Chapter 7
Coexistence of Tree Canopy Species

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Abstract The canopy tree species *Fraxinus platypoda*, *Pterocarya rhoifolia*, and *Cercidiphyllum japonicum* coexist at the Ooyamazawa riparian forest research site. In this chapter, we clarify the coexistence mechanisms of riparian tree species as they pertain to disturbance regimes, life-history strategies, and responses to environmental factors. Reproductive strategies, e.g., seed production and germination, differ widely among these three species and we observed probable reproductive trade-offs in each species. Canopy-height individuals of *F. platypoda* are recruited from advanced saplings, and *P. rhoifolia* and *C. japonicum* both established following large-scale disturbance events. Basal sprouting, i.e., vegetative reproduction, is likely the mechanism by which *C. japonicum* survives and attains co-dominance in riparian forests. *F. platypoda* had greater shade and water tolerance than the other two species. Each of these species is well-adapted to the various disturbances typical of riparian zones. Therefore, the coexistence mechanisms among them are likely a combination of random chance and niche partitioning.

Keywords Coexistence · Disturbance regime · Germination · Life history · Reproductive strategy · Seed production · Seedling survival · Shade tolerance · Vegetative reproduction · Water tolerance

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7.1 Introduction

Natural disturbances and life-history characteristics are key factors influencing the coexistence of tree species (White 1979; Loehle 2000). Disturbances in riparian areas are dynamic and vary more widely in type, frequency, and magnitude compared with those on hillsides. Various disturbance regimes in riparian areas lead to heterogeneous topography (Gregory et al. 1991; Kovalchik and Chitwood 1990) due to repeated destruction and regeneration of riparian forests.

Fraxinus platypoda, *Pterocarya rhoifolia*, and *Cercidiphyllum japonicum* (Fig. 7.1) are the dominant tree species in the riparian forests of the Chichibu

Fig. 7.1 The three dominant canopy tree species in the Ooyamazawa riparian forest of the Chichibu Mountains in central Japan

Mountains in central Japan (Maeda and Yoshioka 1952; Sakio 1997). One such riparian forest, along the Ooyamazawa stream, is an old-growth forest whose high-elevation trees have not been affected by human impacts, e.g., logging or erosion control works (Chap. 1), and are therefore valuable. The dominant canopy tree species in this forest is *F. platypoda*, followed by *P. rhoifolia* and *C. japonicum*.

The life-history characteristics and regeneration processes of these three canopy tree species were explained in detail in Chaps. 2, 3 and 4. In this chapter, we clarify the coexistence mechanism of riparian tree species in terms of disturbance regimes, tree life-history strategies, and responses to environment factors.

7.2 Seed Production

All three dominant canopy species in the Ooyamazawa riparian forest produce wind-dispersed winged achenes (Fig. 7.2). The average dry weights (mean ± standard deviation [SD], $n = 20$) of the fruit of *F. platypoda*, *P. rhoifolia*, and *C. japonicum* are 144 ± 24, 90 ± 11, and 0.82 ± 0.15 mg, respectively. The dry weights (mean ± SD, $n = 20$) of their seeds are 80 ± 17, 70 ± 8, and 0.58 ± 0.14 mg, respectively (Sakio et al. 2002).

The seeds of these three species are released according to different schedules, from autumn to winter (Fig. 7.3).The seeds of *P. rhoifolia* are released in October, whereas those of *F. platypoda* are released in November, during leaf fall. *C. japonicum* seeds are released after leaf fall, from November until spring of the

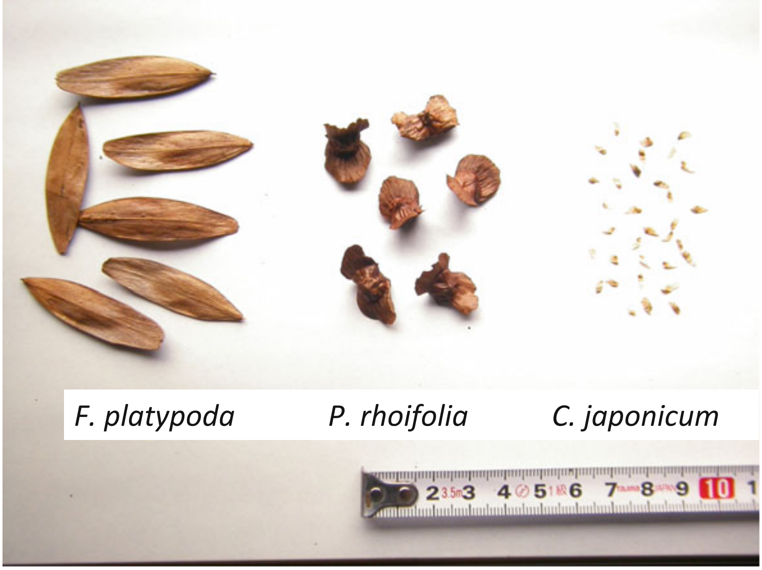
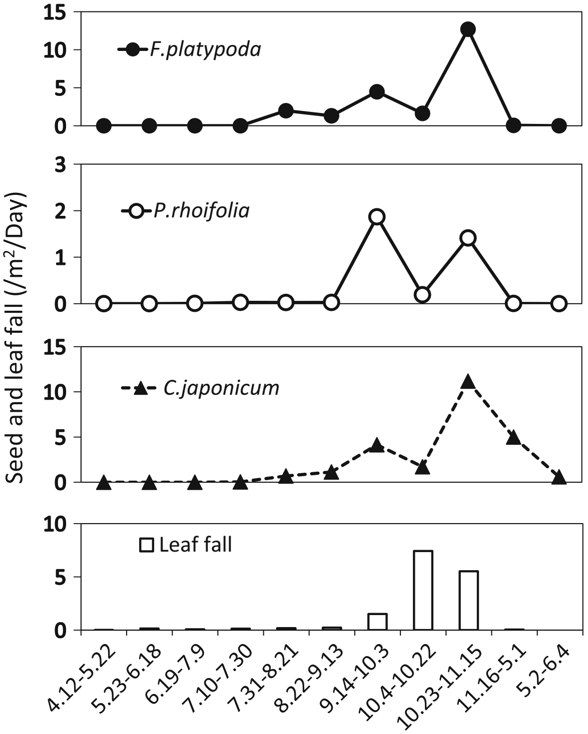


Fig. 7.2 Seeds of the three riparian species

Fig. 7.3 Seed dispersal of the three riparian species and leaf fall in 2002. Leaf fall includes all tree species



following year. The dispersal distances of *P. rhoifolia* and *F. platypoda* are similar, extending to several tens of meters. In contrast, the significantly lighter seeds of *C. japonicum* (Welch's *t*-test, $P < 0.001$) are dispersed over hundreds of meters, with the maximum dispersal distance recorded being 302 m (Sato et al. 2006).

Secondary dispersal of *F. platypoda* seeds can also occur via water, implying an adaptation for waterborne fruit dispersal. We have observed many *F. platypoda* seeds being transported by the flow of mountain streams during mast seed years (Chap. 2); this process allows the establishment of many seedlings on the gravel banks of mountain streams in the following year (Fig. 7.4).

Annual fluctuation in seed production varies among tree species. Generally, late successional species have large seeds and irregular fruiting behavior, whereas pioneer species have small seeds and regular fruiting. *F. platypoda* had non-mast years in 1997, 2001, 2003, 2005, and 2015, and mast years in 1996, 1998, 2002, 2004, 2006, and 2016 (Fig. 7.5). Thus, this species exhibits irregular fruiting behavior, as has also been observed in *Fraxinus excelsior*, which is native throughout mainland Europe (Tapper 1992, 1996). Seed production also fluctuates annually in *P. rhoifolia*, which had non-mast years in 1996, 2006, and 2008, and mast years in 2005, 2007, and 2011. In contrast, *C. japonicum* produces regular amounts of seeds every year, with only slight fluctuation. Among these three species, *F. platypoda* had

Fig. 7.4 Current-year *F. platypoda* seedlings germinated at the stream edge. Some seedlings are submerged

the largest coefficient of variation (CV) of seed production (0.97), followed by *P. rhoifolia* (0.87) and *C. japonicum* (0.48).

7.3 Seedling Germination and Growth

7.3.1 Germination Sites

Seeds of the three species germinate from mid-May to early summer of the year following seed production. Buried seeds in Ooyamazawa riparian forest soil germinated no *F. platypoda* seeds, one *P. rhoifolia* seed, and 12 *C. japonicum* seeds in 30 L of soil (Kubo et al. 2008). Seeds of *P. rhoifolia* and *C. japonicum* have exhibited dormancy in nursery seedling tests; in particular, *P. rhoifolia* seeds have successfully germinated 2 years after sowing.

Germination sites differ among the three species (Fig. 7.6). Figure 7.6 shows the results of a survey conducted in a year following a poor year for *F. platypoda* seed production (all seedlings aged >1 year). But, in the following year, a mast year, *F. platypoda* seeds germinated in all environments. *F. platypoda* can germinate in forest floor environments varying in light, substrate, and water conditions, including at water edges, under herb cover, and on steep slopes and gravel. Most *F. platypoda* seedlings that germinate in the litter layer die due to fungal damage and lack of moisture; however, some individuals survive for several years (Chap. 2). Current-year seedlings have a very high survival rate on the gravel banks of mountain streams, where herbaceous vegetation is rare. *F. platypoda* seedlings are highly shade-tolerant and tend to concentrate in former stream channels and small gravel deposits (Sakio 1997). When a canopy gap forms, thus improving the light environment, *F. platypoda* seedlings begin to grow into canopy trees.

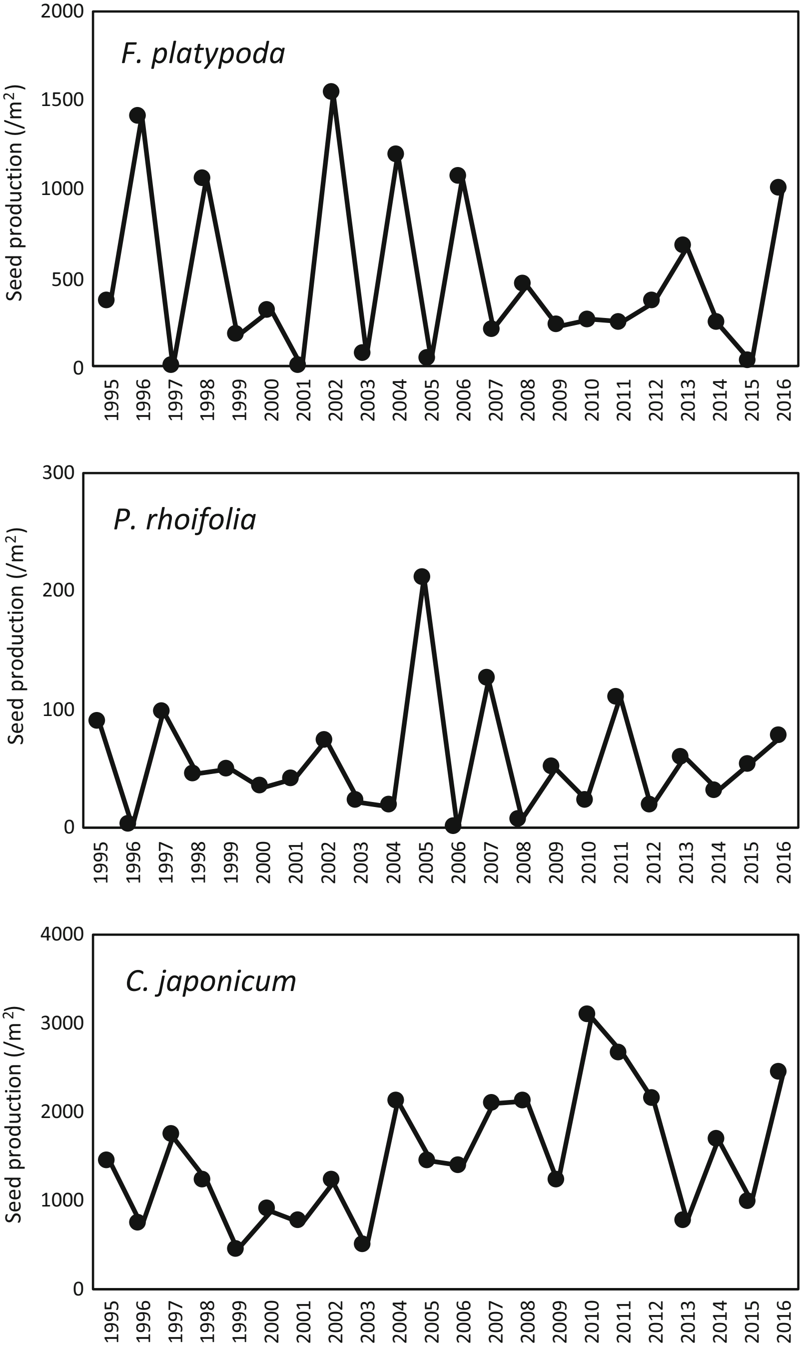


Fig. 7.5 Annual fluctuation of seed production in the three riparian species from 1995 to 2016

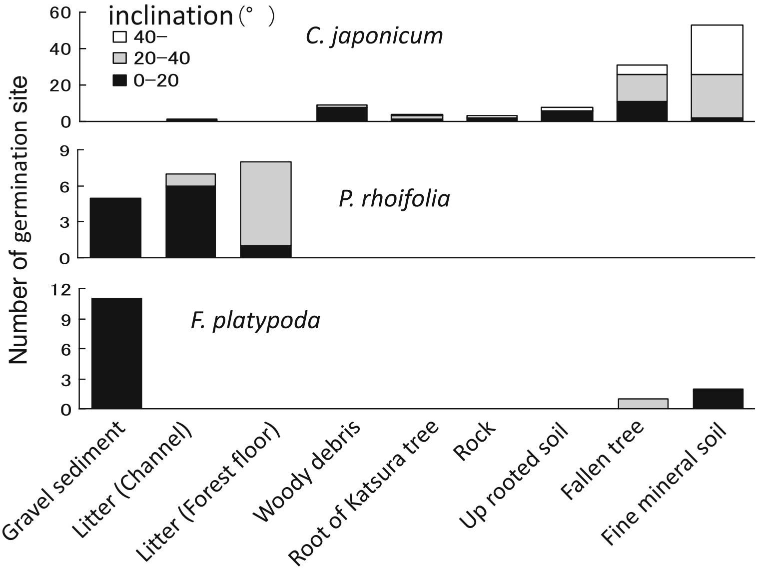


Fig. 7.6 Seed germination sites of the three riparian species (Kubo et al. 2000)

P. rhoifolia can also germinate in any environment, except on steep slopes due to unstable substrates. *P. rhoifolia* germination has been observed under closed canopies, and in gravel deposits and the litter layer; however, seedlings that germinate in the litter layer die within 1–2 months of germination (Sakio et al. 2002). Surviving individuals develop true leaves, but their growth is greatly affected by light availability. *P. rhoifolia* seedlings are affected by herbal pressure, even in canopy gaps; they require a brighter environment for survival than *F. platypoda* and may show arrested tree growth in low-light environments (Kisanuki et al. 1995).

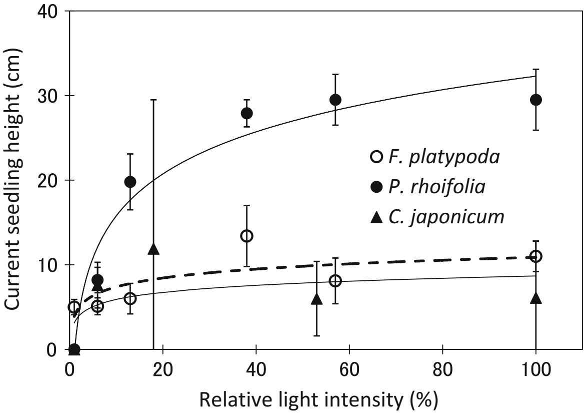
In contrast, *C. japonicum* seeds germinate in a limited range of environments. Most *C. japonicum* seedlings have been found in fine mineral soil and on fallen logs. Seedling emergence of small-seeded species is generally reduced in litter deposits (Seiwa and Kikuzawa 1996); the germination and establishment of small-seeded species, such as birch (*Betula platyphylla* var. *japonica*), is promoted in fine-grained soil (Koyama 1998). These factors also appear to affect *C. japonicum* seed germination. Germination begins in mid-May; however, seedlings can be washed away by surface sediment movement during the rainy and typhoon seasons, with a survival rate of $<10\%$ in late October. This rate is higher at sites with high illuminance, and seedlings found in such environments have been reported to be significantly larger than those in low-light environments (Kubo et al. 2000). Similar results were obtained in a germination experiment examining the effects of soil and relative photosynthetic effective photon flux density on germination in a nursery (Kubo et al. 2004).

7.3.2 Seedling Shade Tolerance

The light environment is among the most important factors for plant growth. Plant responses to light differ among plant species. Pioneer species require more light than late successional species. In forests, canopy gap formation strongly affects light conditions. Improvement of the light environment by gap formation is an important factor for growth from seedling to canopy tree (Suzuki 1980, 1981; Nakashizuka and Numata 1982a, b; Nakashizuka 1983, 1984). For seedlings that have established under the canopy, a lack of canopy gap formation within a few years will result in decreased growth and, eventually, death. If an individual establishes under a small canopy gap, and that gap closes due to branch extension within the surrounding canopy, the individual will be unable to survive.

We compared the effects of light conditions on the growth of seedlings of the three Ooyamazawa riparian species in a nursery. *P. rhoifolia* had the fastest growth rate, growing to 30-cm seedlings within 1 year, whereas *F. platypoda* and *C. japonicum* seedlings measured about 10 cm (Fig. 7.7). However, since *C. japonicum* seeds are much smaller than those of *F. platypoda* (Fig. 7.2), its relative growth rate was very high. *P. rhoifolia* seedling growth decreased sharply under nursery light conditions (<20% of outdoor sunlight), and failed to survive in 1% light. Similarly, *C. japonicum* seedlings did not survive at 1% light. In contrast, all *F. platypoda* seedlings survived for 1 year at 1% light (Fig. 7.7; Sakio 2008). A study conducted at the Ooyamazawa riparian forest research site showed that branch growth was dramatically faster in 1-m-tall *P. rhoifolia* saplings than in *F. platypoda* saplings of the same height beneath a canopy gap (Sakio 1993). At a seedling size of <1 m, *F. platypoda* grew in lower light environments than *P. rhoifolia* and *C. japonicum* at the same research site (Kubo et al. 2000).

Fig. 7.7 Relationship between growth and relative light intensity for current-year seedlings grown in nursery beds for 1 year (Sakio 2008)



7.3.3 Seedling Water Tolerance

Trees in riparian areas are always exposed to a moist environment at the water's edge, and seedlings that have germinated on the gravel banks of mountain streams are affected by flooding during the rainy and typhoon seasons (Fig. 7.4). Water tolerance thresholds differ greatly among the three riparian species. Submergence experiments, in which 1-year-old seedlings were submerged to the soil surface for 1 year (Sakio 2005) and current-year seedlings were submerged for different periods (Fig. 7.8; Sakio 2008), showed that *F. platypoda* has much higher water tolerance

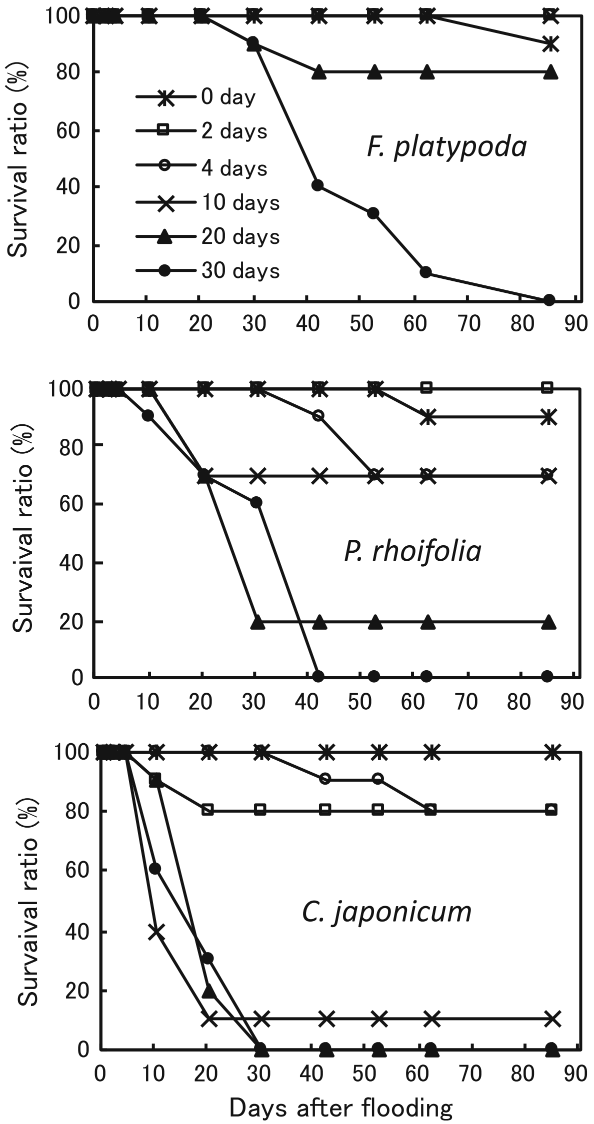


Fig. 7.8 Flooding survival rates of current-year seedlings of the riparian species

than do *P. rhoifolia* and *C. japonicum*. Dry weight was significantly lower in submerged 1-year-old *P. rhoifolia* and *C. japonicum* seedlings than in control individuals; moreover, 80% of *F. platypoda* current-year seedlings survived 20 days of submergence, whereas only 20% of *P. rhoifolia* seedlings survived, and all *C. japonicum* seedlings died. The superior water tolerance of *F. platypoda* may be one reason explaining its dominance in Ooyamazawa riparian forests.

7.4 Sprouting

All three riparian tree species exhibit reproduction by sprouting, with most *F. platypoda* producing single trees (Fig. 7.9; Sakio et al. 2002). *P. rhoifolia* produces intermediate numbers of sprouts; *C. japonicum* produces the most sprouts, with a maximum of 60 observed from one tree. In *C. japonicum*, sprout number was positively correlated with the diameter at breast height (DBH) of the main stem. The role of the *C. japonicum* sprouts is maintenance of the individual; this has also been observed in *Euptelea polyandra*, which maintains individuals by sprouting in areas frequently disturbed by landslides (Sakai et al. 1995). However, it remains unknown whether the sprouting mechanism of *C. japonicum* is related to physical damage to the individual, physiological responses to changes in the light environment, or tree age. In *P. rhoifolia*, sprouting does not play a role in maintenance of the individual in Ooyamazawa riparian forests, although such maintenance by sprouting has been observed in *P. rhoifolia* growing in environments characterized by heavy snow (Nakano and Sakio 2017, 2018).

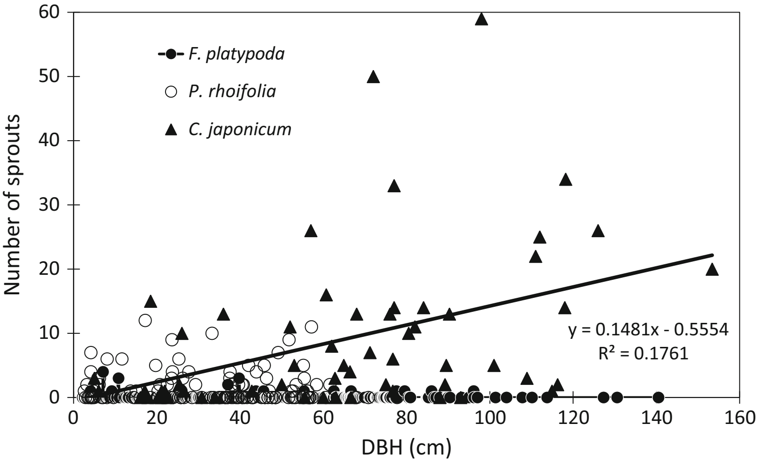


Fig. 7.9 Relationship between the diameter at breast height (DBH) of the main stem and sprout number for each individual of the three riparian species (Sakio 2008)

7.5 Forest Structure

7.5.1 Size Structure

A survey of all living trees (DBH ≥ 4 cm) without sprouts in an area of 4.71 ha showed that the frequency distribution of DBH was similar between *F. platypoda* and *P. rhoifolia*, being characterized by many small individuals with DBH ≤ 10 cm or less (Fig. 7.10). *C. japonicum* exhibited a different DBH distribution, with only two saplings at DBH < 10 cm. Both *F. platypoda* and *P. rhoifolia* showed frequency distribution peaks around DBH = 40. Within a core plot (0.54 ha), there were 811 *F. platypoda*, 192 *P. rhoifolia*, and one *C. japonicum* individual with tree height ≥ 1 m and DBH < 4 cm. Many *F. platypoda* and *P. rhoifolia* seedlings with DBH < 4 cm were distributed beneath the canopy (Chaps. 2 and 3). These results demonstrate that *F. platypoda* and *P. rhoifolia* produce many advanced seedlings that will eventually become canopy trees.

7.5.2 Spatial Distribution and Age Structure

Figure 7.11 shows the spatial distribution of canopy trees (DBH ≥ 20 cm) and young trees (4 cm ≤ DBH < 20 cm) within the 4.71-ha research plot. Canopy and young trees of *F. platypoda* are dominant from upstream to downstream, whereas *P. rhoifolia* canopy trees are distributed in three patches (A, B, and C). Large patches of canopy trees can reach 50 m in diameter, each with an average tree age of about 90 years. These *P. rhoifolia* patches were topographically distributed on

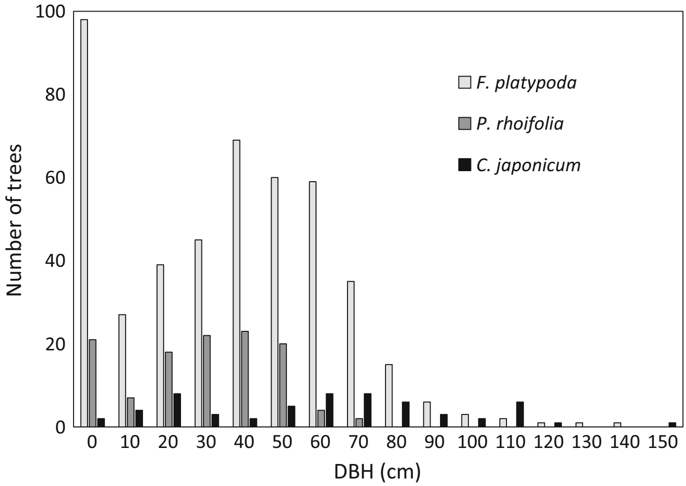


Fig. 7.10 DBH class distributions of the three riparian species (Sakio 2008)

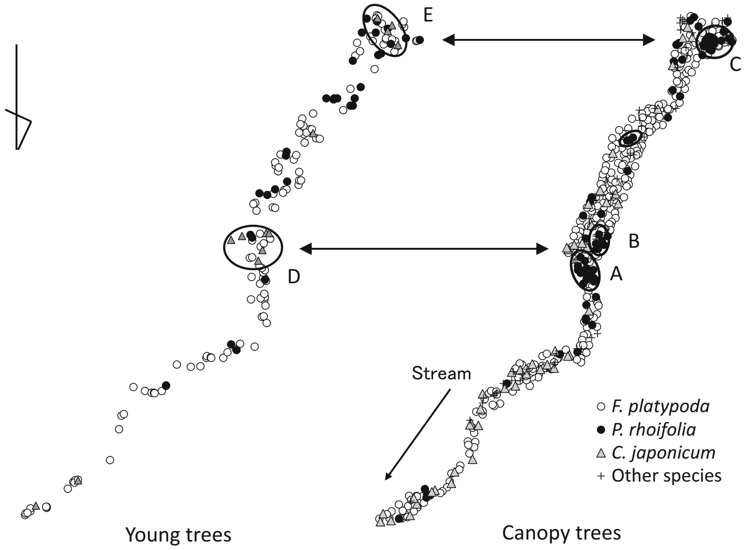


Fig. 7.11 Spatial distribution of young and canopy trees, including at the sites of two large-scale disturbances. *P. rhoifolia* canopy trees and young *C. japonicum* trees coexist at the same sites

large landslide or debris flow paths, suggesting that *P. rhoifolia* established in these large-scale disturbance sites at the same time (Sakio et al. 2002).

C. japonicum canopy trees are few in number and scattered randomly throughout the research area, although young trees showed aggregated distributions in and around *P. rhoifolia* patches (Fig. 7.11, D and E). At approximately 90 years, the ages of young *C. japonicum* and *P. rhoifolia* trees were similar; therefore, these two species are likely to have established at the same time.

7.6 Coexistence Mechanisms of the Three Species

The following coexistence mechanisms of canopy species in the Ooyamazawa riparian forest can be considered (Fig. 7.12).

In the Ooyamazawa riparian forest, *F. platypoda* regenerated to produce canopy trees through seedling establishment on large-scale disturbance sites, such as landslide and debris flow paths, as well as through the release of advanced forest floor seedlings upon the formation of small gaps. *F. platypoda* has higher shade tolerance than *P. rhoifolia* and *C. japonicum*, as demonstrated by seedling field studies and nursery experiments. *F. platypoda* also shows higher tolerance to submergence and flooding than *P. rhoifolia* and *C. japonicum*, and has adapted to germinate and grow on gravel stream banks.

The 4.71-ha research plot contained several large patches of *P. rhoifolia* with DBH of about 50 cm; these were established on the sites of large-scale disturbances

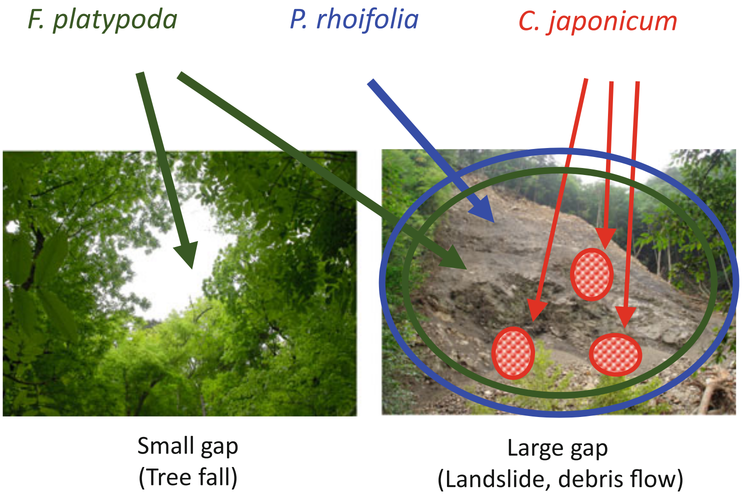


Fig. 7.12 Mechanism for the coexistence of three canopy tree species in the Ooyamazawa riparian area

that occurred about 90 years ago. Thus, *P. rhoifolia* regeneration sites are limited to large-scale disturbance sites where large gaps are formed by landslide or debris flow; the regenerants eventually became canopy trees, forming single-species patches.

Unlike *F. platypoda*, *C. japonicum* cannot form large cohorts of advanced seedlings on the forest floor beneath canopy trees. However, *C. japonicum* seeds can disperse into the large-scale disturbance sites favored by *P. rhoifolia*. The mass production of small wind-dispersed seeds increases the probability of reaching new germination sites cleared by large disturbances (Harper 1977; Augspurger 1984). Thus, *C. japonicum* regeneration in large-scale disturbance sites can co-occur with that of *P. rhoifolia*. In these disturbance sites, organic and inorganic matter such as fallen trees, boulders, soil, and sand are mixed together to form complex substrates. The diversity of microsites produced during this process ensures seed germination, seedling establishment, and growth of *C. japonicum*. Fine inorganic soils, which form in boulders and the cracks of fallen trees, are ideal substrates for *C. japonicum* germination and establishment. These substrates are less susceptible to erosion due to rainfall, such that seedlings can grow stably; if direct sunlight is weak, seedlings may continue to grow because strong light dries out these soils. Thus, *C. japonicum* waits for rare regeneration opportunities, which appear at the scale of decades or centuries; as a trade-off, the lifespan of the individual is prolonged. *C. japonicum* generates many sprouts around the main trunk. In *F. platypoda* and *P. rhoifolia*, the death of the trunk means the inevitable death of the individual; however, if the main trunk of *C. japonicum* dies, one of the many surrounding sprouts will grow to become the main trunk (Fig. 7.13). In this manner, once *C. japonicum* has established, it will survive for long periods by successively producing new trunks.

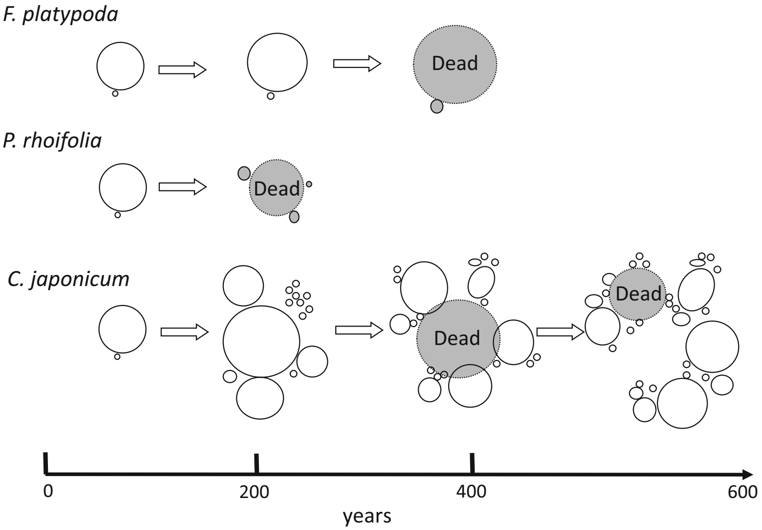


Fig. 7.13 Relationship between tree age and sprouting. In *F. platypoda* and *P. rhoifolia*, the death of the main trunk results in the death of the individual. In contrast, *C. japonicum* individuals are maintained by sprouting for long periods after the death of the main trunk

Therefore, *C. japonicum* trees represent a small population within the Ooyamazawa riparian forest, but this species sustainably coexists with both the shade-tolerant dominant species *F. platypoda* and the pioneer species *P. rhoifolia*.

7.7 Conclusion

The coexistence mechanisms of the three Ooyamazawa riparian canopy species involve a combination of niche partitioning and chance. The three species exhibit trade-offs in reproductive characteristics, e.g., seed size, quantity, and annual variation. Coexistence is generally maintained through niche partitioning, especially in the early life-history stages. Chance can also play an important role in *P. rhoifolia* and *C. japonicum* regeneration, through unpredictable large-scale, low-frequency disturbance. In conclusion, *F. platypoda*, *P. rhoifolia*, and *C. japonicum* are well-adapted to disturbances in the Ooyamazawa riparian zone throughout their life histories.

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