

# Emergence and Survival of *Salix* Seedlings on a Recently Formed Bar in the Ishikari River, Hokkaido, Japan

## 石狩川内の砂州におけるヤナギ属実生の発生と生残

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### 要旨

北海道石狩川上流部の砂州において、ヤナギ属実生の発生と生残過程を検討した。調査地ではオノエヤナギとエゾヤナギが優占し、定着時期の異なる実生群落が成立していた。ヤナギ属の種子散布は融雪洪水後に水位が低下し始める時期に同調して始まるため、地表面が水面より上に現れる時期によりその場所に定着する種が異なっていた。地表面の出現時期は微地形と水位との関係で決定されていた。種子は地表面に到達すると直ちに発芽し、7月には実生数が最高となった。これらの実生は、前年やその前の年に定着していたより大きな実生や草本などに被陰されて枯死することが主な死亡要因であることがわかった。また、オノエヤナギよりもエゾヤナギの方が被陰に対する抵抗性が高いという結果も得られた。このような状況に耐え定着年を生残した実生は、次の春の融雪洪水で流失あるいは埋没して生残個体が減少する可能性も示唆された。定着後2年が経過した実生は融雪洪水で消失するものが相当数あったが、3年が経過した実生は多くが生残していた。このように、ヤナギ属実生は微地形に対応した不均一な立地で水位の変動に呼応して定着していき、その生残に関わる要因は、実生の生長段階に応じて異なることがわかった。

### I. Introduction

The distribution of riparian species depends on factors related to the flood regime, such as elevation from the riverbed (Hupp and Osterkamp, 1985; Nakamura et al., 1997), flood frequency (Hupp and Osterkamp, 1996), and substrate texture (Johnson et al., 1976; Hupp and Osterkamp, 1985; Nakamura et al., 1997). Variations in downstream patterns (Nilsson, 1986; Nilsson et al., 1989) and human disturbance (Nilsson et al., 1991; Hupp, 1992) can also affect it.

*Salix* species form typical pioneer communities in riparian zones subject to frequent flooding. More than 20 riparian *Salix* species occur in Japan, and well-developed mixed *Salix* communities (Ishikawa, 1980) develop along rivers in northern Honshu and Hokkaido. The distribution of these *Salix* species is influenced by the longitudinal gradient of the river, particle size of riverbed deposits, and the micro-topography of the floodplain (Ishikawa, 1979, 1983; Niiyama, 1987). Along the Ishikari River in Hokkaido, Niiyama (1987) studied the relationships between the distribution of *Salix* species, soil texture, and moisture conditions in four river zones with distinct morphologies. *Salix* species distributed along the river with their favorite soil texture.

Both climatic and edaphic factors affect the establishment of plant communities (Jenny, 1958). The main factor affecting the habitat segregation of *Salix* species may be that different species require

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different conditions for seedling establishment (Ellenberg, 1988; Niyama, 1990; Ishikawa, 1994) owing to differences in the “regeneration niche” that subsequently separates adult plants into a “habitat niche” (Grubb, 1977).

The distribution of *Salix* species is also subject to fluvial processes that influence community establishment. In northern Japan, floods caused by snowmelt occur every spring, and disturb established communities and create fresh sites on which new seedlings can emerge. Spring flooding also influences seed dispersal (Niyama, 1990) and the suitability of sites for seedling establishment (Ishikawa, 1994).

Few studies have described the process of the emergence of seedlings and the formation of *Salix* communities (e.g., Niyama, 1990; Yoshikawa and Hokusima, 1999). Sakio (1997) found that seedling dynamics were greatly affected by natural disturbances and river morphology. Niyama (2008) indicated that the direct competition after germination is crucial for the dominance and coexistence of *Salix* species on fine textured substrata. However, the relationships between the emergence and survival of seedlings and such natural conditions are still not well understood. We therefore sought to clarify the processes of emergence and survival of *Salix* seedlings and to determine how they are affected by fluctuations in water level, variation in micro-topography, and competition through seedling growth.

## II. Study site

The study site was on a bar in the Ishikari River (43°53'N, 142°33'E) near the town of Aibetsu, central Hokkaido (Fig. 1-A).

The site was located 181.6 km from the mouth of the river. The Ishikari River is classified as a first-grade river according to the Ministry of Land, Infrastructure, Transport and Tourism. It is 268 km in length, has a drainage area of 14,330 km<sup>2</sup> and a design-flood discharge of 18,000 m<sup>3</sup>/s. The original meandering course of the river has been subject to extensive flood control works (Ishikari River Development and Construction Department, 1980), and many dams have been constructed on the main course and its major tributaries. The reach 5 km upstream and 5 km downstream of the study site was 110–200 m wide, with earthen levees constructed on both sides.

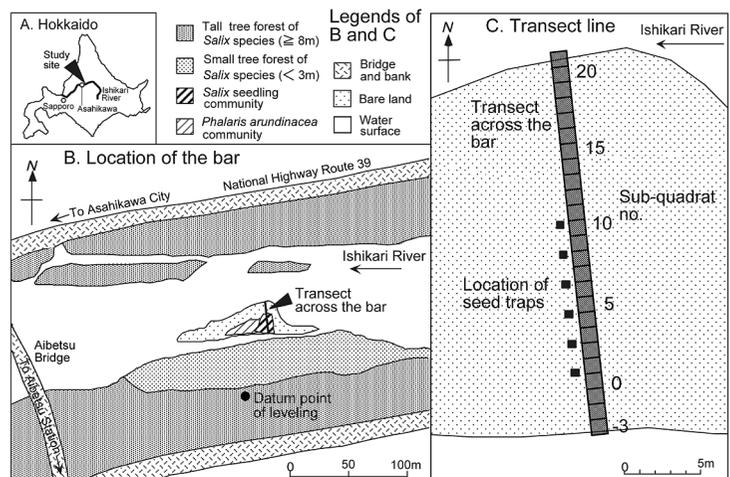


Fig.1. Maps of the study site.

- A : Location of the study site on the Ishikari River in Hokkaido, northern Japan.
- B : Location of the surveyed bar and vegetation within the river channel. (The tall and small tree forests contained *Alnus hirsuta* and the *Salix* species: *S. sachalinensis*, *S. rorida*, *S. jessoensis*, *S. subfragilis*, *S. miyabeana*, *S. pet-susu*, and *S. gracilistyla*.)
- C : Transect across the bar divided into 25 sub-quadrats, each 1 m × 1 m. The location of six water trays to trap seeds during the seed dispersal period are also shown.

The bar is located in the middle of the channel (Fig. 1-B) and was formed some time after 1992, as deduced from its absence in aerial photographs taken in the summer of 1992. The bar is submerged each year during the spring snowmelt flood. The flood alters the shape of the bar through sediment deposition and removal.

Communities of mixed *Salix* species of varying stages of development were present on the bar and on nearby sediment deposits within the channel (Fig. 1-B). Within these communities we recorded seven *Salix* species (*S. sachalinensis*, *S. rorida*, *S. jessoensis*, *S. subfragilis*, *S. miyabeana*, *S. pet-susu*, and *S. gracilistyla*) and *Alnus hirsuta*. The most abundant species was *S. sachalinensis*, followed by *S. rorida* then *S. jessoensis*. *Salix* species were present on the bar only as seedlings, but stands of saplings and small trees had developed on the more elevated older sediment deposits around the bar (Fig. 1-B). A community of *Phalaris arundinacea* occupied the middle of the bar, and a few other herbaceous species also occurred in both the *Phalaris* and *Salix* communities.

### III. Methods

A 25-m  $\times$  1-m transect comprising 25 sub-quadrats of 1 m  $\times$  1 m (numbered from -3 to 21) was laid across the bar (Fig. 1-C). A series of measurements of *Salix* seedling dynamics and surface conditions was then performed in these sub-quadrates.

#### 1. Seedling census

The *Salix* seedlings on the bar were densely spaced. All seedlings in the sub-quadrats were numbered and their position was mapped in September 1996 and September 1997. Stem diameters and lengths were measured. The stems were partly buried by sediment deposited since the seedlings had germinated, so the real base of seedlings could not reliably be found. However, seedlings radicanted near the ground surface, so we regarded a position just above the first roots to be the base of the stem for the purposes of stem length and diameter measurement.

#### 2. Seed dispersal and seedling emergence

Seed traps were located at six positions adjacent the transect during from May to July in 1997 (Fig. 1-C). The traps were square trays, 31 cm  $\times$  21.5 cm  $\times$  5 cm, placed on the ground, and were filled to a depth of 3 cm with water. Seeds that fell into the trays were counted and discarded every 3 to 6 days. Newly emerged seedlings were found and counted in each sub-quadrat from 7 June to 5 September 1997. The number of surviving seedlings was also recorded. All seedlings were counted together until 14 June, after which they could be identified to species level from their leaf morphology.

#### 3. Fluctuations in water level and riverbed morphology

To identify the environmental factors affecting the establishment of seedlings, we collected some information. River discharge data from the Naka-Aibetsu discharge station 5 km upstream of the study area were obtained from the Asahikawa Development and Construction Department, Hokkaido Regional Development Bureau. We sometimes recorded water levels at the transect from 20 May to 7 September in 1997. Then we determined a regression relationship between water level and mean daily discharge of the Ishikari River in 1997. We used the regression equation to calculate water level at the transect line in 1995 and 1996. We recorded the 1997 water levels on both sides of the bar and found that it was lower on the south side than on the north.

We surveyed the riverbed morphology by direct leveling before (19 October 1996) and after (29 April 1997) the spring floods. The reference point for the leveling was located on an elevated sediment deposit in the channel that was free of flood influence during the survey period. The level of sub-quadrat 0 in 1996 was set as zero, and the elevation of each of the other sub-quadrats was expressed relative to that.

To identify the level of the 1995 sediment surface that had since been buried under later deposits, we excavated to reveal the true base of seedlings that had emerged in 1995 (surmised from seedling size and subsequently confirmed from tree ring counts). The depth of the 1995 surface was 22 cm in sub-quadrats 0 and 5. The 1995 surface could not be found in sub-quadrat 13 because the only seedlings growing there emerged in 1997.

#### 4. Gravel size analysis

The substrata texture is very important for seedling establishment. We recorded the coverage of fine sand on the ground surface of all sub-quadrats. Then, we measured the soil texture in three sub-quadrats (0, 5, and 13) in 1997 to examine the effect of soil texture on the emergence and growth of seedlings. To compare the particle sizes of past and present surface deposits, we collected five samples of riverbed substrate in surveyed sub-quadrats. Cobbles (>64 mm in diameter) that covered the present surface were discarded from each sample. We assumed that the retained sediment filled the interstitial spaces between the cobbles. Each sample weighed 400 g.

Each sample was dried in an oven for 24 h at 80°C. It was then sieved for 10 min in a mechanical shaker through 10 sieves with mesh sizes from 0.0625 mm to 32 mm (i.e.,  $2^{-4}$ ,  $2^{-3}$ , ...,  $2^5$  mm). Each size fraction was weighed. To compare the texture of soils between the samples, the diameters of the particles were log-transformed, as follows:

$$\phi = -\log_2 X$$

where  $X$  is the particle diameter in mm.

Soil texture was defined by the mean  $\pm$  standard deviation ( $x \pm \sigma$ ) of  $\phi$ , as per the method of Friedman (1961, 1967):

$$x = 1/100 \sum f_i x_i$$

$$\sigma = (\sum f_i (x_i - x)^2 / 100)^{1/2}$$

where  $x_i$  is the mean and  $f_i$  is the weight percentage of diameter class  $i$ . Since we used sieves that increased in increments of  $1\phi$ , the medians of each diameter class were adopted as  $-5.5\phi$ ,  $-4.5\phi$ ,  $-3.5\phi$ ,  $-2.5\phi$ ,  $-1.5\phi$ ,  $-0.5\phi$ ,  $0.5\phi$ ,  $1.5\phi$ ,  $2.5\phi$ , and  $3.5\phi$ . As there were very few particles larger than  $4\phi$  in the samples, the mean of this particle class was regarded as  $4.5\phi$  for convenience.

#### 5. Statistical analysis for the survival of new seedlings

To understand which factors had the greatest influence on survival of the new seedlings, we performed stepwise multiple linear regression analysis. The objective variables were the survival rate of new seedlings in 1997. The explaining variables were as follows: (1) Relative elevation from base point, (2) Coverage of fine sand on the ground surface, (3)  $\Sigma D^2H$  of seedlings emerged in 1995 and

1996, (4) Coverage of grass species. We used the statistical software package SPSS v. 12.0J (SPSS Inc., Chicago, IL, USA).

#### IV. Results

##### 1. Distribution of *Salix* seedlings

Many *Salix* seedlings emerged in 1995, 1996, and 1997, mainly *S. sachalinensis* and *S. rorida*, hence we restrict our presentation of data to these two species. The total number of seedlings on the bar in 1997 were less than that in 1996 (Table 1). In both species, more seedlings emerged in 1997 than in 1996, especially in *S. rorida*.

The distributions of seedlings of the two *Salix* species along the transect in 1996 and 1997 are shown in Fig. 2. Some seedlings that had emerged in 1995 survived from 1996 to 1997. The 1995 seedlings of *S. sachalinensis* survived best in sub-quadrat 2 (Fig. 2-B, D), and those of *S. rorida* survived best in sub-quadrat 4 (Fig. 2-A, C).

Seedlings that emerged in 1996 had very different patterns of distribution between 1996 and 1997. Although both species were present in many sub-quadrats in 1996 (Fig. 2-A, B), in 1997 the seedlings of *S. sachalinensis* survived in sub-quadrats -1 to 3 (Fig. 2-C), and those of *S. rorida* survived only in sub-quadrats 1 to 9 (Fig. 2-D).

Table 1. Results of seedling censuses in 1996 and 1997.

Year seedlings emerged	Total number of seedlings present	
	1996	1997
	<i>Salix</i>	<i>sachalinensis</i>
1995	311	183
1996	306	23
1997	–	824
	<i>S. rorida</i>	
1995	47	32
1996	33	1
1997	–	1014

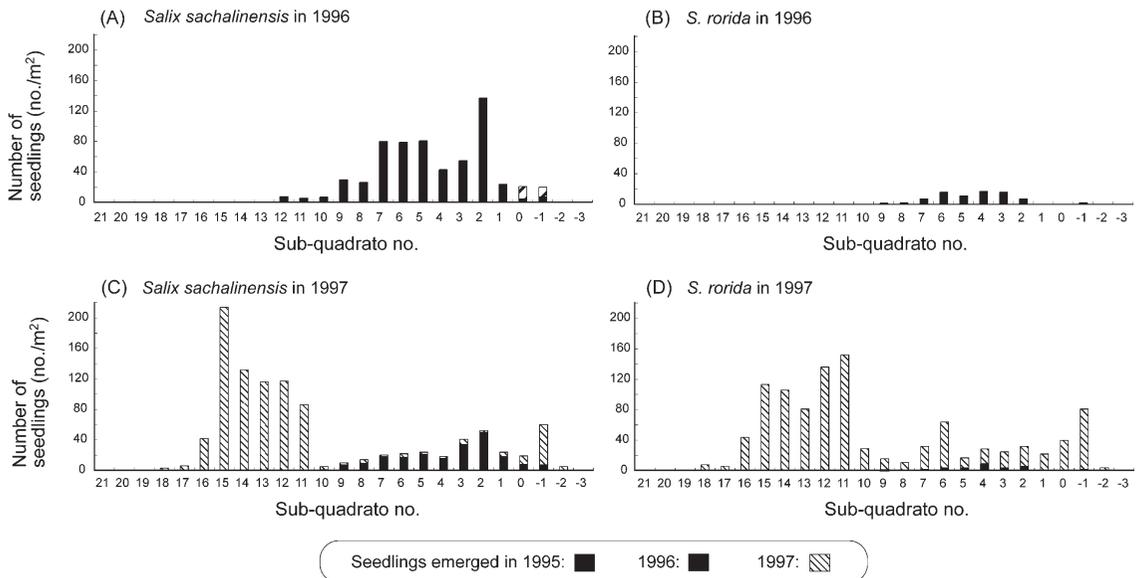


Fig. 2. Distribution of *Salix sachalinensis* and *S. rorida* seedlings in transect sub-quadrats in 1996 and 1997 by year of emergence.

The distributional patterns of new seedlings that emerged in 1997 differed from those of the older seedlings in two ways: (1) The 1997 seedlings appeared mainly in sub-quadrats 11 to 16, where very few seedlings had appeared in previous years. Seedlings of *S. sachalinensis* were particularly scarce in sub-quadrats 2 to 9 (Fig. 2-C), where those of *S. rorida* were more plentiful (Fig. 2-D). (2) The number of 1997 seedlings of *S. sachalinensis* increased with distance from the middle of the bar. However, the number of *S. rorida* seedlings did not display the same trend in either year, and neither did *S. sachalinensis* in 1996.

## 2. Seed dispersal and emergence of new seedlings

*Salix rorida* began to disperse first, in May, and *S. sachalinensis* began to disperse in June and had the longest period of dispersal (Fig. 3). The receding water began to expose the seed traps from 28 May. Most seeds were trapped in June, and the peak occurred on 11 June. Consistent with the dispersal period of each species, the seeds trapped at the peak were mainly *S. rorida* and *S. sachalinensis*.

Many seedlings emerged on the bar during the seed dispersal period. Figure 4 shows the relationship between the number of emerging seedlings and the number of days from when the ground surface became exposed in 1997. The total number of seedlings increased with the length of time the ground surface had been above water.

## 3. Fluctuation in water level and variations in micro-topography

Changes in the discharge of the Ishikari River displayed a clear pattern each year (Fig. 5). In April and May, predictable floods occurred owing to snowmelt. In August or September, large floods sometimes occurred owing to heavy rain. The seed dispersal periods of the *Salix* species coincided with the gradual decline in river discharge through May and June. As the water level fell, bare sites from sediment deposition or erosion were exposed, and the *Salix* seedlings emerged on these first.

The maximum water level on the bar and surface of the bar in 1997 and relationships between water level and river discharge developed from the 1997 measurements are shown in Fig. 6. We calculated the water level in 1995 and 1996 with these equation at both side of the bar. The reconstructed water levels for 1995 and 1996 are shown in Fig. 7 along with measured bar surface in 2006 and 2007 and inferred level of the bar in 2005. When we inferred the surface level of 1995, the depth of the roots of seedlings emerged in 1995 gave

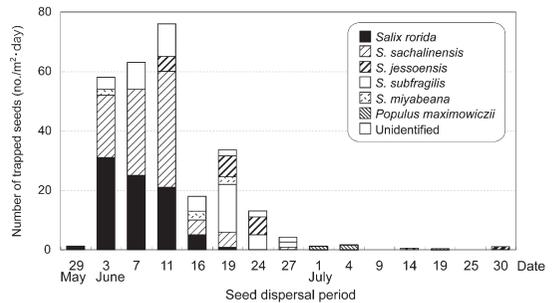


Fig. 3. The number of seeds trapped in water trays on the bar in 1997.

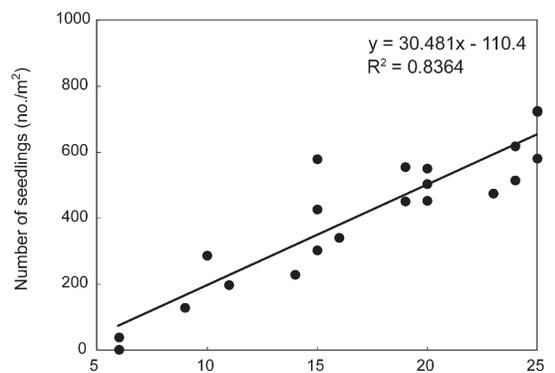


Fig. 4. Relationship between time since exposure of the sub-quadrat and number of new seedlings emerged as of 2 July 1997.

us the important information. Both the river discharge and the geographical features of the riverbed determined when the bar was submerged and when it was exposed. In 1997, the surface was exposed on 28 May after the spring floods, and was estimated to have been exposed on 7 June in 1995 and 9 June in 1996. The surface level along the transect (height of the bar) increased each year owing to sediment deposition. In 1995 and 1996, rainfall-induced floods submerged the bar for durations that depended at any given position on the discharge and micro-topography.

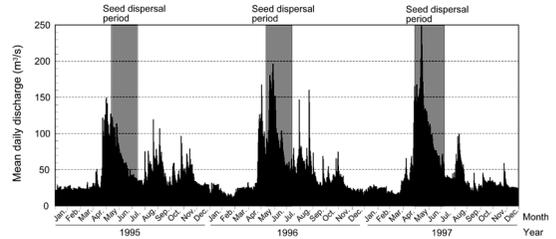


Fig. 5. Fluctuation in discharge of the Ishikari River at Naka-Aibetsu discharge station 5 km upstream of the study area. (Data source: Asahikawa Development and Construction Department, Hokkaido Regional Development Bureau.)

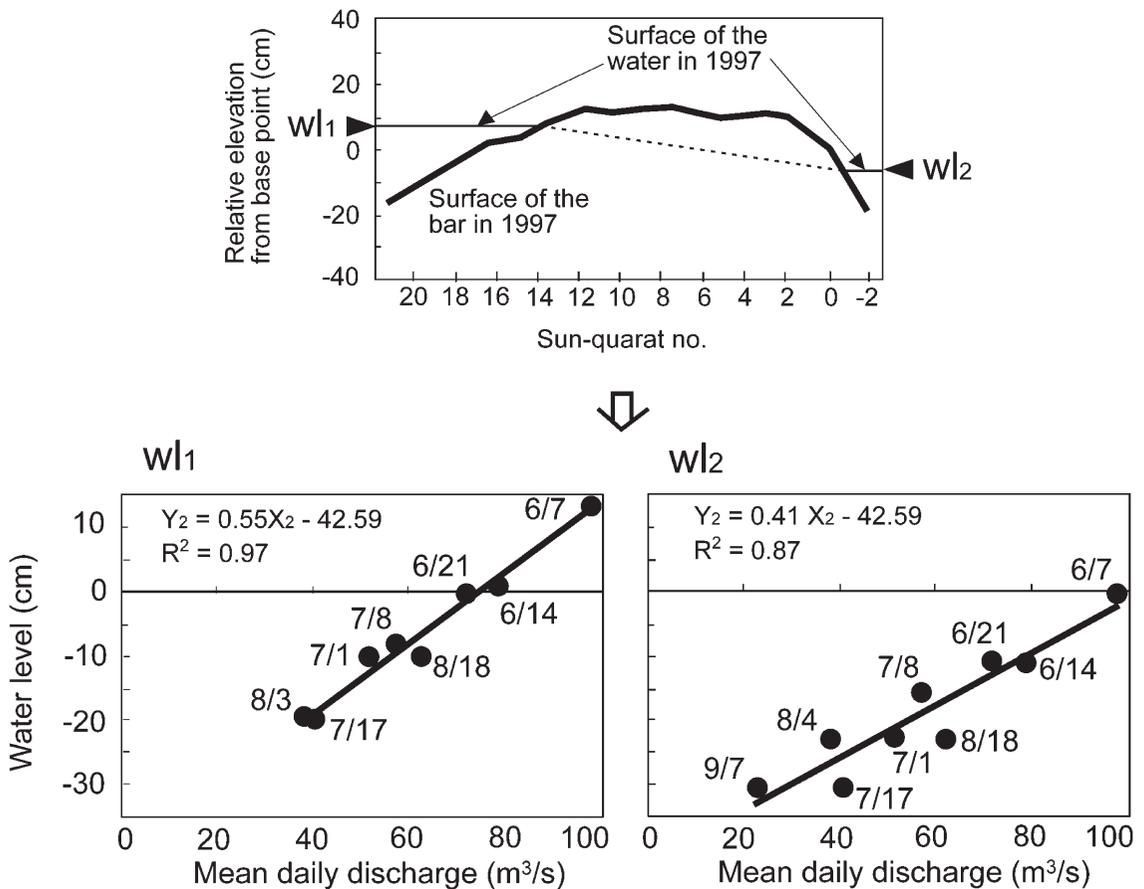


Fig. 6. Relationships between mean daily discharge of the Ishikari River at Naka-Aibetsu discharge station and the water level on either side of the bar as measured at the transect line in 1997. The points wl1 and wl2 indicate either side of the bar as shown in the top diagram.

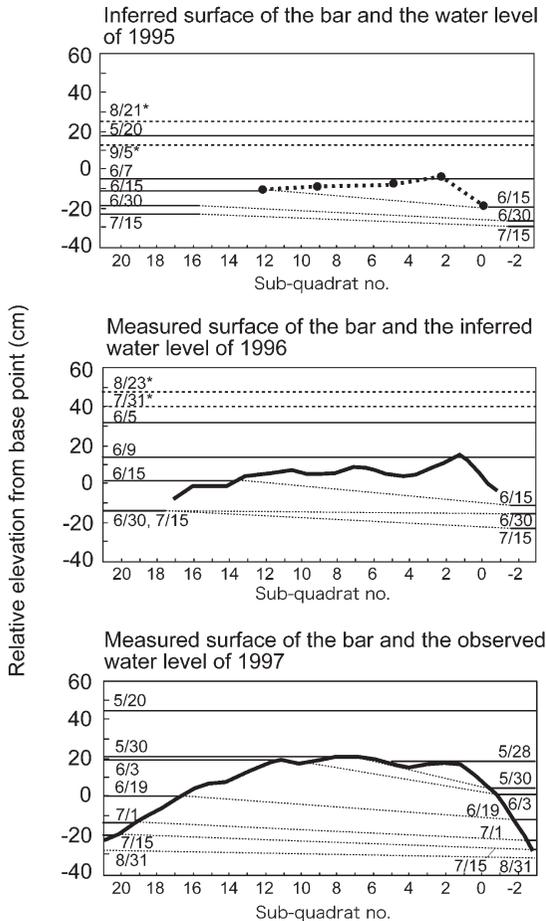


Fig. 7. Fluctuations in water level and elevation of the surface of the bar along the transect in each year from 1995 to 1997. The surface of the bar in 1995 was estimated from the depth of the base of seedlings that emerged in 1995. Asterisks show the dates when rainfall-derived floods occurred during summer.

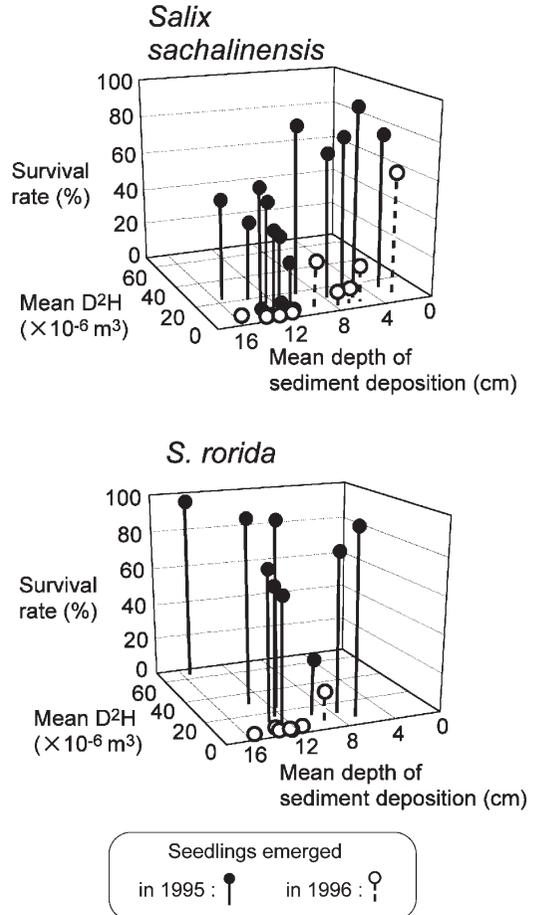


Fig. 8. Relationships between the survival of *Salix sachalinensis* and *S. rorida* seedlings following the 1997 spring flood, mean  $D^2H$  of seedlings, and mean depth of sediment deposition.

Figure 8 shows the relationships between mean sediment depth and the survival rates of seedlings in various size classes. Survival patterns were similar in the two *Salix* species: small seedlings with  $D^2H < 10 \times 10^{-6} \text{ m}^3$  rarely survived. More than 40% of the larger seedlings ( $>10 \times 10^{-6} \text{ m}^3$ ) of *S. sachalinensis* survived. Therefore, seedlings that emerged in 1996 had a lower survival rate than the seedlings that emerged in 1995. If the mean depth of sediment deposition was less than 10 cm, >60% of larger seedlings survived. The larger seedlings of *S. rorida* appeared to survive better than those of *S. sachalinensis* even when sediment deposition was greater than 10 cm.

#### 4. Factors affecting the survival of new seedlings

The seedlings that emerged on the bar grew during summer, but the conditions expected to

influence the survival of newly emerged seedlings differed between sub-quadrats, i.e., relative elevation, particle size of surface sediment, size and abundance of older *Salix* seedlings, and percentage cover of herbaceous species such as *Phalaris arundinacea* and *Trigonotis peduncularis* (Fig. 9).

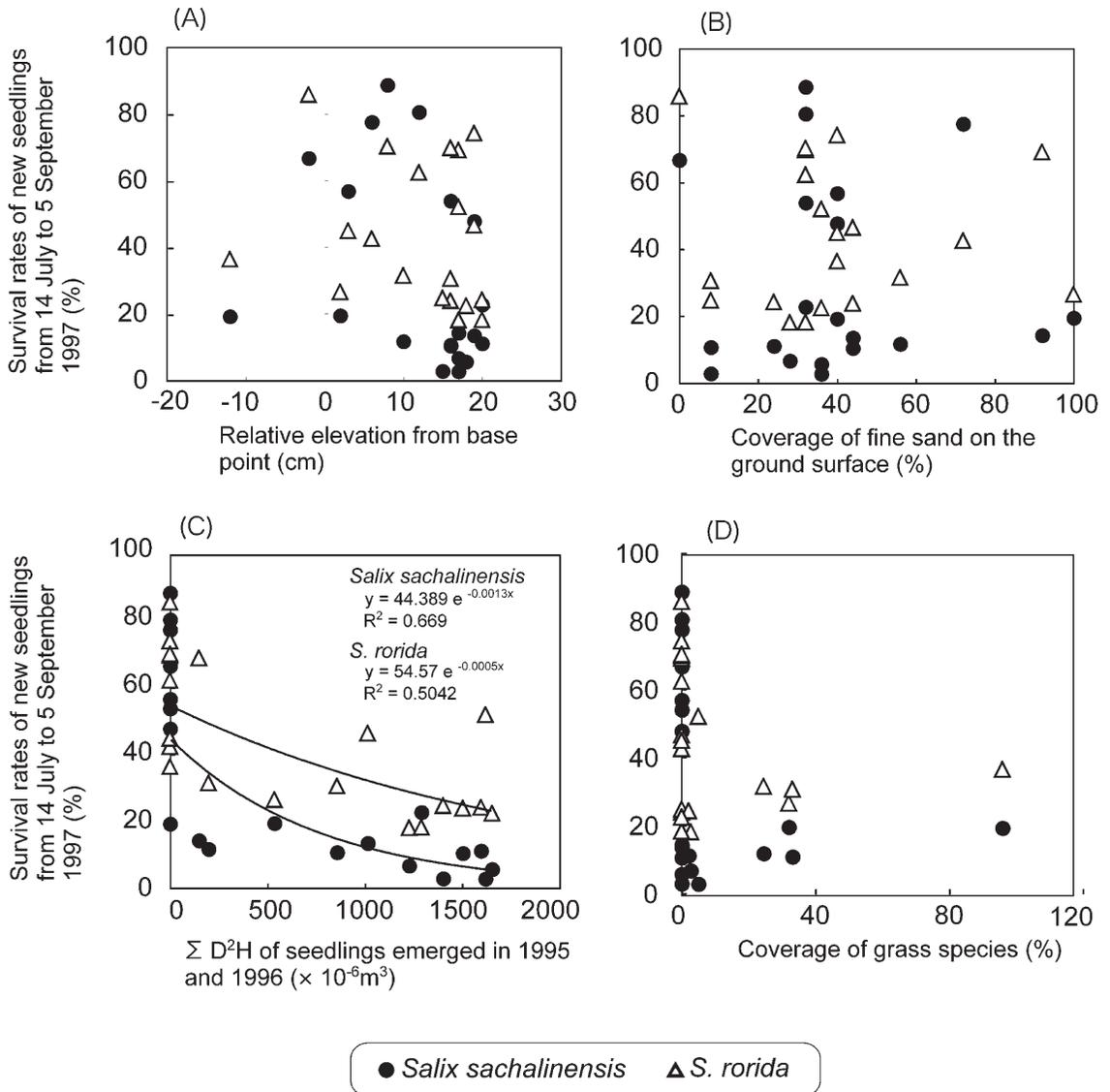


Fig. 9. Influence of (A) microtopographical position, (B) substrate texture, (C) size of older seedlings, and (D) density of herbaceous species cover on the survival of seedlings that emerged between 14 July and 5 September 1997.

The survival rate of new seedlings had not evident trend to decline as the relative elevation from the reference point increased (Fig. 9-A). The particle size distribution of the flood deposits influences moisture, hardness, and porosity of the substrate. The 1997 surface was coarser than that of 1995 (Table 2). Pebbles on the 1997 surface in all three reference sub-quadrats would have been advantageous to the growth of seedlings of *S. rorida*, which has a well developed taproot (Niyama,

1983) and is able to draw water from depth in coarse soil. Our observations suggested that seedlings of *S. rorida* grew better than those of *S. sachalinensis* in the early stages following emergence. However, there was no clear relationship between the percentage cover of fine sand in each sub-quadrat and the survival rate of either species (Fig. 9-B).

The number of older seedlings was represented as the sum of  $D^2H$  in each sub-quadrat, which we used as a proxy for seedling biomass. Lower values of  $\Sigma D^2H$  were associated with higher survival rate of new seedlings (Fig. 9-C). This trend was adopted the logarithmic equation. The value of  $R^2$  were higher in *S. sachalinensis*. The seedlings of *S. rorida* were more tolerant of being shaded by older seedlings than those of *S. sachalinensis*. Those of *S. jessoensis* did not reveal any trend (data not shown). The relationships between the coverage of herbaceous species and survival rate had not so clear trend (Fig. 9-D).

The most important factors to emerge from this analysis for both species were  $\Sigma D^2H$  and percentage cover of herbaceous species. The selected model for survival rate of *S. sachalinensis* seedlings ( $Z_s$ ) was:

$$Z_s = 58.896 - 0.035 \times [\Sigma D^2H] - 0.507 \times [\% \text{ cover of herbaceous species}]$$

$R^2$  was 0.925 ( $P < 0.01$ ) and the standardized regression coefficients were  $-0.824$  ( $\Sigma D^2H$ ) and  $-0.401$  (% cover of herbaceous species), showing that  $\Sigma D^2H$  had the stronger influence on survival.

The selected model for survival rate of *S. rorida* seedlings ( $Z_r$ ) was:

$$Z_r = 62.558 - 0.024 \times [\Sigma D^2H] - 0.350 \times [\% \text{ cover of herbaceous species}]$$

$R^2$  was 0.599 ( $P < 0.01$ ) and the standardized regression coefficients were  $-0.759$  ( $\Sigma D^2H$ ) and  $-0.376$  (% cover of herbaceous species). In other words, these two factors affected the survival of *S. rorida* and *S. sachalinensis* seedlings in similar ways.

## V. Discussion

The emerging *Salix* seedlings displayed site differences between years. Those that emerged in 1995 and 1996 grew on the higher sub-quadrats. This is because as the water level gradually receded after the spring floods, the higher ground surface was the first to be exposed and colonized by new seedlings. Sub-quadrats at lower relative levels (numbers  $-3$  and  $-2$  and  $10$  to  $21$ ) were largely free of seedlings in 1996, but were then colonized in 1997. Seedling distribution was therefore heavily influenced by the micro-topography of the riverbed.

*Salix* species are tolerant of burial and are able to sprout from stems or roots (Krasny et al., 1988). Seedlings that were large or were buried by only a small amount of sediment survived better. So older (larger) seedlings on higher positions (less sediment deposition) were better able to survive the spring floods, while later emerging seedlings at lower levels were smaller, and thus survived less well. Therefore, a much higher proportion of the seedlings that had emerged in 1995 survived the

Table 2. Textures of riverbed deposits in 1997 and 1995.

Sub-quadrat no.	Mean ( $\pm \sigma$ ) particle sizes (in $\phi$ )	
	Inferred surface of 1995	Surface of 1997
0	$-1.0 \pm 2.7$	$-2.0 \pm 2.6$
5	$-1.4 \pm 2.5$	$-2.1 \pm 2.3$
13	–	$-2.7 \pm 2.1$

1997 spring flood than those that had emerged in 1996.

The lower  $R^2$  and coefficients for *S. rorida* suggest that its seedlings might be more tolerant of competition than those of *S. sachalinensis*. These results are consistent with the fact that *Salix* seedlings have high light requirements that prevent their establishment under existing trees or herbs (Johnson et al., 1976). Shading by older seedlings and grass species greatly influenced the emergence and survival of new *Salix* seedlings.

The coincidence of timing for seed dispersal and receding water level from spring floods is an important trait in *Salix* species, because their seeds are small and short-lived (Niiyama, 2008). The receding water level is a favorable time for seedling emergence, owing to the elevated moisture in the soil or sediment that is exposed as the water level recedes (Niiyama, 1990). The seeds of these species can also germinate under water, and pronounced seedling zonation has been observed in areas subject to repeated rising and receding water level (Krasny et al., 1988; Niiyama, 1990). Seed dispersal by water is a known feature of riparian plant species (Skoglund, 1990; Hughes and Cass, 1997).

The dominance of *S. sachalinensis* at this site is a function of its regeneration traits, namely, a longer period of seed dispersal and adaptation to a wider range of soil textures for seedling emergence than the other *Salix* species present in this area. *Salix rorida* was able to coexist with the dominant *S. sachalinensis* on account of its ability to occupy and persist in extremely coarse soil, in which *S. sachalinensis* is less able to survive (Niiyama, 2008). If changes in the geomorphic processes caused the ground surface to become coarser at this site, it is likely that seedlings of *S. rorida* would be able to achieve dominance.

The first woody plants to dominate bare and wet sediment along streams grow rapidly, are tolerant of burial, and lack seed dormancy (Hupp, 1992). Species such as *Salix* and *Populus* typically display these traits. Their patterns of distribution are determined to a large extent by the river flow during their establishment (Stromberg et al., 1991). New sediment deposits are prime sites for seedling emergence since they offer low shade stress owing to the absence of herb and litter layers. Natural disturbances, such as flooding and landslides, play important roles in the regeneration of riparian forests (Gregory et al., 1991; Nakamura, 1990).

## VI. Conclusion

Emergence of new seedlings were closely related with the coincidence of the seed dispersal periods and exposure of ground surface after spring floods. Sediment deposit made the bar higher and higher, and the ground surface could expose from early times. *Salix* species which disperse the seeds in the early period could establish on that bar.

The most serious factors affecting the survival of new seedlings was shading by older seedlings. But, it may be different tolerance to shading between *Salix sachalinensis* and *S. rorida*. This competitive exclusion process helps to explain the formation of almost even-aged *Salix* community.

These results contribute the broader interpretation for the process of colonization of *Salix* communities.

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