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## 10. Riparian Forests in the Region along the Northwestern Pacific Side

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### 1. Riparian Landscape and Forests

Riparian landscapes are transition zones from terrestrial to aquatic ecosystems; they are characterized by scenic elements including waterfalls, rivers, lakes, and wetlands<sup>1</sup>. These landscapes are visually distinct from the adjacent terrestrial landscape, attracting the attention of both tourists and researchers. Because of their natural beauty, photographs of riparian landscapes are used as illustrations in many contexts, from web pages to travel guidebooks.

An important phenomenon in riparian landscape is water table fluctuation caused by various hydrological factors such as rainfall and sea tide changes (Figure 1)<sup>1, 2, 3</sup>. Water table rising can lead to physiological water stress in the living organisms of riparian landscapes, thus promoting the growth of hygrophilous species and decline of terrestrial species. Lateral water flow in riparian areas is accompanied by sedimentation and erosion, which represent physical disturbances that also affect organisms. Although the intensity and frequency of water stresses and physical disturbances vary among riparian landscape types, they tend to decrease with distance from aquatic ecosystems. These environmental conditions caused by lateral water flow create a wide variety of habitat combinations within riparian landscapes.

Riparian forests are among the most developed ecosystems along the coasts of the northwestern Pacific



Figure 1 Changes in water table during (left, Aug 5, 2003) and after floods (right, Aug 6, 2003), and riparian forest dominated by *Salix* species in Kamikouchi, Matsumoto, Central Japan.

Rim. For example, *Salix arbutifolia*, *Salix rorida*, and *Salix cardiophylla* var. *urbaniana* dominate riparian forests on the floodplain of the Azusagawa River, Kamikochi, central Japan (Figure 1). In southeastern Russia, riparian forests are composed mainly of *Salix* species, *Pinus koraiensis*, *Picea jezoensis*, and *Betula platyphylla* (Figure 2, left); *Salix pierotii* and *Salix chaenomeloides* dominate forests along the Nakdong-gang River, Republic of Korea (Figure 2, right). These forests can be classified according to their topography and aquatic environments, as follows.

#### Riparian forests in mountainous areas

In mountainous areas, riparian forests occur on valley bottoms or steep slopes; they are predominantly influenced by physical disturbances related to erosion via flowing water. The dominant species in cool temperate regions of Japan include *Fraxinus platypoda*, *Pterocarya rhoifolia*, and *Cercidiphyllum japonicum*<sup>4, 5</sup>.

#### Riparian forests on alluvial fans and lowlands

Riparian forests on alluvial fans are influenced by both physical disturbance and water stress, whereas riparian forests on lowlands are predominantly affected by water stress during floods. Forests along the floodplain of the Azusagawa River (Figure 1) are classified as alluvial fan riparian forests. Lowland riparian forests are mainly dominated by *Salix* species (Figure 2).

#### Swamp forests

Swamp forests occur in areas with a high water table (e.g., riverine backswamps, swamps, and valley bottoms). The dominant species in swampland forests of the cool temperate regions of Japan are *Alnus japonica* and *Fraxinus mandshurica* var. *japonica*. These forests presumably occupied vast lowland areas in the past; however, most of these regions are now deforested.

Riparian forests influence ecosystem functions within riparian landscapes and their adjacent aquatic environments; they provide essential ecosystem services such as soil stabilization and habitat for other taxa<sup>2, 6, 7</sup>. These forests once occupied substantial areas along the coasts of the northwestern Pacific Rim. In



Figure 2 Riparian forests in the Bolshaya Ussurka River, Russian Far East (left), and the Nakdong-gang River, Republic of Korea (right).

Japan, most natural riparian forests were lost to deforestation during World War II, followed by afforestation efforts and subsequent river improvement and dam construction projects<sup>4, 6</sup>. Decreased ecosystem function and services related to the loss of riparian forests caused by human activities are common problems, both in the northwestern Pacific Rim and worldwide. Conservation and restoration of riparian forests is therefore essential for maximizing their ecosystem services. This chapter will provide a brief overview of the current knowledge regarding riparian forests in mountainous areas, particularly in Japan.

## 2. Montane Riparian Forests

The steep slopes and valley bottoms of mountain river systems are often subject to natural disturbances such as sedimentation and erosion, which occur after heavy precipitation during storms and the rainy season<sup>2, 4, 7, 8</sup>. Plants on mountain slopes survive with difficulty in these unstable riparian habitats; however, several plant species persist despite (or have adapted to) these disturbance regimes and water stress environments<sup>4, 5, 9</sup>. For example, in the cool temperate regions of Japan, *F. platypoda*, *P. rhoifolia*, and *C. japonicum* dominate montane riparian forests<sup>4, 5</sup>, while *Euptelea polyandra* has adapted to unstable (i.e., intermittently eroded) slopes by producing large numbers of sprouts<sup>10</sup>. Most of these species are early successional species with low shade tolerance; thus, they are rare in riparian forests. Riparian forests that grow on these unstable mountain habitats tend to have distinct tree species composition and stand structure, compared with forests on adjacent gentle slopes and crests<sup>11, 12, 13</sup>.

The Ooyamazawa riparian forest is an old-growth natural forest located in the cool temperate zone of Japan (Figure 3); it lies along a mountain tributary of the Arakawa River in Chichibu-Tama-Kai National Park, Saitama Prefecture, central Japan (35°57'30"N, 138°46'32"E, 1,200-1,620 m a.s.l.). Sakio (1997) reported climate data for a study site in the Ooyamazawa riparian forest based on data collected at Nakatsugawa (700 m a.s.l.), a nearby settlement (4.6 km) that had an annual mean temperature of 10.7°C, annual precipitation of 1,100 mm, and maximum snow depth of 30 cm, respectively. Based on these data and a temperature lapse rate of 0.6°C per 100-m increase in elevation, the estimated annual mean temperature at this site (1,450 m a.s.l.) was 6.5°C<sup>14</sup>. The site lies in the upper part of a cool temperate, deciduous broadleaf forest zone<sup>14</sup>; the dominant canopy species (height > 30 m) include *F. platypoda*, *P. rhoifolia*, and *C. japonicum* (Table 1). This montane riparian forest also contains *Acer* species<sup>15</sup>. In Japan, 28 *Acer* species are distributed throughout subtropical, warm temperate, cool temperate, and subalpine forests. In the Ooyamazawa riparian forest, the subcanopy includes mainly *Acer shirasawanum* and *Acer pictum*, while the understory includes mainly *Acer carpinifolium* and *Acer argutum* (Table 1); nine other species are also present<sup>15</sup>.

During the past few decades, studies conducted in montane riparian forests in the cool temperate regions of Japan have reported information concerning species composition<sup>13, 16</sup>, species richness and forest structure<sup>5, 11, 16</sup>, and the ecology of dominant and common species<sup>4, 5, 10</sup>. For example, *F. platypoda*, whose



Figure 3 An old-growth montane riparian forest in Ooyamazawa.

Table 1 Tree species composition, life form, and size structure of the Ooyamazawa riparian forest (4.71 ha). LF: life form. D: deciduous. E: evergreen. B: broad-leaf. C: needle-leaf. T: tall tree. S: small tree or shrub. L: liana. N. ind: number of individuals. N. tree: number of standing trees. BA: basal area (m<sup>2</sup>). RBA: relative basal area (%). From Higa et al. 2020.

| Species   | LF      | N. ind | N. tree | BA    | RBA  | Max.<br>DBH |
|---|---------|--------|---------|-------|------|-------------|
| <i>Fraxinus platypoda</i>                             | D, B, T | 460    | 463     | 88.61 | 55.2 | 140.5       |
| <i>Cercidiphyllum japonicum</i>                       | D, B, T | 59     | 59      | 25.02 | 15.6 | 153.4       |
| <i>Pterocarya rhoifolia</i>                           | D, B, T | 118    | 118     | 14.07 | 8.8  | 77.7        |
| <i>Acer shirasawanum</i>                              | D, B, T | 428    | 428     | 7.33  | 4.6  | 62.8        |
| <i>Acer pictum</i>                                    | D, B, T | 271    | 272     | 6.16  | 3.8  | 92.0        |
| <i>Ulmus laciniata</i>                                | D, B, T | 95     | 95      | 6.32  | 3.9  | 89.4        |
| <i>Acer carpinifolium</i>                             | D, B, S | 484    | 508     | 2.82  | 1.8  | 47.0        |
| <i>Tilia japonica</i>                                 | D, B, T | 9      | 9       | 1.92  | 1.2  | 93.9        |
| <i>Betula maximowicziana</i>                          | D, B, T | 4      | 4       | 1.42  | 0.9  | 73.0        |
| <i>Abies homolepis</i>                                | E, C, T | 12     | 12      | 1.70  | 1.1  | 93.0        |
| <i>Carpinus cordata</i>                               | D, B, T | 52     | 52      | 0.76  | 0.5  | 21.6        |
| <i>Kalopanax septemlobus</i>                          | D, B, T | 3      | 3       | 0.84  | 0.5  | 78.0        |
| <i>Fagus crenata</i>                                  | D, B, T | 6      | 6       | 0.52  | 0.3  | 62.6        |
| <i>Betula grossa</i>                                  | D, B, T | 4      | 4       | 0.52  | 0.3  | 50.8        |
| <i>Padus buergeriana</i>                              | D, B, T | 1      | 1       | 0.31  | 0.2  | 62.7        |
| <i>Acer argutum</i>                                   | D, B, S | 138    | 141     | 0.37  | 0.2  | 13.2        |
| <i>Acer palmatum</i>                                  | D, B, S | 6      | 6       | 0.11  | 0.1  | 23.9        |
| <i>Acer rufinerve</i>                                 | D, B, S | 11     | 11      | 0.18  | 0.1  | 33.6        |
| <i>Pterostyrax hispida</i>                            | D, B, S | 89     | 89      | 0.38  | 0.2  | 16.5        |
| <i>Phellodendron amurense</i>                         | D, B, T | 1      | 1       | 0.10  | 0.1  | 35.5        |
| <i>Actinidia argute</i>                               | D, B, L | 13     | 13      | 0.10  | 0.1  | 16.2        |
| <i>Acer maximowiczianum</i>                           | D, B, T | 2      | 2       | 0.14  | 0.1  | 39.0        |
| <i>Fraxinus lanuginosa</i> f. <i>serrata</i>          | D, B, T | 2      | 2       | 0.03  | <0.1 | 19.5        |
| <i>Aria alnifolia</i>                                 | D, B, T | 4      | 4       | 0.07  | <0.1 | 25.5        |
| <i>Schizophragma hydrangeoides</i>                    | D, B, L | 8      | 8       | 0.03  | <0.1 | 10.1        |
| <i>Acer amoenum</i> var. <i>amoenum</i>               | D, B, S | 3      | 3       | 0.03  | <0.1 | 15.5        |
| <i>Carpinus japonica</i>                              | D, B, T | 1      | 1       | 0.00  | <0.1 | 7.0         |
| <i>Tsuga sieboldii</i>                                | E, S, T | 2      | 2       | 0.07  | <0.1 | 24.5        |
| <i>Hydrangea petiolaris</i>                           | D, B, L | 1      | 1       | 0.01  | <0.1 | 8.0         |
| <i>Acer nipponicum</i>                                | D, B, T | 16     | 16      | 0.15  | 0.1  | 28.7        |
| <i>Trochodendron aralioides</i> f. <i>longifolium</i> | E, B, T | 2      | 2       | 0.02  | <0.1 | 13.2        |
| <i>Acer japonicum</i>                                 | D, B, T | 3      | 3       | 0.00  | <0.1 | 3.9         |
| <i>Acer tenuifolium</i>                               | D, B, T | 7      | 7       | 0.04  | <0.1 | 15.0        |
| <i>Euptelea polyandra</i>                             | D, B, S | 10     | 10      | 0.08  | <0.1 | 16.0        |
| <i>Euonymus sieboldianus</i>                          | D, B, T | 7      | 7       | 0.05  | <0.1 | 20.0        |
| <i>Swida controversa</i>                              | D, B, T | 2      | 2       | 0.08  | <0.1 | 23.9        |
| <i>Acer cissifolium</i>                               | D, B, T | 1      | 2       | 0.03  | <0.1 | 18.2        |
| <i>Acer tschonoskii</i>                               | D, B, T | 1      | 1       | 0.00  | <0.1 | 4.1         |
| <i>Fraxinus apertisquamifera</i>                      | D, B, T | 9      | 9       | 0.05  | <0.1 | 15.3        |
| <i>Vitis coignetiae</i>                               | D, B, L | 4      | 4       | 0.02  | <0.1 | 10.0        |
| <i>Clethra barbinervis</i>                            | D, B, T | 3      | 3       | 0.01  | <0.1 | 6.4         |
| <i>Viburnum furcatum</i>                              | D, B, S | 7      | 7       | 0.01  | <0.1 | 6.8         |
| <i>Stewartia pseudocamellia</i>                       | E, B, T | 2      | 2       | 0.04  | <0.1 | 17.6        |
| <i>Padus grayana</i>                                  | D, B, T | 1      | 1       | 0.10  | 0.1  | 35.0        |
| <i>Acer distylum</i>                                  | D, B, S | 1      | 1       | 0.02  | <0.1 | 14.0        |
| <i>Celtis jessoensis</i>                              | D, B, S | 1      | 1       | 0.00  | <0.1 | 4.1         |

seedlings and saplings have high shade tolerance, forms sapling banks that allow rapid regeneration after small-scale disturbance events<sup>14, 17</sup>. These characteristics allow *F. platypoda* to be more abundant than other species in mature riparian forests<sup>14, 17</sup>. *P. rhoifolia* has lower shade tolerance, but a higher shoot growth rate, than does *F. platypoda*; therefore, *P. rhoifolia* persists on riparian sites after large-scale disturbance events<sup>17</sup>. In contrast, *C. japonicum* is more sparsely distributed in riparian forests because its germination sites are limited to fallen trees and fine mineral soils<sup>18</sup>; however, it sprouts prodigiously and is presumed to extend its lifespan by continuously replacing the main trunk with these sprouts<sup>19</sup>, which allows it to survive in unstable sites. *E. polyandra* has also adapted to unstable slopes through vigorous sprout production<sup>9, 10, 20</sup>. Cool temperate montane riparian forests are also characterized by high tree species richness (Figure 4A)<sup>11, 21</sup> and the presence of various herbaceous plants and ferns<sup>13</sup>, whose diversity is related to the complexity of the terrain and microsite conditions that result from flooding disturbance<sup>16, 22</sup>. For example, Kanumazawa riparian forests have higher species richness than do non-riparian forests on mountain slopes, according to species-area curves (Figure 4A)<sup>16, 22</sup>.

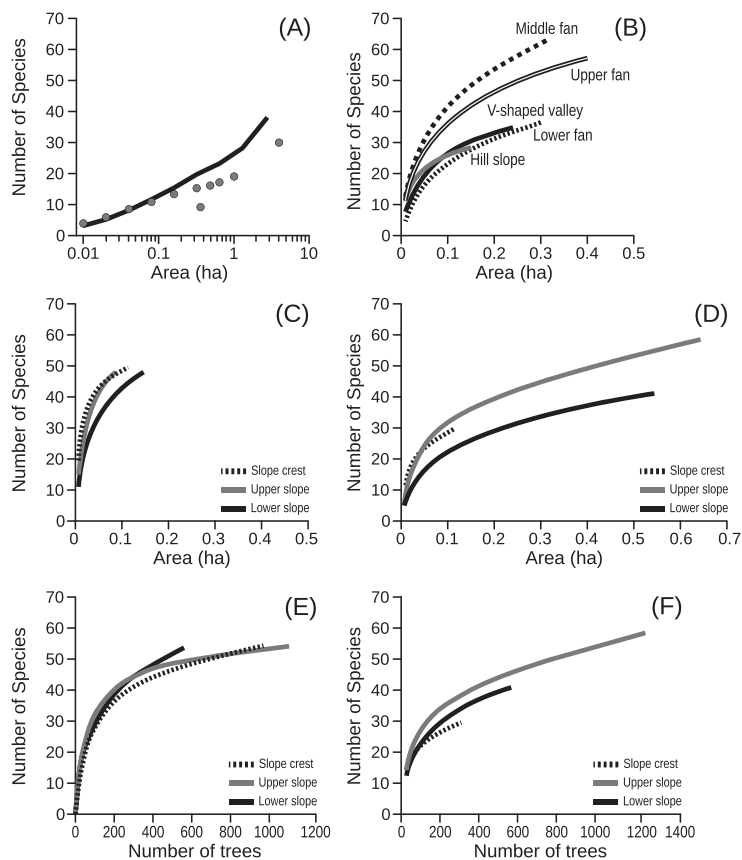


Figure 4 Species-area (A, B, C, and D), and species-density (E and F) curves for montane riparian forests in Japan. Species-area curves for (A) the Kanumazawa riparian forest (solid line), and other temperate non-riparian forests (closed circles) in cool temperate regions of Japan (after Masaki et al. 2008) and (B) old-growth forest on alluvial fans in warm temperate regions of Japan (after Ito et al. 2007). Species-area and species-density curves estimated using the jackknife method in (C, E) warm temperate secondary forests (after Ito et al. 2006) and (D, F) warm temperate secondary forests (after Akiyama et al. in press).



In comparison with cool temperate riparian forests, there is limited knowledge concerning the ecology of warm temperate montane riparian forests in Japan; most old-growth forests in mountainous areas were harvested and replaced with plantations or coppices. One example of an existing old-growth forest in the warm temperate climate of Japan is the Ichinomata Conservation Forest<sup>23</sup>. At an elevation of 500 m, this forest is located in the upper warm temperate forest zone and is characterized by steep relief. The bedrock is Shimanto zone Mesozoic sandstone and shale<sup>24</sup>. During 1981–2010, the mean annual rainfall in this region was 2,704 mm; the mean annual temperature was estimated to be 13°C at a lapse rate of 0.6°C/100 m. The tree species of the three main topographic units of this forest (slope crest, upper slope, and lower slope) are listed in Table 2. Slope crests have gentle gradients and occupy the uppermost portions of slopes; upper slopes are located below crests, and typically have steep gradients; whereas lower slopes have the steepest gradients and include lower side slopes, foot slopes, talus cones, landslide areas, debris flow terraces, and channels, which correspond to unstable riparian habitats. Tree density is greatest among slope crests, followed by upper and lower slopes. The five species with the greatest summed dominance ratios on slope crests are *Cleyera japonica*, *Symplocos prunifolia*, *Pieris japonica* subsp. *japonica*, *Chamaecyparis obtusa*, and *Tsuga sieboldii*; the corresponding species on the upper slope unit are *Cl. japonica*, *Camellia japonica*, *Quercus salicina*, *T. sieboldii*, and *Ch. obtusa*; and the corresponding species on the lower slopes are *Cl. japonica*, *Machilus japonica*, *Neolitsea aciculata*, *Q. salicina*, and *Abies firma*. Thus, species that are abundant or dominant on lower slopes are also common on slope crests and upper slopes<sup>23</sup>. Similar results were reported on the basis of studies conducted in a secondary broadleaf evergreen forest<sup>25</sup> and an old-growth forest<sup>26, 27</sup>. Species composition does not significantly differ among montane riparian forests and surrounding forests; no typical dominant species or specialists have been identified in the warm temperate forests of Japan, in contrast to the forests in cool temperate regions<sup>23</sup>.

Topographic conditions also influence tree species distribution in warm temperate evergreen broadleaf forests. In the Ichinomata Conservation Forest, the abundance and biomass of broadleaf evergreen, broadleaf deciduous, and coniferous trees vary among the three topographic units (Table 2)<sup>23</sup>. In both broadleaf deciduous trees and conifers, density and basal area gradually increase from slope crest to lower slope. Deciduous broadleaf trees are more abundant than are broadleaf evergreen trees in unstable riparian habitats<sup>25, 26</sup>, perhaps because of their shade tolerance<sup>28</sup>. Valley bottoms may provide canopy gaps of different sizes, potentially in the form of debris flow terraces after major disturbance events<sup>4, 5</sup>, which allow trees to establish and reach maturity<sup>9, 26</sup>. Valley bottoms may therefore serve as critical habitats for broadleaf deciduous trees in old-growth forests in warm temperate regions.

Forests have higher species richness in cool temperate regions than in warm temperate regions<sup>11, 23, 16</sup>. However, few studies have assessed species richness in riparian forests of warm temperate regions<sup>e.g., 25, 26</sup>. Based on species-area curves, Ito et al. (2006) showed that riparian habitats, particularly upper and middle fan zones, had higher tree species richness than did forests on the surrounding mountain slopes (Figure 4B); however, Ito et al. (2007) reported contrasting results, with lower tree species richness on lower slopes (i.e., riparian areas) than in upland forests (Figure 4C). This result may have been related to low tree density in riparian areas caused by frequent disturbance<sup>29</sup>. Therefore, Ito et al. (2007) additionally assessed species-density curves within the three topographic units; they found that species richness was highest in riparian areas (Figure 4E). Thus, lower slopes appear to be dominated by many species with small populations, such that species richness is more closely related to tree density than to area<sup>25</sup>. In the Ichinomata Conservation Forest<sup>23</sup>, species richness is lowest in riparian areas (i.e., on lower slopes; Figure 4D), even when normalized according

Table 2 Tree species composition (tree density and basal area) among the three topographic units (crest, upper, and lower slopes) in the Ichinomata Coneservation Forest. Combined tree census data, our survey data from the VBP, and PFMP data are shown. The total area of each topographic unit is shown in parentheses. SC = slope crest, US = upper slope, LS = lower slope. From Akiyama et al. in press.

| Species   | SC (0.14 ha) |                            | US (0.77 ha) |                            | LS (0.65 ha) |                            |
|---|--------------|----------------------------|--------------|----------------------------|--------------|----------------------------|
|   | Dt<br>(/ha)  | BA<br>(m <sup>2</sup> /ha) | Dt<br>(/ha)  | BA<br>(m <sup>2</sup> /ha) | Dt<br>(/ha)  | BA<br>(m <sup>2</sup> /ha) |
| <i>Cleyera japonica</i>                                   | 371.4        | 2.93                       | 472.7        | 5.37                       | 235.4        | 3.87                       |
| <i>Chamaecyparis obtusa</i>                               | 228.6        | 97.42                      | 24.7         | 11.36                      | 6.2          | 1.59                       |
| <i>Tsuga sieboldii</i>                                    | 142.9        | 39.74                      | 33.8         | 7.85                       | -            | -                          |
| <i>Quercus salicina</i>                                   | 57.1         | 1.81                       | 85.7         | 5.16                       | 44.6         | 4.60                       |
| <i>Abies firma</i>  | —            | —                          | 13.0         | 5.22                       | 12.3         | 6.57                       |
| <i>Camellia japonica</i>                                  | 85.7         | 0.52                       | 135.1        | 2.11                       | 75.4         | 1.27                       |
| <i>Symplocos prunifolia</i>                               | 314.3        | 2.00                       | 153.2        | 1.11                       | 3.1          | 0.04                       |
| <i>Machilus japonica</i>                                  | 7.1          | 0.02                       | 55.8         | 0.60                       | 144.6        | 2.32                       |
| <i>Castanopsis</i> spp.                                   | 142.9        | 1.76                       | 113.0        | 2.24                       | 3.1          | 0.33                       |
| <i>Eurya japonica</i> var. <i>japonica</i>                | 214.3        | 0.71                       | 109.1        | 0.31                       | 49.2         | 0.14                       |
| <i>Neolitsea aciculata</i>                                | 64.3         | 0.21                       | 58.4         | 0.29                       | 106.2        | 0.96                       |
| <i>Illicium anisatum</i>                                  | 50.0         | 0.51                       | 58.4         | 0.64                       | 32.3         | 0.47                       |
| <i>Distylium racemosum</i>                                | —            | -                          | 41.6         | 1.01                       | 47.7         | 0.60                       |
| <i>Quercus sessilifolia</i>                               | 7.1          | 0.21                       | 23.4         | 2.30                       | 3.1          | 1.19                       |
| <i>Pieris japonica</i> subsp. <i>japonica</i>             | 228.6        | 1.90                       | 44.2         | 0.49                       | -            | -                          |
| <i>Quercus acuta</i>                                      | 50.0         | 1.74                       | 15.6         | 1.95                       | -            | -                          |
| <i>Litsea coreana</i>                                     | —            | -                          | 18.2         | 0.51                       | 16.9         | 0.44                       |
| <i>Symplocos myrtaea</i>                                  | 121.4        | 0.55                       | 28.6         | 0.08                       | -            | -                          |
| <i>Betula grossa</i>                                      | 7.1          | 0.63                       | 3.9          | 0.39                       | 3.1          | 1.00                       |
| <i>Ternstroemia gymnanthera</i>                           | 35.7         | 0.15                       | 16.9         | 0.39                       | -            | -                          |
| <i>Cephalotaxus harringtonia</i> var. <i>harringtonia</i> | —            | -                          | 1.3          | 0.01                       | 21.5         | 0.56                       |
| <i>Rhododendron weyrichii</i>                             | 50.0         | 0.22                       | 16.9         | 0.15                       | -            | -                          |
| <i>Cornus controversa</i> var. <i>controversa</i>         | —            | -                          | 1.3          | 0.06                       | 7.7          | 0.70                       |
| <i>Cinnamomum yabunikkei</i>                              | 7.1          | 0.03                       | 13.0         | 0.13                       | 4.6          | 0.02                       |
| <i>Neoshirakia japonica</i>                               | 7.1          | 0.02                       | 6.5          | 0.03                       | 12.3         | 0.06                       |
| <i>Quercus glauca</i>                                     | —            | -                          | 7.8          | 0.12                       | 4.6          | 0.10                       |
| <i>Phellodendron amurense</i> var. <i>amurense</i>        | —            | -                          | 1.3          | 0.21                       | 1.5          | 0.33                       |
| <i>Carpinus tschonoskii</i>                               | —            | -                          | -            | -                          | 3.1          | 0.56                       |
| <i>Magnolia obovata</i>                                   | —            | -                          | 6.5          | 0.31                       | -            | -                          |
| <i>Premna microphylla</i>                                 | —            | -                          | 1.3          | 0.05                       | 10.8         | 0.10                       |
| <i>Machilus thunbergii</i>                                | 7.1          | 0.03                       | 6.5          | 0.08                       | 3.1          | 0.02                       |
| <i>Carpinus laxiflora</i>                                 | —            | -                          | 3.9          | 0.22                       | 1.5          | 0.09                       |
| <i>Acer amoenum</i> var. <i>amoenum</i>                   | —            | -                          | 1.3          | 0.31                       | -            | -                          |
| <i>Lyonia ovalifolia</i> var. <i>elliptica</i>            | 7.1          | 0.15                       | 5.2          | 0.08                       | -            | -                          |
| <i>Stewartia monadelpha</i>                               | —            | -                          | 1.3          | 0.19                       | 1.5          | 0.05                       |
| <i>Acer palmatum</i>                                      | —            | -                          | 1.3          | 0.25                       | -            | -                          |
| <i>Mallotus japonicus</i>                                 | —            | -                          | -            | -                          | 4.6          | 0.13                       |
| <i>Actinidia arguta</i> var. <i>arguta</i>                | —            | -                          | -            | -                          | 6.2          | 0.04                       |
| <i>Ilex macropoda</i>                                     | —            | -                          | 3.9          | 0.07                       | -            | -                          |
| <i>Daphniphyllum macropodum</i> subsp. <i>macropodum</i>  | 7.1          | 0.03                       | 1.3          | 0.01                       | 1.5          | 0.01                       |
| <i>Diospyros japonica</i>                                 | —            | -                          | -            | -                          | 1.5          | 0.10                       |
| <i>Cerasus jamasakura</i>                                 | 7.1          | 0.03                       | 1.3          | 0.02                       | -            | -                          |
| <i>Vaccinium bracteatum</i>                               | —            | -                          | 2.6          | 0.02                       | -            | -                          |
| <i>Ligustrum japonicum</i>                                | —            | -                          | 1.3          | <0.01                      | 1.5          | 0.01                       |
| <i>Idesia polycarpa</i>                                   | —            | -                          | -            | -                          | 1.5          | 0.07                       |
| <i>Ilex rotunda</i>                                       | —            | -                          | 1.3          | 0.06                       | -            | -                          |
| <i>Ilex pedunculosa</i>                                   | —            | -                          | 1.3          | 0.06                       | -            | -                          |
| <i>Nekemias cantoniensis</i>                              | —            | -                          | -            | -                          | 3.1          | 0.01                       |
| <i>Ilex goshiensis</i>                                    | 7.1          | 0.15                       | -            | -                          | -            | -                          |
| <i>Buxus microphylla</i> var. <i>japonica</i>             | —            | -                          | 1.3          | <0.01                      | -            | -                          |
| <i>Dendropanax trifidus</i>                               | —            | -                          | 1.3          | <0.01                      | -            | -                          |
| <i>Ilex buergeri</i>                                      | —            | -                          | 1.3          | <0.01                      | -            | -                          |
| <i>Ilex micrococca</i>                                    | —            | -                          | 1.3          | <0.01                      | -            | -                          |
| <i>Neolitsea sericea</i>                                  | —            | -                          | 1.3          | <0.01                      | -            | -                          |
| Total   | 2228.6       | 153.47                     | 1607.8       | 52.24                      | 876.9        | 28.37                      |
| Evergreen broadleaf species                               | 1778.6       | 15.27                      | 1470.1       | 25.05                      | 776.9        | 16.40                      |
| Deciduous broadleaf species                               | 78.6         | 1.05                       | 57.1         | 2.34                       | 58.5         | 3.24                       |
| Evergreen coniferous species                              | 371.4        | 137.15                     | 72.7         | 24.43                      | 40.0         | 8.72                       |

to tree density (Figure 4F). Understory plants were not strongly associated with lower slopes, and species composition was similar among the three topographical units (Figure 5). Thus, understory species richness remained low on lower slopes, even when forbs were included (Figures. 4D, F and 5). Taken together, these results indicate that montane riparian forests in warm temperate broadleaf evergreen forests are not necessarily species richness hotspots<sup>23</sup>, unlike montane riparian forests in cool temperate broadleaf deciduous forests<sup>11, 13, 16</sup>. These differences in species richness among montane riparian forests may be influenced by riparian habitat microtopography. Studies comparing species richness among microtopographic classes may be required to better understand the montane riparian forests in warm temperate regions of Japan.

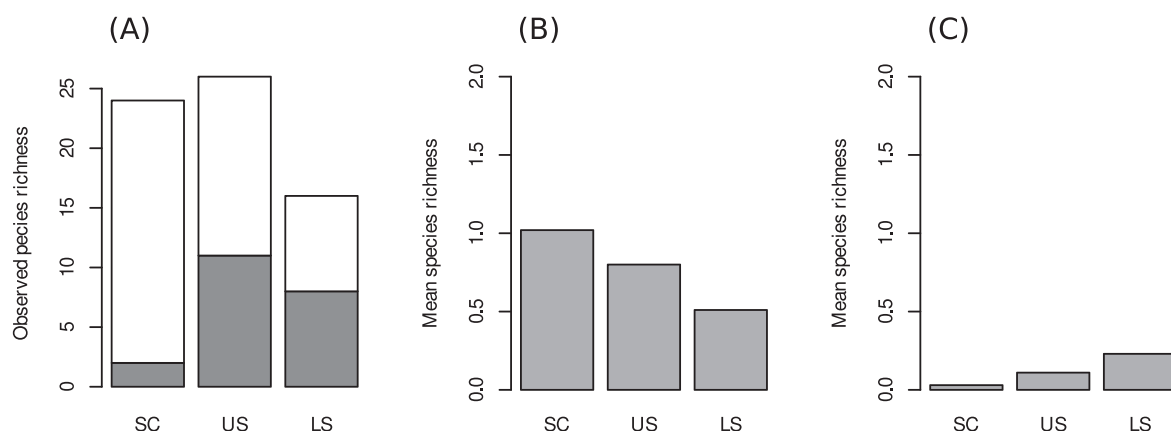


Figure 5 Species richness of understory vegetation in the survey plot. (A) Total observed species richness. Gray and white bars indicate the numbers of forest floor and non-forest floor species, respectively. (B) Mean observed species richness (/m<sup>2</sup>). (C) Mean forest floor species richness (/m<sup>2</sup>). LS, lower slope; SC, slope crest; US, upper slope. After Akiyama et al. in press.

### 3. The Threat of Sika Deer to Montane Riparian Forests

Although riparian forests are important and unique ecosystems<sup>1, 30, 31</sup>, most riparian forests in Japan were cleared during the 20<sup>th</sup> century because of increased industrial or agricultural land use and the construction of embankments for river management<sup>4</sup>; several of the remaining forests are currently under heavy browsing pressure by the sika deer, *Cervus nippon*.

Browsing by large herbivores can drastically modify the structure, environment, and tree species composition of forests<sup>32, 33</sup>. In recent decades, deer populations have increased because of decreased human activity in mountainous areas, the absence of predators, and a gradual decline in hunting; such populations have become a major problem for forest ecosystems in several regions of Japan<sup>34, 35, 36</sup>. In areas with excessive deer density, plant species diversity has decreased because of a drastic decline in forest floor vegetation<sup>37, 38</sup> and increased mortality among palatable plant species<sup>39, 40</sup> caused by heavy browsing and debarking by deer. The adverse effects of these activities on tree regeneration in natural forests have become a major concern<sup>37, 39, 40, 41</sup>. Increasing deer populations have other negative impacts on forest ecosystems and resources, including timber resource quality reduction<sup>38, 41, 42, 43, 44</sup>, decreased insect community



diversity<sup>45, 46</sup>, altered soil microbial food web structure and function<sup>47</sup>, and increased risks of soil erosion and landslides in mountainous areas<sup>48</sup>.

Deer occur in both the Ooyamazawa riparian forest<sup>49</sup> and Ichinomata Conservation Forest<sup>50</sup>; however, severe deer browsing damage has been reported only in the Ooyamazawa riparian forest<sup>49</sup>. Prior to the recent deer population increase, a 3.1-ha permanent study plot (upper and middle subplots) was established in the Ooyamazawa riparian forest in 1991, then extended by a 1.5-ha lower plot in 1998, for a total area of 4.71 ha. Tree censuses were conducted in each subplot at 5-year intervals from 1991 to 2008. During the 1980s and 1990s, the deer density around the study site was 0–6.3 head/km<sup>2</sup>. Deer density began to increase in the late 1990s, reaching 20.9 head/km<sup>2</sup> in the 2000s<sup>51, 52, 53</sup>. Recently, temporal changes in the dietary selections of deer and species-specific differences in browsing damage over time were reported using these long-term tree census data (Figure 6)<sup>49</sup>. In the first survey (1991–1992), no trace of browsing damage was found on any standing tree in the upper or middle subplots. In the second survey (1996–1998), evidence of debarking was found on three *Ulmus laciniata* trees and one *A. shirasawanum* tree (Figure 6). Thereafter, evidence of deer browsing increased rapidly; it was observed on 170 trees of eight species in the third survey (2001–2003). Among these tree species, *A. argutum*, *U. laciniata*, *Pterostyrax hispida*, and *A. carpinifolium* were preferentially browsed by deer, compared with *F. platypoda*, *A. pictum*, and *A. shirasawanum* (Figure 6). Browsing damage was initially recorded primarily on trees with smaller diameter at breast height (DBH; 4–20 cm); however, browsing distribution gradually expanded to include larger trees (DBH > 20 cm). Prior to the sharp increase in deer abundance, the forest floor had dense vegetation cover, with greater plant species richness, including *Parasenecio tebakaensis*, *Parasenecio delphiniifolius*, *Chrysosplenium macrostemon* var. *macrostemon*, *Laportea bulbifera*, *Impatiens nolitangere*, *Dryopteris crassirhizoma*, *Dryopteris polylepis*, and *Polystichum tripterum*; after the increase, only unpalatable and poisonous plants such as *Veratrum album* subsp. *oxysepalum*, *Aconitum tonense*, and *Scopolia japonica* remained on the forest floor, and in low abundance<sup>54</sup>.

In deer, diet is determined by the physical ease of feeding, as well as the nutritional and lignin contents of

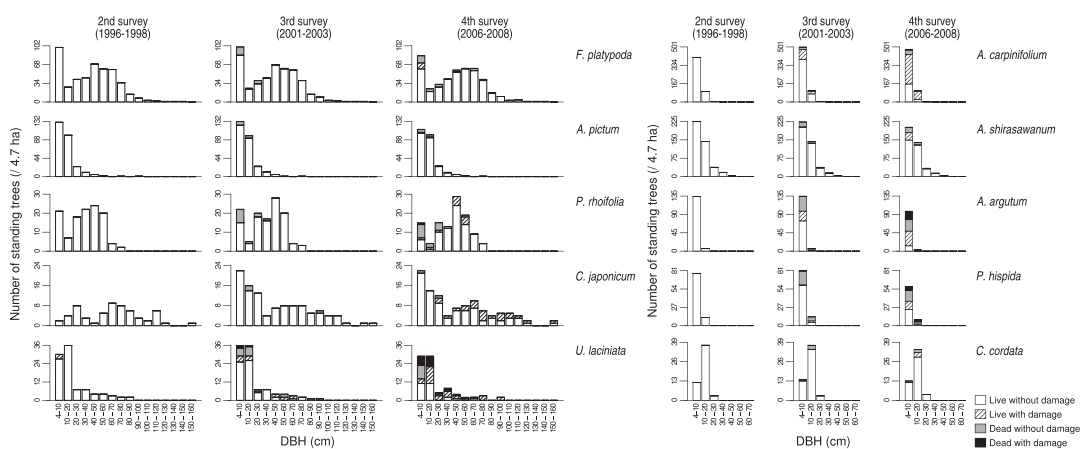


Figure 6 Temporal changes in browsing damages by sika deer and DBH distributions (number of standing trees in 4.7 ha) of the main 10 tree species in the Ooyamazawa riparian forest from the second to fourth survey. Browsing damage included feeding damage to leaves and stems, bark-stripping, and fraying damages to bark. From Higa et al. 2020.

plants<sup>32, 55, 56</sup>. Higa et al. (2020) reported that the severe browsing damage experienced by *A. argutum*, *A. carpinifolium*, and *P. hispida* may have been related their comparative small size among tree species in this forest. DBH and tree height generally vary among species in natural forests. These three species have low tree height and small maximum DBHs; they also produce many sprouts without scarring related to disturbance. Smaller trees have more leaves and stems at lower heights, which are accessible to deer. In addition, tree bark becomes thicker, harder, rougher, and more suberizing with increasing tree diameter. Therefore, these three species may have been easier for deer to browse<sup>49</sup>. In contrast, *F. platypoda* and *A. pictum* have greater tree heights and trunk diameters. Forest floor vegetation, which includes the seedlings and saplings of these two species, has almost disappeared because of heavy deer browsing pressure, except for poisonous herbs such as *V. album* subsp. *oxysepalum*, *Aco. tonense*, and *S. japonica*. Thus, despite their palatability, deer may show lower preference for these species because they produce comparatively fewer leaves and stems at lower heights; they also have thicker bark than do other species. These results indicate that deer browsing activity can greatly reduce tree species diversity among functional types such as shrub species, which have low height and small maximum DBHs, in montane riparian forests. Furthermore, *U. laciniata* experienced the most deer browsing damage among the four preferred species, which is consistent with the reports of previous studies<sup>36, 57</sup>. This species may be preferentially targeted because of its low bark lignin content<sup>56, 57</sup> and the physical ease of bark strip peeling<sup>57</sup>.

In an old-growth riparian forest dominated by *Ulmus davidiana* var. *japonica* in the Nikko district in central Japan, heavy browsing and debarking by deer have resulted in a decline in forest floor vegetation and dieback of mature trees<sup>58</sup>. The deer population is expected to continue to increase and expand throughout less snowy regions of Japan. Therefore, riparian forests are expected to experience increasingly serious damage because of deer browsing activity.

## 4. Concluding Remarks

This chapter provide brief overview of the current knowledge about riparian forests in mountainous areas in Japan. The montane riparian forests in cool-temperate regions of Japan are characterized by distinctive species composition, high species richness, and species specialized to the conditions in riparian habitats; however, these characteristics are not necessarily correspond to the montane riparian forest in warm-temperate regions<sup>23</sup>. In addition, some montane riparian forests are facing to the threat caused by overpopulation of sika deer<sup>49</sup>. Although, riparian forests are important and unique ecosystems, there are limited studies in the Kuroshio regions except Japan, to the best of my knowledge. Therefore, several knowledge gaps remain. For example, do montane riparian forests in subtropical and tropical regions have similar characteristics to the warm-temperate montane forests of Japan? Similarly, do those forests in northern regions have different characteristics to those in cool-temperate regions in Japan? Further studies is required to fulfill our ecological knowledge gaps of montane riparian forests in the region along the northwestern Pacific side.

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