Forest Ecology and Management 261 (2011) 1143–1151

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Review

Methods for studying treefall gaps: A review

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ARTICLE INFO

Article history:
Received 15 November 2010
Received in revised form 12 January 2011
Accepted 13 January 2011

Keywords:
Treefall gap
Gap size
Gap shape
Gap age
Gap models
Disturbance

ABSTRACT

As silvicultural objectives have changed over the last several decades, managers are increasingly designing cutting regimes that mimic natural disturbance with the hopes that such systems will restore forests to a more natural condition while optimizing harvest yield. Treefall gaps, canopy openings caused by the death of one or more trees, are the dominant form of disturbance in many forest systems worldwide. These gaps play an important role in forest ecology by helping to maintain bio- and pedo-diversity, influencing nutrient cycling, and preserving the uneven-age nature of late-successional forests. In gap literature, there are inconsistencies with regard to gap terminology, methods for identifying and studying gaps, and modeling gap disturbances. From the papers reviewed, the size of treefall gaps ranges widely from 10 to >5000 m^2; we suggest that the maximum gap size should be set at 1000 m^2. Larger openings tend to have microclimates and return intervals significantly different than smaller treefall gaps. Two main definitions of treefall gaps exist: *canopy gap*: a 'hole' in the forest through all levels down to an average height of 2 m above ground and *extended gap*: canopy gap plus the area that extends to the bases of surrounding canopy trees. Although researchers have assumed a variety of gap shapes to simplify measuring gap size, gaps are often irregularly shaped and so we recommend that gap areas and shapes be determined from detailed field measurements. Gap age may be determined from tree ring analysis of released trees in or near the gap edge, the spacing of whorls on released saplings, or from decomposition of gap-making trees. Windthrow is the main cause of canopy gaps in a variety of ecosystems; other causes include insects, diseases, acidic deposition, drought, and climate change. Treefall-gap models have been developed to predict the following processes during gap making or infilling: (i) gap abundance, (ii) forest structure, (iii) spatial and temporal variations in light levels, (iv) canopy dynamics, and (v) soil nutrient and water regimes. We recommend a protocol for gap studies and identify future research topics.

Contents

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doi:10.1016/j.foreco.2011.01.011

Fig. 1. Typical treefall gap in temperate hardwood forest.

1. Introduction

Over the last century, large scale forestry practices focused primarily on timber production have left many forests with a simplified structure, age distribution, and species composition (Boucher et al., 2009). These changes are generating concern as forestry objectives are shifting in many parts of the world from a focus on maximum production to a wider perspective that includes biodiversity preservation and ecosystem functioning (Lindenmayer and Franklin, 2002). To address these new objectives, managers are increasingly designing cutting regimes that mimic natural disturbance with the hopes that such systems will restore forests to a more natural condition while optimizing harvest yield.

While it is now generally recognized that disturbance plays an important role in all natural systems, late-successional forests were thought to be essentially static and homogeneous prior to Watt's (1947) landmark paper. Watt emphasized the need to study spatial pattern and process even in apparently stable ecosystems. In particular, he pointed out that systems must be analyzed at multiple scales since many seemingly stable large systems have complex dynamics at smaller scales. With the exception of Bray (1956), Watt's (1947) paper was largely ignored until the late 1970s when the importance of disturbance in forest ecology was eventually widely accepted (e.g. Grubb, 1977; Bormann and Likens, 1979; White, 1979; Shugart, 1984).

In many forests throughout the world, treefall gaps (Fig. 1), openings in the canopy caused by the death of one or more trees (Whitmore, 1989), are the dominant form of disturbance. These gaps not only help maintain the characteristic uneven-aged nature of late successional forests, but also they influence nutrient cycling, preserve soil and plant species diversity, and change the microtopography in many forests. Windthrow gaps have been documented in a variety of ecosystems on every continent (except Antarctica). This research has clearly demonstrated the importance of gaps to these systems (Runkle, 1982; Pickett and White, 1985; Denslow, 1987; Yamamoto, 1989; Brokaw and Busing, 2000).

Perhaps the most thoroughly studied impact of gap formation is how increased light helps to maintain floristic richness. Denslow (1987) theorized that the significant species diversity in tropical systems exists because each species is competitively superior for a portion of its life. Since most trees have long life spans, they exist in a variety of microenvironments as they grow. The death of a nearby tree dramatically changes light, temperature, soil moisture, and available nutrients. These conditions will favor some species, but not all. As the gap is filled, the microclimate and nutrient status slowly return to pre-disturbance levels and the resulting conditions will tend to favor a different suite of species. If a growing tree is competitively superior for a portion of its life, it will persist (Denslow, 1987; Wright, 2002). In temperate systems, moderate to large-sized gaps maintain species diversity because the higher light conditions created in these larger gaps are ideal for shade intolerant species. These species germinate only in open areas with full sun at least part of the day. Following germination, shade intolerant species tend to grow rapidly and are able to reach the canopy more quickly than shade tolerant species, and so are maintained in the forest (Shugart, 1984; Kobe et al., 1995; Pacala et al., 1996; Woods, 2004; Hanson and Lorimer, 2007).

Forest gaps have also been termed nutrient "hot spots" because they tend to be areas with high rates of decomposition and mineralization, leading to increased levels of nutrients (Collins and Pickett, 1987; Poulson and Platt, 1996; Denslow et al., 1998; Ritter, 2005; Scharenbroch and Bockheim, 2007a, 2008b). Thus, gaps play an important role in the overall biogeochemistry of forest systems.

Over the last 30 years, numerous reviews have been written describing gap dynamics (Denslow, 1987; Yamamoto, 1992; Kuuluvainen, 1994; Ulanova, 2000; K. Yamamoto, 2000; S.I. Yamamoto, 2000; Bugmann, 2001; McCarthy, 2001; Wright, 2002). These reviews focus on gap impacts on forest structure, nutrient cycling, microclimate, and forest management. Although there is extensive literature on gap dynamics, it is often hard for managers to interpret results due to inconsistent methods. This paper will review 47 articles and summarize generally accepted methods for analyzing gap characteristics critical to developing a successful forest management system. Please refer to Appendix A for a list of common terms pertaining to gap research.

2. Methods

2.1. Gap size

2.1.1. Gap definition and types

The size of a gap can strongly influence vegetation growth and nutrient cycling (Zhang and Zak, 1995; Gray et al., 2002; Muscolo et al., 2007). Therefore, gap size is an important characteristic to record. In this review, we intend to focus solely on gaps created through treefall. Gaps ranging from 10 to >5000 m^2 have been reported (Table 1). However, we argue that treefall gaps were originally defined to describe small openings in the forest that were created through the death of branches or one or more trees (Watt, 1947). Large openings (>1000 m^2), created through fires, tornadoes, downdrafts, or hurricanes, have characteristics sufficiently different from treefall gaps as to make comparison between them difficult. In particular, very large openings have reduced shading from surrounding trees and consequently have higher solar radiation and soil temperature than small openings. These large openings also tend to have higher soil moisture due to a reduction in transpiration (Zhang and Zak, 1995; Gray et al., 2002; Muscolo et al., 2007). In many cases, these exceptionally large gaps also have a significantly different return-time than smaller treefall gaps. In particular, forests dominated by small-scale treefall gaps tend to approach a steady-state, while those characterized by large-scale disturbances do not (Turner et al., 1993). Yamamoto (1992) also recognized this issue and suggested a maximum gap size of 1000 m^2, which we here endorse.

Before the size of a treefall gap can be quantified, a gap definition must be established. The most commonly used definition is that of Brokaw (1982a,b). He defined a treefall gap as an opening in the forest canopy down through all foliage levels to an average regeneration height of 2 m. This definition is convenient as it is straight forward and easy to apply in the field. However, it has been criticized because, in a treefall gap, the changes in microclimate associated with gap formation are not limited to the area directly under the gap. Gap edges will also experience changes to their microclimate. Consequently, Runkle (1982) identified two types of gaps: canopy and expanded. A canopy gap is essentially a gap as defined by Brokaw (1982a,b), and an expanded gap is the canopy gap plus the area extending to the bases of the canopy trees surrounding the gap.

There is disagreement on the definition of gap closure (death of a gap). Runkle (1982) contended that regrowth in the gap must be 10–20 m above ground for a gap to be considered closed, while Brokaw (1982a,b) argued that a regrowth height of 2 m was sufficient. Tyrrell and Crow (1994) presented three criteria to assess whether a gap is closed: trees in a gap are one half to two thirds the height of the surrounding canopy, trees in the gap are >25 cm dbh, or the tree canopy is so dense that the original gap is not easily distinguished.

2.1.2. Gap shape and size

Once the gap has been clearly defined, gap size may be quantified. Most methods focus on the two dimensional projection of the canopy gap to the forest floor. For two dimensional measurements, there are three main strategies: (i) assume uniform, elliptical shape and make two measurements; (ii) assume irregular shape and take many measurements; and (iii) assume irregular shape and calculate area based on photographic data (Table 2). To quantify the three dimensional shape, Hu and Zhu (2009) proposed a method using hemispherical photographs. Other researchers have suggested calculating a gap diameter to canopy height ratio as an appropriate measure of effective size (Table 2).

Most methods for measuring two-dimensional gap size are based on assumptions about gap shape. The geometry of a forest gap can impact photosynthetically active radiation (PAR) at the forest floor of gaps (Canham, 1988). In general, narrow gaps, shaded by surrounding trees, will receive far less PAR at ground level than circular gaps of the same size. Numerous shapes have been recognized, including dumb-bell or chablis (Oldeman, 1978), ellipse (Runkle, 1981), and triangle (Salvador-Van Eysenrode et al., 1998). However, gaps often are, in fact, irregularly shaped (Lertzman and Krebs, 1991; Battles et al., 1996; Gagnon et al., 2004).

The size of uniform, ellipse-shaped gaps may be calculated quickly by measuring the length and width of each gap (Runkle, 1981). Such uniform-shaped gaps are rare, and gap sizes calculated in this manner may be imprecise (Lertzman and Krebs, 1991; Battles et al., 1996; Gagnon et al., 2004). Irregularly shaped gaps can be subdivided into smaller sections and each section measured (Brokaw, 1982b; Green, 1996; de Lima, 2005). Rather than projecting the canopy gap onto the forest floor, K. Yamamoto (2000) and S.I. Yamamoto (2000) utilized two photographs of the canopy gap, taken at different heights, and a series of geometric calculations to calculate the gap area.

The height of gap border trees will affect PAR at the forest floor as taller tress will block more light. Therefore, to accurately describe gap shape, the three dimensional shape of the gap must be measured. This measurement is especially important when comparing different study sites or gaps with different canopy species. Hu and Zhu (2009) used hemispherical photographs to characterize the three dimensional shape. For man-made, circular gaps, a gap diameter to canopy height ratio has also been used to account for the effect of trees surrounding the gap (Gray et al., 2002; Ritter et al., 2005). For natural gaps, which tend to be irregularly shaped, the orientation should also be taken into account since a long, narrow gap would receive more light with a north/south orientation than with an east/west orientation.

Gap size and shape are often fluid measurements since new gaps may form adjacent to pre-existing gaps and size may be enlarged for several years before the gap is filled in with new growth.

2.2. Gap age

After a gap forms, increased solar radiation allows vegetation to grow quickly. Over time, microsite characteristics within the gap slowly revert to those of a closed forest. Consequently, the age of a gap is an important parameter to note. There are three main methods for determining gap age: (i) tree ring analysis, (ii) whorl counts, and (iii) degree of decomposition. The most widely

Table 1
Properties of natural gaps.

Location	Forest cover type	Forest age (y)	Disturbance extent (%)	Canopy gap size (m^2)[a]	Cause(s) of gap	Study
Canary Islands	*Lauraceae*	–	–	<100–268	Windthrow?	Arévalo and Fernández-Palacios (2007)
TN, USA	*Liriodendron-Prunus-Quercus-Fraxinus*	"Old growth"	–	90–242	Fire, windthrow	Barden (1981)
India	Subtropical broad-leaved	"Old growth"	–	34–950	Mortality (insects), fire, windthrow	Barik et al. (1992)
BC, Canada	Boreal, sub-boreal, temperate, subalpine	"Old growth"	32–73	9-1570 (70–154)	Mortality	Bartemucci et al. (2002)
NH, USA	*Picea rubra*	"Old growth"	8–29 (18)	47–590	Mortality (insect)	Battles and Fahey (2000)
Panama	Tropical	100–300	–	20–705	–	Brokaw (1985)
Germany	*Fagus sylvatica*	146	–	–	Mortality (acid deposition)	Brumme (1995)
TN, NC, USA	*Tsuga*-mixed deciduous	–	–	100–300	–	Busing and White (1997)
WI, USA	*Acer-Tilia-Fraxinus*	140–311	–	–	Windthrow, ice storms	Choi et al. (2001)
NC, USA	*Acer-Quercus-Liriodendron*	–	–	181–4043 (1175)	Windthrow (hurricane)	Clinton and Baker (2000)
NE Alberta, Can.	*Populus tremuloides*	44–67	3.6–17	10–>90	Wildfire	Cumming et al. (2000)
NW MI, USA	*Acer-Tilia-Fraxinus*	65–149	–	37–49	Windthrow, mortality (drought)	Dahir and Lorimer (1996)
Quebec, Can.	*Abies-Betula*	<200	18–64 (42)	25–101	Mortality (insects), fire	de Römer et al. (2007)
Chile	*Nothofagus pumilio*	"Old growth"	13–24 (19)	50–500	Windthrow	Fajardo and de Graaf (2004)
NH, USA	*Picea-Abies*	"Virgin"	–	25–500	Windthrow, mortality (insects, diseases)	Foster and Reiners (1986)
Japan	*Fagus crenata*	–	11–13	<100–1200	Windthrow	Henbo et al. (2004)
MA, USA	*Tsuga-Quercus-Betula-Acer*	115	–	30–450	Windthrow (hurricane)	Hibbs (1982)
Poland	*Picea*	–	34	25–>400	Windthrow?	Holeksa (2003)
Germany	*Betula pendula*	>80	–	21–2157 (75)	–	Huth and Wagner (2006)
Germany	*Picea abies*	"Virgin"	–	25–5676 (213)	Mortality (climate warming), windthrow	Kathke and Bruelheide (2010), Kirchner et al. (2009)
Quebec, Can.	Boreal conifers, deciduous	50–234	7.1–41 (30)	4.1–390	Fire	Kneeshaw and Bergeron (1998)
IL, USA	*Acer-Quercus-Ulmus*	–	–	–	Windthrow	Lin et al. (2004)
Sweden	*Picea abies*	∼200	31	9–370 (82)	Windthrow, mortality (insects, diseases)	Liu and Hytteborn (1991)
Argentina	*Blepharocalyx-Cinnamomum-Pisonia*	"Mature"	–	15–>110	–	Malizia and Grau (2008)
NW MI, USA	*Acer-Tsuga-Betula-Tilia*	"Old growth"	9.5	90–>300	–	Mladenoff (1987), Mladenoff (1990)
Germany	*Fagus sylvatica*	"Old growth"	–	116–1410	Windthrow	Naaf and Wulf (2007)
Quebec, Can.	*Abies-Picea*	<220	30–82 (54)	12–520	Mortality (insects), windthrow	Pham et al. (2004)
TN, NC, USA	*Tsuga-Fagus-Acer-Halesia*	–	–	1–1490 (65)	–	Runkle and Yetter (1987)
MI, WI, USA	*Tsuga canadensis*	120–>300	3.1–17	12–121 (149)	Windthrow	Tyrrell and Crow (1994)
Venezuela	*Kaatinga*, terra firme	–	–	79–4100	Windthrow	Uhl et al. (1988)
Russia	*Picea abies*	"Primeval"	6.2–25 (12)	200–700	Windthrow	Ulanova (2000)
NW WI, USA	*Tsuga-Acer-Betula*	–	–	<50–800	–	Webster and Lorimer (2002)
N. MI, USA	*Tsuga-Fagus-Acer*	∼300	–	–	Windthrow	Woods (2004)
China	*Castanopsis kawakamii*	"Climax natural"	–	<20–>700	Mortality, windthrow	Zhang and Zak (1995)

[a] Median value in parentheses.

accepted method for determining the age of gaps is tree-ring analysis. Lorimer and Frelich (1989) pointed out that when a gap is formed, the increase in light allows trees that were overtopped by the gap maker to experience growth release as reflected in increased ring width. Runkle (1982) suggested that release may be reflected in the spacing of branch whorls. A tree growing in a gap will have wider spacing due to increased light and the resulting increase in growth rate. The gap age may also be calculated from the degree of decomposition of the gap maker, although this method is less precise, especially within older gaps (Liu and Hytteborn, 1991). As noted above, gaps may be formed from more than one event and so, parts of the gap may be different in age.

Table 2
Gap size measurement.

Study	2D/3D	Method
Runkle (1981)	2	Measure length and width of gap. Calculate area using ellipse formula
Brokaw (1982a,b), Green (1996)	2	Measure distance from gap center to 8 (Brokaw) or 16 (Green) equally spaced points around the periphery of the gap. Calculate area based on these polygons
de Lima (2005)	2	Divide the gap into triangles. Triangles need not share a common vertex. Calculate area of all triangles
K. Yamamoto (2000) and S.I. Yamamoto (2000)	2	Using two photographs, at different heights in the same position, the area of the canopy gap is calculated
Hu and Zhu (2009)	3	Using two hemispherical photographs, the three-dimensional gap is calculated
Ritter et al. (2005)	3	Gap diameter: canopy height ratio

2.3. Stand-level disturbance extent

To investigate gap dynamics at the landscape level, researchers must devise a sampling scheme to characterize disturbance for the forest as a whole. Several techniques have been proposed for evaluating the aerial extent of gaps, including (i) long-term plots, (ii) aerial photography, (iii) GIS, (iv) increment cores at random points, and (v) transects.

In the northern Great Lakes region, Woods (2000) utilized a historical forest inventory to track long-term forest dynamics. The inventory was started in 1935 with 240 plots of 800 m^2 area on a 40 m × 100 m grid. In each plot, the species and dbh of all trees >12.7 cm were recorded. The measurements were repeated in 1948 (on every other plot), 1974–78, and 1992–94 (upland plots). From this inventory, Woods described the mortality rates for each cataloged species and changes in species abundance for the forest as a whole. He also used this information to make predictions about future species composition (Woods, 2000, 2004).

Historical imagery may also be used along with a geographic information system (GIS). Kathke and Bruelheide (2010) utilized historical aerial photographs and ArcGIS 9.0 to investigate forest dynamics in a remnant natural forest in Germany. They obtained high-quality aerial photographs from 1945, 1991, 2000, and 2003, scanned and geo-referenced them. Geo-referencing ensures that each photograph is aligned to the same coordinate system and allows for comparisons and calculations to be made between them. In ArcGIS 9.0, each gap 25–10,000 m^2 is identified by drawing a polygon over it, and the size is calculated using the spatial statistics tool. Gap areas between years were compared to determine the fate of each. With this information, gap turnover rate, rotation time, formation rate, closure rate, and changes in overall gap frequency were calculated.

In late successional forests of the Upper Great Lakes region, Lorimer and Frelich (1989) developed a method to characterize the disturbance regime using increment cores. They identified 70 random points spread over the study area. At each point, they established a plot and recorded the species, dbh, and crown class (greater than or less than 10% crown in direct sun) for all trees over 1.4 m. In addition, increment cores were collected from 10 to 30 trees closest to the random point. They theorized that for the northern hardwood hemlock system, every tree in the canopy must have germinated in a gap or been released by gap formation. By analyzing the cores for release of trees, they were able to identify timing of gap formation. Assuming that each tree represents the disturbance history for a particular point, they were able to calculate the percentage of trees showing disturbance in a particular decade, and in turn, the canopy disturbance intensity over time.

Intersect or strip transects may also be employed to characterize canopy gap distribution (Brokaw, 1982a; Runkle, 1982, 1992; Nakashizuka, 1984). For intersect transects, Runkle (1982) recorded the length of each transect and the lengths of each gap encountered along the transect. Using this information, he calculated the percent of each transect in gaps and subsequently, the fraction of the forest in gaps. For each gap encountered, he calculated the areas of the canopy gap and expanded gap, assuming an elliptical shape. He used this size information to calculate the overall gap extent and size distribution across the study area.

For strip transects, the method is similar, but instead of a line, the transect is a swath of constant width. Using strip transects ensures that more gaps will be intersected and included in the study. The research can further control the number of gaps included by changing the criteria by which a gap is determined to fall within the strip. Brokaw (1982a) used a 20 m width and counted gaps in which the gap maker fell within the strip. To increase the number of gaps counted, Runkle (1992) suggested counting a gap if any part of it intersected the strip.

2.4. Determining the origin of gaps

2.4.1. Causes of canopy gaps

Gap formation is generally attributed to wind, snowfall, insects, disease, acidic deposition, drought, climate change, and fires. However, several studies indicate that soil properties and tree species characteristics may also be important. Of the 47 gap case studies reviewed, 13 involve artificially created gaps; in exploring assessment of gap origins, we review only the remaining 34 (Table 1).

In the few studies that observed the influence of soil characteristics on gap formation, the effective rooting depth was measured and the soil was characterized, noting features including a fragipan layer, a shallow depth to bedrock or a paralithic layer, abundant coarse fragments, a high water table and poor drainage (Habecker et al., 1990; Liu and Hytteborn, 1991; Bockheim, 1997; Lin et al., 2004; Woods, 2004; Scharenbroch and Bockheim, 2007b).

In addition to the severity of the storm, tree characteristics influence their susceptibility to wind-throw and gap formation. Based on limited studies in which species and dbh were recorded for gap-makers, trees with a larger dbh and a flat-rooted or heart-rooted pattern (e.g., Tsuga, Picea, and Abies), as opposed to a tap-rooted pattern (e.g., *Pinus*, *Quercus*, and *Acer*) tend to be the gap-maker or "storm" trees (Liu and Hytteborn, 1991; Clinton and Baker, 2000; Lin et al., 2004).

3. Modeling processes in treefall gaps

There are two main types of models important for gap research. Forest-gap models are designed to simulate the dynamics of a forest by following the fates of individual trees (Shugart, 2002). These models are useful for investigating stand, ecosystem, or landscape changes. In contrast, many models have been developed to simulate processes occurring at smaller scales within individual treefall gaps. Models have been developed to predict the following processes during gap making or infilling: (i) gap abundance; (ii) forest structure, (iii) spatial and temporal variations in light levels, (iv) canopy dynamics, and (v) soil nutrient and water regimes (Table 3). In many cases these studies use existing registered models, including FORMIX3, CASA, LINKAGES, JABOWA-FORET, SAFE, SWEAT, and ZELIG.

About half of the modeling studies predicted population structure during the gap making or infilling process, including patterns of trees, height and diameter growth of trees within and adjacent to the gap, regeneration, and changes in species composition (Table 3). Some of these studies focused on tropical, temperate, or boreal ecosystems, while others targeted a specific species within the ecosystem.

Several of the modeling studies in gaps dealt primarily with spatial and temporal variations in light levels. These studies employed tree inventory and allometric data, hemiplots, solar positioning algorithms, the model tRAYci, and computer-aided design software. Hemiplot is a program that uses hemispherical photographs to analyze vegetation and light (Pinto et al., 2008). The model tRAYci simulates direct and diffuse light using submodels (Brunner, 1998). Several studies solely addressed changes in the canopy of gap vegetation, including leaf-area index and canopy density. These studies employed light detection and ranging (LIDAR), canopy height models, air photos, and digital elevation models (DEMs).

Only a few studies modeled moisture and nutrient levels in soils of gaps. Belanger et al. (2004) used the SAFE model and regression equations for throughfall to simulate throughfall contributions of protons and base cations to the acid–base status of gap soils. In temperate forest gaps, Scharenbroch and Bockheim (2008a) used WATBAL to model the monthly soil water drainage flux from the effective rooting zone (0–50 cm). Using meterological data, and the

Table 3
Models for simulating processes in treefall gaps.

Model Name	Purpose	Approach	Study
CANOPY	Canopy dynamics and stand density	Forest-gap model	Choi et al. (2001)
CASA-3D	C cycling in tropical forests after disturbance	Satellite images; modified CASA model	Huang et al. (2008)
DRYADES	Forest structure and succession; Douglas fir; BC	Spatial gap model	Mailly et al. (2000)
FORMIND	Stand dynamics; tropics	FORMIX3 model individual trees	Kohler and Huth, 1998
Ising	Regeneration and species diversity	Spatial tree data; lattice models	Kubo et al. (1996), Schlicht and Iwasa (2004, 2006)
JABOWA-FORET	Forest structure and dynamics	JABOWA-FORET model application to gaps	Acevedo et al. (1995)
LINKADIR	Tree damage from ice storms	Logistic regression; LINKAGES model	Lafon (2004)
SAFE	Predict throughfall contribution of nutrients	Regression equations; SAFE model	Belanger et al. (2004)
SEIB-DGVM	Forest structure and succession	Adaptation of FORMIX3 gap dynamics model	Sato (2009)
SORTIE	Spatial and temporal variations in light levels	Allometric data; age-estimation models	Dube et al. (2001), Dube et al. (2005), Menard et al. (2002)
SWEAT	Soil and water regimes; tropical forests	Meteorological data; SWEAT model	Marthews et al. (2008a)
WATBAL	Soil and water regimes; temperate forests	Meteorological, soil, canopy data	Scharenbroch and Bockheim (2008a)
ZELIG	Stand-level development; Douglas fir	Forest growth data; ZELIG model	Pabst et al. (2008)
N/A	Canopy dynamics; boreal forest	LIDAR; canopy height models	Vepakomma et al. (2008)
N/A	Canopy dynamics and stand density	Forest inventory data; air photos and DEM	Henbo et al. (2004, 2006)
N/A	Patterns of trees in gaps	Remote sensing; Ripley's K function	Koukoulas and Blackburn (2005)
N/A	Forest structure and succession	Point-process modeling	Shimatani and Kubota (2004)
N/A	Changes in gap-edge tree diameters	Hierarchical regression analysis	Pedersen and Howard (2004)
N/A	Canopy openness and sunlight penetration	Tree inventory data; CAD software	Silbernagel and Moeur (2001)
N/A	Retrospective gap distribution and size	Historical air photos	Axelsson and Ostlund (2001)
N/A	Spatial patterning of trees and light availability	Stem maps and trayci light model	Sprugel et al. (2009)
N/A	Radiation in canopy gaps; tropics	Tree allometry; solar positioning algorithms	Marthews et al. (2008b)
N/A	Gap light index	Hemiplots	Yoshida et al. (1998)
N/A	Gap cycle	Gap survey; age structure; cellular-automata model	Cumming et al. (2000)
N/A	Gap detection	Air photos; high-resolution dems	Betts et al. (2005)
N/A	Gap cycle	Tree density data; cellular-automaton model	Pagnutti et al. (2007)

SWEAT model, Marthews et al. (2008a) simulated water regimes in gaps of tropical forests. Finally, Huang et al. (2008) used satellite images, and a modified CASA model to simulate carbon cycling in tropical forests after a disturbance.

4. Natural vs. created gaps

Throughout much of the literature, man-made gaps are used as a proxy for naturally created ones. This practice allows for the control of size, shape, location, and timing of gap formation. However, in many cases, man-made gaps may be sufficiently different from natural ones as to make generalizing between the two difficult.

Soil disruption and biomass removal in particular are different in man-made and natural gaps. Traditional harvesting techniques can lead to soil compaction or displacement, mixing of mineral and organic horizons, and loss of litter layer due to erosion (Jurgensen et al., 1997; Klepac et al., 1999; Block et al., 2002). In addition, man-made gaps are often cleared of cut trees, while the stumps are left in the ground. In contrast, in natural gaps created by windthrow, the tree remains in the gap, often with the root ball exhumed from the soil, but attached to the tree. These natural gaps are not free from soil disruption. In fact, tip-ups can mix considerable quantities of soil, and may lead to localized erosion (Clinton and Baker, 2000). Clearly, removing biomass from the gap will impact the biogeochemistry of the remaining area by removing nutrients. The type of soil disruption can also impact nutrient cycling as increases in bulk density (through compaction), loss of soil structure (through compaction and erosion), and displacement (through erosion) can negatively impact microbial growth (Tan and Chang, 2007).

While most studies involving man-made gaps use traditional harvesting techniques, with careful execution, natural treefall gaps may be replicated. In 1990, researchers in the Harvard Experimental Forest mimicked a hurricane blow-down by pulling trees down with a winch situated outside the plot. They were careful to avoid mechanical damage to the soil (Cooper-Ellis et al., 1999). While this study did not investigate small-scale treefall gaps, a similar method could be employed to do so.

5. Recommendations and conclusions

We recommend that when designing silvicultural systems based on treefall gap dynamics, managers first consult existing literature on the disturbance regime in the target area. If such data are unavailable or unreliable, and a suitable target stand exists in the area, we recommend that a study be conducted to determine the characteristics—shape, size, age, stand-level disturbance intensity—of gaps in the area. Such a study would provide managers with the necessary information to design a management system that would closely mimic the natural disturbance regime. Such a system would optimize harvest yield while maintaining the species diversity and structural characteristics of late successional forests.

We also recommend that all future gap research report gap size, shape, age, cause, primary cover type, and if possible, the overall aerial extent of gaps in the system. Clearly, there are a wide variety of methods available to measure each. We recommend that, whenever possible, the method with the highest degree of precision be employed. For example, to measure gap size, we would caution against any method that assumes a uniform shape as such assumptions have been shown to be invalid in many systems. Furthermore, we recommend that the specific methods in measuring each of these characteristics be clearly stated. Finally, we recommend that natural treefall gaps be used in studies of natural processes and man-made gaps be used in studies focused on impacts of logging, unless the methods are designed to specifically mimic natural processes, such as seen in the Harvard forest.

When a gap is formed by multiple events, the shape, size, and age change through time. In these cases, we recommend that researchers proceed as suggested by Runkle (1992) and treat the gap both as a single, large gap and as subsections of the larger gap and record shape, size, age, and origin of each. If such measurements are not possible, Runkle (1992) suggested focusing on the earliest and latest events.

Much of gap research has focused on impacts of gap formation on above ground processes, especially vegetation growth. Our knowledge of below ground responses remains weak.

Future research focused on below ground processes, including biogeochemistry, microbial growth and composition, and soil characteristics, would greatly further our overall understanding of gap dynamics and their impact on the forest as a whole. In general, the unique microclimate of gaps—increased soil temperature, increased soil moisture, and increased solar radiation—is known to influence nutrient cycling and microbial dynamics. However, more research is needed to truly understand how belowground processes are impacted by many gap characteristics including gap size, shape, age, and cover type.

Acknowledgments

This project was supported by grants from the United States Department of Agriculture (McIntire-Stennis) and the Huron Mountain Wildlife Foundation. We thank Drs. B.C. Scharenbroch and K.D. Woods for reviewing an earlier draft of this manuscript.

Appendix A

Terms pertaining to the study of canopy gaps.

Area-based turnover rate—the area that is subjected to any change due to gap formation or closure (%/yr) (Pickett and White, 1985)
Canopy gap—a ‘hole’ in the forest through all levels down to an average height of 2 m above ground (Runkle, 1982; Brokaw, 1982a,b); also development gap (Lertzman et al., 1996)
Domino effect—the disturbance of nearby trees from the falling of gap-maker trees (Lin et al., 2004)
Expanded gap—canopy gap plus the area extending to the bases of the canopy trees surrounding the gap (Runkle, 1982)
Gap abundance or density—the number of gaps intersected from transects (#/m) (Fajardo and de Graaf, 2004)
Gap age—time since gap formation (Sernander, 1936; Liu and Hytteborn, 1991)
Gap closure rate—a historical change in a tract from gap to closed forest (%/yr) (Fujita et al., 2003)
Gap filler—trees that reach canopy height and eventually fill the gap (Kneeshaw and Bergeron, 1998)
Gap formation rate—a historical change in a tract from closed forest to gap (%/yr) (Fujita et al., 2003)
Gap fraction—the proportion of a tract that is in gaps (%) (Runkle, 1982)
Gap maker—the tree or trees that initially form the gap (Lertzman, 1992)
Mode of mortality—the proportion of the trees in a gap that were uprooted, snapped, or standing dead (%) (Yamamoto, 1992)
Return time—the average time between disturbances at a particular point (Everham and Brokaw, 1996)
Rotation time—the time it takes until the whole study area is converted from a closed forest to a gap, or vice versa (yr) (Pickett and White, 1985)
Turnover time—calculated by dividing the total area of interest by the total disturbed area per unit time (Everham and Brokaw, 1996)

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