Canopy Gap Characteristics of an Oak-Beech-Maple Old-Growth Forest in Northeastern Ohio[1]

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Abstract. **Forests are gap-driven systems as openings within the tree canopy directly influence species composition, structure, and regeneration. Most gap studies have occurred in small, mesic, old-growth remnants. This study sought to further the understanding of gap characteristics by examining gaps in one of Ohio's largest old-growth forests, which has wet-mesic site conditions and high species diversity. A modification of the methodology recommended by Runkle (1992) was used to obtain data on gap characteristics. An important portion (17.7%) of this old-growth forest was in gaps. Most of the gaps sampled were large (100-400 m²), and multiple-tree gaps were significantly larger than single-tree gaps. Tip-up and basal shear of a canopy tree were the primary means by which a gap was created (origin type). These findings differ from some other similar gap studies, and the contrasts may be due to the advanced age and particular species composition of this forest, the poor soil drainage conditions, and the large size and stressed condition of the overstory trees.**

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INTRODUCTION

Small canopy gaps created by the mortality of one or a few overstory trees are currently the primary form of disturbance in many eastern deciduous forests (Runkle 1990). Canopy gaps directly influence forest regeneration, species composition, growth rates, density, and age structure (Lorimer 1989; Whitmore 1975; Busing 1998). The fundamental attributes of canopy gaps are their size, mode of origin, and shape, as these have the most effect on forest characteristics (Runkle 1992).

The canopy gap characteristics of several different forest types in the eastern US have been previously described, especially those of small, mesic, old-growth stands (Runkle 1982; Runkle 1990; Cho and Boerner 1991; Dahir and Lorimer 1996). This study examined the canopy gap characteristics of a wet-mesic forest that is one of the largest old-growth remnant stands in Ohio.

MATERIALS AND METHODS

Study Area

This study was conducted over a two-day period during March 2001 at Johnson Woods State Nature Preserve in Wayne County, northeastern Ohio (40° 53' N and 81° 44' W). The preserve is 83.4 ha in size, with 75.2% of this considered old-growth. Elevation ranges from 332.2-335.3 m and slope varies from 0-6%. The preserve is located on the glaciated Appalachian Plateau and has relatively flat terrain with several depressions and low swells. Nearly 70% of Johnson Woods is situated on somewhat poorly drained soils that occasionally have standing water (Bureau and others 1984).

Braun (1950) described the preserve as a "virgin white oak [*Quercus alba*] forest occupying a morainal area" and delineated five plant communities, namely: 1) red maple (*Acer rubrum*)–American elm (*Ulmus americana*) in depressions, 2) red maple–white oak on flats, 3) white oak with an admixture of mesophytic and wet-mesic species occupying low swells, 4) white oak on well-drained mesic sites, and 5) an American beech (*Fagus grandifolia*) community. Today, white oak, sugar maple (*Acer saccharum*), and American beech comprise the majority of the canopy trees, with importance values of 16.5%, 15.3%, and 21.4%, respectively (P. A. Heimberger, unpublished data). These importance values were calculated by species as the average of relative density and relative basal area for stems >10 cm in diameter at breast height (dbh) (Hix and Pearcy 1997).

Data Collection

A modification of the methodology recommended by Runkle (1992) was used to obtain data on canopy gap characteristics. Fourteen line transects were established and distributed 50.0 m apart following a random start. Transects began and ended 20.0 m from any old-growth forest edge. The total length of transect sampled was 6,178 m.

Measurements (length of transect) were made for each of the following canopy conditions: unbroken (closed) canopy or canopy gap. Gaps were considered any area of the forest where the height of the canopy was ≤50% of that in adjacent areas. For each gap encountered, the number (single- or multiple-tree) and dbh of the gap maker(s) were recorded (Runkle 1992). Canopy gap size was estimated by measuring the longest (A_{major}) and second longest (A_{minor}) perpendicular lines between the trunks of border trees. Mode of gap origin was determined as one of the following: tip-up, basal shear, standing dead (snag), or other (broken branch, geologic, and so forth). For each gap, the most important origin type for each gap was determined in the field. A single-tree gap was created by the death of one canopy tree, while a multiple-tree gap was one created by the death of two or more canopy trees. Gap maker dbh was measured using a diameter tape, and only trees having a diameter of at least 20.0 cm at 1.37 m above the ground were considered capable of creating a gap. For eight

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gaps, no gap maker tree could be determined. Sixty-three gaps were encountered.

Data Analysis

The fraction of the old-growth forest in canopy gaps was calculated following the method of Runkle (1992) as the proportion of the total transect distance in canopy openings divided by the total length of the transect. Gap size was calculated using the area formula for an ellipse: area = $(\pi \times (A_{major} \times A_{minor})/4)$. Eccentricity of gap shape was calculated by dividing A_{major} by A_{minor}; a value of 1 indicates a circular shape and a value greater than 1 indicates an elliptical shape (Battles and others 1996). Gap size, fraction, and dbh of gap makers between single-tree and multiple-tree gaps were analyzed with *t*-tests using each transect as an independent sample. Data on gap origin and shape was analyzed using chi-square methods of contingency analysis for categorical data. The relationship between gap size and gap maker dbh was analyzed using simple regression. The relationship between gap size and mode of origin was analyzed using one-way Analysis of Variance (ANOVA). All analyses were done on MINITAB version 11 statistical software and evaluated at a significance level of $P = 0.05$.

RESULTS

Gap Fraction

Overall, 17.7% of the old-growth forestland area was in canopy gaps (Table 1). An estimated 6.4% of the land area was in single-tree gaps, while 11.3% was in multiple-tree gaps. These two estimates were significantly different.

TABLE 1

Canopy gap fractions (%) for single- and multiple-tree gaps.

	Single-tree gaps	Multiple-tree gaps
Mean	6.4[1]	11.3[1]
SE	3.4	9.0

[1]Significantly different (95% confidence interval).

Gap Size

Most gaps were <400 m² and the overall mean gap size was 386.0 ± 247.7 m² (Fig. 1; Table 2). Large gaps (≥100.0 m²) comprised 96.9% of the sample and ranged in size from 112.3-1105.3 m². Small gaps (<100.0 m²) made up 3.1% of the sample and ranged in size from 81.6-94.2 m². The mean size of single-tree gaps was 248.4 ± 124.3 m², while the multiple-tree gaps averaged 506.9 ± 280.3 m² in size. These means were significantly different.

Gap Origin

The most frequent type of origin for single-tree gaps was a standing dead tree (snag), while multiple-tree

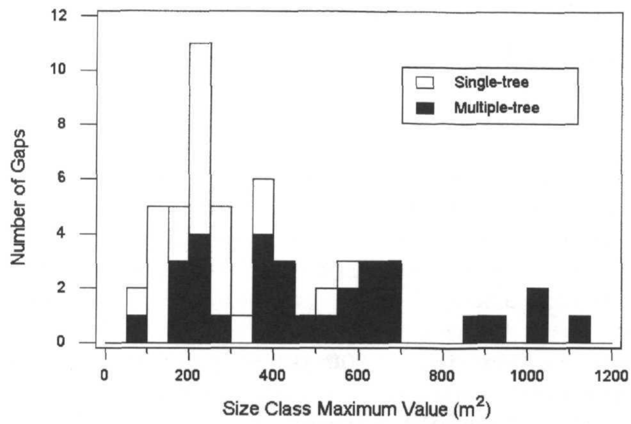

FIGURE 1. Size distribution (m²) of single- and multiple-tree gaps.

gaps most often resulted from the tip-up of canopy trees. Significant differences were found between single-tree and multiple-tree gap origin types (Table 3). Multiple-tree gaps also commonly formed from the basal shear of canopy trees. Mean gap size differed significantly among origin types (Table 4). Tip-ups tended to create the largest gaps followed by basal shears and snags, respectively.

Gap Makers

Twenty-four of the gaps sampled were formed by a single tree, while thirty-one were created by two or more trees. The overall average gap maker size was 71.8 ± 21.7 cm (Fig. 2; Table 5), and the range was from 23.7-133.7 cm. Mean gap maker size for single-tree gaps was 79.4 ± 23.0 cm, while the average gap maker in multiple-tree gaps was 69.0 ± 21.0 cm. The mean diameter of the main gap maker (defined as the gap maker with largest dbh in multiple-tree gaps) was 74.9 ± 20.41 cm. There were no significant differences in main gap maker size or in mean gap maker size between single-tree and multiple-tree gaps.

Gap Shape

Most gaps had eccentricity values greater than 1 (Fig. 3). Almost all (88%) of the single-tree gaps were

TABLE 2

Gap size characteristics (m²) for single- and multiple-tree gaps.

	Single-tree gaps (n = 24)	Multiple-tree gaps (n = 31)
Mean ± Std. Dev.	248.4[1] ± 124.3	506.9[1] ± 280.3
Median	230.8	500.8
Maximum	578.5	1105.3
Minimum	94.2	81.6

[1]Significantly different (95% confidence interval).

TABLE 3

Mode of gap origin by the number of gap makers. Upper value represents number of observed, lower number (in parentheses) is expected value according to chi-square contingency analysis.

	Single-tree gaps (n = 24)	Multiple-tree gaps (n = 31)
Tip-up	2 (8.89)	18 (11.11)
Basal shear	8 (8.44)	12 (10.56)
Snag	13 (6.22)	1 (7.78)
Other	1 (0.44)	0 (0.56)
Chi-square value =	24.390	
Critical value (p = 0.05, 3 d.f.) =	7.815	

elliptical, while 71% of the multiple-tree gaps were elliptical. A few of the multiple tree-gaps would be considered circular (6%). The chi-square analysis indicated no statistically significant differences in observed gap shape between single-tree and multiple-tree gaps (Table 6).

TABLE 4

Mean gap size (m²) for the four gap origin categories.

	Tip-up	Basal shear	Snag	Other
Mean	519.6[1]	348.5[1]	252.0[1]	209.2[1]
Std. Dev.	274.7	211.3	154.1	0.0
N	24	23	15	1

[1]Significantly different (95% confidence interval).

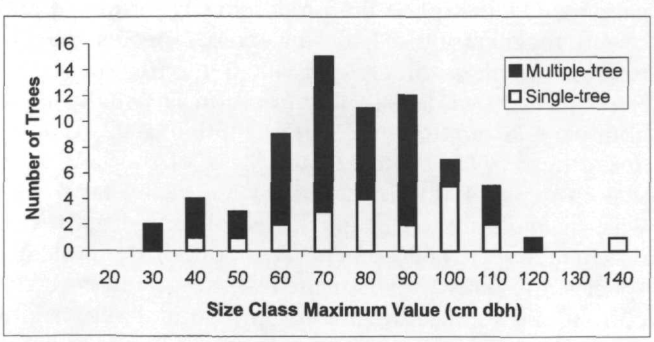

FIGURE 2. Size class distribution (cm dbh) of gap-maker trees for single- and multiple-tree gaps.

TABLE 5

Gap maker size (cm dbh) for single- and multiple-tree gaps.

	Single-tree gaps (n = 21)	Multiple-tree gaps (n = 49)
Mean ± Std. Dev.	79.4 ± 23.0	69.0 ± 21.0
Median	78.5	67.7
Maximum	133.7	110.0
Minimum	36.0	23.7

DISCUSSION

An important portion of this old-growth forest was in gaps. Most of the gaps sampled were large (≥100.0 m²), with multiple-tree gaps tending to be significantly larger than single-tree gaps. Tip-up and basal shear of canopy trees were the primary means by which multiple-tree gaps were created, while snags most often resulted in single-tree gaps. Gap size was influenced by its mode of origin. A similar number (24 versus 31, respectively) of single-tree and multiple-tree gaps were found. Most gaps were elliptical in shape, and in this sample, more single-tree gaps were elliptical than were multiple-tree gaps.

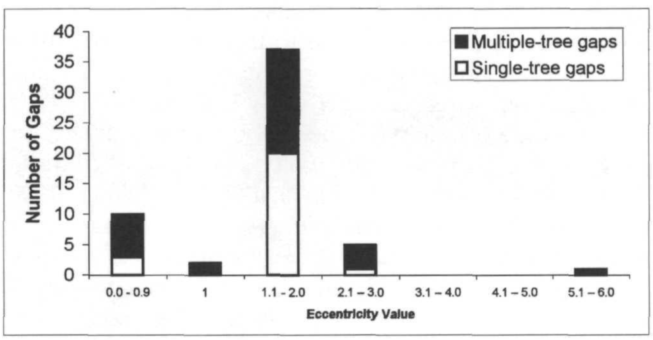

FIGURE 3. Distribution of gap eccentricity values by the number of gap makers. A value greater than one indicates an elliptical shape and a value of one implies a circular shape.

These gap fractions and gap sizes are higher than those reported from forests with similar site characteristics (Ward and Parker 1989; Cho and Boerner 1991). The differences might possibly be explained by the deteriorating overstory trees and the predominance of poorly drained soils. McCarthy and others (2001) found oaks in a southeastern Ohio old-growth forest to be in a "disease decline spiral" caused by advanced age, their large size, topography, chronic air pollution, drought, and Armillaria root rot disease. This phenomenon may be occurring in Johnson Woods since some of the oaks are nearly 400 years old. The deaths of these old trees would create a more open canopy than in other old-growth forests where the canopy trees are not nearly as

TABLE 6

Gap shape by number of gap makers. The upper value represents number of observed, the lower number is the expected value according to contingency chi-square analysis.

	Single-tree gaps (n = 24)	Multiple-tree gaps (n = 31)
Other	3 (4.36)	7 (5.64)
Circular	0 (0.87)	2 (1.13)
Elliptical	21 (18.76)	22 (24.24)
Chi-square value =	2.777	
Critical value (p = 0.05, 2 d.f.) =	5.991	

old and large. The majority of Johnson Woods is also situated on poorly drained soils, which occasionally have standing water (Bureau and others 1984). These anaerobic soil conditions do not allow for tree roots to fully develop, which makes the trees more susceptible to windthrow. Finally, the gap fraction and mean gap size might have been overestimated in this study due to the use of line transects, which are more likely to intersect larger gaps than small ones (Runkle 1992). Despite these contrasts, the mean gap size in this study was similar to Lorimer's (1989) suggestion that average gap sizes in old deciduous forests are generally large (280–375 m^2).

Gap mode of origin has been shown to influence gap microenvironment and size, which affect the distribution of species regenerating within that stand (Helfrich 1998; Putz and others 1983). The primary modes of gap origin found in Johnson Woods were more similar to those found in second-growth mixed-mesophytic forests of southeastern Ohio than to those of other old-growth forests. Keller and Hix (1999) and Helfrich (1998) found tip-ups to be the primary mode of gap origin in the second-growth forests, while most gaps reported in old-growth deciduous forests are caused by snags and basal shears (Runkle 1982; Cho and Boerner 1991; Dahir and Lorimer 1996; Cook 2000). The higher incidence of tip-ups in this study when compared to other studies in old-growth forest may be a reflection of the differences in species composition and the poorly drained soils. Putz and others (1983) determined that large tree species relatively short in height with dense, stiff, strong wood (for example, oaks) had a greater tendency to uproot than trees with lower density wood. The occurrence of basal shears can probably be attributed to the advanced age of the stand and the susceptibility of oaks to biotic diseases. The lower number of gaps caused by snags in this study may indicate a lack of major regional stress events in this area's recent history (Keller and Hix 1999). Clinton and others (1994) found that gaps created by snags were most common following landscape-wide stress events such as droughts or pest outbreaks. Also, tip-ups are often a result of the wind toppling intermediate-size trees (Helfrich 1998). Thus, it can be inferred that the dominant underlying gap mode of origin for this study is wind, which may make pit-and-mound microsites an important factor influencing species composition and distribution in this forest (Helfrich 1998).

Important differences in the size and number of gap makers were found in this study when compared to similar studies. Most gap studies in old-growth have found that gaps were usually created by the mortality of one or two canopy trees (Runkle 1990; Cho and Boerner 1991; Dahir and Lorimer 1996). Clinton and others (1994) found multiple-tree gaps to be more associated with regional stress episodes, while single-tree gaps are probably the most common in old-growth because of the predominance of small-scale disturbances (Runkle 1990). This study indicated that a similar number of gaps were caused by one and by several canopy trees. This may be a reflection of gap maker size and the mode of gap origin of this forest. The mean gap maker size was similar or larger than that found in other studies. This coupled with the fact that most gaps were created by tip-up or basal shear means that a gap-creating event had a higher probability of involving more than one tree. This higher incidence of multiple-tree gaps may also explain the larger gap fraction and the greater mean gap size observed in this study.

Gap shape, for both single-tree and multiple-tree gaps, was more eccentric than in some other studies, meaning that the gaps were more elongated and less circular in this study. Runkle (1990) found that nearly 65% of the gaps in a maple-beech old-growth forest in Ohio were approximately circular. Some gap sizes in this study may been overestimated compared with those determined in other similar studies because the more elongated the ellipse, the greater the overestimation (Battles and others 1996). However, the mean gap eccentricity value for all gaps observed in this study was 1.4. Battles and others (1996) found that when the eccentricity value was 2 or less, the error was less than 10% when estimating the gap size by assuming an ellipsoidal shape. The more elongated gaps also have centers that are not far from the gap edge, which does not allow as much direct light to reach the forest floor as in more open gap shape.

The inferred low light levels resulting from elongated gaps may help explain the predominance of maple and beech regeneration. Shade-intolerant species usually require openings of at least 400.0 m^2 for successful regeneration, while oak regeneration is usually most abundant in multiple-tree gaps (Runkle 1982; Clinton and others 1994). An estimated 7.8% of the land area was in gaps >400.0 m^2, while 11.3% of the land area was in multiple-tree gaps. This observed gap size distribution seems sufficient to allow both shade-intolerant species and oaks to persist in this forest. However, the current disturbance regime of primarily large, wind-created gaps seems to favor the regeneration of sugar maple and American beech over oak species. These findings support the idea of Beckage and others (2000) that the disturbance type is a more important factor in determining species regeneration patterns than are the size and frequency of gaps. Further research is needed on the age distribution, formation rates, and species compositions of canopy gaps in Johnson Woods to confirm and fully describe the forest's current disturbance regime.

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