

17 Diversity of tree species in mountain riparian forest in relation to disturbance-mediated microtopography

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17.1 Introduction

17.1.1 Riparian forests with high species richness

In riparian forests, concurrent disturbances of the canopy and ground is thought to be responsible for the high hardwood and herb species diversity, both in terms of species richness as well as equitability (Baker 1990; Nillson et al. 1989; Pabst & Spies 1999).

The riparian forests of northern Honshu Island in Japan are also characterized by a high diversity of tree species (Suzuki et al. 2002). Fig. 1 shows an example of a species-area curve for riparian forest in the Kanumazawa Riparian Research Forest (KRRF) (Hoshizaki et al. 1997, 1999; Masaki et al. 1999, 2005; Suzuki et al. 2002), compared to other temperate forests on Honshu Island for similar climatic conditions to those of KRRF (cf. Hara et al. 1995; Masaki 2002; Masaki et al. 1999; Nakashizuka & Numata 1982a, 1982b). The KRRF was observed to

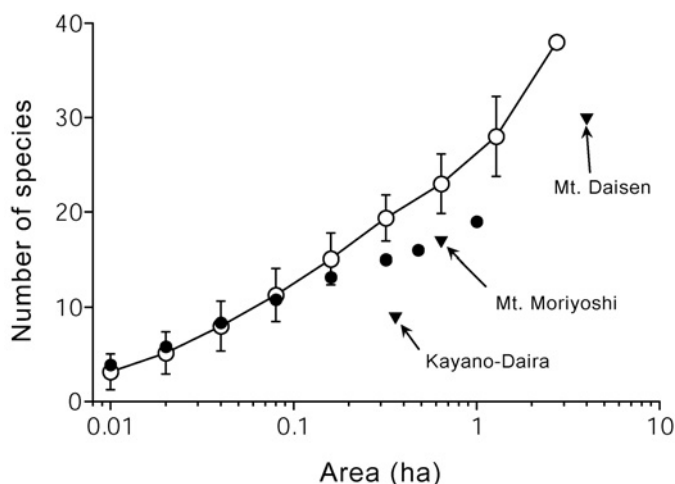


Fig. 1. The number of tree species (for stems ≥ 5 cm DBH) in a temperate riparian forest (KRRF: open circle) and other temperate non-riparian forests (closed symbols) as a function of stand area. Closed circles represent the number of species at the upper terrace KRRF. Closed triangles are based on the reports by Nakashizuka and Numata (1982a, 1982b) and Hata et al. (1995). Vertical bars show standard errors

have a higher associated species richness than non-riparian forests at spatial scales greater than 0.1 ha. The majority of the non-riparian forests examined had a beech (*Fagus crenata* Blume) and an oak (*Quercus crispula* Blume) as dominant species, and were also characterized as having a lower overall richness of tree species. Conversely, riparian forests were characterized as having a greater diversity of species, including *Cercidiphyllum japonicum* Sieb. et Zucc., *Aesculus turbinata* Blume, *Pterocarya rhoifolia* Sieb. et Zucc., in the KRRF (Suzuki et al. 2002) as well as elsewhere (e.g., Kaneko et al. 1999; and also see Chapter 6).

One possible explanation for the higher species richness in riparian forests is the greater heterogeneity of the riparian forest microenvironment, which provides riparian species with a variety of specific habitats to which they are better adapted. While this is a deterministic interpretation underlying the high species richness, a number of stochastic mechanisms are also possible. For example, multiple and complex disturbance regimes, such as canopy gaps and flooding may provide less adapted species the opportunity to recruit (cf. Chesson 1986; Masaki et al. 2007).

Among these two mechanisms, in this chapter, we examine the following deterministic hypothesis: heterogeneous microenvironments should facilitate the coexistence of numerous species in riparian forests, as well as be responsible for the higher diversity of tree species *in situ*. The data for the analyses was obtained during tree censuses in the KRRF.

17.1.2 Diversity at different scales

Given that species richness is usually dependent on spatial scale (e.g., Pollock et al. 1998), we examined diversity patterns at two spatial scales. One is at the local stand-level while the other is on a larger scale, such as at the landscape level. Diversity at the larger level refers to a change in the species assembly along the gradient from the riparian to the higher altitude area (i.e., gamma diversity). This will provide us with the information on how riparian ecosystems function as species pools in the landscape. Conversely, diversity at the local level means how tree species differently colonize microhabitats within riparian areas (i.e., alpha diversity). To examine species diversity at these different scales, the large-plot studies covering this wide range of habitats within the KRRF have provided useful information.

Previously, Suzuki et al. (2002) briefly analyzed species diversity within KRRF at these spatial scales. They showed that the high species richness in the KRRF was largely attributed to greater number of riparian species and the increased occurrence of locally rare species. In addition, many of the species that prefer xeric environments, such as the upper terraces, also occurred in the riparian area. However, these authors restricted their analysis of tree communities to only include trees of a certain minimum size (diameter at breast height (DBH) \geq 5 cm). In forests, difference in species characteristics that will affect mature tree distribution will often occur during the seedling and sapling stages of tree life history. Masaki et al. (2005) reported that water stress experienced by seedlings on the upper terraces often inhibited growth and survival of species that prefer riparian habitats (e.g., *Acer mono* Maxim), and that this would have a lasting influence on the distribution of the mature trees of these species. It is therefore important to consider the younger stages in analyses of diversity.

In addition, in the study of Suzuki et al. (2002), classification of the microtopographic characteristics within the riparian region was too simplified. The authors only distinguished between two types of microtopographic sites based on relative elevation above water level. However, in practice, lower elevation sites can be further divided into several types depending on the occurrence of the last river disturbance (i.e., flooding, erosion, sedimentation, etc.), each of which reflect the stability of the forest floor and developmental stage of organic soil. Such heterogeneity in forest floor types can often affect the success of seedling establishment in riparian forests (Kubo et al. 2000, 2004; Sakio 1997; Sakio et al. 2002), and may consequently promote coexistence among species in riparian forests. It is thus necessary to classify the microtopography of riparian forests more comprehensively in analyses of the relationships between the diverse species characteristic of this environment. Consequently, in this chapter, we analyze community structure by also considering the earlier stages of life history, and by characterizing microtopographic sites in greater detail.

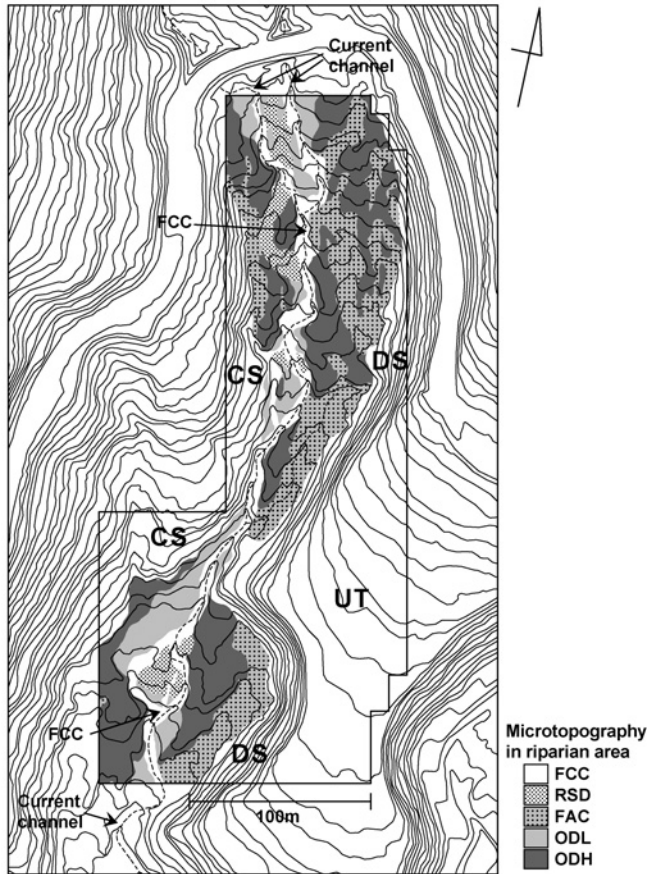


Fig. 2. The topography of KRRF. The 4.71-ha plot is shown by the polygon in solid line. The contour interval is 2 m. The dashed line represents the current channel. Abbreviations are as follows: FCC: floodplain around the current channel, RSD: recent sediment deposition, FAC: floodplain around the abandoned channel, ODL: older deposition at lower elevation, ODH: older deposition at higher elevation, CS: colluvial slope, DS: denudation slope, UT: upper terrace

17.2 Methods

17.2.1 Census methods

The study plot (4.71 ha; Fig. 2) was established in KRRF (39°N, 141°E, 400 to 460 m a.s.l.) in 1993. Mean annual temperature is 9.2 °C, while mean annual precipitation is 2060 mm and a maximum snow depth in winter of up to 2 m. This area has never been logged and appears to exhibit the mature conditions associated

with old-growth forests. The plot includes a riparian area and an adjacent upper terrace with a relief distance of ca. 20 m. These two major topographic units are separated by a denudation slope. The other side of riparian area is bounded by a colluvial slope.

The dominant species within the riparian area of this forest is *Cercidiphyllum japonicum* (26% of total basal area at breast height), followed by *Aesculus turbinata* (19%), *Fagus crenata* (15%), *Quercus crispula* (13%), *Pterocarya rhoifolia* (9%), and *Acer mono* (8%) (Suzuki et al. 2002). All of these species are tall, deciduous trees. In terms of maximum size, *C. japonicum* reaches >150-cm DBH, followed by *A. turbinata*, *F. crenata* and *Q. crispula* (100 to 120-cm DBH) and *P. rhoifolia* and *A. mono* (ca. 80-cm DBH). Of these, *F. crenata* and *Q. crispula* were distributed in both the riparian and upper terrace areas, while other species were specific to the riparian area.

In this plot, censuses were conducted on several occasions for trees with DBH 5 cm (referred as 'mature trees' for convenience) during the eleven years from 1993 to 2003. The mean DBH was calculated for each of the standing trees for the period that the tree was alive, and transformed into basal area (BA) using the equation: $BA = DBH^2\pi/4$. For the census of saplings, 315 quadrats ($2\times 2\text{ m}^2$) were made in $10\times 10\text{ m}$ grids of the plot: 192 for the riparian area, 110 for the upper terrace, and 13 for the slopes. In this study, a sapling was defined as a tree with stem length $\geq 10\text{ cm}$ and DBH $< 5\text{ cm}$. The number of trees was used to create an index of the specific dominance at the sapling stage because most of the saplings did not reach breast height.

17.2.2 Topography and microtopography

As mentioned above, four major topographic units were recognized: riparian area (RA), colluvial slope (CS), denudation slope (DS), and upper terrace (UT) (Fig. 2). The upper terrace is drier than the riparian area, with the summer soil matrix potentials at a 10-cm depth from the surface decreasing to -0.14 MPa in the riparian area and -0.25 MPa in the upper terrace (Masaki et al. 2005).

Within the riparian area, identification of microtopographic sites was also visually assessed and as a result, five microtopographic units were recognized: a floodplain around the current channel (FCC), a floodplain around an abandoned channel (FAC), recent sediment deposition (RSD), and older deposits. Older deposits were also classified into those at a lower elevation (ca. <2 m above water level (a.w.l.); ODL) and those at a higher elevation (ca. 2-4 m a.w.l.) (ODH), which were identified visually by apparent steps. To summarize, in order of ascending elevation above water level, microtopographic sites within the plot were as follows: FCC, RSD, FAC, ODL, ODH, CS, DS, and UT.

17.2.3 Analysis

To test for any distribution bias to any topographic or microtopographic sites for

each species, parametric tests such as the χ^2 -test are not useful because the carrying capacity of these sites differ with respect to each other (see Fig. 7 below). Consequently, the null hypothesis that the probability of a species occurring is proportional to the area of each (micro) topographic site is thus not valid.

We therefore permuted species randomly among tagged stems. This procedure was repeated 10,000 times and the confidence interval of expected dominance was estimated at each site. For representing specific dominance, basal area was used for mature tree populations and the number of stems was used for sapling populations.

17.3 Diversity on a larger scale

17.3.1 Topographic preference of mature trees

Based on the distribution patterns of mature trees, species were categorized into the four representative categories shown in Fig. 3. Certain species, such as *Cercidiphyllum japonicum* and *Pterocarya rhoifolia*, exhibited a biased distribution toward the riparian area. *Aesculus turbinata* and several other species preferred both the riparian area and the colluvial slope. As in other riparian forests

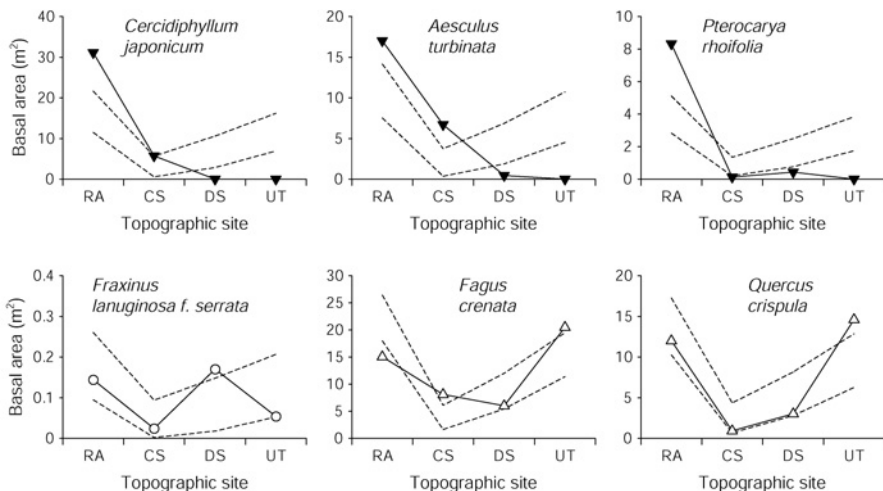


Fig. 3. Basal area of some representative species at each of the topographic sites within the plot. Data with solid lines are observed values and those with dashed lines represent 95% confidence envelopes. Abbreviations are as follows: RA: riparian area, CS: colluvial slope, DS: denudation slope, UT: upper terrace

Table 1. Species ordination based on preference of mature trees and saplings for topographic sites

Preference of mature trees	Preference of saplings				
	RA	CS	DS	UT	No significance
RA	<i>Acer mono</i> , <i>Ulmus laciniata</i> , <i>Cercidiphyllum japonicum</i> , <i>Zelkova serrata</i> , <i>Pterocarya rhoifolia</i> , <i>Aesculus turzinata</i> , <i>Kalopanax pictus</i> , <i>Magnolia obovata</i> , <i>Morus bombycis</i> , <i>Acer palmatum</i> var. <i>amoenum</i> , <i>Swida controversa</i>	-	-	-	-
CS	<i>Euonymus oxyphyllus</i>	-	-	-	<i>Acer nipponicum</i> , <i>Tilia maximowicziana</i>
DS	<i>Fraxinus lanuginosa</i> , <i>Carpinus laxiflora</i>	-	-	-	<i>Sorbus alnifolia</i> , <i>Prunus sargentii</i> , <i>Alnus pendula</i>
UT	<i>Quercus crispula</i>	<i>Acanthopanax sciadophylloide</i>	<i>Acer distylum</i> , <i>Hamamelis japonica</i> var. <i>obtusata</i>	<i>Prunus grayana</i> , <i>Magnolia salicifolia</i> , <i>Acer japonicum</i> , <i>Rhus trichocarpa</i> , <i>Clethra barvinervis</i>	<i>Acer sieboldianum</i> , <i>Acer micranthum</i> , <i>Fagus crenata</i>
No significance (rare species)	<i>Clerodendrum trichotomum</i>	<i>Benthamidia japonica</i>	-	-	<i>Castanea crenata</i> , <i>Euonymus alatus</i> f. <i>ciliatodentatus</i> , <i>Ilex macropoda</i> , <i>Phellodendron amurense</i> , <i>Styrax obassia</i> , <i>Salix caprea</i> , <i>Alnus hirsuta</i> var. <i>sibirica</i> , <i>Betula maximowicziana</i> , <i>Acer rufinerve</i> , <i>Tilia japonica</i> , <i>Salix dolichostyla</i> , <i>Aralia elata</i> , <i>Sorbus commixta</i> , <i>Euonymus macropterus</i>

in Japan (e.g., Kaneko 1999), these above species appeared to be specific to the riparian area and were collectively referred to as the RA-preferring species. Other species, such as *Fraxinus lanuginosa* Koidz. preferred the denudation slope (DS-

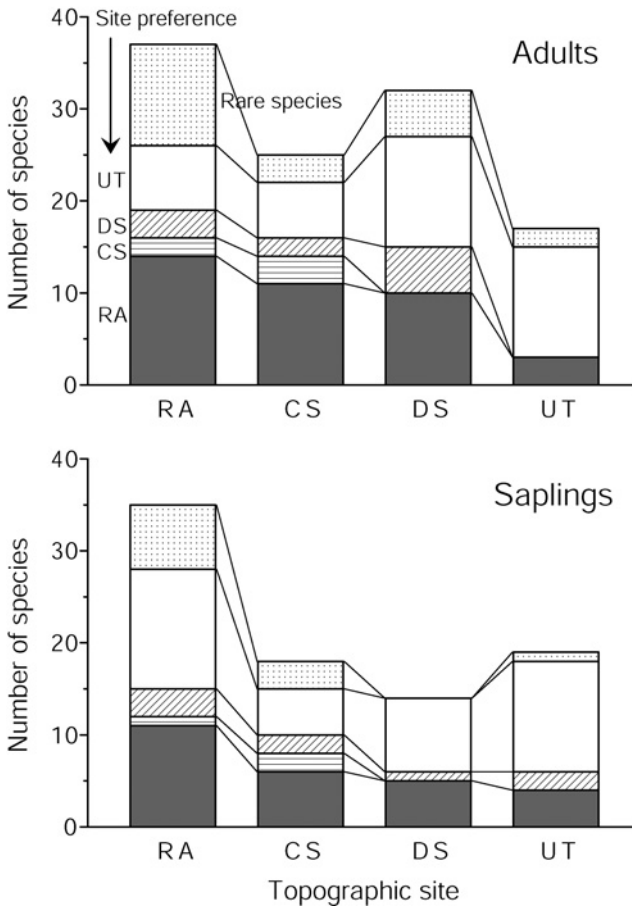


Fig. 4. The number of species at each of the topographic sites within the plot for mature trees (≥ 5 -cm DBH; upper) and saplings (≥ 10 -cm length; lower). The data are shown for each of the distribution types. Abbreviations for topographic sites are given in the caption for Fig. 3

preferring species), while others such as *Fagus crenata* and *Quercus crispula*, preferred the upland upper terraces (UT-preferring species).

Based on this analysis, specific preference could be summarized as shown in Table 1. The table shows that eleven of forty-seven species were RA-preferring. For other categories of distribution, there were three CS-preferring species, five DS-preferring species, and 12 UT-preferring species.

The other 16 species did not exhibit any significant bias ($p > 0.05$). Since none of the species had basal areas exceeding $0.07 \text{ m}^2 \text{ ha}^{-1}$ (0.18 % of the total) in this plot, these sixteen species were considered to be too scarce to test for distribution patterns (i.e. rare species).

17.3.2 Occurrence of mature trees

Using this classification of species, the occurrence of species on each topographic site was examined. As shown in Fig. 4, the number of species at the mature tree stage was highest in the riparian area and lowest on the upper terraces. DS had a comparable number of species compared to RA, even though the sample area of DS was smaller than RA. However, as discussed below, DS was characterized by having the lowest basal area of all the sites due to repeated disturbance by denudation attributed to the gliding action of snow.

The riparian area was characterized by an abundance of rare species as well as by RA-preferring species. Seven of the UT-preferring species inhabited the RA. Conversely, the upper terrace was characterized mostly by UT-preferring species. Only three RA-preferring species inhabited the upper terrace. In addition, species preferring slopes were found to inhabit the riparian area but not the upper terrace. These patterns appear, in part, to be caused by the sporadic removal of evergreen shrubs and dwarf bamboos by river disturbances in the RA. These results mean that the riparian area functions as the species pool for this region.

17.3.3 Topographic preferences of saplings

We then tested whether the observed site preferences of mature trees could be extended to the distribution of saplings (Fig. 5, Table 1). It is clearly shown that saplings of RA-preferring species are more commonly found in the riparian area.

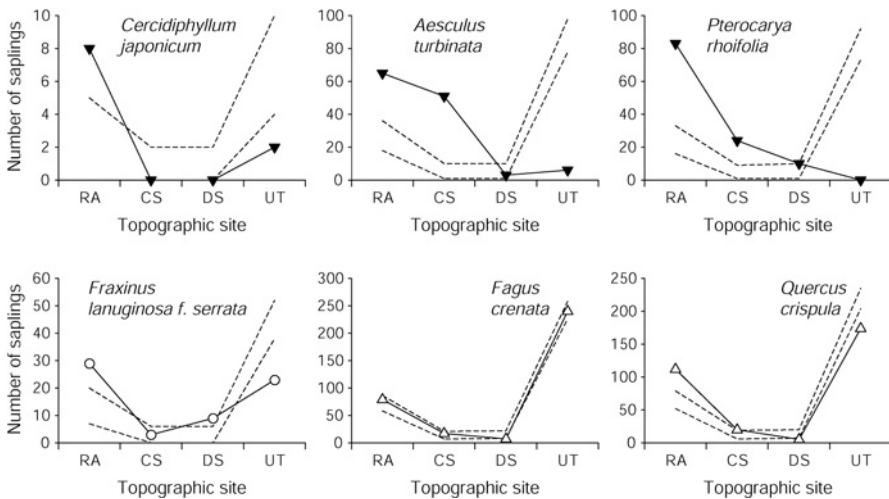


Fig. 5. Number of saplings for several representative species at each of the topographic sites within the plot. Data with solid lines are observed values and those with dashed lines represent 95% confidence envelopes. Abbreviations of topographic sites are the same as those in Fig. 3

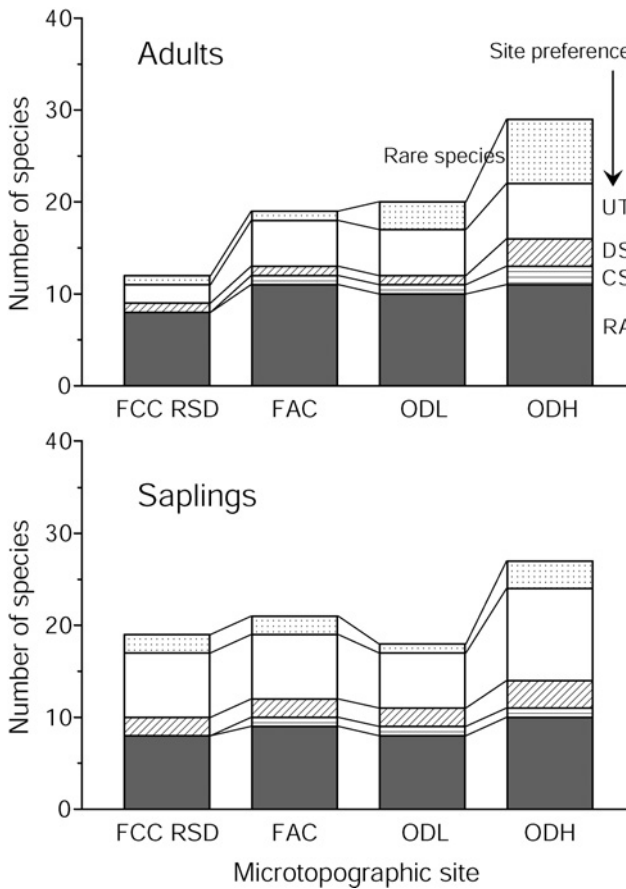


Fig. 6. The number of species at each of the microtopographic sites within the riparian area of the plot for mature trees and saplings. The data are shown for each of distribution types. Abbreviations for topographic sites are given in the caption for Fig. 2

Meanwhile, saplings of UT-preferring species varied in their preference at the sapling stage. For example, saplings of *Quercus crispula* were more commonly found in the riparian area, while distribution of *Fagus crenata* appeared to be a site-generalist. As a result, more than half of these species did not exhibit any significant bias to the upper terrace ($p > 0.05$).

This means that the saplings of many species prefer mesic sites to xeric sites. This is probably because, as saplings grow into mature trees, they will be selected by factors such as soil condition, resulting in a more apparent differentiation with respect to site preference in mature trees. The riparian area is likely to have favorable conditions for the saplings of most tree species. However, during the latter life-history stages of the trees, successful RA-preferring species may out-

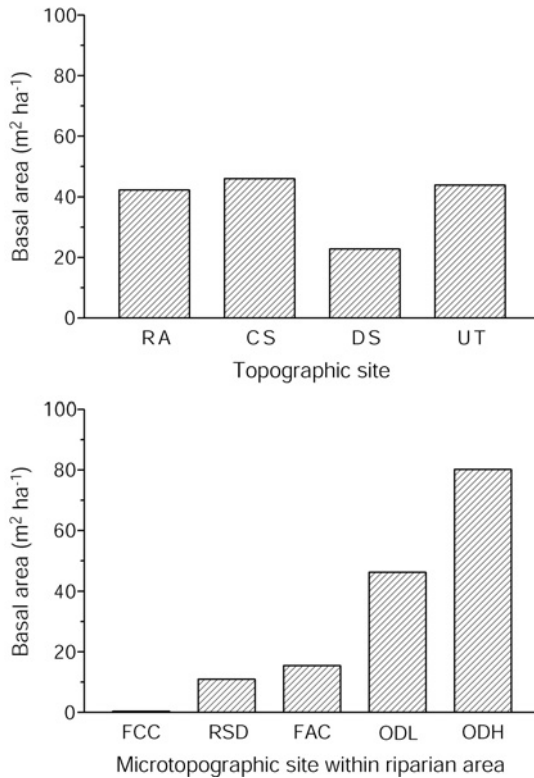


Fig. 7. Basal area of standing trees at each of topographic sites (upper) and of microtopographic sites (lower). See caption of Fig. 2 and 3 for the abbreviations of sites

compete, by superior growth, survival, resistance to external disturbance, etc., other species in the riparian area to a certain degree, resulting in niche differentiation in mature trees.

17.4 Diversity at the local stand level

17.4.1 Occurrence of hardwood species within the riparian area

The next theme is how tree species coexist within the riparian area. The occurrences of species based on the distribution categories are shown in Fig. 6, with similar patterns observed in mature trees and saplings. The number of species increased monotonically with the elevation above water level. The lowest sites (i.e., FCC and RSD) had the least number of species (12 species) while the highest

site had a three-fold increase in the number of species.

The RA-preferring species had an almost even distribution at any of the microtopographic sites surveyed within the riparian area. Conversely, UT- and DS-preferring species, as well as rare species tended to occur in greater numbers at more stable sites. Thus, riparian-specific species occur anywhere within the riparian area, but species specific to other topographic sites tended to inhabit relatively more stable sites.

17.4.2 Specific microtopographic preferences

Specific differences in microtopographic site-preference, and whether such differences, if they existed, could fully explain the patterns described above, were also investigated. Before assessing site preference however, we examined the stability and productivity of microtopographic sites using basal area (Fig. 7).

The BA for the entire riparian area (40 to $45 \text{ m}^2 \text{ ha}^{-1}$) was comparable to other topographic sites, except for DS where BA was only half that observed for the others (due to repeated surface disturbance and soil denudation, caused primarily by the glide of heavy snow). Conversely, BA was very heterogeneous within the riparian area. BA increased monotonically with elevation sequence from FCC ($<0.5 \text{ m}^2 \text{ ha}^{-1}$) to ODH (nearly $80 \text{ m}^2 \text{ ha}^{-1}$), implying that site stability at ODH was relatively high. At the same time, this also suggests greater productivity at ODH because for UT, which is also free from channel disturbance, had a BA of only ca. $40 \text{ m}^2 \text{ ha}^{-1}$. Thus, the riparian area had a mosaic distribution of microtopographic sites, each of which differed with respect to stability and productivity (e.g., Pabst & Spies 1999).

Tables 2 and 3 show the distribution bias for each life-history stage of RA- and UT-preferring species, respectively. Other categories (CS- and DS-preferring species) did not exhibit any specific preferences to any of the microtopographic sites. Rare species, which were mostly found in the riparian area, exhibited no significant bias except for *Alnus hirsuta* Turcz. var. *sibirica* (Fischer) C. K. Schn. (more mature trees at FCC and RSD), and *Clerodendrum trichotomum* Thunb. and *Salix caprea* L., formerly *Salix bakko* Kimura (more saplings at ODL).

For mature trees of the RA-preferring species, some exhibited a biased distribution toward ODH, while others showed no significant bias. It appeared that the occurrence of RA-preferring species was not significantly biased toward unstable microtopographic sites such as FCC, FAC and RSD. However, the distribution of saplings exhibited markedly different patterns, with some preferring less stable sites and others preferred more stable sites. Niche differentiation appeared to exist at the sapling stages among the RA-preferring species. Potentially, this has long term effects on the coexistence of RA-species within the riparian area, but destructive disturbances at unstable microtopographic sites can disrupt this pattern and consequently, result in a greater number of mature trees colonizing more stable microtopographic sites. This shift in the distribution of RA-species was analogous to those exhibited by UT-preferring species in larger-scale analyses (Table 1).

Table 2. Ordination of RA-preferring species based on preference of mature trees and saplings for microtopographic sites

Preference of mature trees	Preference of saplings				
	FCC, RSD	FAC	ODL	ODH	No significance
FCC, RSD	-	-	-	-	-
FAC	-	-	-	-	-
ODL	-	-	-	-	-
ODH	<i>Acer mono</i>	-	<i>Cercidiphyllum japonicum</i>	-	<i>Kalopanax pictus</i>
No significance	<i>Zelkova serrata</i>	<i>Morus australis</i> , <i>Acer palmatum</i> var. <i>amoenum</i>	<i>Ulmus laciniata</i> , <i>Aesculus turbinata</i>	<i>Magnolia obovata</i>	<i>Pterocarya rhoifolia</i>

Table 3. Ordination of UT-preferring species based on preference of mature trees and saplings for microtopographic sites

Preference of mature trees	Preference of saplings				
	FCC, RSD	FAC	ODL	ODH	No significance
FCC, RSD	-	-	-	-	-
FAC	-	-	-	-	-
ODL	-	-	-	-	-
ODH	-	-	-	<i>Quercus crispula</i>	<i>Acer japonicum</i> , <i>Fagus crenata</i> , <i>Hamamelis japonica</i> var. <i>obtusata</i>
No significance	-	-	-	<i>Acer micranthum</i>	<i>Prunus grayana</i> , <i>Acanthopanax sciadophylloides</i> , <i>Acer sieboldianum</i> , <i>Magnolia salicifolia</i> , <i>Acer distylum</i> , <i>Clethra barvinervis</i> , <i>Rhus trichocarpa</i>

On the other hand, saplings of UT-species exhibited no significant preference ($p > 0.05$) to any of the microtopographic sites, except for *Quercus crispula* and *Acer micranthum* Sieb. et Zucc. which had more saplings at the ODH. For mature trees, four species exhibited a significant bias toward ODH, while others did not. Thus, UT-species appeared to be generalists with respect to microtopography

during the early stages of their life history, subsequently being more specific with respect to habitat preference as some of these species exhibit a bias toward ODH.

17.5 Conservation of diversity at different scales

In the riparian forest described here, riparian disturbances formed a microtopographic mosaic, and provided various sites that were favorable for species within the riparian area. It has been reported that riparian forests experience both canopy disturbance by tree deaths and ground disturbance (flooding, erosion, deposition, of debris, etc.), create a diverse mosaic of vegetation, consequently resulting in a high diversity of plant species (Hughes & Cass 1997; Nillson et al. 1989). This study contributed positively to this hypothesis and corroborated previously published reports.

This study showed that microtopographic differentiation at the sapling stage occurs in riparian-specific species. In general, different soil condition preferences during the seedling and saplings stages often determine the structure of forests (e.g., Clark et al. 1999; Liang & Seagle 2002; Palmiotto et al. 2004). In other riparian forests in Japan, the seedlings of some species become established in abandoned channels and floodplains (Sakio 1997). Our results are consistent with these findings. Such differentiation would help promote coexistence of tree species within the riparian forests at a local scale.

Meanwhile, the microtopographic preferences of mature trees did not differ as clearly among species, including UT-species. In the riparian area, many of the mature trees exhibited a biased distribution at more stable sites such as sites of older deposits at higher elevation. As a result, species richness was greatest at stable microtopographic sites compared to other relatively unstable sites. Similar patterns have been reported elsewhere in Japanese riparian forests (Nakamura et al. 1997). As shown in Fig. 7, older deposits at higher elevation is most favorable for tree growth, probably reflecting soil moisture and more abundant organic content (Nakamura et al. 1997). Such stability at microtopographic sites may play a more critical role in the maintenance of locally higher species richness, than river-disturbed sites such as floodplains.

At a larger scale, this riparian forest appeared to act as a pool of tree species diversity in the landscape (e.g., Metzger 1997). Many species were found to be specific to the riparian area (i.e., RA-species), with rare species most commonly found within the riparian area. Consequently, the riparian forest was demonstrated to be important for regional species diversity. This is deterministic conclusion, also shown previously (see Suzuki et al. 2002).

In addition, the riparian forest can also act as a sink of diversity because, as opposed to RA-species which live in stable and fertile sites in the riparian area, UT-, CS-, DS- and rare species were less selective there. In the riparian forest, the populations of these species are thus expected to be less stable and closer to local

extinction than when compared to the RA-species.

This implies that some dynamic processes within the riparian forest can greatly alter species diversity in the riparian forest (Sakio et al. 2002). For example, a rare chance event such as flooding may promote colonization by rare species (cf. Chesson 1986) while concomitantly causing the local extinction of some UT-species. Therefore, the diversity in the landscape cannot be maintained by the potential of the riparian forest alone as a species pool. From the dynamic perspective, both the riparian and the surrounding forests are considered to be important for the conservation of woody flora at the level of the landscape. Long-term monitoring of the community dynamics at KRRF will illustrate how valid these expectations actually are.

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