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RELATIONSHIP BETWEEN THE SOIL SEED BANK AND STANDING VEGETATION IN THE BAR OF A GRAVEL-BED RIVER

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SYNOPSIS

The purpose of this study was to investigate the distribution pattern and density of seeds in soil in a gravel-and-sand bar as well as the influence of the seedbank on standing vegetation. Median densities of the seeds in soil were 928 seeds/m^2 for the disturbed environment characterized by gravel materials and 5,344 seeds/m^2 for the environment characterized by sand materials. The seeds of all species were widely distributed in the soil. However, the distribution of plants was heterogeneous, suggesting that vegetation cover is not dependent on seed distribution but on the environmental conditions of the sites. Consequently, it can be deduced that although the seeds in soil and vegetation cover were significantly correlated, the local physical environment can be a more dominant factor than the seeds in soil in determining the bar vegetation in this gravel-bed river.

INTRODUCTION

Studies have shown that riverine plant communities can be destroyed by increases of discharge volume and bed load volume, or plant communities on the bankface can deposit amount of soil (1, 2). These studies provided evidence of the dynamics of river vegetation on the basis of a physical index, the shearing force on the river bed. In river floodplains, these dynamics may help rejuvenate plant communities. However, more studies are necessary to explain most schemes of river vegetation succession.

From an ecological point of view, it seems likely that seeds in soil play an essential role in the composition of the plant community at a particular locality. However, to the best of our knowledge, no studies have measured seedbanks in sandy riverbeds that experience heavy flood pulses and heavy sand deposition to clarify the relationship between seeds in the soil and standing river vegetation.

Studies of seedbanks have shown that the amount of seeds differs among land uses, and the species of seeds also may differ from the species of the aboveground plants (3–6). For example, one study revealed that farmland had dense seedbanks (29,000–70,000 seeds/m^2), whereas the density of forest seedbanks was far less (200–3300 seeds/m^2) (4). Another study reported low species similarity between seedbanks and the aboveground plants (5).

Other studies using channel experiments and numerical analysis (7–9) reported that seed dispersal contributes to the formation of plant communities. These studies are important to understand how seedbanks are produced in river systems.

The purpose of this study was to investigate the distribution pattern and density of seedbanks in a gravel-and-sand bar for better understanding the influence of seedbanks on standing vegetation in general, not only particular species as in the studies above.

STUDY SITE

This research was conducted on a gravel-and-sand bar which was about 0.1km^2 in the Naka River, located in northeastern Japan (Fig. 1). The river's drainage area is 3,270 km^2 from the Nasu valley at an elevation of 1,915m. The Naka River has a length of 150 km, and flows to Ibaraki Prefecture through parts of neighboring Fukushima Prefecture and Tochigi Prefecture. This site is located at an elevation of about 50m. The river slope at the study site is 1/770, and average grain size of the substrate is 25 mm. The mean annual maximum discharge is 1,400 m^3/s at this site. For several kilometers on either side of this site, other single gravel-and-sand bars exist. A massive water discharge has not occurred for about 10 years at this site, and the focal gravel-and-sand bar has remained essentially in the same location.

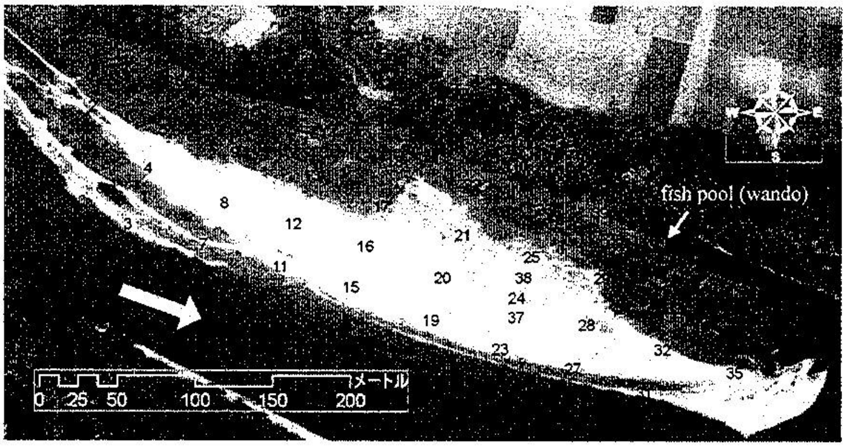


Fig. 1. An aerial photograph of the bar in the Naka River. Values are the sample site numbers.

The vegetation on the focal bar is characterized by Artemisia capillaries and Anaphalis margaritacea, which formerly grew on the riverside. Moreover, this site has more indigenous species growing in the dry riverbed and in marshy places on the bar than other bars in the Naka River.

MATERIALS AND METHODS

Geographical and vegetation maps of the overall study site

To map the topography at this site, more than 1,000 points were obtained by means of a real-time kinematic GPS survey from July 5 to 20 in 2007. Based on the points, a map of the bar surface was made by using a triangulated irregular network (TIN) layer using Geographic Information System (GIS) software(ArcGIS ver.9.1). A vegetation map was also created by means of ArcGIS using an aerial photograph and the vegetation survey data (see below) gathered around the same time as the topographical survey.

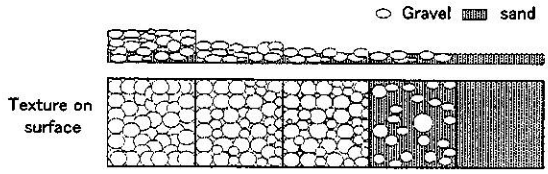
Distribution surveys of the aboveground vegetation and seedbanks

a) Setting of sampling points

Thirty-six sampling sites (each 0.5 m × 0.5 m) were located on each intersection point of vertical direction with crossing direction. Moreover, we added a sampling site in a backwater area that contains, one site in a plant community of rare species, and two sites in two plant communities of invasive species. When sampling sites were placed, if several plant communities occurred in a selected site, the site was relocated to a single plant community by moving it around 2–3 m.

b) Gravel-and-sand structure and vegetation on surface

The gravel-and-sand structure and vegetation community were investigated at each site. These structures were classified into five types according to the amount of gravel and sand on the surface (Fig. 2) (1,11). In the vegetation survey we recorded the plant species and the vegetation cover (%) by each species.



Gravel layer	Over 2	Over 1	—	—	—
Gravel rate on surface	100%	100%	Over 90%	Under 90%	0%
Sand rate on surface	0%	0%	Under 10%	Over 10%	100%
Type	I	II	III	IV	V

Fig. 2. An illustration of the five types of gravel-and-sand structures on the bar surface

c) Excavating gravel and sand

At each site, gravel-and-sand samples were gathered to 0.1-m depth. We assumed that the seeds gathered at this depth would have a high probability of germination (11).

Grain and seed analyses

a) Analysis of grain size

The grain size analysis followed the sedimentation method(JIS-A-1204), which entails examining the granularity of the soil after sun drying. We used the grain diameter classes recognized internationally by river engineers(12).

b) Extraction of seed

In the gravel-and-sand samples, the presence of seeds was confirmed visually when the seed diameter was more than 8 mm(e.g. Sicyos angulatus). For those seeds with a diameter of 8 mm or less, seeds and organic matter were extracted by the flotation method. For flotation processing, each sample was stirred for 5 min in 50% potassium carbonate (K_2CO_3) solution with a specific gravity of 1.54, and the floating seeds and organic matter were collected. The process was repeated three times, and the collected floating materials were oven-dried at 50 degrees Celsius for about 6 h. After such processing, only about 1/8 of the organic material was removed. Seeds were removed manually under a microscope, and both the species and the number of seeds were recorded.

Almost all of the seeds were discolored and distorted by dryness, shrinkage, having passed through an animal gut or having been partially consumed by microorganisms, making it difficult to identify seeds to the species level. Therefore, most seeds were identified only to the family or genus level. When a plant of a family or genus was noted in the aboveground vegetation, then we judged as that species had existed in the seedbank at least once.

Data analysis

a) Data analysis by GIS

We used ArcGIS to analyze the relationships among surface geography, aboveground vegetation, each grain size, and the seedbank at the sampling sites. Both the vegetation map and the surface geography map were divided into a 1-m mesh, and the plant community name and the elevation value were stored in each cell.

b) Analysis of relationship between seedbank species and aboveground vegetation

As an index of the relationship between the seedbank species and the aboveground vegetation, we calculated the appearance rate. This ratio equals the number of sites at which plants of a species grew, divided by the number of sites at which the species' seeds were found. However, the appearance rate was calculated by adding to the number of species within the seedbank, as the species had existed previously in the seedbanks even if certain seed species no longer existed in the seedbank, but existed in the standing vegetation.

RESULTS

Relationship between geographical features and vegetation in the study area

Geographical features and gravel-and-sand structural types in the study area are shown in Figures 3 and 4. The relative elevation, the difference between watermark amount at investigating and growth altitude, rose about 3-4 m from the waterside line in the main current part to the left bank side. Plant communities changed with this elevation gain in the order of Phragmites japonica community nearest to the water, Artemisia princeps community, and a variety of Kummerowia stipulacea communities. Almost all of the gravel-and-sand structures around this area were types I–III. A wando had formed between the

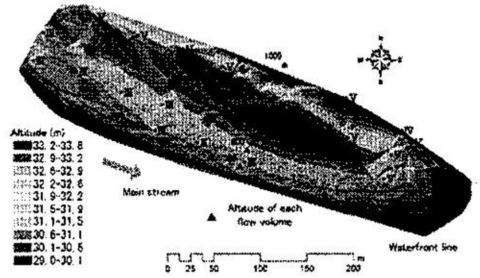
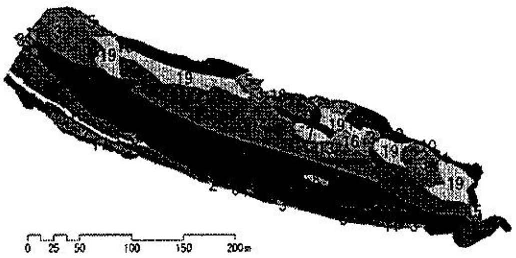


Fig. 3. Distributions of relative elevation and gravel-and-sand structure types



Community name
1.Sicyos angulatus
2.Persicaria lapathifolia
3.Miscanthus sacchariflorus
4.Humulus japonicus
5.Humulus japonicas-Phragmites japonica
6.Phalaris arundinacea
7.Pueraria lobata- Artemisia princeps
8.Eragrostis curvula
9.Oenanthe javanica-Phalaris arundinacea
10.Salix subfragilis
11.Phragmites japonica
12.Erigeron Canadensis-Setaria faberi
13.Kummerowia stipulacea-Artemisia capillaris
14. Kummerowia stipulacea-Artemisia princeps
15.Persicaria thunbergii
16.Lespedeza cuneata-Artemisia capillaris
17.Persicaria hydropiper
18.Salix subfragilis
19.Phragmites australis
20.Artemisa princeps

Fig.4 Vegetation map

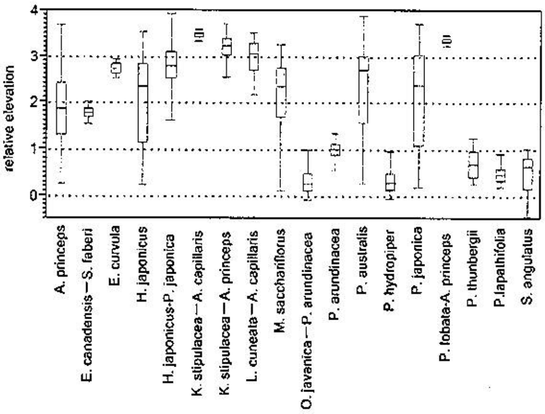


Fig. 5. The growth range of communities

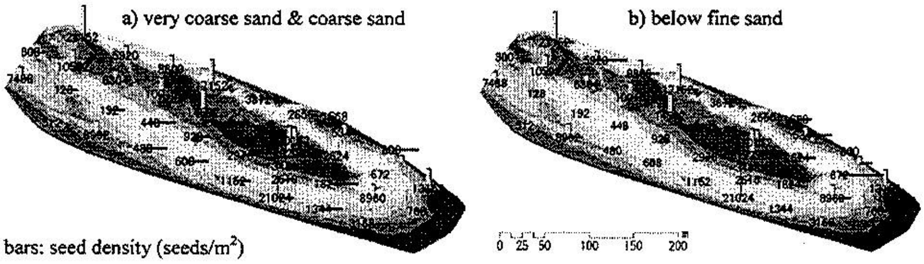
sand bar edge and the left bank. Almost all of the gravel-and-sand structures around this area were types IV and V. Moreover, many plant communities formed a mosaic in the vicinity of the wando.

Annual indigenous herbaceous communities (e.g., Oenanthe javanica–Phalaris arundinacea community, Persicaria hydropiper community, Polygonum thunbergii community) existed in the marshy area. The median relative elevation was about 0.5 m, and the growth range was narrow, about 1 m (Fig. 5).

Perennial indigenous herbaceous communities existed in both wet and dry conditions along with the annual Humulus japonicus, a climbing plant; the median relative elevation was about 2–3 m, and the growth range was wide, about 3 m. However, plant communities growing at the same relative elevation differed greatly on either side of the bar top. The P. thunbergii community (with a plant height of about 1 m) existed mainly from the channel side to the bar top. The Phragmites australis community and the A. princeps community (with a plant height of about 2–3 m) existed from the sand bar top to the wando area near the left bank.

Spatial distribution pattern of seedbanks

The seed density and the amount of sand (sand density) at each sampling site are shown in Figure 6; panel (a) shows the density values for very coarse and coarse sand, and panel (b) shows the density values for below the fine sand. There was a



Vertical bars: seed density (seeds/m^2)
Horizontal bars: sand density (seeds/m^2)
Numerical values are seed densities.

Fig.6 The distribution pattern of seeds and grain sizes close relationship between sand density and seed density. The seed density increased moving away from the main channel side of the bar. Areas of low seed density tended to be in localities with large amounts of below the fine sand and small amounts of coarse and very coarse sand, whereas high seed density showed the opposite trend.

With regard to gravel structure, the seed density was low in types I–III (i.e., >90% gravel) and high in types IV and V. In types I–III, the seed density ranged from 96 to 20,928 seeds/m^2, with a median of 928 seeds/m^2, whereas in types IV and V the range was 448 to 21,152 seeds/m^2, with a median of 5,344 seeds/m^2.

Seedbanks and aboveground vegetation at the study site

The seedbank species were found at 38 of the 40 sampling sites(Table 1). The species whose seeds were distributed widely across the bar were Portulaca oleracea at 37 sites, Persicaria sp. (Persicaria macrantha or Persicaria lapathifolia) at 36 sites, and Cyperaceae at 35 sites. Some groups were represented by numerous seeds, in the following order: P. oleracea > Poaceae C (e.g., Eragrostis curvula, Digitaria ciliaris) > Cyperaceae. Moreover, there were many seedbank species that were not observed in the aboveground vegetation. For instance, P. oleracea did not exist in the vegetation on the bar, although it is widely distributed in the area and there were many seeds of this species in the seedbanks. This was also the case with Cyperaceae. In addition, the seeds of many tree species in nearby mountainous areas and upstream areas of the watershed were included in the seedbanks.

The aboveground vegetation at the sampling sites belonged to 21 families (Table 2). The species distributed widely across the bar were Artemisia indica at 22 sites, P. japonica at 18 sites, and Humulus scandens at 35 sites. Many species in the aboveground vegetation were not represented in the seedbanks such as A. indica and Conyza canadensis, which were distributed widely on the bar. The seeds of Artemisia and Conyza reportedly do not persist in seedbanks because they are prone to drying and shrinkage (15). Consequently, there is a strong possibility that the seeds of these species had degraded due to weathering because dryness is especially pronounced on the bar.

Table 1. The species in seedbanks at the study sites

species		sampling point(No.)																																								NS	SB
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40		
Portulaca oleracea		512	16	0	0	144	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	24	[illegible]	[illegible]	208	[illegible]	120	32	240	16	[illegible]	[illegible]	320	[illegible]	304	9,624	37
Polygonum(Persicaria lapathifolia)	○	112	88	0	0	[illegible]	[illegible]	[illegible]	0	[illegible]	[illegible]	[illegible]	40	16	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	104	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	120	[illegible]	[illegible]	[illegible]	6,104	36
Cyperaceae		240	8	24	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	120	[illegible]	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	[illegible]	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	5,024	35
PoaceaeD	○	64	16	0	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	[illegible]	0	[illegible]	0	0	[illegible]	[illegible]	[illegible]	[illegible]	72	0	[illegible]	[illegible]	24	[illegible]	[illegible]	0	[illegible]	832	30
PoaceaeC	○	40	0	0	[illegible]	[illegible]	40	[illegible]	0	0	16	0	40	64	0	0	104	[illegible]	[illegible]	[illegible]	400	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	72	160	816	[illegible]	[illegible]	976	0	0	0	128	512	1,872	[illegible]	[illegible]	7,600	29
Chenopodium centrorubrum	○	64	0	0	0	88	[illegible]	24	16	[illegible]	80	[illegible]	0	[illegible]	160	0	0	[illegible]	[illegible]	[illegible]	0	[illegible]	[illegible]	16	0	[illegible]	[illegible]	0	[illegible]	[illegible]	24	0	[illegible]	[illegible]	16	16	[illegible]	[illegible]	0	0	24	1,888	28
Persicaria thunbergii	○	8	0	0	0	[illegible]	[illegible]	40	0	24	[illegible]	0	[illegible]	[illegible]	[illegible]	[illegible]	0	[illegible]	[illegible]	0	24	0	0	[illegible]	[illegible]	[illegible]	0	[illegible]	16	[illegible]	32	16	72	[illegible]	0	[illegible]	[illegible]	8	0	16	32	904	28
PoaceaeB	○	64	8	24	0	16	[illegible]	24	[illegible]	0	104	40	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	40	0	[illegible]	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	16	[illegible]	0	0	0	0	0	240	[illegible]	0	0	[illegible]	0	1,024	27
Boehmeria longispica		112	24	16	8	[illegible]	400	48	0	[illegible]	32	0	[illegible]	160	[illegible]	0	0	120	[illegible]	[illegible]	0	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0	0	0	64	[illegible]	32	0	8	0	[illegible]	96	0	0	64	2,904	27
Mollugo stricta		16	16	0	0	88	144	0	0	40	[illegible]	0	0	32	[illegible]	0	0	[illegible]	48	0	0	0	[illegible]	[illegible]	[illegible]	16	[illegible]	[illegible]	0	[illegible]	[illegible]	[illegible]	8	0	8	0	32	0	[illegible]	16	0	768	24
Persicaria hydropiper	○	0	0	0	0	0	32	88	0	72	16	0	0	[illegible]	16	[illegible]	0	[illegible]	[illegible]	0	[illegible]	16	0	16	[illegible]	0	0	0	0	[illegible]	[illegible]	16	112	16	0	8	1,400	[illegible]	16	64	0	2,040	23
Cardamine parviflora	○	168	0	0	0	240	272	0	0	72	32	0	0	152	24	0	[illegible]	96	40	0	[illegible]	0	[illegible]	72	[illegible]	176	8	0	0	[illegible]	32	0	0	[illegible]	0	0	0	16	8	0	32	1,544	22
PoaceaeA	○	8	0	0	0	16	16	24	0	32	8	0	0	40	0	0	0	0	216	0	8	0	[illegible]	16	[illegible]	16	0	[illegible]	16	0	40	0	40	0	0	0	48	16	32	0	8	656	21
Oenothera elata	○	144	0	0	0	[illegible]	104	0	0	56	48	0	0	248	88	0	0	80	[illegible]	[illegible]	40	0	[illegible]	[illegible]	24	432	0	0	0	[illegible]	[illegible]	0	16	0	0	0	8	[illegible]	0	0	0	2,904	20
Setaria italica		8	0	0	0	0	0	24	0	48	8	[illegible]	0	16	0	0	0	0	[illegible]	0	[illegible]	[illegible]	0	[illegible]	[illegible]	[illegible]	0	[illegible]	[illegible]	[illegible]	0	[illegible]	32	0	0	0	[illegible]	[illegible]	[illegible]	0	0	376	20
PoaceaeE	○	48	0	0	8	8	40	120	0	24	0	0	[illegible]	8	0	0	0	[illegible]	[illegible]	0	0	0	0	[illegible]	0	[illegible]	[illegible]	0	0	0	[illegible]	[illegible]	[illegible]	0	[illegible]	0	1,008	0	0	192	0	2,648	19
subgen. Chamaesyce		24	0	0	0	16	72	16	0	0	16	0	0	[illegible]	16	0	0	32	24	8	0	0	[illegible]	[illegible]	[illegible]	[illegible]	0	[illegible]	0	0	0	0	16	0	0	[illegible]	0	32	120	0	0	1,096	19
Humulus scandens	○	0	0	0	0	8	[illegible]	0	0	[illegible]	144	0	0	0	280	0	8	[illegible]	[illegible]	0	0	0	96	0	0	0	[illegible]	0	0	[illegible]	16	[illegible]	16	[illegible]	8	0	0	0	0	[illegible]	136	1,472	18
Arabis serrata		8	0	0	0	[illegible]	0	0	0	[illegible]	32	0	0	[illegible]	16	0	0	16	24	0	0	[illegible]	0	120	0	32	0	[illegible]	[illegible]	64	0	0	0	0	0	8	[illegible]	0	16	0	0	880	17
Oxalis corniculata		16	0	0	0	[illegible]	[illegible]	0	0	0	24	0	0	0	24	0	8	40	40	0	8	0	24	0	0	0	[illegible]	0	0	8	0	0	40	0	0	[illegible]	0	[illegible]	[illegible]	0	40	392	17
Monochoria vaginalis	○	16	0	0	0	[illegible]	0	[illegible]	0	0	[illegible]	0	0	0	24	0	0	8	24	0	0	0	0	16	8	8	0	0	16	0	[illegible]	16	8	0	0	0	0	0	0	0	24	240	15
Silene gallica		32	0	40	0	[illegible]	[illegible]	[illegible]	0	240	64	0	0	160	56	0	0	8	[illegible]	0	0	0	0	0	0	0	0	0	0	0	0	[illegible]	[illegible]	0	0	0	16	0	0	0	0	664	14
Rubus		0	0	0	0	[illegible]	[illegible]	0	0	[illegible]	[illegible]	8	0	0	12	0	0	0	72	0	0	0	8	0	0	0	0	0	0	0	[illegible]	[illegible]	16	8	0	0	[illegible]	0	0	0	24	248	14
Eleusine indica		8	0	0	0	40	[illegible]	16	0	0	8	0	0	8	8	0	0	48	0	0	0	0	8	0	0	0	0	0	0	0	8	0	8	0	0	0	0	8	0	0	8	184	13
Mosla punctulata		0	0	0	0	0	16	8	0	0	0	0	0	16	8	0	0	16	16	0	0	0	0	0	0	8	0	8	0	8	0	0	8	0	0	0	0	8	0	0	0	120	11
Solanum nigrum	○	16	0	8	0	[illegible]	16	[illegible]	0	0	0	0	0	16	56	0	0	0	72	0	0	0	0	0	0	0	0	0	0	8	8	0	24	0	0	0	0	0	0	0	0	280	11
Zelkova serrata		16	0	0	0	0	[illegible]	0	0	0	16	0	0	0	0	8	0	0	0	0	0	0	0	0	8	0	0	8	0	0	0	0	40	0	0	0	112	16	[illegible]	0	0	256	10
Lemna trisulca		56	0	0	0	[illegible]	[illegible]	0	0	0	0	0	0	32	24	0	0	8	40	0	0	0	0	0	0	0	56	0	0	0	[illegible]	0	0	0	0	0	0	0	0	0	0	432	9
Scenedesmus quadricauda		32	0	[illegible]	0	[illegible]	[illegible]	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	24	0	0	0	0	0	0	8	0	8	0	0	0	0	0	8	0	0	0	136	9
Sambucus racemosa		0	0	0	0	0	[illegible]	[illegible]	0	0	8	0	0	0	8	0	0	16	0	0	0	0	8	0	0	0	0	0	0	8	0	24	16	0	0	0	0	0	0	0	0	104	9
Asteroideae		0	0	8	0	24	[illegible]	[illegible]	0	16	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	8	0	0	0	8	0	0	0	0	0	0	0	0	0	0	88	8
Lespedeza	○	0	0	0	0	0	0	0	0	8	0	0	0	8	0	0	0	0	0	0	40	0	0	16	0	16	0	0	0	0	0	0	8	0	0	0	0	0	24	0	8	128	8
Amaranthus		0	0	0	0	0	16	0	0	0	0	0	0	8	32	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	8	0	8	0	0	112	7
Schoenoplectus lacustris		0	8	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	40	0	0	0	8	0	0	112	6
Eclipta thermalis		0	0	0	0	8	32	0	0	0	0	0	0	40	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	8	0	0	112	6
Morus australis		0	0	0	0	0	0	8	0	0	0	0	8	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	16	0	0	0	8	0	0	0	0	56	6
Rumex obtusifolius	○	8	0	0	0	0	16	0	0	8	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	8	0	0	0	0	0	0	0	0	64	6
Bidens pilosa	○	0	0	0	0	0	0	0	0	0	0	0	0	8	0	8	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	8	0	0	0	48	5
Actinidia polygama		0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	8	16	0	0	0	0	0	0	8	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	48	5
Rubia argyi		0	0	0	0	0	8	56	0	0	0	0	0	0	0	0	0	1,520	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	1,592	4
Aralia elata		0	0	0	0	0	16	8	0	0	0	0	0	8	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	4
Sagittaria trifolia (2)		8	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	8	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	4
Carpinus tschonoskii		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	8	0	8	0	0	0	16	0	0	0	0	40	4
Prunus Sect.Sargentiella		0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	8	0	0	0	0	8	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	32	4
Actinidia deliciosa		0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	16	0	0	0	8	0	0	0	0	48	4

Oryza sativa		8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8	0	0	0	0	0	0	0	0	0	0	0	0	24	3
Sicyos angulatus	○	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	64	3
Broussonetia kazinoki		8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	40	3
Swida controversa		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	8	8	0	0	24	3
Cornus macrophylla		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	8	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	24	3
Trigonotis		0	0	0	0	0	0	0	0	0	0	0	0	152	0	0	0	0	0	0	0	0	8	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	168	3
Chelidonium majus		0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	2
Ajuga pygmaea		8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	16	2
Sambucus chinensis		0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	2
Murdannia keisak		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	24	2
Impatiens textorii		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8	0	0	0	0	0	0	0	0	16	2
Galium spurium		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	224	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	224	1
Poaceae(fragment)	○	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	8	1
PoaceaeF	○	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1
Sagittaria trifolia (1)		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	8	1
Hemistepta lyrata		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	8	1
Corydalis ochotensis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	8	1
Quercus Quercus		0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	1
Lamiaceae		0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1
Commelina communis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	8	1
Vitis		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1
Actinidia arguta		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8	1
Fabaceae		0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	1
Vigna angularis	○	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1
none		0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1
sum		1,872	200	128	24	2,648	5,288	2,248	48	1,576	1,480	112	112	2,504	2,200	144	232	3,648	4,288	288	744	264	944	5,232	872	2,528	664	304	456	656	1,336	752	2,184	168	200	168	3,288	640	4,824	392	1,032	56,688	
appearance species		30	9	7	3	30	34	28	5	21	25	7	6	29	27	12	9	32	35	11	14	10	20	20	19	23	12	16	13	21	24	20	40	9	10	11	24	22	19	10	18	70	

1. The number of seeds indicated is 8 times the analysis result because the hyperbaric method only removed 1/8 of the organic material from sediment samples.

2. The values are the seed numbers, with presence indicated by a gray cell.

3. The species identities of Poaceae A, D, and F are uncertain; Poaceae B represents *Phragmites japonica*, *Phragmites australis*, *Lolium ×hybridum Hausskn*, *Lolium perenne*, *Vulpia myuro*, *Bromus remotiflorus*, *Elymus tsukushiensis*, and so on, Poaceae C represents *Eragrostis curvula*, *Digitaria ciliaris* and so on, and Poaceae E represents *Phalaris arundinacea*, *Poa trivialis*, *Poa ochotensis*, and so on.

4. An open circle indicates that the species (family/genus level) existed in the standing vegetation on the bar.

5. Sum in this table contains the seed numbers of other species.

Table 2. The standing vegetation in the study sites

species	sampling point(No,)																																								F	SB	AR
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40			
Artemisia indica		40			20		1	3	1	1	5	2	5		10	1	3		1	5			3	1	3		10	1	70			2						1			22	—	—
Phragmites japonica	▨30	▨40	▨10	2	▨60	▨	▨10	▨	100	▨70	▨1		▨100	▨20	▨	▨	▨100	▨80		▨		▨	▨	▨	▨	▨	▨	▨	▨90		90	70			▨70	▨			▨		18	27	58
Humulus scandens					▨30	▨100			▨	▨90			20	▨100		▨	▨20	▨				▨		1		▨100			▨	▨	▨30	▨50	▨30	▨	20				▨	▨50	15	18	71
Persicaria lapathifolia	▨	▨	30	1	▨	▨	▨		▨	▨	▨1	▨	▨	▨	▨	▨	▨	▨1	▨	▨	▨	▨	▨	▨1	▨		▨	▨1	▨1	▨	▨1	▨1	▨	▨	▨30	▨20	▨	▨	▨	▨	13	36	34
Poaceae sp.		1		1										5	1	1			2		3			5				2			1	3			3		1				13	—	—
Phalaris arundinacea	▨20			▨	▨	▨	▨80		▨			▨	▨	10			▨	▨					▨		▨	▨60				▨90	▨	▨30		▨		▨50			▨80	20	9	19	43
Persicaria thunbergii	▨				▨	▨	▨5		▨1	▨		▨	▨1	▨	▨		▨	▨		▨			▨	▨	▨		▨	▨	▨	▨30	▨5	▨1	▨		▨5	▨60	▨		▨10	▨	9	28	32
Conyza canadensis			2				5	1								3	3	1		1	1																	3			9	—	—
Kummerowia striata					▨							1			1				3		1			3	1												1	10			8	1	89
Elymus tsukushiensis	▨	▨5	▨		▨	▨	▨	▨	1	▨	▨		▨	▨10	▨	▨	▨	▨	1	▨	1	▨	▨	▨	▨	▨	▨	▨	▨5						▨	▨			▨		7	27	23
Lepidium virginicum				5												1					3		3					2										5			6	—	—
Commelina communis		1							1									1			1											▨1									5	1	100
Glycine max		5			▨															1	1								5								1				5	1	83
Sicyos angulatus					▨5								10				▨	10															5			▨				80	5	3	71
Bidens frondosa							1		1				▨		▨		▨	5												1		▨					▨	5			5	5	50
Equisetum arvense		3				5			5									10																						3	5	—	—
Pueraria lobata		10			▨70								50												3																4	1	100
Kummerowia stipulacea					▨															3	5				3			3													4	1	80
Lolium multiflorum	▨	▨	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨	▨	3	▨	1	▨	▨	▨1	▨	▨	▨	▨1	▨						▨	▨			▨		4	27	14
Pilea pumila										1			5																	1		1									4	—	—
Lespedeza cuneata									▨				▨							▨20	1		▨		▨							▨						▨		▨	3	8	33
Trifolium repens		10			▨		8																																		2	1	67
Bidens pilosa													▨		▨		▨							1				1				▨					▨				2	5	29
Poa trivialis	▨			▨	▨	▨	▨		▨			▨	▨				▨	▨					▨		▨	▨				▨	▨	▨		▨		▨			▨		2	19	11
Chamaesyce maculata	▨		1		▨	▨	▨			▨			▨	▨			▨	▨	▨			▨	▨	▨	▨		▨					▨			▨		▨	▨			2	19	10
Oenothera parviflora	▨				▨	▨			▨	▨			▨	▨			▨	▨	▨	▨	1	▨	▨	▨	▨				▨	▨		▨				▨	▨				2	20	10
Cardamine scutata	▨		5		▨	▨			▨	▨			▨	▨		▨	▨	▨		▨		▨	▨	▨	▨	▨			▨	▨			▨				▨	▨		▨	2	22	9
Persicaria hydropiper						▨	▨		▨	▨			▨	▨	▨		▨	▨		▨	▨		▨	▨					▨	▨	▨	▨	▨		▨	▨	▨	▨	▨		2	23	9
Hordeum nodosum	▨	▨	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨1	▨	▨		▨	2	▨	▨	▨	▨	▨	▨	▨	▨						▨	▨			▨		2	27	7
Vulpia myuros	▨	▨	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨	▨		▨	5	▨	▨	▨	▨	▨	▨	▨	▨						▨	▨			▨		2	27	7
Poaceae sp2.																								1				3													2	—	—
Artemisia capillaris																									1													50			2	—	—
Glechoma hederacea					20												3																								2	—	—
Stellaria media																	1															1									2	—	—
Cerastium glomeratum																							1									1									2	—	—
Sedum bulbiferum									1									3																							2	—	—
Vigna angularis					▨																														1						1	1	50
Trifolium pratense					▨																				1																1	1	50
Amphicarpaea bracteata					▨				5																																1	1	50
Vicia sepium					▨				1																																1	1	50
Rumex acetosella	▨					▨			▨						▨										3					▨		▨									1	5	17
Poa ochotensis	▨			▨	▨	▨	▨		▨			▨	▨				▨	▨					▨		▨	▨				▨	▨	▨		▨		▨			▨		1	19	5
Bromus remotiflorus	▨	▨	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨	▨		▨		▨	▨	▨	▨	▨	▨	▨	▨						▨	▨			▨		1	24	4
Lolium x hybridum Hausskn	▨	▨	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨	▨		▨		▨	▨	▨	▨	▨	▨	▨	▨						▨	▨		3	▨		1	27	4
Phragmites australis	▨	▨	▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨	▨		▨		▨	▨	▨	▨	▨	▨	▨	▨						▨	▨			▨	70	1	27	4
Chenopodium album	▨				▨	▨	▨	▨	▨	▨	▨		▨	▨			▨	▨	▨		▨	▨	▨		▨	▨		▨	▨	▨		▨	▨	▨	▨10	▨	▨			▨	1	28	4
Eragrostis curvula	▨			▨	▨	▨	▨			▨		▨	▨			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨				▨	▨	▨	▨	▨	1	29	3
Digitaria ciliaris	▨			▨	▨	▨	▨			▨		▨	▨			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨				▨	▨	▨20	▨	▨	1	29	3

Paederia foetida					10																																				1	—	—
Miscanthus sacchariflorus																																	100								1	—	—
Metaplexis japonica																																	1								1	—	—
Solidago altissima													1																												1	—	—
Galinsoga quadriradiata										1																															1	—	—
Ambrosia artemisiifolia																			1																						1	—	—
Mosla scabra																								1																	1	—	—
Viola grypoceras	1																																								1	—	—
Oenanthe javanica																																							80		1	—	—
Persicaria longiseta																																1									1	—	—
Persicaria senticosa																		5																							1	—	—
Acalypha australis																							3																		1	—	—
Stellaria aquatica																																								5	1	—	—
Arenaria serpyllifolia							1																																		1	—	—
Stellaria uliginosa																																1									1	—	—
Achyranthes japonica																		1																							1	—	—
Cayratia japonica										10																															1	—	—
sum	4	10	6	5	8	4	9	3	13	7	4	3	9	6	4	6	9	12	7	6	14	1	6	10	12	3	2	9	6	7	6	15	5	1	8	4	6	10	5	7		mean:36	
structure type	3	3	2	3	5	5	4	3	5	5	3	3	5	5	2	3	5	5	3	3	3	5	1	4	4	5	1	4	5	5	5	5	5	4	5	5	4	3	5	5		median:30	

1. The values indicate vegetation coverage rate (%).

2. When a species is included in the seedbank at a sampling site, the cell is shaded gray.

3. The appearance rate (%) is defined as the number of sites at which plants of a species grew divided by the number of sites at which the species' seeds were found. F, the existence points of seedbanks; SB, the total number of sites at which the species was included in the seedbank; AR, the appearance ratio.

4. Sum in this table contains the species numbers of other species.

DISCUSSION

This study investigated the relationship between distribution patterns of seedbanks and standing vegetation on a gravel-and-sand bar. Seeds were distributed widely across the bar, although the density of seeds differed between areas with mostly gravel zone versus areas with mostly sandy zone. Our results indicate that, although there was a strong correlation between the seedbanks and the standing vegetation, the physical environmental conditions had a greater influence on which species grew in particular localities.

Spatial distribution characteristic of seedbanks

The density of the seedbanks varied among the sampling sites. The seed density of sites dominated by sand (i.e., types VI and V, hereafter collectively called the sandy zone) was about six times greater than that of gravel beds (i.e., types I–III, hereafter collectively called the gravel zone; Fig. 6). However, the density of seeds in both the sandy zone and the gravel zone was sufficient to supply the vegetation communities with seedlings, and the densities were never less than those reported for seedbanks in forests (4). The difference in the seed density between the sandy zone and gravel zone was related to the grain size of the sand, suggesting that this difference depends on the amount of seed washed away by the river during flooding events.

However, we observed no species that were strictly located only in the gravel zone or the sandy zone. We noted that seedbanks were distributed widely across the sand bar. Some plants were observed living over the entire bar, such as P. oleracea, Poaceae, Cyperaceae, and Polygonum spp. Some of the species' seeds were distributed at only half of the sampling sites, such as Setaria italica, Eleusine indica, and Chamaesyce spp (Table 1).

Relationship between seedbank species and standing vegetation

Seedbanks were distributed widely across the bar. However, the degree of the growth range of standing vegetation depended on the environmental gradient of each community (Fig. 5). To explain this discrepancy, we examined how seedbanks influence the vegetation based on the relationship between seedbank species and vegetation species shown in Table 2.

First, we explain this phenomenon using Persicaria thunbergii as an example. Persicaria thunbergii plants were found growing at 9 sites, yet this species' seeds were found evenly distributed among 28 sites. Thus, the appearance rate was 32% (9/28), which is comparable to the overall mean. The plants grew in the sandy zone (types IV and V) and on wet sites (nos. 30, 36, 39) and had a high coverage rate (10–60%). However, P. thunbergii seeds were found at sites where the plants did not exist in the standing vegetation or where the vegetation rate was remarkably low; these sites were in the gravel zone (types I–III),and in low-lying areas on the main channel side of the bar, or in the sandy zone and (P. japonica community) where the relative elevation was high. Thus, although P. thunbergii seeds were widely distributed, the environmental conditions were only favorable for germination at some of the sites.

Poaceae seeds were also widely distributed. However, the appearance rate of plants was 10% or less, except for the species P. japonica and P. arundinacea. Phragmites japonica showed a wide distribution and grew at sites ranging from low to high relative elevation. The plants had high vegetation cover on gravel-and-sand structures of types IV and V and low vegetation cover on types II and III. Phalaris arundinacea plants grew mostly on the channel side of the bar on gravel-and-sand structures of types IV and V. Thus, these findings also support the hypothesis that vegetation cover was a function of the environmental conditions.

The seeds of H. scandens, an annual vine, were found at many sampling sites and the plants had a high appearance rate. This species grew in the sandy zone at sites with high relative elevation away from the main stream. The high appearance rate likely resulted because seed is not easily flushed from the sandy zone, but also many seeds are dispersed widely as the vines grow over the upper parts of P. australis and Tiarrhena sacchariflora. Although H. scandens seeds were found in the type III structure at site no. 16, no plants of this species were found at this site.

The seedbanks did influence the composition of the standing vegetation, but the effect of environmental conditions on germination was more important. Thus, we conclude that the local physical environment is a more dominant factor than the seeds in the soil in determining the bar vegetation in this gravel-bed river.

CONCLUSIONS

We investigated the distribution pattern and density of seeds in soil in a gravel-and-sand bar by excavating gravel and seeds as well as the influence of the seedbank on standing vegetation. As a result, median densities of the seeds in soil were 928 seeds/m^2 for the disturbed environment characterized by gravel materials and 5,344 seeds/m^2 for the environment characterized by sand materials. However, many seedbank species were not observed in the aboveground vegetation. For instance, P. oleracea did not exist in the vegetation on the bar, although it was widely distributed in the area where there were many seeds of this species in the seedbanks.

From the results, we can conclude the following;

- The seed density tended to be high in localities with large amounts of below the fine sand and low in small amounts of coarse and very coarse sand.
- The seeds of all species were widely distributed in the soil. However, the distribution of plants was uneven.
- The density of seeds in both the sandy zone and the gravel zone was sufficient to supply the vegetation communities with seedlings, and the densities were never less than those reported for seedbanks in forests.
- Our findings suggest that the physical environmental conditions had a greater influence on which species grew in particular localities(e.g. 15) , although there was a strong correlation between the seedbanks and the standing vegetation.

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APPENDIX – NOTATION

The following symbols are used in this paper:

I, II, III, IV, V = types of gravel-and-sand textures on the bar surface;

NS = the total number of seeds;

SB = the total number of sites at which the species was included in the seedbank;

SP = the total number of sites at which the standing plants were observed; and

AR = the appearance ratio.

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