# Chapter 12
# General Conclusion

**Hitoshi Sakio**

**Abstract** The research conducted at Ooyamazawa highlights the importance and value of long-term ecological research (LTER). The studies discussed here demonstrate that tree life-history strategies and regeneration are strongly correlated with disturbance regimes in riparian zones. Coexistence mechanisms among canopy tree species at Ooyamazawa reflect niche partitioning at early stages; however, long-term coexistence was more related to unpredictable large-scale disturbance events. LTER documented the unexpected effects of a rapid increase in sika deer populations. Deer browsing led to the decline of understory vegetation and trees at Ooyamazawa and the resulting cascade effects led to changes in the ground beetle and bird communities. Our 28-year research record indicated that global warming has impacted flowering and fruiting in *Fraxinus platypoda*. Our findings highlight the necessity of ongoing, long-term monitoring in capturing ecosystem change.

**Keywords** Avifauna · Cascade effect · Global warming · Ground beetle decline · Long-term ecological research · Ooyamazawa riparian forest · Phenology · Riparian forest conservation · Sika deer

## 12.1 Research at Ooyamazawa Riparian Forest Research Site

In the 1980s, long-term ecological research (LTER) sites were established across Japan. Research at the Ooyamazawa riparian forest research site was initiated early relative to other locations, in 1983 (Chap. 1); this included the establishment of the Ogawa Forest Reserve by the Forestry and Forest Products Research Institute (Nakashizuka and Matsumoto 2002). Pilot experiments were conducted from 1983 to 1986. In 1987, full-scale research began, focused on forest structure and

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regeneration. In the same year, 20 seed traps were established within a core plot of 0.54 ha. Subsequent research regarding forest structure and seed production focused on the dominant canopy species *Fraxinus platypoda*. In 1991, the survey area was expanded to encompass 4.71 ha; research on canopy species was then broadened to include *Pterocarya rhoifolia* and *Cercidiphyllum japonicum*. In 1997, collaborating researchers began additional surveys. In December 2006, the site was registered within the Japan long-term ecological research network (JaLTER). In addition, a 1-ha plot, which included the existing core plot, was registered as a core site within the Ministry of Environment's Monitoring Sites 1000 Project.

Over 35 years, LTER at Ooyamazawa focused on the life-history strategies of riparian trees (Chap. 2) and coexistence mechanisms among riparian plants (Chaps. 6 and 7). Long-term phenological observations, which were made using seed traps and binoculars, revealed changes in the flowering and seed production cycles of *F. platypoda* (Chap. 2). During the course of the study period, dramatic changes occurred at Ooyamazawa. Sika deer (*Cervus nippon*) heavily influenced the understory vegetation after 2000, wherein overbrowsing caused a rapid decline in vegetation cover (Chap. 8). The effects of sika deer have been significant throughout Japan (Miura and Tokida 2008). The observed decline in understory vegetation at Ooyamazawa precipitated significant cascade effects on the ground beetle community (Chap. 10) and the local avifauna (Chap. 11).

## 12.2 Tree Life Histories and Dynamics

Based on the assumption that an understanding of life history is vital for understanding coexistence and ecosystem dynamics in forested stands, LTER at Ooyamazawa focused on tree life-history strategies within the riparian forest. These studies focused on the dominant canopy species *F. platypoda*, *P. rhoifolia*, and *C. japonicum*, as well as four *Acer* species (Chaps. 2–5). For each of the three dominant canopy species, the population structure and size and spatial distributions were quantified. Annual variation in seed production was also assessed, as were germination characteristics; notably, germination characteristics were investigated using both field and nursery observations. For the four *Acer* species, the sizes and spatial distributions of mature individuals, as well as characteristics of vegetative reproduction, were assessed.

Some tree species reproduce both sexually and asexually (i.e., vegetatively). Some species may favor vegetative reproduction in areas where their growth is limited, such as at the thresholds of their tolerance to light and substrate conditions (Koop 1987). *Acer argutum* often propagates asexually via suckers, while *C. japonicum* and *Acer carpinifolium* both produce suckers at the base of their main stems; these changes lead to trunk modification on long- and short-term timescales, respectively. Suckering at the base of the trunk is likely a response to the need to balance photosynthesis and respiration under a dense canopy. Furthermore,

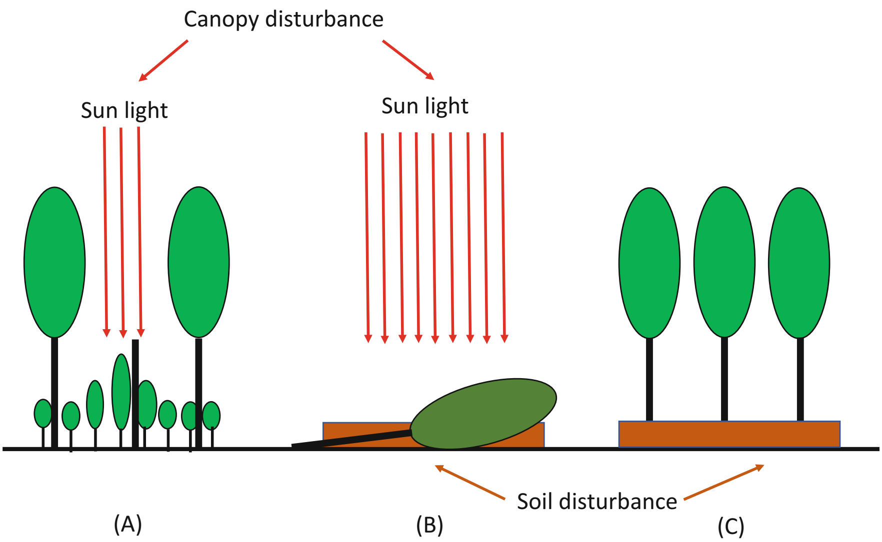


**Fig. 12.1** Disturbance processes in riparian areas. Type A reflects canopy gap formation that alters light conditions. Type B reflects large-scale debris flows and landslides that alter both light and soil conditions. Type C reflects sediment flow that removes understory vegetation and alters soil conditions

individuals of the *P. rhoifolia* species are maintained via suckering in areas with heavy snowfall (Nakano and Sakio 2018).

The studies conducted at Ooyamazawa revealed that the regeneration of these species is strongly related to disturbance regimes in riparian zones. Major disturbances typical of mountain basins include predictable flooding and typhoons in the rainy season, as well as sporadic debris flows caused by large typhoons. Large-scale landslides also occur at low frequency, but with a high degree of unpredictability. Three disturbance processes were identified within the riparian zone (Fig. 12.1): (1) gap formation due to withering and truck breakage in canopy trees, which increases light availability in the understory (Fig. 12.1A); (2) small-scale sediment movement associated with mountain streams, which alters the soil environment without altering light conditions (Fig. 12.1C); and (3) large-scale landslides and debris flows, which significantly alter the soil, vegetation, and light conditions (Fig. 12.1B). The seven riparian tree species studied at Ooyamazawa were closely associated with disturbance events and environmental changes typical of mountain basins.

## 12.3 Plant Species Coexistence

Chapter 6 discusses the life histories of herbaceous plant species with respect to topography. In 1983, 76 species were identified in the herbaceous layer (Sakio et al. 2013). Six landform types were identified along the Ooyamazawa basin valley: debris flow terrace, alluvial fan, terrace scarp, new landslide site, old landslide slope, and talus. Herbaceous plant diversity was associated with mosaic surface soil conditions, which are a product of disturbances such as debris flows, landslides, and soil erosion. A strong association was found between micro-scale soil heterogeneity (caused by disturbance) and the growth of herbaceous plants.

Herbaceous plants may adapt to environmental conditions through vegetative growth, as well as through sexual and asexual reproduction. At Ooyamazawa, three major groups of herbaceous plants were defined. The first were perennial herbs and ferns with rhizomes growing on stable debris flow terraces and alluvial fans. This group included spring ephemerals, such as *Corydalis lineariloba* and *Allium monanthum*. The remaining two groups included annual species (e.g., *Impatiens noli-tangere* and *Persicaria debilis*) and two subgroups of perennials: those with bulbils (e.g., *Elatostema umbellatum* var. *majus* and *Laportea bulbifera*) and those with replacement rhizomes (e.g., *Chrysosplenium macrostemon*, *Cacalia delphiniifolia*, and *Cacalia farfaraefolia*). The annual species and perennials groups tended to dominate in areas with frequent annual disturbance, such as sandbars and new landslide sites with unstable soils.

Coexistence mechanisms were investigated among the dominant canopy species, *F. platypoda, P. rhoifolia*, and *C. japonicum*, based on life-history characteristics and disturbance regimes (Chap. 7). *F. platypoda* was the dominant species at Ooyamazawa, comprising >60% of all canopy trees. Seedlings and saplings were common in the understory; peaks were observed for small seedlings and those with a diameter at breast height between 40 and 50 cm. *F. platypoda* has high shade tolerance and many saplings of this species were found in the understory. Furthermore, mature individuals were found to have regenerated following a major disturbance event at Ooyamazawa, approximately 200 years ago. Seedlings and saplings typically have greater resistance to flooding; therefore, they can survive at stream edges and grow rapidly to reach canopy height when gaps are formed.

Canopy-layer, mature individuals of the *P. rhoifolia* species formed a large patch approximately 50 m in diameter. Presumably, these individuals were approximately the same age and had regenerated following a past disturbance event. *P. rhoifolia* exhibited a faster growth rate under direct sunlight relative to other species, a trait that was also observed in a nursery experiment. However, its lifespan is relatively short, with a maximum of 150 years; thus, mature individuals are replaced by other species after death.

*C. japonicum* displayed a relatively uniform age and diameter at breast height size class distribution at Ooyamazawa. Larger individuals were clustered near the mountain stream, while seedlings and saplings were uncommon in this area. This indicated limited regeneration opportunity for *C. japonicum* at Ooyamazawa. Sub-canopy layer individuals of *C. japonicum* were located within the regenerated stand of *P. rhoifolia*, which suggested that the regeneration potential of *C. japonicum* also relies on large-scale disturbance. *C. japonicum* typically has high annual seed production and its seeds are dispersed over long distances (Sato et al. 2006), which allows for the colonization of newly disturbed areas. Once established, individuals are maintained by suckering around the main trunk. Coexistence mechanisms in the riparian forest at Ooyamazawa reflected niche partitioning at early stages; however, long-term coexistence relied on unpredictable large-scale disturbance events. These results reflect a similar trend observed in the understory herbaceous species at the site.

The rough topography at Ooyamazawa is the result of an earthquake that occurred 200 years ago (Sakio 1997) and a massive landslide that occurred 100 years ago (Sakio et al. 2002). More recently, climate change has caused changes in the disturbance regime, especially in the riparian area. The frequency and magnitude of large-scale disturbance events has increased, exemplified by typhoon Hagibis (Typhoon No. 19) in 2019. These changes may affect long-term patterns in plant regeneration and life-history strategies at the site.

## 12.4 Effects of Global Warming on Tree Reproduction

Global warming has progressed over the past century and has been related to various ecosystem-level changes. The effects of global warming will first become evident in polar and high-altitude ecosystems (Grabherr et al. 1994; Kullman 2001; Sanz-Elorza et al. 2003; Sturm et al. 2001; Wardle and Coleman 1992). Grabherr et al. (1994) demonstrated significant ecological impacts of global warming in terms of the upwards advance of alpine-nival flora. The timberline of Mt. Fuji advanced rapidly upwards from 1978 to 1999 (Sakio and Masuzawa 2011). Furthermore, Kudo and Suzuki (2003) showed accelerated growth in a few restricted species using artificial warming over a 5-year period; they also showed a change in vegetation structure in a mid-latitude alpine ecosystem. The maximum, average, and minimum temperatures in Chichibu increased by 1.09 °C, 1.15 °C, and 1.69 °C, respectively, from 1926 to 2018 (Fig. 12.2).

Phenological change was documented in *F. platypoda* at Ooyamazawa over a 28-year survey period (Chap. 2). The flowering interval of *F. platypoda* was 2–3 years for both female and male trees, and flowering of the two sexes showed clear synchronization, until 2002. After 2002, an increasing number of males flowered annually, while females retained a flowering interval, and synchronization was lost. The reason for this change is unclear, but is presumably related to an increase in the photosynthetic rate due to rising temperature and an increase in net production due to a prolonged photosynthetic period.

In the past, significant changes in the distribution of forest vegetation have been recorded in the Japanese archipelago due to climate change, such as during the glacial and interglacial periods. In many instances, species' ranges may shift due to

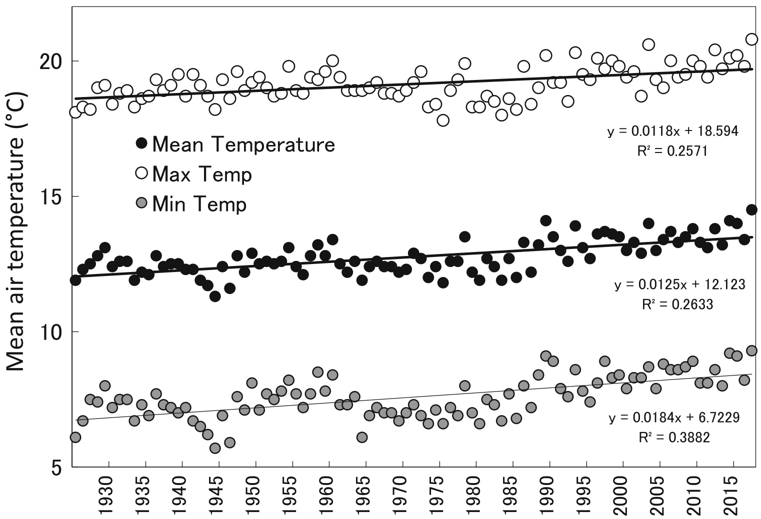


**Fig. 12.2** Maximum, average, and minimum temperatures in Chichibu city from 1926 to 2018 (Japan Meteorological Agency 2013)

the direct physiological effect of temperature; however, there may also be instances in which local populations are extirpated due to unsuccessful reproduction.

## 12.5 Sika Deer Browsing and Riparian Forest Ecosystems

### *12.5.1 Understory Vegetation and Tree Species*

LTER documented an unexpected phenomenon at Ooyamazawa (Chap. 8). The sika deer population in Japan has nearly doubled over the past few decades (Miura and Tokida 2008). After 2000, herbaceous vegetation cover sharply declined at the site (Sakio et al. 2013); in particular, vegetation cover quickly decreased to only a few percent and species richness was reduced by half. The majority of herbaceous species were affected by deer browsing, excluding the toxic *Aconitum sanyoense*, *Scopolia japonica*, and *Veratrum album* ssp. *oxysepalum*. Small spring ephemeral species were also less affected due to their short growing season.

Sika deer browsing further influenced tree species populations at Ooyamazawa. Many trees, including canopy-layer individuals, died due to girdling by deer. This damage was species-specific, wherein *Ulmus laciniata* exhibited the greatest damage. *Acer* spp., especially *Acer carpinifolium*, were also extensively damaged. Browsing on suckers of *Acer carpinifolium* was sufficiently extensive to cause the death of some individuals. To restore the vegetation by exclusion of deer predation, fences were installed in the Ooyamazawa basin, excluding the riparian area, in 2016 (Fig. 12.3). Long-term monitoring will be critical to determine the effectiveness of the fencing.

**Fig. 12.3** Exclusion fencing for sika deer at Ooyamazawa. Fencing was established in 2016

**Fig. 12.4** Decline in a Sasa borealis community on a hillside slope. This decline was a result of sika deer browsing and simultaneous flowering

## *12.5.2 Avifauna*

Within the Ooyamazawa riparian forest research site, 44 species were recorded during the breeding season and 23 were recorded in the wintering season between 2010 and 2017. An 8-year survey that began in 2010 suggested that the avifauna community dramatically changed at this site over time.

Sika deer browsing (Chap. 8) led to the decline of the *Sasa borealis* community on hillside slopes (Fig. 12.4), which has not yet recovered since blooming in 2013.

The abundance of bird species that feed in shrubs, namely *Cettia diphone*, *Luscinia cyane*, *Luscinia akahige*, and *Leiothrix lutea*, significantly decreased over the 8-year period; therefore, these species were nearly absent by 2017. Furthermore, the abundance of bird species that nest in shrubs, such as *Phylloscopus borealoides* and *Phylloscopus coronatus*, also decreased.

### *12.5.3 Ground Beetle Community*

Ground beetle monitoring at Ooyamazawa, conducted from 2008 to 2017, captured 2381 individuals from 19 families (including 1969 individuals of 36 carabid species). The carabid community was characterized by high species richness and a high proportion of Japanese endemic species, relative to other forest monitoring sites across Japan. Similar to the avifauna, the ground beetle community showed major changes over the course of the survey period. Most carabid species exhibited dramatic declines and the annual catch of carabids decreased by 80% over the sampling period. While some of this decline was related to the decline in understory vegetation due to deer browsing, it may also have been related to climate change and warming.

### *12.5.4 Cascade Effects of Sika Deer Browsing*

Sika deer alter the structure and composition of forests through herbivory. Consequently, regeneration is prevented (Takatsuki 2009). The sika deer population increase in Japan has resulted from deer protection policies, increased food resources related to establishment of plantations after World War II, reduced hunting pressure, and reduced snow cover in winter. Cascade effects that result from deer browsing are described in Fig. 12.5. At Ooyamazawa, sika deer browsing led to a reduction in forest floor vegetation (Chap. 8), alterations in beetle and bird communities (Chaps. 10 and 11), and a decline in tree populations due to girdling (Chap. 9).

Although not addressed in this study, the reduction in understory vegetation would be expected to increase surface soil erosion, leading to deterioration in stream water quality and detrimental effects on aquatic life, particularly breeding fish (Sakai 2013). Previous research suggested that the increase in deer population affected fish populations in the upper reach of the Yura River, located in the Ashiu Forest Research Station of the Kyoto University Field Science Education and Research Center, Kyoto Prefecture, Japan (Nakagawa 2019).

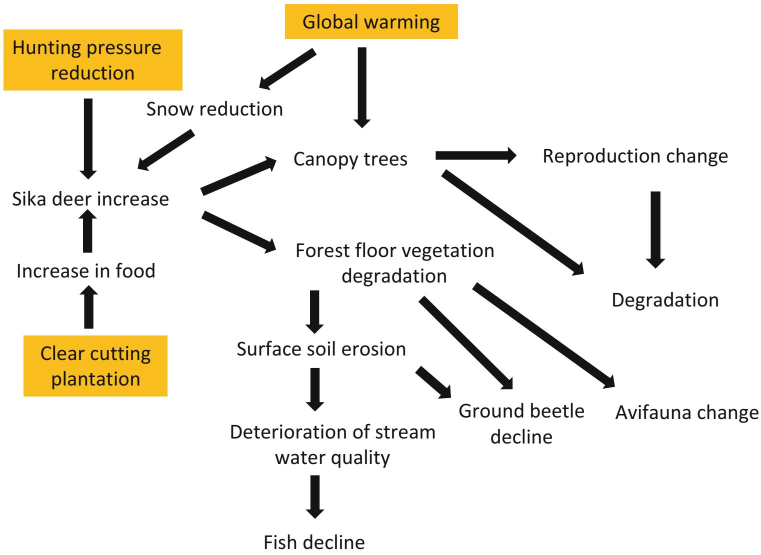


**Fig. 12.5** Cascade effects on riparian ecosystems caused by human impacts and global change

## 12.6 Conservation of Riparian Forest Ecosystems

Following World War II, dams were constructed in mountain basins in Japan (Fig. 12.6). Additionally, plantations of *Cryptomeria japonica* and *Chamaecyparis obtusa* were established, often directly adjacent to riparian zones (Fig. 12.7). As a result, many riparian forests were lost, and mountain stream ecosystems were degraded (Sakio and Suzuki 1997). Given this legacy, conservation of the remaining areas of intact riparian forest is critical. These forests can become models for conservation and rehabilitation, while serving as important genetic

**Fig. 12.6** Erosion control dams in mountain streams

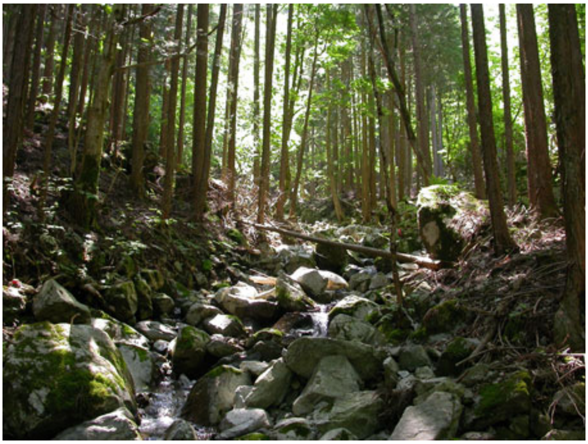

**Fig. 12.7** *Cryptomeria japonica* plantation in a riparian zone following clear cutting of native forest

resources. Although sika deer pose an ongoing threat, deer management and exclusion fencing efforts are beginning to show positive effects in some areas in Japan. Deer fencing was installed in 2016 at Ooyamazawa (Chap. 9), but recovery has not yet been observed. Future monitoring efforts will determine the feasibility of understory vegetation restoration. Existing long-term survey data will allow for comparison between recovering exclusion areas and the vegetation community composition prior to intensive deer browsing.

## 12.7 Future Directions

The research conducted at Ooyamazawa highlights the importance and value of LTER. The initial research objectives included understanding life-history characteristics in riparian forests and determining long-term forest dynamics. However, deer browsing intensified after the establishment of the site and provided an excellent opportunity to study the influence of browsing on forest dynamics. Existing vegetation survey data allowed us to directly assess changes in vegetation caused by sika deer (Chaps. 8 and 9). Effects on avifauna and ground beetle communities were also assessed. Our 28-year analysis of *F. platypoda* clearly demonstrated changes in flowering and seed production resulting from climate change and rising temperatures.

LTER requires consistent research effort and continuous funding. Thus far, LTER has been conducted at survey sites throughout Japan and produced important findings. We note that researchers who are invested in LTER from its conception often remain highly motivated; however, wardens may see routine monitoring as burdensome. The continuation of manipulative experiments and long-term monitoring is an important concern for the future. Fortunately, research at Ooyamazawa has benefited from the addition of young researchers, which is reflected in the efforts of

JaLTER and the Monitoring Sites 1000 Project. We look forward to continued research efforts.

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