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Tree Replacement in Small Canopy Gaps of a *Tsuga canadensis* Forest in the Southern Appalachians, Tennessee

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Summary. Tree species replacement was studied in 95 canopy gaps created by the fall of single trees in an undisturbed, old-growth forest in Great Smoky Mountains National Park, Tennessee. When large trees (dbh > 70 cm) of the very shade tolerant species, *Tsuga canadensis*, die and fall, they are usually replaced by less tolerant species such as *Betula alleghaniensis, Liriodendron tulipifera,* and *Magnolia fraseri*. Species diversity of the replacement trees, measured by the index, $1/\Sigma p_i^2$, was 5.77 compared to a diversity of 1.66 for the fallen trees.

Forest development after endogenous disturbances such as the death and fall of individual trees has recently received renewed attention (Bormann and Likens, 1979; Botkin et al., 1972; Brewer and Merritt, 1978; Connell, 1978; Fox, 1977; Forcier, 1975; Harcombe and Marks, 1978; Skeen, 1976; Williamson, 1975) after an early beginning of pioneering studies (Watt, 1947; Bray, 1956). A central and unresolved question in these studies is whether species replacement in small canopy gaps will lead to greater dominance by shade tolerant species or maintenance of less tolerant species through opportunistic capture of canopy gaps. The present study is an attempt to answer this question in a 40 ha hemlock (*Tsuga canadensis*) forest which has apparently been protected by its geography, history, and mesic climate from exogenous disturbances such as damaging fires, violent windstorms, and cutting.

The canopy of the study forest, which is located between 940 and 1,130 m elevation in the Ramsay Prong watershed of Great Smoky Mountains National Park, Tennessee, consists primarily of hemlock, yellow birch (*Betula alleghaniensis*), and red maple (*Acer rubrum*). An evergreen shrub, *Rhododendron maximum*, dominates the subcanopy. Similar forests occur in valleys elsewhere in the southern Appalachians (Oosting and Billings, 1939; Whittaker, 1956). The climate is perhumid mesothermal, or temperate rain forest (Shanks, 1954). Nomenclature follows Little (1953).

I examined all gaps created by the fall of single canopy trees in the 40 ha forest. Of the 103 gaps found, 95 were chosen for study because they contained one replacement tree which was taller and broader in crown diameter than any other tree in the gap and could, therefore, be considered the gap successor. Eight gaps formed within the last ten years were excluded because the replacement outcome was still unclear. Gap size and species composition of the surrounding canopy were determined by visually fitting an ellipse to the canopy opening (Brewer and Merritt, 1978), measuring the major and minor axis with a modified Biltmore stick, and using the perimeter of the ellipse as a curved line intercept. The modified Biltmore stick is a 50 cm ruler held at a right angle and constant distance from the eye with a cord which is attached to the ruler at both ends. The height of the canopy was measured by rangefinder, and the gap width determined by proportions: width/height = ruler intercept/ruler distance. The curved line intercept measures coverage of trees contiguous to the gap and most likely to affect the replacement process in the gap. The species of each fallen tree was determined from bark and wood characteristics (Panshin and de Zeeuw, 1970). Age of each gap was estimated from release dates observed in increment cores from neighboring trees and from the stage of decomposition of the fallen tree.

Of the 95 canopy gaps studied, 73 were created by the fall of large hemlock (average dbh 99 cm), and the remaining 22 by hardwoods (avg. dbh 82 cm, Table 1). Species coverage of the surrounding undisturbed canopy forms a declining geometric series led by hemlock, yellow birch, and red maple (Whittaker, 1975; $r^2 = 0.98$, regression of rank versus logarithm of coverage). Median size of gaps in 1978 was 65 m^2, which is small considering the size of fallen trees (Bormann and Likens, 1979), but this area does not include lateral expansion of surrounding trees. Lateral expansion is normally 4 to 8 cm per year for mature trees (Trimble and Tryon, 1966; Runkle, 1978). The use of a radial expansion estimate of 6 cm per year times the estimated age of the gap yields a median gap size of 130 m^2 at the time of gap formation.

Of the 73 gaps formed by the fall of hemlock, that species replaced itself in only seven gaps; seven species of hardwood, led by yellow birch, filled the other 66 gaps (Table 1). In the 22 hardwood gaps, hardwoods captured the gap in 11 cases and hemlock was the successor in the remainder. Heterogeneity of species composition among the fallen and successor trees, as measured by the diversity index, $1/\Sigma p_i^2$, increased from 1.66 to 5.77, entirely as a result of greater equitability among species (Peet, 1974).

There was no significant difference in the species composition of replacement trees in gaps larger and smaller than the median ($P > 0.5$, chi square = 3.28, df = 5, *Acer, Halesia,* and *Liriodendron* grouped because of small numbers). There was also no significant difference between hemlock and hardwood replacement frequencies related to slope angle, slope azimuth, *Rhododendron* coverage, or elevation (Mann-Whitney U-test, $P > 0.05$).

Recently Connell (1978) proposed that in undisturbed old-growth forests dominant, shade tolerant species should replace themselves and other species in small canopy gaps, leading to a forest of lower species diversity. Although originally proposed for tropical

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Table 1. Relative canopy coverage of species contiguous to gaps and numbers of former and replacement trees.

Species	Surrounding canopy (%)	Former trees (no.)	Replacement trees	
			Tsuga gaps (no.)	Non-*Tsuga* gaps (no.)
Tsuga canadensis	40	73	7	11
Betula alleghaniensis	22	9	22	5
Acer rubrum	13	4	6	0
Fagus grandifolia	7	1	13	3
Liriodendron tulipifera	6	2	6	1
Magnolia fraseri	4	2	7	2
Halesia carolina	3	1	3	0
Betula lenta	2	2	9	0
Prunus serotina	1	1	0	0
Total	98[a]	95	73	22

[a] Remainder consists of *Acer saccharum, Aesculus octandra, Fraxinus americana, Magnolia acuminata, Picea rubens, Quercus rubra,* and *Tilia heterophylla.*

rain forests (Connell, 1978), this hypothesis is supported by recent studies in temperate forests (Brewer and Merritt, 1978; Harcombe and Marks, 1978). In the present study hemlock, a very shade tolerant tree (Baker, 1949), replaced itself less frequently than expected from the composition of fallen trees or from the composition of the surrounding canopy (chi square = 185 and 28, df = 1). Species less shade tolerant than hemlock (*Acer rubrum, Betula alleghaniensis, B. lenta, Liriodendron tulipifera, Magnolia fraseri*; Baker, 1949; Lorimer, 1977) replaced hemlock in 50 of 73 gaps. In particular, yellow-poplar (*Liriodendron tulipifera*), an intolerant species, has apparently maintained itself in approximately the same proportion as it exists in the surrounding intact canopy (Table 1; Buckner and McCracken, 1978). Thus, the results of this study suggest that minor endogenous disturbances such as the death and fall of single canopy trees can maintain low and mid-tolerant species in an old-growth hemlock forest.

Results of this study raise the question of how the observed replacement rates can account for the large representation of hemlock in the canopy (Table 1). A possible answer to this question is that the high percentage of hemlock in the canopy (40 percent) results from the species' ability to survive prolonged suppression and slowly force its way into an undisturbed overstory (Harlow and Harrar, 1958).

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