

Chapter 2

Fraxinus platypoda



Hitoshi Sakio

Abstract The ash species *Fraxinus platypoda* is the dominant canopy tree species at Ooyamazawa riparian forest. I investigated flowering, seed production, germination, seedling survival and growth, and structural measures in *F. platypoda*. Flowering and seed production demonstrated a clear masting pattern over a 28-year period. The seeds of *F. platypoda* germinated in most environments, but seedling survival was regulated by microtopographic factors. I suggest that gap formation processes may be vital to the establishment of canopy-height individuals. The overall forest structure and spatial distribution of *F. platypoda* suggested that all individuals of this species occurring at Ooyamazawa regenerated simultaneously following a large-scale disturbance event 200 years ago. Since this event occurred, saplings of *F. platypoda* have regenerated in canopy gaps. It is probable that *F. platypoda* succeeds as a dominant species in riparian forests by regenerating in response to disturbance at multiple scales.

Keywords Advanced sapling · Dioecy · Disturbance regime · Flowering · Germination · Life history · Microtopography · Reproductive strategy · Seed production · Seedling

2.1 Introduction

Native riparian forests are distributed along the Ooyamazawa stream in the Chichibu Mountains of the Kanto region, central Japan. In these forests, *Fraxinus platypoda* Oliv. (*Oleaceae*) is one of the dominant canopy tree species, coexisting with *Pterocarya rhoifolia* and *Cercidiphyllum japonicum*. The Chichibu Mountains harbor a very complex topography characterized by steep slopes, with tree diversity distributed among the resulting microhabitats. For example, *Tsuga sieboldii* and

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Chamaecyparis obtusa forests are distributed along ridges, *Fagus crenata* and *Fagus japonica* on mountain slopes, and *F. platypoda*, *P. rhoifolia*, and *C. japonicum* in valleys (Maeda and Yoshioka 1952; Tanaka 1985). The regeneration mechanisms of *T. sieboldii*, *F. crenata*, and *F. japonica* have been extensively studied by Suzuki (1979, 1980, 1981a, b), Nakashizuka and Numata (1982a, b) and Nakashizuka (1983, 1984a, b), and Ohkubo et al. (1988, 1996), respectively. These researchers examined forest regeneration within the context of gap dynamics theory. Gaps are open spaces within the forest canopy layer formed by die back, trunk breakage, and uprooted trees. In general, gaps occur on a small scale and are not often accompanied by soil disturbance, with the exception of uprooted trees.

On the other hand, disturbances within riparian zones vary in type, frequency, magnitude, and size compared to canopy gap formation on hillslopes. In steeper mountain regions, valley floor landforms are sculpted by fluvial processes and a variety of mass soil movement processes from tributaries and adjacent hillslopes (Gregory et al. 1991).

The ash species, *Fraxinus platypoda*, is a late successional species in riparian habitats of cool temperate forests distributed along the Pacific coast of Japan. This species is distributed from Tochigi Prefecture in the north to Miyazaki Prefecture in the south (Fig. 2.1). Kisanuki et al. (1992) and Ann and Oshima (1996) examined regeneration mechanisms within a gap dynamics framework in mixed forests of *F. Platypoda* and *P. rhoifolia*. However, the regeneration of *F. platypoda* may also be related to large-scale natural disturbances such as debris flows and landslides in the riparian zone. In this chapter, I present long-term research related to the life history and regeneration process of *F. platypoda* with respect to natural disturbances within the riparian zone.

2.2 Study Species

Fraxinus platypoda is a deciduous canopy species that can reach up to 40 m in height and 150 cm in diameter at breast height (DBH, 130 cm) (Fig. 2.2). This species is well adapted to stream disturbances that vary in frequency and size, and it dominates forests in riparian zones (Sakio 1997).

Branching occurs above the trunk of the tree. Most individuals have a single trunk and rarely exhibit sprouts, similar to species such as *P. rhoifolia* and *C. japonicum*. Leaves are impari-pinnate compound, consisting of 7–9 leaflets, and leaf length is about 25–35 cm and decussate-opposite (Fig. 2.3). The base of the petiole markedly bulges and holds the stem. Open hairs occur along the middle vein on the back of the leaf, but others are hairless. The apical leaflet is oblong-ellipsoid oblanceolate in shape, and is 8–20 cm in length and 3–7 cm in width, with a small petiole of 1–2 cm in length. The side leaflets lack a petiole, and the base is wedged with fine serrations. Twigs are thick, gray-brown, and hairless, and many are oval lenticel. The pith is thick. Branches grow rapidly in early spring and stop growing in June (Sakio 1993). The root system is concentrated in the shallow part of the ground surface. *Fraxinus*

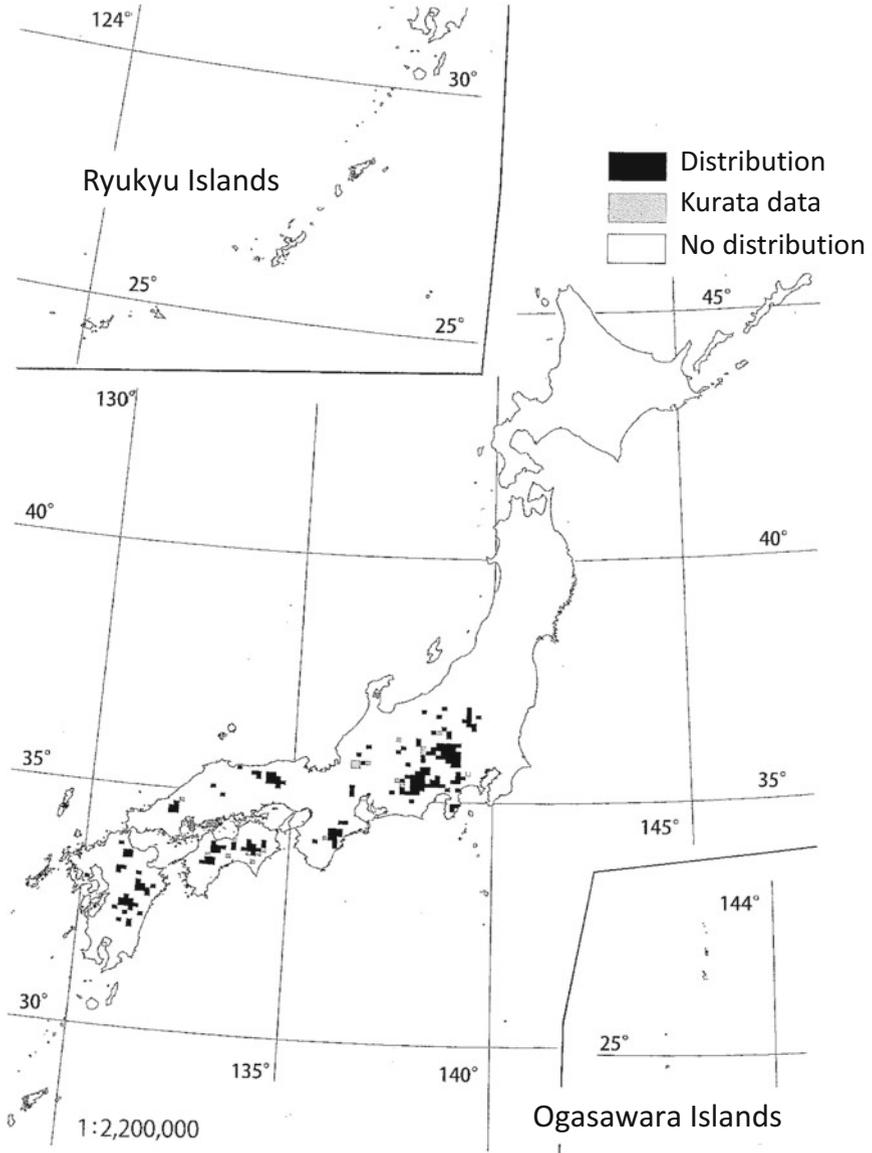


Fig. 2.1 Distribution of *F. platypoda*. Modified after Kawahara et al. (2009)

platypoda has medium to large-diameter straight roots and horizontal roots and is classified as a deep root type. Fine roots are dense, but root hairs are rare (Karizumi 1979). The species is easily uprooted by scouring running water. In saplings, sedimentation by soil and sand easily produces adventitious roots (Sakio 2002).

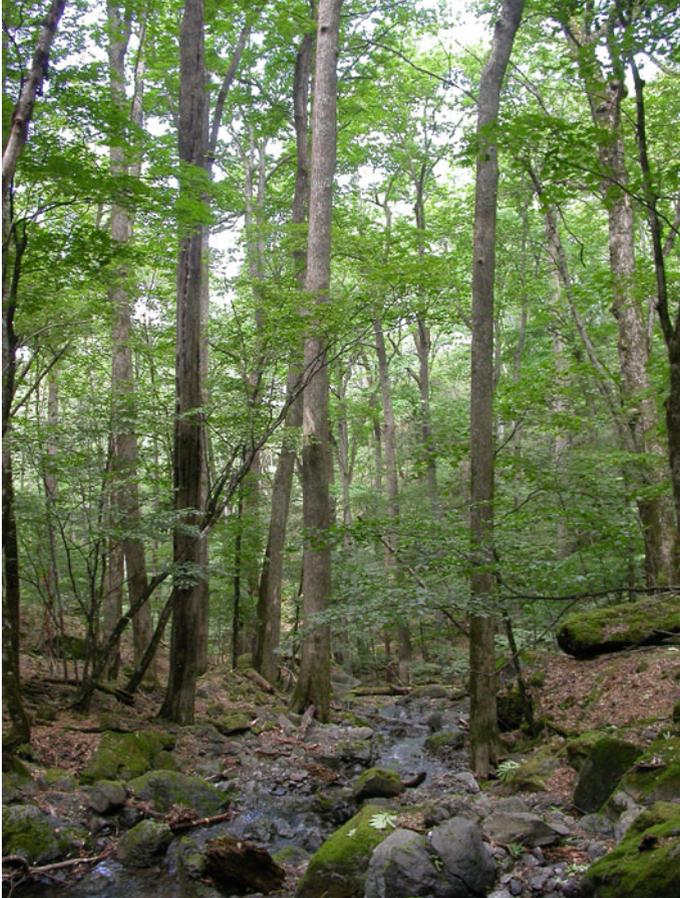


Fig. 2.2 *F. platypoda* forest in the Ooyamazawa riparian forest

2.3 Reproductive Traits

2.3.1 Flower

Sexual expression of *F. platypoda* is not obvious. The species exhibits two morphological types: one with male flowers and the other with hermaphrodite flowers (Fig. 2.4). Both flowers lack a perianth. Male flowers have one stamen with a pair of anthers, while hermaphrodite flowers have one pistil with a pair of anthers. Whether the male portion of hermaphrodite flowers of *F. platypoda* is functional is unknown. However, sexual expression of *F. platypoda* may be functionally considered to be androdioecy, as the pollen of hermaphrodite flowers exhibits germination ability. Because the breeding characteristics of *F. platypoda* are not clearly understood, I



Fig. 2.3 Leaves of *F. platypoda*



Hermaphrodite flower



Male flower

Fig. 2.4 Two types of flowers of *F. platypoda*

treat the sexual expression of *F. platypoda* as dioecy, i.e., female trees and male trees, in this chapter.

The timing of flowering in *F. platypoda* differs depending on altitude but, typically, occurs in mid-April (700 m a.s.l.) to mid-May (1500 m a.s.l.). In the Ooyamazawa riparian forest (1500 m a.s.l.), flowering occurs from the beginning of May to mid-May. However, the exact timing fluctuates annually.

Flowering data collected over 28 years have demonstrated clear fluctuations of flower values for *F. platypoda* in the core research plot (Fig. 2.5). The numbers of female and male trees in the core plot (0.54 ha) were 26 and 20, respectively. The rank of flowering for female and male trees was scored from 1 to 5 by observation using binoculars. The average flowering rank of all individuals was 3.22 for females

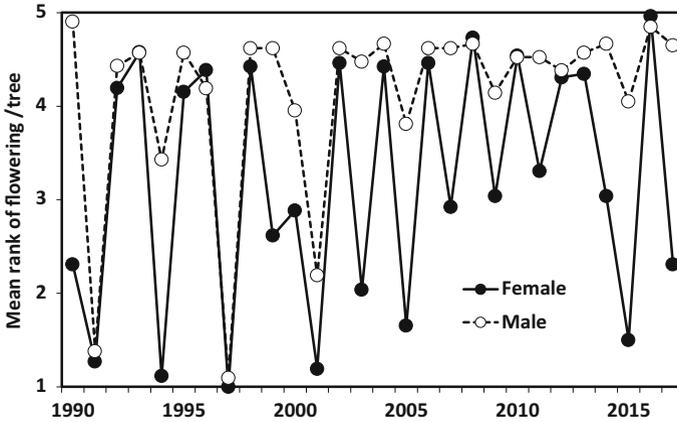


Fig. 2.5 Mean rank of flowering of female and male trees of *F. platypoda* from 1990 to 2017. The numbers of female and male trees were 26 and 20, respectively

and 4.11 for males; values were significantly higher in males. The coefficient of variation (CV) was 0.48 for females and 0.28 for males; values were significantly higher in females. In this forest, although the flowering interval was 2–3 years, the interval changed over the 28 years. The flowering of the two sexes exhibited clear synchronization until 2002, but synchronization ceased thereafter. After 2002, more males have flowered every year, while females have retained a distinct interval. The change in flowering fluctuation after 2002 may have been driven by external factors, such as climate warming.

2.3.2 Seed Production

After flowering, fruit (samara) of *F. platypoda* continues to grow, causing abortion. The pericarp finishes growing at the end of August, at which point seeds begin to grow. Oven-dried matured fruit of *F. platypoda* weighed 144 ± 24 mg, and the dry weight of seeds was 80 ± 17 mg (Fig. 2.6; Sakio et al. 2002). Seeds mature in mid-October and are dispersed by wind and stream water in November (Fig. 2.7). Many mature seeds occur in mast years, but a large number of seeds are empty or insect-damaged during non-mast years.

Clear fluctuations in seed production and flowering of *F. platypoda* occurred over the 28 years (Fig. 2.8). Because seed production was strongly positively correlated with the extent of flowering, the former is presumed to be regulated by the latter (Fig. 2.9).



Fig. 2.6 Fruits and seeds of *F. platypoda* in autumn

2.4 Germination

The seeds of *F. platypoda* germinate from the end of June to mid-July. Current-year seedlings are found on litter, gravel, mineral soil, and fallen logs, except after non-mast years. As long as the light environment is not very strong, current-year seedlings of *F. platypoda* only have cotyledons (Fig. 2.10), and the true leaf does not expand during the germination year. The germination site of *F. platypoda* is not strongly restricted by the soil and light environment, unlike *C. japonicum*, whose germination sites are limited. *F. platypoda* does not exhibit seed dormancy. The seeds of *F. platypoda* produced in autumn germinate in the early summer of the following year and do not germinate thereafter.



Fig. 2.7 Fruits of *F. platypoda* in the stream in autumn (Sakio 2008)

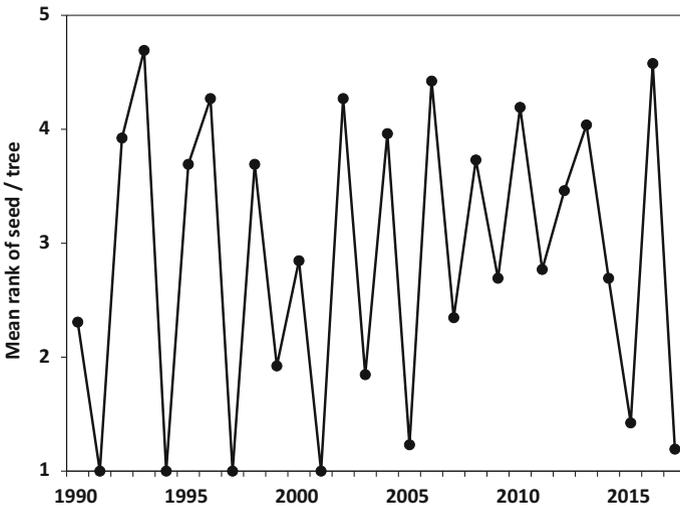


Fig. 2.8 Mean rank of seed production of *F. platypoda* from 1990 to 2017

2.5 Seedling Survival

The seeds of *F. platypoda* are randomly dispersed. Therefore, the distribution of current-year seedlings of *F. platypoda* is not affected by microenvironments such as soil and light conditions. However, the distribution pattern of seedlings of *F. platypoda* changes with the growth of seedlings, shifting from random or uniform

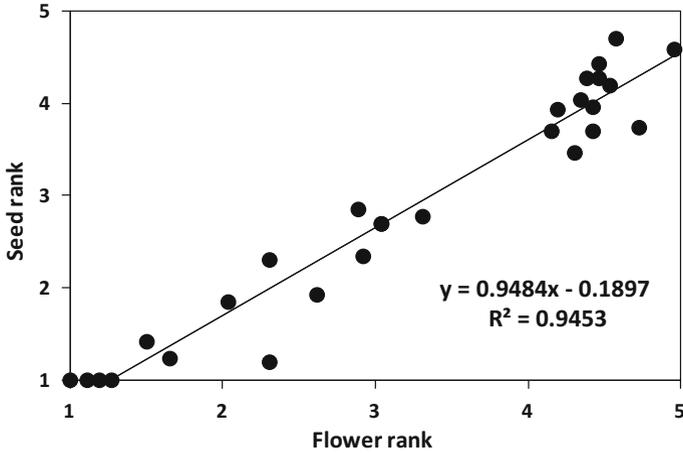


Fig. 2.9 Relationship between flower and seed rank



Fig. 2.10 Current seedling of *F. platypoda*

distribution to aggregated throughout growth (Fig. 2.11). Small-sized seedlings (height < 20 cm) tend to be distributed around the active channel (Figs. 2.11 and 2.12), while the distribution of larger seedlings (20 cm \leq height < 1 m) is more closely related to the microtopography than to canopy gaps. These larger seedlings tend to be aggregated in abandoned channels. On hillslopes where the forest floor vegetation is dense, *F. platypoda* seedlings disappear after several years due to the effects of shade. The mean longevity of *F. platypoda* seedlings in various environments is 1.19 ± 0.58 years (Sakio et al. 2002). On the other hand, seedlings near

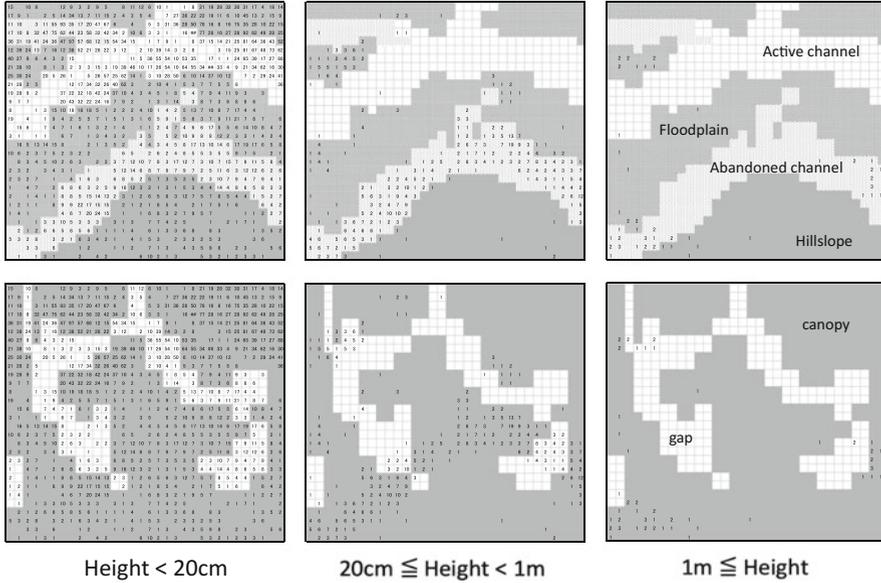


Fig. 2.11 Distribution of *F. platypoda* seedlings. Upper and lower graphs show the relationship with microtopography and canopy gaps, respectively. The six plots in the figure are each 30×32 m, and numbers indicate the number of individuals in 1 m^2



Fig. 2.12 Advanced sapling communities of *F. platypoda* along the stream

active channels exhibit long life spans and high density due to the absence of forest floor vegetation (Fig. 2.11). However, seedling communities can be destroyed by flooding, often caused by large typhoons. Gravel deposits formed during flooding

events can serve as new seedling establishment sites. When the seedling community stabilizes due to channel fluctuations, it continues to grow into a large-sized seedling community ($20\text{ cm} \leq \text{height}$).

In other words, the distribution of *F. platypoda* seedlings is regulated by the microtopographic variation in forest floor vegetation. In riparian forests, the light environment depends not only on the presence of canopy gaps but also on gaps in the forest floor vegetation due to stream disturbance. The dynamics of *F. platypoda* seedlings are thought to be strongly influenced by the latter.

2.6 Seedling Growth

Large-sized seedlings ($1\text{ m} \leq \text{height}$) that have established on stable sites exhibit variation in growth rates depending on the light environment. New shoots of *F. platypoda* begin to elongate rapidly in early spring and stop growing in June (Sakio 1993). Seedlings under canopy gaps grow faster than seedlings under the canopy (Fig. 2.13) and have more leaves. In many forests, canopy gaps appear to be necessary for the growth of canopy trees (Suzuki 1980, 1981a; Nakashizuka and Numata 1982a, b; Nakashizuka 1983, 1984a). Therefore, even in riparian forests, gap formation via the death of canopy trees may be necessary for seedlings of *F. platypoda* to grow into the canopy.

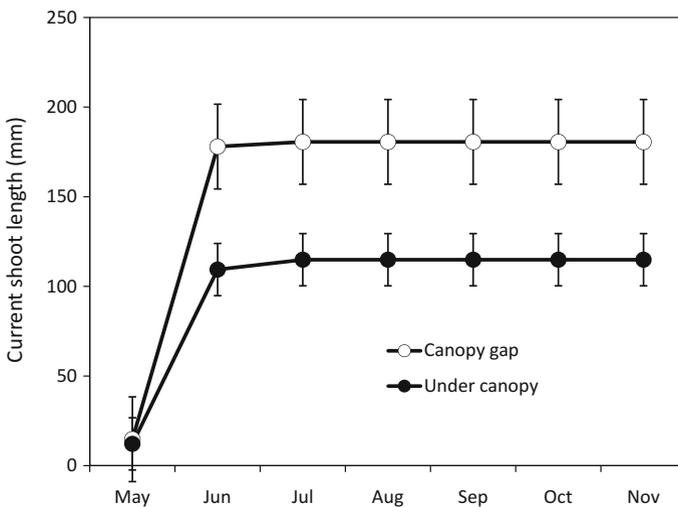


Fig. 2.13 Seasonal changes of current shoot lengths of *F. platypoda* saplings in canopy gaps and under the canopy. Modified after Sakio (1993)

2.7 Forest Structure and Spatial Distribution

In the 4.71-ha study plot within the Ooyamazawa riparian forest, we observed 418 *F. platypoda* individuals out of a total of 2214 trees ($4 \text{ cm} \leq \text{DBH}$) (Sakio et al. 2002). Canopy trees, subcanopy trees ($10 \text{ cm} \leq \text{DBH}$), and the shrub layer ($\text{DBH} < 10 \text{ cm}$) accounted for 304, 59, and 55 individuals, respectively. The mean DBH of *F. platypoda* canopy trees was $56.9 \pm 19.0 \text{ cm}$, with a maximum of 140.5 cm (Sakio et al. 2002). The DBH distribution of *F. platypoda* was continuous from saplings to large canopy trees (Fig. 2.14). *F. platypoda* exhibited two peaks in DBH distribution: one formed by small trees ($\text{DBH} < 10 \text{ cm}$) and the other formed by the 40-cm DBH class. These data suggest that *F. platypoda* maintains sapling banks. The peak of the 40-cm class suggests synchronous regeneration caused by a large-scale disturbance. The relative density of dominant canopy trees of *F. platypoda* is high and does not exhibit distinct fluctuations along the stream.

In the core plot ($60 \times 90 \text{ m}$), one peak of *F. platypoda* individuals occurred within the 40–60-cm DBH class, similar to the pattern observed in the 4.71-ha plot (Sakio 1997). In addition, increment cores of all *F. platypoda* individuals larger than 4-cm DBH were obtained using an increment borer in November 1998, in the core plot. The age distribution of *F. platypoda* individuals was continuous from saplings to older canopy-aged trees (Sakio 1997). Figure 2.15 presents the spatial distribution of tree age for *F. platypoda* in the core plot. The age of most individuals was aggregated around 200 years, but several young aggregated groups also occurred (e.g., small patches A, C, and F). These results suggest that a large-scale disturbance occurred around 200 years ago in the Ooyamazawa riparian forest and that *F. platypoda* regenerated simultaneously. Since that time, *F. platypoda* advanced saplings have regenerated under canopy gaps. Thus, *F. platypoda* is likely to become

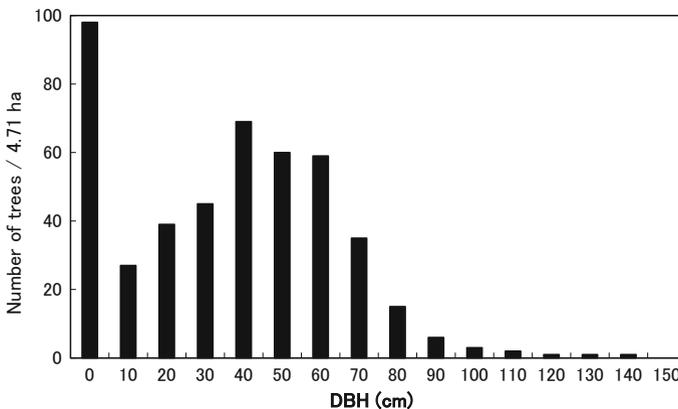


Fig. 2.14 DBH distribution of *F. platypoda* individuals in the Ooyamazawa riparian plot (4.71 ha). Only individuals over 4 cm in DBH were measured. Modified after Sakio (2008)

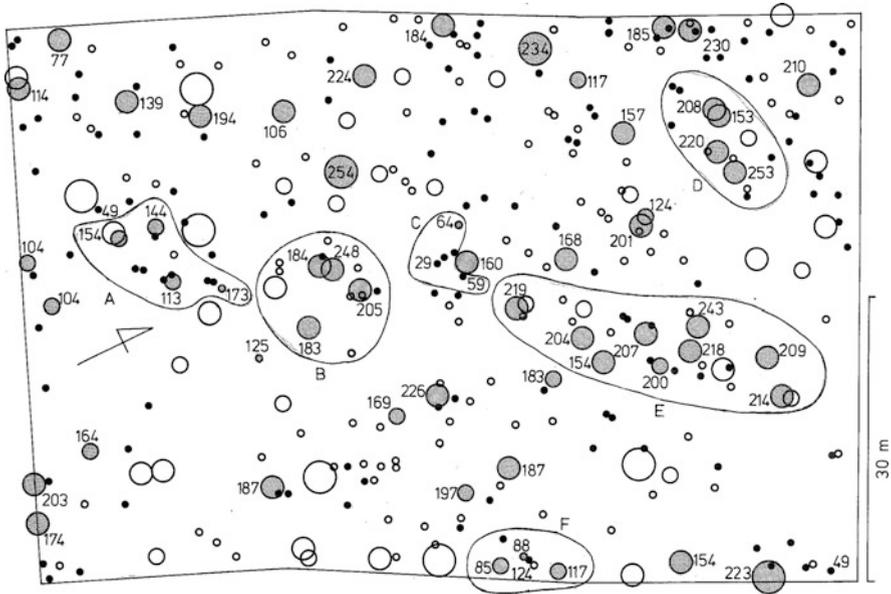


Fig. 2.15 Spatial distribution of *F. platypoda* individuals in the core plot (60 × 90 m). Numbers show the age of *F. platypoda* individuals. The size of circles reflects the DBH. Gray and black circles show *F. platypoda* individuals, and open circles show other species

an overwhelmingly dominant species within the basin because it can regenerate within sites of large-scale disturbance as well as within small gaps.

2.8 Conclusion

Fraxinus platypoda produces a large number of seeds once every few years, thus forming young advanced sapling communities within various microtopographic habitats. In particular, advanced sapling communities are formed in gravel deposits along mountain streams. These sapling communities continue to be regenerated after repeated destruction by mountain stream disturbances and subsequent regeneration on new gravel deposits. After large disturbances, *F. platypoda* regenerates within all river basins and also fills canopy gaps by advanced saplings when small gaps are formed. Thus, *F. platypoda* succeeds as a dominant species in riparian forests by regenerating in response to various scales of disturbances throughout its life history.

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