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Long-term fluctuations and mechanisms of seed production of riparian tree canopy species

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Abstract

Annual seedfall was measured over a 24-year period for three canopy species, *Fraxinus platypoda*, *Pterocarya rhoifolia*, and *Cercidiphyllum japonicum*, in a riparian forest in the Chichibu Mountains, central Japan. We collected seeds from 20 traps approximately every month, except in the winter. *Fraxinus platypoda* and *P. rhoifolia* seedfall fluctuated, with a 2-year cycle. The seedfall of *C. japonicum* also fluctuated, but this species produced seeds every year, with an approximate 4-year cycle. The simple moving average over 5 years for *F. platypoda* and *P. rhoifolia* was maintained at a constant level over the 24-year period, but it gradually increased for *C. japonicum*. Each year's seedfall for the three species was influenced by the previous year's seedfall. The results for *F. platypoda* suggest that the fluctuations in the amount of seedfall were almost entirely dependent on fluctuations in stored resources, regardless of the previous year's weather. Conversely, the amount of seedfall for *P. rhoifolia* and *C. japonicum* was influenced by fluctuations in stored resources and the average temperature or precipitation in the summer of the year before flowering. These differences in seed production patterns were associated with differences in life history characteristics such as seed size and regeneration mechanisms.

KEYWORDS

Cercidiphyllum japonicum, *Fraxinus platypoda*, life history strategy, masting behavior, *Pterocarya rhoifolia*

1 | INTRODUCTION

In some tree species, there is a phenomenon known as mast seeding, in which seed production is synchronized among individuals and shows irregular intervals (Fernández-Martínez et al., 2019; Kelly, 1994; Norton & Kelly, 1988). Mast seeding appears in long-lived plants, such as woody plants or perennial herbs, and affects the cost of reproduction in some years (Kelly, 1994). Because seed production is directly related to forest regeneration (Daskalakou et al., 2019; Piovesan & Adams, 2005) and has a significant effect on the population dynamics of seed-eating animals and insects (Kelly & Sork, 2002; Shibata et al., 2002), predicting seed production is important for forest management and the conservation of forest ecosystems.

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Hypotheses to explain masting can be divided into the following two categories: ultimate (evolutionary) and proximate (mechanistic) (Kelly, 1994; Pearse et al., 2016). Pearse et al. (2016) outlined the ultimate hypotheses (economies of scale), including predator satiation, pollination efficiency, and environmental prediction. For many wind-pollinated plants, synchronized flowering in a given year can increase the fruit set. In addition, masting allows trees to produce enough fruit to enable enough seed to escape predation and leave offspring. Alternatively, there are two types of proximate hypotheses (i.e., environmental constraints and weather cues) (Pearse et al., 2016). The environmental constraints-related hypotheses are based on the belief that plant resources, including pollen, limit seed set. Bogdziewicz et al. (2020) reviewed the proximate mechanisms underlying mast seeding, which were determined on the basis of experiments examining resource dynamics, pollen limitation, and genetic and hormonal regulation. For the hypotheses involving weather cues, it is assumed that at least one weather condition at the time of flower bud differentiation influences abundance because many flower buds must form to produce a large amount of fruit (Burns, 2012; Kon, 2009; Tanaka, 1995). However, there is no evidence that climate is the only contributing factor.

Among the proximate hypotheses, the resource budget hypothesis assumes the accumulation and release of carbohydrates affects mast seeding (Isagi et al., 1997; Satake & Iwasa, 2000). Isagi et al. (1997) used a resource budget model (RBM) to show that masting occurs because of the balanced resources of each plant, even without any interannual environmental fluctuations. In practice, some plants exhibit resource (nonstructural carbohydrates, phosphorus, and nitrogen) depletion after seed production and density-dependent pollen limitation (Crone & Rapp, 2014). In addition, the RBM likely explains the synchrony in many masting species (Crone & Rapp, 2014; Satake & Iwasa, 2000).

Conversely, Hoch et al. (2013) observed that seed production relies exclusively on current-year photoassimilates (i.e., not stored carbohydrates), which is inconsistent with the resource budget hypothesis involving carbohydrate accumulation and release. Han et al. (2014) reported that flower bud differentiation in *Fagus crenata* requires nitrogen, and in good crop years, the same amount of nitrogen is used for the production of firm fruit and leaf clusters. Therefore, flower buds do not form in the year following a good crop year. In other words, resource budgeting occurs for nitrogen, but not for carbohydrates. In the relatively poor soil conditions in the tropical rainforests of Southeast Asia, the accumulation of phosphorus, but not nitrogen or potassium, in *Dryobalanops aromatica* may be the decisive factor influencing the occurrence and frequency of mast reproduction (Ichie & Nakagawa, 2013). Fernández-Martínez et al. (2019) observed that masting is stronger in species growing under limiting conditions and suggested that this reproductive behavior might have evolved as an adaptation to nutrient (nitrogen and phosphorus) limitations and imbalances. Therefore, these RBMs should be interpreted more generally in terms of the dynamics of stored resources (carbohydrates and/or nutrients), depending on what resources limit reproduction in different species, such as whitebark pine (*Pinus albicaulis*) (Sala et al., 2012).

Long-term monitoring in the field is essential for testing these hypotheses. Although long-term analyses of seed production in various tree species have been performed to elucidate the masting mechanism, most of these studies involved only one tree species or compared multiple tree species within the same genus (*Quercus*: Koenig et al., 1994; *Carpinus*: Shibata et al., 1998; *Acer*: Tanaka, 1995), and relatively few studies have compared different taxonomic groups (Kelly et al., 2013; Zlotin & Parmenter, 2008) or different locations (Nussbaumer et al., 2016). Previous research showed that pioneer species, such as *Populus* (J. Richardson et al., 2014) as well as *Salix dolichostyla* subsp. *dolichostyla* and *Salix hukaoana* (H.S., personal observation), tend to produce many seeds synchronously every year. Conversely, conifer and late successional species show distinct masting behavior, including *Dacrydium* (Norton & Kelly, 1988), *Pinus* (Chen et al., 2018; Moony et al., 2011; Nussbaumer et al., 2016), *Picea* (Lamontagne & Boutin, 2007; Mencuccini et al., 1995; Nussbaumer et al., 2016; Peters et al., 2005), *Nothofagus* (Allen & Platt, 1990; Allen et al., 2014; Monks & Kelly, 2006;), *Quercus* (Clotfelter et al., 2007; Koenig et al., 1994; Nussbaumer et al., 2016; Pérez-Ramos et al., 2010), *Fagus* (Hilton & Packham, 2003; Kaji et al., 2001; Nussbaumer et al., 2016; Övergaard et al., 2007; Suzuki et al., 2005), and *Fraxinus* (Tapper, 1992, 1996).

In this study, seedfall was investigated for three tree species with different life history characteristics that coexist in the same forest canopy over a 24-year period to analyze how differences in life history characteristics affect the annual variation in seedfall. The tree species included in this study were *Fraxinus platypoda*, *Pterocarya rhoifolia*, and *Cercidiphyllum japonicum*, which are canopy trees in a riparian forest.

The objectives of this study were as follows: (1) to determine the seedfall patterns of three tree species with different life history characteristics over a 24-year period; (2) to determine the proximate (mechanistic) mechanisms of masting in relation to resources and weather variables; and (3) to discuss how masting patterns are related to life history characteristics.

2 | MATERIALS AND METHODS

2.1 | Site description

The study site (35°57′30″ N, 138°45′32″ E) was located in a riparian zone along a small stream (Ooyamazawa) of the Nakatsugawa branch of the Arakawa River in the Chichibu Mountains, central Japan (Figure 1). This site is in the Saitama Prefecture Forest and is protected as part of the Class II special zone of Chichibu-Tama-Kai National Park, which has been designated as a Natural Monument of Saitama Prefecture and is part of the Kobushi Biosphere Reserve. This site ranged from 1210 to 1530 m above sea level. There were no records of logging in the old growth forest prior to 1936, but selective cutting was conducted in the downstream part of Ooyamazawa from 1936 to 1941. However, the upper part of this area was unaffected by human activities, such as logging or erosion control practices, and the old growth forest was conserved (Sakio, 2020a).

The mean annual precipitation at the AMeDAS (Automated Meteorological Data Acquisition System) Chichibu Meteorological Station in Saitama Prefecture, located 40 km from the Ooyamazawa research site, was 1337.0 mm from 1980 to 2018 (https://www.data.jma.go.jp/obd/stats/etrn/index.php). The maximum snow depth was approximately 30 cm between January and March. The mean annual temperature at the study site (1450 m above sea level) was 7.1°C from 2008 to 2018 (Sakio, 2020a). The mean air temperature is 18.3°C in the warmest month (August) and −5.2°C in the coldest month (January) (Sakio, 2020a). The mean annual air humidity was 81.9% from 2014 to 2018 (Sakio, 2020a).

In terms of its geological characteristics, the study area comprises Paleozoic graywacke and sandstone. The Chichibu Mountains have a complex topography with steep slopes (greater than 30°) and a network of mountain streams. The study plot was located in the upstream riparian area. Sakio (1997) described the microtopography and substratum in the study plot. The riparian area in the study plot contained an active channel, abandoned channel, floodplain, and hillslope. There was no vegetation in the active channel, except for the young seedlings of woody plants on the channel bar. The substratum of the active channel consisted of sand and/or gravel, while that of the hillslope contained mature soil.

The study site was situated in the upper areas of a cool temperate, deciduous broad-leaved forest zone that ranged from 700 to 1600 m above sea level (Figure 2a). Ohno (2008) classified the Ooyamazawa riparian forest as *Cacalio yatabei–Pterocaryetum rhoifoliae* on the basis of the riparian forest communities in the mountainous area of the Chubu and Kanto regions. Canopy tree species in this area are over 30 m high and the dominant species are *F. platypoda*, *P. rhoifolia*, and *C. japonicum* (Sakio, 1997). The subcanopy tree species are *Acer shirasawanum* and *A. pictum*, and the lower layer is dominated by *A. carpinifolium* and *A. argutum*. In 1983, the herbaceous layer was approximately 1 m high and consisted of large ferns (*Dryopteris crassirhizoma* and *Polystichum ovatopaleaceum*) and large

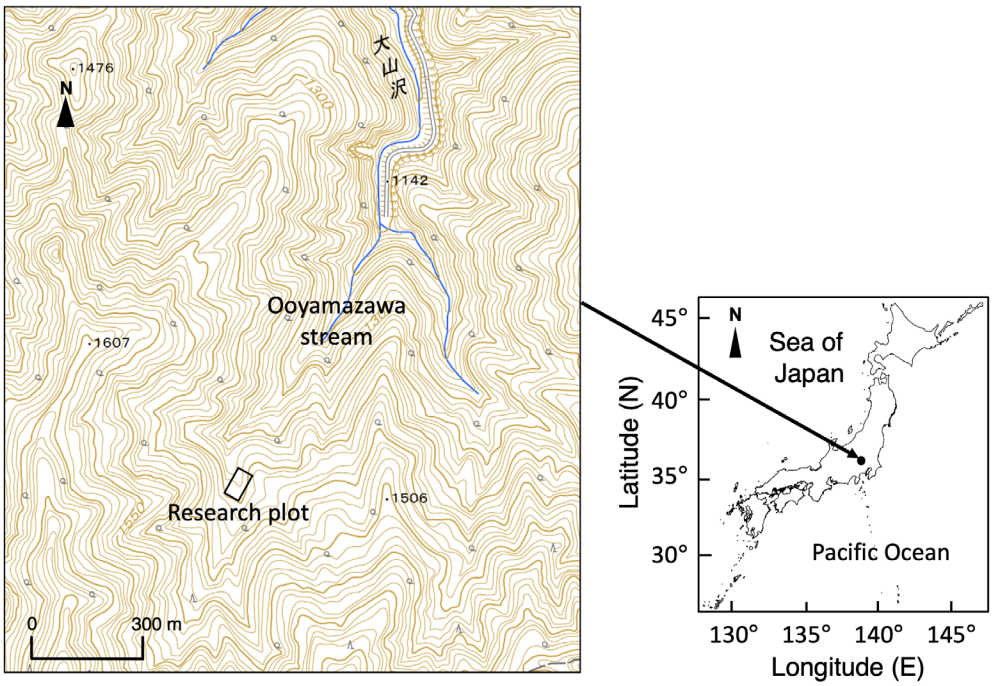


FIGURE 1 Research location and plot in the Ooyamazawa riparian forest in the Chichibu Mountains, central Japan. [Color figure can be viewed at wileyonlinelibrary.com]

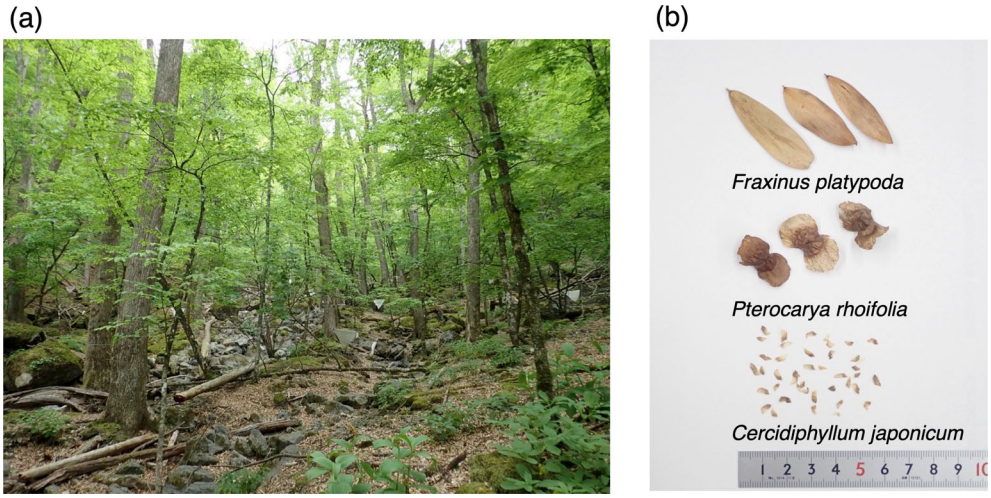


FIGURE 2 (a) Canopy trees at the research site in the Ooyamazawa riparian forest in the Chichibu Mountains, central Japan, dominated by *Fraxinus platypoda*, *Pterocarya rhoifolia*, and *Cercidiphyllum japonicum*. (b) Fruits (*F. platypoda* and *P. rhoifolia*) and seeds (*C. japonicum*) of the riparian species examined in this study. [Color figure can be viewed at wileyonlinelibrary.com]

herbs (*Cacalia yatabei* and *Spuriopimpinella nikoensis*), with a coverage of approximately 90%. However, the coverage of the forest floor vegetation decreased from 80% in 1998 to 5% in 2004 because of a rapid increase in the Sika deer (*Cervus nippon*) population (Sakio et al., 2013).

This study site was registered as an Associate Site of the Japan LTER Network (JaLTER; http://www.jalter.org/en/researchsites/) and as a Core Site of the Monitoring Sites 1000 Project by the Ministry of the Environment, Japan (http://www.biodic.go.jp/moni1000/index.html).

2.2 | Study species

2.2.1 | *Fraxinus platypoda*

Ash, *F. platypoda* Oliv. (Oleaceae), is one of the late successional species in the riparian habitats of the cool temperate forests that are distributed along the Pacific coast of Japan (Kawahara et al., 2009). It is a deciduous canopy species that grows up to 40 m tall and 150 cm in diameter at breast height (DBH). *Fraxinus platypoda* has two sexual morphotypes, one with only male flowers and the other with hermaphroditic and male flowers in an inflorescence (Sakio, 2020b). Because these flowers are fertile, this tree species is considered functionally androdiecious (Sakio & Nirei, 2022). Moreover, it is a wind-pollinated species and its seeds are dispersed by wind. Seeds are completely empty between May and August, but their contents are filled after August and then mature seeds fall after September (Sakio & Nirei, 2022). The maximum tree life span of this species is approximately 300 years (Sakio, 1997). *Fraxinus platypoda* is well adapted to disturbances that vary in frequency and size, and it dominates the forest in riparian zones (Sakio, 1997).

2.2.2 | *Pterocarya rhoifolia*

Japanese wingnut, *P. rhoifolia* Siebold et Zucc. (Juglandaceae), is a representative riparian element in the cool temperate forests of Japan, in which it is widely distributed from southern Hokkaido to Honshu, Shikoku, and Kyusyu (Kawahara et al., 2009), growing in regions with heavy and light snowfall (Nakano & Sakio, 2017, 2018). This species is a deciduous canopy tree that grows up to 35 m tall and 120 cm in DBH (Hayashi, 1969). *Pterocarya rhoifolia* is a monoecious species with wind-pollinated unisexual flowers that produce wind-dispersed seeds. The maximum tree life span of this species is approximately 100–150 years (Kaneko, 2009).

2.2.3 | *Cercidiphyllum japonicum*

Katsura tree, *C. japonicum* Siebold et Zucc. ex Hoffm. et Schult. (Cercidiphyllaceae), is also a representative riparian element in the cool temperate forests of Japan, occurring in riparian areas in Hokkaido, Honshu, Shikoku, and Kyushu. It also grows in China. It is a tall, straight-stemmed species that grows up to 30 m tall and 100 cm in DBH. *Cercidiphyllum japonicum* is a deciduous canopy species, and is dioecious with female and male trees. It is wind-pollinated and its seeds are dispersed by wind over hundreds of meters, with a maximum recorded dispersal distance of 302 m (Sato et al., 2006). The maximum trunk life span of this species is approximately 300 years, and the tree life span is estimated to be 500 years or more because *C. japonicum* can continue to maintain individuals via sprouts around the trunks (Kubo & Sakio, 2020).

2.2.4 | Comparison of the life history strategies of the three study species

The coexistence of these three species is explained by their life history stages, natural disturbances, and the environment (Sakio et al., 2002). *Fraxinus platypoda*, *P. rhoifolia*, and *C. japonicum* produce wind-dispersed fruits with wings (Figure 2b). Although *F. platypoda* and *P. rhoifolia* disperse fruits, while *C. japonicum* disperses seeds, these dispersants are collectively defined as seeds in this paper. The seeds of *F. platypoda* and *P. rhoifolia* are larger than those of *C. japonicum*, which are very small. In a medium seed production year, oven-dried mature seeds of *F. platypoda*, *P. rhoifolia*, and *C. japonicum* (mean ± *SD*, $n = 20$) weighed 144 ± 24 mg, 90 ± 11 mg, and 0.82 ± 0.15 mg, respectively (Sakio et al., 2002). The *F. platypoda* and *P. rhoifolia* seeds germinate on gravel sediment or litter, whereas *C. japonicum* seeds germinate on fine mineral soil or fallen trees (Kubo et al., 2000). In terms of light and seedling growth, *P. rhoifolia* seedlings grow fastest among the three species under bright conditions (Sakio, 2008). In contrast, *F. platypoda* seedlings exhibit the highest shade tolerance, enabling it to grow in dark conditions (1% light) (Sakio, 2008).

As described above, *F. platypoda* has the characteristics of a typical late successional species such as *Fagus crenata*. *Pterocarya rhoifolia* has the characteristics of a late successional species in its early life history stages (seed and germination) and of a pioneer species in its later stages (growth and maturity). *Cercidiphyllum japonicum* has the opposite characteristics to *P. rhoifolia*. In other words, *C. japonicum* has the characteristics of a pioneer species in its early life history stages (seed and germination) and of a late successional species in its later stages (growth and maturity).

2.3 | Methods

2.3.1 | Seedfall

Seedfall was studied for 24 years between 1995 and 2018. We set a permanent plot (60 × 90 m; 0.54 ha) in the Ooyamazawa riparian forest area. This plot included 62 (female: 29, male: 22, vegetative: 11), 9 (adult: 7, vegetative: 2), and 7 (female: 4, male: 3) *F. platypoda*, *P. rhoifolia*, and *C. japonicum* individuals, respectively (Sakio, 1997), of which 29, 7, and 4 *F. platypoda*, *P. rhoifolia*, and *C. japonicum* individuals, respectively, were producing seeds. We set 20 conical seed traps approximately 1.0 m above the ground in a regular matrix within the plot (0.54 ha). The seed traps were made of nylon netting (approximately 1.0-mm mesh) with openings (0.5-m radius). After this site became the long-term research site for the Monitoring Site 1000 Project (https://www.biodic.go.jp/moni1000/), the radius of the seed trap openings was changed to the standard (0.4 m) in 2010. We collected the contents of the seed traps and brought them back to the laboratory approximately every month between May and November. In the winter, these traps were left at the research site. In the laboratory, we selected the *F. platypoda*, *P. rhoifolia*, and *C. japonicum* seeds and dried them to a constant weight at 80°C for 48 h. The seed weight and seed number were determined for each seed trap. These measurements were made without distinguishing the degree of seed maturity and insect infestation. Thus, immature seeds that had aborted just after flowering and insect-eaten seeds were included when determining the seed number and seed weight.

2.3.2 | Analysis of the seed set in *F. platypoda*

To determine the effect of current-year branch leaves on fruiting, *F. platypoda* trees underwent a leaf-clipping treatment (N: natural pollination and NL: natural pollination with all new leaves removed from current-year branches) in May 1992 and 2006. Both N and NL were completed using 10 branches and the same trees were analyzed in 1992 and 2006. We counted the number of hermaphroditic flowers per inflorescence before the flowering stage. The fruits of all inflorescences were collected in mid-October and counted to analyze the fruit set for each treatment. Fruit length, seed length, fresh fruit weight, and maturity were also analyzed. To evaluate maturity, pericarps lacking seeds, seeds shorter than 1 cm, and undeveloped seeds longer than 1 cm were defined as immature seeds. All of the seeds produced in 1992 were sown in nursery fields in the spring of 1993 and the germination rates were determined. The study site for this experiment was the Ohchigawa section of The University of Tokyo Chichibu Forest (Sakio & Nirei, 2022). The experimental site was located in the same Arakawa River basin as Ooyamazawa.

2.3.3 | Weather data

Temperatures were measured at the study site from 2008 to 2018 (Sakio, 2020a) and compared with temperatures at the AMeDAS Chichibu Meteorological Station; the mean monthly temperatures at the two sites were highly positively correlated. Spearman's rank correlation coefficient of the mean monthly temperature between the two sites was 0.907 ($p < 0.001$) in May, 0.855 ($p < 0.01$) in

June, 0.849 ($p < 0.001$) in July, and 0.862 ($p < 0.001$) in August from 2008 to 2018. Therefore, the temperature data from the Chichibu Meteorological Station were used for this analysis (https://www.data.jma.go.jp/obd/stats/etrn/index.php) for 24 years. The precipitation data from the Chichibu Meteorological Station were also used, although no data were available for the study site. From 2006 to 2018, precipitation levels were measured at the Ohkanmuri Precipitation Station, Arakawa Dam Integrated Operation and Maintenance Office, Japan Water Agency, which is located 4 km from the study plot. The monthly precipitation at the two sites were highly positively correlated. Spearman's rank correlation coefficient of the monthly precipitation between the two sites was 0.962 ($p \fallingdotseq 0$) in May, 0.835 ($p < 0.0001$) in June, 0.654 ($p < 0.05$) in July, and 0.747 ($p < 0.01$) in August from 2006 to 2018.

Because the flower buds of broadleaf trees form in the early summer of the previous year (Lester, 1963; Merkle et al., 1980; Taniguchi et al., 2002; Yoshino, 2000, 2003), the average temperature and precipitation from May to August of the previous year were used.

2.4 | Data analysis

Because seed weight was not measured for *P. rhoifolia* and *C. japonicum* from 1995 to 2007, seed number was used as the seedfall data. The number of seeds and the seed weight were highly correlated for the three tree species (Spearman's rank correlation, $p < 0.00001$). The seed data count was the total number of seeds, including insect-eaten seeds and immature seeds.

The seed production trends (increase or decrease) of the three species over 24 years were predicted on the basis of moving average values for 5 years, and were tested using the Jonckheere–Terpstra test.

Seasonal changes in seedfall per day were expressed as the number of seeds collected divided by the number of days elapsed since the previous collection. The data were then averaged over the 24-year study period.

To test the periodicity of seedfall, the autocorrelation coefficient was obtained by shifting the first-order difference data of seedfall from 1 to 9 years using Pearson correlation coefficients and evaluated in a graphical correlogram. The correlogram assumes that the time lag (year) with the highest positive correlation is the period.

To determine if resource dynamics affected the annual variation in the amount of seedfall, the autocorrelation coefficient of the first-order difference in the amount of seedfall from the previous year to the current year and from 2 years prior to 1 year prior was determined using Pearson correlation coefficients. The relationship between seed abortion and the total seedfall was determined by same method.

To determine if weather affected the annual variation in the amount of seedfall, single correlation coefficients between the amount of seedfall (first-order difference) and each weather variable (first-order difference) were determined using Pearson correlation coefficients. Meteorological variables included monthly average temperature, average maximum temperature, average minimum temperature, and total precipitation. The weather at the time of flower bud differentiation reportedly affects seed production (Allen & Platt, 1990; Norton & Kelly, 1988), with most flower buds differentiating in June and July of the year before flowering (Taniguchi et al., 2002). Therefore, the period of flower bud formation is expected to be around June to July of the year before flowering for the target tree species in this study; the target period of May to August was selected to include the months before and after flower bud formation.

Weather variables were significantly correlated with the amount of seedfall. Therefore, the weather variable model was selected as the best model based on the comparison of Akaike Information Criterion (AIC) values by

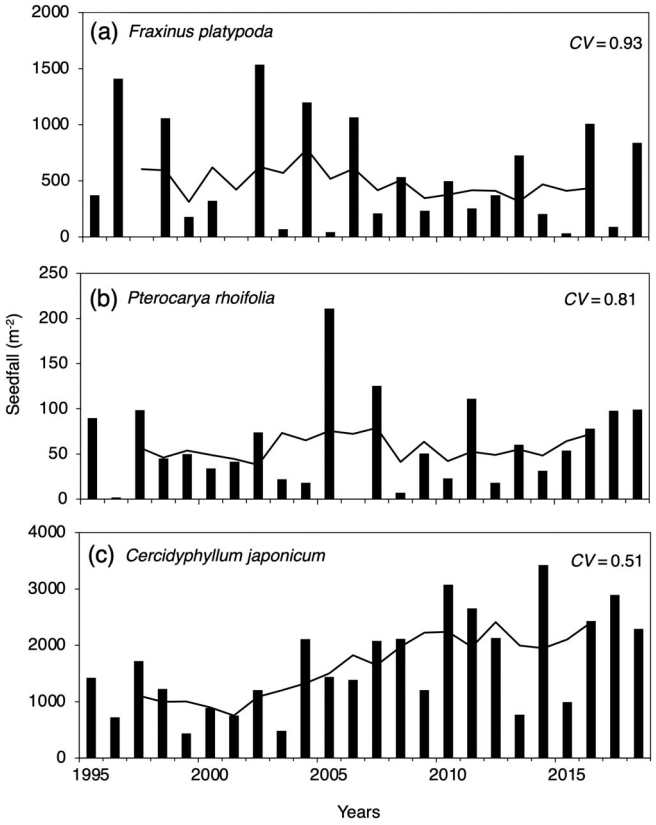


FIGURE 3 Total seedfall (including immature seeds that aborted just after flowering and insect-eaten seeds) of three tree species over 24 years. Black lines show the moving average value for 5 years. *CV*, coefficient of variation.

single and multiple regression analyses to simultaneously evaluate the effects of storage resources and weather variables. The model with the lowest AIC value is the one that best explains the amount of seedfall. The objective variable was the amount of seedfall and the explanatory variables were the weather variables and the amount of seedfall in the previous year for which significant correlations were found. Single and multiple regression analyses were performed using R3.6.0 (R Development Core Team 2019).

3 | RESULTS

3.1 | Annual seedfall

Irregular seed production was revealed in the three species over the 24-year study period (Figure 3). *Fraxinus platypoda* seedfall clearly fluctuated, with values ranging from 0 to 1536 seeds m^{-2}. The annual variation in seedfall was smaller during 2007–2014. *Fraxinus platypoda* had non-mast or very poor years in 1997, 2001, 2003, 2005, 2015, and 2017. The seed fall of *P. rhoifolia* also fluctuated, with values ranging from 0 to 211 seeds m^{-2}. *Pterocarya rhoifolia* had non-mast or very poor years in 1996, 2006, and 2008. Although the seedfall of *C. japonicum* also fluctuated, seeds were produced every year, with values ranging from 436 to 3424 seeds m^{-2}.

There was a difference in the fluctuation pattern of seedfall in the three species. The largest and smallest variations in seed production were observed for *F. platypoda* and *C. japonicum*, respectively. The coefficient of variation (*CV*) was highest for *F. platypoda* (0.93), followed by *P. rhoifolia* (0.81), and *C. japonicum* (0.51). For the simple moving average over 5 years, *F. platypoda* and *P. rhoifolia* maintained a constant level (Jonckheere–Terpstra test, *ns*) during the 24-year period, but *C. japonicum* had a gradually increasing trend (Jonckheere–Terpstra test, $p < 0.01$).

The seed production cycle of *F. platypoda* was clearly 2 years (Figure 4), while that of *P. rhoifolia* was also approximately 2 years. Conversely, the seed

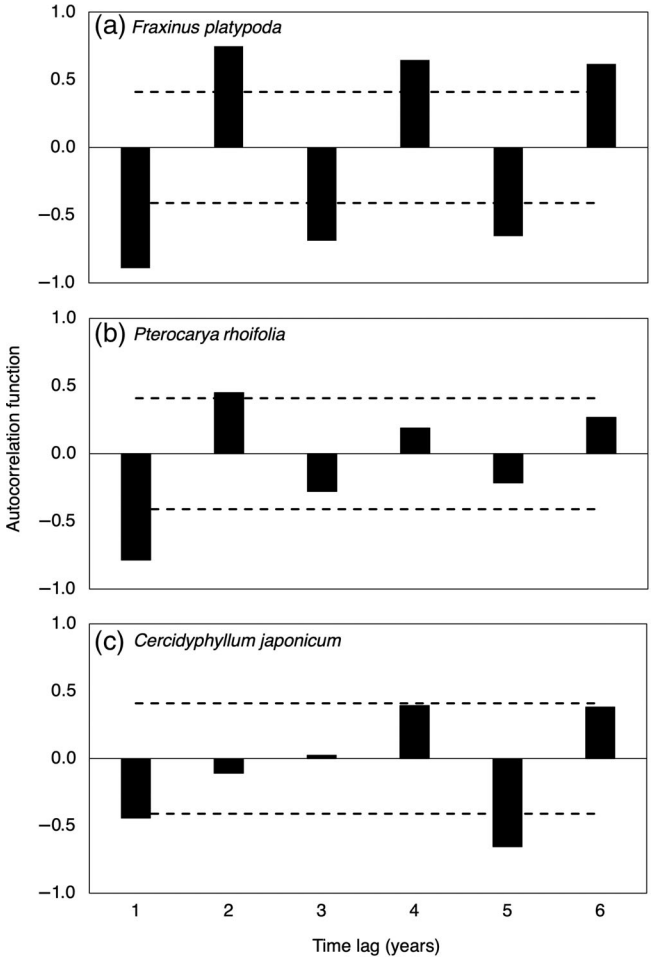


FIGURE 4 Correlogram with upper and lower 95% confidence limits for the autocorrelation of the total seedfall presented in Figure 3. The autocorrelation coefficient was obtained by shifting the first-order difference data of seedfall from 1 to 9 years.

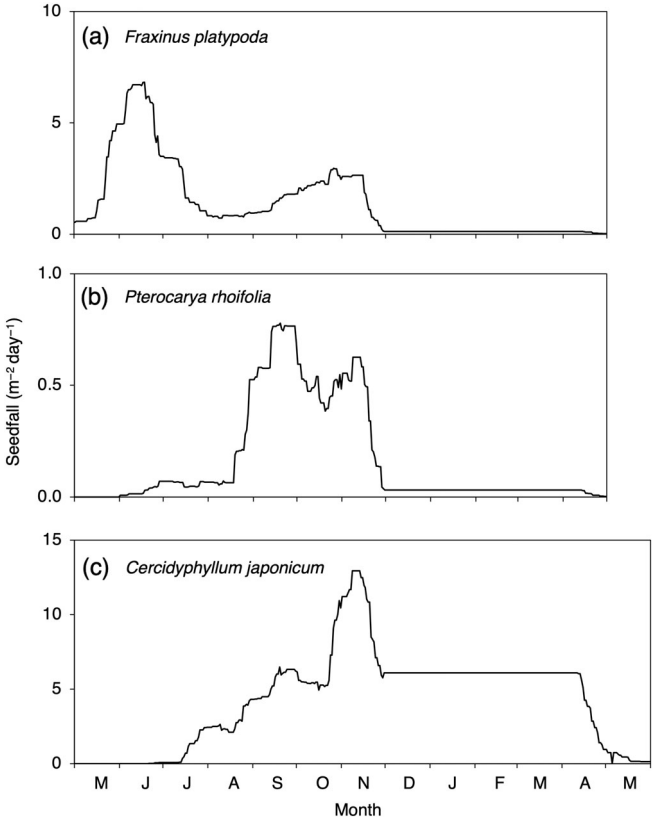


FIGURE 5 Seasonal total seedfall per day (including immature seeds that aborted just after flowering and insect-eaten seeds) of three tree species. In the winter from November to April, these traps were left at the research site.

production cycle of *C. japonicum* was not clear, but it tended to be 4 years.

3.2 | Seasonal seedfall

Seasonal changes in the amount of seedfall per day differed greatly among the three species (Figure 5). The seedfall of *F. platypoda* rose sharply in June and again rose in October and November, showing an autumn pattern with two peaks. The seeds of *F. platypoda* that fell in June were empty and very small. The *P. rhoifolia* seeds fell from September to November, with very few falling before maturity. *Fraxinus platypoda* and *P. rhoifolia* showed no seedfall after December. The seedfall of *C. japonicum* started in mid-July and increased sharply in November, continuing until the next spring. The seedfall rates of *F. platypoda*, *P. rhoifolia*, and *C. japonicum* in winter from December to April were 3.5%, 7.5%, and 52.9%, respectively. However, because the seed traps were left unattended from December to April, we do not know the seedfall pattern of *C. japonicum* during the winter.

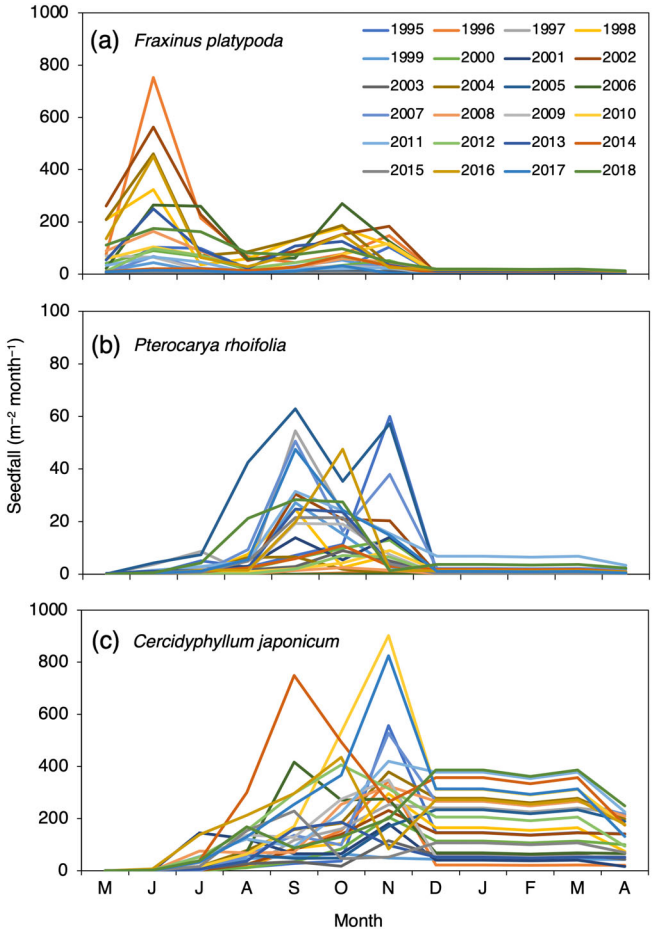


FIGURE 6 Seasonal changes in the total seedfall per month of three tree species for 24 years. [Color figure can be viewed at wileyonlinelibrary.com]

The seasonal changes in the amount of seedfall per month differed for each year of the 24-year study period, but the patterns were almost the same for each species (Figure 6). The *F. platypoda* seedfall pattern included two peaks in most years, except for the years with poor seedfall. There was a very strong positive relationship between the seed abortion from May to August and the total seedfall for the 24 years (Figure 7). Spearman's rank correlation coefficient between seed abortion and the total seedfall was 0.993 ($p \fallingdotseq 0$).

3.3 | Fruit set in *F. platypoda*

Table 1 shows the fruit set rate and seed properties. The fruit set rate of NL was more than double that of N in both years ($p < 0.001$). The fruit length and weight were greater for N than for NL in 1992 ($p < 0.001$). Seed maturity and the germination rate were more than 2-times higher for N than for NL in 1992 ($p < 0.001$). The number of mature seeds per inflorescence was higher for NL (11.4, 3.7) than for N (8.4, 1.9) in 1992 and 2006, respectively. In 1992, the mean fruit length was greater for N than for NL, but the fruit weight per inflorescence was greater for NL (5.3 g) than for N (3.4 g).

3.4 | Effect of the previous year's seedfall

For all three species, each year's seedfall was influenced by the previous year's seedfall (Figure 8).

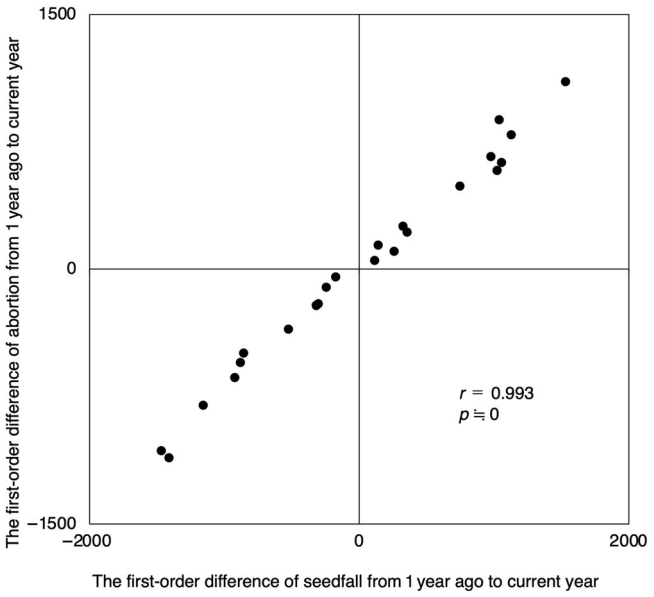


FIGURE 7 Relationships between the seed abortion and total seedfall of *Fraxinus platypoda* for 24 years. *r*, Pearson correlation coefficient.

TABLE 1 Fruit characteristics of 1992 and 2006 in various treatments at autumn.

Treatments		Fruit set rate (%)	Fruit length (mm)	Seed length (mm)	Fruit weight (g)	Maturity (%)	Germination rate (%)
1992	N (n = 97, 2194)	4.42***	35.55 ± 5.80***	21.05 ± 2.34	0.35 ± 0.12***	86.60***	54.64***
	NL (n = 265, 2063)	12.85	27.24 ± 10.39	20.88 ± 2.38	0.20 ± 0.17	42.86	21.51
2006	N (n = 34, 1836)	1.85***	32.32 ± 9.37	16.25 ± 4.76	–	55.88	–
	NL (n = 62, 1703)	3.64	30.84 ± 9.49	15.97 ± 3.15	–	59.68	–

Note: Treatment N: Natural pollination (n = fruit set, flowers); NL: Natural pollination with leaves removed (n = fruit set, flowers). Fruit length, seed length, fruit weight (Mann–Whitney U-test, ***$p < 0.001$). Fruit set rate, maturity, and germination rate (χ^2 test, ***$p < 0.001$).

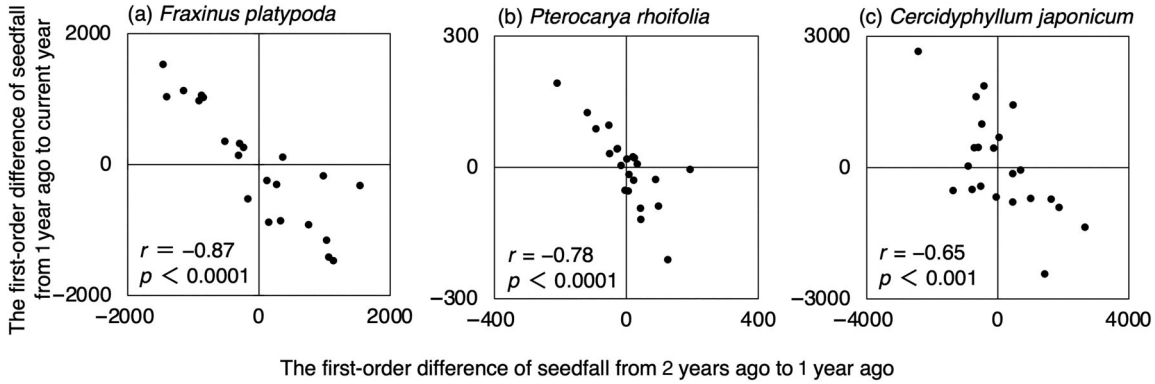


FIGURE 8 Relationships of the total seedfall of three species between the current year and the previous year. r, Pearson correlation coefficient.

TABLE 2 Pearson correlation coefficient of one-order difference between seed production and weather variable.

Species	Weather variable	May	June	July	August
Fraxinus platypoda	Mean air temperature	0.11	−0.08	−0.31	−0.04
	Mean maximum air temperature	−0.02	0.00	−0.34	−0.14
	Mean minimum air temperature	−0.01	0.03	−0.31	0.15
	Precipitation	−0.28	−0.41	−0.07	0.29
Pterocarya rhoifolia	Mean air temperature	0.21	0.18	0.57**	−0.13
	Mean maximum air temperature	0.10	0.09	0.58**	−0.06
	Mean minimum air temperature	0.27	0.08	0.58**	−0.29
	Precipitation	0.18	0.57**	0.47	−0.13
Cercidiphyllum japonicum	Mean air temperature	0.19	0.52	−0.22	−0.13
	Mean maximum air temperature	0.30	0.40	−0.22	−0.21
	Mean minimum air temperature	−0.02	0.55**	−0.21	−0.06
	Precipitation	0.16	0.02	−0.03	−0.29

**Pearson correlation coefficient, $p < 0.01$.

There were clear negative relationships between each year's seedfall and the previous year's seedfall among the three species, and the correlation coefficient was highest for *F. platypoda* (0.87), followed by *P. rhoifolia* (0.78) and *C. japonicum* (0.65).

3.5 | Climate effect on seedfall

Correlation coefficients between the amount of seedfall (first-order difference) and weather variables (first-order difference) from May to August the year before flowering

TABLE 3 Comparison of combinations of explanatory variables for number of seedfall by regression analysis.

Species	Weather variable	R^2	Adjusted R^2	AIC
Pterocarya rhoifolia	Seedfall	0.60	0.58	178.0
	Mean air temperature in July	0.33	0.30	198.1
	Seedfall + mean air temperature in July	0.79	0.77	165.7
	Precipitation in June	0.33	0.30	198.1
	Seedfall + precipitation in June	0.69	0.66	174.4
Cercidiphyllum japonicum	Seedfall	0.43	0.40	301.3
	Mean air temperature in June	0.27	0.23	320.0
	Seedfall + mean air temperature in June	0.71	0.68	288.3

Note: Models were compared by regression analysis with the number of seedfall as the objective variable and the number of seedfall in the previous year and weather variables as explanatory variables. The model with the lowest AIC was selected.

are shown in Table 2. For *F. platypoda*, there was no significant correlation between the amount of seedfall and the climatic variables. The amount of seedfall for *P. rhoifolia* was significantly positively correlated with the precipitation in June the year before flowering as well as the mean temperature, mean maximum temperature, and mean minimum temperature in July the year before flowering. There was a significant positive correlation between the amount of seedfall for *C. japonicum* and the average minimum temperature in June the year before flowering.

To simultaneously evaluate the effects of storage resources and weather, models were compared by regression analysis using the amount of seedfall in the previous year and weather variables as explanatory variables; significant correlations were found (Table 3). The model with the lowest AIC value was selected. It combined the amount of seedfall in the previous year and the average temperature in July of the year before flowering for *P. rhoifolia*, whereas it combined the amount of seedfall in the previous year and the average temperature in June of the year before flowering for *C. japonicum*.

4 | DISCUSSION

4.1 | Comparison of annual seedfall patterns

This study revealed the differences in the seedfall patterns of the three dominant tree species in a riparian forest over a 24-year period (Figure 3). Among the three tree species, the highest variation in seedfall was observed for *F. platypoda* ($CV = 0.93$). *Fraxinus platypoda* reportedly has a distinct seedfall pattern, with a fruiting cycle of 2 years (Haibara et al., 1989) or 3–4 years (Sakio et al., 2002), but these reports were based on a short study period of approximately 6 years. In this study, long-term observations over a period of 24 years indicated that *F. platypoda* has a 2-year fruiting cycle (Figure 4).

The seedfall of *P. rhoifolia* also varied ($CV = 0.81$). There are reports that mast seeding repeat every other year (Sakio et al., 2002) and sometimes 2 years in a row (Sawada et al., 1998). The present study was characterized by many years of intermediate seedfall and rare mast years (Figure 3). However, the amount of seedfall per trap increased or decreased each year, and the correlogram showed a 2-year cycle similar to that of *F. platypoda*.

There were also large annual fluctuations in the amount of seedfall for *C. japonicum*, but it produced some seeds every year (Figure 3; Sakio & Kubo, 2022) and had the lowest variation of the three species ($CV = 0.51$). There have been reports that *C. japonicum* has a long interval between mast years (Mizui, 1993) and that the cycle is more than 5 years (Sasaki, 1986). The long-term observation data in this study further confirm that the cycle is more than 4 years (Figure 4). Conversely, there was a long-term increasing trend in the amount of seedfall for *C. japonicum*. The number of female seed-producing *C. japonicum* trees in the study area did not increase or decrease over the 24-year period, and the diameter growth of these individuals was slight because they were mature. Therefore, this increasing trend in seedfall may be due to an increase in photosynthesis as the air temperature increased. No increase in seedfall was observed for *F. platypoda* and *P. rhoifolia*, but the fluctuations in seedfall for *F. platypoda* have been small since 2007.

The seasonal variation in the amount of seedfall differed among the three species (Figure 5). *Fraxinus platypoda* was characterized by bimodal peaks of seedfall with many immature seeds in June and July, just after flowering. Most of the *F. platypoda* seeds that fall in autumn

are mature seeds. This abortion, in which immature seeds are dropped at an early stage of development, is considered more effective in terms of resource allocation than dropping them just before maturity. The seed abortion from May to August was significantly highly correlated with the total seedfall for the 24-year period (Figure 7). Thus, seed abortion is considered to be spontaneous and unaffected by external factors (e.g., weather conditions).

Conversely, *P. rhoifolia* seed abortion was relatively rare in June, July, and August, similar to *Betula* sp. (Mizui, 1993), and most of the seeds dropped from September to November. However, in some years, most *P. rhoifolia* seeds were empty, even though they appeared to be mature seeds. The reproductive strategy of *F. platypoda* ensures the production of mature seeds by limiting the number of seeds in advance. In contrast, *P. rhoifolia* seeds develop after flowering, and if the summer weather is favorable, it produces a large number of mature seeds. However, if the weather and other conditions are unfavorable, all of the seeds will be empty and that year's reproductive efforts will be lost. The seasonal variation in the amount of seedfall is similar between *C. japonicum* and *P. rhoifolia*, but immature fruits drop from *C. japonicum* trees after flowering (Mizui, 1993). We did not analyze the immature fruits in this study. It is possible that many seeds (i.e., in immature fruits) dropped after flowering, similar to the aborted *F. platypoda* seeds.

4.2 | The cause of masting

In this study, there was a significant negative correlation between the amount of seedfall in the current year (first-order difference) and the amount of seedfall in the previous year (first-order difference) for the three riparian canopy tree species (Figure 8). This strongly suggests that the amount of seedfall in the current year is affected by the allocation of resources to reproduction in the previous year, and that the stored resources are invested in mast years. Thus, it is clear that the seedfall of the three species is affected by fluctuations in stored resources.

In particular, the strong negative correlation for *F. platypoda* suggests that the fluctuations in the amount of seedfall are almost entirely dependent on fluctuations in stored resources. Moreover, the regular 2-year cycle of seedfall in *F. platypoda* also reflects the influence of resource accumulation on masting. The *F. platypoda* flower buds form at the top of the previous year's branches and bloom before the leaves develop. Inflorescence formation, shoot elongation, and leaf development are dependent on the stored carbohydrates from the previous year. Shoot elongation and leaf development occur simultaneously after flowering and only once during the growing season (Sakio, 1993). These results indicate that the stored carbohydrates from the previous year contribute significantly to the flowering and fruiting of *F. platypoda*.

Inflorescences produced more seeds when leaves were removed from the current-year branches (NL) than under natural conditions (N) (Table 1). This implies that seed production depends on the stored carbohydrates from the previous year or is influenced by the translocation of carbohydrates from other branches. However, it is possible that the photosynthetic activities during the current year affect seed maturation after summer (Hoch et al., 2013) and the translocation of carbohydrates from other branches, as in *Styrax obassia* (Miyazaki et al., 2007). Because 1992 was a mast year, during which many branches were fruiting, the translocation of carbohydrates from other branches may have been limited. While not negating the effects of accumulated minerals, this means that carbohydrates accumulated in the previous year contributed to the fruit set. Experiments with a stable carbon isotope (^{13}C) are needed to accurately clarify these phenomena (Hoch et al., 2013; Miyazaki et al., 2007).

Similarly, the 2-year seedfall cycle observed for *P. rhoifolia* was thought to be dependent on stored resources. However, it was unclear in this study whether these resources were carbohydrates or minerals such as nitrogen (Han et al., 2014) or phosphorus (Ichie & Nakagawa, 2013). As described above, various substances, including carbohydrate, nitrogen, and phosphorus, or resource allocation strategies are the causal factors of masting, but these may differ depending on the region and tree species (Wang et al., 2022). The data supporting the resource budget hypothesis are very limited (Crone et al., 2009; Ichie & Nakagawa, 2013; Sala et al., 2012; Satake & Bjørnstad, 2008). Thus, additional data are needed.

In many previous studies, climatic factors, such as temperature and precipitation, have been revealed to induce masting. In European beech (*Fagus sylvatica*), mast years have followed years in which the summer temperature was relatively high (Hacket-Pain et al., 2015; Övergaard et al., 2007). In *Picea glauca*, mast years may be related to hot and dry summers at the time of bud differentiation (Nienstaedt & Zasada, 1990). In *Nothofagus solandri*, seedfall is positively correlated with the mean daily temperature in the period immediately before the formation of floral primordia in the previous year (Allen & Platt, 1990; S. J. Richardson et al., 2005). An analysis of meteorological records for the Pasoh Forest Reserve, Peninsular Malaysia, suggests that the floral induction in *Shorea* section *Mutica* is caused by a drop of roughly 2°C or more in the minimum nighttime temperature for three or more nights (Ashton et al., 1988). In another study, which was

conducted in Lambir Hills National Park, Borneo, the magnitude of a flowering event depended on the timing of droughts associated with the El Niño southern oscillation cycle (Sakai et al., 2006). Using a phenology model, Numata et al. (2022) observed that the general flowering in 57% of the species in the family Dipterocarpaceae is affected by both drought and low-temperature cues. Additionally, cone production in longleaf pine (*Pinus palustris*) forests is correlated with the average annual air temperature and precipitation (on a decade scale) (Chen et al., 2018). As described above, weather cues that trigger masting vary among tree species and regions.

Many trees that flower in spring tend to have flower buds that differentiate in June or July of the year before flowering (Taniguchi et al., 2002; Yoshino, 2000, 2003). The amount of seedfall of *F. platypoda* was not significantly correlated with weather in May–August in the year before flowering (Table 2), suggesting that the amount of seedfall was not affected by weather at the time of flower bud differentiation. Conversely, the amount of seedfall of *P. rhoifolia* was significantly positively correlated with the amount of precipitation in June and the average temperature in July of the year before flowering. A model combining the amount of seedfall in the previous year and the average temperature in July of the year before flowering was selected in the multiple regression analysis (Table 3). Significant positive correlations were found between the amount of seedfall of *C. japonicum* and the temperature in June of the year before flowering. For *C. japonicum*, a model combining the amount of seedfall in the previous year and the average temperature in June of the year before flowering was selected in the multiple regression analysis. These results suggest that for *P. rhoifolia* and *C. japonicum*, masting is caused by a combination of storage resources and climatic conditions.

4.3 | Masting and life history strategies

In a study of 11 hardwood species, population-based *CV*s in seedfall ranged from 0.22 for *Phellodendron amurense* var. *amurense* to 1.69 for *Betula maximowicziana* (Yasaka, 2007). Compared with these species, *C. japonicum* is a low-*CV* tree species, while *F. platypoda* and *P. rhoifolia* have moderate *CV*s. Tree species that show distinct annual fluctuations like *F. platypoda* and *P. rhoifolia* include *Fraxinus mandshurica*, *Kalopanax septemlobus*, *Tilia japonica*, *Tilia maximowicziana*, and *B. maximowicziana* (Mizui, 1993), and *F. crenata*, *Quercus crispula* var. *crispula*, *Castanea crenata*, *Zelkova serrata*, *Juglans mandshurica* var. *sachalinensis*, and *Padus grayana* (Tambara, 1999). Similar to the species described above, these species that have masting years are late successional species, except for *B. maximowicziana*.

Conversely, pioneer tree species or disturbance-dependent species are expected to have lower seedfall *CV*s. Trees located near watercourses, such as *Populus* (J. Richardson et al., 2014) and *S. dolichostyla* subsp. *dolichostyla* and *S. hukaoana* (H.S., personal observation), in temperate forests tend to produce many seeds every year, likely because resources are abundant and disturbances are very frequent (Piovesan & Adams, 2005). These riparian tree species produce large amounts of very small seeds every year. Regarding seed production, there is a trade-off relationship between seed size and number. An earlier comparison of 30 deciduous tree species indicated that trees with larger seeds produce fewer seeds, while trees with smaller seeds produce more seeds (Mizui, 1993).

Many previous studies on seed production focused on a single tree species or compared species within the same genus (*Quercus*: Koenig et al., 1994; *Carpinus*: Shibata et al., 1998; *Acer*: Tanaka, 1995), but few compared trees with different life histories. In this study, we compared the seedfall patterns of forest canopy trees in a riparian forest. The selected species are the riparian canopy trees that form old growth forests, but they have different life histories and vary in terms of seed size and seedfall patterns. Earlier research confirmed *C. japonicum* produces small seeds in large quantities, whereas *F. platypoda* and *P. rhoifolia* produce relatively small quantities of relatively large seeds (Sakio et al., 2002). *Fraxinus platypoda*, *P. rhoifolia*, and *C. japonicum* are all wind-pollinated trees. *Fraxinus platypoda* is the most dominant species in the study forest and has the most late transitional species characteristics of the three species. *Pterocarya rhoifolia* trees form concentrated forests with large patches comprising trees of the same age. Thus, masting of these tree species has advantages for pollination. Conversely, *C. japonicum* individuals are scattered (Sakio et al., 2002) dioecious species. Moreover, *C. japonicum* can regenerate after very rare large-scale disturbances such as landslides or debris flow. This species produces many small seeds (Sakio et al., 2002), which are then widely dispersed (Sato et al., 2006) every year, thereby ensuring regeneration after rare catastrophic events. On the basis of its relatively late initiation of reproduction, large size, and long lifespan, *C. japonicum* appears to be a late transitional species, but its reproduction-related characteristics, such as seed size, seed dispersal distance, and masting behavior, are similar to those of pioneer species.

5 | CONCLUSIONS

This study revealed masting in three riparian tree species over a 24-year period. The *F. platypoda* and *P. rhoifolia*

seedfall clearly fluctuated, with a 2-year cycle. The seedfall of *C. japonicum* also fluctuated, but seeds were produced every year, with an approximate 4-year cycle. These results suggest that the fluctuations in the amount of seedfall of *F. platypoda* are almost entirely dependent on the fluctuations in stored resources, regardless of the previous year's weather. Conversely, the amount of seedfall of *P. rhoifolia* and *C. japonicum* is dependent on the fluctuations in stored resources and the average temperature in June of the year before flowering. These differences in seed production patterns were related to differences in life history characteristics such as seed size and regeneration mechanisms.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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