Characteristics of typhoon disturbed gaps in an old-growth tropical montane rainforest in Hainan Island, China

Huai Yang, Shirong Liu, Kunfang Cao, Jingxin Wang, Yide Li & Han Xu

Journal of Forestry Research

ISSN 1007-662X
Volume 28
Number 6

J. For. Res. (2017) 28:1231-1239
DOI 10.1007/s11676-017-0402-y

Springer

J. For. Res. (2017) 28(6):1231–1239
DOI 10.1007/s11676-017-0402-y

ORIGINAL PAPER

Characteristics of typhoon disturbed gaps in an old-growth tropical montane rainforest in Hainan Island, China

Huai Yang[1,2] · Shirong Liu[2] · Kunfang Cao[3] · Jingxin Wang[4] · Yide Li[1] · Han Xu[1]

Received: 8 May 2015 / Accepted: 19 September 2015 / Published online: 8 May 2017

Abstract Disturbances that create gaps can shape the structure and function of forests. However, such disturbance regimes in Asian tropical montane rainforests remain largely unquantified. Least studied are typhoon disturbances that are attributable to climate change. We investigated gap characteristics in terms of size, age, and gap-maker to quantify the gap disturbance regimes in an intact old-growth tropical montane rainforest on Hainan Island, China. The intensity of typhoons has increased since 1949, and typhoon winds blow mostly (45.5%) from the northeast corner of Hainan Island, resulting in a higher frequency of gaps in the northeast. A total of 221 gap-makers (trees that fell to create canopy gaps) and 53 gaps were observed in a 3.16 ha old-growth rainforest. Most canopy gaps (85%) were <200 m^2. The average size of canopy gaps was smaller in the rainforest than in other tropical forests, while the average size of expanded gaps was similar to those in other tropical forests. The maximum age of gaps was 23.5 years indicating that gaps had more rapid turnover than other parts of tropical forests. The frequency distribution of gap-makers followed a lognormal distribution with a distinctive peak at three gap-makers, which was different from the inverse J-shaped curve typical of other tropical forests. Gaps were recorded mainly on slopes between 20° and 35° and wood density of gap-makers was between 0.6 and 0.7 g cm^{-3}. Our results suggest that small-scale disturbance was the dominant agent of gap formation in this old-growth rainforest that is subject to increasing typhoon disturbances.

Keywords Gap characteristics · Gap-makers · Old-growth · Slope · Tropical montane rainforest · Typhoon disturbance · Wood density

Project funding: This study is jointly supported by the Ministry of Science and Technology (2012BAD22B01 and 2006BAD03A04) and special funds of Research Institute of Tropical Forestry, Chinese Academy of Forestry (RITFYWZX2012-02; CAFYBB2014QA010).

The online version is available at http://www.springerlink.com

Corresponding editor: Chai Ruihai.

✉ Shirong Liu
liusr@caf.ac.cn

1 Research Institute of Tropical Forestry, Chinese Academy of Forestry, 510520 Guangzhou, People's Republic of China

2 Key Laboratory of Forest Ecology and Environment of State Forestry Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, People's Republic of China

3 State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, and College of Forestry, Guangxi University, Nanning 530005, Guangxi, People's Republic of China

4 Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV 26506, USA

Introduction

Gap disturbances are one of the fundamental determinants of forest structure, composition, and dynamics (Turner 2010), and their ecological effects vary with size, severity, and frequency (White and Jentsch 2001). The gaps created by strong winds, such as storms, hurricanes or typhoons, are an important component of natural disturbance regimes in many forest ecosystems (Foster 1988; Ulanova 2000). Gaps created by hurricanes or typhoons not only help maintain or restore the old-growth characteristic of virgin forests, but also create variations in microclimates and niches (Schliemann and Bockheim 2011). Storms and typhoons cause wind throw and windbreak, which can create gap patterns of varying sizes depending on the disturbance intensity (Greenberg and McNab 1998; Harcombe et al. 2002). Generally, the disturbance intensity of storms and typhoons increases with decreasing latitude from the north to south in China. Thus, wind throws and trunk breakage resulting from storms and typhoons show an increasing trend from the north to south in China. It is known that wind disturbances selectively damage larger trees in a given stand, and that species with heartwood rot are generally vulnerable to wind damage (Peterson 2007). Earlier studies indicated that functional properties of tree species might be as important as wind in determining the characteristics of gap formation (Arihafa and Mack 2013; Grainger and Aarde 2013). Therefore, understanding of gap creation regimes is of importance to sustainable forest management practices (Felton et al. 2006; Kukkonen et al. 2008).

Forests at latitudes between 5° and 20° south or north are frequently subject to hurricanes or typhoons (Gray 1979; McDowell 2011; Zhang et al. 2011). Consequently, these forests have higher heterogeneity of canopy structure, higher percentages of gap area and diversified gap growth-phase, and higher density of trees, but lower height and smaller size of trees (Vandermeer et al. 2000; Dale et al. 2001; Uriarte and Papaik 2007). Tropical rainforest on Hainan Island, China is disturbed by typhoons about 8–10 times annually (Jiang and Lu 1991). Of these storms, about 3–5 affect the montane rainforests (Zhang et al. 2011; Chen et al. 2012). Typhoon impacts on forests of Hainan are seen as relatively short tree height, higher percentage of gap area, and fewer tree species of high or low wood density (Jiang and Lu 1991; Li 1995). Zang et al. (1999) studied the gap characteristics of forests in Bawangling, located in the southwest of Hainan Island, where typhoon disturbance was slight. However, little is known about the effect of typhoons and site condition on the gap creation regimes of Asian tropical montane forests under a changing environment in the context of climate change.

In this study, we conducted a quantitative assessment of gap characteristics of a tropical montane rainforest at Jianfengling National Nature Reserve (JNNR), Hainan Island, China, where typhoons are a major driver of gap formation. The objectives of this study were to: (1) describe the gap characteristics (i.e., gap size, age, and makers) in a tropical montane old-growth rainforest, and (2) quantify the relationships between gap properties and the wind direction of typhoons, slope gradient, and wood density of gap-makers.

Materials and methods

Study sites

This study was conducted within the core zone of JNNR (18°23′N–18°50′N, 108°36′E–109°05′E), in Ledong County in southwestern Hainan Island, the southernmost part of terrestrial China. The region has one of the most well protected and most typical old-growth tropical montane rainforests at the northern edge of tropical Asia, and therefore, is an ideal place to study natural gap creation by typhoons. The reserve is approximately 47,000 ha in total area, of which tropical mountain rainforests cover nearly 15,000 ha (Jiang et al. 2002; Wang et al. 2014).

This region is characterized as a tropical monsoon climate with distinct wet (May to November) and dry (December to April) seasons. The mean annual air temperature is 19.8 °C, ranging from 14.8 °C (January) to 23.3 °C (June). The annual average precipitation is 2449 mm, of which 80–90% falls during May to October (Zhou et al. 2013). The site has irregular topography with granite as the predominant soil parent material. The most common soil type is the montane lateritic red or yellow earth. The forest is dominated by the families *Fagaceae*, *Myrtaceae*, *Lauraceae*, *Rubiaceae*, *Palmaceae*, *and Euphorbiaceae*, with the presence of *Hopea hainanensis* (Dipterocarpaceae) representing the typical tropical flora of Southeast Asia. The mean canopy height (diameter at breast height, DBH > 60 cm) is 23.7 m, and the mean total basal area per ha is 56 m^2 (Jiang and Lu 1991).

Transect survey on forest gaps

A complete gap field survey was conducted during June to September 2013 after typhoon Bebinca's disturbance in a 60 ha forest stand at approximately 870–1015 m asl. We sampled a 60-ha plot (1000 m × 600 m) made up of 1500 subplots (20 m × 20 m). We used the transect method to sample gaps and estimate gap parameters following Yamamoto et al. (2011). Two perpendicular transects of 20 m width and 600 m length (transect 1) or 1000 m length (transect 2) were demarcated across the center of the 60 ha plot. We sampled 79 subplots, of which 30 subplots were oriented from south to north and the remaining 49 subplots were oriented from west to east. All gaps were investigated and recorded along the two transects. The slope of subplots of the two transects ranged from 4.9° to 40.7°.

Following Runkle (1982) and Veblen (1985), two types of gaps were recognized and defined: canopy gaps (CG) and expanded gaps (EG). A CG is the vertical projection onto the ground of the opening caused by the snapping or uprooting of a tree or by standing dead trees. The border of the EG (Veblen 1985) is defined by the trunks of the trees, the canopy of which defines the CG. The criteria used to determine gap closure were proposed by Runkle (1982) and Tyrrell and Crow (1994). They defined gaps as "closed" if one or more of the following criteria is met by trees filling the gap from below: (1) average height of these trees is one-half to two-thirds or more of the adjacent canopy height, (2) average DBH of these trees is >25 cm, and (3) the canopy of these trees is dense enough that the original canopy gap opening could not be easily recognized. We recorded physical site characteristics, including slope, aspect, elevation, geographical coordinates and canopy height when gaps were not identified as closed. The slope was measured in such a way that each quadrat was divided into four triangular planes and each plane was formed by joining three corners of the quadrat. The average angle of the four triangular planes that deviated from the horizontal plane and the north direction provides the slope and aspect of each quadrat, respectively. Gap length was set as the longest distance from one gap edge to another gap edge, and the width was set as the longest perpendicular to length. In irregular shaped gaps, we measured actual radii as in Lertzman and Krebs (1991). CG and EG areas were calculated by fitting width and length dimensions to the formula for an ellipse (Lima 2005).

Gap-makers were the fallen trees that created gaps, and one, two or more of those fallen trees could form gaps. For each gap, the species of gap-makers were recorded, DBH was measured and type of mortality and state of decay were recorded. Gap-maker mortality was grouped as: (1) uprooted (downed trees with at least some of the root-ball attached), (2) standing dead (a dead tree from which the leaves and most of the branches had fallen), (3) breaks on trunk (the trees with the bole completely broken somewhere between the ground line and the base of the live crown), or (4) breaks at trunk base. The height of the residual trunk (Hs) was categorized as: $Hs < 2$ m = snapped off at the trunk base, $2 \leq Hs < 10$ m = snapped off at the trunk, and $Hs \geq 10$ m = standing (Zang et al. 1999). Wood density was determined from cores of the trunks. The cores were taken with an increment borer from trees of DBH ≥ 5 cm. Core lengths were then measured with a dial caliper and core volumes computed for cylinders of the measured length and inner diameter of the corer. For some shrub species, we had to sample trunks <5 cm DBH, in which cases we removed the phloem and bark and measured fresh volume by water displacement. After drying in an oven at 103 °C for 72 h, wood density was computed as oven dry mass/fresh volume and averaged for each species (Baker et al. 2004; Harmon et al. 2011; Iida et al. 2012). A decay class was assigned based on morphological characteristics to estimate the relative age of each gap-maker (Triska and Cromack Jr. 1980). Experienced local forest workers estimated the death age of each gap-maker. Gap age classes were assigned according to the age of the oldest gap-maker in each gap (Fogel and Cromack 1977; Maser et al. 1979), and the criteria used to determine gap age were taken from Runkle (1992) and Fraver et al. (2002).

Data collection and analysis

Data sets of typhoon intensity and frequency on Hainan Island were collected from the data source of China Typhoon Network. Regression analysis was conducted to evaluate the relationship between the numbers of gaps, gap size, gap age, and the numbers of gap-makers. The $P < 0.05$ level was considered to be statistically significant. All statistical analyses were performed using SPSS 12.0. Graphs were drawn using SigmaPlot 10.

Results

Typhoon intensity and frequency

In total, 156 typhoons hit Hainan Island between 1949 and 2014 for a mean of 2.4 typhoons per year (Fig. 1). About half of these landed on Hainan Island's northeast corner so the prevailing typhoon wind direction at Jianfengling was from the northeast. Before the 1980s, there were several small typhoons after every big one. Since then, the average intensity of typhoon has increased to 2.5 from 2.2 levels, and this has been conducive to the creation of gaps.

Relation between cumulative frequency of gaps and wind direction of typhoon

The cumulative frequency of gaps increased in transects aligned south to north and west to east (Fig. 2), gap number distribution decreased from northeast to southwest, which was consistent with the data on prevailing wind direction of typhoons in Hainan Island.

Gap size

We recorded 53 gaps within our 3.16 ha study area. CG and EG accounted for 21.3 and 50.5% of the study area, respectively. The total EG and CG area documented from all 53 gaps was 15,945 and 6746 m^2, respectively.

The area of CG ranged from 19 to 349 m^2, with an average of 127 ± 76 m^2. The proportion of forest area in EG ranged from 51 to 654 m^2, with an average of 301 ± 138 m^2 (Fig. 3). The size distribution of CG was strongly skewed to the smaller classes, with approximately 85% of CG being less than 200 m^2.

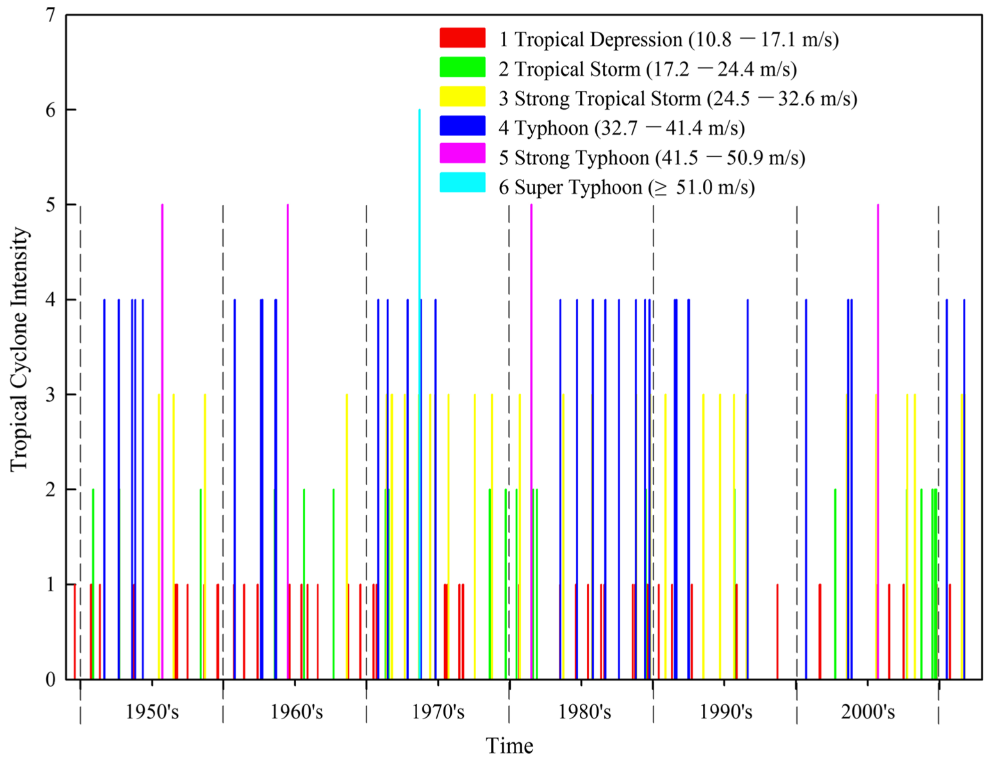

Fig. 1 Typhoon intensity and frequency on Hainan Island from 1949 to 2014 (data collected from China Typhoon Network). The maximum average wind speed near the *bottom center* is shown in brackets

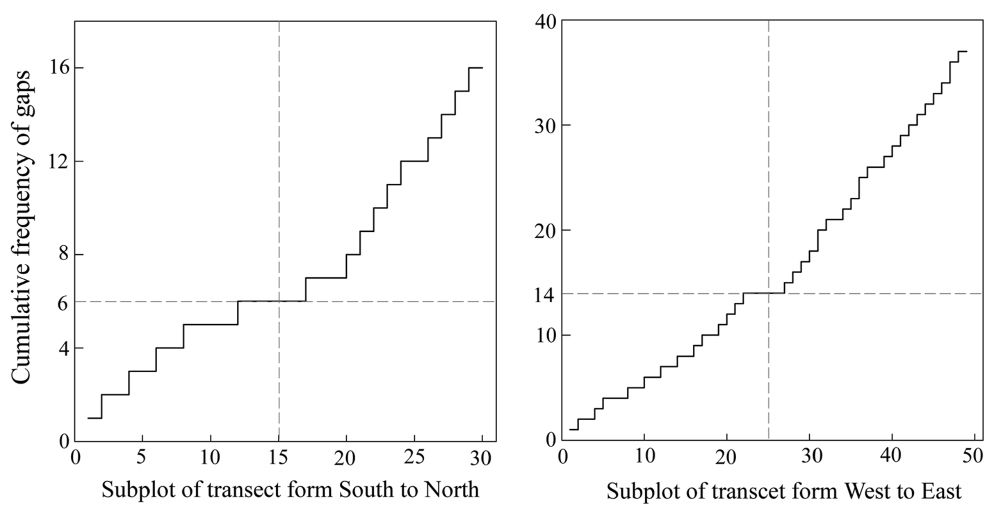

Fig. 2 Relation between cumulative frequency of gaps and transect from south to north and from west to east

Gap age structure and recovery time

The estimated gap ages ranged from 1 to 23.5 years, with an average of 11.61 ± 6.10 years (Fig. 4). 20 gaps formed from 0 to 10 years ago, 23 gaps formed from 10 to 20 years ago, and only 10 gaps were estimated older than 20 years. Gap age and gap size were not correlated (CG: $R = 0.046$, $P = 0.745$; EG: $R = 0.144$, $P = 0.304$).

Gap density was 16.8 gaps ha^{-1} (53 gaps/3.16 ha). On a basis of the oldest gap (formed approximately 30 years ago), the gap formation rate was 0.56 gaps ha^{-1} a^{-1} (16.8 gaps ha^{-1}/30 a). By area percentage, the CG formation rate was 0.71% a^{-1} (21.3%/30 a). By the disturbance frequency of CG, the recovery time of typhoon disturbed sites was 141 a (1/0.0071 a^{-1}).

Causes of gap-makers

Gap-makers numbered 1–9, and 3 was the most common count, accounting for 26.4% of the gaps. The majority of gaps were created by multiple gap-makers (92.5%) (Fig. 5).

We recorded 221 gap-makers in the 53 gaps. The causes of mortality of the gap-makers were: uprooting (55% 122

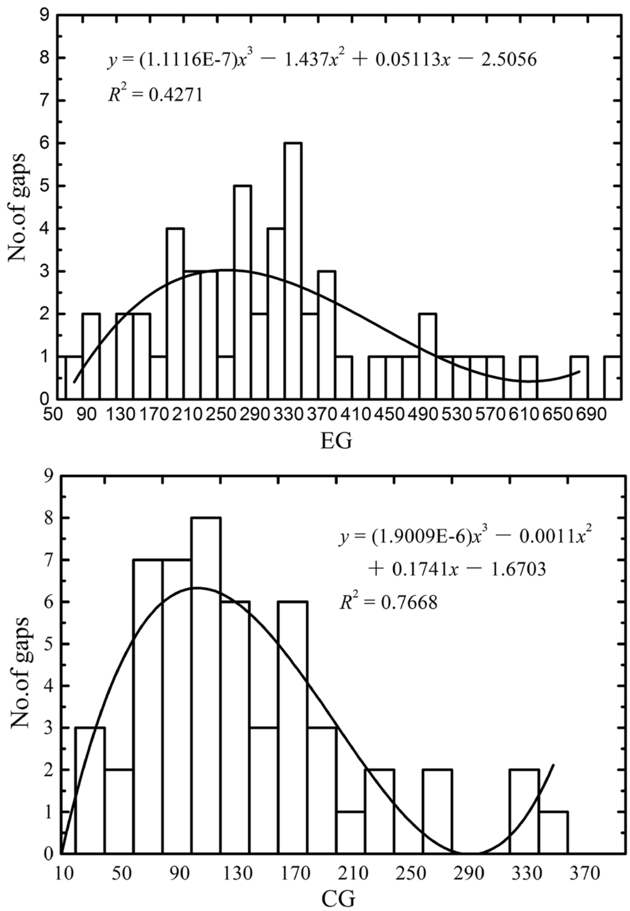

Fig. 3 Distribution patterns of EG and CG area (defined by 40 m^2 size classes). *Open bars* indicate numbers of gaps by area of EG and CG (the total number of gaps was 53)

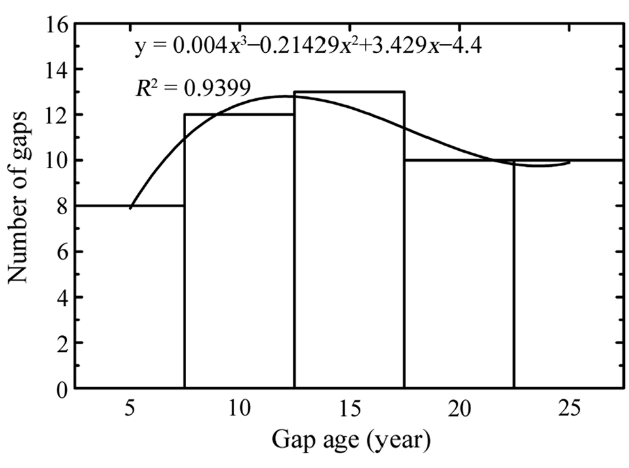

Fig. 4 Distribution patterns of gap age (defined by 5-year age class). *Open bars* indicate the number of gaps by gap age (the total number of gaps was 53)

gap-makers); broken trunks (24% 52 gap-makers); standing dead (11% 24 gap-makers); and breaks at the trunk base with (10% 23 gap-makers).

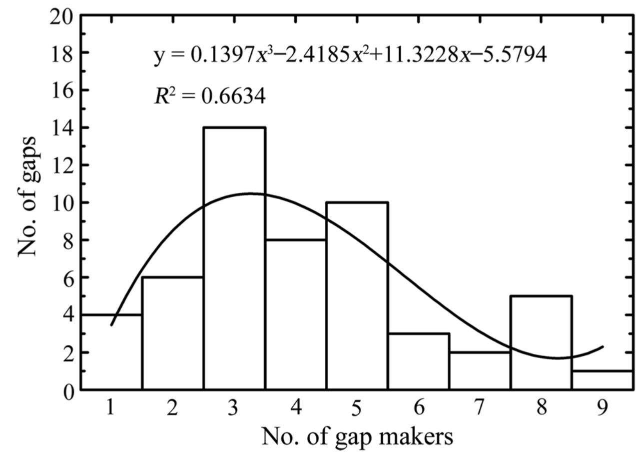

Fig. 5 Frequency distribution of gap-makers. *Open bars* represent the number of gap-makers. *Solid curve* shows the trend between the number of gaps and the number of gap-makers (the total number of gaps was 53)

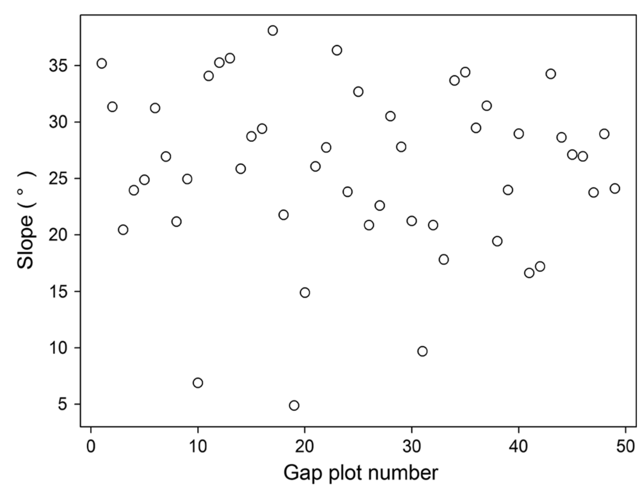

Fig. 6 Scatter plot of slope angle in gap plots. *Open circles* represent the slope of the gap plot, which was independent and disorderly

Gap and slope, wood density

The average slope of the gap plots was 25.8 ± 7.4°, ranging from 20° to 35° (Fig. 6). The wood density of gap-makers mainly ranged from 0.6 to 0.7 g cm^{-3} (Fig. 7).

Discussion

Relationships among typhoon, wind and gap formation

The annual occurrence of typhoons on Hainan Island averaged twice during 1884–1948 (Lin 1989; Liu et al. 2001). However, it increased to 2.4 times per year during 1949–2014. The average intensity of typhoons that

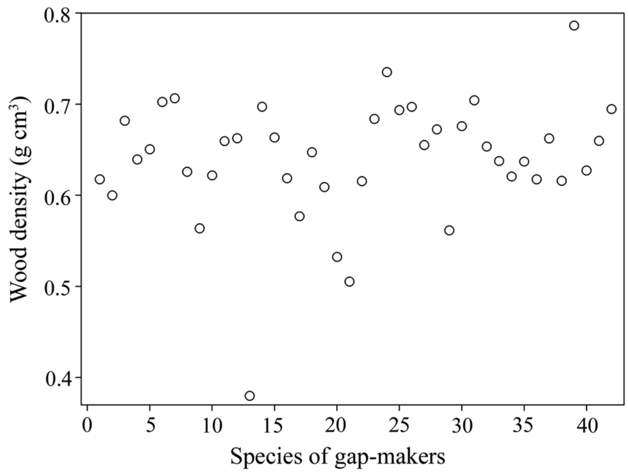

Fig. 7 Wood density distribution of gap-makers

occurred on Hainan Island from 1980 to 2014 increased to 2.5 levels compared to 2.2 levels from 1949 to 1979, and this has been conducive to gaps formation (Bellingham et al. 1996; Lin et al. 2011). So gap area percentage has increased to 21.3% from 12.1% in 1980s (unpublished data, Jianfengling Natural Research Station of Forest Ecosystems). Gap number distribution decreased from northeast to southwest, because Hainan Island is located in the western path of northwest pacific typhoons with annual 2.5 times of typhoons. It was recorded that typhoon landed on Hainan Island from east and northeast during 1957–2006 accounted 89.6 and 25.6%, respectively (Zhang et al. 2010), and the northeast wind direction of typhoon landing in Ledong County (JNNR location county) accounted 45.5% during 1949–1986 (Yin 1987).

The proportion of the trunk breakage in forests shows a progressively increasing trend from the north to south in China due to typhoons disturbance, with a change from 1.6% in temperate regions (Zang et al. 1998) to 24.41% in subtropical regions (Liu et al. 1999), and to 32.47% in tropical regions (Zang et al. 1999). Additionally, in the present study, a large proportion of gap-makers with uprooted are 55%. However, the characteristics in Bawangling located in the southwest of Hainan Island, and to the north of our study site where less typhoon disturbance occurs (rainfall 1500–2000 mm while 1700–3600 mm in JNNR), showed that the proportion of gap-makers with uprooted was only 16.88% (Zang et al. 1999).

Comparisons of gap features among different tropical forests

The average size of CG (127 m^2) at JNNR was smaller than that reported for other tropical forests (218 m^2 with a range of 86–628 m^2) (Brokaw 1985b). In contrast, our EG areas were similar to those of other tropical forests (Brokaw 1985a) (Tables 1, 2). In this study, trees height ranged 25–30 m compared to 30–60 m in a similar forest in Xishuangbanna, Southwest China (Zhu and Zhou 2002). Therefore, the gap size is smaller in the montane rainforest with the shorter trees in Hainan Island than in other tropical forests. Moreover, the gap percentage in forests is generally higher with typhoon disturbance than without typhoon disturbance (Runkle 1982).

Forty-seven percent of our CGs covered areas less than 100 m^2 in the forest. This percentage was larger than reported for premontane tropical wet forest (42%) in La Selva, Costa Rica (Sanford et al. 1986), middle mountain moist evergreen broad-leaved forest (33.4%) in Ailaoshan, Yunnan, China (Li et al. 2003) and other tropical forests in Table 2.

Our maximum gap age was 23.5 years, the turnover time (141 years) was calculated by the methods of Hartshorn (1978) and Clinton et al. (1993), younger than that in Bawangling (160 years) (Zang et al. 1999), EI Cielo, Mexico (157.3 years) (Arriaga 1988), Ivory Coast, Taï, Africa (216–314 years) (Jans et al. 1993), Barro Colorado Island, Panama (159 years) (Brokaw 1982). This suggests rapid recovery in the JNNR forest compared to other tropical forests. This can be explained by the following reasons. First, increased typhoon occurrences might have two effects: increased rainfall and atmospheric nitrogen deposition, providing moisture and additional nutrients for plant growth (Hietz et al. 2011; Liu et al. 2011; Phoenix et al. 2012). Second, the gap areas are smaller in this forest, thus, the time required for seedlings to fill gaps would be shortened (Zhu and Zhou 2002).

The frequency of gap-makers in our study tended to follow a lognormal distribution with a distinctive peak at the first three gap-makers, differing from the often reported inverse J-shaped curve in other tropical forests (Nagel and Svoboda 2008; Kucbel et al. 2010). This can be explained by the fact that the major gap-makers in this study were tree-uprooting and snapping (together creating >4/5 of all gaps) resulting from a typhoon, and these types of gap-makers can damage nearby trees as they fall, leading to two or more gap-makers in one gap.

Relationships between gap and wood density

We observed that neither fast-growing trees with low wood density nor very slow-growing trees with high wood density were gap-makers. Trees with medium wood density most commonly fell under typhoon disturbance, and became gap-makers. Wood density is an important factor affecting the wind resistance of trees (Harmon et al. 2011). Generally, fast growing tree species have relatively wide

Table 1 Comparison of canopy gap traits for different forest types and locations

Forest type	Location	Area percentage (%)	Average gap-makers (range)	Average gap size (m^2)	Study
Tropical montane rainforest	Jianfengling, Hainan, China	21.3	4.2 (1–9)	127	This study
Tropical montane rainforest	Bawangling, Hainan, China	25.2	1–6	80	Zang et al. (1999)
Premontane tropical wet forest	La Selva, Costa Rica			161	Sanford et al. (1986)
Panama	Tropical			20–705 (range)	Brokaw (1985b)
Hemlock-hardwoods[a]	Wisconsin, Michigan, USA	3.1–16.9	2.6 (1.6–3.5)	48.3	Tyrrell and Crow (1994)
Maple-mixed hardwoods[b]	North Carolina, Tennessee, USA	8.9–24.2		65.4	Runkle (1982)
Douglas-fir (old growth)	Oregon and Washington, USA	13.1	2.3 (0–6)	85 (median)	Spies et al. 1990
Monsoon evergreen broad-leaved forest	Dinghushan, Guangdong, China			230.2	Peng et al. (2002)
Middle mountain moist evergreen broad-leaved forest	Ailaoshan, Yunnan, China		2.4 (1–6)	89.1	Li et al. (2003)
Subtropical evergreen broad-leaved forest	Heishiding, Guangdong, China		2.6 (1–4)	66	Liu et al. (1999)

[a] Twenty-five stands

[b] Eight stands in Great Smoky Mountains National Park

Table 2 Gap area percentage for different forest types and locations

Forest type	Location	Gap area percentage (%)		Source
		<100 m^2	<20 m^2	
Tropical montane rainforest	Jianfengling, Hainan, China	47	85	This study
Premontane tropical wet forest	La Selva, Costa Rica	42	76	Sanford et al. (1986)
Lowland tropical moist forest	Barro Colorado Island, Panama		95	Denslow (1987)
Middle mountain moist evergreen broad-leaved forest	Ailaoshan, Yunnan, China	33.4	100	Li et al. (2003)
Tropical wet forest	Heredia Province, Costa Rica	22.2	55.6	Denslow et al. (1998)
Tropical semi-deciduous forest	Estação Ecológica de Caetetus, Gália	10.8	36.6	de Lima et al. (2008)
Tropical moist forest	Bolivia, Brazil	26	62	Myers et al. (2000)
Tropical moist floodplain	Cocha Cashu, Peru		44	Cintra and Horna (1997)
Subtropical evergreen broad-leaved forest	Heishiding, Guangdong, China	79.8		Liu et al. (1999)

tree rings and low wood density, and these trees are normally shorter in height, and therefore, they are not readily felled by high winds. In contrast, slow-growing trees have narrower tree rings, higher wood density, and stronger bending strength, all leading to greater resistance to typhoon winds. Thus, trees with high wood density do not often become gap-makers. This implies that selecting appropriate species with designated wood density is important for constructing resilient windbreaks in areas with frequent typhoons.

Implications for sustainable forest management

Mimicking the size and frequency of natural disturbance in terms of gap formation is considered to be the most effective way to ensure sustainable forest management

(Bengtsson et al. 2000; Franklin et al. 2007). Accordingly, group selection or selective harvesting should be considered as suitable management practices before natural death of larger trees. The average area of CG and EG after selective cutting should be around 130 and 300 m^2, respectively, in tropical montane rainforest. Furthermore, the ratio of CG and EG should be 25% and 50%, respectively, if the selective cutting intensity is determined by the gap area percentage. Because the gap-makers are easily broken at the trunk base, we recommend to saw trees close to the stem base. Our results suggest that natural gap disturbance regime should be used as a reference for guiding sustainable management of tropical forests.

Conclusions

This study reveals that small-scale disturbance is an important component of the disturbance regime in old-growth tropical montane rainforest on Hainan Island. Canopy gaps accounted for a high proportion total tropical rainforest area subject to typhoon disturbance. Our study forest recovered quickly from typhoon damage. The gaps mainly resulted from uprooted and snapped-off trees of multiple species with intermediate wood density. The wind direction of typhoons and the site slope are important factors influencing the occurrence and distribution of gaps.

Acknowledgements We are grateful to Jianfengling National Key Field Research Station for providing their assistance in field work.

References

Arihafa A, Mack AL (2013) Treefall gap dynamics in a tropical rain forest in Papua New Guinea. Pac Sci 67:47–58

Arriaga L (1988) Gap dynamics of a tropical cloud forest in northeastern Mexico. Biotropica 20:178–184

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biol 10:545–562

Bellingham P, Kohyama T, Aiba SI (1996) The effects of a typhoon on Japanese warm temperate rainforests. Ecol Res 11:229–247

Bengtsson J, Nilsson SG, Franc A, Menozzi P (2000) Biodiversity, disturbances, ecosystem function and management of European forests. For Ecol Manag 132:39–50

Brokaw NVL (1982) Treefalls: frequency, timing, and consequences. In: Leigh EG, Rand AS, Windsor DM (eds) The ecology of a Neotropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, pp 101–108

Brokaw NVL (1985a) Gap-phase regeneration in a tropical forest. Ecology 66:682–687

Brokaw NVL (1985b) Treefalls, regrowth, and community structure in tropical forests. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, pp 53–69

Chen B, Cao J, Wang J, Wu Z, Tao Z, Chen J, Yang C, Xie G (2012) Estimation of rubber stand age in typhoon and chilling injury afflicted area with Landsat TM data: a case study in Hainan Island, China. For Ecol Manage 274:222–230

Cintra R, Horna V (1997) Seed and seedling survival of the palm *Astrocaryum murumuru* and the legume tree Dipteryx micrantha in gaps in Amazonian forest. J Trop Ecol 13:257–277

Clinton BD, Boring LR, Swank WT (1993) Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74:1551–1558

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ (2001) Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. Bioscience 51:723–734

De Lima RAF, Martini AMZ, Gandolfi S, Rodrigues RR (2008) Repeated disturbances and canopy disturbance regime in a tropical semi-deciduous forest. J Trop Ecol 24:85–93

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Syst 18:431–451

Denslow JS, Ellison AM, Sanford RE (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. J Ecol 86:597–609

Felton A, Felton AM, Wood J, Lindenmayer DB (2006) Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. For Ecol Manag 235:186–193

Fogel R, Cromack K Jr. (1977) Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. Can J Bot 55:1632–1640

Foster DR (1988) Species and stand response to catastrophic wind in central New England, USA. J Ecol 76:135–151

Franklin JF, Mitchell RJ, Palik BJ (2007). Natural disturbance and stand development principles for ecological forestry. Gen. Tech. Rep. NRS-19. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. p. 44

Fraver S, Wagner RG, Day M (2002) Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, USA. Can J For Res 32:2094–2105

Grainger MJ, Aarde RJ (2013) The role of canopy gaps in the regeneration of coastal dune forest. Afr J Ecol 51:11–20

Gray WM (1979) Hurricanes: their formation, structure and likely role in the tropical circulation. Meteorol Trop Oceans 77:155–218

Greenberg CH, McNab WH (1998) Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. For Ecol Manage 104:179–191

Harcombe P, Bill C, Fulton M, Glitzenstein J, Marks P, Elsik I (2002) Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. J Ecol 90:947–957

Harmon ME, Woodall CW, Fasth B, Sexton J, Yatkov M (2011) Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species. Res. Pap. NRS-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. p. 40

Jiang YX, Lu JP (1991) Tropical forest ecosystems of jianfengling in Hainan Island. Science Press, Beijing **(in Chinese)**

Hartshorn GS (1978) Tree falls and tropical forest dynamics. In: Tomlinson PB, Zimmerman MH (eds) Tropical trees as living systems. Cambridge University Press, Cambridge, pp 617–638

Hietz P, Turner BL, Wanek W, Richter A, Nock CA, Wright SJ (2011) Long-term change in the nitrogen cycle of tropical forests. Science 334:664–666

Iida Y, Poorter L, Sterck FJ, Kassim AR, Kubo T, Potts MD, Kohyama TS (2012) Wood density explains architectural differentiation across 145 co-occurring tropical tree species. Funct Ecol 26:274–282

Jans L, Poorter L, van Rompaey RS, Bongers F (1993) Gaps and forest zones in tropical moist forest in Ivory Coast. Biotropica 25:258–269

Jiang Y, Wang B, Zang R, Jin J, Liao W (2002) The biodiversity and its formation mechanism of the tropical forests in Hainan Island. Science Press, Beijing **(in Chinese)**

Kucbel S, Jaloviar P, Saniga M, Vencurik J, Klimaš V (2010) Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. Eur J Forest Res 129:249–259

Kukkonen M, Rita H, Hohnwald S, Nygren A (2008) Treefall gaps of certified, conventionally managed and natural forests as regeneration sites for Neotropical timber trees in northern Honduras. For Ecol Manag 255:2163–2176

Lertzman KP, Krebs CJ (1991) Gap-phase structure of a subalpine old-growth forest. Can J For Res 21:1730–1741

Li GC, He YT, Han XG (2003) Features of gaps of middle mountain moist evergreen broad-leaved forest in Ailao Mountain. Chin J Ecol 22:13–17

Li YD (1995) Biodiversity of tropical forest and its protection strategies in Hainan Island, China. For Res 8:455–461 (**in Chinese**)

Lima RAF (2005) Gap size measurement: the proposal of a new field method. For Ecol Manag 214:413–419

Lin C (1989) Annual variation characteristics of the typhoons making landfalls in the Hainan Island over the past 100 years and their relation to the southern oscillation. Mar Forecasts 3:8–10

Lin TC, Hamburg SP, Lin KC, Wang LJ, Chang CT, Hsia YJ, Vadeboncoeur MA, McMullen CMM, Liu CP (2011) Typhoon disturbance and forest dynamics: Lessons from a northwest Pacific subtropical forest. Ecosystems 14:127–143

Liu J, Wang B, Zang R (1999) Gap formation and its characteristics in south subtropical evergreen broadleaved forest. J Appl Ecol 10:385–388

Liu Kb, Shen C, Louie Ks (2001) A 1000-year history of typhoon landfalls in Guangdong, Southern China, reconstructed from Chinese historical documentary records. Ann Assoc Am Geogr 91:453–464

Liu X, Duan L, Mo J, Du E, Shen J, Lu X, Zhang Y, Zhou X, He C, Zhang F (2011) Nitrogen deposition and its ecological impact in China: an overview. Environ Pollut 159:2251–2264

Maser C, Anderson RG, Cromack K Jr, Williams JT, Martin RE (1979) Dead and down woody material. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric Handb 553:78–95

McDowell WH (2011) Impacts of hurricanes on forest hydrology and biogeochemistry. In: *Forest Hydrology and Biogeochemistry* (pp. 643–657). Berlin: Springer

Myers GP, Newton AC, Melgarejo O (2000) The influence of canopy gap size on natural regeneration of Brazil nut (Bertholletia excelsa) in Bolivia. For Ecol Manag 127:119–128

Nagel TA, Svoboda M (2008) Gap disturbance regime in an old-growth Fagus—Abies forest in the Dinaric Mountains, Bosnia-Herzegovina. Can J For Res 38:2728–2737

Peng S, Huang Z, Zhou G, Zhou X, Zhang C, He W (2002) Gap formation characteristics and its effects on sapling composition and diversity in Dinghushan Biosphere Reserve. J Trop Subtrop Bot 11:229–235

Peterson CJ (2007) Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. For Ecol Manage 250:96–108

Phoenix GK, Emmett BA, Britton AJ, Caporn SJ, Dise NB, Helliwell R, Jones L, Leake JR, Leith ID, Sheppard LJ (2012) Impacts of atmospheric nitrogen deposition: Responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. Global Change Biol 18:1197–1215

Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63:1533–1546

Runkle JR (1992) Guidelines and sample protocol for sampling forest gaps. US Department of Agriculture, Forest Service, Pacific Northwest Research Station

Sanford RL, Braker HE, Hartshorn GS (1986) Canopy openings in a primary neotropical lowland forest. J Trop Ecol 2:277–282

Schliemann SA, Bockheim JG (2011) Methods for studying treefall gaps: A review. For Ecol Manage 261:1143–1151

Spies TA, Franklin JF, Klopsch M (1990) Canopy gaps in Douglas-fir forests of the Cascade Mountains. Can J For Res 20:649–658

Triska FJ, Cromack K Jr (1980) The role of wood debris in forests and streams. In: Waring RH (ed) Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, pp 171–190

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849

Tyrrell LE, Crow TR (1994) Structural characteristics of old-growth Hemlock–Hardwood forests in relation to age. Ecology 75:370–386

Ulanova NG (2000) The effects of windthrow on forests at different spatial scales: A review. For Ecol Manag 135:155–167

Uriarte M, Papaik M (2007) Hurricane impacts on dynamics, structure and carbon sequestration potential of forest ecosystems in Southern New England, USA. Tellus A 59:519–528

Vandermeer J, de la Cerda IG, Boucher D, Perfecto I, Ruiz J (2000) Hurricane disturbance and tropical tree species diversity. Science 290:788–791

Veblen TT (1985) Forest development in tree-fall gaps in the temperature rain forests of Chile. Natl Geogr Res 1:162–183

Wang A, Fang YT, Chen DX, Koba K, Makabe A, Luo TS, Yoh M (2014) Variations in nitrogen-15 natural abundance of plant and soil systems in four remote tropical rainforests, southern China. Oecologia 174:567–580

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. In: Kadereit JW (ed) Progress in botany. Springer, Berlin, pp 399–450

Yamamoto SI, Nishimura N, Torimaru T, Manabe T, Itaya A, Becek K (2011) A comparison of different survey methods for assessing gap parameters in old-growth forests. For Ecol Manag 262:886–893

Yin X (1987) The main harmful-wind directions of typhoon on Hainan Island. Chin J Trop= Crops 2:9

Zang RG, Guo ZL, Gao WT (1998) Gap regeneration in a broadleaved Korean pine forest in Changbai Mountain Natural Reserve. Chin J Appl Ecol 9:349–353

Zhang K, Song C, Chen Y (2010) Records and disaster assessment of typhoons in East Hainan Island in recent 50 years. J Anhui Agric Sci 38:12880–12882 **(in Chinese)**

Zang RG, Yang YC, Liu JY, Yu SX, Yang XS (1999) Gaps and their natural disturbance regimes in the tropical montane rain forest of Hainan Island. Sci Silvae Sin 35:2–8

Zhang ZW, Zhang JH, Zhao ZZ, Liu SJ, Xie RH, Fan N (2011) Analysis of risks in Hainan Island typhoon hazard factor based on GIS. Meteorol Environ Res 2:31–34

Zhou Z, Jiang L, Du E, Hu H, Li Y, Chen D, Fang J (2013) Temperature and substrate availability regulate soil respiration in the tropical mountain rainforests, Hainan Island, China. J Plant Ecol 5:1–10

Zhu H, Zhou HX (2002) A comparative study on the tropical rain forests in Xishuangbanna and Hainan. Acta Bot Yunnanica 24(1):1–13