Basic Characteristics of Woody Plant Seed Rain and Its Influencing Factors in Fragmented Habitats of Qiandao Lake: Postprint

Authors: Bao Minghui, Fang Zhongping, Hu Laiting, Southern Song, Xu Gaofu, Mingjian Yu

Date: 2022-07-05T00:00:00+00:00

Abstract

To investigate the fundamental characteristics of seed rain of woody plants in fragmented habitats, this study utilized monthly seed rain data collected from 2015–2020 within long-term monitoring plots of plant communities on sample islands in Qiandao Lake. Kruskal-Wallis tests were employed to analyze inter-annual variations in seed rain density of woody plants and monthly variations in seed rain density among species with different dispersal modes. Linear mixed-effects models were used to examine the effects of island spatial characteristics (island area, distance to the nearest island, distance to mainland) and climatic factors (accumulated temperature above 0 °C, precipitation) on seed rain density of woody plants and species with different dispersal modes. The results demonstrated that: (1) Over the six-year period, a total of 877,178 mature seeds of woody plants were collected across 240 seed traps on 29 sample islands, representing 52 species in 40 genera and 26 families. (2) Animal dispersal constituted the primary seed dispersal mode for woody plants. Species with different dispersal modes exhibited substantial differences in the temporal dynamics of seed rain. (3) Annual seed rain density of woody plants was significantly positively correlated with island area and annual accumulated temperature, and significantly negatively correlated with annual precipitation. (4) Monthly seed rain density of autochorous species was significantly positively correlated with distance to the nearest island, whereas monthly seed rain density of zoochorous species was significantly positively correlated with distance to mainland, and monthly seed rain density of anemochorous species was extremely significantly positively correlated with monthly accumulated temperature. Habitat fragmentation influenced the temporal dynamics of woody plant seed rain through island spatial characteristics.

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Full Text

Basic Characteristics and Influencing Factors of Seed Rain of Woody Plants in Fragmented Habitats in the Thousand Island Lake

Minghui Bao[1], **Zhongping Fang**[2], **Laiting Hu**[3], **Ge Nan**[4], **Gaofu Xu**[2], **Mingjian Yu**[1*] [1]College of Life Sciences, Zhejiang University, Hangzhou 310058, China [2]Chun' an Xin' anjiang Ecological Development Group Co., Ltd., Chun' an 311700, Zhejiang, China [3]Forestry Administration of Chun' an, Chun' an 311799, Zhejiang, China [4]Weinan Junior High School, Weinan 714099, Shaanxi, China

Abstract: Seed rain fundamentally influences species composition, forest community diversity, and the regeneration of plant populations and communities. Understanding seed rain characteristics is crucial for investigating plant regeneration strategies and population restoration. To explore the basic characteristics of seed rain in fragmented habitats, this study analyzed monthly seed rain data collected from 2015 to 2020 in plant community monitoring plots on sample islands in the Thousand Island Lake. We used Kruskal-Wallis tests to examine interannual differences in seed rain density of woody plants and monthly variations among species with different dispersal syndromes. Linear mixed-effects models were then employed to investigate the effects of island spatial attributes (island area, distance to nearest island, distance to mainland) and climatic factors (accumulated temperature above 0 °C, precipitation) on seed rain density of woody plants and species with different dispersal syndromes. The results showed: (1) Over the six-year period, 240 seed traps across 29 sample islands collected a total of 877,178 mature seeds of woody plants, belonging to 26 families, 40 genera, and 52 species. (2) Zoochory was the dominant dispersal syndrome for woody plants, with significant differences in temporal dynamics among dispersal syndromes. (3) Annual seed rain density of woody plants was significantly positively correlated with island area and annual accumulated temperature, but significantly negatively correlated with annual precipitation. (4) Monthly seed rain density of autochorous species was significantly positively correlated with distance to the nearest island, while that of zoochorous species was significantly positively correlated with distance to mainland, and anemochorous species showed a highly significant positive correlation with monthly accumulated temperature. Habitat fragmentation affects the temporal dynamics of woody plant seed rain through island spatial attributes.

Keywords: seed rain, dispersal syndrome, habitat fragmentation, temporal dynamics, woody plants

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Seed rain, defined as the process by which seeds or fruits fall from parent plants to the ground surface, represents a critical factor in forest population and community regeneration. The temporal dynamics of seed rain constitute one of its fundamental characteristics, manifesting as seasonal and interannual variations at community, population, and individual levels. Seed rain also serves as an indicator of population and community dynamics because it is influenced by both biotic and abiotic environmental factors, including temperature and precipitation, as well as species-specific biological and ecological traits such as seed dispersal mode. Previous research has demonstrated that elevated temperatures and increased annual rainfall can enhance seed production in species like *Erica multiflora*. Studies in the 50 hm^2 Barro Colorado Island (BCI) forest dynamics plot revealed that among 41 tree species with the same dispersal syndrome, heavier seeds tend to have shorter dispersal distances.

Seed dispersal modes can be categorized into autochory (self-dispersal) and allochory (dispersal via external agents). Allochory is further divided into hydrochory (water dispersal), anemochory (wind dispersal), and zoochory (animal dispersal). Autochory refers to seeds leaving the parent plant or entering soil through their own structural mechanisms via gravity, bouncing, or drilling. Zoochory involves seed transport by animals, while anemochory relies on wind. Seasonal dynamics of seed rain are driven by different dispersal strategies: anemochorous species tend to fruit during dry seasons, whereas zoochorous species typically fruit during rainy seasons. This pattern has been validated in multiple studies, including research in seasonally dry tropical forests of Ecuador and the Caatinga dry forest of Brazil. Although seed dispersal is crucial for maintaining population and community structure, it is also one of the most severely disrupted processes in fragmented habitats.

Habitat fragmentation refers to the process by which continuous habitats are divided into multiple isolated patches, leading to reduced habitat area, increased isolation, and enhanced edge effects. Fragmentation often results in biotic homogenization, favoring light-demanding and drought-tolerant species, while intensifying competition and reducing species diversity. Moreover, habitat fragmentation can alter the abundance and richness of seed dispersers, particularly large-seed dispersers, disrupting effective animal-mediated seed dispersal, reducing recruitment of animal-dispersed plants, and increasing plant extinction risk by up to tenfold.

In forest community succession, seed rain dynamics represent a limiting factor for plant population regeneration. Therefore, investigating seed rain characteristics and their influencing factors is essential for understanding plant population renewal and community succession trends. Previous studies in fragmented habitats have focused on basic seed rain characteristics, species attributes (richness, life form, dispersal syndrome, successional status, seed mass), and relationships with patch spatial characteristics (area, number, edge gradients). However, few studies have examined how habitat fragmentation affects seed rain density across different dispersal syndromes. The Thousand Island Lake in China' s subtropical region, formed by reservoir dam construction creating over 1,000 isolated land-bridge islands, provides an ideal platform for studying habitat fragmentation effects on plant population renewal and community succession. Using seed rain data from 2015–2020, this study employed non-parametric tests and linear mixed models to address: (1) the basic characteristics of woody plant seed rain on Thousand Island Lake islands; (2) the temporal dynamics of seed rain; and (3) whether and how climatic factors and habitat fragmentation influence seed rain temporal dynamics.

1.1 Study Area Description

The study site is located in the Xin' anjiang Reservoir (29°22 -29°50 N, 118°34 - 119°15 E) in Chun' an County, Hangzhou City, Zhejiang Province, also known as the Thousand Island Lake. Formed in 1959 by hydroelectric dam construction, the reservoir covers approximately 540 km^2. The region experiences a typical subtropical monsoon climate, characterized by warmth, humidity, distinct seasons, and concurrent rainfall and heat. The mean annual temperature is 17 °C, with maximum and minimum extremes of 41.8 °C and -7.6 °C, respectively, and mean annual precipitation of 1,430 mm. Following dam construction, the original forest on the islands was largely cleared, initiating secondary succession that has continued for over 60 years. Forest coverage exceeds 88.5%, dominated by secondary *Pinus massoniana* forests. The understory is primarily composed of small trees and shrubs including *Loropetalum chinense*, *Vaccinium carlesii*, and *Rhododendron simsii*.

1.2 Seed Rain Collector Deployment

We selected 29 islands with minimal human disturbance and dominated by *Pinus massoniana* forests as plant community sample islands [FIGURE:1, TABLE:1]. Between 2009 and 2010, we established 12.7 ha of permanent plant community monitoring plots on these islands, tagging and surveying all woody plants with diameter at breast height $ $1 cm, with the first recensus completed in 2014–2015 . Within the plots on each of the 29 islands, we installed seed rain collectors at 10–15 m intervals in every 5 m × 5 m subplot. Each collector consisted of a 0.71 m × 0.71 m (0.5 m^2) PVC frame with 1 mm mesh nylon netting, secured by four 0.8 m PVC pipes. A total of 240 seed collectors were deployed across the 29 islands. From January 2015 to December 2020, we collected seeds and fruits monthly from each collector. Samples were oven-dried at 80 °C for 48 hours in the laboratory, then sorted into eight categories: mature fruits, mature seeds, peels/pods, fragments, immature fruits, flowers, animal-damaged fruits, and animal-damaged seeds. Species identification was conducted using reference atlases of flowers, fruits, and seeds, with counting and weighing performed (seeds within multi-seeded fruits were also counted). Maturity was determined based on size, shape, color, and when necessary, embryo morphology and texture.

1.3 Data Analysis and Processing

This study utilized 71 monthly seed rain datasets collected from January 2015 to December 2020 (with only one collection between August and September 2020). Dispersal syndromes for each species were determined based on fruit type, seed characteristics, field observations, and literature references, classifying species into three categories: zoochory, autochory, and anemochory. Seed rain density was expressed as the number of seeds collected per square meter: seed rain density (seeds · m^{-2}) = total seeds collected for a species on an island / total collector area on that island. Meteorological data were obtained from Chun' an County records for 2015–2020 [Attached Figure 1].

Due to non-normal distribution and heterogeneity of variance in seed rain density data, we used Kruskal-Wallis tests to analyze interannual differences in woody plant seed rain density and monthly differences among dispersal syndromes. Linear mixed-effects models examined the influence of island spatial attributes (island area, distance to nearest island, distance to mainland) and climatic factors (accumulated temperature above 0 °C, precipitation) on seed rain density. To account for non-independence of seed rain data across months and islands, month and island ID were included as random intercepts in monthly density models, while island ID served as a random intercept in annual density models. Both seed rain density and island area were log-transformed for all analyses. Since accumulated temperature above 0 °C was highly correlated with temperature (Pearson' s $r = 0.99$, $P < 0.001$), only accumulated temperature was included as a fixed effect. Linear mixed-effects models were performed using the lmer package, with ggplot2 used for visualization, all conducted in R 4.1.0.

2.1 Overview of Seed Rain

Between 2015 and 2020, the 240 collectors across 29 islands gathered 877,178 mature seeds of woody plants, representing 52 species in 40 genera and 26 families. Notably, *Rosa laevigata*, *Melia azedarach*, and *Broussonetia papyrifera* were collected but not recorded in the plot surveys. The 2014–2015 recensus documented 74 woody species across the 29 islands, with 25 species not yielding mature seeds in our collections. The ten most abundant species in seed rain were: *Lyonia ovalifolia* var. *hebecarpa*, *Vaccinium carlesii*, *Eurya muricata*, *Rhododendron ovatum*, *Pinus massoniana*, *Liquidambar formosana*, *Vitex negundo* var. *cannabifolia*, *Loropetalum chinense*, *Juniperus formosana*, and *Schima superba*. The dominant fruit types were drupes and capsules . Zoochory was the predominant dispersal syndrome, accounting for 73.58% of species, compared to 13.21% for anemochory and 13.21% for autochory .

2.2.1 Interannual Variation in Woody Plant Seed Rain

Kruskal-Wallis tests revealed that seed rain density in 2017 and 2018 was significantly higher than in 2015 ($P < 0.05$), with no significant differences among other years [Figure 2: see original paper].

2.2.2 Seasonal Variation in Seed Rain Among Dispersal Syndromes

Temporal dynamics differed substantially among dispersal syndromes. Zoochorous species peaked from August to January and reached minima from March to May. Anemochorous species peaked in January–February and were lowest from June to August. Autochorous species showed increasing trends from February to June but lacked distinct peaks or troughs due to high variability [Figure 3: see original paper].

2.3.1 Factors Influencing Temporal Dynamics of Woody Plant Seed Rain

Linear mixed-effects models indicated that annual seed rain density of woody plants was significantly positively correlated with island area and annual accumulated temperature ($P < 0.05$), and significantly negatively correlated with annual precipitation ($P < 0.05$) [Figure 4: see original paper].

2.3.2 Factors Influencing Temporal Dynamics of Different Dispersal Syndromes

Model results showed that monthly seed rain density of different dispersal syndromes responded variably to monthly accumulated temperature, monthly precipitation, island area, distance to nearest island, and distance to mainland. Autochorous species density was significantly positively correlated with distance to nearest island ($P < 0.05$). Anemochorous species density was highly significantly positively correlated with monthly accumulated temperature ($P < 0.001$). Zoochorous species density was significantly positively correlated with distance to mainland ($P < 0.05$) [Figure 5: see original paper].

Over the six-year study period, seeds of 52 woody species were collected, representing 67% of the total woody plant species recorded in Thousand Island Lake plots. The remaining 33% of species were not collected, primarily due to seed limitation, including both dispersal limitation and source limitation. Dispersal limitation occurs when seeds cannot reach all suitable germination sites, while source limitation arises from low seed production by parent trees. Most uncaptured species exhibited low abundance (accounting for only 0.2% of total species abundance), lacked parent trees, and produced few seeds. Additionally, over half were shrubs with low stature (mean height 1.7-3.3 m), resulting in limited dispersal distances that hindered collection. These species will likely face severe recruitment challenges in coming years.

3.1 Seasonal Dynamics of Seed Rain Among Dispersal Syndromes

Zoochory represents the primary dispersal mode for woody plants in Thousand Island Lake' s *Pinus massoniana* forests, consistent with findings from other subtropical and tropical forest studies. The main dispersers are birds and rodents, with bird-dispersed species outnumbering mammal-dispersed ones. Birds are typically the most important seed dispersers in fragmented forests, participating in seed dispersal during early forest recovery and resulting in higher proportions of bird-dispersed plants. Their high mobility makes them effective seed dispersers in forest patches, connecting different habitat fragments through seed deposition.

Plants tend to reproduce when conditions favor dispersal and seedling establishment to maximize fitness. Our results show that both anemochorous and zoochorous species peaked during autumn and winter. This pattern can be explained by seedling establishment dynamics. Stronger winds in autumn and winter facilitate dispersal of winged seeds, while low humidity promotes dehiscence of capsules and pods in autochorous species. In subtropical forests, seeds dispersed during the rainy summer season would germinate quickly, subjecting seedlings to a prolonged winter that hampers establishment. Conversely, seeds dispersed in autumn and winter remain dormant due to moisture and temperature constraints, germinating in March–April when conditions become favorable. This allows seedlings to grow sufficiently strong to withstand subsequent winter drought and cold, similar to findings from Hong Kong shrubland phenology studies. Additionally, winter cold stratification can break seed dormancy and enhance germination rates. In contrast, studies in tropical dry forests show rainy seasons as peak fruiting and dispersal periods for zoochorous species, as rainy seasons coincide with peak activity of animal dispersers.

3.2 Factors Influencing Temporal Variation in Seed Rain

Our study demonstrates that annual seed rain density of woody plants is significantly positively correlated with island area. Liu et al. (2019b) found that shade-tolerant species biomass increased significantly with island area in Thousand Island Lake, whereas light-demanding species showed no such trend. Shade-tolerant plants accounted for 40% of total seed rain production, and tree biomass is positively correlated with seed production within certain ranges. Thus, increased shade-tolerant biomass on larger islands enhances seed production, resulting in higher seed rain density. Additionally, smaller islands are more susceptible to edge effects and environmental disturbances such as soil erosion, further reducing seed production.

Seed production is linked to flowering phenology, which is primarily influenced by temperature, photoperiod, and precipitation—factors significantly altered by climate change. In Thousand Island Lake, annual seed rain density was significantly negatively correlated with annual precipitation. Increased air humidity can reduce pollen dispersal efficiency, thereby affecting seed production. Consequently, higher precipitation negatively impacts pollination and seed rain density. The significant positive correlation between seed rain density and annual accumulated temperature can be explained by temperature effects on plant performance. Elevated temperatures can mitigate negative effects of low temperatures during flowering, enhancing reproductive performance. Previous studies also show that experimental warming promotes vegetative growth, which can increase seed production through enhanced nutritional status and reproductive capacity.

Zoochorous species seed rain density was significantly positively correlated with distance to mainland, following island biogeography theory' s "distance effect" —islands farther from mainland have lower immigration rates. Higher immigration rates on near-mainland islands mean more plants and animals colonize, including mammals that consume or disperse seeds of zoochorous species. Since our collectors primarily captured fruits/seeds falling directly from trees or those defecated by birds, increased mammalian seed consumption on near-mainland islands reduces seed rain collection.

Autochorous species seed rain density increased with distance to nearest island. Liu et al. (2020) demonstrated that conspecific negative density dependence intensifies with increasing distance to nearest islands in fragmented habitats. In fragmented landscapes, limited dispersal of both plants and their natural enemies intensifies host-enemy interactions and intraspecific competition. Given autochorous species' strong dispersal limitation, intense competition may drive plants to increase seed quantity at the expense of quality to enhance survival. Thus, autochorous seed rain density increases with isolation.

Anemochorous species seed rain density was highly significantly positively correlated with monthly accumulated temperature, while temperature showed negative effects on autochorous and zoochorous species. Seed production variation represents an evolutionary strategy responding to environmental factors like temperature and precipitation. Different life-history strategies manifest in seed number variation: large-seeded species produce fewer, heavier seeds, while small-seeded species produce numerous, lighter seeds. Anemochorous species have the smallest average seed mass, zoochorous the largest, and autochorous intermediate. Temperature increases may cause anemochorous plants to produce more, smaller seeds, while zoochorous and autochorous plants produce fewer, larger seeds. However, because zoochorous and autochorous seed rain densities were also significantly correlated with distance to mainland and nearest island, respectively, temperature' s negative effects on these syndromes were not significant.

Zoochory is the dominant dispersal mode for woody plants in Thousand Island Lake. Seed rain densities of woody plants and different dispersal syndromes respond differently to climatic factors and island spatial attributes, with habitat fragmentation affecting seed rain temporal dynamics through island spatial characteristics. This study utilized six years of monitoring data; continued monitoring and comparative studies linking seed rain to subsequent life-history stages could further elucidate plant community regeneration mechanisms in fragmented habitats.

Acknowledgments: We thank the Chun' an County Xin' anjiang Ecological Development Group Co., Ltd. and Chun' an County Forestry Administration for project support. We appreciate contributions to seed collection and sorting from Donghao Wu, Zhen Ruan, and local residents including Chengxian Jiang, Jianchun Yan, Quangui Jiang, Guo' e Zhou, and Liying Tong. We thank Juan Liu, Boliang Wei, Lei Zhong, and Jinliang Liu for valuable comments on the manuscript.

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Attached Figure 1: Monthly accumulated temperature above 0 °C and precipitation in Chun' an County during the study period

Attached Table 1: Basic information on 29 study islands in the Thousand Island Lake (Island ID, Area (hm^2), Perimeter (hm), Distance to mainland (m), Distance to nearest island (m), Number of seed traps)

Attached Table 2: Species information table for recensus of woody plant community on 29 study islands in the Thousand Island Lake from 2014 to 2015 (Species, Family, Abundance)

Attached Table 3: Basic information on species with different dispersal syndromes in 29 study islands in the Thousand Island Lake (Species, Family, Dispersal syndrome, Fruit type, Seed mass)

Note: Figure translations are in progress. See original paper for figures.