme is the ability to grow slowly but consistently beneath a closed canopy, without significant response to gaps. Individuals that reach subcanopy size by this mode of growth may then fill a gap that forms overhead before the gap is closed by neighboring canopy trees or saplings of faster growing species. At the other extreme are species that show negligible aboveground growth beneath a closed canopy, but respond significantly to gaps formed nearby (Canham 1988a, 1989). It has been suggested that this gradient in the magnitude of response to gaps is accompanied by an inverse gradient in the duration of periods of suppression that can be tolerated by species (Poulson and Platt 1989). Beech saplings show a much more modest response to gaps than sugar maple (Canham 1988a), but in the present study, canopy recruitment by beech occurred after less total suppression than in sugar maple. While my observations do not directly address Poulson and Platt's (1989) hypothesis, the results of this study indicate that species with more modest responses to gaps do not necessarily require the ability to withstand longer periods of suppression or greater total length of suppression than species with stronger gap responses.

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