Chapter 3
Pterocarya rhoifolia

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Abstract *Pterocarya rhoifolia* is a dominant canopy species of the Ooyamazawa riparian area of central Japan. In this study, to clarify how the life history of *P. rhoifolia* has adapted to riparian disturbance, we investigated the seed production, seedling regeneration, sprouting, distribution pattern, and size structure of this species in the Ooyamazawa riparian area. Annual seed production by mature *P. rhoifolia* fluctuated between years, with seeds produced during most years from 1995 to 2014. *P. rhoifolia* diameter at breast height (DBH) showed continuous distribution from saplings to mature trees, with some peaks. *P. rhoifolia* trees formed patches of various sizes along streams, with large, high-density patches observed on large landslide deposits; stands on such patches were generally even in age. Although current-year *P. rhoifolia* seedlings were found on litter, gravel, mineral soil, and fallen logs, almost all such seedlings died within several years. We found up to 10 sprouts per *P. rhoifolia* individual, including a few large sprouts per stem; however, no significant correlation was detected between sprout number and the DBH of the main stem. Therefore, we conclude that *P. rhoifolia* populations are generally maintained by seedling regeneration following large riparian disturbances in the Ooyamazawa riparian area.

Keywords Japanese wingnut · Life history · Seed production · Seedling regeneration · Spatial pattern · Disturbance regime

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H. Sakio (ed.), *Long-Term Ecosystem Changes in Riparian Forests*, Ecological Research Monographs, https://doi.org/10.1007/978-981-15-3009-8_3

3.1 Introduction

The genus *Pterocarya* belongs to the family Juglandaceae and was once widely distributed in the Northern Hemisphere, with fossils dating to the early Oligocene (Manchester 1987, 1989; Manos et al. 2007; Kozlowski et al. 2018). Currently, the extant *Pterocarya* comprise six generally accepted species, with one species in western Eurasia (Turkey, Georgia, Azerbaijan, and Iran) and five others in eastern Asia (China, the Korean Peninsula, Laos, Vietnam, Taiwan, and Japan) (Kozlowski et al. 2018). All of those *Pterocarya* species are elements of riparian forests in each region. In Japan, Juglandaceae comprises three species in three genera: *Pterocarya rhoifolia* Sieb. et Zucc., *Platycarya strobilacea* Sieb. et Zucc., and *Juglans mandshurica* Maxim. var. *sachalinensis* (Komatsu) Kitam.

The Japanese wingnut *P. rhoifolia* is the only volunteer species of *Pterocarya* in Japan. Although reports refer to the presence of an adjunct *P. rhoifolia* population from China (Laoshan, East Shandong), there is no reliable record and the presence of this species in China remains unclear (Kozlowski et al. 2018). The standard Japanese name for *P. rhoifolia* is "*Sawagurumi*," which is derived from the fact that this species grows near mountain streams. *P. rhoifolia* is a representative riparian element in the cool temperate forest of Japan, is widely distributed from southern Hokkaido to Kyusyu, and grows in regions with heavy and light snowfall (Hotta 1975; Kawahara et al. 2009; Nakano and Sakio 2017; Fig. 3.1). In snowy regions on the Japan Sea side and Tohoku region (northeastern Honshu), *P. rhoifolia* forms the riparian forest canopy with *Aesculus turbinata* Blume and *Cercidiphyllum japonicum* Sieb. et Zucc. (Kikuchi 1968; Suzuki et al. 2002). On the Pacific Ocean side, *Fraxinus platypoda* Oliv. coexists with these species (Sakio 1997; Sakio et al. 2002).

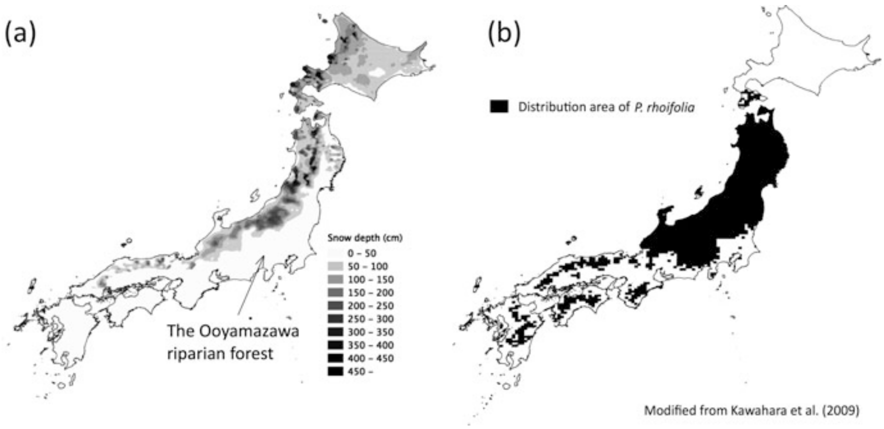

Fig. 3.1 (**a**) Annual maximum snow depth in Japan depth derived from Japanese Meteorological Agency mesh climate data (Nakano and Sakio 2017 revised), (**b**) map of the *P. rhoifolia* distribution

Pterocarya rhoifolia forests develop on stream banks, mud flow terraces, and flood terraces in floodplains, and on the alluvial cone and talus in lower hill slopes along mountain streams (Sato 1988; Kaneko and Kawano 2002). These habitats characteristically undergo land-surface disturbance, e.g., floods, debris flows, and landslides. Therefore, *P. rhoifolia* maintains its populations by adapting its life history to disturbance regimes in riparian areas.

In the Ooyamazawa riparian area on to the Pacific Ocean side of Japan, *P. rhoifolia* forms the canopy with *F. platypoda* and *C. japonicum*. Although *P. rhoifolia* dominates the canopy with *F. platypoda* in the Ooyamazawa riparian area, *P. rhoifolia* canopy trees also grow in patches along streams. In this chapter, we clarify the life history of *P. rhoifolia* in riparian forest based on studies in the Ooyamazawa riparian forest, and discuss the adaptation of the *P. rhoifolia* life history to riparian disturbances.

3.2 Study Species

Pterocarya rhoifolia is a deciduous canopy tree species with straight trunks and can reach 35 m in height and 1.2 m in diameter at breast height (DBH) (Hayashi 1969). It has a single large trunk or a few large trunks in a stool. It often produces sprouts, although not as frequently as *C. japonicum*. In the Ooyamazawa riparian forest, almost all *P. rhoifolia* had a single large trunk in a stool. In 2011, we recorded a maximum DBH and tree height of *P. rhoifolia* of 89.8 cm and 39.9 m, respectively (Fig. 3.2). Its bark is gray and split lengthwise in the mature tree stage. The terminal bud has 1–3 bud scales that fall between autumn and winter and overwinters as a naked bud with pubescence. Its leaves are alternate and imparipinnate compound, 20–30 cm long. The leaves have 9–21 leaflets (Fig. 3.3). The petiole and rachis are finely pubescent. The leaf rachis of the closely related species *Pterocarya stenoptera* is often winged, while that of *P. rhoifolia* is not.

3.3 Reproductive Characteristics

Pterocarya rhoifolia is a monoecious species with unisexual flowers. It is an anemophilous species, and flowers bloom and new leaves develop simultaneously. *P. rhoifolia* produces a female catkin hanging from the terminal part of a current-year shoot and some green male catkins hanging from the axil at the base of a current-year shoot (Fig. 3.4). It flowers in late May in the Ooyamazawa riparian forest. Although the male catkins fall off after pollen dispersal, the female catkins develop into infructescences. One infructescence has 20–60 fruit (Kaneko 2009; Figs. 3.5 and 3.6). One *P. rhoifolia* fruit is a nut with two wings that develop from bractlets; hence, the English name of *P. rhoifolia* is “Japanese wingnut.” The nut is about 0.8 cm in size, and about 2.2 cm including the wings; the oven-dried nut and

Fig. 3.2 The typical mature tree form of *P. rhoifolia* (in the Ooyamazawa riparian forest)

nut including wings of *P. rhoifolia* (mean ± SD) weighed 70 ± 8 and 90 ± 11 mg, respectively (Sakio et al. 2002). A fruit contains one seed. In the Ooyamazawa riparian forest, *P. rhoifolia* fruit matures and is dispersed by wind from September to November (Fig. 3.7).

Pterocarya rhoifolia can live for up to 150 years (Kaneko 2009) and starts producing fruit at 40–80 years, at which point the DBH is 28 cm and the tree height is 16 m (The Japanese Riparian Forest Research Group 2001). Although *P. rhoifolia* reaching the canopy layer with stems larger than 30 cm DBH can bloom, small-diameter individuals released from suppression and understory individuals cannot bloom (Kaneko 2009). Therefore, to reach reproductive maturity, *P. rhoifolia* requires sufficient size and light.

Mature *P. rhoifolia* produce seeds most years, although the annual seed production fluctuates (Sawada et al. 1998; Kaneko and Kawano 2002; Sakio et al. 2002). In

Fig. 3.3 The leaves of *P. rhoifolia*

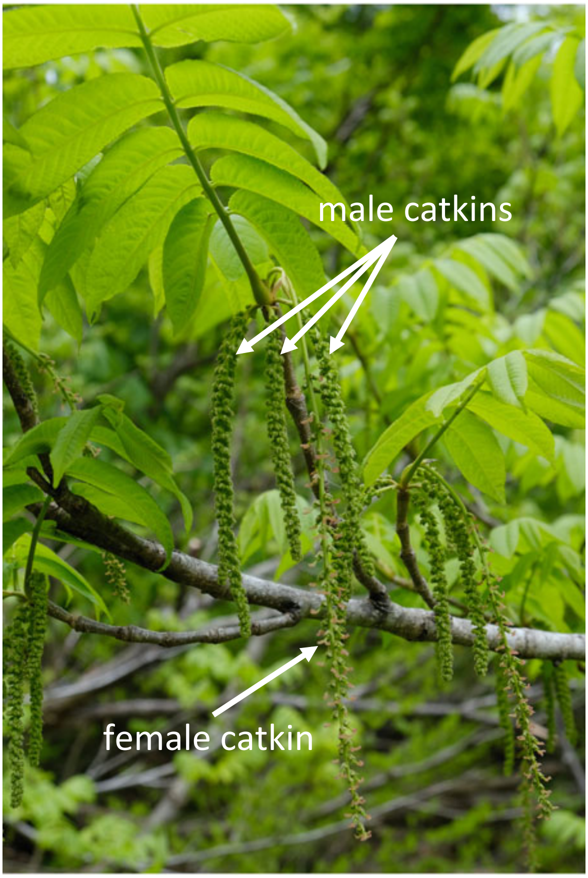

Fig. 3.4 A flowering branch of *P. rhoifolia* with male and female catkins

Fig. 3.5 Fruiting individual of *P. rhoifolia*

Fig. 3.6 A branch with leaves and a fruiting spike

the Ooyamazawa riparian forest, *P. rhoifolia* produced seeds almost every year between 1995 and 2014, although very few were produced in 1996 and 2006 (Fig. 3.8). Moreover, the annual variation in seed production has tended to alternate yearly since 2005. The coefficient of variation (CV) between 2005 and 2014 was

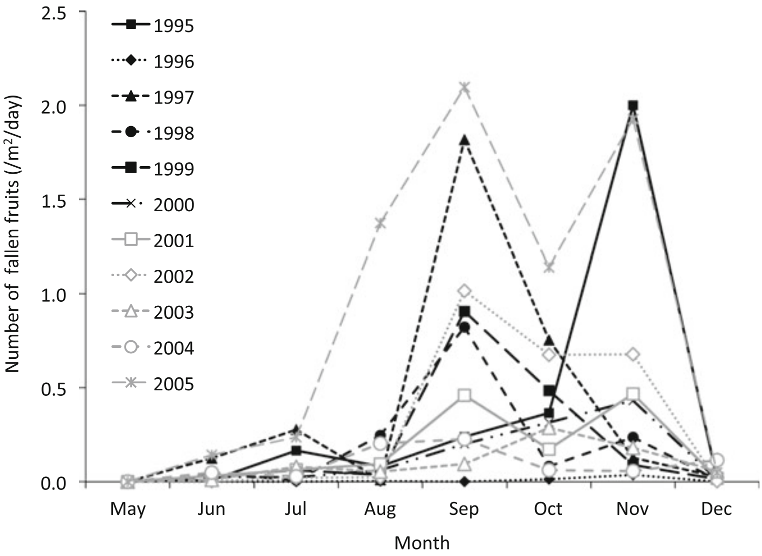

Fig. 3.7 Seasonal change in amount of fallen *P*. *rhoifolia* fruit in the Ooyamazawa riparian forest (1995–2005)

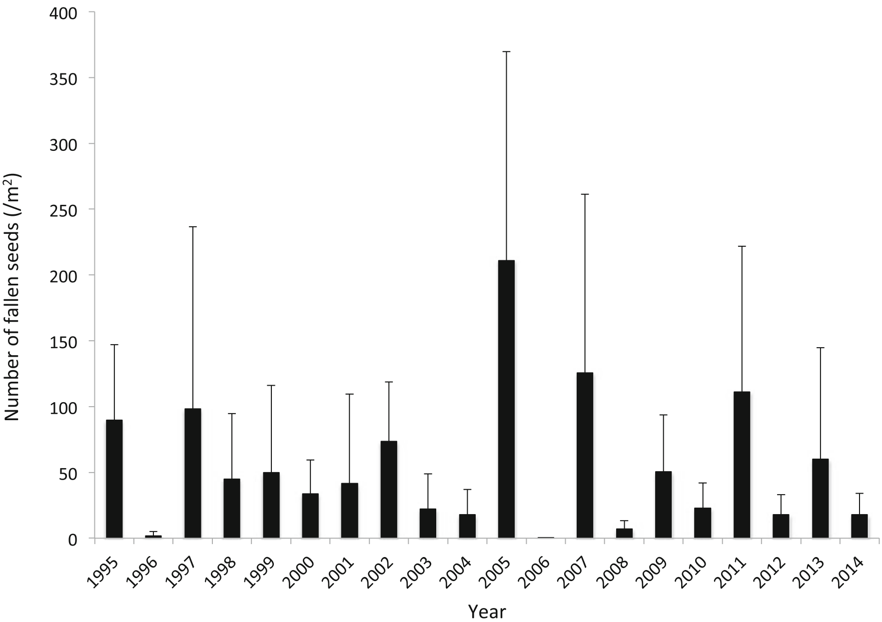

Fig. 3.8 Annual change in the number of dispersed seeds of *P*. *rhoifolia* in the Ooyamazawa riparian forest (1995–2014). Vertical bars indicate the standard deviation

larger than that between 1995 and 2004 ($CV_{1995–2004} = 0.75$, $CV_{2005–2014} = 0.89$). The variation in annual seed production in *P. rhoifolia* is intermediate between that of *F. platypoda* and *C. japonicum* (Sakio et al. 2002).

3.4 Structure and Distribution

According to Sakio et al. (2002), a 4.71 ha study plot in the Ooyamazawa riparian forest contained 112 *P. rhoifolia* over 4 cm in DBH, of which 80 (71.4%) were in the canopy layer. The mean DBH of the *P. rhoifolia* canopy trees was 44.6 ± 11.5 cm, with a maximum of 77.7. The DBH distribution of the *P. rhoifolia* population was continuous from saplings to large individuals (Fig. 3.9), but there were some peaks: one for small trees <5 cm in DBH (suggesting that *P. rhoifolia* maintains sapling banks) and another at 35–40 cm in DBH (suggesting that synchronous regeneration of *P. rhoifolia* has occurred several times in the past). The trees form patches of various sizes along a stream, with some large high-density patches on large landslide deposits (Sakio et al. 2002; Fig. 3.10). The mean age of the *P. rhoifolia* trees forming these patches is about 90 years and most are even-aged. These results suggest that *P. rhoifolia* invades the sites of large disturbances, such as floods, debris flows, and landslides, where it forms colonies.

3.5 Seedling Regeneration

The dispersed seeds of *P. rhoifolia* generally germinate in the spring of the following year. *P. rhoifolia* forms almost no soil seed bank. Kubo et al. (2008) investigated the species composition of the soil seed bank (to 5 cm depth) for the Ooyamazawa

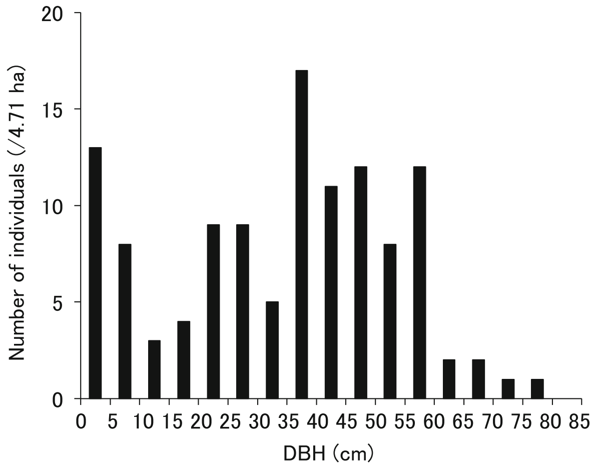

Fig. 3.9 Frequency distribution of the DBH of *P. rhoifolia* in a 4.71-ha study plot in the Ooyamazawa riparian forest

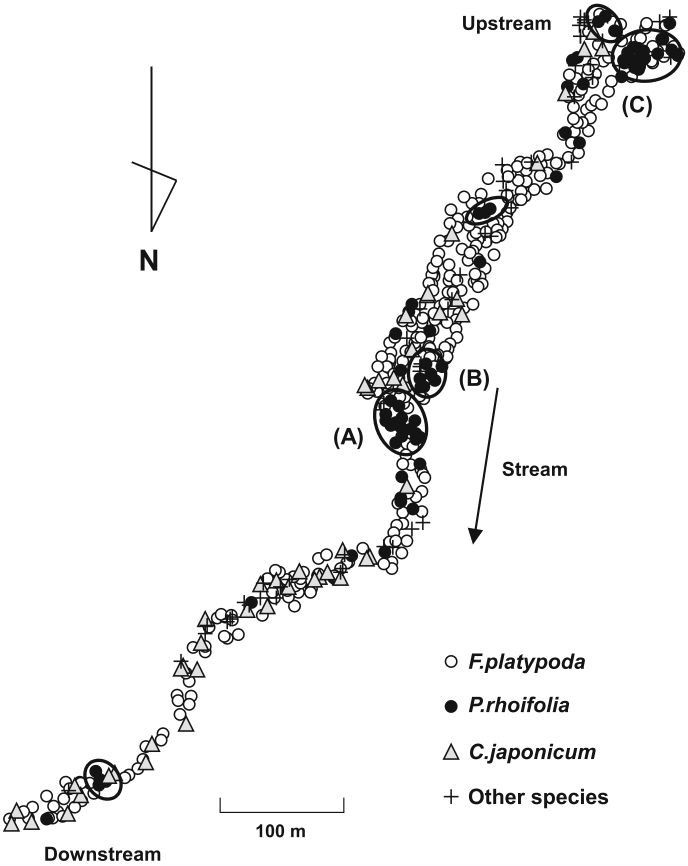

Fig. 3.10 Distribution of three canopy trees along a stream in the Ooyamazawa riparian forest. Patches (A–C) where a large landslide occurred about 90 years ago were dominated by *P. rhoifolia* canopy trees with a few *C. japonicum* trees (Sakio et al. 2002)

riparian forest and found only one buried viable *P. rhoifolia* seed in 30 L soil. The current-year seedlings of *P. rhoifolia* are epigeal cotyledons type, which have two opposite cotyledons deeply palmately four-clefted at germination (Fig. 3.11). Their alternate primary leaves are simple leaves until the first or second leaf stage, and become imparipinnate compound leaves at larger leaf stages.

The germination sites of current-year seedlings of *P. rhoifolia* in the Ooyamazawa riparian forest are on litter, gravel, mineral soil, and fallen logs (Sakio et al. 2002). On Chichibu Mountain, *P. rhoifolia* seeds germinate both under closed canopy and in gaps in the riparian forest dominated by *F. platypoda* and *P. rhoifolia* (Kisanuki et al. 1995). These results suggest that the germination sites of *P. rhoifolia* in riparian areas are not markedly limited.

In the Ooyamazawa riparian forest, current-year seedlings that germinate on litter tend to die in the current year because of low light intensity and drought, while

Fig. 3.11 Current-year seedling of *P. rhoifolia* with four-part cotyledons

current-year seedlings on gravel, mineral soil, and fallen logs die within 3 years (Sakio et al. 2002). Furthermore, almost all current-year *P. rhoifolia* seedlings that germinate under a closed canopy die in the current year (Kisanuki et al. 1995). Taking this into consideration, under what conditions can current-year seedlings of *P. rhoifolia* survive and grow? Nursery experiments have indicated that the height of current-year *P. rhoifolia* seedlings increases with relative light intensity (RLI), reaching about 30 cm at over 40% RLI (Sakio et al. 2008). An investigation of the relationship between the distribution of *P. rhoifolia* saplings (height >1 m and DBH <4 cm) and topography in the Ooyamazawa riparian forest found that more saplings were distributed in abandoned channels and floodplains than on hillslopes or in active channels (Sakio et al. 2002, Table 3.1; Fig. 3.12). The abandoned channels and floodplains were directly affected by stream flow and lacked an understory. Moreover, the microhabitats in the Ooyamazawa riparian forest in which *P. rhoifolia* saplings ($\geq$1 years old) tend to thrive consist of deposited gravel with thin soil and no herbaceous layer (Kubo et al. 2000).

There are no statistical relationships between canopy gaps and the distribution of *P. rhoifolia* saplings (height >1 m and DBH <4 cm) in the Ooyamazawa riparian forest (Table 3.1; Fig. 3.13). However, Sato (1992) investigated the regeneration of *P. rhoifolia* saplings in a *P. rhoifolia* forest in Hokkaido and found a weak positive correlation between the distribution of *P. rhoifolia* saplings (2 m $\leq$ tree height $\leq$ 4 m)

Table 3.1 Number of grids with *P. rhoifolia* saplings (height ≥1 m) and the mean number of saplings per grid (Sakio et al. 2002 revised)

Grid condition	Presence grids of saplings (%)	Total number of saplings	Mean number of saplings per grid (±s.d.)
Topography (number of grids)			ns[a]
Hillslope (428)	15 (3.5%)	17	1.13 ± 0.35
Active channel (161)	9 (5.6%)	10	1.11 ± 0.33
Abandoned channel (208)	44 (21.2%)	71	1.61 ± 0.97
Floodplain (553)	55 (9.9%)	94	1.71 ± 1.54
Canopy (number of grids)			ns[b]
Under canopy (1052)	96 (9.1%)	157	1.64 ± 1.30
Gap (298)	27 (9.1%)	35	1.30 ± 0.72

s.d. standard deviation, *ns* not significant
[a]Results of Tukey–Kramer test
[b]Results of *t*-test

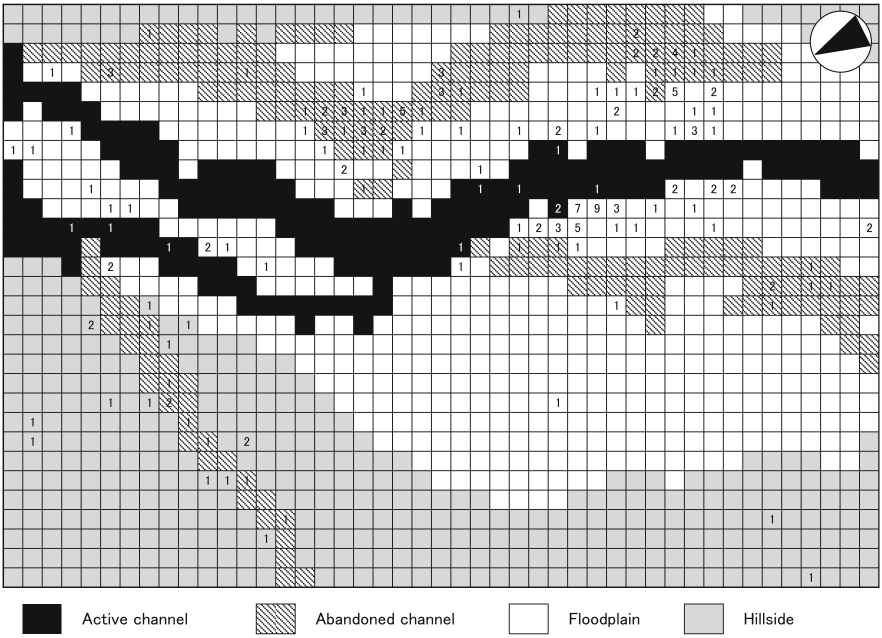

Fig. 3.12 Microtopography and distribution of *P. rhoifolia* saplings in a 0.54-ha study plot in the Ooyamazawa riparian forest (Sakio et al. 2002 revised). This plot was divided into 1350 quadrats (2×2 m^2). The microtopography was recorded in each quadrat and was classified into the following categories: hillside, active channel, abandoned channel, and floodplain. The figures show the numbers of *P. rhoifolia* saplings in each quadrat

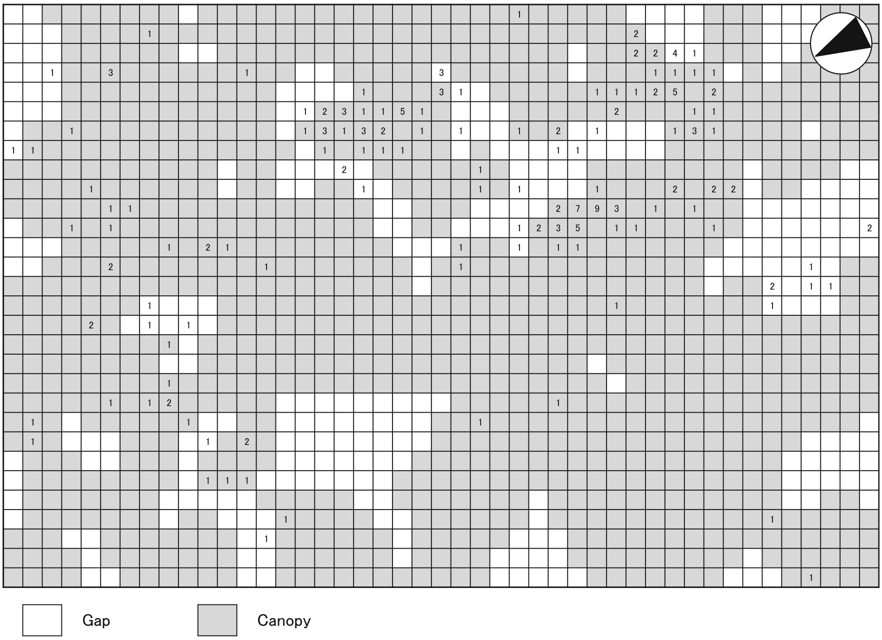

Fig. 3.13 Canopy gaps and distribution of *P. rhoifolia* saplings in a 0.54-ha study plot in the Ooyamazawa riparian forest. This plot was divided into 1350 quadrats (2 × 2 m^2)

and relative illumination, and reported that *P. rhoifolia* saplings were distributed contiguously around canopy gaps. Moreover, Sakio (1993) investigated the pattern of leaf expansion and shoot elongation of *P. rhoifolia* saplings in Ooyamazawa riparian forest, and found that *P. rhoifolia* saplings (height = 80.3±13.3 cm) in a canopy gap continued to expand their leaves and develop current-year shoots from May to August.

The factors that enable the survival and growth of *P. rhoifolia* seedlings and saplings have not been explained completely. However, many investigations have suggested that, for *P. rhoifolia* to regenerate seedlings, bare ground caused by land-surface disturbance with destruction of the herbaceous layer and a canopy gap are probably needed.

3.6 Sprouting Traits

Pterocarya rhoifolia produces some sprouts from the root collar and lowest part of the stem, but lacks root suckers. In the Ooyamazawa riparian forest, *P. rhoifolia* has a maximum of 10 sprouts/individual and there are no significant correlations between the number of sprouts and DBH of the main stem (Sakio et al. 2002). In an unpublished study, overall, 79.2% of individuals had sprouts, 95.3% of which

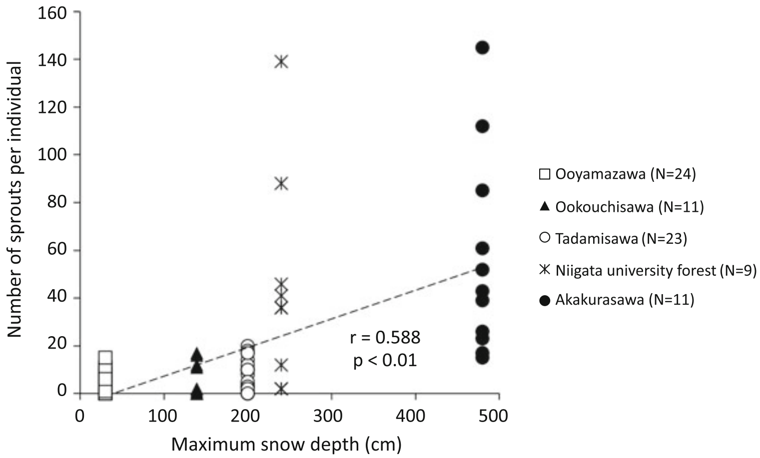

Fig. 3.14 Relationship between the maximum snow depth and number of sprouts per mature *P. rhoifolia*. *N* number of individuals (Nakano and Sakio 2017 revised)

were less than 50 cm high (Y. Nakano, unpublished data). In the Ooyamazawa riparian forest, such sprouts have no role in maintaining the population (Nakano and Sakio 2017).

However, the sprouting traits of *P. rhoifolia* change in response to maximum snow depth. Nakano and Sakio (2017) comparing several areas with maximum snow depths from 30 to 480 cm in a cool temperate mountainous area in central Japan, which includes the Ooyamazawa riparian forest as a low-snow region, and reported that the number of sprouts per *P. rhoifolia* individual increased with maximum snow depth (Fig. 3.14). In deep snow, the sprouts of *P. rhoifolia* may play a role in repairing individuals damaged by the snowpack to maintain the population (Nakano and Sakio 2018). They also found that, with increasing maximum snow depth, the DBH decreased, maximum stem length and tree height shortened, trees tended toward a "dwarf shrub" form, and seed production decreased (Nakano and Sakio 2017). These results suggest trade-offs between clonal growth (producing sprouts) and sexual reproduction (seed production) and between producing sprouts and height growth (Nakano and Sakio 2017; Fig. 3.15). This sprouting ability could conceivably be due to *P. rhoifolia* growing in an environment that tends to be influenced by disturbances specific to riparian areas, such as floods and landslides. Therefore, the sprouting ability of *P. rhoifolia* is insurance enabling it to survive when threatened.

Ito (1992) investigated dry matter partitioning in seedlings and sprouts of *P. rhoifolia* and showed that the slopes of the regression lines of the allometric relationship between basal trunk diameter and tree height were greater in sprouts than in seedlings, suggesting a change in growth characteristics from the "waiting" type (diameter-preferred growth) in seedlings to the "competing" type (elongation-preferred growth) in sprouts.

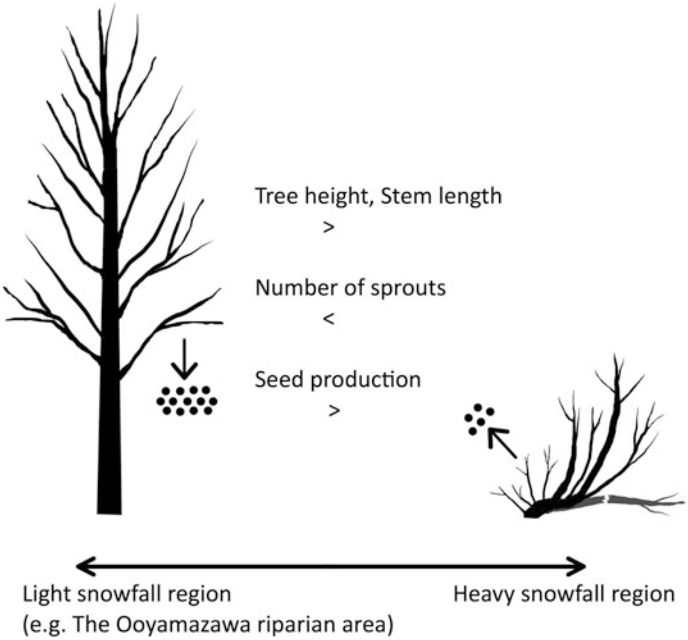

Fig. 3.15 Schematic diagram relating the life history traits of *P. rhoifolia* and snowfall conditions (Nakano and Sakio 2017 revised)

3.7 Conclusion

In the Ooyamazawa riparian forest, *P. rhoifolia* forms the canopy with *F. platypoda* and *C. japonicum*. Sato (1992) compared the distribution, growth, and survival of saplings of the main canopy tree species (*P. rhoifolia*, *Acer mono*, *Alnus hirsute*, and *Ulmus laciniata*) in a *P. rhoifolia* forest in Hokkaido. Defining a pioneer species by its high germinating capacity, high growth rate, and high survival rate under sufficient light, they concluded that *P. rhoifolia* is not a typical pioneer species, but is intermediate between a pioneer and non-pioneer species. In the Ooyamazawa riparian forest, *P. rhoifolia* is more of a pioneer than *F. platypoda* and *C. japonicum*, particularly in terms of the growth rate during the seedling and sapling stages (cf. Chap. 7).

Mature *P. rhoifolia* produce and disperse seeds almost every year. *P. rhoifolia* seeds invade the sites of large disturbances, including floods, debris flows, landslides, and canopy gaps, and establish there. Moreover, *P. rhoifolia* can grow rapidly with sufficient light. Consequently, this tree species can form the canopy and even-aged populations in the Ooyamazawa riparian forest. In this forest, *P. rhoifolia* does not produce many sprouts. Hence, sprouts may not contribute to maintaining *P. rhoifolia* individuals for a long time, such as *C. japonicum* (cf. Chap. 4), and the lifespan of *P. rhoifolia* appears to be about 150 years (Kaneko 2009). Consequently, the dominance ratio of late-successional tree species in the canopy such as *F. platypoda* and *C. japonicum* may increase after the lifespan of *P. rhoifolia* without large disturbances. However, if large disturbances occur along rivers and generate suitable sites for *P. rhoifolia* regeneration, even-aged *P. rhoifolia* forest may reestablish (Sato 1988). Therefore, the life history traits of *P. rhoifolia* are adapted to disturbances in riparian areas and the species may be able to maintain its population in the Ooyamazawa riparian forest.

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