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ARTICLE

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# Grow or die: A 49-year growth history of a Japanese warm-temperate tree species

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## Abstract

The growth trajectories of trees are not fully understood due to their long life span. We characterized the population dynamics of the canopy tree *Castanopsis cuspidata* (Thunb.) Schottky in a Japanese warm-temperate forest over 49 years (1966–2015). Our study was initiated approximately 50 years after our study site was clear-cut. The forest had a closed canopy for the first 23 years of the study. Strong typhoons in 1991 and 1993 seriously damaged the forest, and since then the forest has been recovering from these disturbances. The diameter distribution of this species was bell-shaped in 1966, suggesting that the trees emerged simultaneously after the clear-cut in the 1910s, and the recruitment of trees has remained unchanged since then. The lack of recruitment of *C. cuspidata* before the typhoon disturbance supports this conclusion. Assuming that the *C. cuspidata* trees in 1966 were cohorts that were established soon after the clear-cut, the size differences reflect differences in growth rate, with small trees corresponding to slow growers and large trees corresponding to fast growers. Before the typhoon, slow growers had low survival, and the mortality rate of fast growers was low. Many fast growers were uprooted or snapped by strong winds by the typhoons. However, their mortality rate did not differ from that of slow growers because many slow growers were killed by large fallen trees. The growth of some slow-growing survivors increased after the typhoon, which allowed them to rapidly reach the canopy. Therefore, the typhoon altered the distribution of canopy trees among slow and fast growers. Survivors experienced faster growth than trees that died during the census period, suggesting that growth rate provides a robust indicator of future survival. Before the typhoon, the survival of fast growers was higher than that of slow growers. This suggests that fast growers disproportionally contribute to reproduction compared with slow growers. However, no recruited tree was observed in this subperiod, suggesting that fast growers

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made no contribution to reproduction. Fast growers might not play a more significant demographic role than slow growers in this species.

**KEYWORDS**
*Castanopsis cuspidata*, growth rate, long-term ecological research, mortality, population dynamics, population growth, recruitment, typhoon

## INTRODUCTION

Trees are characterized by a prolonged sterile stage (seeds, seedlings, and saplings). Most trees do not initiate reproduction unless they reach a certain size (hereafter referred to as "reproductive size") (Thomas, 1996; Wright et al., 2005). However, after the initial flowering, trees have a prolonged fertile stage (mature). Therefore, reaching reproductive size is critically important for the reproductive success of trees.

The growth trajectories of mature trees vary. Temporal autocorrelation in tree growth (a fast grower tends to maintain a high growth rate, whereas a slow grower tends to maintain a slow growth rate) has been observed in many trees (Bullock et al., 2004; Kohyama, 1982; Kohyama et al., 2005; Kohyama & Hara, 1989; Nakashizuka et al., 1997). This causes fast growers to reach reproductive size sooner than slow growers (Zuidema et al., 2009). Dendrochronological studies have often revealed decadal differences in the age of trees similar in size (Brienen et al., 2006; Kanzaki, 1984; Nakashizuka & Numata, 1982; Rozendaal et al., 2010; Suzuki, 1981; Suzuki & Usuda, 1989).

Tree (annual) rings provide insights into the growth trajectory of trees. However, a dendrochronological approach is often lacking important information, such as the growth history of dead trees (only the growth history of live trees can be traced using this approach); nevertheless, some studies have analyzed the tree rings of dead trees that were resistant to decomposition (Angers et al., 2017). Decomposition can lead to the disappearance of many dead trees from forests. The growth history of dead trees may provide important insights into population dynamics.

Observing a forest for years is the only way to determine the growth trajectories of trees, including dead trees (except those that recruited and died between consecutive censuses). During the monitoring period, some juvenile trees may attain maturity, and others may die before attaining maturity. A complete set of growth data of a forest can be obtained via forest monitoring. We monitored a population of *Castanopsis cuspidata* (Thunb.) Schottky, a canopy tree species that begins to reproduce after reaching the canopy layer, for 49 years in a Japanese warm-temperate forest. We used these data to address several fundamental ecological questions.

The forest understory is strongly light-limited and has a low compensation point for many trees (Chazdon, 1987; Clark & Clark, 1999; Nakashizuka, 1985; Poorter & Arets, 2003; Yamada et al., 2014; Yoda, 1978). This forces trees to grow slowly and to remain for long periods in the forest understory where they face high risks of death because of light shortages and damage from falling debris (Clark & Clark, 1991). These trees appear to have little chance of reaching the canopy (Baker, 2003; Swaine et al., 1987). Hence, we hypothesize that fast growers can rapidly pass through the forest interior and have greater survival than slow growers that remain in the forest interior longer. To test this hypothesis, we determined whether the survival of fast growers was greater than that of slow growers. In addition, we determined whether survivor trees grew faster than dead trees.

A fast grower of *C. cuspidata* should rapidly reach the forest canopy, initiate reproductive activities, and possibly remain reproductively active for a longer period than conspecific slow growers. Brienen et al. (2006) and Zuidema et al. (2009) used a population matrix approach and data from tropical trees to show that fast growers played more significant roles in sustaining populations than slow growers.

This finding applies to trees in forests with few disturbances such as tropical forests. However, this might not apply to trees in Japanese warm-temperate forests, which are occasionally damaged by strong typhoons (Bellingham et al., 1996; Hirayama et al., 2019; Ida, 2000; Naka, 1982; Saito, 2002; Sato, 2004; Sato et al., 2010; Takafumi & Hiura, 2009; Yamamoto, 1992). Canopy trees are exposed to stronger winds compared with forest interior trees; consequently, the mortality of canopy trees by wind storms is high (Hirayama et al., 2019; Ida, 2000; Saito, 2002). These storms might limit the longevity of canopy trees.

The death of canopy trees creates canopy gaps, which leads to accelerated stem diameter growth of trees that have been suppressed by the dead canopy trees (Naka, 1982; Nakashizuka & Numata, 1982; Suzuki, 1981). Consequently, slow growers may take over the canopy trees after the death of the fast growers. If slow growers in the forest understory can survive the typhoon disturbance, they have an opportunity to reach the canopy

layer and reach reproductive maturity. Here, we evaluated the importance of fast growers in sustaining a *C. cuspidata* population in a Japanese warm-temperate forest vulnerable to typhoon disturbance.

## MATERIALS AND METHODS

### Study site

This study was performed in a warm-temperate evergreen forest in Minamata, Kyushu, Japan (33°19′ N, 130°80′ E, 400 to 637 m above sea level [asl]). A 33-ha secondary forest at our study site was designated as a forest reserve for the conservation of genetic resources for timber trees by the Japanese government. The forest is dominated by the evergreen broad-leaved trees *C. cuspidata*, *Quercus acuta* Thunb. ex Murray, *Quercus salicina* Blume, and *Machilus thunbergii* Sieb. et Zucc., which regenerated after the clear-cut between 1910 and 1920 for charcoal production (Kira, 1978). Therefore, the trees in the forest were established after the clear-cut from coppices, dispersed seeds, or soil seed banks.

In total, 174 woody species have been documented in the forest (Kira, 1978). The average canopy height is approximately 20 m, and the diameter of the stem at breast height (dbh, 130 cm from the ground) is greater than 50 cm for some large trees. According to meteorological records collected at Minamata (6 m asl and approximately 15 km west of the forest) from 1981 to 2010, the average annual precipitation is 2100 mm, and the average monthly rainfall is never less than 50 mm. The mean annual temperature is 16.8°C; the warmest and coolest months are August (27.1°C) and January (6.6°C), respectively.

Typhoons frequently make landfall in southwestern Japan, and typhoon disturbances have major effects on forest structure, species composition, and the regeneration of warm-temperate forests (Naka, 1982; Saito & Sato, 2007; Taoda, 1987; Yamamoto, 1992). Strong typhoons occasionally affect the study site, and typhoons in 1991 and 1993 induced serious damage to the forest. Many trees in the forest were uprooted or snapped, which resulted in high mortality (Yamada et al., 2011; Yamamoto & Manabe, 1997). No other typhoons have caused such serious damage to the forest during our observation period.

### Study species

In this study, we focused on the growth, recruitment, and mortality of the most dominant tree species in this forest, *C. cuspidata*. This species is a common evergreen broad-leaved tree species in Japanese warm-temperate forests (Kira, 1991; Tagawa, 1995; Yamada et al., 2002, 2011; Yamanaka, 1966). *C. cuspidata* grows to approximately 20 m tall and over 100 cm in dbh. This species has the ability to sprout when the stem breaks, which can result in multiple-stemmed individuals (Hirayama et al., 2010, 2019). This species has a moderate level of shade tolerance, and the saplings can survive for some years under closed canopies (Cho et al., 2005; Hirayama et al., 2010; Hiroki & Ichino, 1998; Tanouchi, 1996). Reproduction in this species typically begins when trees reach the canopy layer. Annual fluctuations in seed production in this species are large (Hiroki & Matsubara, 1982; Shimada, 2001). Numerous seeds are produced in a mast seeding year, which occurs once approximately every 4 years; seed production is low in other years.

### Field methods

Within the forest, a permanent plot (P-1 of Yamada et al., 2011) of 40 × 40 m was established in 1966 approximately 50 years after the clear-cut for studies of the International Biological Program (Kira, 1978), and it has been monitored since then (Yamada et al., 2011). Thus, 49 years of data were collected. All tree stems with dbh ≧ 4.5 cm were monitored in the plot. These stems were tagged, mapped, and identified, and dbh measurements were taken. Instances in which trees had multiple stems because of coppice regeneration were noted. All trees inventoried in previous censuses were remeasured to estimate growth and mortality rates. Trees were recorded as recruits, and their size was measured when new trees reached dbh ≧ 4.5 cm during the census period. Censuses were conducted yearly from 1966 to 1976, in 1978, 1980, 1981, and every 2 years thereafter.

### Analysis

We divided our census period into three subperiods; the pre-typhoon period before the 1991 typhoon (23 years from 1966 to 1989), the typhoon disturbance subperiod (12 years from 1989 to 2001), and the post-typhoon subperiod (14 years from 2001 to 2015). The pre-typhoon subperiod was characterized by a high density of trees and basal area (BA) of forest (Appendix S1: Figure S1a,b). The forest interior was extremely dark, and the self-thinning process predominated (Appendix S2: Figure S1). In this subperiod, the tree density of the forest decreased and the BA increased (Appendix S1: Figure S1a,b). In the typhoon disturbance subperiod, the

forest was affected by two strong typhoons in 1991 and 1993, which induced severe damage to the forest. Because trees damaged by the typhoons gradually died, stand BA continued to decrease until 2001 (Appendix S1: Figure S1a). Recovery occurred during the post-typhoon subperiod. The BA and density of trees in the forest increased during this subperiod.

The *C. cuspidata* population was divided into three size categories: small (10.0 cm > dbh ≧ 4.5 cm), medium-sized (25.0 cm > dbh ≧ 10.0 cm), and large (dbh ≧ 25.0 cm). A logistic regression analysis between the crown position (1 = approaching the forest canopy layer and 0 = below the forest canopy) and dbh suggests that this species reaches the canopy layer when the dbh of the trees is approximately 25 cm (Appendix S3: Figure S1). Thus, we assumed that only large trees (dbh ≧ 25.0 cm) reached the canopy layer and thus were reproductively mature. Given that the cohort of *C. cuspidata* trees in the plots was established soon after the clear-cut in the 1910s, the difference in tree size should largely reflect differences in growth rate among them (small trees should be equal to slow growers and large trees should be identical to fast growers).

Stem diameter growth rates were measured using the relative growth rate (RGR), which is calculated as follows:

$$(\ln(\mathrm{dbh}_{\mathrm{final}}) - \ln(\mathrm{dbh}_{\mathrm{initial}}))/t,$$

where $\mathrm{dbh}_{\mathrm{initial}}$ and $\mathrm{dbh}_{\mathrm{final}}$ are the initial and final dbh in each census period, respectively, and $t$ is the census interval in years. RGR for survivors for each subperiod was calculated for all size categories. In addition, RGR for dead trees when they were alive was calculated for all size categories within each subperiod. Therefore, $t$ for dead trees was always shorter than that for survivor trees. RGR tends to decrease with tree size (Kohyama et al., 2020). This pattern leads to a decline in RGR as $t$ increases, given that tree size usually increases with time. Therefore, the RGRs of surviving trees in longer census periods are higher than those of dead trees in shorter census periods, and this reveals major differences between survivor and dead trees.

The mortality rate was calculated for all size categories for all subperiods per the following formula from Sheil et al. (1995):

$$\text{Mortality rate} = 1 - (1 - N_{\mathrm{dead}}/N_{\mathrm{initial}})^{1/t},$$

where $N_{\mathrm{dead}}$ is the number of dead trees during the census period and $N_{\mathrm{initial}}$ is the number of dead trees at the beginning of each census period. We calculated the duration as the number of large trees (in years) for all trees found in 1966 from the beginning (1966) to the end (2015) or until they died.

The effects of tree size on mortality were analyzed using Fisher's exact test for count data. Pairwise comparisons of the dbh growth rate and periods as large trees were made among size categories or between dead and survivor trees using pairwise Wilcoxon rank-sum tests with the Benjamini–Hochberg correction (Benjamini & Hochberg, 1995), if necessary. All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022).

## RESULTS

In the study plot, *C. cuspidata* was the most dominant tree species among the 42 species detected in the plot in terms of both BA and density from the beginning to the end of the study period.

In the pre-typhoon subperiod, the temporal change in BA and density of the *C. cuspidata* population followed stand-level trends (Appendix S1: Figure S1a,b). The density and BA of *C. cuspidata* decreased and increased over time, respectively. In this subperiod, stand-level self-thinning that followed the power 3/2 law occurred (Appendix S2: Figure S1) (Aiba et al., 2022; Nakashizuka, 1984; Yamakura, 1985; Yoda et al., 1963); thus, the forest canopy was densely packed with many trees. Throughout this subperiod, *C. cuspidata* comprised approximately 70% and 35% of the total BA and density of trees, respectively (Appendix S1: Figure S1c). In the following typhoon disturbance subperiod, the density and BA of *C. cuspidata* decreased because of the death of the typhoon-damaged trees. The BA and density of *C. cuspidata* were only 47% and 17% in 2001, respectively (Appendix S1: Figure S1c). In the post-typhoon subperiod, the BA and density recovery of *C. cuspidata* were lower than the stand-level average; the BA and density of this species were 36% and 15% in 2015, respectively.

The frequency distribution of dbh of *C. cuspidata* was bell-shaped; the number of small and large trees was small, and the number of medium-sized trees was large in 1966 (Figure 1), suggesting that the recruitment of this species to the forest has long been limited before the establishment of the plot. No tree was recruited in the pre-typhoon subperiod until 1989, suggesting again that the recruitment of *C. cuspidata* in this stand is low. Recruitment increased after the typhoon disturbance, and a total of 47 trees had been recruited by 2015. Seven out of 47 of the recruited trees died before 2015. The densities of *C. cuspidata* declined from 195 in 1966 to 58 in 2015; only 18 trees among the initial 195 trees survived for 49 years.

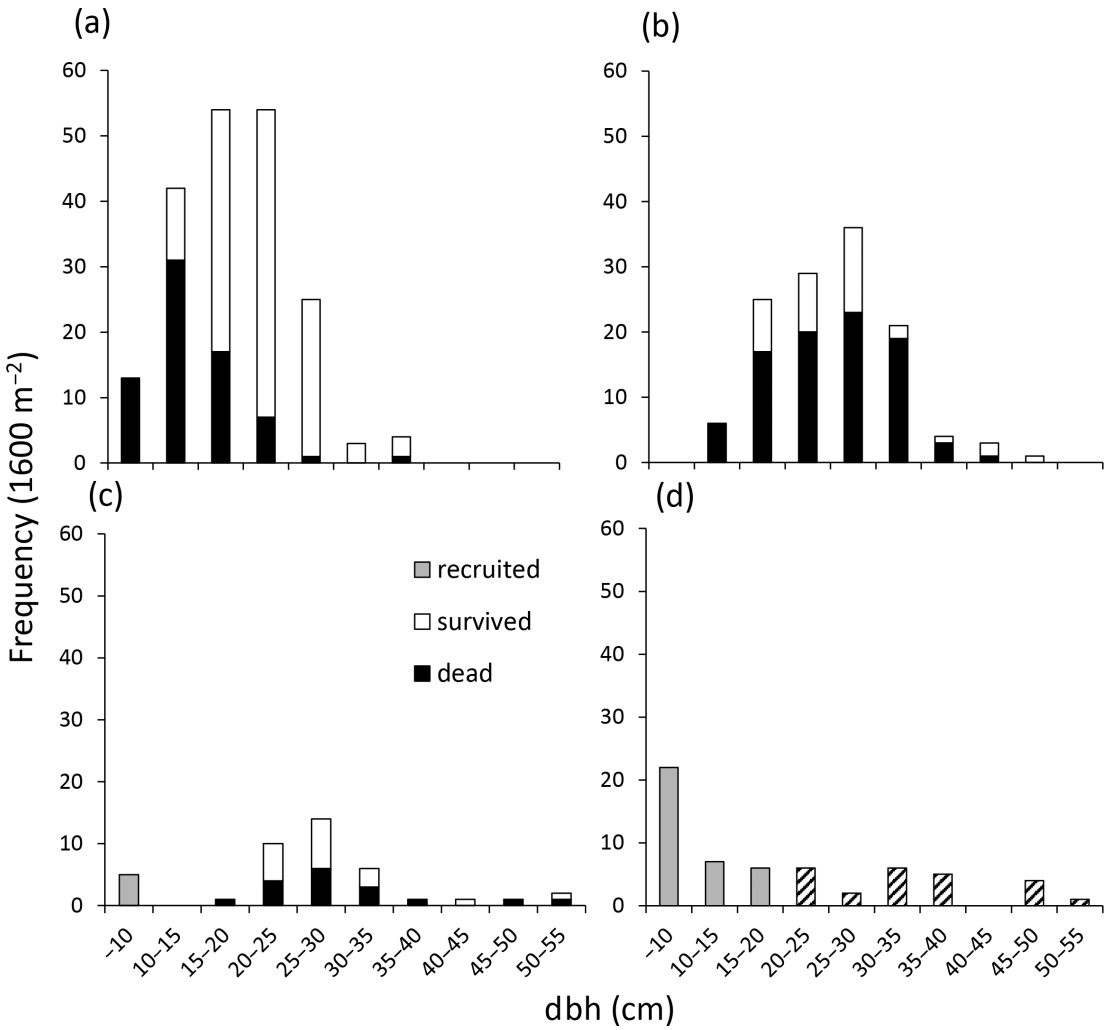



**FIGURE 1** Frequency distribution of dbh of *Castanopsis cuspidata* at (a) the beginning of the pre-typhoon subperiod (=1966), (b) at the beginning of the typhoon disturbance subperiod (=1989), (c) at the beginning of the post-typhoon subperiod (=2001), and (d) at the end of the post-typhoon subperiod (=2015) in a Japanese warm-temperate forest. Open, black, and gray bars show the trees that survived to the next subperiod, those that died before the next subperiod, and those that were recruited after 1966, respectively. Hatched bars show the trees that were present in 2015, for which their survival to the next subperiod could not be evaluated.

In the pre-typhoon subperiod, *C. cuspidata* showed a distinct size-dependent pattern of mortality (Figure 2). No single small tree survived this subperiod, and only 2 out of 32 large trees died in the same subperiod. Medium-sized trees had an intermediate mortality rate. This pattern drastically changed in the typhoon disturbance subperiod. Both medium-sized and large trees had higher mortality rates than trees observed in the pre-typhoon subperiod because of typhoon-related damage. Forty-six trees out of 65 large trees were uprooted or snapped by the typhoon, and 43 trees out of 60 medium-sized trees were killed by fallen large trees. No statistically significant difference in mortality rate was observed between medium-sized and large trees. The mortality rate was lower in the post-typhoon subperiod than in the typhoon disturbance subperiod. No size-dependent patterns in the mortality rate were observed.

Figure 3 shows the growth trajectories of 242 *C. cuspidata* trees. The dbh of some medium-sized trees sharply increased after the typhoons. According to the RGR values of survivors in the pre-typhoon subperiod, large trees grew faster than medium-sized trees, but this difference was marginally insignificant ($p = 0.08$, Wilcoxon rank-sum tests, Figure 4a). No small tree survived this subperiod (all small trees died in this subperiod); thus, we were unable to calculate the RGR of these trees. Five small trees survived for 10 years from 1966 to 1976. Comparison of RGR values in this 10-year period among small, medium-sized, and large trees revealed that small trees had the lowest RGR, whereas large trees had the highest RGR (Figure 4b). This size-dependent difference in RGR was unclear in the typhoon disturbance subperiod (Figure 4c). The size-dependent pattern in RGR differed in the post-typhoon and pre-typhoon subperiods (Figure 4d).

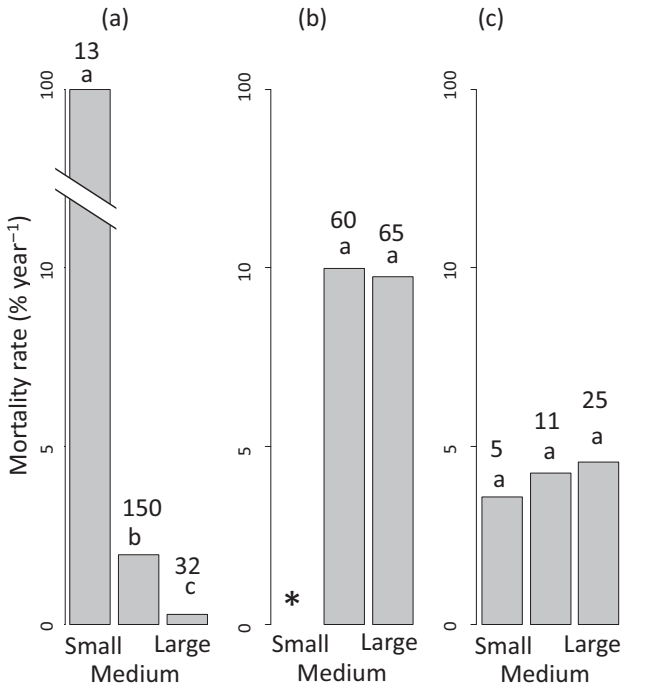



**FIGURE 2** Mortality rate of *Castanopsis cuspidata* in (a) the pre-typhoon subperiod (1966–1989), (b) the typhoon disturbance subperiod (1989–2001), and (c) the post-typhoon subperiod (2001–2015) for small trees (10.0 cm > dbh ≧ 4.5 cm), medium-sized trees (25.0 cm > dbh ≧ 10.0 cm), and large trees (dbh ≧ 25.0 cm) in a Japanese warm-temperate forest. Different letters above the bars indicate significant differences among size categories within a subperiod (Fisher's exact test for count data). Because all small trees died during the pre-typhoon subperiod, there were no small trees in the typhoon disturbance subperiod (asterisk). Numbers above the bars show the sample sizes.

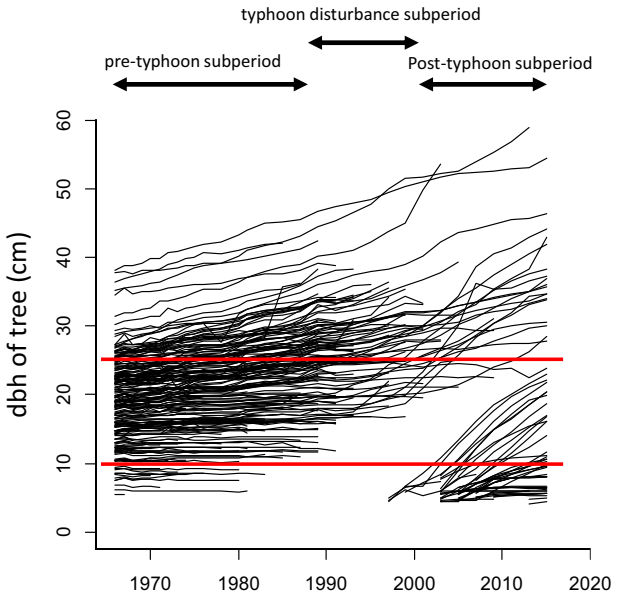



**FIGURE 3** dbh growth trajectory of *Castanopsis cuspi* data from 1966 to 2015 in a Japanese warm-temperate forest. One line represents the growth trajectory of a single tree. Red lines correspond to the boundary between small, medium-sized, and large trees. Arrows indicate the subperiods.

The RGR of trees in all three size classes increased in this subperiod. The increase in RGR was significantly higher for small trees than for medium-sized and large trees.

The RGR was significantly higher in survivor trees than in dead trees in the pre-typhoon subperiod among medium-sized trees (Figure 5a). However, no significant difference in RGR was observed between survivor and dead trees in the same subperiod (Figure 5b); this might be explained by the small sample size and low statistical power (only two large trees died in the pre-typhoon subperiod). In the typhoon disturbance subperiod, the RGR of both medium-sized and large survivors was significantly higher than that of dead trees in the same size class (Figure 5c,d). In the post-typhoon period, the RGR of dead trees was lower than that of survivor trees (Figure 5e,f); however, differences in RGR were not statistically significant for both cases, which might stem from the small sample size (e.g., only three dead medium-sized trees were observed).

After 1989, 47 trees were recruited. Five trees were vegetatively regenerated from large trees, and the remaining 43 trees did not show any evidence of vegetative sprouting from other trees. The RGR of dead trees (7 trees) was significantly lower than that of survivor trees (40 trees) (Figure 6). Variation in RGR was greater among survivor trees than among dead trees.

Figure 7 summarizes the population dynamics of trees in the three size categories. All small trees died in the pre-typhoon subperiod. In this subperiod (Figure 7a), no recruitment was observed. The transition from medium-sized trees to large trees (35 trees) was minor compared with trees that remained in the medium size category (60 trees) or trees that died (55 trees). The mortality rate of large trees was low. In the typhoon disturbance subperiod, most of the medium-sized and large trees were killed by the typhoons (Figure 7b). Five trees were recruited immediately after the typhoon disturbance. In the post-typhoon subperiod (Figure 7c), the recruitment of trees was increased, and 15 fast-growing recruited trees became medium-sized trees. The dbh of the fastest grower among the recruited trees was 23.0 cm in 2015.

In the 49-year study period, large trees in 1966 remained as large trees for a significantly longer period than medium-sized or small trees in 1966 (Figure 8). However, according to the growth history of the 18 large trees in 2015 (Figure 7), 16 and 2 trees were medium-sized and large trees, respectively, in 1966, suggesting that large trees were almost completely

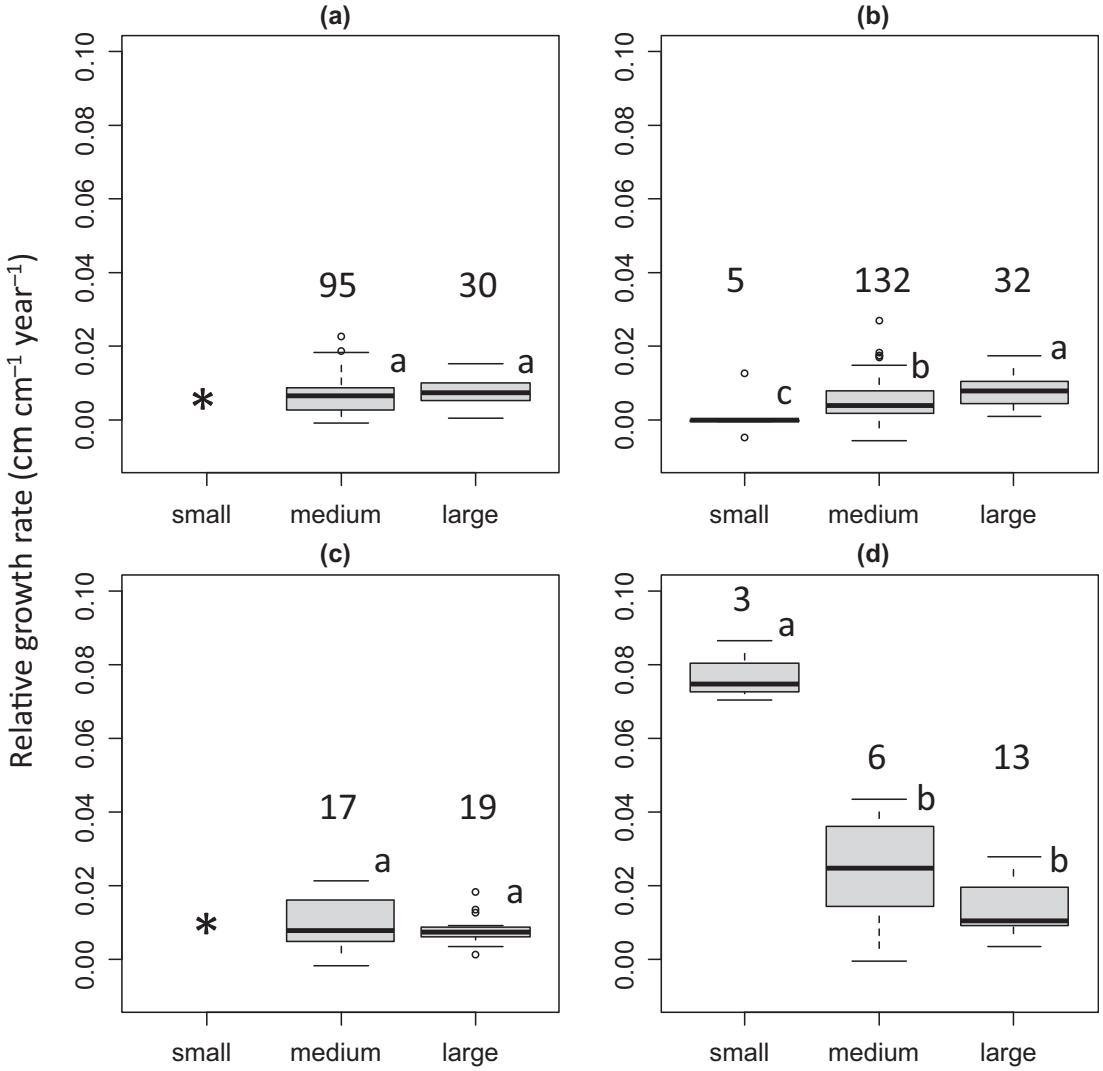



**FIGURE 4** Relative growth rate (RGR) of the dbh of *Castanopsis cuspidata* for small trees (10.0 cm > dbh ≧ 4.5 cm), medium-sized trees (25.0 cm > dbh ≧ 10.0 cm), and large trees (dbh ≧ 25.0 cm) (a) in the pre-typhoon subperiod (1966–1989), (b) in the initial 10 years of the pre-typhoon subperiod (1966–1976), (c) in the typhoon disturbance subperiod (1989–2001), and (d) in the post-typhoon subperiod (2001–2015) in a Japanese warm-temperate forest. RGRs were determined for survivors throughout the subperiods. Shown are the median (horizontal line), interquartile range (box), data range (whiskers), and outliers (circle). Different letters above the boxes indicate significant differences among size categories within a subperiod (pairwise Wilcoxon rank-sum tests with Benjamini–Hochberg correction). No small tree survived throughout the pre-typhoon subperiod and typhoon disturbance subperiod (asterisk). Numbers above the boxes show the sample size.

replaced by trees that were medium in size in 1966. This means that only 2 out of 32 large trees in 1966 survived for 49 years.

## DISCUSSION

### Do fast growers have higher survival than slow growers?

Our results provide strong evidence to support the idea that fast growers have higher survival than slow growers. The forest was clear-cut in the 1910s. There was wide variation in dbh in *C. cuspidata* in 1966. Assuming that the whole trees at the initial census in 1966 were cohorts that were established at the clear-cut, size differences reflect differences in growth rate. Thus, small trees were assumed to be slow growers, and large trees were assumed to be fast growers. In the pre-typhoon subperiod when the forest interior was extremely dark (Yoda, 1978), extremely slow growers (small trees) could not survive, many slow growers (medium-sized trees) died, and the mortality rate of fast growers (large trees) was low (Figure 2a). This may stem from the suppression of the

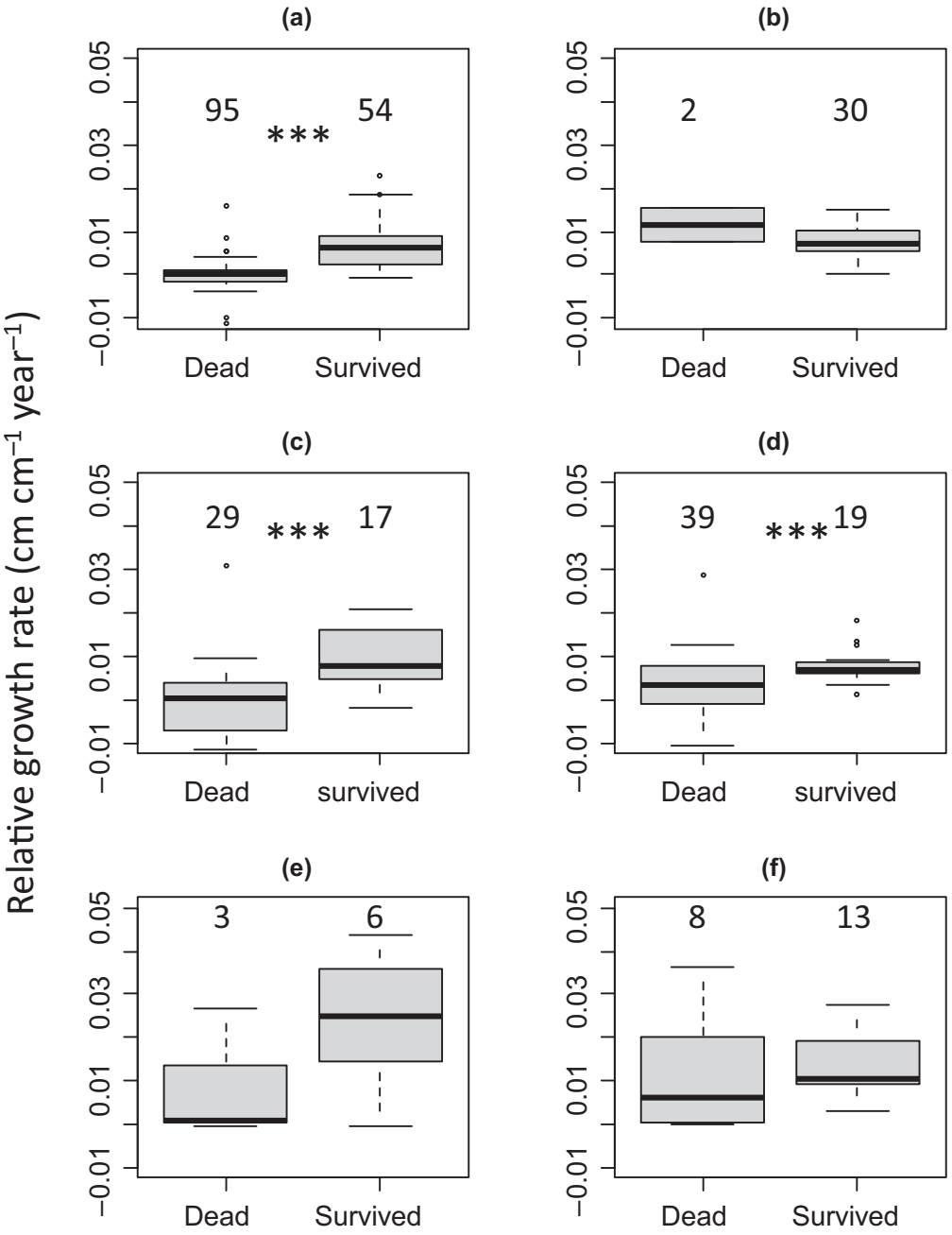



**FIGURE 5** Comparison of the relative growth rate of the dbh of *Castanopsis cuspidata* between survivor trees and dead trees for (a) medium-sized trees (25.0 cm > dbh ≧ 10.0 cm) and (b) large trees (dbh ≧ 25.0 cm) in the pre-typhoon subperiod (1966–1989), (c) medium-sized trees, and (d) large trees in the typhoon disturbance subperiod (1989–2001), and (e) medium-sized trees and (f) large trees in the post-typhoon subperiod (2001–2015) in a Japanese warm-temperate forest. Shown are the median (horizontal line), interquartile range (box), data range (whiskers), and outliers (circle). Asterisks indicate significant differences; *$p < 0.05$; ***$p < 0.001$ (Wilcoxon rank-sum test). Numbers above the boxes show the sample size.

slow growers by fast growers; once this structural relationship between fast growers and slow growers was formed, slow growers may have low survival.

However, in the typhoon disturbance subperiod, the size of the fast growers was no longer advantageous. Many large fast growers in the canopy might have been uprooted and snapped by the strong winds of the typhoons (Figure 1b). This increased the mortality of large trees in this subperiod (Figure 2b). However, the mortality of slow growers was also substantial during this period because many slow growers were killed by fallen large trees. The mortality risk by typhoon damage did not differ between fast growers and slow growers.

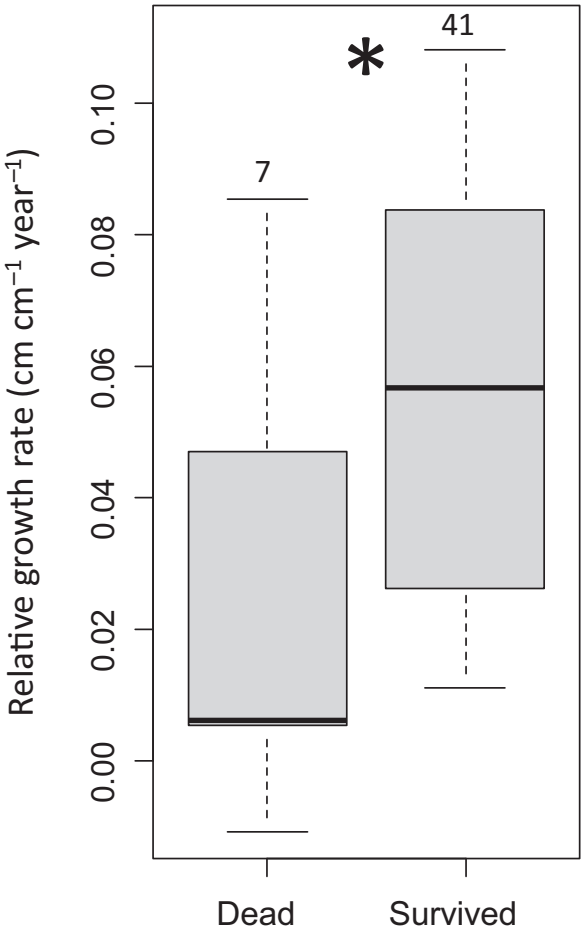



**FIGURE 6** Comparison of the relative growth rate of the dbh of *Castanopsis cuspidata* between survivor trees and dead trees among recruited trees during the census period in a Japanese warm-temperate forest. Shown are the median (horizontal line), interquartile range (box), and data range (whiskers). Asterisks indicate significant differences; *$p < 0.05$ (Wilcoxon rank-sum test). Numbers above the boxes show the sample size.

The growth of some slow-grower survivors increased rapidly after the typhoons (Figure 3). This might reflect a release from severe suppression by fast growers. Slow growers are not competitive in a dark forest; however, if they survive a forest disturbance, slow growers have the opportunity to reach the canopy. The typhoons thus altered the identity of the trees that comprised the canopy. Therefore, our first hypothesis that fast growers that can rapidly pass through the forest interior have higher survival than slow growers that remain in the forest interior was supported, but this was only the case for disturbance-free periods.

Our data showed that survivors had faster growth than trees that died in the census period. This may suggest that fast growers have higher survival than slow growers. However, this interpretation is only valid if the growth rate of this species is determined exclusively by inherent variation (genetic makeup) among trees. Although the genetics of trees affect their growth, microenvironmental conditions related to resource availability also have major effects on the growth of trees (Brienen et al., 2006; Kohyama et al., 2005; Kohyama & Hara, 1989). For example, a tree in sunny conditions may be able to grow faster than a tree under dark conditions. These conditions are also favorable for tree survival. Therefore, the association of survival with the growth rates of trees may simply reflect variation in microhabitat suitability. Our data suggest that growth rate can be a good indicator of the future survival of *C. cuspidata* trees.

Variation in growth rate was high among recruited trees. The growth rate of some trees was slow, and they remained in the small category; by contrast, the growth of other trees was rapid, and these trees reached the large category in the same period (dbh = 23.0 cm in 2015). The difference in growth rate among recruited trees can provide insights into variation in dbh observed in *C. cuspidata* trees in 1966. One possibility is that trees that germinated earlier than other trees may be able to grow faster. Alternatively, the difference in growth rate may be explained by the genetic characteristics of trees and/or the microenvironmental conditions. The recruited trees could be used to study the mechanisms underlying variation in growth rate.

## Do fast growers contribute to population growth more than slow growers?

The present results indicate that the regeneration of *C. cuspidata* occurs only when a canopy gap is formed by a sporadic forest disturbance. That is, this species cannot regenerate under closed canopies. The role of disturbance in the regeneration of trees has received much attention from ecologists (Brokaw, 1985; Denslow, 1987; Runkle, 1985), and disturbance-dependent regeneration has been observed in many tree species (Ida, 2000; Kanzaki, 1984; Naka, 1982; Nakashizuka & Numata, 1982; Suzuki, 1981; Suzuki & Usuda, 1989). The size distribution of this species in 1966 was bell-shaped (Figure 1a), suggesting that the trees all emerged at the time of the clear-cut in the 1910s and that trees were recruited a long time after the clear-cut. No recruitment of *C. cuspidata* trees in this forest was observed in the pre-typhoon subperiod when disturbance was absent, and forest canopies were densely packed with many trees (Figure 7a); this suggests that the regeneration of this species depends on disturbance. A sudden increase in recruitment after the typhoon disturbance (Figure 7b,c) provides further support for this conclusion.

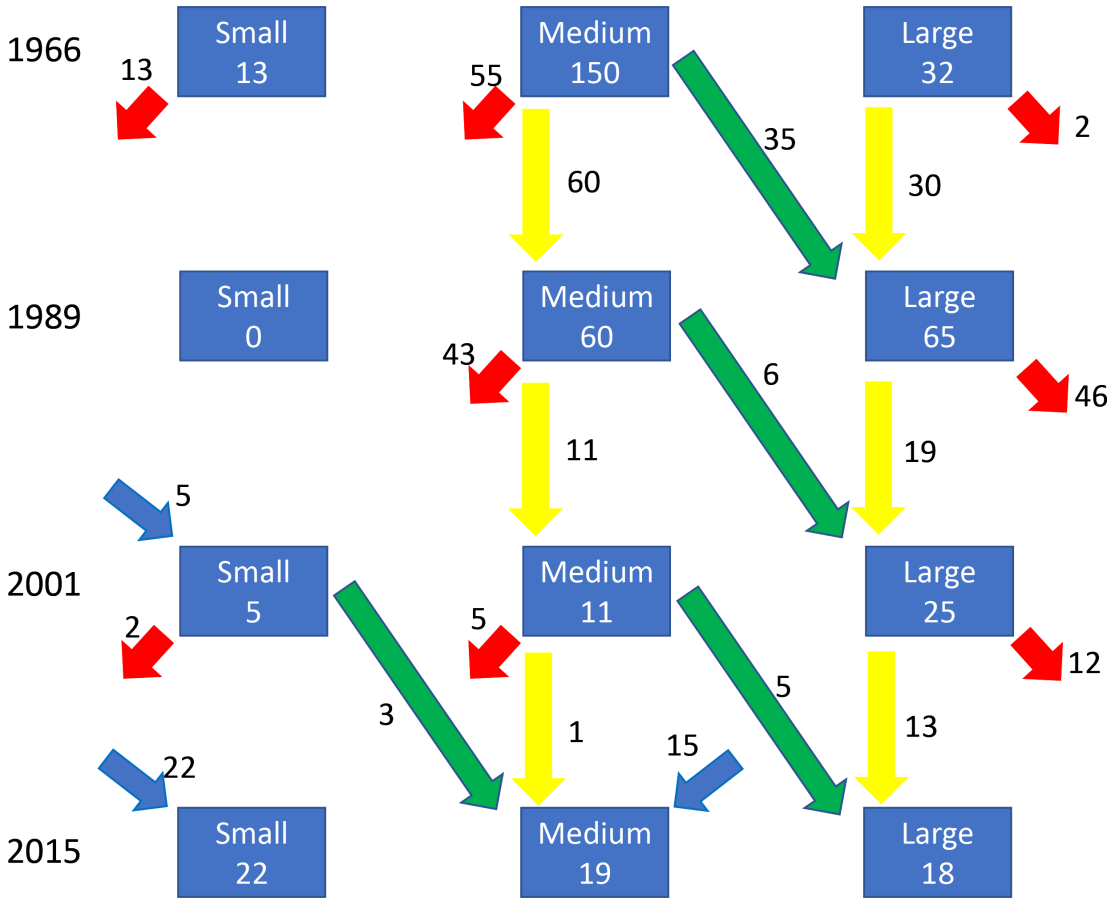



**FIGURE 7** Number of small, medium-sized, and large *Castanopsis cuspidata* trees in 1966, 1989, 2001, and 2015 in a Japanese warm-temperate forest (numerals in the boxes). Dynamics in the pre-typhoon subperiod (1966–1989), typhoon disturbance subperiod (1989–2001), and post-typhoon subperiod (2001–2015) are also indicated by arrows; blue, red, green, and yellow arrows indicate recruitment, death, progression from a size category to the next size category, and stasis in the same size category, respectively.

Because *C. cuspidata* can sprout rapidly when trees are damaged, the importance of vegetative sprouting for this species during the regeneration process, including regeneration by coppices, has been recognized by various scientists (Chen et al., 2017; Hirayama et al., 2019; Yamashita et al., 2018). However, our data do not support this observation. Only 5 trees among the 47 recruited trees were derived from the coppices of other trees. This result suggests that the contribution of vegetative sprouting to the regeneration of this species is quite limited in this forest and that regeneration via seed production was key during the regeneration process after typhoon disturbance.

Our data showed that fast growers could remain as large trees (reproductively mature trees) significantly longer than slow growers when large disturbances were absent (Figure 8). This might suggest that fast growers contribute disproportionately to population increases compared with slow growers (Rozendaal et al., 2010; Zuidema et al., 2009). Zuidema et al. (2009) used a population matrix approach to show that fast growers have much stronger effects on the population growth rate than slow growers. Indeed, this is the case if trees can produce offspring that can survive and regenerate. Although almost all large trees that reached the canopy layer in 1966 survived (Figure 7a) and probably produced a certain number of seeds over 23 years in the pre-typhoon subperiod, no recruitment of *C. cuspidata* trees was observed in this subperiod. The acorns of *C. cuspidata* do not remain dormant for long periods, and this species does not form a seed bank in soil (Hiroki & Matsubara, 1982). Some tree species make seedling or sapling banks (Abe & Yamada, 2008; Yamada & Suzuki, 1996, 2004), but we were unable to find seedlings and saplings smaller than 4.5 cm in dbh in the plot before the typhoon (T. Yamada, Hiroshima University, unpublished observation). This, coupled with the lack of seed production observed, suggests that their contribution to the population growth rate was zero in this subperiod.

Seed production in the typhoon disturbance and/or the post-typhoon subperiods may have played a more significant role in changes in population size over time in

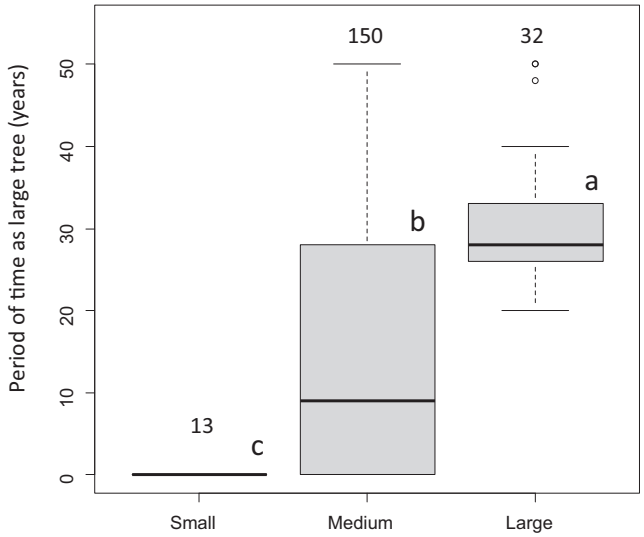



**FIGURE 8** Period of time as a large tree (dbh ≧ 25.0 cm) for large, medium-sized, and small trees in 1966 for *Castanopsis cuspidata* in a Japanese warm-temperate forest. Shown are the median (horizontal line), interquartile range (box), data range (whiskers), and outliers (circle). Different letters above the boxes indicate significant differences among size categories within a subperiod (pairwise Wilcoxon rank-sum tests with the Benjamini–Hochberg correction, $p < 0.001$). Numbers above the boxes show the sample sizes.

this species than in the pre-typhoon subperiod because more recruits were observed after the disturbances, and they were assumed to have mostly originated from seeds. For this reason, larger trees in the typhoon disturbance and the post-typhoon subperiods contributed more to population growth than trees that were large in the pre-typhoon subperiod but died during disturbances. Larger and survivor trees from the pre-typhoon subperiod might have had an advantage because they can produce seeds immediately after the typhoon disturbance; by contrast, medium-sized trees might have needed some time after the disturbance to attain reproductive size, which would result in a delay in seed production. Therefore, the hypothesis that fast growers played a more significant role in sustaining populations than slow growers (Brienen et al., 2006; Zuidema et al., 2009) was only supported for survivor trees but not for dead trees in the presence of disturbance. It would be premature to conclude that fast growers always play a more significant demographic role than slow growers in this species. However, this conclusion is based solely on demographic rates like growth rate, survival rate, and recruitment rates. To fully evaluate the importance of fast growers in population growth rates, an analysis of population growth rate using population model (Zuidema et al., 2009) is obviously needed.

Approximately 88.8% of large trees in 2015 (16 out of 18 trees) were medium-sized trees in 1966, suggesting that large trees were almost completely replaced over a 49-year period. The maximum attainable size (in dbh) of this species in Japan is over 100 cm. These large *C. cuspidata* trees might have survived for more than a few hundred years. Therefore, the 18 large trees potentially have the opportunity to keep producing seeds for more than 100 years if they can survive future disturbances. They might thus greatly contribute to sustaining populations. Continued monitoring efforts are needed to clarify the future population dynamics of *C. cuspidata* and distinguish between general patterns and exceptions relating to the contribution of fast-growing trees to population dynamics.

The fast–slow continuum is a typical life historical variation among trees (Rüger et al., 2018; Salguero-Gómez et al., 2016). However, surprisingly few is known as the concrete theoretical foundations underlying it. Further studies linking the fast–slow continuum with other ecological traits like life span, survival, and reproduction are needed (Rüger et al., 2018). Also, the plasticity of growth rate within a species, which may relate to environmental factors, should be uncovered.

Japan was projected to experience more numbers of more intense typhoons in future (Yoshida et al., 2017). This study showed that typhoons play a key role in the growth and regeneration of *C. cuspidata*. Because *C. cuspidata* is a predominating tree species in many Japanese warm-temperate forests, enhanced frequency and intensity of typhoon in future may affect the population dynamics of this species and forest ecosystem severely. Further study is needed to attempt assessments of future impacts of typhoon on the forests.

## AUTHOR CONTRIBUTIONS

Toshihiro Yamada, Masahiro Nagano, and Hisayuki Maenaka designed the study. Toshihiro Yamada wrote the manuscript, and the others edited it. All authors played key roles in fieldwork. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Yamada et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.tx95x6b3q.

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## SUPPORTING INFORMATION

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