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Shifting mosaic in maintaining diversity of floodplain tree species in the northern temperate zone of
Japan

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Abstract

We examined the relationships between floodplain forest structure and disturbance frequencies in bar-braided and incised-meandering channel sections of the Rekifune River, northern Japan. This was undertaken with special reference to the life history traits at seedling and reproductively mature stages of eight dominant species (Chosenia arbutifolia, Populus maximowiczii, Toisusu urbaniana, Salix sachalinensis, Salix pet-susu, Alnus hirsuta, Ulmus japonica, and Fraxinus mandshurica var. japonica). These species were generally arranged along the flood frequency and intensity gradient represented by five geomorphic surface types: gravel bar, lower and upper floodplain, secondary channel, and terrace. However, habitat separation between seedlings and conspecific mature stands occurred with geomorphic surface type in four of the eight species, suggesting that these species require more than one geomorphic surface type to complete their life cycles. Comparisons of stand-replacement disturbances between the bar-braided and incised-meandering rivers suggested that the shifting mosaic pattern in association with the evolution of land surfaces plays a vital role in maintaining variety in regeneration habitats and development of riparian forests in a half-century time scale. We conclude that the key factors maintaining the diversity of floodplain tree species in the studied northern temperate forests are (1) the development of diverse geomorphic surfaces providing regeneration and habitat niches, and (2) the timing of maturation and lifespan of early and mid-successional species consistent with the disturbance frequency.

Keywords: braided channel; incised-meandering channel; stand-replacement disturbance; disturbance frequency; land surface evolution; Rekifune River

Introduction

Mechanisms that maintain species richness and coexistence in forests are a central issue in plant community ecology. Using an environmental gradient analysis, Whittaker (1956) examined the vegetation in the Great Smoky Mountains and concluded that tree and shrub species were arranged along complex gradients of moisture and elevation. He emphasized that habitat partitioning is a key process in the maintenance of species diversity (Whittaker, 1965, 1967). Grubb (1977) later asserted the importance of a 'regeneration niche' in explaining the indefinite persistence of many species. This assertion was determined by focusing on niche partitioning in reproduction, dispersal, seedling establishment, and the further development of immature plants. Since then, niche-partitioning processes have been examined at each developmental stage of a life history. Nakashizuka (2001) reviewed the status of community ecology regarding the coexistence mechanism in temperate mixed deciduous forests. He suggested that selecting a particular regeneration strategy (e.g., small seeds capable of dispersing long distances) might be a disadvantage in other life stages of the tree life cycle, and emphasized the importance of investigating seed and seedling stages in the context of the entire life cycle. More recently, Strykstra et al. (2002) developed a theoretical framework using a range of trait combinations (seed bank, dispersal, and lifespan) and disturbance and safe site reliabilities to explain plant communities and to define the characteristics of safe site dynamics within communities. 'Safe site' refers to the edaphic conditions or opportunities suitable for successful seedling recruitment (Harper, 1977; Strykstra et al., 2002).

Many floodplain tree species depend on frequent flood disturbances that cause erosion and the deposition of sediments, creating heterogeneous habitats in a riverbed. Several studies have described the composition and structure of floodplain tree species with particular emphasis to their relationships with the edaphic floodplain environment (referred to as 'habitat niche' by Grubb, 1977) both in Japan (Niiyama, 1987, 1989; Ishikawa, 1988; Aruga et al., 1996) and in other countries (Johnson et al., 1976; Nilsson et al., 1989; Hughes, 1990; Girel and Pautou, 1997; Gom and Rood, 1999). Dominant species are distributed on specific geomorphic surfaces suitable for their physiological requirements. These surfaces vary by soil texture, moisture, and organic content. Such soil conditions generally

exhibit a gradient across a valley floor. The moisture retention capacity and organic content tend to vary with elevation from a riverbed because of the progressive development of alluvial deposits and differential depth to the groundwater table. However, on lower elevation sites, soils tend to be coarser because of frequent flooding, and are relatively dry during periods of low flow. Thus, elevation gradients and sediment deposition can strongly influence the spatial arrangement and succession of floodplain plant communities (Bell and del Moral, 1977; Bell, 1980; Hodges, 1997; Nakamura *et al.*, 1997). Shin and Nakamura (2005) demonstrated a geomorphic surface classification method for characterizing floodwater recurrence intervals and resultant soil conditions that successfully describes the distribution of dominant tree species. However, Harper (1977) pointed out that relationships between the distribution and abundance of adult plants and environmental features are unlikely to provide insights into establishment conditions. This is because the scale of environmental heterogeneity for mature plants is of quite a different order to that of individual seeds.

Studies on niche separation on the regeneration of floodplain tree species are limited. Karrenberg *et al.* (2002) reviewed the life history traits of *Salix* and *Populus* species on floodplains, and identified many strategies that allowed them to survive in such highly disturbed environments. Niiyama (1990) examined the coexistence of various *Salix* species at both seed dispersal and seedling stages of their life cycles and related niche partitioning to flood seasonality and soil heterogeneity. Many pioneer species in floodplain forests are light demanding, and their seedlings are not found within mature stands: thus, recruitment must occur in open spaces (Kikuzawa, 1983). This suggests that the regeneration of pioneer species requires a particular geomorphic surface that differs from that supporting mature stands of their own species (Streng *et al.*, 1989) Thus, the mechanisms of niche partitioning in floodplain trees should vary with the developmental stage of their life history.

Another mechanism for maintaining species richness is disturbance (Connell, 1978; Sousa, 1984). The floodplain ecosystem is highly dynamic, and disturbances are integral to it. Riverbeds in the northern temperate zone are seasonally or episodically eroded by either floodwaters caused by snowmelt in spring or heavy rainfall associated with storms in summer. These geomorphic disturbances create a shifting mosaic pattern of habitat patches with different disturbance frequencies and turnover times (Suzuki *et al.*, 2002). Here, the 'shifting mosaic' refers to the mosaic of floodplain

habitat patches that continually change their spatial distributions in floodplain valleys throughout successional development (Bormann and Likens, 1979). The relationship between life history traits of riparian tree species and disturbance was mainly examined at the seedling stage (Streng *et al.*, 1989; Niiyama, 1990; Jones *et al.*, 1994; Dixon, 2003). The referenced studies examined seed dispersal and seedling demography with reference to intensity and timing of specific flood disturbance events in a short time frame such as several years. However, the role of stand-replacement disturbance in maintaining diversity of floodplain tree species has not been clarified in a longer time frame of more than several decades and in a spatial scale of the entire floodplains.

The purposes of this study are (1) to examine safe site characteristics for seedling establishment of floodplain tree species in relation to the location of their mature stands using geomorphic surface classifications that reflect disturbance frequencies, and (2) to determine a role of the shifting mosaic in maintaining the diversity of floodplain tree species with special reference to the turnover time of geomorphic surfaces and the lifespan of tree species. The latter purpose is linked to a difference in the shifting mosaic between bar-braided and incised-meandering channels. Mosaic patterns of floodplain forests are developed by the recurrence of flood disturbances having a variety of magnitudes over a long period of time, rather than by specific disturbance events in a short period. We focus on the stand-replacement disturbance creating a shifting mosaic in a half-century time scale using a time series of aerial photographs and on key life stages linking with life history traits.

Study site

The study was conducted along the Rekifune River (catchment area: 539.8 km²; 42°30'N, 143°17'E) and its tributary, which runs from Mt. Yaoromappu (1794 m above sea level; part of the Hidaka mountain range) to the south of Tokachi, Hokkaido, Japan. The annual mean air temperature is 5.3 °C: the monthly mean air temperature is 13.7 °C from May to October and –3.0 °C from November to April. The annual mean precipitation from 1979 to 2002 was 1176 mm, with maximum and minimum records of 1624 mm and 786 mm, respectively. The Rekifune River basin consists of Pleistocene and Holocene sedimentary rocks.

The alluvial fan of the Rekifune River develops along a 25 km segment from its mouth, with an upstream and downstream gradient from the fan-head of 8.4% and 3.9%, respectively. The Rekifune River is an incised-meandering river in its middle reaches, beneath which it forms braided channels (Figure 1). The channel floor is about 300 m wide in the meandering reaches and 1 km wide in the braided reaches. Mature floodplain forests are widely distributed along the river, their species composition being relatively constant throughout both the meandering and braided reaches. The dominant species are C. arbutifolia, Toisusu urbaniana, Populus maximowiczii, Salix sachalinensis, Salix pet-susu, Alnus hirsuta, Ulmus japonica, and Fraxinus mandshurica var. japonica (Shin and Nakamura, 2005). These are the focus of our study.

Figure 1

The study sites were comprised of a section characterized by bar-braided channels and a section characterized by an incised-meandering channel where the bed floor is scoured (Figure 1). Drainage areas above the bar-braided and incised-meandering sections are 533.1 and 129.4 km², respectively. The braided study section is about 2 km long of the Rekifune River and is situated 1 km upstream from the river mouth. The meandering study section is a 1.5 km long stretch of a tributary of the Rekifune River, the Rekifune-nakano River, which is located about 20 km above the braided section. In the braided section, the mean floor width was about 1 km, with a gradient of 4.6%. The mean diameter and standard deviation of bed materials, obtained using a linear-lattice sampling method (Kawamura and Ozawa, 1970), was 11.5 ± 6.6 cm. In the incised-meandering section, the channel floor width was about 200 m with a gradient of 5.1%; the mean diameter and standard deviation of bed materials was 8.8 ± 7.5 cm.

Methods

We examined the distribution of seedlings and reproductively mature trees and the seed production ages and lifespans of dominant tree species from the combined data of braided and meandering sections. We compared the stand-replacement disturbance rates (destruction rates of the floodplain forests) and successive plant colonization between the two sections.

Classification of geomorphic surfaces

The gauging station used to obtain hydrological data was situated between the two study sections (Figure 1). We estimated the water discharge of each section by multiplying the ratio between the drainage area above the gauging station with that above each study section. We used hydrological data between 1976 and 1995 to calculate the recurrence interval (T_r) of a flood event using the following formula.

$$T_r = (\underline{n}+1)/\underline{m}$$

where \underline{n} is the number of years of record and \underline{m} is the rank of the magnitude of the event (Dunne and Leopold, 1978)

We produced a straight line expressing the relations between the highest yearly water level and the recurrence interval of these levels to obtain the highest water level under various recurrence intervals (for detailed information regarding recurrence calculations, see Shin and Nakamura, 2005).

First, we surveyed cross-sectional profiles of the riverbed. To include various geomorphic surfaces, we established five and six transect lines in the braided and meandering sections, respectively. For each section, we divided the riverbed into five geomorphic surfaces, classified by inundation frequencies for 2- and 20-year flood recurrence intervals (Shin and Nakamura, 2005). We defined each geomorphic surface type as follows: gravel bars as surfaces inundated during bankfull events; lower floodplains as areas inundated in a 1/2 return period (one occurrence every two years) next to the active main channel; secondary channels as areas along side channels inundated in 1/2 return period; upper floodplains as the upper parts of floodplains inundated in a 1/20 return period; terraces as floodplains higher than the upper floodplains. Based on this classification scheme, we produced a geomorphic surface map along transect lines. We filled the gaps between lines, using 1/2500 and 1/5000 topographic maps for the bar-braided and meandering sections, respectively, and conducted field verifications of the geomorphic surface maps in 1998.

Vegetation survey

We randomly established five quadrats on each of the five geomorphic surface types classified above in each river section ($n = 5 \times 5 \times 2$) to examine the relationships between geomorphic

classifications and the distribution of seedlings and mature floodplain tree species. We conducted the field vegetation surveys from 1997 to 1999. Because tree stands varied greatly in height, diameter, and density, we used three different quadrat sizes to include most of the representative tree species present in a small community patch: 5 m × 5 m, 10 m × 10 m, and 20 m × 20 m (Shin and Nakamura, 2005). The height of the crown layer and the stem density determined the choice of quadrat size. In each quadrat, we measured diameters at breast height (DBH) for trees taller than 1.3 m and at the bottom of the trunks for smaller trees.

We selected the five largest diameter trees from each quadrat and estimated the ages from ring counts on cores using an increment borer or on cross-sectional disks when trees were too small to be cored. Tree ages were averaged to determine the stand age of each geomorphic surface type. Within each quadrat, we established a 5 m × 5 m sub-quadrat specifically for seedlings, defined in this study as individuals with heights less than 1.3 m. For reproductively mature trees, we conducted vegetation survey in all quadrats during periods in which they dispersed seeds in 1999 (May and June for *U. japonica*, *F. mandshurica* var. *japonica*, *C. arbutifolia*, *T. urbaniana*, and *P. maximowiczii*, May for *S. sachalinensis* and *S. pet-susu*, and September for *A. hirsuta*). We identified seedlings and mature trees to the species level, counted the number of individuals, and recorded their heights from the ground to the tallest living bud. To determine the relative dominance of each species on each of the five geomorphic surface types, we first summed basal areas of all trees in each quadrat and calculated the basal area per unit area for each species (Nakamura et al. 1997). In each quadrat, we calculated the ratio of the basal area of each species among the eight dominant species. These data were averaged for each geomorphic surface type. We also determined the distributions of mature trees and seedlings separately across geomorphic surface types for each species based on the ratio of tree counts among the five geomorphic surface types.

We estimated both the age of initial reproduction and the maximum age for each species to examine the relationship between maturation time and longevity. In this study, the age of initial reproduction was defined as the youngest age of reproductively mature trees. We therefore measured the ages of five trees producing seeds with the smallest DBH in each quadrat and averaged for each species. Similarly, we obtained maximum ages from five individuals with the greatest DBH. Exact

estimations of maximum age are difficult because floodplain trees often die before physiological senescence in highly disturbed river environments. We defined the maximum age of a mature tree as the number of years the individual survived at a given site (hereafter, lifespan). All nomenclature follows Ohwi and Kitagawa (1983).

Environmental variables

We measured relative light intensities and volumetric soil moisture contents to determine the environmental conditions suitable for seedling recruitment and establishment. At 10 randomly selected points in each quadrat, we measured relative light intensities 90 cm above the ground in both open spaces and within young and mature stands. We used a Minoruta Digital Illuminometer from 10 am to 2 pm for the measurements. We then averaged the 10 measurements for each quadrat.

We measured soil moisture force (pF) with a tensiometer in one representative quadrat on each geomorphic surface. To obtain pF values in all quadrats, we initially established a relation between pF values and the time-domain reflectometry (TDR) percentage (soil moisture percentage on a dried soil basis). Since this relationship varies with soil texture, we measured the pF and TDR percentage simultaneously at the above five sites on six sunny days from June to August 1999. This enabled us to establish the relationship between the two factors on each of the geomorphic surface types. Finally, we conducted TDR measurements in all quadrats on July 27, 1999 (fair weather) under dry conditions (no rainfalls were recorded over the preceding 10 days except for 1-mm rainfall on July 24). We then converted the TDR values into pF values to compare the amount of soil moisture available to plants on the five geomorphic surface types. Note that high pF values indicate low soil moisture levels. Although soil moisture varies with soil texture and/or preceding rainfall amount, we considered that pF values measured on the same day under dry conditions should reflect the relative differences of available water contents among the quadrats. We carefully interpreted pF values in consideration of other soil data (texture and nutrients etc.) published in Shin and Nakamura (2005).

We estimated the intensity of flood disturbance based upon shear stress (τ) at a given geomorphic surface type. We used 20-yr recurrence interval flood as a representative high-magnitude

disturbance and compared the shear stress on each geomorphic surface type. The shear stress was calculated by the following equation:

$$\tau = \rho \underline{g} \underline{h} \underline{I}$$

where ρ is the water density ($102 \text{ kgf} \cdot \text{s}^2/\text{m}^4$), \underline{g} is the gravitational acceleration (9.8 m/s^2), \underline{h} is water depth at each surface (m) and \underline{I} is bed gradient. The shear stress was calculated at intervals of 10m on each transect line and averaged for each geomorphic surface type. This averaged shear stress was obtained for the eleven transect lines of the two sections.

We examined statistical differences in relative light intensities, soil moisture, and shear stress between the geomorphic surface types using Kruskal–Wallis one-way ANOVA (SPSS, ver. 6x). When the variables differed significantly ($\underline{P} < 0.05$), we performed multiple comparisons using Mann–Whitney \underline{U} tests. Because we tested more than a pair-wise comparison, we adjusted probabilities conservatively to α / \underline{k} using the Bonferroni procedure, where α is the desired level of significance and \underline{k} is the number of comparisons (Neter *et al.*, 1990; SYSTAT Inc., 1992).

We determined boundaries and frequencies of flood disturbances from aerial photographs taken in 1947, 1963, 1977, 1992, and 1997. The most recent photographs used for the bar-braided and incised-meandering sections were in 1997 and 1992, respectively. We rectified photographic distortion caused by the curvature of the earth and lens irregularities. We identified stream channels, gravel bars, and forests from these photographs, and examined historical changes in such areas. We estimated the frequency of stand-replacement disturbance from the number of disturbances at a given site over 50 years. The destruction rates were area-weighted for each river section to compare shifting mosaics and woody plant colonization between bar-braided and incised-meandering sections.

Results

Safe sites for seedlings and the distribution of mature trees with geomorphic surface type

Differences in both dominant species composition and stand age occurred among the geomorphic surface types (Figure 2). Dominance of *C. arbutifolia* was clear on gravel bars and lower and upper floodplains. Some pioneer species (*S. sachalinensis*, *S. pet-susu*, and *A. hirsuta*) comprised

Figure 2

dominant stands on secondary channels. The mid-successional species (U. japonica and F. mandshurica var. japonica) was most common on terraces, where all pioneer species were mostly absent. The stand age generally followed the flood frequency represented by geomorphic surface type. The different distribution pattern between pioneer and mid-successional species was more apparent at two life stages (Figure 3). Seedlings of pioneer species were most abundant on either gravel bars, lower floodplains or secondary channels whereas those of mid-successional species colonized the upper floodplains.

Figure 3

Overall, floodplain tree species occurred on more than one geomorphic surface type at different stages of their life cycles. Seedlings and conspecific mature individuals of some species were clearly distributed on different geomorphic surface types, whereas other species shared the same geomorphic surface type at both stages. The five geomorphic surface types were then analyzed in greater detail for each species. Although the gravel bars had abundant C. arbutifolia seedlings, none were found on the lower and upper floodplains. Conversely, mature trees of this species were absent on the gravel bars, and occurred mostly on the lower floodplains. Similar species that exhibited different distribution sites between seedlings and conspecific mature trees included P. maximowiczii, A. hirsuta, and F. mandshurica var. japonica. These species also dominated specific geomorphic surface types as mature trees, whereas their seedlings were distributed on geomorphic surface types subject to more frequent flooding.

In contrast, both life stages of T. urbaniana, S. sachalinensis, and S. pet-susu shared the same type of geomorphic surface. T. urbaniana seedlings were most abundant on gravel bars, on which mature trees of the same species were also found. Mature S. pet-susu trees and seedlings co-occurred (60% and 40%, respectively) along secondary channels, where this species was highly dominant.

We examined light and soil moisture conditions to characterize safe sites for seedling establishment, and shear stress to estimate disturbance intensity when the 1/20 recurrence interval flood occurs (Table 1). Even such a magnitude of flood would not inundate over the terrace deposits, and therefore no evaluation of shear stress on this surface. Gravel bars, which were exposed to sunlight, exhibited high light intensities and dry conditions on the exposed mineral soil, and suffered from the most intensive flood disturbance. Although lower and upper floodplains had similar light

Table 1

conditions, the soil of upper floodplains was the driest of the five geomorphic surface types. Except for terrace, the shear stress was lowest on upper floodplains with shallower flood depths on this surface. Ground surfaces on terraces were shaded by the large canopies of mature trees and understory vegetation. The fine sediments that accumulated on terrace surfaces retained soil-water by capillary force, even though their elevations were the highest. On secondary channels soil moisture and light conditions were similar to those on terraces (dark and wet). Alder and willow trees densely covered the exposed mineral soil. The shear stress was second highest.

Seed production age and lifespans of dominant tree species

The seeds of all eight dominant species investigated in this study are dispersed by air and/or water, and most are short-lived and germinate immediately on moist surfaces. The seeds of Salix sp. in the studied rivers are very small, ranging from 0.12 to 0.14 mg (Table 2). Seeds of other Salicaceae species, C. arbutifolia, T. urbaniana, and P. maximowiczii, are larger, ranging from 0.20 to 0.70 mg. These are followed by seeds of A. hirsuta, which range from 0.66 to 0.77 mg. Seeds of U. japonica and F. mandshurica var. japonica are much larger and heavier than those of pioneer species, ranging from 4.6 to 5.8 mg and 41.0 to 83.0 mg, respectively.

Table 2

The age at first seed production varied among the dominant eight species in this study (Table 2). Some of the earliest ages were 7.8 and 9.0 years for S. sachalinensis and S. pet-susu, respectively. When gravel bars are stable for such periods, S. sachalinensis and S. pet-susu trees can survive long enough to mature and produce seeds. The time required for maturation and seed production for C. arbutifolia, T. urbaniana, and A. hirsuta was longer, ranging from 12.9 to 15.9 years. Thus, the latter pioneer species require substrates that are stable for longer periods than are provided by gravel bars. P. maximowiczii had the longest time to maturation (48.8 years), indicating that this species requires considerably stable surface for seed production. This was roughly at the level of higher floodplains and terraces in the studied rivers (Figure 2).

We assumed that the maximum age of canopy trees found in the sampled quadrats represented the lifespan of the species in the studied rivers. Species with a shorter lifespan tends to start producing seeds earlier (Table 2). Of the eight dominant species, those with early seed

production such as S. sachalinensis and S. pet-susu had short lifespans (20–35 years), whereas F. mandshurica var. japonica required a longer period to mature (47 years) and a longer lifespan (65.4 years). C. arbutifolia, T. urbaniana, and A. hirsuta were ranked between the Salix sp. and F. mandshurica var. japonica in terms of reproduction age and lifespan (about 35 years). P. maximowiczii was an anomaly amongst the pioneer species, having both a long maturation period and lifespan. This was shown by large numbers of mature stands on upper floodplains and terraces (Figure 3).

Shifting mosaic and woody plant colonization

The destruction and colonization of woody plant species associated with flood disturbances were examined with a time-series analysis of aerial photographs. Figure 4 shows part of the riverbed in the bar-braided section from 1947 to 1997 superimposed with a geomorphic surface classification map showing the same location in 1997. The circled area was a gravel bar in 1947 that showed unvegetated open spaces near the active channel. Sparse crowns appeared in the same area in 1963, indicating woody plant colonization. The photographs in 1977 and 1997 show that the sparse stands found in 1963 had formed a dense canopy closure. The gravel bar initially identified in 1947 had evolved into a higher floodplain by 1997.

Figure 4

In the incised-meandering section, the floodplain forest was relatively unchanged (average destruction rate: 1/49.8, Figure 5, Table 3), with 44% undisturbed riverbeds (0/50, representing zero occurrences in 50 years). The proportion of most frequently destroyed areas (3/50, once in 16.7 years on average) was only 12%. In contrast, the braided section was frequently disturbed (average destruction rate: 1/35.7). Combined the areas of 3/50 and 2/50 destruction rates, 46% of the braided section was destroyed once every 25 years on average.

Table 3

Figure 5

The areas of gravel bars, lower and upper floodplain, and terrace almost corresponded to those of 3/50, 2/50, 1/50 and 0/50 destruction rates, respectively (Table 3). In the braided section, the gravel bars, lower and upper floodplains, and secondary channels accounted for 76% of its valley floor in which pioneer species C. arbutifolia, T. urbaniana, P. maximowiczii, and other Salix species, dominated (Figure 2). However, in the incised-meandering section, terraces accounted for more than

40% in which mid-successional species dominated.

Discussion

Distributions of seedlings and mature trees on the diverse geomorphic surfaces

Stand age generally corresponded with the flood frequency of geomorphic surface type. Young stands were established on the gravel bars because these surfaces suffered from frequent flooding, whereas old stands were on the terraces because of lack of disturbance. The relative dominance of the eight tree species was arranged along the flood frequency gradient represented by the five geomorphic surface types (Figure 2). However, for pioneer species, the dominant life stage on gravel bars and upper floodplains was seedlings and mature trees, respectively. As such, the regeneration niche should be further examined (Grubb, 1977; Niiyama, 1990). Although light and soil moisture conditions were similar within a same geomorphic surface type, they differed among types (Table 1). Seedlings of each species were concentrated on either one or two geomorphic surface types, indicating that species-specific safe sites could be characterized by different types of geomorphic surfaces. Salicaceae requires higher light intensities for seed germination and establishment compared with U. japonica and F. mandshurica var. japonica (mid-successional species). However, intraspecific differences in the efficiency of light utilization also exist among the Salicaceae (Maruyama et al., 1972; Koike and Haruki, 1985). Soil moisture requirements for seed germination also vary among these species (Nagasaka et al., 1994). For example, although P. maximowiczii and S. sachalinensis can germinate under limited moisture conditions, C. arbutifolia cannot. Past studies have addressed the importance of substrate conditions for initial recruitment and subsequent establishment and determined species-specific requirements for substrate texture and moisture conditions (Niiyama, 1987, 1989; Ishikawa, 1988; Aruga et al., 1996; Nagasaka, 1996).

Substrate preference at seedling and sapling stages is particularly important and may determine community composition at the mature stage (Kobe, 1996). Upland forest studies have demonstrated that seedling survival or distribution along topographic gradients is consistent with adult distribution (Shibata and Nakashizuka, 1995; Stohlgren et al., 1998). On the contrary, Sakio (1997)

found a segregated distribution between saplings and mature trees of Fraxinus platypoda in a floodplain forest. Streng et al. (1989) and Jones et al. (1994) also found negative associations between adults and conspecific seedling survival or sapling density. Seedlings of a species whose seeds are dispersed over a short distance must have strategies to survive near conspecific mature trees, whereas species capable of dispersing seeds over a long distance have a greater chance of arriving at a distant safe site. The latter strategy may be more advantageous in floodplain habitats where frequent flood disturbances promote the availability of exposed surfaces. Consequently, segregated colonization occurs between seedling and adult stages within the same species (Sousa, 1984). Our study demonstrated that seedlings and mature trees of some species in floodplain forests were distributed on different types of geomorphic surfaces arranged along the disturbance frequency gradient on the valley floors. For example, whereas gravel bars are recruitment sites for C. arbutifolia seedlings, the lower and higher floodplains are growing sites for older or mature trees producing seeds.

The past studies on seedling dynamics of several years suggested that timing, duration and intensity of flooding as well as drought, herbivory and canopy shade determined the survival rate of seedlings, and that their influences differed among the species (Streng et al., 1989; Jones et al. 1994). In a longer time frame, this study suggests that flood frequencies and intensities, which interact with light availability and edaphic conditions and channel dynamics can be another important determinant directing the successive development of floodplain forests (Akashi, 1988). For example, although C. arbutifolia dominates gravel bars (greater than 60%), the trees are too immature to produce seed (about seven-years old on average). These seedlings may grow into mature trees only if the gravel bars are stabilized without extreme scouring by a high shear stress (Table 1) and unpredictable sediment deposition by flooding. The fast growth of C. arbutifolia axial roots in coarse gravel deposits might be a great advantage in resisting strong floodwaters and allowing continued growth on gravel bars (Ishikawa, 1994; Ishikawa and Asahina, 1997). Although the geomorphic surface types necessary for seedling establishment are determined by species-specific requirements of the substrate environment, the surfaces required by mature trees are determined by flood frequencies and intensities. Sakai et al. (1999) also suggested that the survival of floodplain tree species in old mature patches could be determined by their longevity and long intervals between disturbances rather than shade

tolerance characteristics during the seedling stage.

The role of a shifting mosaic in maintaining the diversity of floodplain tree species

The time-series analysis of aerial photographs clearly exhibited the dynamic features of bar-braided rivers. This frequent lateral migration creates a shifting mosaic structure of the floodplain landscape (Bormann and Likens, 1979). The floodplain landscape development identified in this study could also be explained by geomorphic processes. Between 1947 and 1963, the channel migrated laterally to the left bank, thereby leaving the right bank as a stable geomorphic surface (Figure 4). Trees established on this surface act as effective roughness elements, promoting gradual over-bank sedimentation in association with flooding (Friedman *et al.*, 1996; Scott *et al.*, 1996; Nakamura *et al.*, 1997). Successive chronic sedimentation elevated the original low surface on the right bank and decreased the resultant flood frequency and intensity. In contrast, the vegetation on the left bank was destroyed by channel migration, which scoured the channel bed sediment and created a large area of open space on the left bank. These open spaces in 1997 could be classified as gravel bars, which are recruitment sites for pioneer species. Canopy cover on the left bank in 1947 indicated that it was a stable geomorphic surface and could be classified as a lower or higher floodplain where late successional species could colonize. This left bank surface changed substantially over the 17 years following 1947, from a stable surface to gravel bars or flowing channels. Lower floodplains distributed along the stream channels in 1997 had been likely disturbed before 1963. Likewise, upper floodplains situated along the right bank areas were subject to disturbance before 1947. Terraces have not been disturbed for more than 50 years. The geomorphic surfaces in the actively migrating channel were subject to relatively continuous disturbances. This shifting mosaic pattern in association with the evolution of land surfaces plays a vital role in maintaining variety in regeneration habitats. The geomorphic surfaces in the actively migrating channel were subject to relatively continuous disturbances. This shifting mosaic pattern in association with the evolution of land surfaces plays a vital role in maintaining variety in regeneration habitats.

In the bar-braided section in this study, the number of flowing channels averaged 6.4 ± 1.1 (mean \pm 1SD), which represents the number of dividing and rejoining channels around multiple gravel

bar islands and vegetated floodplains. In the meandering section, although bank erosion following lateral channel migration destroyed floodplain forests, the incised-meandering pattern was developed by the stream channel in association with the entrenchment of previous floodplains. Thus, in the meandering section, downward erosion prevailed over lateral erosion, with only a limited extent of channel migration. Accordingly, the incised-meandering section was characterized by a lower average number of flowing channels (mean \pm 1SD: 2.3 ± 0.8). Therefore, flood disturbances in the meandering section were limited to the narrow valley floor that consisted mainly of gravel bars and adjacent lower floodplains.

Inundation frequencies and intensities of floodplain habitats in association with river morphology determine the distribution of geomorphic surfaces and the heterogeneity of regeneration habitats required by floodplain tree species. In the bar-braided river in this study, geomorphic surfaces with high flood frequencies and intensities occupied major parts of the riverbed. This provided spatially extensive habitats for both the seedlings and reproductively mature trees of pioneer species. The average stand-replacement disturbance frequency in the bar-braided section (1/35.7 years) was consistent with the average lifespans of C. arbutifolia, T. urbaniana, S. sachalinensis, and A. hirsuta (Table 2). For these pioneer species, geomorphic surfaces stable for about 35 years provide sufficient time for trees to reach reproductive maturity. In addition, periodic and intensive flooding creates newly exposed substrates for germination, prevents successional replacement by mid-successional species, and thereby sustains the regeneration of pioneer forests over time (Table 3). However, in the incised-meandering section, about 44% of the riverbed evolved into stable surfaces (terraces). The disturbance intensity on the higher surfaces is quite low and its frequency averaged 49.8 years, which is longer than the average lifespan of Salicaceae species (20–37 years) other than P. maximowiczii. Therefore, pioneer forests established after disturbances would be replaced by mid-successional forests comprising U. japonica or F. mandshurica var. japonica. This is because pioneer species fail to regenerate without substrate replenishment for seedling recruitment.

In general, energy investment in longevity results in lower growth rates and delayed maturation. Loehle (1988) analyzed the relationship between life history characteristics and energy investment in a large number of tree species and found a correlation between reproductive maturation

time and longevity (lifespan). We found the same trend between ages to reproductive maturity and longevity among the eight tree species examined in this study (Table 2). The short-lived salicaceous species annually produce a large number of light seeds, which are dispersed over long distances by wind to reach safe sites created by frequent floods. Thus, both the lifespan of the tree and its life-history traits, such as seed dispersal, germination, establishment, and reproduction, have developed according to the frequency, intensity, and spatial extent of flood disturbances (Nakamura and Inahara, in press). All these disturbance regimes contribute to the dominance of salicaceous species along bar-braided rivers.

We conclude that the key factors maintaining the diversity of floodplain tree species in the studied northern temperate forest are (1) the development of diverse geomorphic surfaces providing regeneration and habitat niches, and (2) the timing of maturation and lifespan of early and mid-successional species being consistent with the disturbance frequency. Although this study did not examine flow regimes in great detail (seasonality, timing and duration etc.) and other disturbances such as drought and herbivory that influence the survival of post-seedling establishment, the resulting mature forests were generally explained by the availability of recruitment sites, regeneration strategies and evolution of land surface.

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Table 1. Comparison of relative light intensity, soil moisture, shear stress and floor condition among geomorphic surfaces using Kruskal-Wallis one-way ANOVA.

	Gravel bar	Lower floodplain	Upper floodplain	Secondary channel	Terrace	Kruskal-Wallis one-way ANOVA	
						χ^2	P
Light intensity (%)	82.05 ^a (61.01-93.07)	15.50 ^{bc} (5.76-21.31)	20.66 ^c (15.32-22.86)	7.56 ^b (5.47-11.94)	9.13 ^b (5.45-10.82)	32.85	<0.001
pF value	1.79 ^a (1.48-1.94)	1.96 ^a (1.84-2.10)	2.34 ^d (2.17-2.56)	1.02 ^c (0.79-1.66)	1.02 ^{bc} (0.48-1.59)	35.96	<0.001
Shear Stress (kgf m ⁻²)	8.82 ^a (7.52-10.01)	4.16 ^a (4.03-4.65)	1.53 ^b (1.41-3.59)	5.37 ^a (4.95-7.01)	---	23.84	<0.001
Floor condition	mineral soil, exposed	mineral soil, partially exposed	covered by floor vegetation	mineral soil, exposed	covered by floor vegetation		

Median and quartile range (25th and 75th percentiles; in parentheses) of environmental variables are shown. Values followed by the same letter are not significantly different from each other ($p > 0.05/10$; Mann-Whitney U-test with Bonferroni adjustment).

Table 2. Maturation, lifespan and seed weight of dominant tree species in the study river sections.

	Age at initial seed production		Life span (year)		Seed weight (mg)
	Mean	S.D.	Mean	S.D.	
	<i>Chosenia arbutifolia</i>	13.9	2.3	36.7	
<i>Toisusu urbaniana</i>	12.9	3.7	35.7	3.4	0.20-0.27 ¹⁾
<i>Populus maximowiczii</i>	48.8	6.4	49.9	7.2	0.35-0.70 ¹⁾
<i>Salix sachalinensis</i>	7.8	1.6	34.8	10.3	0.12-0.14 ¹⁾
<i>Salix pet-susu</i>	9.0	0.7	20.0	3.6	0.12-0.13 ²⁾
<i>Alnus hirsuta</i>	15.9	3.0	36.7	4.4	0.66-0.77 ²⁾
<i>Ulmus japonica</i>	not found		82.2	6.6	4.6-5.8 ²⁾
<i>Fraxinus mandshurica</i> var. <i>japonica</i>	47.0	4.3	65.4	9.6	41.0-83.0 ²⁾

1) Provided by You Nagasaka, Hokkaido Forestry Research Institute.

2) After Katsuta *et al.* (1998).

Table 3. Comparison of destruction rates and current distribution of geomorphic surface type* between braided and incised-meandering sections.

Destruction rates	Braided	Meandering
3/50	28 (%)	12 (%)
2/50	18	22
1/50	20	22
0/50	34	44
Mean frequency	1/35.7	1/49.8
Geomorphic surface types		
Gravel bar	27 (%)	20 (%)
Lower floodplain	17	16
Upper floodplain	24	19
Secondary channel	8	4
Terrace	24	41

* The geomorphic surface areas are after Shin and Nakamura (2005).

Figure captions

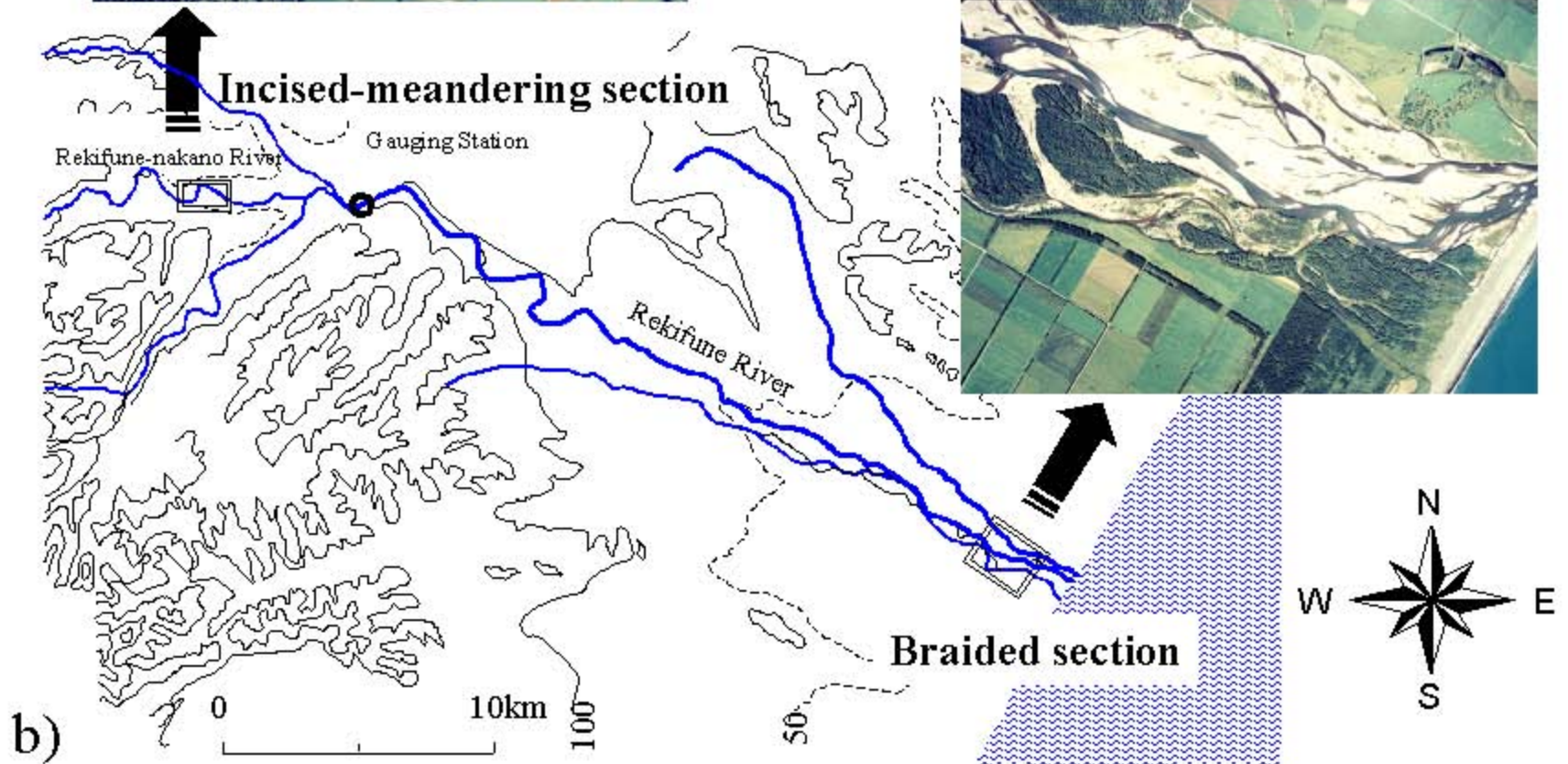
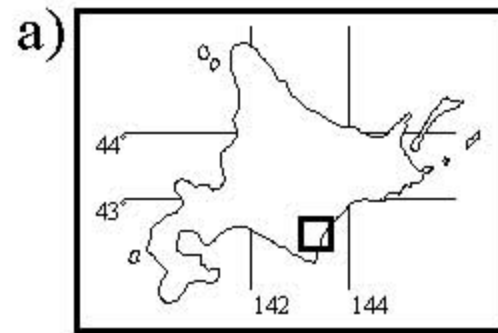
Figure 1. a) Location of the Rekifune River in Hokkaido, northern Japan. b) Locations and aerial views of the investigated river sections. The circle indicates the gauging station used to measure water levels and discharge.

Figure 2. Species composition and age structure of the studied floodplain communities. This is represented by the relative dominance of the basal area at DBH of the dominant tree species and the average maximum tree age for each geomorphic surface type. Bars represent the standard deviation of each mean.

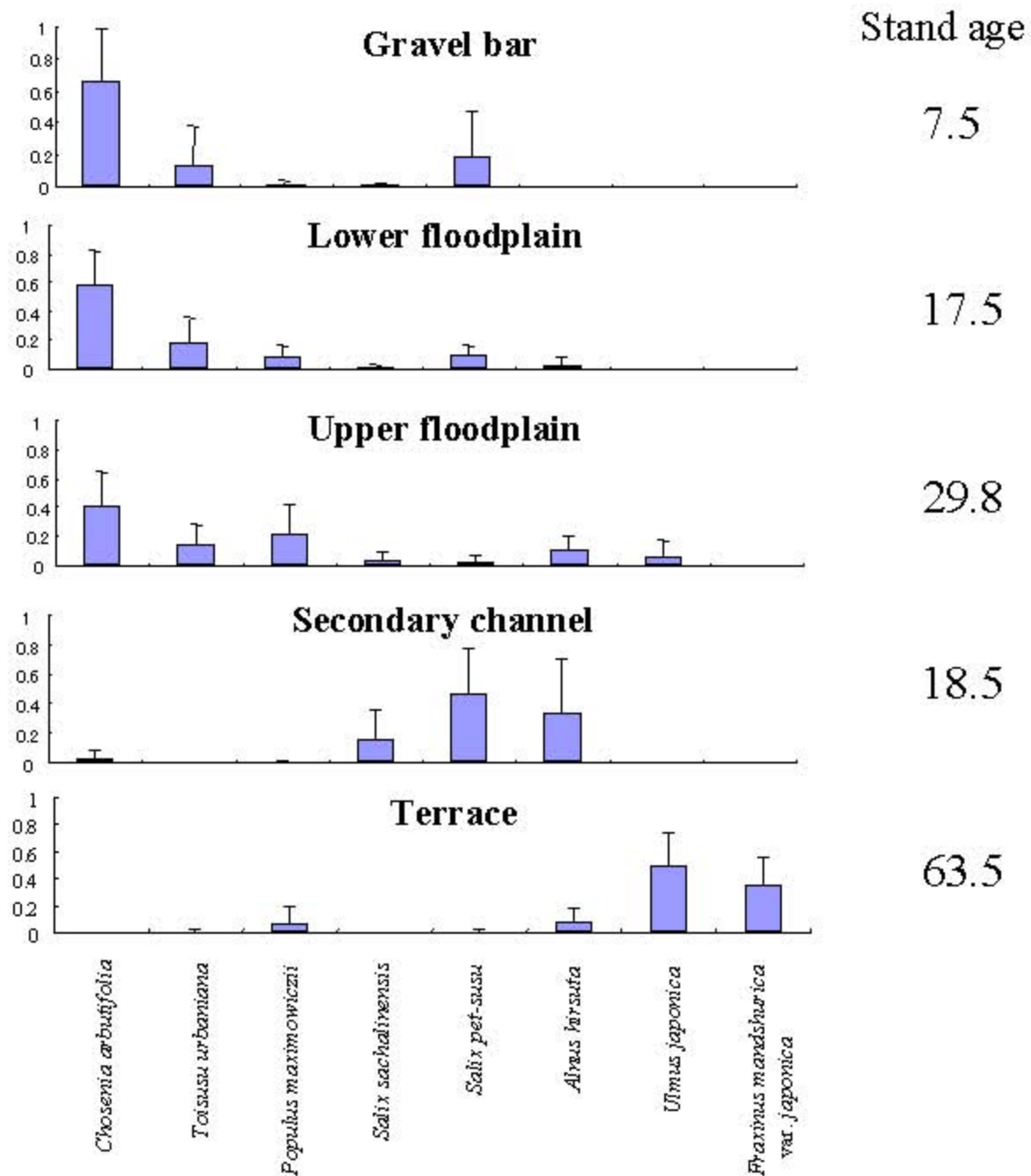
Figure 3. Distributions of seedlings and conspecific reproductively mature trees across the five geomorphic surface types. The proportions of seedlings and mature trees are based on the ratios of tree counts among the five geomorphic surface types.

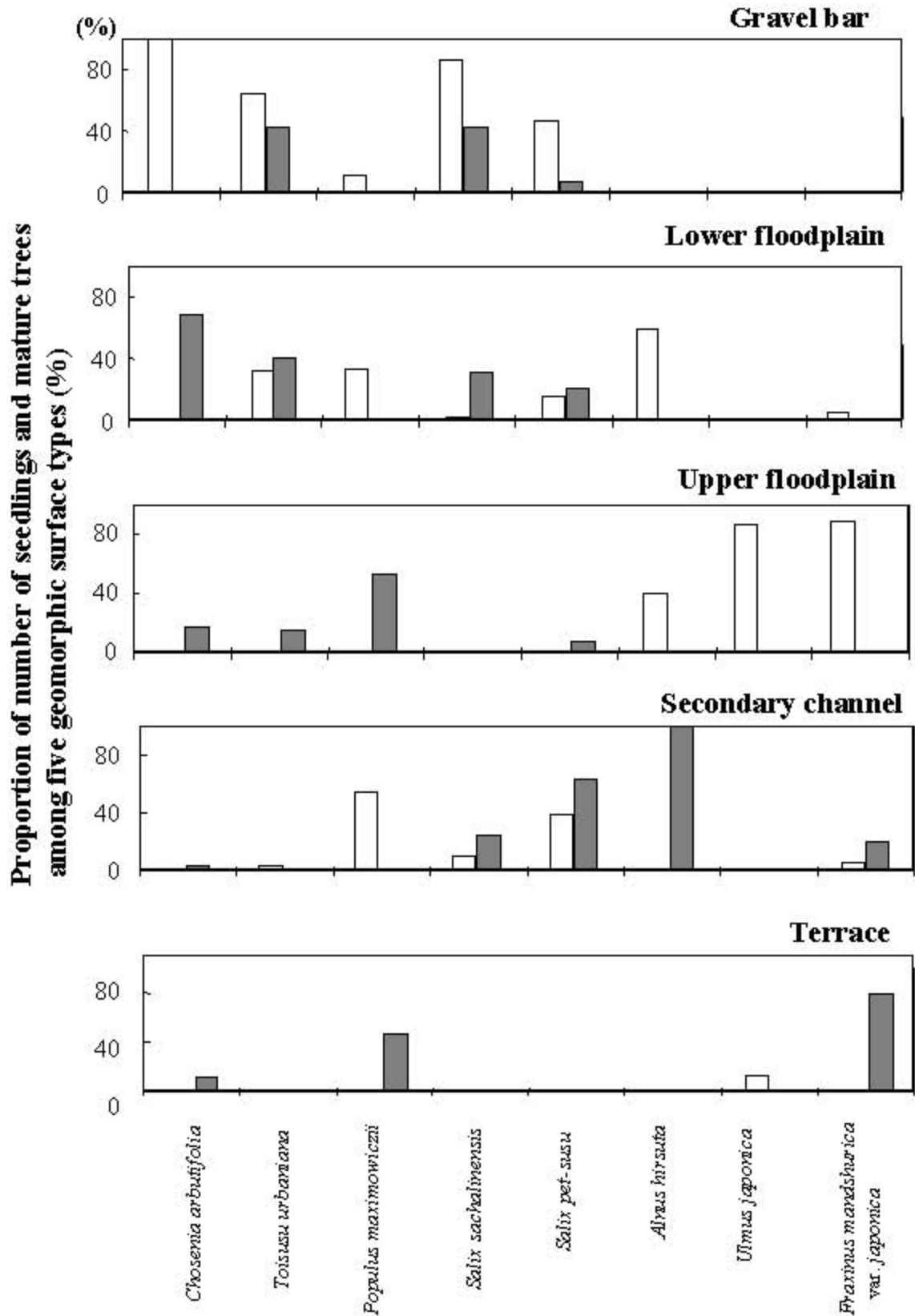
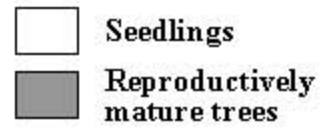
Figure 4. Historical series of part of the bar-braided section from 1947 to 1997, and the geomorphic surface map showing the same site in 1997. Circled areas indicate the same areas of the riverbed throughout different years and the geomorphic surface map.

Figure 5. Aerial views of the riverbeds for braided and incised-meandering sections showing the distributions of destructed areas with four different flood frequencies. 0/50, 1/50, 2/50, and 3/50 represents nil, one, two, and three floodings every 50 years, respectively. Note the different scales on the two maps.

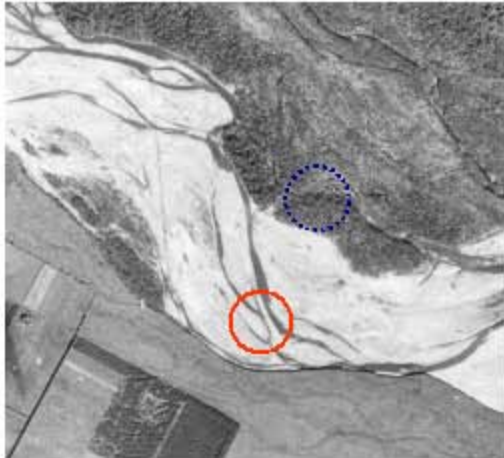


Relative dominancy

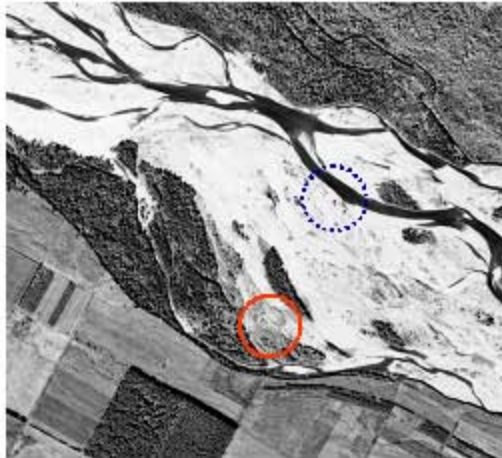




1947



1963



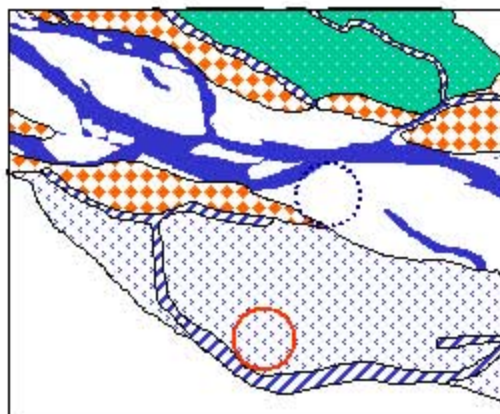
1977



1997



Geomorphic surfaces in 1997



- Channel
- Gravel bar
- Lower floodplain
- Secondary channel
- Upper floodplain
- Terrace



0 500m

