Gap dynamics in a hemlock–hardwood forest

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The dynamics of small openings in a hemlock–hardwood stand at the Harvard Forest, Petersham, Massachusetts, were studied. Rates of lateral growth of canopy tree species into openings ranged from 6 to 14 cm/year with a maximum of 26. Red oak (*Quercus rubra* L.) (RO) had the highest rate of lateral expansion. In small openings ($r < 0.25 \times$ tree height), regenerating species ranked by rate of height growth were as follows: black birch (*Betula lenta* L.) (BB) > red maple (*Acer rubrum* L.) (RM) > yellow birch (*B. alleghaniensis* Britton) (YB) > hemlock (*Tsuga canadensis* (L.) Carr.) (HK) = red oak; in moderate size openings ($r = 0.25$ to $0.5 \times$ tree height), the ranking was birches = RM > RO > HK; in open grown even-aged stands, the ranking was RO > BB = RM = YB > paper birch (*B. papyrifera* Marsh.) ≫ HK. A comparison of rates of height growth with opening closure rates indicates that tree reproduction is not successful in openings of less than about $0.5 \times$ tree height in diameter. This is primarily because small openings close quickly by lateral growth of the surrounding canopy trees and is not simply a factor of changes in rates of height growth with opening size.

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La dynamique des trouées dans un peuplement de tsuga–feuillus a été étudiée à la Forêt de Harvard, Massachusetts. Le taux de croissance latérale des essences du couvert foliacé dans les trouées a varié de 6 à 14 cm/an, avec un maximum de 26. Le chêne rouge (*Quercus rubra* L.) a exhibé l'expansion latérale la plus rapide. Dans le cas des petites trouées dont le rayon était inférieur au quart de la hauteur des arbres (h), les essences en régénération ont montré une croissance en hauteur dans l'ordre décroissant suivant: bouleau noir (*Betula lenta* L.) > érable rouge (*Acer rubrum* L.) > bouleau jaune (*B. alleghaniensis* Britton) > tsuga (*Tsuga canadensis* (L.) Carr.) = chêne rouge; dans le cas des trouées de grandeur moyenne (r = 0,25 à 0,5 h), l'ordre fut le suivant: bouleaux = érable rouge > chêne rouge > tsuga; avec les peuplements équiennes clairiérés, l'ordre fut chêne rouge > bouleau noir = érable rouge = bouleau jaune > bouleau à papier (*B. papyrifera* Marsh.) ≫ tsuga. La comparaison de la croissance en hauteur avec la vitesse de fermeture des trouées montre que la reproduction n'est pas satisfaisante dans les trouées dont le diamètre est inférieur à la demi-hauteur des arbres. La raison tient au fait que les petites trouées se referment rapidement par suite de la croissance latérale des arbres adjacents et non seulement que la croissance en hauteur fluctue en fonction de la dimension des trouées.

[Traduit par le journal]

Forest managers have long been interested in the dynamics of small forest openings because harvesting timber in small patches represents one forest management alternative (e.g., Eyre and Zillgitt 1953; Gilbert and Jensen 1958). Today, ecologists are aware of the importance and relative frequency of disturbance in forests, and so are interested in the dynamics of natural openings (Woods and Shanks 1959; Skeen 1976; Ehrenfeld 1980; Runkle 1982). They have recognized that the frequency of disturbance and the size of the area disturbed have profound effects on the composition and structure of mature forests (Whitmore 1978; Hibbs *et al.* 1980; Lorimer 1980; Runkle 1982.) Small disturbances create small openings in the forest canopy and so can provide temporary growing space for understory trees and shrubs (Hibbs *et al.* 1980). These are openings small enough to close by lateral canopy growth before a canopy species can grow up in them. Moderate disturbances open larger canopy gaps and provide growing space in which the more shade-tolerant species can grow into the canopy; large disturbances cause extensive canopy destruction and tend to produce a shift in relative rates of height growth to favor less shade-tolerant species (Gilbert and Jensen 1958; Oliver and Stephens 1977; Hibbs *et al.* 1980; Runkle 1982). These larger openings may contain a mixture of species, but shade-intolerant species tend to be dominant. The interaction of this growth response spectrum of different forest species with the disturbance regime of a particular area provides a scheme that regulates forest composition by affecting species growth and so affecting species composition.

There are few studies of the actual height growth of different species in openings. Shifts in relative density of species with varying opening size have been documented (Minckler and Woerheide 1965; Skeen 1976; Leak and Filip 1977; Runkle 1982). As would be expected, shade-tolerant species were found in smaller openings. In larger openings, shade-tolerant and shade-

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TABLE 1. Lateral growth of overstory trees into forest openings, measured as mean of the last 5 years of radial growth from the tree into the opening. Samples taken in nine openings from a height of 15 to 18 m

Species	No. of trees	No. of branches	Lateral growth: Centimetres per year	± SE	Maximum
Red oak	8	52	14.03	1.65	26.4
Paper birch	3	22	10.87	1.39	24.2
Black and yellow birch	2	15	10.68	1.58	24.0
Hemlock	8	51	9.21	0.50	16.2
Red maple	6	41	8.00	0.72	20.2
White pine	2	12	6.10	0.94	11.7

intolerant species were found together, with the intolerant species growing faster. Minckler and Woerheide (1965) concluded that increasing opening size beyond about one tree height in diameter caused little further change in species composition or growth rate.

As seedlings grow up in a forest opening, the canopy surrounding the opening is growing laterally into the opening, extending over the seedlings. Trimble and Tryon (1966) found a lateral extension rate into openings of 16.5 cm/year in a red oak (*Quercus rubra* L.) overstory and 9.2 cm/year in a yellow poplar (*Liriodendron tulipifera* L.) overstory. Runkle (1982) has found rates of 8.3 cm/year in sugar maple (*Acer saccharum* Marsh.) and 7.0 cm/year in hemlock (*Tsuga canadensis* (L.) Carr.). Thinning studies have found rates of 7.5 cm/year in black walnut (*Juglans nigra* L.) (Phares and Williams 1971) and up to 25 cm/year in young yellow birch (*Betula alleghaniensis* Britton) (Erdman *et al.* 1975).

The importance of soil moisture and root growing space to regeneration in a forest has been demonstrated by Toumey and Kienholz (1931) and others. Since the rooting space of a canopy tree may extend well beyond the boundary of the tree's canopy, the measurement and study of root growing space and its effect on soil moisture are difficult. This study was done on a mesic site, and opening size was small relative to overstory tree rooting distance so it was assumed that light (not soil moisture) was the primary limiting factor.

This paper presents a case study of several openings within a small area of forest and examines the interaction of opening size, species composition, and growth with opening closure as they affect forest dynamics and composition.

Study area

This 3-ha forest stand is an old woodlot in compartment PH 4 on the Harvard Forest, Petersham, Massachusetts. The stand covers a hilltop and its north slope with the openings being on the more or less level hilltop. The soil is a moderately well drained bouldery till.

The trees forming the canopy of the stand date from heavy cuttings done in 1865 and 1885. All present overstory trees date from these or more recent disturbances so these two early cuts probably removed most of the then current canopy. Openings in the canopy were made in the 1920's following the chestnut blight, in 1938 by a hurricane, and in 1959 when small groups of hemlocks were removed to encourage hemlock regeneration. In addition, single trees have occasionally been lost to wind and (or) ice. The present composition of the forest overstory is about 50% hemlock with red oak, red maple (*A. rubrum* L.), black birch (*B. lenta* L.), white pine (*Pinus strobus*), yellow birch, and paper birch (*B. papyrifera* Marsh.) making up the rest. These trees are 18 to 24 m tall. Understory vegetation occurred in well defined groups under canopy openings in an otherwise dark (because of the overstory hemlock component) understory.

Methods

A grid of 10-m squares was established in 1.4 ha of the stand, and stem position and crown projection of trees > 5 cm dbh (diameter at 1.4 m) were mapped to the nearest 10 cm. Tree height was measured with a Haga altimeter. Openings were delineated from crown projections, and the area of an opening was defined by the projection, not as in the case of Runkle's (1982) extended opening, by stem position of surrounding trees. Opening radius is the radius of a circle with an area equal to that of the opening.

Within each of the 15 openings, three of the larger individuals of each tree species present were cut into 20-, 40-, or 60-cm-long sections (depending on tree size) and aged at each cut. When the regeneration in an opening was over 10 m tall, its height was measured and age determined from an increment core. Growth rate was calculated as total height / total age. Growth rate of open grown 40-year-old trees in an adjacent stand was also determined this way: five individuals of each species except yellow birch (n = 2) were sampled.

In nine openings, a 12-m tower was erected and 193 lateral branches growing into the opening were clipped from 29 canopy trees with a 6-m pole clipper at a height of 15 to 18 m. Lateral growth rate was determined by measuring the length of the last 5 years of horizontal extension into the openings along a horizontal radius from the tree into the opening. Locating this horizontal radius involves some approximations (tip of branch to bole of tree), but it gives a more realistic

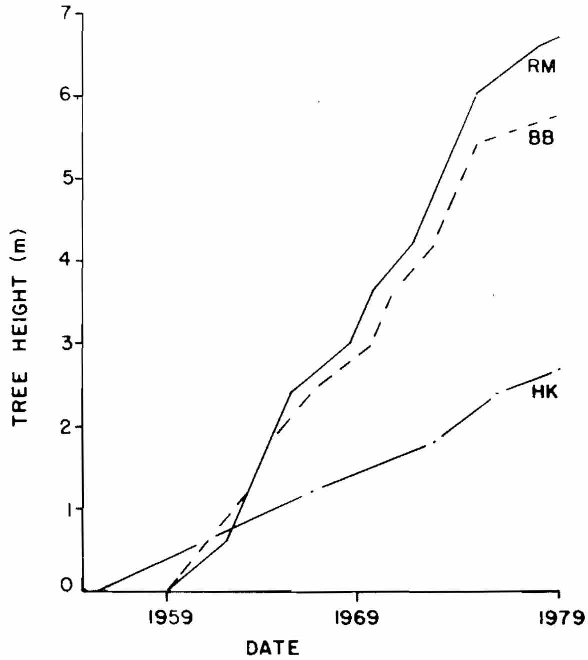

FIG. 1. Growth of three seedlings (one each of three species) in an opening with a radius of 4.2 m surrounded by 18- to 21-m-tall trees. RM, red maple; BB, black birch; HK, hemlock.

figure for lateral growth rate into openings than the inflated figure that would come from measuring the total length of growth in the last 5 years.

Nomenclature is after Little (1979) for trees and Seymour (1969) for shrubs and herbs.

Results and discussion

Lateral growth of trees into openings ranged from 6 to 14 cm/year (Table 1). Maximum observed values were considerably larger, however, indicating that closure of an opening by lateral canopy growth may be considerably faster than suggested by mean figures. For example, an opening with a 5-m radius surrounded by red oak will close in about 36 years at the average rate and in only 19 at the maximum rate. The actual rate of closure probably lies somewhere between the average and maximum values.

In general, the rate of growth of lateral branches might be expected to slow after some age or length is achieved, but when and how growth slows is a function of species and environmental conditions. There is little literature on this phenomenon, especially for hardwoods. This makes accurate prediction of opening closure difficult, but as long as the overstory trees are large relative to the opening they surround, the above projections are probably reasonable.

Within a given opening, individuals of the same species grew in height at about the same rate although there was frequently a great difference between species. As an example, Fig. 1 gives the growth of three seedlings in one opening, the growth rate of hemlock being considerably lower than that of the other species. The growth of the largest three individuals of each species in this and each other opening was measured. Linear regression on height and age at each section point of the three individuals of each species sampled in this opening gave r^2 values of 0.96, 0.89, and 0.91, respectively, for red maple, black birch, and hemlock. Thus, growth rates within a species within an opening were very similar and, surprisingly, steady over considerable time periods. It will be noted, however, that in the examples given, as in many other openings studied, growth rate in the last few years for the hardwoods in smaller openings dropped, probably indicating that the trees were being overtopped by the surrounding canopy. Also, in all openings, hemlock never grew as fast as the hardwoods and, when found with hardwoods, was found under and in the shade of the hardwood seedlings.

Figure 2 shows height growth of species in openings of a range of sizes. Opening size, while not being a direct measure of the light available in an opening, is easily measured in the field and, on level ground, does have a predictable relationship with light. Opening size can also be adjusted if necessary for closure knowing the age of the regeneration and closure rate. In fact, the steady growth of species in openings (e.g., Fig. 1) probably means that one need not be too concerned with opening size in the past because, in at least a figurative sense, the height of the photosynthetic surface in the opening has been rising as the opening has been closing to maintain a constant light level on that surface. A more general and perhaps more accurate interpretation would be that, within limits, the photosynthetic production necessary for this height growth (a function of light level and leaf surface area) is maintained by a balance between tree growth and opening closure. Why this balance should produce such a constant growth rate is not clear. In Fig. 1 it appears, for black birch especially, this balance has shifted by 1979.

In even-aged forests, trees of different species grow in height at different rates, and these rates change with time (Oliver 1978). This phenomenon was not observed here even though the age of some trees was sufficient to show it if it occurred. The simplest explanation of this is that this regeneration was resource (light) limited, and the species-specific potential growth rates were not achieved.

There are several generalizations that can be made about the rate of height growth of each species shown in Fig. 2. Hemlock was the slowest growing species in practically all openings as well as in the even-aged

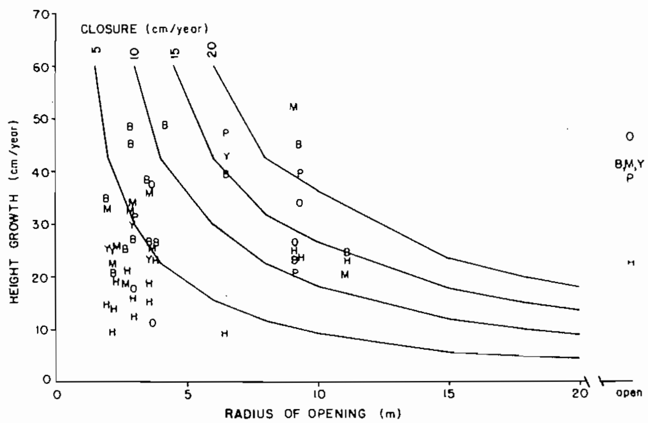

FIG. 2. Height growth of regeneration in openings in an 18-m-high canopy and a set of curves for different rates of canopy closure above which height growth must be in an opening of a given size for the regeneration to reach the canopy before the opening will close. All points represent a mean of three tallest trees of each species per opening except the rare instance where less than three individuals of each species were present. "Open" grown is from a 40-year-old even-aged stand. B, black birch; H, hemlock; M, red maple; O, red oak; P, paper birch; Y, yellow birch.

stand. In the 11 smaller openings ($r < 5$ m), species ranked by rate of height growth were, generally, black birch (B) > red maple (M) > yellow birch (Y) > hemlock (H) = red oak (O). Paper birch and red oak were rare in these openings. In the four moderate-sized openings, the ranking shifted to birches = M > O > H. Red maple was rare, and yellow birch was missing. These moderate-sized openings were all 40 or more years old so the absence of certain species may reflect the results of competition and mortality through this time. The relative scarcity of red maple in these older openings, a common component of regeneration in small openings and in even-aged forests, is noteworthy, but an explanation for the scarcity is not obvious. In the high light situation of even-aged stands, the ranking was O > B = M = Y > paper birch ≫ H. Over this range of opening size, the absolute rate of height growth of red oak, red maple, and hemlock did increase to a greater or lesser degree.

Plotted with the data of Fig. 2 are a set of curves for four different rates of canopy closure.The rate of height growth of an individual seedling in an opening of given size must fall above the curve representing the rate of closure of that opening for the seedling to reach the canopy before the opening will close by lateral growth of the surrounding trees. For example, a seedling growing in an opening with $r = 5$ m and with a lateral canopy growth rate of 10 cm/year must grow in height at least 37 cm/year to survive. If it grows more slowly, the opening will close from above before the seedling can become part of the canopy. These curves assume an 18-m-tall canopy but can be generalized by expressing opening radius in units of canopy tree height. In this case, an r of one tree height = 18 m.

This interpretation of Fig. 2 assumes that the rates of height growth and crown closure are constant. In this case, height growth did tend to be constant although there is no *a priori* reason that this should be so. In an intuitive way, a tree in an opening can be visualized as gaining photosynthetically or losing photosynthetically, these two states corresponding to trees that will or will not eventually achieve a canopy position. This gain or loss is a function of many factors including regeneration height growth and leaf area, and canopy closure and other light-reducing behaviors like canopy leaf density increase and height growth of the canopy trees. To simplify this situation and to provide a useful interpretive tool, the minimum rate of height growth a seedling must have to reach the canopy (Fig. 2) can be viewed as somewhat analogous to this break point between gaining and losing photosynthetically. When viewed in this way, the curves in Fig. 2 have a more general biological meaning.

It is apparent from this figure and Table 1 that few or no tree seedlings found in this study will reach the canopy level in openings where $r < 5$ m. In openings larger than this, the faster growing individual(s) may reach the canopy, but this success is not so much a function of improved growth with improved light conditions in the larger opening as simply the longer time available to grow before crown closure from above can be completed. Even in these larger openings, it is important to note that there is only sufficient space for one or two trees to become dominant.

Small openings represent temporary growing space because they close quickly by lateral growth of the surrounding canopy. They are not sites for regenerating tree species. Woods and Shanks (1959) and others have made similar observations in the case of canopy closure following the death of single chestnut (*Castanea dentata*) trees. This study showed that new seedlings grew in these openings but their rate of height growth was too slow to reach the canopy before it closed over them. Small forest openings may, however, be a site for successful growth and reproduction by understory woody and herbaceous species. The case of striped maple (*A. pensylvanicum*), a small tree growing and reproducing under the canopy in temporary openings in the northern hardwood forest, is an example (Hibbs 1979; Hibbs *et al.* 1980). Hemlock may also utilize the growing space of small openings, alternating periods of growth and suppression and only eventually reaching the canopy after several cycles of disturbance, growth, and canopy closure (Marshall 1927; Oliver and Stephens 1977).

Larger openings are the site of successful growth of both tree and herb species. Success of tree species is achieved not so much by higher rates of height growth in the increased light of these larger openings but simply by the longer time required to close the opening by lateral growth of the surrounding canopy. As opening size increases through the range above that which can be considered temporary, however, the competitive advantage can shift among the species present (e.g., Minckler and Woerheide 1965).

In this fashion, opening size interacts with species' requirements to regulate forest composition. This study indicates that those species growing faster in moderate-sized openings, black birch and red maple, may be able to regenerate successfully in these openings. As opening size is increased, the competitive advantage of these moderately shade-tolerant species is eroded to the point where, in large openings that provide conditions similar to the open, the advantage shifts to favor red oak. In between, no species has a clear advantage. Hemlock has a competitive advantage in no situation but can, as previously mentioned, survive suppression to respond to later canopy disturbance.

Oliver and Stephens (1977), in reconstructing the history of a mature forest plot at the Harvard Forest, found evidence of the effect of past openings and support for the findings of this study. The age distribution reflected the past disturbance history, with almost all trees dating from past canopy disturbances. Red oak was found to regenerate in and quickly dominate large openings. Black birch, red maple, and hemlock also established in these openings but became subdominants. They could later be released following a small canopy disturbance that removed a dominant tree. The spatial distribution of age-classes also indicated that most openings were small enough to be dominated by a single individual and so did not produce a small even-aged patch of reproduction. Aging of white pine (*Pinus strobus*) in the adjacent forest (Hibbs 1982) indicates that it also reproduced in openings in this forest.

Two (at least) questions are not answered by this study. The first question deals with the interaction of opening size and seedling establishment. How does opening size affect germination and initial survivial? This study utilizes already established regeneration and so misses this phase of gap dynamics.

The second question relates to the dynamics of older openings and the observation by Oliver and Stephens (1977) that moderately shade-tolerant subdominants such as red maple and black birch eventually reach the canopy following small canopy disturbances. The implication is that if an opening is large enough to allow the successful regeneration of a tree species (Fig. 2), then it is large enough for and will be dominated by a shade-intolerant species like red oak. Smaller openings will rarely allow the successful regeneration of any canopy species, and the more shade-tolerant species will generally go through a subdominant phase before eventual release.

Conclusions

Small forest openings (diameter $< 0.5 \times$ tree height) offer only temporary growing space and, as such, may be utilized only by understory woody and herbaceous species. Larger openings provide growing space for trees. These species are successful in these openings, primarily because these larger openings take longer to close by lateral growth of the surrounding canopy and secondarily because the regeneration grows faster in them. Changes in rates of height growth over that range of opening size studied, however, does indicate a shift in competitive advantage among species over that range.

Average lateral canopy growth rate ranged from 6 to 14 cm/year among the seven species, with a maximum of 26. This maximum rate may play an important role in the closure of openings.

Differences in species composition and growth rate over the range of opening sizes studied suggest that the size of opening created by a disturbance can ultimately affect forest structure and composition.

EHRENFELD, J. G. 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bull. Torrey Bot. Club, **107**: 29–41.

ERDMANN, G. G., R. M. GODMAN, and R. R. OBERG. 1975. Crown release accelerates diameter growth and crown development of yellow birch saplings. U.S. For. Serv. Res. Pap. NC-117.

EYRE, F. H., and W. M. ZILLGITT. 1953. Partial cuttings in northern hardwoods of the Lake States. U.S. Dep. Agric. Tech. Bull. No. 1076.

GILBERT, A. M., and V. S. JENSEN. 1958. A management guide for northern hardwoods in New England. U.S. For. Serv. Stn. Pap. No. 112.

HIBBS, D. E. 1979. The age structure of a striped maple population. Can. J. For. Res. **9:** 504–508.

——— 1982. White pine in the transition hardwood forest. Can. J. Bot. **60**. In press.

HIBBS, D. E., B. F. WILSON, and B. C. FISCHER. 1980. Habitat requirements and growth of striped maple (*Acer pensylvanicum* L.). Ecology, **61**: 490–496.

LEAK, W. B., and S. M. FILIP. 1977. Thirty-eight years of group selection in New England northern hardwoods. J. For. **75**: 641–643.

LITTLE, E. L., JR. 1979. Checklist of United States trees (native and naturalized). U.S. Dep. Agric. Agric. Handb. No. 541.

LORIMER, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology, **61**: 1169–1184.

MARSHALL, R. 1927. The growth of hemlock before and after release from suppression. Harv. For. Bull. No. 11.

MINCKLER, L. S., and D. WOERHEIDE. 1965. Reproduction of hardwoods 10 years after cutting as affected by site and opening size. J. For. **63**: 103–107.

OLIVER, C. D. 1978. The development of northern red oak in mixed stands in central New England. Yale University School of Forestry and Environmental Studies, Bulletin No. 91.

OLIVER, C. D., and E. P. STEPHENS. 1977. Reconstruction of a mixed-species forest in central New England. Ecology, **58**: 562–572.

PHARES, R. E., and R. D. WILLIAMS. 1971. Crown release promotes faster diameter growth of pole-size black walnut. U.S. For. Serv. Res. Note NC-124.

RUNKLE, J. R. 1982. Patterns of disturbance in some old growth mesic forests of eastern North America. Ecology. **63**. In press.

SEYMOUR, F. C. 1969. The flora of New England. Charles E. Tuttle Co., Rutland, VT.

SKEEN, J. N. 1976. Regeneration and survival of woody species in a naturally-created forest opening. Bull. Torrey Bot. Club, **103**: 259–265.

TOUMEY, J. W., and R. KIENHOLZ. 1931. Trenched plots under forest canopies. Yale University, School of Forestry, Bulletin No. 30.

TRIMBLE, G. R., JR., and E. H. TRYON. 1966. Crown encroachment into openings cut in Appalachian hardwood stands. J. For. **64**: 104–108.

WHITMORE, T. C. 1978. Gaps in the forest canopy. *In* Tropical trees as living systems. *Edited by* P. B. Tomlinson and M. H. Zimmermann. Cambridge University Press, New York.

WOODS, F. W., and R. E. SHANKS. 1959. Natural replacement of chestnut by other species in the Great Smokey Mountains National Park. Ecology, **40**: 349–361.