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Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains

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Abstract

Relationships between canopy cover and tree regeneration were determined for various species in cove forests of the Great Smoky Mountains. Old-growth stands were sampled with six plots covering a total area of 4.8 ha. Each plot was subdivided into contiguous 10 × 10 m quadrats. Canopy cover overlying each of the 480 quadrats was characterized with three different indices based on visual estimates of cover. Influences of: (1) overlying cover, (2) proximate openings, and (3) total area of proximate openings on quadrat regeneration densities were determined. Most species reproducing by seed and some species reproducing by vegetative means had higher densities in quadrats with openings, but only the intolerants were highly dependent on gaps. *Tsuga canadensis*, a very shade-tolerant species, was one of the few species with abundant regeneration beneath dense canopy cover. In general, understory areas near gaps had somewhat higher regeneration densities than other areas with overlying cover. Several shade-tolerant species showed a positive regeneration density response to canopy openings and an ability to regenerate in gaps 0.01–0.03 ha in area. These openings were too small for intolerant species. Many species exhibited a positive response to total size of the proximate opening(s). A sharp increase in regeneration density with area of the opening(s) was evident at approximately 0.04 ha for the shade-intolerant species.

Nomenclature: Radford et al. (1968).

Introduction

Recent interest in the role of canopy gaps in forest dynamics has produced a wealth of information on tree regeneration in canopy gaps (e.g., Hartshorn 1978; Whitmore 1978; Barden 1979, 1981; Denslow 1980; Runkle 1981; Hibbs 1982; Nakashizuka 1984; Brokaw 1985; Stewart 1986; Uhl *et al.* 1988; Veblen 1989; Spies *et al.* 1990; Stewart *et al.* 1991). Clearly, both shade-intolerant and shade-tolerant species can regenerate in temperate deciduous forest gaps. The comparative abundance of regeneration beneath a closed canopy and the importance of gaps in canopy recruitment of individuals that do not originate in gaps are not as clear. Pickett *et al.* (1987) state that shade tolerants 'do not simply grow slowly up through the closed canopy', while Lorimer *et al.* (1988) estimate that more than one-third of the shade-tolerant canopy trees do not originate in canopy gaps. Nakashizuka (1984), Woods (1984) and Ward & Parker (1989) present evidence of abundant tree regeneration in a variety of understory situations in temperate forests, including closed-canopy areas. Preliminary observations in an Appalachian cove forest suggest that most seed regeneration of deciduous species occurs in or near canopy gaps, and that shade tolerants often regenerate beneath the forest canopy adjacent to gaps (Clebsch & Busing 1989). Further characterization of regeneration patterns in understory areas bordering, or away from canopy gaps of species-rich cove forests may elucidate regeneration requirements for a variety of species and help clarify the role of gap versus understory origin in stand dynamics.

Table 1. Characteristics of old-growth forest study plots in the northeastern Great Smoky Mountains.

Location	Plot size[a] (ha)	Elev. (m)	Slope (deg)	Aspect	Basal area (m^2ha^{-1})	Dominants
Long Branch	0.6	920	11	N	45	*Acer-Tsuga-Halesia*
Long Branch	0.6	950	16	N	39	*Halesia-Acer-Tsuga-Aesculus*
Porters Creek	0.6	720	18	N	40	*Halesia-Aesculus-Acer*
Roaring Fork	1.0	995	10	N	48	*Tsuga-Halesia-Fagus-Acer*
Roaring Fork	1.0	960	10	N	55	*Tsuga-Halesia-Acer-Fagus*
Roaring Fork	1.0	1140	20	N	40	*Tsuga-Halesia-Aesculus*

[a] Dimensions are 50×120 m for 0.6-ha plots and 100×100 m for 1.0-ha plots.

The complexity of canopy structure has been ignored in many studies of gap phase tree regeneration. For these studies, solitary canopy openings with sharply defined boundaries were often selected. The dichotomous characterization of canopy structure as gap or non-gap is now recognized as an oversimplification of canopy cover and its influence on tree regeneration and growth (Lieberman *et al.* 1989; Canham 1989). Canopy gaps are not always single openings with clearly defined edges; they vary in size, shape, orientation and dispersion within a stand (Poulson & Platt 1989). In temperate deciduous forests the light regime of understory areas within ca. 10 m of gaps may be affected (Canham *et al.* 1990), so characterization of canopy cover within the immediate area (ca. 0.01 ha) overlying a point on the forest floor may be insufficient (Ward & Parker 1989). In temperate deciduous forests of the southeastern United States, the light regime of a point on the forest floor is influenced by canopy gaps within 10–15 m to the south, east and west of the point (Canham *et al.* 1990). As a result, regeneration levels in certain understory areas near gaps may differ from those in other closed-canopy areas.

A central tenet of patch dynamics theory is that disturbance patch size affects species composition of the assemblage colonizing the patch (Pickett 1980; Pickett & White 1985). Certain species are favored by small patches while others are favored by large patches. In forests, it does appear that canopy gap size affects the species composition of regeneration (Whitmore 1978; Denslow 1980; Runkle 1982; Brokaw 1987). Shade tolerant species are generally more successful invaders of small gaps, while shade intolerant species are more successful in large gaps. Whitmore (1982) suggests that the cutoff between large and small gaps occurs at approximately 0.1 ha. Certainly, intolerant species are successful in openings of this size in a wide variety of forests; in some forests, however, intolerants are highly successful in much smaller gaps (Prentice & Leemans 1990). For example, Hartshorn (1978) and Pickett (1983) note that some tropical intolerants are successful in gap areas greater than 0.05 ha. In deciduous forests of temperate regions the gap size threshold occurs at approximately 0.04 ha as the abundance of intolerant species increases markedly in gaps at or beyond this size (Runkle 1985; Stewart *et al.* 1991). Information on the comparative abundance and success of intolerant and tolerant species in gaps of different sizes adds to our understanding of forest community dynamics. Given that canopy openings are not always solitary, well-defined gaps, however, it also may be useful to estimate the area that single or multiple openings cover in the shade bearing canopy around a point. Contrasting responses between intolerant and tolerant species to the combined area of openings would conform to theory.

The general objective of this study was to find relationships between old-growth canopy cover and abundance of regeneration for a variety of tree species, and for groups of tree species with similar biological traits. Three simple indicators of canopy structure, based on levels of canopy shading, were used to test for effects of: (1) overlying canopy cover, (2) proximate openings, and (3) total area of overlying and proximate openings on regeneration.

Study area

Data were collected in two adjacent watersheds in the northeastern Great Smoky Mountains, Tennessee (35°40′ N, 83°23′ W). Cove sites in the Roaring Fork and Middle Prong of the Little Pigeon River watersheds were selected for sampling (Table 1). The sites were in a vast expanse of old-growth forest with no history of logging or catastrophic natural disturbance (Harmon *et al.* 1983; Pyle 1988). All sites were on north-facing, lower slopes of mountain coves.

Elevation and topographic position of the sites were characteristic of species-rich cove forests (Braun 1950; Whittaker 1956; Golden 1981). Canopy dominants ($>$ 4 m^2/ha) included *Acer saccharum*, *Tsuga canadensis*, *Halesia carolina*, *Aesculus octandra* and *Fagus grandifolia*. Of these species, only *Halesia carolina* was a dominant at all sites. *Tsuga canadensis* and *Acer saccharum* were dominants at most sites, while *Aesculus octandra* and *Fagus grandifolia* were dominants in at least a third of the sites. Shrub cover was negligible at all sites. The vegetation was typical of undisturbed coves of the middle elevations of the Great Smoky Mountains without *Rhododendron maximum*. Shanks (1954) and Whittaker (1956) provide further information on the environment and vegetation of cove forests.

Methods

Each of the six study plots was sampled with a grid system of 10 × 10 m quadrats. Within each of the 480 quadrats, data were collected for all live tree stems $>$ 1.37 m tall. Sprouts emanating at or below ground level from the base of trees were included. Species and size were noted for each stem. Individuals $<$ 2.1 cm diameter at breast height (dbh) were pooled by species into one size class, while dbh was measured to the nearest millimeter on all larger individuals. Following Ward & Parker (1989), data were subsequently summarized for an additional regeneration class of stems 2.1–10.0 cm dbh.

Canopy cover of each quadrat was quantified by an index based on four visual estimates. Canopy cover overlying each 5 × 5 m quadrant of a given quadrat was assigned a value of 0 for canopy opening, 1 for light to moderate cover, or 2 for dense canopy cover. The four values were then averaged to give an index of 0.01 ha canopy cover from 0 to 2. The distance and direction to canopy openings ($>$ 25 m^2) outside each large plot, but within 10 m of the plot's edge, were noted.

Effects of canopy cover density on tree regeneration were analyzed with the index of canopy cover overlying each 0.01 ha quadrat. Three canopy cover classes were delineated for the index in a way that produced a gap class with 10–15% of the total number of quadrats, and a dense cover class with 30–40% of the quadrats. The remaining quadrats comprised an intermediate cover class. Average stem density across all quadrats in each cover class was then calculated for three regeneration size classes: (1) stems 0.1–2.0 cm dbh, (2) stems 2.1–10.0 cm dbh, and (3) all stems 0.1–10.0 cm dbh. Density values were calculated for each species or other biological grouping. For example, a vegetative regeneration group consisted of four species with a moderate to strong tendency for basal or root sprouting from live canopy trees (*Fagus grandifolia*, *Halesia carolina*, *Magnolia fraseri*, and *Tilia heterophylla*). A seed regeneration group consisted of all other species, and a total regeneration group consisted of all tree species encountered.

Two methods were used to test for differences in regeneration densities among canopy cover classes: (1) a chi-square test, and (2) a Monte Carlo test. For each species or other grouping the relationship between density and canopy cover was tested with a chi-square statistic calculated across all cover classes. In this test, observed values were the stem tallies by class and expected values were the fraction of quadrats in a given class multiplied by the total number of stems across all three classes. A Monte Carlo test helped to determine which classes had regeneration densities substantially higher or lower than the expected values. In this test, stem tallies based on random drawings of quadrats from the entire pool of 480 quadrats were made for each species or group of species by cover class. In each case, the number of quadrats drawn from the pool was equal to the number of quadrats in the cover class being tested. The range of stem tallies across 19 random sets of quadrats provided a 95% confidence interval ($19/(19 + 1) \times 100\%$; Leemans 1991) for comparison with the actual tally for a given class. An actual stem tally outside this range indicated deviation from the expected density. These tests were also performed in the two analyses that follow. Test results were not presented for species with less than 60 stems in the entire sampling area.

A second analysis involved the categorization of each quadrat as gap, gap border, or closed canopy. Gap quadrats contained an opening $>$ 25 m^2. Gap border quadrats were non-gap quadrats within 10 m of an opening $>$ 25 m^2 to the south, east or west. Other quadrats were assigned to a closed-canopy class. As above, average density values in each class were calculated for individual species and for groups of species.

Table 2. Stem density of the tree regeneration stratum in old-growth cove forests of the northeastern Great Smoky Mountains.

Species	Tolerance[a]	Density (stems/ha) by diameter class (cm) 0.1–2.0	2.1–10.0	Total 0.1–10.0
Acer saccharum	VT	254.0	84.4	338.4
Halesia carolina	T	200.4	88.3	288.7
Fagus grandifolia	VT	151.7	63.8	215.5
Tsuga canadensis	VT	74.8	93.5	168.3
Aesculus octandra	T	92.3	69.6	161.9
Acer pensylvanicum	VT	69.6	41.5	111.1
Tilia heterophylla	T	19.8	15.8	35.6
Magnolia fraseri	M	18.3	4.0	22.3
Betula lutea	M	14.8	6.0	20.8
Liriodendron tulipifera	I	12.3	0.6	12.9
Fraxinus americana	I	11.0	1.5	12.5
Acer spicatum	–	7.3	2.9	10.2
Prunus serotina	I	2.9	2.3	5.2
Acer rubrum	T	3.3	0.2	3.5
Amelanchier arborea	–	2.1	0.8	2.9
Cornus alternifolia	–	1.7	1.0	2.7
Hamamelis virginiana	–	1.5	0.8	2.3
Carya cordiformis	I	1.9	0	1.9
Cornus florida	VT	0	1.9	1.9
Betula lenta	I	1.5	0.4	1.9
Ilex opaca	VT	0.4	0.4	0.8
Magnolia acuminata	M	0.4	0.2	0.6
Quercus rubra	M	0.6	0	0.6
Ostrya virginiana	T	0.2	0.2	0.4
Castanea dentata	M	0.2	0	0.2
Prunus pensylvanica	VI	0	0.2	0.2
Ilex ambigua	–	0.2	0.0	0.2
All species		944.0	482.5	1426.5

[a] VT = very shade tolerant, T = tolerant, M = intermediate, I = intolerant, and VI = very intolerant (Burns & Honkala 1990).

A third analysis involved an estimate of the open canopy area within the path of direct sunlight for each quadrat. For each quadrat, the number of neighboring quadrats to the south, east and west with a canopy gap (> 25 m^2) was tallied. The focal quadrat was included in the tally and an integer value from 0 to 6 representing a large gap or a series of gaps spread across an area of 0.0 to 0.06 ha, respectively. Four classes of the gap area index were delineated and stem densities were calculated for each class. These included: (1) a non-gap class of quadrats without overhead or adjacent gaps, (2) a 0.01–0.02 ha gap dispersion class, (3) a $\geq$ 0.02 – $<$ 0.04 ha gap dispersion class, and a $\geq$ 0.04 ha gap dispersion class.

Results

High regeneration densities ($>$ 100 stems/ha) were exhibited by six shade-tolerant species (Table 2). Of these six species, only *Acer pensylvanicum* was not a canopy dominant. Some species in this group had a moderate to strong tendency toward vegetative regeneration (e.g., *Fagus grandifolia* and *Halesia carolina*). Moderate regeneration densities (10–50 stems/ha)

Table 3. Mean quadrat regeneration density (stems/ha) by class of overlying 0.01-ha canopy cover. Significant Monte Carlo test results are provided in parentheses: a '+' indicates a density greater than the 95%-confidence interval, and a '−' indicates a density less than the interval.

	Cover index class			
Species	<1	1–1.5	>1.5	Chi-square
Acer pensylvanicum	160	84 (−)	137	39.5**
Acer saccharum	525 (+)	326	293	68.9**
Aesculus octandra	265 (+)	209 (+)	52 (−)	194.5**
Betula lutea	33	16	24	7.7*
Fagus grandifolia	104	236 (+)	191	42.3**
Halesia carolina	390	307	225 (−)	46.0**
Liriodendron tulipifera	100 (+)	2 (−)	1 (−)	378.9**
Magnolia fraseri	21	25	19	1.5
Tilia heterophylla	53	32	35	5.4
Tsuga canadensis	116 (−)	165	193	15.4**
All intolerant species	133 (+)	25	23	158.0**
Primary means of regeneration				
All seed species	1277 (+)	861 (−)	756 (−)	131.0**
All sprouting species	567 (+)	600 (+)	470 (+)	30.8**
Diameter class (cm)				
0.1–2.0	1239 (+)	962	812 (−)	82.8**
2.1–10.0	605 (+)	498	415	34.3**
All species	1844 (+)	1460	1226 (−)	116.3**

* $P<0.05$
** $P<0.01$

were exhibited by six species with a range of shade tolerances. The remaining 15 species had low regeneration densities (< 10 stems/ha).

Most species and biological groups of species showed a significant response to canopy cover overlying each 0.01 ha quadrat (Table 3). Peaks in average regeneration density for quadrats directly beneath gaps > 25 m^2 in area (index < 1) were common. *Acer saccharum*, *Aesculus octandra*, *Liriodendron tulipifera*, the intolerant species group, the seed regeneration group, and the all species group showed this trend. Only *Fagus grandifolia* and the vegetative regeneration group had peak densities in quadrats with moderate canopy cover (index 1–1.5). According to the Monte Carlo tests, both peaks were significant. Peak densities in quadrats with high canopy cover (index > 1.5) were rare. *Tsuga canadensis* was the sole species showing this trend, and the Monte Carlo test indicated that this peak was not significant. Two vegetative species, *Magnolia fraseri* and *Tilia heterophylla*, did not exhibit a significant response to this cover index.

Most species and biological groups of species showed a significant response of regeneration density to distance from gaps (Table 4). Many species had significantly high regeneration densities in gap quadrats and significantly low regeneration densities in closed-canopy areas away from gaps. Moderate densities in non-gap quadrats within 10 m of a gap were common. *Magnolia*, *Tilia*, *Tsuga*, and the vegetative regeneration group did not have elevated densities in quadrats near gaps.

Most species had increasing regeneration densities with increasing area of the canopy opening(s) (Table 5). A few shade-tolerant species did not exhibit this trend, however. *Aesculus octandra* regeneration, for example, was clearly most abundant in or near small openings (0.01–0.03 ha). *Tsuga* had significantly high regeneration beneath a closed canopy. By contrast, the intolerant species group had high regeneration densities only in the largest openings.

Occasionally, the Monte Carlo test indicated a significantly high density for a class even though the

Table 4. Mean quadrat regeneration density (stems/ha) by gap and non-gap classes. Significant Monte Carlo test results are provided in parentheses: a '+' indicates a density greater than the 95%-confidence interval, and a '−' indicates a density less than the interval.

Species	Gap	Non gap		Chi-square
		Near gap	Other	
Acer pensylvanicum	226 (+)	113	90 (−)	69.9**
Acer saccharum	736 (+)	376	244 (−)	320.0**
Aesculus octandra	177	222	108 (−)	79.8**
Betula lutea	45	14	18	17.2**
Fagus grandifolia	370 (+)	213	155 (−)	104.8**
Halesia carolina	368 (+)	236	225 (−)	34.7**
Liriodendron tulipifera	121 (+)	0	2 (−)	473.3**
Magnolia fraseri	34	22	21	3.2
Tilia heterophylla	47	23	34	6.5*
Tsuga canadensis	245	148	147	25.7**
All intolerant species	177 (+)	27	20 (−)	271.1**
Primary means of regeneration				
All seed species	1711 (+)	1114	746 (−)	468.3**
All sprouting species	734 (+)	327	351	168.5**
Diameter class (cm)				
0.1–2.0	1738 (+)	978	713 (−)	510.0**
2.1–10.0	706 (+)	463	384 (−)	101.4**
All species	2445 (+)	1441	1097 (−)	588.6**

* $P<0.05$

** $P<0.01$

actual tally was low (e.g., *Halesia carolina*, Table 5). Apparently, the test was not highly effective for species with a strongly clumped spatial pattern. Limitations of the overall study design for determining the effects of canopy cover on species regenerating in vegetative clumps (e.g., *Halesia* and *Tilia*) were evident and the results for such species must be interpreted with caution.

Discussion

All species regenerating primarily by seed show a marked response of regeneration density to canopy cover. Usually, densities are high in or near openings. Maximal densities often occur in the larger gaps. This is particularly true for shade-intolerant species. Only *Tsuga canadensis*, a very shade-tolerant species, is most abundant beneath a closed canopy. Regeneration of one shade-tolerant species, *Aesculus*, is clearly most abundant in or near small gaps.

Seed regenerating species classified as intolerant show a strong tendency of higher regeneration densities in or near canopy openings. As a whole, these species have much higher regeneration densities in or near the larger openings ($\geq$ 0.04 ha). *Liriodendron tulipifera*, an intolerant capable of prolific regeneration, is almost absent from the shaded understory, but it is abundant in some of the largest openings.

Several species with a strong tendency toward vegetative regeneration have mixed responses among the various analyses presented. As mentioned above, the study design is not well suited for the analysis of cover effects on species regenerating in vegetative clumps. Nonetheless, it is clear that these species can produce abundant regeneration beneath a closed canopy.

These findings are compatible with current generalizations concerning forest regeneration strategies. Veblen (1992) recognizes three modes of regeneration: (1) a catastrophic regeneration mode, (2) a gap-phase regeneration mode, and (3) a continuous regeneration mode. In the old-growth system studied here catas-

Table 5. Mean quadrat regeneration density (stems/ha) by index of area of openings in the overlying and adjacent canopy (0.06 ha). Index values correspond to the area over which openings are dispersed. Data for gap quadrats with an index value >0.02 are pooled into one class for chi-square tests. Significant Monte Carlo test results are provided in parentheses: a '+' indicates a density greater than the 95%-confidence interval, and a '−' indicates a density less than the interval.

	Gap area index (ha)				
Species	≥0.04	0.02-<0.04	0.01–0.02	0	Chi-square
Acer pensylvanicum	270 (+)	171	110	102	26 .5**
Acer saccharum	830 (+)	425	345	314	48 .0**
Aesculus octandra	90	242 (+)	242 (+)	127	77 .5**
Betula lutea	90 (+)	54 (+)	14	19	34 .9*
Fagus grandifolia	280	67	194	217	12 .7**
Halesia carolina	510	363	290	276 (+)	17 .8**
Liriodendron tulipifera	260 (+)	13	22	2 (−)	178 .3**
Magnolia fraseri	10	38	23	21	1 .0
Tilia heterophylla	90	71	25	36	19 .9**
Tsuga canadensis	180	146	109 (−)	193 (+)	37 .8**
All intolerant species	330 (+)	30	50	20 (−)	96 .0**
Primary means of regeneration					
All seed species	1890 (+)	1078	916 (−)	812	92 .6**
All sprouting species	890	539	531 (+)	550 (+)	5 .7
Diameter class (cm)					
0.1–2.0	2020 (+)	1025	976	892	60 .4**
2.1–10.0	760	592	471	470 (+)	18 .8**
All species	2780 (+)	1617	1447	1362	76 .5**

** P<0.01

trophic natural disturbances are rare. For this reason, species adhering exclusively to the catastrophic regeneration mode are rare or absent in old stands. Information on tree species colonizing an old field in a cove site suggests that *Robinia pseudoacacia* and *Sassafras albidum* exhibit catastrophic regeneration in this system (Clebsch & Busing 1989). *Robinia pseudoacacia* is rarely observed in old stands, but it is often a prolific colonizer of areas disturbed by humans (Boring & Swank 1984). The data presented in this paper provide clear evidence for both the gap-phase regeneration mode and the continuous regeneration mode in this system. Most species show a positive regeneration density response to gaps < 0.15 ha and can be considered gap-phase species. Few species have exclusively catastrophic or continuous regeneration in cove forests.

Gap-phase regeneration can be further divided into two types based on gap size requirements (Whitmore 1982, 1988, 1989). Whitmore's pioneer species group requires large openings for regeneration, while his climax species group does not. The pioneer group includes Veblen's catastrophic type and a portion of his gap-phase type. The climax group includes Veblen's continuous type and a portion of his gap-phase type. As discussed earlier, the gap size threshold between pioneer and climax groups occurs in the 0.04–0.1 ha range. Pioneer species regeneration is uncommon in smaller openings simply because such species are unable to germinate (Swaine & Whitmore 1988; Whitmore 1989).

In cove forests, the best example of a pioneer species is *Liriodendron tulipifera*. It shows a clear pattern of regeneration in gaps, and it is particularly abundant in large gaps. Presumably, other intolerants exhibit this pattern; however, small sample sizes for most intolerants prohibited conclusive analysis in this study. Many species exhibit the climax species strategy of regeneration in or near small gaps. The shade tolerants *Aesculus octandra*, *Acer saccharum* and *Acer pensylvanicum* fit this pattern well. Most species have elevated regeneration in or near gaps. In contrast, a few species do not appear to require any type of gap for sapling establishment. *Tsuga canadensis* is a good example, and it represents Veblen's continuous regeneration type rather than his gap-phase type. Whether species capable of continuous regeneration require gaps for growth and recruitment into the canopy is not fully resolved. Further long-term study of understory populations may reveal influences of canopy cover on the survival, growth and reproduction of such species.

Canopy gaps are regeneration sites for many species in a variety of temperate forests. In this study of a temperate deciduous forest rich in species, most species tend to regenerate at higher levels in gaps. The shade-intolerant species regenerate almost exclusively in gaps. However, regeneration of most species occurs beneath a closed canopy as well as in gaps. Nakashizuka (1984), Woods (1984), Stewart (1988), Ward & Parker (1989), and Peters *et al.* (1992) also found substantial regeneration, of seed and vegetative origin, beneath temperate forest canopies. Several of these studies suggest that canopy composition and density influence regeneration. Shade-tolerant species originating beneath a closed canopy may advance to the overstory, particularly in less dense areas of the canopy (Veblen 1992). The idea that a range of canopy conditions influences regeneration and its long-term success deserves further consideration.

In conclusion, although regeneration of many species tends to be higher in or near canopy gaps, regeneration of shade-tolerant species also occurs beneath a closed canopy. For this reason, gaps may not be critical to the regeneration and maintenance of many shade-tolerant species in temperate deciduous forests. Gaps are often critical to the success of intolerant species, however. The sharp increase in regeneration of intolerant species with increasing gap size appears to be a widespread phenomenon.

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References

Barden, L. S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians. Oecologia 44: 141–142.

Barden, L. S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian mountains. Oikos 37: 205–209.

Boring, L. R. & Swank, W. T. 1984. The role of black locust (*Robinia pseudoacacia*) in forest succession. Journal of Ecology 72: 749–766.

Braun, E. L. 1950. Deciduous forests of eastern North America. Blakiston, Philadelphia, Pennsylvania, USA.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66: 682–687.

Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. Journal of Ecology 75: 9–19.

Burns, R. M. & Honkala, B. H. 1990. Silvics of North America. Vol. 2, Hardwoods. USDA, Washington, DC.

Canham, C. D. 1989. Different responses to gaps among shade-tolerant tree species. Ecology 70: 548–550.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A. & White, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20: 620–631.

Clebsch, E. E. C. & Busing, R. T. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. Ecology 70 :728–735.

Denslow, J. S. 1980. Gap partitioning among tropical rain forest trees. Biotropica 12: 47–55.

Golden, M. S. 1981. An integrated multivariate analysis of forest communities of the central Great Smoky Mountains. American Midland Naturalist 106: 37–53.

Harmon, M. E., Bratton, S. P. & White, P. S. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. Vegetatio 55: 129–139.

Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. In: Tomlinson, P. B. & Zimmerman, M. H. (eds.), Tropical trees as living systems, pp. 617–638. Cambridge University Press, Cambridge, England.

Hibbs, D. E. 1982. Gap dynamics in a hemlock-hardwood forest. Canadian Journal of Forest Research 12: 522–527.

Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forests in central Sweden. Vegetatio 93: 157–165.

Lieberman, M., Lieberman, D. & Peralta, R. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. Ecology 70: 550–552.

Lorimer, C. G., Frelich, L. E. & Nordheim, E. V. 1988. Estimating gap origin probabilities for canopy trees. Ecology 69: 778–785.

Nakashizuka, T. 1984. Regeneration process of climax beech (*Fagus crenata* Blume) forests IV. Gap formation. Japanese Journal of Ecology 34: 75–85.

Peters, R., Nakashizuka, T. & Ohkubo, T. 1992. Regeneration and development in beech-dwarf bamboo forest in Japan. Forest Ecology and Management 55: 35–50.

Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club 107: 238–248.

Pickett, S. T. A. 1983. Differential adaptation of tropical tree species to canopy gaps and its role in community dynamics. Tropical Ecology 24: 68–84.

Pickett, S. T. A. & White, P. S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Pickett, S. T. A., Collins, S. L. & Armesto, J. J. 1987. Models, mechanisms and pathways of succession. Botanical Review 53: 335–371.

Poulson, T. L. & Platt, W. J. 1989. Gap light regimes influence canopy tree diversity. Ecology 70: 553–555.

Prentice, I. C. & Leemans, R. 1990. Pattern and process and the dynamics of forest structure: a simulation approach. Journal of Ecology 78: 340–355.

Pyle, C. 1988. The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. Castanea 53: 183–196.

Radford, A. E., Ahles, H. E. & Bell, C. R. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, North Carolina.

Runkle, J. R. 1981. Gap regeneration in some old-growth mesic forests of the eastern United States. Ecology 62: 1041–1051.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests in eastern North America. Ecology 63: 1533–1546.

Runkle, J. R. 1985. Disturbance regimes in temperate forests. In: Pickett, S. T. A. & White, P. S. (eds.), The ecology of natural disturbance and patch dynamics, pp. 17–33. Academic Press, New York.

Shanks, R. E. 1954. Climates of the Great Smoky Mountains. Ecology 35: 354–361.

Spies, T. A., Franklin, J. F. & Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research 20: 649–658.

Stewart, G. H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research 16: 558–568.

Stewart, G. H. 1988. The influence of canopy cover on understorey development in forests of the western Cascade Range, Oregon, USA. Vegetatio 76: 79–88.

Stewart, G. H., Rose, A. B. & Veblen, T. T. 1991. Forest development in canopy gaps in old-growth beech (*Nothofagus*) forests, New Zealand. Journal of Vegetation Science 2: 679–690.

Swaine, M. D. & Whitmore, T. C. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75: 81–86.

Uhl, C., Clark, K., Dezzeo, N. & Maquino, P. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology 69: 751–763.

Veblen, T. T. 1989. Tree regeneration responses to gaps along a transandean gradient. Ecology 70: 541–543.

Veblen, T. T. 1992. Regeneration dynamics. In: Glenn-Lewin, D. C., Peet, R. K. & Veblen, T. T. (eds.). Plant succession: theory and prediction, pp. 152–187. Chapman and Hall, London.

Ward, J. S. & Parker, G. R. 1989. Spatial dispersion of woody regeneration in an old-growth forest. Ecology 70: 1279–1285.

Whitmore, T. C. 1978. Gaps in the forest canopy. In: Tomlinson, P. B. & Zimmerman, M. H. (eds.), Tropical trees as living systems, pp. 639–655. Cambridge University Press, Cambridge, England.

Whitmore, T. C. 1982. On pattern and process in forests. In: Newman, E. I. (ed.), The plant community as a working mechanism, pp. 45–59. Blackwell Scientific Publications, Oxford.

Whitmore, T. C. 1988. The influence of tree population dynamics on forest species composition. In: Davy, A. J., Hutchings, M. J. & Watkinson, A. R. (eds.), Plant population ecology, pp. 271– 291. Blackwell Scientific Publications, Boston.

Whitmore, T. C. 1989. Canopy gaps and the two major groups of forest trees. Ecology 70: 536–538.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26: 1–80.

Woods, K.D. 1984. Patterns of tree replacement: canopy effects on understory pattern in hemlock-northern hardwood forests. Vegetatio 56: 87–107.