

Article

Size-Dependent Patterns of Seed Rain in Gaps in Temperate Secondary Forests, Northeast China

Qiaoling Yan ^{1,2}, Qun Gang ^{1,2,3} and Jiaojun Zhu ^{1,2,*}

¹ CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang 110016, China; qlyan@iae.ac.cn (Q.Y.); gangqun1988@outlook.com (Q.G.)

² Qingyuan Forest CERN, Chinese Academy of Sciences, Shenyang 110016, China

³ University of Chinese Academy of Sciences, Beijing 100049, China

* Correspondence: jiaojunzhu@iae.ac.cn; Tel.: +86-24-83970303; Fax: +86-24-83970300

Received: 23 November 2018; Accepted: 22 January 2019; Published: 4 February 2019



Abstract: Secondary forests have become the major forest type worldwide, and are experiencing various disturbances and exhibiting obvious vegetation degradation (e.g., reduced biodiversity and decreased productivity) compared with primary forests. Forest gap is a common small-scale disturbance in secondary forests. Promoting natural regeneration under gap disturbance is an important approach to recover biodiversity and ecosystem services for temperate secondary forests. The gap size is the crucial characteristic controlling natural regeneration of many tree species. However, little is known about the spatiotemporal pattern of seed rain for gravity-dispersed and wind-dispersed tree species in gaps of varying sizes. The objectives of this study were to determine how seed rain of dominant tree species depend on gap size, and consequently, to explore some gap-based silviculture solutions for restoring secondary forests from the view of seed dispersal. The spatial distribution of seed rain in gaps with three sizes (large gaps of 250–350 m², medium gaps of 150–250 m², and small gaps of <150 m²), the temporal dynamics of seed rain over three years, and the relationship between seed rain and soil seed banks were explored in temperate secondary forests. The results showed that more than 90% of the seeds in seed rain were wind-dispersed, and their seed rain density and the contribution of seed rain to soil seed bank in medium gaps reached the highest ($p = 0.03$). The results suggest that establishing medium-sized gaps (i.e., gap size with 150–250 m²) in the secondary forests is more favorable for improving the natural regeneration potential (arrival of seeds and forming soil seed bank) of gap-dependent and wind-dispersed species (e.g., *Acer mono*) in gaps.

Keywords: gravity-dispersed species; wind-dispersed species; mast seeding; medium-sized gaps; gap-dependent species; gap-based management

1. Introduction

Secondary forests have become the major forest type worldwide, and have currently accounted for more than 50% of the total forest area of China [1]. Furthermore, one-third of the national forests are distributed in Northeast China, more than 70% of which have become the secondary forests due to a century of excessive timber harvesting [2]. Secondary forests are derived from natural regeneration after the original forests suffering from the destructive disturbances [1] and are presenting obvious vegetation degradation (e.g., reduced biodiversity, decreased productivity) [3]. Poor natural regeneration of dominant tree species is the primary cause for these problems [1]. Thus, it is one of the top priorities for forest managers to restore the structure and function of secondary forests by promoting natural regeneration [1,4–6]. The natural regeneration of plants involves several stages (i.e., seed rain, seed bank, seedling bank, sapling bank and advance regeneration) and is considered to

be an effective forest restoration strategy due to its low cost and high productivity [4,5]. Successful natural regeneration from seeds is largely dependent on the arrival of seeds, which represents the start of a natural regeneration that links the end of the reproductive cycle of adult plants and subsequent population renewal and recruitment [7].

As one of the most important disturbances in secondary forests, canopy gaps created by the fall of single or multiple trees play a critical role in stand dynamics, forest cycle [8], and biodiversity of temperate secondary forests [9,10]. Promoting the natural regeneration of secondary forests under gap disturbances is crucial to the restoration and sustainable management of secondary forests [5,11]. After gap formation in broadleaved secondary forests, there are two sources of natural regeneration: seed regeneration and sprout regeneration. Although stump sprouts after gap formation can grow much faster than seedlings germinated from seeds and can quickly dominate the gap [12], seed regeneration (seed rain, soil seed bank, and seedling bank) can be used to predict the direction of future regeneration [5,6]. Nonetheless, few studies have documented the process of seed rain (i.e., an interface between the adult and seedling stages) regarding the presence of gap disturbances [13]. Consequently, the dynamics of canopy gaps are not fully understood and it is urgent to find out some gap-based silviculture and possible solutions for secondary forests [14]. The characteristics of seed rain, combined with the soil seed bank (i.e., correlations between propagule production and seed reserves in soil), determine the distribution pattern of seeds in disturbed habitats [15] and can be used to predict recruitment patterns and vegetation structure [16]. Furthermore, seed rain, as a type of regeneration strategy, increases the chance of seeds arriving at safe sites in sufficient numbers [15]. Thus, a study of the spatiotemporal patterns of seed rain in gaps could enhance the understanding of the role of gaps in the regeneration dynamics of temperate forest communities.

The spatiotemporal patterns of seed rain are determined by both abiotic and biotic conditions [17,18]. The canopy openness increases after gap formation, subsequently influencing the colonization opportunity (density and diversity) of species and, consequently, seed regeneration. After a gap is formed, more seeds may fall into the gap due to the reduced obstacles to seed rain, followed by the 'more individuals hypothesis' (MIH), i.e., species diversity increases with density and tends to be higher in gaps than in the understory [19]. However, the effects of gap formation on species density in soil seed bank are quite different in temperate secondary forests, e.g., forest gaps can promote species diversity/richness, but either have little effect [5,20] or play critical roles [21] in the seed density of soil seed bank. It is necessary to know whether the different effects of gap formation on species density in soil seed bank are related to the effects of gap formation on seed rain in temperate secondary forests. After all, seed rain is the primary source for seed bank and there are close relationships between them [15].

Gap size, one of the most important gap characteristics, has a critical effect on environmental factors (e.g., light, temperature, moisture) and particularly affects the airflow (including wind speed and direction) above, within and below the canopy [22]. Due to the airflow heterogeneity resulting from different sizes of gaps, the seed dispersal and deposition for wind-dispersed tree species should be dramatically altered. The dispersal mode should be regarded as a biotic factor influencing the changes in seed rain characteristics under gap disturbances [22]. However, much attention has been paid to the seedfall density and diversity between gaps and the forest understory in tropical/subtropical forests [23,24], and no definite conclusions have been reached. Of the few studies that have compared seed rain in the understory and in gaps, some found that the seeds of wind-dispersed trees were more abundant in the treefall gaps than those in the understory [25]; others, however, found the opposite phenomenon [23,24,26]. More empirical studies are, therefore, needed to investigate whether gaps with various sizes support the contribution to seed density of wind-dispersed tree species in temperate secondary forests.

Beyond gap size, the within-gap position strongly influences the spatial patterns of natural regeneration (i.e., seed rain, soil seed bank, seed germination/seedling emergence, seedling establishment, and seedling/sapling growth) for a given species within gaps. Species may partition

resources along resource gradients that change greatly from the gap center to the closed-canopy [27]. All the spatial patterns of natural regeneration are mainly focused on the establishment and growth of different tree species at various positions within gaps [28,29]. Of the few studies that have explored the spatial patterns of seed rain along with within-gap positions, Zang et al. [30] found that the distribution of seed rain was related to the gap position (including the gap, gap border, and non-gap) in a tropical montane rainforest, but the effects of gap size on distribution of seed rain were not addressed in their study. There are significant differences in environmental factors at the same position in different sizes of gaps [28,31]; thus, it should be expected substantial effects of the gap position combined with the gap size on the patterns of seed rain.

Inter-annual variations in seed rain are quite common in temperate forest ecosystems [32] and have an important effect on the temporal (annual) dynamics of seed rain in stands with different tree densities (e.g., gaps) [33]. Little is known about whether there are different responses of seed rain density to a mast-seeding year for varying sizes of gaps, leading to a limited understanding of the later recruitment patterns in the gaps of secondary forests.

Our hypothesis was that the spatiotemporal patterns of the seed rain density in gaps were size-dependent. Based on this hypothesis, the spatial distribution of seed rain for gravity-dispersed and wind-dispersed species at three within-gap positions (Gap, Edge, and Understory), the temporal dynamics of seed rain over three years (2011–2013), and the relationship between seed rain and potential vegetation (seed bank) were studied in ten scattered canopy gaps of various sizes in temperate secondary forests of China. We attempted to answer the following questions: (1) How does the forest gap size affect the spatiotemporal variation in seed rain density? (2) How does the seed rain spatially vary at different positions in gaps? (3) Are the relationships between seed rain and potential vegetation (i.e., soil seed bank) in forest gaps size-dependent? Finally, some new insights into the gap-based restoration measures by promoting regeneration may be provided to the secondary forests.

2. Materials and Methods

2.1. Study Site

This study was conducted at the Qingyuan Forest CERN, Chinese Academy of Sciences, located in a mountainous area in Liaoning Province, China (124°54' E, 41°51' N, 500–1100 m a.s.l.). The region has a continental monsoon climate with a windy spring, a warm and humid summer, and a dry and cold winter. The mean annual air temperature is 4.7 °C, ranging from −37.6 °C in January to 36.5 °C in July. The annual precipitation fluctuates from 700 to 850 mm, of which 80% falls during June–August. The growing season lasts from early April to late October [5]. The soil is a typical brown forest soil, classified as Udalfs according to the second edition of the USDA soil taxonomy. The soil textures in the stands were averaging 25.6% sand, 51.2% silt, and 23.2% clay [34].

Mixed broadleaved-Korean pine forests originally covered the study site at Qingyuan Forest CERN until the 1930s and were subsequently removed over decades of timber production. In the early 1950s, the original forests were completely cleared by a large fire and the site was replaced by secondary forest stands [35]. A mixture of naturally regenerating broadleaved native tree species represents the selected secondary forest stands at Qingyuan Forest CERN, which is dominated by *Fraxinus rhynchophylla* Hance, *Acer mono* Maxim., and *Quercus mongolica* Fisch., among others [36]. By ideally mimicking natural gaps, ten approximately elliptical gaps of various sizes with a length to width ratio of 3:2 were scattered in the study area and created by cutting and removing all vegetation higher than 2 m in early April of 2010 (spring). There were three large gaps of 250 to 350 m² (LGs) ($2.0 < \text{gap diameter (D)} < \text{border tree height (H)} < 3.5$), four medium gaps of 150 to 250 m² (MGs) ($1.0 < \text{D:H} \leq 2.0$), and three small gaps of < 150 m² (SGs) ($0.49 < \text{D:H} \leq 1.0$) in size [37]. This is because it was very difficult to find suitable sites for creating large gaps without complicating the topographical conditions and vegetation types, and removal of canopy trees in natural forests was highly regulated by the policy under China's Natural Forest Protection Project. Thus, the maximum size was less than 350 m², and only ten gaps were artificially created in

natural secondary forests of China. These gaps were approximately 20 m apart from each other. The sizes of artificial canopy gaps were accurately calculated by using the two hemispherical photographs method [38]. A Laser Ranging System (LI-RD1000, Laser Technology, Inc., Centennial, CO, USA) was used to determine the height of the gap border trees. Under the same history of forest management, the basic characteristics (including soil type, topography (i.e., altitude and slope), and vegetation composition) of the ten artificial gaps were quite similar. The summary of the site characteristics for the canopy gaps in this study is presented in Table 1.

2.2. Sampling Points Setting

According to our preliminary experiment, it was sufficient to represent the spatial distribution characteristics of the seed regeneration potential (e.g., seed banks) by collecting samples from two transects running along the longitudinal and latitudinal axes in each gap [5]. Therefore, only two transects were investigated in the present study: one longitudinal transect ran along the south-north direction of the canopy gap and one latitudinal transect ran along the east-west direction of the gap (Figure 1). Three categories of positions were determined according to the distance from the gap center: Gap, Edge, and Understory (Figure 1). The Edge plots were those ahead the transect entered the Understory. The gap's boundaries were those to the edge of the projected canopy, and the Edge positions were 3 m apart extended from these boundaries along two transects. The number of sampling points (i.e., four points) for both Edge and Understory positions along two transects remained consistent and did not change with gap size. However, the number of sampling points for Gap position changed with gap size, i.e., there were five, nine, and 13 sampling points for small gaps, medium gaps, and large gaps, respectively (Figure 1). There were 170 sampling points in total for all ten canopy gaps (13 sampling points for the SGs, 17 points for the MGs, and 21 points for the LGs) (Table 1), and points were set 3 m apart. At each sampling point, the seed rain and soil seed bank were monitored from 2011 to 2013. Five within-gap positions (north, south, center, east and west) were identified by dividing the east-west and south-north transects at intervals of 3 m from the gap center to the edge of gaps and to the closed-canopy adjacent to the gaps (Figure 1).

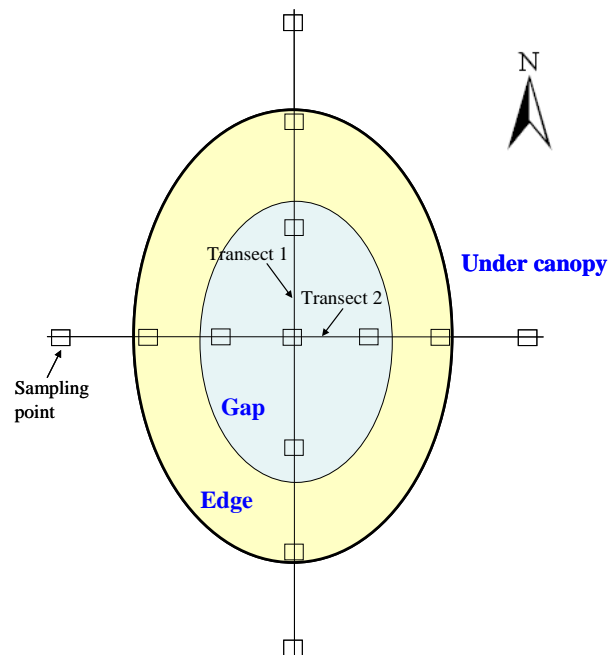


Figure 1. Transects and sampling points used to investigate the seed rain and soil seed banks, and three categories of positions (i.e., gap, edge, and under canopy) determined according to the distances from the center of each artificial forest gap.

Table 1. Description of the forest gaps investigated in the study of temperate secondary forests.

Gap Size Category	Forest Gap	Area (m ²)	Altitude (m)	Slope (°)	Height of Gap Border Trees (m)	DBH of Gap Border Trees (cm)	Vegetation Composition of Gap Border Trees (%)	Quadrats Along the South-North Direction of Gap	Quadrats Along the East-West Direction of Gap	Canopy Openness (%)	
										In Gap	Under Canopy
Large gaps	G1	346.5	756	16	16.33 ± 0.65	14.36 ± 1.16	<i>Fraxinus rhynchophylla</i> (43), <i>Acer mono</i> (20), <i>Quercus mongolica</i> (18)	11	10	24	17
	G2	323.3	760	15	17.58 ± 0.45	16.17 ± 1.98	<i>Acer mono</i> (37), <i>Fraxinus rhynchophylla</i> (20), <i>Quercus mongolica</i> (18)	11	10	22	16
	G3	286.2	743	15	16.35 ± 1.21	18.13 ± 1.32	<i>Acer mono</i> (35), <i>Quercus mongolica</i> (25), <i>Juglans mandshurica</i> Maxim. (15)	11	10	21	18
Medium gaps	G4	196.9	752	17	16.47 ± 1.22	13.24 ± 1.75	<i>Quercus mongolica</i> (56), <i>Fraxinus rhynchophylla</i> (21), <i>Acer mono</i> (15)	9	8	19	15
	G5	176.8	741	17	17.55 ± 1.07	12.54 ± 1.71	<i>Acer mono</i> (34), <i>Fraxinus rhynchophylla</i> (30), <i>Quercus mongolica</i> (16)	9	8	19	16
	G6	162.3	758	18	16.75 ± 0.63	11.77 ± 1.09	<i>Fraxinus rhynchophylla</i> (31), <i>Acer mono</i> (36), <i>Juglans mandshurica</i> (15)	9	8	17	13
	G7	150.6	753	19	17.01 ± 1.34	12.34 ± 2.65	<i>Acer mono</i> (44), <i>Fraxinus rhynchophylla</i> (21), <i>Tilia tuan</i> Szyszyl. (15)	9	8	16	13
Small gaps	G8	121.8	748	16	15.73 ± 0.98	12.13 ± 1.78	<i>Fraxinus rhynchophylla</i> (45), <i>Acer mono</i> (24), <i>Juglans mandshurica</i> (15)	7	6	15	12
	G9	98.7	755	16	16.15 ± 1.16	10.62 ± 1.39	<i>Acer mono</i> (47), <i>Fraxinus rhynchophylla</i> (25), <i>Ulmus laciniata</i> (Trautv.) Mayr (15)	7	6	14	11
	G10	51.5	743	18	15.58 ± 0.71	10.32 ± 1.77	<i>Quercus mongolica</i> (36), <i>Acer mono</i> (26), <i>Fraxinus rhynchophylla</i> (15)	7	6	13	11

DBH = mean tree diameter at breast height (± S.E.).

2.3. Seed Rain Investigation

At each sampling point, a seed trap was arranged in early May 2011, prior to the current-year seed shedding. Each trap was 0.5 m above the ground, 0.50 m × 0.50 m, made of a fine and flexible mesh of 1 mm and was supported on four PVC tubes. Although the tree species occurring in the seed rain belong to different propagule types (e.g., nut, seed, and samara) (Table 2), “seeds” were used to collectively name these propagule types [39]. The seeds were collected at intervals of 20 days from late June to late October for three years (2011–2013). The species composition and the amount of seed rain were determined by the seed extraction method [5]. All seeds, fruits, capsules, flowers, and other reproductive parts of plants falling into the traps were identified to the species level and recorded. The fruits were categorized as aborted, immature, damaged, fragmented and mature [26]. The seeds were judged to be mature and viable after the tetrazolium dyeing test [5], and only the viable seeds (including both germinable and dormant seeds) were included in the present study. Because the seed traps were set above the ground, fruits and seeds after first dispersal (i.e., falling directly from trees by wind or gravity) mainly dominated the traps; fruits and seeds resulting from secondary dispersal by rodents and other terrestrial animals were not, however, recorded in this study [26].

Table 2. Species, abundance class and common dispersal type for the seeds of broad-leaved woody species occurred in the seed rain collection of 3 years (2011, 2012 and 2013).

Species	Family	Life Form	Propagule Type	Appendages	Abundance Class	Common Dispersal Type for the Primary Dispersal	Viability Rate of Seeds after 1-year Burial
<i>Quercus mongolica</i>	Fagaceae	Tree	Nut	None	Rare	Gravity	-
<i>Bothrocaryum controversum</i> (Hemsl.) Pojark.	Cornaceae	Tree	Drupe	None	Rare	Gravity	-
<i>Fraxinus rhynchophylla</i>	Oleaceae	Tree	Samara	Wing	Rare	Wind	-
<i>Fraxinus mandshurica</i> Rupr.	Oleaceae	Tree	Samara	Wing	Common	Wind	10% [40]
<i>Juglans mandshurica</i>	Juglandaceae	Tree	Nut	None	Common	Gravity	82% [40]
<i>Acer mono</i>	Aceraceae	Tree	Samara	Wing	Common	Wind	-
<i>Acer pseudosieboldianum</i> (Pax) Kom.	Aceraceae	Tree	Samara	Wing	Rare	Wind	-
<i>Phellodendron amurense</i> Rupr.	Rutaceae	Tree	Seed	None	Rare	Gravity	-
<i>Betula costata</i> Trautv.	Betulaceae	Tree	Nutlet	Wing	Common	Wind	-

2.4. Soil Seed Bank Sampling

The samples were collected at points < 0.5 m from the points of seed rain collection at the end of most of the seed fall into the seed bank (i.e., in late October) in 2011–2013. For each sampling period, a composite sample combined with three soil samples was collected at each point [5]. A hollow steel cylinder 70 mm in diameter was used to collect soil samples from the forest floor litter and 0–2 cm in the soil. The species composition in soil seed bank was assessed by the seed extraction method, which was the same method used for determining the species composition in seed rain. Only the viable seeds (including both germinable and dormant seeds) were included in the present study [41].

2.5. Data Analysis

Data of the seeds for woody species collected in both seed rain and seed bank were converted to the number of viable seeds m^{-2} (i.e., seed density). There was a value of seed density for each seed-trap or each soil sample. The average position-scale estimates of seed density (i.e., “Gap”, “Edge”, and “Understory”) were used when considering the effects of within-gap position during data analysis.

Based on the fruit morphology and consumption [32,42], each species found in the seed rain was assigned to gravity (gravity-dispersed species) or wind (wind-dispersed species) as the dispersal mode (Table 2). The abundance of species existing in the seed rain was divided into two categories, i.e., “rare” species were defined as those species occurring at less than 15% of all sampling points [43], and all other species were defined as “common” (Table 2).

The similarity indices in the species composition between the seed rain and the corresponding soil seed bank were calculated following Sokal and Sneath [44]. The Sokal and Sneath similarity index was calculated as follows:

$$I = 2c / (a + b) \quad (1)$$

where I is the similarity index, c is the number of common species in both seed rain and soil seed bank, a is the total number of species in the seed rain, and b is the total number of species in the soil seed bank.

All data were tested for the homogeneity of variance before performing specific statistical procedures. Mixed-model repeated measures analysis of variance (RMANOVA) was used to test the effects of gap size and within-gap position on the seed density of seed rain, the similarity between seed rain and seed bank, and the contribution of seed rain to seed bank in seed density (i.e., the ratio of seed density in the seed rain to seed density in the seed bank) at the sampling points across the three years. In RMANOVA, the gap size, within-gap position and their two-way interaction effects were treated as fixed effects, and time was treated as a random effect [45] (SAS 9.4 software, SAS Institute Inc., Cary, NC, USA). Furthermore, the separate sampling points from the same gap were ever used as independent data samples. When the interactions between the gap size and the within-gap position were significant, one-way ANOVA and Tukey's HSD post-hoc tests were applied (SPSS software, 16th edition, Chicago, IL, USA) to determine the effects of gap size by within-gap position. Differences were considered significant at the level of $p < 0.05$.

One-way ANOVA and Tukey's HSD tests were also applied post hoc (SPSS software, 16th edition, Chicago, IL, USA) to distinguish the density of all seeds and two main dispersal types of seeds among the three categories of positions. Simple linear regressions were used to determine the relationships between the gap size and the density of seed rain and between the densities of seed rain and the corresponding seed bank.

3. Results

3.1. Spatiotemporal Variation in the Seed Rain and Its Relationship with Gap Size

According to RMANOVA, the gap size \times position interaction had no significant effects on seed density ($df = 4$, $F = 0.11$, $p = 0.9769$). However, gap size ($df = 2$, $F = 5.72$, $p = 0.0061$), sampling year ($df = 2$, $F = 9.91$, $p = 0.0001$), and sampling year \times gap size ($df = 4$, $F = 3.72$, $p = 0.0075$) significantly influenced seed density of all woody species and wind-dispersed species. The seed density in 2013 was the highest at almost all of the within-gap positions of large and medium gaps, but no dramatic changes in the seed density were found in small gaps during the three years of this investigation (Figure 2).

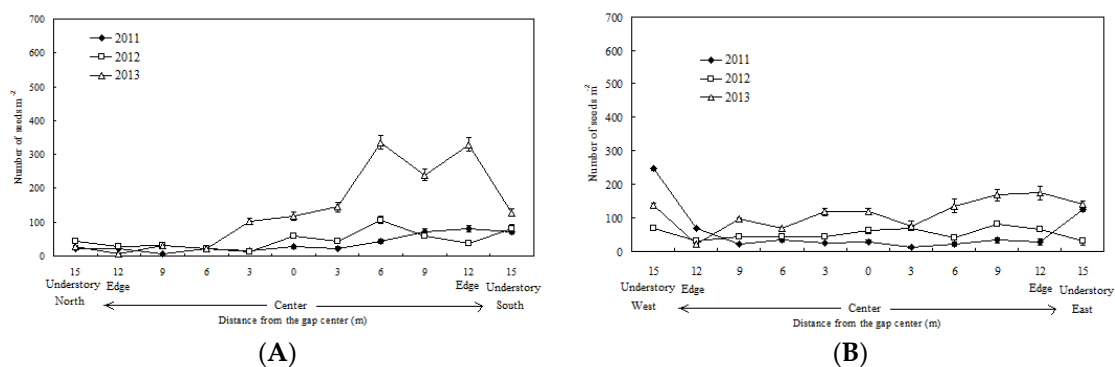


Figure 2. Cont.

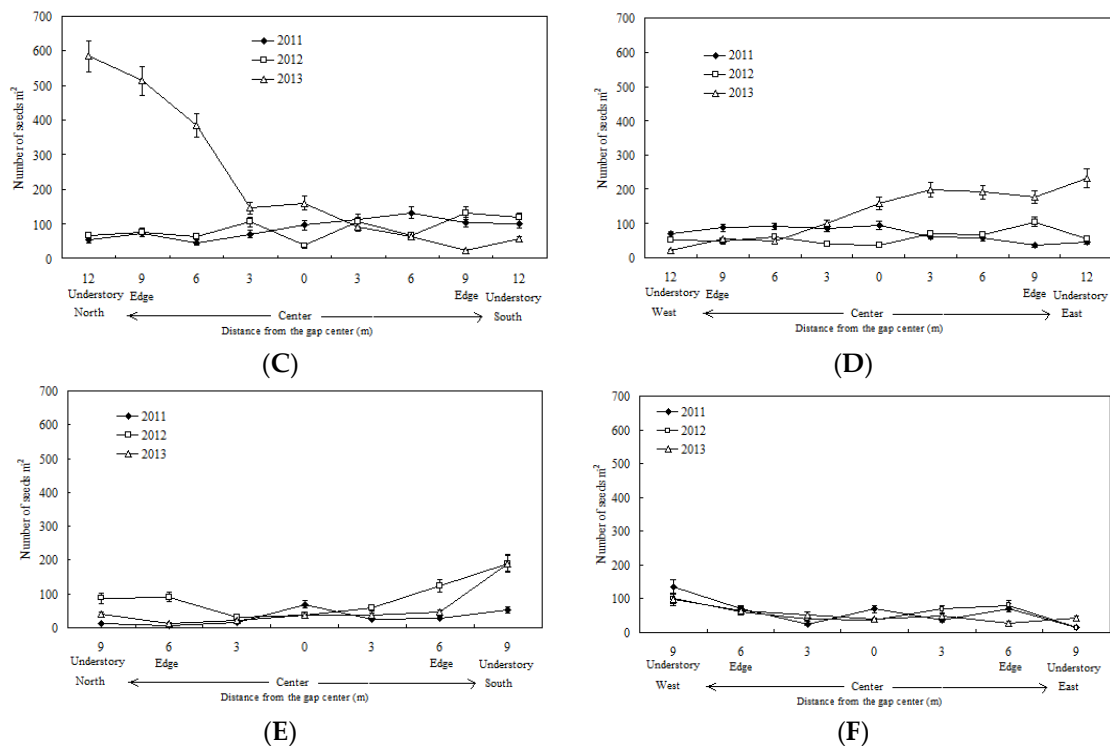
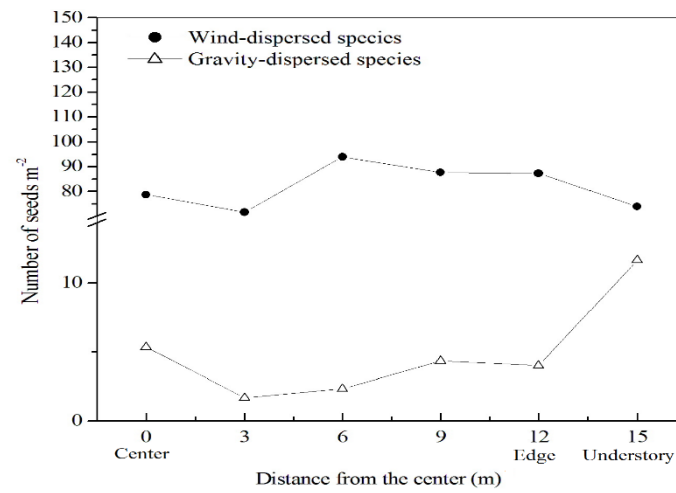


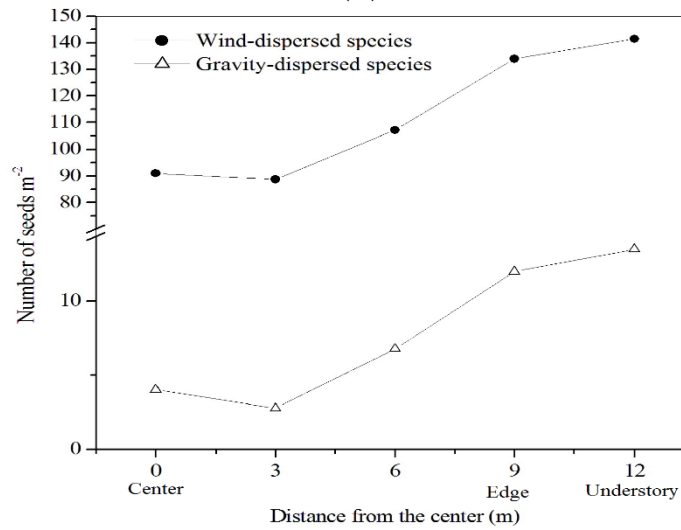
Figure 2. Spatiotemporal distribution patterns of the seed rain density. (A) north-south transect in large gaps; (B) west-east transect in large gaps; (C) north-south transect in medium gaps; (D) west-east transect in medium gaps; (E) north-south transect in small gaps; (F) west-east transect in small gaps.

For all of the woody species in seed rain, the seed density fluctuated at three categories of positions of the large gaps (Understory (90 ± 7 seeds/m²) > Edge (74 ± 8 seeds/m²) \approx Gap (68 ± 3 seeds/m²)) (Figure 2A,B), the medium gaps (Understory (121 ± 5 seeds/m²) \approx Edge (118 ± 4 seeds/m²) > Gap (100 ± 6 seeds/m²)) (Figure 2C,D), and the small gaps (Understory (89 ± 9 seeds/m²) > Edge (63 ± 4 seeds/m²) > Gap (42 ± 7 seeds/m²)) (Figure 2E,F), respectively.

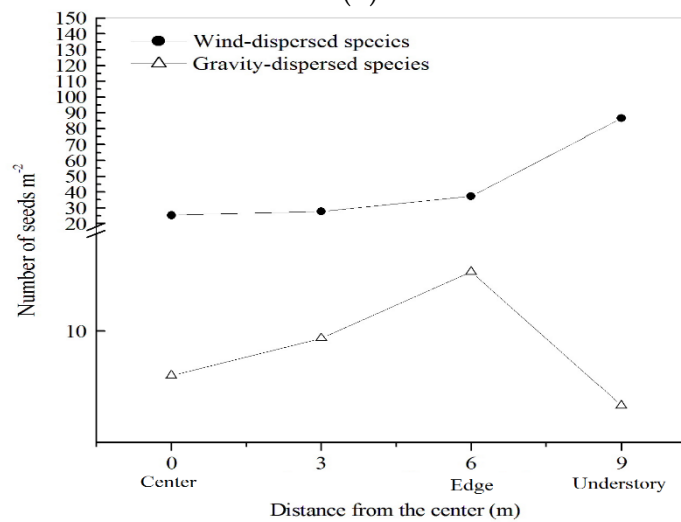
For the wind-dispersed species in seed rain, the seed density ranked as follows: Understory (74 ± 3 seeds/m²) < Edge (87 ± 3 seeds/m²) \approx Gap (83 ± 2 seeds/m²) in the large gaps (Figure 3A), Understory (142 ± 2 seeds/m²) > Edge (134 ± 3 seeds/m²) > Gap (96 ± 5 seeds/m²) in the medium gaps (Figure 3B), and Understory (87 ± 5 seeds/m²) > Edge (37 ± 3 seeds/m²) > Gap (27 ± 3 seeds/m²) in the small gaps (Figure 3C). For the gravity-dispersed species, however, the density of seed rain varied in the following orders: Understory (12 ± 2 seeds/m²) > Edge (4 ± 1 seeds/m²) \approx Gap (3 ± 1 seeds/m²) in the large gaps (Figure 3A), Understory (14 ± 1 seeds/m²) \approx Edge (12 ± 3 seeds/m²) > Gap (5 ± 1 seeds/m²) (Figure 3B) in the medium gaps, and Edge (13 ± 2 seeds/m²) > Gap (9 ± 1 seeds/m²) \approx Understory (7 ± 3 seeds/m²) in the small gaps (Figure 3C).



(A)



(B)



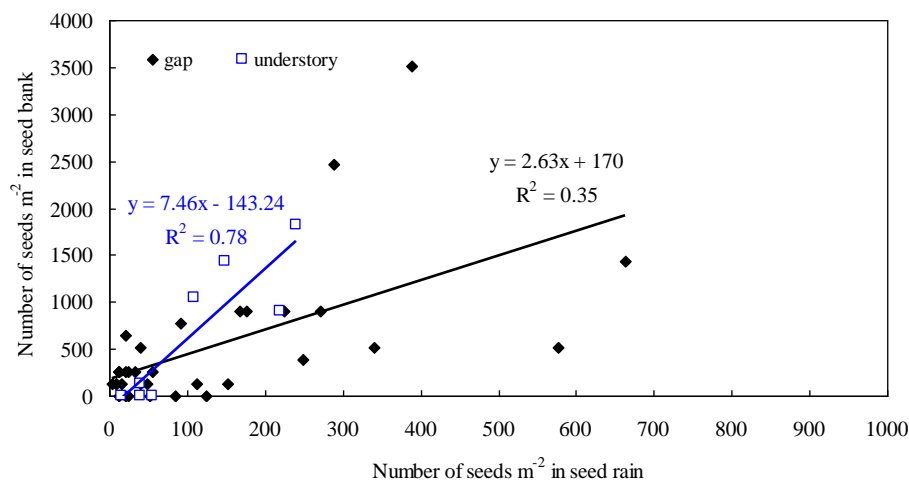
(C)

Figure 3. Spatial distribution patterns of the seed rain density for two main types of seed dispersal (i.e., gravity-dispersed species and wind-dispersed species) in large gaps (A), medium gaps (B), and small gaps (C) shown as the mean value for three years.

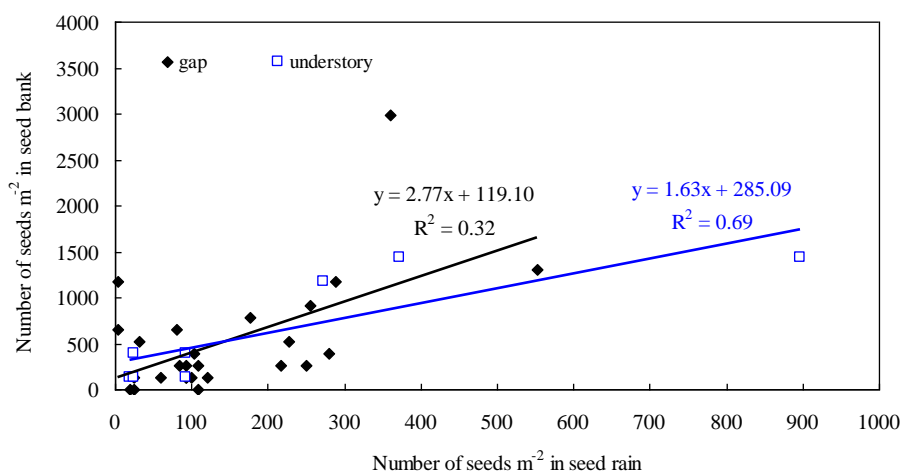
Among the three sizes of gaps, the seed densities were the highest in the medium gaps ($p = 0.03$) for all of the woody species (105 ± 14 seeds/m²) and wind-dispersed tree species (98 ± 6 seeds/m²).

3.2. Relationship Between Seed Rain and Soil Seed Bank

Only for the large and medium gaps, the density of seed rain was positively correlated with that of seed bank at the Gap and Understory positions (Figure 4). In particular, close relationships were found for the wind-dispersed tree species at these two positions.



(A)



(B)

Figure 4. Relationship between the seed density of seed rain and that of the soil seed bank for all types of tree species in large gaps (A) and medium gaps (B).

The Sokal and Sneath similarity index in the species-composition between seed rain and seed bank was ranked as follows: Gap (0.41 ± 0.04) \approx Edge and Understory (0.38 ± 0.04) in the large gaps, Understory (0.55 ± 0.02) > Gap (0.49 ± 0.01) > Edge (0.38 ± 0.03) in the medium gaps, and Gap (0.44 ± 0.04) > Edge and Understory (0.33 ± 0.02) in the small gaps.

For all types of seeds and the wind-dispersed seeds found in the large and medium gaps, the contribution of seed rain to the seed density of seed bank tended to decline along the Gap ($24 \pm 1\%$ in large gaps, $43 \pm 2\%$ in medium gaps) -Edge ($21 \pm 2\%$ in large gaps, $40 \pm 3\%$ in medium gaps)-Understory ($18 \pm 1\%$ in large gaps, $31 \pm 2\%$ in medium gaps) gradient. However, an opposite pattern of contribution occurred in the small gaps, i.e., the contribution tended to increase along the

Gap ($22 \pm 1\%$)-Edge ($28 \pm 2\%$)-Understory ($49 \pm 4\%$) gradient. The contribution of seed rain to soil seed bank for the gravity-dispersed tree species was less than 5% at any position of various sizes of gaps.

4. Discussion

By comparing gaps with different sizes, we found that the gap size played an important role in the density of the species in seed rain and in the relationships between seed rain and soil seed bank. Our results indicated that the seed density in the medium gaps was significantly higher than in the large and small gaps (Figure 3). The relationships between seed rain and seed bank were mainly dependent on the gap size, which was represented as that the positive correlation between seed rain and seed bank and the highest contribution and similarity of seed rain to seed bank occurred in the medium gaps. Compared with other two extreme canopy conditions (large gaps and closed canopy), the medium gap size can provide a more moderate microclimate and resources for seed arrival and deposition [5] and the regeneration and growth of tree species [46].

Although some studies have explored the establishment and growth of different tree species at the seed bank and seedling/sapling stages across various within-gap positions [5,28,29], this study is the first report for the spatial distribution patterns of seed rain along the gradients of within-gap positions from the gap center to the closed-canopy over a range of gap sizes in temperate secondary forests. Our findings showed that the spatial distribution patterns of seed rain relied on the gap size. First, the seeds of all species tended to be deposited in larger numbers in the forest understory than in treefall gaps for various sizes of gaps, except for the wind-dispersed species in the large gaps (Figure 3). This result is supported by previous studies [23,24,26] in tropical/subtropical forests. Because seed traps were used to collect the seed rain, only the fruits/seeds after the first dispersal (i.e., wind- or gravity-dispersed seeds) were considered [26], and the effects of gap size on the dispersal of zoochorous seeds were not explored in this study. We found that more than 90% of the seeds in seed rain were wind-dispersed (including gap-dependent species *A. mono*, pioneer species *Betula costata* and so on). During the period of seed fall from August to late October, the wind speed in the forest stands at the Qingyuan Forest CERN was not strong enough (varying between 1, 6 and 2.0 m/s) to carry wind-dispersed seeds to a great distance [30], and the gaps were generally farther from the mother trees than the understory. Consequently, the seed rain densities in the closed-canopy adjacent to the small/medium gaps were greater than in the gaps [26]. However, the morphological structure of the wind-dispersed seeds, together with the airflow at the edge between the understory and the open area in large gaps, may facilitate their dispersal into the gaps [23]. Then, the arrived wind-dispersed seeds in the gaps will have more opportunities to complete their regeneration due to the favorable microenvironments created by gap formation, such as greater light availability [6]. Consequently, it is reasonable to predict that the establishment of these wind-dispersed seeds in the gaps will modify the dynamics of the secondary forests that are experiencing gap disturbances [6,17,47]. Second, the density of species in the seed rain was the highest only at the edge of the medium gaps (Figure 2). The fact that the edge effects of seed rain only occurred in the medium-sized gaps is consistent with the spatial characteristics of the seed bank in temperate forests [5], which further confirms the close relationships between seed rain and seed bank in the medium gaps. The edge effects of seed rain occur mainly because the gap edges combine the traits of canopy gap and closed-canopy in the transition area for seed arrival [13].

Gaps with different sizes have various responses to the inter-annual variations in the seed rain. Our results indicated that a consistent number of seeds occurred in small gaps among the three investigating years, but more seeds were deposited in large and medium gaps during a mast-seeding year (in 2013) (Figure 2). Although the number of seeds was lowest in the small gaps relative to other two sizes of gaps, consistent seed resources can be supplied for later recruitment in the small gaps of secondary forests without being affected by seed production [33]. All of these results in the present study strongly support our working hypothesis and we suggest establishing medium/large-sized

gaps (i.e., gap size with 150–350 m²) to improve the natural regeneration potentials of wind-dispersed tree species in secondary forests.

5. Conclusions

Because seed traps were used to collect the seed rain, only the fruits/seeds after the first dispersal (i.e., wind- or gravity-dispersed seeds) were considered, and the effects of gap characteristics (i.e., gap size and within-gap position) on the dispersal of zoochorous seeds were not explored in this study. We found that more than 90% of the seeds in seed rain were wind-dispersed (including gap-dependent species *A. mono*, pioneer species *B. costata* and so on). Fewer wind-dispersed seeds reached the treefall gaps than into their corresponding forest understory. Medium-sized gaps facilitate the seed arrival of a greater number and more categories of wind-dispersed species. We also found that the effects of within-gap positions on the characteristics of seed rain, the inter-annual variations in seed rain, and the relationships between seed rain and potential vegetation (i.e., soil seed bank) are strongly dependent on the gap size. Thus, from the perspective of improving the natural regeneration potentials (arrival of seeds and forming soil seed bank) of gap-dependent and wind-dispersed species (e.g., *A. mono*) in gaps, it would be more favorable forest establishing medium/large-sized gaps (i.e., gap size with 150–350 m²) in secondary forests.

Author Contributions: Q.Y. and J.Z. designed the experiments, carried out data analysis and wrote the manuscript; Q.Y. and Q.G. carried out the experiments in the field and laboratory.

Funding: This work was supported by grants from the National Natural Science Foundation of China (31330016), Key Research Program of Frontier Sciences, CAS (QYZDJ-SSW-DQC027), and the Youth Innovation Promotion Association CAS (2011158).

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Zhu, J.J.; Liu, S.R. Conception of secondary forest and its relation to ecological disturbance degree. *Chin. J. Appl. Ecol.* **2007**, *267*, 1085–1093, (In Chinese with English Abstract).
2. Chen, X.W.; Li, B.L.; Lin, Z.S. The acceleration of succession for the restoration of the mixed-broadleaved Korean pine forests in Northeast China. *For. Ecol. Manag.* **2003**, *117*, 503–514. [[CrossRef](#)]
3. Zhu, J.J.; Liu, Z.G. A review on disturbance ecology of forest. *Chin. J. Appl. Ecol.* **2004**, *15*, 1703–1710. (In Chinese with English Abstract)
4. Chazdon, R.L. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science* **2008**, *320*, 1458–1460. [[CrossRef](#)] [[PubMed](#)]
5. Yan, Q.L.; Zhu, J.J.; Zhang, J.P.; Yu, L.Z.; Hu, Z.B. Spatial distribution pattern of soil seed bank in canopy gaps of various sizes in temperate secondary forests, Northeast China. *Plant Soil* **2010**, *329*, 469–480. [[CrossRef](#)]
6. Yan, Q.L.; Zhu, J.J.; Yu, L.Z. Seed regeneration potential of canopy gaps at early formation stage in temperate secondary forests, Northeast China. *PLoS ONE* **2012**, *7*, e39502. [[CrossRef](#)] [[PubMed](#)]
7. Nathan, R.; Muller-Landau, H.C. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* **2000**, *15*, 278–285. [[CrossRef](#)]
8. Gagnon, J.L.; Jokela, E.J.; Moser, W.K.; Huber, D.A. Characteristics of gaps and natural regeneration in mature longleaf pine flatwoods ecosystems. *For. Ecol. Manag.* **2004**, *187*, 373–380. [[CrossRef](#)]
9. Košulič, O.; Michalko, R.; Hula, V. Impact of canopy openness on spider communities: Implications for conservation management of formerly coppiced Oak forests. *PLoS ONE* **2016**, *11*, e0148585. [[CrossRef](#)]
10. Greenberg, C.H. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. *For. Ecol. Manag.* **2001**, *148*, 135–144. [[CrossRef](#)]
11. van Kuijk, M.; Anten, N.P.R.; Oomen, R.J.; van Bentum, D.W.; Werger, M.J.A. The limited importance of size-asymmetric light competition and growth of pioneer species in early secondary forest succession in Vietnam. *Oecologia* **2008**, *157*, 1–12. [[CrossRef](#)] [[PubMed](#)]
12. Bond, W.J.; Midgley, J.J. Ecology of sprouting in woody plants: The persistence niche. *Trends Ecol. Evol.* **2001**, *16*, 45–51. [[CrossRef](#)]

13. Zhu, J.J.; Lu, D.L.; Zhang, W.D. Effects of gaps on regeneration of woody plants: A meta-analysis. *J. For. Res.* **2014**, *25*, 501–510. [[CrossRef](#)]
14. Kern, C.C.; Burton, J.I.; Raymond, P.; D'Amato, A.W.; Keeton, W.S.; Royo, A.A.; Walters, M.B.; Webster, C.R.; Willis, J.L. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry* **2017**, *90*, 4–17. [[CrossRef](#)]
15. Grime, J.P. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd ed.; John Wiley & Sons Ltd.: Chichester, UK, 2001.
16. Wang, B.C.; Smith, T.B. Closing the seed dispersal loop. *Trends Ecol. Evol.* **2002**, *17*, 379–385. [[CrossRef](#)]
17. Martini, A.M.Z.; dos Santos, F.A.M. Effects of distinct types of disturbance on seed rain in the Atlantic forest of NE Brazil. *Plant Ecol.* **2007**, *190*, 81–95. [[CrossRef](#)]
18. de Andrés, E.G.; Camarero, J.J.; Martínez, I.; Coll, L. Uncoupled spatiotemporal patterns of seed dispersal and regeneration in Pyrenean silver fir populations. *For. Ecol. Manag.* **2014**, *319*, 18–28. [[CrossRef](#)]
19. Evans, K.L.; Gaston, K.J. Can the evolutionary-rates hypothesis explain species-energy relationships? *Funct. Ecol.* **2005**, *19*, 899–915. [[CrossRef](#)]
20. Busing, R.T.; White, P.S. Species diversity and small-scale disturbance in an old-growth temperate forest: A consideration of gap partitioning concepts. *Oikos* **1997**, *78*, 562–568. [[CrossRef](#)]
21. Forrester, J.A.; Leopold, D.J. Extant and potential vegetation of an old-growth maritime *Ilex opaca* forest. *Plant Ecol.* **2006**, *183*, 349–359. [[CrossRef](#)]
22. Bohrer, G.; Katul, G.G.; Nathan, R.; Walko, R.L.; Avissar, R. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *J. Ecol.* **2008**, *96*, 569–580. [[CrossRef](#)]
23. Loiselle, B.A.; Ribbens, E.; Vargas, O. Spatial and temporal variation of seed rain in a tropical lowland wet forest. *Biotropica* **1996**, *28*, 82–95. [[CrossRef](#)]
24. Jones, F.A.; Chen, J.; Weng, G.J.; Hubbell, S.P. A genetic evaluation of seed dispersal in the Neotropical tree *Jacaranda copaia* (Bignoniaceae). *Am. Nat.* **2005**, *166*, 543–555. [[CrossRef](#)] [[PubMed](#)]
25. Denslow, J.S.; Diaz, A.E.G. Seed rain to tree-fall gaps in a Neotropical rainforest. *Can. J. For. Res.* **1990**, *20*, 642–648. [[CrossRef](#)]
26. Du, Y.J.; Mi, X.C.; Ma, K.P. Comparison of seed rain and seed limitation between community understory and gaps in a subtropical evergreen forest. *Acta Oecol.* **2012**, *44*, 11–19. [[CrossRef](#)]
27. Denslow, J.S. Gap partitioning among tropical rainforest trees. *Biotropica* **1980**, *12*, 47–55. [[CrossRef](#)]
28. Gray, A.N.; Spies, T.A. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *J. Ecol.* **1996**, *84*, 635–645. [[CrossRef](#)]
29. Schnitzer, S.A.; Mascaro, J.; Carson, W.P. Treefall gaps and the maintenance of plant species diversity in tropical forests. In *Tropical Forest Community Ecology*; Carson, W.P., Schnitzer, S.A., Eds.; Blackwell Publishing Ltd.: Oxford, UK, 2008; pp. 196–209.
30. Zang, R.G.; Zhang, W.Y.; Ding, Y. Seed dynamics in relation to gaps in a tropical montane rainforest of Hainan Island, South China: (I) seed rain. *J. Integr. Plant Biol.* **2007**, *49*, 1565–1572. [[CrossRef](#)]
31. Liu, G.X.; Mao, P.S.; Wang, Y.W.; Han, J.G. Effects of adult neighbour and gap size on seedling emergence and early growth of *Bromus inermis* Leyss. *Ecol. Res.* **2008**, *23*, 197–205. [[CrossRef](#)]
32. Li, B.H.; Hao, Z.Q.; Bin, Y.; Zhang, J.; Wang, M. Seed rain dynamics reveals strong dispersal limitation, different reproductive strategies and responses to climate in a temperate forest in northeast China. *J. Veg. Sci.* **2012**, *23*, 271–279. [[CrossRef](#)]
33. Rossi, S.; Morin, H.; Laprise, D.; Gionest, F. Testing mast seeding mechanisms of boreal forest species at different stand densities. *Oikos* **2012**, *121*, 665–674. [[CrossRef](#)]
34. Yang, K.; Zhu, J.J.; Yan, Q.L.; Zhang, J.X. Soil enzyme activities as potential indicators of soluble organic nitrogen pools in forest ecosystems of Northeast China. *Ann. For. Sci.* **2012**, *69*, 795–803. [[CrossRef](#)]
35. Chen, D.K.; Zhou, X.F.; Zhu, N. *Natural Secondary Forest-Structure, Function, Dynamics and Management*; Northeast Forestry University Press: Harbin, China, 1994. (In Chinese)
36. Hu, L.L.; Mao, Z.H.; Zhu, J.J.; Liu, Z.G.; Chen, G.H. Classification and ordination of secondary forests in montane zone of eastern Liaoning Province. *Acta Ecol. Sin.* **2005**, *25*, 2848–2854. (In Chinese with English Abstract)
37. Zhu, J.J.; Zhang, G.Q.; Wang, G.G.; Yan, Q.L.; Lu, D.L.; Li, X.F.; Zheng, X. On the size of forest gaps: Can their lower and upper limits be objectively defined? *Agric. For. Meteorol.* **2015**, *213*, 64–76. [[CrossRef](#)]

38. Hu, L.L.; Zhu, J.J. Determination of the tridimensional shape of canopy gaps using two hemispherical photographs. *Agric. For. Meteorol.* **2009**, *149*, 862–872. [[CrossRef](#)]
39. Thompson, K.; Band, S.R.; Hodgson, J.G. Seed size and shape predict persistence in soil. *Funct. Ecol.* **1993**, *7*, 236–241. [[CrossRef](#)]
40. Gang, Q.; Yan, Q.L.; Zhu, J.J. Effects of thinning on early seed regeneration of two broadleaved tree species in larch plantations: Implication for converting pure larch plantations into larch-broadleaved mixed forests. *Forestry* **2015**, *88*, 573–585. [[CrossRef](#)]
41. Simpson, R.L.; Leck, M.A.; Parker, V.T. Seed banks: General concepts and methodological issues. In *Ecology of Soil Seed Bank*; Leck, M.A., Parker, V.T., Simpson, R.L., Eds.; Academic Press: San Diego, CA, USA, 1989; pp. 3–8.
42. Wu, Z.Y.; Raven, P.H.; Hong, D.Y. *Flora of China*; Science Press: Beijing, China; Missouri Botanical Garden Press: St. Louis, MO, USA, 2013; pp. 11–52.
43. Romermann, C.; Tackenberg, O.; Jackel, A.K.; Poschold, P. Eutrophication and fragmentation are related to species' rate of decline but not to species rarity: Results from a functional approach. *Biodivers. Conserv.* **2008**, *17*, 591–604. [[CrossRef](#)]
44. Sokal, R.R.; Sneath, P.H.A. *Principles of Numerical Taxonomy*; W.H. Freeman and Company: San Francisco, CA, USA, 1963.
45. Gurevitch, J.; Chester, S.T. Analysis of repeated measures experiments. *Ecology* **1986**, *67*, 251–255. [[CrossRef](#)]
46. Kern, C.C.; Reich, P.B.; Montgomery, R.A.; Strong, T.F. Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? *For. Ecol. Manag.* **2012**, *267*, 134–143. [[CrossRef](#)]
47. Puerta-Piñero, C.; Muller-Landau, H.C.; Calderón, O.; Wright, S.J. Seed arrival in tropical forest tree fall gaps. *Ecology* **2013**, *94*, 1552–1562. [[CrossRef](#)]



© 2019 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).