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Relationship between dominant species, vegetation composition and species attributes in spring and autumn on a riverbank: implications for river management to enhance ecosystem functions

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Abstract

An important ecosystem function of vegetation on riverbanks is the control of soil erosion. Riverbanks also offer potential semi-natural habitats for grassland species. Previous classification of riverbank vegetation in Japan ignored both seasonal changes of dominant species and species composition, offering no information on ecosystem functions. Here we aimed at clarifying the association between dominant species, vegetation composition and species attributes in spring and autumn. We surveyed vegetation in 125 plots on a riverbank in Japan. We identified seven vegetation types on the basis of dominant species in autumn. *Imperata cylindrica* var. *koenigii* (Type I) and *Pleioblastus chino* (Type P) dominated their vegetation year-round. Dominant species changed seasonally in the other five vegetation types, but *Lolium multiflorum* was dominant in spring. Since the dominance of annuals is linked to fast turnover of root systems and thus poor control of soil erosion, Types P and I are superior in controlling soil erosion. Both the total number of species and the number of grassland species were small, showing species-poor grasslands in all vegetation types. There were no clear differences in numbers of species between species attributes. Nevertheless, this classification was linked to differences in species composition, reflecting several representative species in each vegetation type. Type P has more indigenous representative species and typical grassland species. Since some representative species may be suitable for natural processes (e.g., for pollination), this classification reflects biodiversity functions.

Keywords Seasonal vegetation change · Semi-natural grassland · Ecosystem function · Representative species · Species attribute

Introduction

Biodiversity is important for ecosystem functions (Millennium Ecosystem Assessment 2005), which sustain both human needs (through supporting, provisioning, regulating and cultural functions) and ecological needs (through natural processes). The assessment of ecosystem functions is a valuable planning and management tool (Cardinale et al. 2012). Research should focus on both human and ecological needs at the same time for both existing and planned sustainable ecosystems (Cardinale et al. 2012; Higgs 2017).

Flooding caused by embankment breaches can have devastating consequences for surrounding areas. An important regulating ecosystem function of vegetation is the control of soil erosion (e.g., De Groot et al. 2002; Wallace 2007). Both above- and below-ground plant parts are important (Gyssels et al. 2005; Vannoppen et al. 2016). Vegetation cover reduces splash detachment and inter-rill erosion (Zuazo and Pleguezuelo 2009). Plant roots are effective in controlling concentrated flow erosion and shallow mass movements by contributing to both mechanical and hydrological soil properties (e.g., Simon and Collison 2002; Eviner and Chapin 2003), and they are more pronounced on splash detachment

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and inter-rill erosion (e.g., Zuazo and Pleguezuelo 2009; Shinohara et al. 2016). Although less reliable than below-ground traits, above-ground traits are useful for predicting root length density when information on below-ground traits is lacking (Helsen et al. 2016).

Riverbanks are traditionally revegetated with perennial grass species in Asia (Ezaki and Sakurai 1992; Lee and Nakagoshi 2010) and in Europe (Coppin and Stiles 1995; Scheres and Schüttrumpf 2019), which provide year-round soil cover, limiting erosion sometimes even with continued biomass harvest (Zuazo and Pleguezuelo 2009). They support typical species-rich plant communities (Liebrand and Sykora 1996; Bátori et al. 2016; Koyanagi et al. 2019). This also enhances other trophic groups, leading to important roles as semi-natural grassland in natural processes (e.g., habitat creation, ecological connectivity enhancement, integrated pest control; Reijers et al. 2014; Korvroëdan et al. 2021). Berendse et al. (2015) and Gould et al. (2016) demonstrated the positive influences of greater plant species richness and functional diversity on preventing soil erosion in grasslands on a simulated embankment. If this is applicable for real riverbanks, it is important to evaluate the effectiveness of components of species diversity in mitigating runoff and soil erosion (Hazebroek and Sprangers 2002). However, positive influences are still debatable. Scheres and Schüttrumpf (2020) suggested that species mixtures with a greater percentage of herbs and higher diversity lead in early development stages and lessen erosion resistance relative to a standard grass-dominated mixture. Thus, the engineering of embankments should consider both ecological needs and human needs at the same time for more sustainable design (Sasaki et al. 2000).

In Japan, means of improving the cost efficiency of managing embankments include reducing the frequency of mowing, which leads to unfavourable vegetation changes that replace short-grass monocultures with taller species (Asami et al. 1994). The mown plant material is removed and incinerated to improve surface visibility on riverbanks. At a given root density, a fibrous root system is hypothesized to have a larger erosion-reducing potential than a taproot system, owing to the larger root–soil contact (Dissmeyer and Foster 1985). Taller grass species are less suitable for land managers owing to their sparse root systems (Sasaki et al. 2000), and their large above-ground biomass is unsuitable because of the high incineration costs (Yamamoto and Yatsuki 2019).

The distribution of vegetation can be patchy along riverbanks (Koyanagi et al. 2019; Tisserant et al. 2021). Vegetation classification is important in evaluating the ecosystem functions in riverbank sections. Riverbanks are currently classified on the basis of dominant species. This is reasonable because local river managers can identify the vegetation type easily, even if they are unfamiliar with the species; and the mass ratio hypothesis (Grime 1998) stipulates that ecosystem properties are driven by the traits of the dominant species in the community. Sasaki et al. (2000) indicated seven vegetation types on riverbanks in Japan, among which they paid attention to three major types, dominated in turn by *Zoysia japonica*, *Imperata cylindrica* var. *koenigii* and *Lolium multiflorum*. They measured root densities as an indicator of the potential to control soil erosion (Hattori et al. 1997) and found that vegetation dominated by *Z. japonica* had the highest root density, and therefore high soil erosion control, followed by *I. cylindrica* var. *koenigii* and *L. multiflorum*. However, this classification does not take into account floristic composition: it remains unclear whether it is linked to differences in floristic diversity (i.e., species richness in each species attribute) among vegetation types. Moreover, it does not focus on seasonal vegetation change. Although *L. multiflorum* is replaced by other species in summer and later, the identity of those species is unclear. Understanding the relationship of vegetation between spring and autumn is important to evaluating ecosystem functions year-round.

This study was designed to compare the vegetation of major vegetation types on a riverbank in spring and autumn. We aimed at clarifying the association of both dominant species, floristic composition and species attributes between spring and autumn, and we discuss the evaluation of ecosystem functions desirable for riverbanks.

Materials and methods

Study site

The study site is located in Ageo, Saitama Prefecture, Japan (35°56′20″N, 139°33′03″E; Fig. 1). The mean annual precipitation (30 years period, between 1991 and 2020), recorded at the nearby Saitama meteorological station, is 1371 mm; the mean annual temperature is 15.2 °C, the mean minimum is 3.9 °C (January), and the mean maximum is 27.0 °C (August) (JMA 2022). The study site is on the east bank (left bank), and both the land- and the river side of the Arakawa River, with a slope of 20°. The vegetation was mown twice a year, which is conventional for maintaining the riverbank. This bank was constructed before the 1950s. Since then, no broadscale reconstructions have taken place. Nevertheless, patchy maintenance (introduction of surface soil and subsequent planting of *Z. japonica* or *Ophiopogon japonicus*) has been done, though it is difficult to clarify where and when (personal communication with H. Sugama, former Head of the Organization for the Conservation of Arakawa River, Japan).
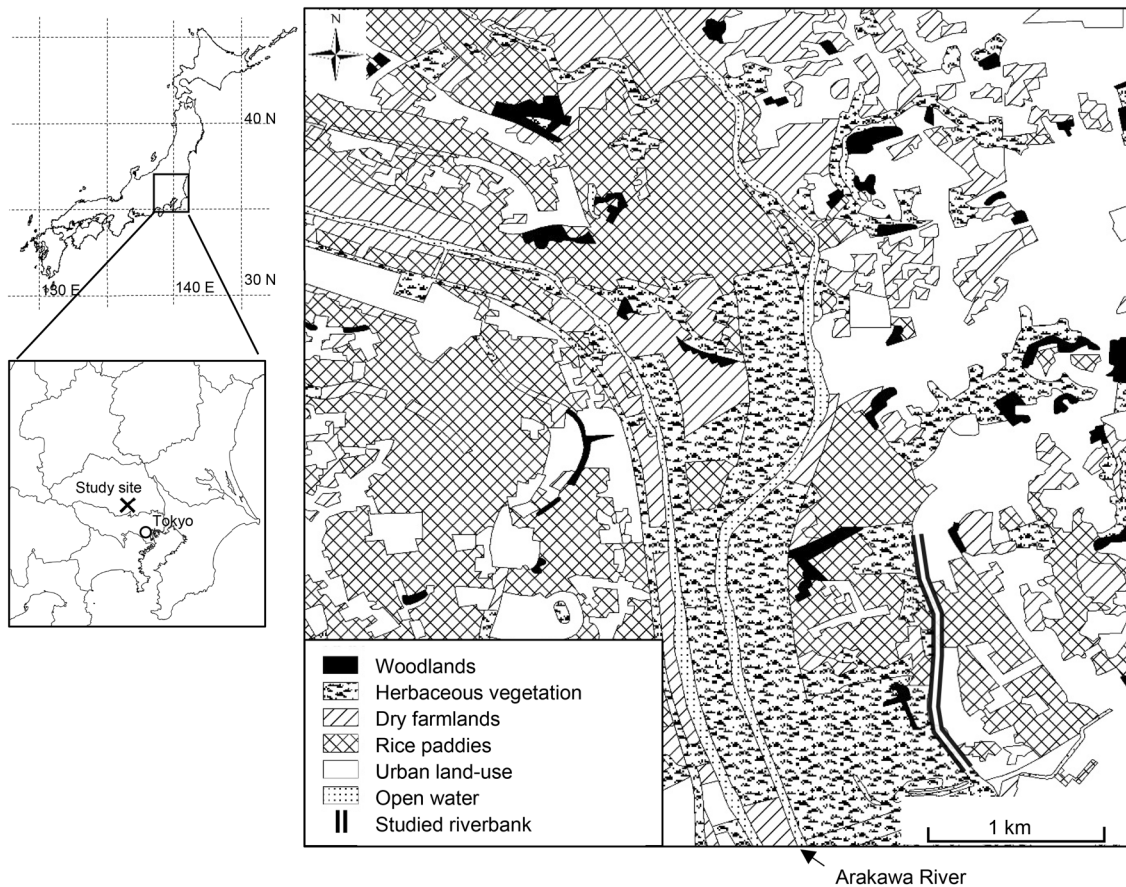
Fig. 1 Location of the study site

Vegetation survey

The data were obtained by one of us (Saito H.) to evaluate the effects of past grazing activities on the vegetation composition on the riverbank. The riverbank had been grazed by cattle owned by a farmer until sixty years ago. According to the interview with the farmer (Sugama H.) the nearer the location of the riverbank, the higher the grazing intensity. Vegetation plots were established on the riverbank which had been grazed until sixty years ago along 1700 m of the riverbank. The effects of grazing on the vegetation were unclear (unpublished data). The survey monitored a total of 43 transects from the bottom to the top of the riverbank. In each transect, up to six consecutive quadrats were established, for a total of 125 plots. To monitor species diversity, the percentage cover of each species was estimated by eye from 15 to 28 May, on 18 June and on 6 and 11 September 2016. The plot size was $3 \, \text{m} \times 3 \, \text{m}$ ($9 \, \text{m}^2$) in 120 plots but was either $6.0 \, \text{m}^2$ or $7.5 \, \text{m}^2$ in 5 plots owing to limited slope length. The difference in the number of species between those 5 plots and the other 120 plots was not significant ($P = 0.140$). Hence, we used all 125 plots for the analyses.

Major dominant species

We based our classification of vegetation type on dominant species in autumn (Sasaki et al. 2000). Dominant species in each plot were defined as those with highest cover and those with $\geq 20\%$ cover.

Species attributes

All plants collected were classified as exotic or native and as annuals (plus biennials), perennial herbs or woody species, as per Numata and Yoshizawa (1979). Characteristic species representing grassland vegetation in *Miscanthetea sinensis* communities were defined as "typical grassland species" (Miyawaki 1994). Following Chiba Historical Materials Research Foundation (2003), all species were distinguished among short plants, medium-statured plants and larger perennials. Plant height classification was applied only to perennials (though not climbers), too, as per Numata and Yoshizawa (1979). The reference classified *P. chino* as tall, but it reached only 50 cm in our study area, as seen also on other riverbanks (Yamada et al. 2017). Continuously mown *P. chino* remains low for several years even if mowing is

resumed (Hori et al. 1998). Therefore, we classified *P. chino* as medium-statured. Nomenclature is based on BG Plants (Yonekura and Kajita 2003).

Analysis

To confirm any differences in species composition among vegetation types, we analysed the data by detrended correspondence analysis (DCA; Hill and Gauch 1980) of presence–absence data. To evaluate the occurrence of each species in different vegetation types and in different seasons, we performed indicator species analysis (INSPAN, Dufrêne and Legendre 1997) of cover data. INSPAN identified "representative species" considered representative of each habitat type ($P < 0.05$, Monte Carlo test; McCune and Mefford 1999) in PC-ORD for Windows v. 6 software (McCune and Mefford 1999).

We calculated one-way ANOVA and Tukey's post hoc test to test differences in number of species, coverage and DCA axis scores between vegetation types. We modelled numbers of species with a Poisson error distribution, coverage with a negative binomial error distribution and DCA axis scores with a Gaussian error distribution. $P < 0.05$ was considered significant. Statistical analyses were performed in R v. 2.13.1 software (R Development Core Team 2015). As the monitoring period in spring spanned 2 months and thus may affect species cover, we included the month (May or June) as an explanatory variable in models of cover in spring. Because total vegetation cover was ~5% lower in June than in May and it is unlikely that any species would be competitively excluded under the less competitive conditions, we believe that the difference in the number of species and vegetation composition in the survey period had little effect.

Evaluation of ecosystem function in each vegetation type

We used vegetation cover as an indicator of the control of splash detachment and inter-rill erosion (Zuazo and Pleguezuelo 2009; Shinohara et al. 2016). We used the cover of annuals as an indicator of root instability (Scheres and Schüttrumpf 2019), cover of tall species as an indicator of incineration cost, and species richness, number of indigenous species and occurrence of typical grassland species as indicators of positive natural processes (Reijers et al. 2014; Korvroëdan et al. 2021). As the precise assessment of the ecological function and conservation value of different habitats cannot be based solely on species-based diversity indices, which are not sensitive to functional redundancy and other functional consequences of species identity (Petchey and Gaston 2006), we also evaluated each representative species in each vegetation type to evaluate natural processes.

Results

General description

We recorded 161 species, including 1 unknown: 56 annuals, 95 perennials and 9 woody species (Appendix 1). Of these, 104 species were indigenous and 56 were exotic. Seven species were typical grassland species; the most frequent was *Arundinella hirta*, followed by *Miscanthus sinensis* and *Cirsium oligophyllum*. In spring, half of the plots were dominated by *Lolium multiflorum* (Table 1). In autumn, *I. cylindrica* var. *koenigii*, *S. altissima*, *Causonis japonica*, *P. chino* and *Sorghum halepense* were dominant, with frequencies of >5% (7/125 plots).

Table 1 Major dominant species

| Season	Species	Frequency	
		Dominance ≥ 20% cover	Dominance with the highest cover and ≥ 20% cover
Spring	*Lolium multiflorum*	0.696	0.488
	Imperata cylindrica var. *koenigii*	0.296	0.144
	Pleioblastus chino	0.152	0.144
	Agrostis gigantea	0.088	0.040
	Solidago altissima	0.072	0.024
	Ophiopogon japonicus	0.064	0.000
	Sorghum halepense	0.056	0.032
Autumn	*Imperata cylindrica* var. *koenigii*	0.400	0.232
	Solidago altissima	0.184	0.072
	Causonis japonica	0.184	0.088
	Pleioblastus chino	0.152	0.112
	Pennisetum alopecuroides	0.088	0.048
	Sorghum halepense	0.080	0.056

Most plots (108) were represented by seven vegetation types. *Pleioblastus chino* (Type P) and *Imperata cylindrica* var. *koenigii* (Type I) are indigenous perennials. *Solidago altissima* (Type Sa) and *Sorghum halepense* (Type Sh) are tall exotic perennials. Climber-dominated plots, all featuring and most dominated by *Causonis japonica*, were defined as Type C. Plots dominated by *Ophiopogon japonicus* or *Zoysia japonica*, both planted during construction of the riverbank, were combined as short species (Type OZ). Plots dominated by annuals such as *Bidens pilosa* var. *pilosa* were defined as Type A. Ten plots were dominated by other species, and seven plots had no dominant species. Plots in Type P and plots in Type I in autumn were linked to dominance by the same species in spring (Fig. 2). Most plots in Types Sa, C, A, Sh and OZ in autumn were dominated by *Lolium multiflorum* in spring.

Floristic composition

The proportion of variance in the distance matrix of the DCA ordination in autumn totalled 0.539 on the first three axes (1, 0.391; 2, 0.097; 3, 0.051; Fig. 3). Plots in Types P and I were located to the left. Their scores differed significantly from those of the other five types on axis 1 (Appendix 2). Differences in scores between Types P and I on axes 1, 2 and 3 were not significant. Scores of Type OZ differed
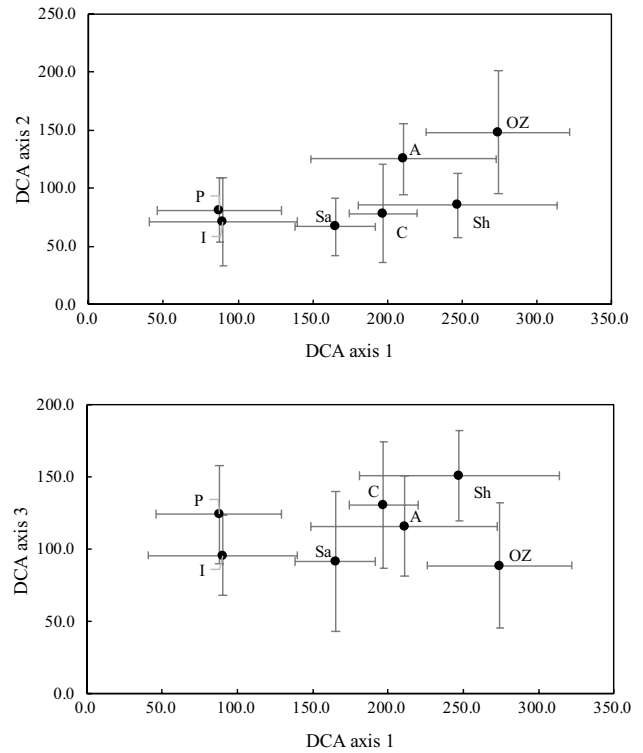
Fig. 3 Mean and SD of ordination scores in each quadrat in autumn by detrended correspondence analysis (DCA) in the first three dimensions
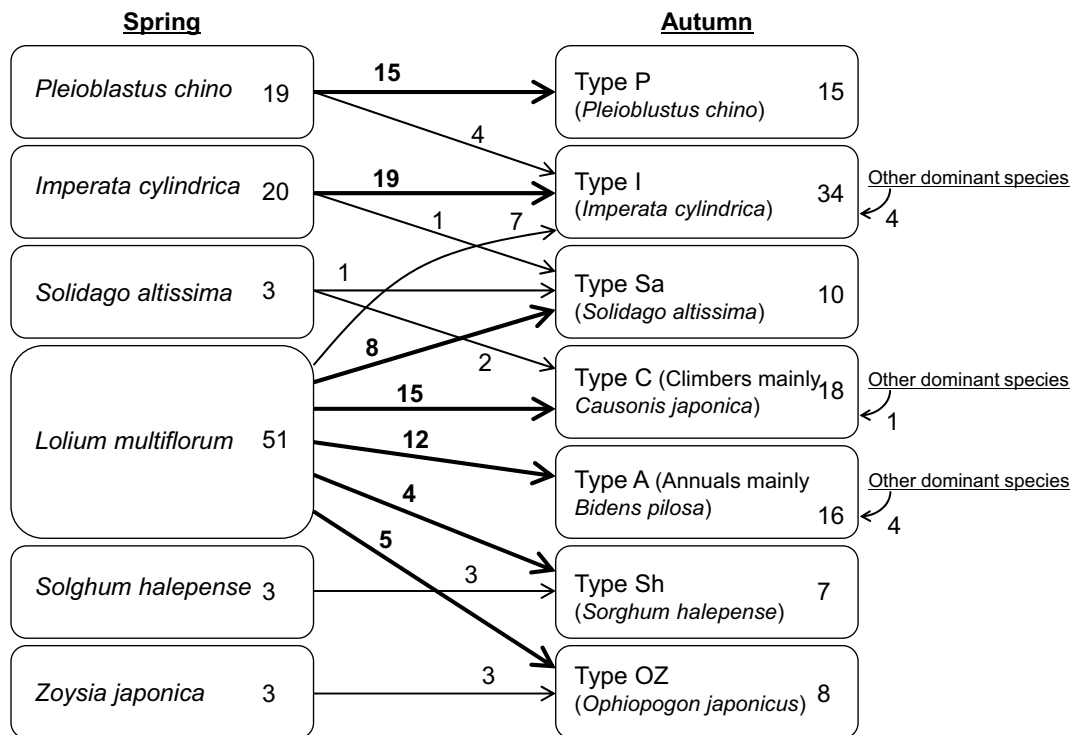

Fig. 2 Change of dominant species between spring and autumn. Values show the number of plots. Bold arrows show that more than half of plots in each vegetation type (right) originated from a dominant species

significantly from the other six types on axis 2. The proportion of variance in the distance matrix of the DCA ordination in spring totalled 0.497 on the first three axes (1, 0.250; 2, 0.142; 3, 0.105; Fig. 4). Again, scores of Types P and I differed significantly from those of the other five types on axis 1. Scores differed significantly between Types P and I on axis 3. The other five types were not significantly distinguished on any DCA axis.

Number of species and cover values in each species attribute

Vegetation cover tended to be low in Type A in autumn but was generally > 80% in all vegetation types (Table 2). Cover of tall species was significantly larger in Types Sa and Sh than in the other five vegetation types, which nevertheless had moderate cover. All vegetation types had high total cover in spring, too. Species richness was significantly lower in Type OZ than in Type Sa in spring and autumn but was not significantly different between most vegetation types. There were more perennials than annuals and more indigenous than exotic species in all vegetation types. Type P averaged significantly more typical grassland species than several other vegetation types in autumn, but still < 1.0.
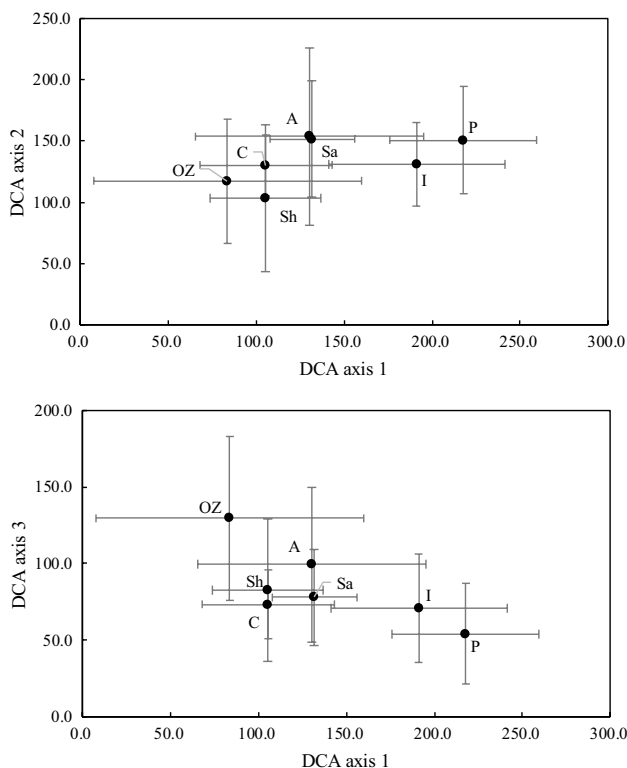
Fig. 4 Mean and SD of ordination scores in each quadrat in spring by detrended correspondence analysis (DCA) in the first three dimensions

Representative species

Solidato altissima and *Paederia foetida* in Type Sa and *Zoysia japonica*, *Ophiopogon japonicus* and *Calystegia pubescens* in Type OZ were representative in both spring and autumn (Table 3). All representative species in Type P were native perennials.

Discussion

Association of vegetation types in spring and autumn

Species dominant in both spring and autumn were linked to an extent (Fig. 2). Dominant species in Types P and I were consistent throughout the year in most plots. Conversely, dominant species changed seasonally in the majority of plots in the other five vegetation types. Most of these plots were dominated by *L. multiflorum* in spring. Most plots in Types Sa, Sh, A, C and OZ were dominated by *L. multiflorum* in spring. Types Sa and Sh produced tall vegetation in summer and autumn, whereas Types C and OZ produced shorter vegetation. Yet despite this difference, the vegetation compositions were not distinct in either season (Figs. 3, 4). A high dominance of *L. multiflorum* until June would strongly determine species available in these plots in spring and thereafter. Indeed, several species dominant in autumn can grow fast: warm temperatures promoted rhizome bud sprouting and rapid shoot growth in *Sorghum halepense* (Monaghan 1980); and climbers are generally known to quickly spread over the ground (Dickinson et al. 2021).

Although vegetation composition in Type I was not distinct from that in Type P (Fig. 3), the cover of exotic species and *L. multiflorum* was significantly larger in Type I in spring (Table 2). Asami et al. (1994) reported vegetation characteristics of *I. cylindrica* var. *koenigii* on riverbanks and suggested that vegetation dominated by it was composed mostly of perennials, along with 10% to 40% exotic species, as observed here. The root system of *I. cylindrica* var. *koenigii* stretches from shallow to deep soil layers (Tominaga 2003). This range would probably enable coexistence between *I. cylindrica* var. *koenigii* and *L. multiflorum*, with their roots in different layers (McKane et al. 2002).

Vegetation characteristics of this study site

We classified vegetation on a riverbank into seven major types on the basis of dominant species in autumn. Among them, *Z. japonica*, *I. cylindrica* var. *koenigii*, *P. chino* and annual weeds were reported as major vegetation types by Sasaki et al. (2000). The other three types were reported as dominant species on riverbanks elsewhere (Suzaki and

Table 2 Numbers of species [mean (SD)] within each group in each vegetation type

Group	Vegetation type						
	Type P	Type I	Type Sa	Type C	Type A	Type Sh	Type OZ
	$N=15$	$N=34$	$N=10$	$N=18$	$N=17$	$N=7$	$N=7$
Spring							
Coverage (%)							
Vegetation cover	97.1 (5.4)a	96.5 (5.7)a	90.1 (15.0)a	89.0 (12.8)a	89.1 (13.3)a	98.9 (2.0)a	99.8 (0.7)a
Sum of cover in each type	132.4 (19.2)a	118.4 (22.7)ab	108.1 (23.4)ab	98.3 (22.6)ab	102.1 (20.2)b	115.6 (16.3)ab	114.2 (13.8)ab
Annuals	12.7 (9.8)c	28.1 (22.3)b	58.1 (19.3)a	57.2 (24.4)a	62.8 (38.7)a	49.2 (30.3)ab	56.0 (49.6)ab
Perennials	119.7 (23.4)a	90.2 (33.8)ab	49.6 (28.6)bc	40.8 (28.0)c	38.8 (32.6)c	57.8 (33.5)ac	58.2 (37.2)bc
Tall species	2.3 (2.3)a	7.4 (14.1)a	15.3 (15.8)a	13.9 (23.9)a	7.4 (11.5)a	33.3 (26.5)a	7.4 (13.1)a
Medium species	122.5 (15.5)a	103.5 (27.8)ab	83.6 (21.7)ab	73.1 (28.2)ab	83.0 (21.4)ab	57.0 (31.4)bc	52.1 (42.4)c
Indigenous species	111.0 (23.4)a	67.4 (37.3)ab	38.3 (30.3)bcd	17.5 (11.6)cd	22.9 (26.6)d	23.8 (14.1)bcd	57.8 (37.3)ac
Exotic species	21.3 (21.7)b	51.0 (29.7)a	71.7 (20.0)a	79.9 (21.9)a	79.0 (32.4)a	91.9 (16.3)a	56.4 (49.7)a
Lolium multiflorum	11.5 (9.9)c	27.5 (22.6)b	58.0 (19.3)a	54.9 (23.4)a	57.7 (35.0)a	43.1 (34.7)ab	47.5 (40.4)ab
Number of species							
Total	11.5 (3.8)ab	11.4 (2.8)ab	13.9 (2.7)a	11.4 (2.1)ab	10.3 (4.2)ab	10.7 (2.9)ab	7.6 (2.6)b
Annuals	2.3 (1.1)a	1.9 (0.9)a	1.6 (0.7)a	1.3 (0.5)a	2.7 (1.4)a	2.3 (1.1)a	2.3 (1.3)a
Perennials	9.2 (3.0)ab	9.2 (2.7)ab	11.7 (2.4)a	9.9 (2.3)ac	7.3 (3.4)bc	8.1 (2.6)ac	5.3 (1.8)c
Indigenous species	7.9 (2.9)ac	7.6 (2.4)ab	10.1 (2.2)a	8.1 (2.2)ab	5.8 (3.2)bc	6.0 (2.0)ac	4.5 (1.4)c
Exotic species	3.5 (1.8)a	3.8 (1.4)a	3.9 (1.3)a	3.4 (1.1)a	4.4 (1.3)a	4.7 (2.2)a	3.1 (2.0)a
Autumn							
Coverage (%)							
Vegetation cover	99.0 (2.1)ab	97.9 (5.6)a	93.8 (8.9)ac	90.0 (17.7)ac	80.1 (19.4)c	80.7 (27.0)ac	80.6 (16.1)bc
Sum of cover in each type	175.9 (30.8)a	136.8 (26.2)b	136.6 (27.9)abc	131.8 (42.6)bc	104.8 (38.7)cd	110.5 (43.1)bd	85.8 (19.3)d
Annuals	0.8 (1.3)b	3.7 (7.3)b	10.5 (15.2)b	7.3 (8.4)b	49.6 (22.4)a	7.6 (8.3)b	8.2 (11.2)b
Perennials	173.8 (29.2)a	132.8 (27.5)b	118.8 (25.3)bc	124.3 (38.6)bc	54.2 (33.5)d	102.0 (39.3)bc	77.3 (20.5)cd
Tall species	17.7 (24.1)b	15.5 (21.4)b	75.2 (20.5)a	25.2 (25.2)b	16.5 (20.9)b	81.4 (32.8)a	4.5 (6.4)b
Medium species	140.2 (27.3)a	110.1 (31.4)b	33.4 (29.5)cd	21.6 (15.4)d	63.8 (30.3)c	14.3 (22.0)d	13.6 (14.9)d
Indigenous species	162.2 (34.9)a	114.4 (30.9)b	54.5 (33.9)c	108.3 (34.6)b	55.8 (43.3)c	20.1 (17.4)d	73.0 (19.6)bc
Exotic species	13.7 (17.0)c	22.5 (20.7)c	82.1 (17.2)a	23.5 (21.8)c	49.0 (28.7)b	90.4 (35.8)a	12.7 (13.6)c
Number of species							
Total number of species	12.8 (4.1)ab	10.4 (2.8)ab	14.0 (2.8)a	12.7 (4.6)ab	13.6 (3.5)a	11.9 (5.9)ab	9.0 (3.2)b
Annuals	1.6 (2.0)bc	1.6 (1.3)c	2.0 (1.4)ac	1.7 (1.1)bc	4.0 (3.4)a	3.4 (3.4)ab	2.3 (1.6)ac
Perennials	11.1 (2.6)a	8.5 (2.3)ab	11.3 (2.9)ab	10.9 (4.3)ab	9.4 (3.0)ab	7.9 (2.9)ab	6.6 (2.2)b
Indigenous species	9.5 (3.4)ab	7.2 (2.4)b	11.0 (3.3)a	8.8 (3.9)ab	8.7 (3.4)ab	7.7 (4.1)ab	5.9 (2.0)b
Exotic species	3.3 (1.9)a	3.2 (1.5)a	3.0 (1.2)a	3.9 (1.2)a	4.9 (1.9)a	4.1 (2.0)a	3.1 (1.8)a
Species representing semi-natural grasslands	0.8 (0.9)a	0.2 (0.4)b	0.4 (0.7)ab	0.5 (0.7)ab	0.1 (0.3)b	0.1 (0.4)ab	90.0b

Values within a species group with the same letter are not significantly different among vegetation types at $P < 0.05$ by Tukey's test. Woody species, low stature species in both spring and autumn, *Lolium multiflorum* in autumn and species representing semi-natural grasslands in spring were scarce and are not shown

Tanaka 2004; Aizawa et al. 2015; Yamane et al. 2016; Koyanagi et al. 2019; Yamada and Nemoto 2020). Therefore, we assumed that all seven vegetation types were more or less commonly distributed on riverbanks in Japan.

The literatures suggest that species-rich semi-natural grasslands on riverbanks in Japan are dominated by either *I. cylindrica* var. *koenigii* or *P. chino* (Yamada et al. 2017; Koyanagi et al. 2019). However, neither Type I nor Type P resembled semi-natural grasslands. Yamada et al. (2017) reported 34.1 species per 5 m^2 in the semi-natural grasslands on a riverbank; our numbers were distinctly lower: 10.4 species in Type I and 12.8 species in Type P per 9 m^2. These lower values are in line with the report that species-poor meadow has 10–20 species per 25 m^2 and species-rich meadow has 30–40 species in 25 m^2 in the Netherlands (Hazebroek and Sprangers 2002). We assume

Table 3 Representative species in each vegetation type (percentage of sites)

Species	Life history	Exotic species	Indicator value (IV)	P-value	Type P N=15	Type I N=34	Type Sa N=10	Type C N=18	Type A N=17	Type Sh N=7	Type OZ N=7
Spring											
Carex leucochlora var. *leucochlora*	P		20.0	0.015	27	9	0	0	0	0	0
Pleioblastus chino	P		66.3	0.000	100	29	10	6	6	0	0
Luzula capitata	P		16.0	0.046	27	18	0	0	0	0	0
Houttuynia cordata	P		16.7	0.047	27	0	10	0	6	0	0
Imperata cylindrica var. *koenigii*	P		30.9	0.000	67	91	60	11	12	14	14
Viola betonicifolia var. *albescens*	P		17.0	0.042	13	24	40	11	6	0	0
Solidago altissima	P	E	29.4	0.003	67	47	90	28	29	14	0
Rosa multiflora	P		19.2	0.028	0	15	40	11	18	0	0
Paederia foetida	P		27.5	0.005	0	24	70	44	12	29	0
Hydrocotyle ramiflora	P		16.7	0.040	0	0	0	17	0	0	0
Lolium multiflorum	A	E	16.3	0.008	80	97	100	100	94	86	57
Causonis japonica	P		28.9	0.002	13	24	50	100	59	57	43
Avena fatua	P	E	19.8	0.019	0	0	0	0	29	0	14
Sorghum halepense	P	E	43.5	0.000	0	0	0	6	12	71	29
Glechoma hederacea subsp. *grandis*	P		21.2	0.044	27	21	70	22	29	0	71
Stellaria media	A		19.5	0.029	13	0	0	0	0	0	29
Zoysia japonica	P		28.8	0.003	7	0	0	0	0	14	43
Ophiopogon japonicus	P		19.7	0.037	7	3	30	17	24	29	57
Calystegia pubescens	P		28.6	0.009	0	0	0	0	0	0	29
Autumn											
Cyperus brevifolius var. *brevifolius*	P		20.0	0.022	1	0	0	0	0	0	0
Pleioblastus chino	P		63.2	0.000	100	21	20	0	18	0	0
Pennisetum alopecuroides	P		21.8	0.013	40	6	10	0	18	0	0
Bromus remotiflorus	P		13.3	0.037	13	0	0	0	0	0	0
Agrostis gigantea	P	E	24.0	0.005	7	29	0	0	0	0	0
Imperata cylindrica var. *koenigii*	P		37.5	0.000	93	100	40	33	0	0	0
Elymus tsukushiensis var. *transiens*	P		18.9	0.046	20	53	30	17	0	0	0
Glechoma hederacea subsp. *grandis*	P		26.3	0.014	7	18	70	6	29	0	57
Equisetum arvense	P		22.7	0.000	87	97	100	44	41	71	0
Solidago altissima	P	E	25.1	0.000	80	71	100	61	29	14	43
Paederia foetida	P		27.7	0.002	20	32	90	72	35	43	0
Artemisia indica var. *maximowiczii*	P		20.3	0.042	53	65	80	61	41	0	14
Agrimonia pilosa var. *japonica*	P		15.0	0.047	7	0	20	0	0	0	0
Achyranthes bidentata var. *fauriei*	P		21.3	0.050	13	21	50	83	59	57	43
Aster iinumae	P		15.2	0.043	0	9	0	28	0	14	0

Table 3 (continued)

Species	Life history	Exotic species	Indicator value (IV)	P-value	Type P N=15	Type I N=34	Type Sa N=10	Type C N=18	Type A N=17	Type Sh N=7	Type OZ N=7
Rumex obtusifolius	P	E	26.2	0.011	7	3	0	39	71	14	57
Bidens pilosa var. pilosa	A	E	20.3	0.029	7	6	0	28	59	57	14
Amaranthus blitum	A		17.6	0.027	0	0	0	0	18	0	0
Vicia sativa subsp. nigra	A		17.5	0.038	27	15	0	0	41	14	0
Sicyos angulatus	A	E	23.9	0.013	0	0	0	6	0	29	0
Stellaria aquatica	A		23.9	0.010	0	0	0	6	0	29	0
Sorghum halepense	P	E	46.6	0.000	0	3	20	28	35	100	29
Solanum emulans	P	E	18.4	0.036	0	0	10	0	6	29	0
Setaria viridis	A		23.5	0.013	7	3	0	6	6	14	43
Zoysia japonica	P		32.1	0.001	0	0	0	0	0	14	43
Ophiopogon japonicus	P		26.2	0.010	7	0	0	11	35	14	57
Brassica juncea	A	E	33.2	0.003	0	0	0	0	41	0	57
Calystegia pubescens	P		17.7	0.046	0	0	0	0	18	0	29

Percent of sites in a given group where given species is present. A, annual; P, perennial herb; E, exotic species

that all vegetation types belong to species-poor grasslands. One reason for the marked difference in species richness would be the difference in the cover of dominant species: total cover in Type P in autumn (175.9%) was significantly larger than the total cover in all other vegetation types except Sa (Table 2). Abe et al. (2015) reported that species-rich semi-natural grassland on a riverbank was sparse, with a biomass of ~350 g/m². Vigorous overgrowth would inhibit the persistence of diverse species in the vegetation, as generally known in grassland (Vermeer and Berendse 1983).

Implications for the evaluation of vegetation on riverbanks

A major ecosystem function required of the vegetation on riverbanks is the control of erosion (De Groot et al. 2002; Wallace 2007). Since vegetation dominated by *Z. japonica* is desirable to control erosion (Hattori et al. 1997), Type OZ is superior among the seven vegetation types. However, it is generally difficult to maintain such low vegetation on lowland riverbanks by mowing twice a year (Asami et al. 1994). Indeed, Type OZ was overgrown by medium species to some extent in spring (Table 2). It is likely that *Z. japonica* and *O. japonicus* here were planted recently. Persistence of the vegetation type in this area is uncertain.

This study clarified the relationship of vegetation between spring and autumn, enabling us to evaluate the ecosystem function of vegetation on riverbanks all year round. The dominance of annuals is linked to fast turnover of root systems and thus poor control of erosion on riverbanks (Scheres and Schüttrumpf 2019). Types P and I were superior to other vegetation types (except Type OZ), being dominated by the same species throughout the year (i.e., *P. chino* and *I. cylindrica* var. *koenigii*, respectively), and were not dominated by annuals (e.g., *L. multiflorum*). *Imperata cylindrica* var. *koenigii* has relatively large root biomass (Hattori et al. 1997; Sasaki et al. 2000) and is assumed to be persistent. *I. cylindrica* has smaller above-ground biomass than taller species (Yamada et al. 2021). Thus, *I. cylindrica* is more suitable because of the low incineration costs than taller species. This is applicable to *P. chino*, too, because continuously mown *P. chino* remains short for several years even if mowing is resumed (Hori et al. 1998). Information on the root system of *P. chino* is lacking; further research is needed to evaluate its root system for the control of soil erosion. Information on the root systems of Types Sa, Sh, C and A is needed, too.

Dense vegetation cover is important to prevent erosion by rain and water flow (Zuazo and Pleguezuelo 2009; Shinohara et al. 2016). However, vegetation cover was consistently high (>80%) in each vegetation type in both spring and autumn, and it was similar or much larger in the six other vegetation types than in Type OZ. The relationship between vegetation

cover and soil erosion has usually been reported as a negative exponential curve in a wide range of environmental conditions (Gyssels et al. 2005), meaning that a wide range of vegetation offers similarly high soil erosion resistance. Therefore, vegetation cover in all vegetation types would be large enough to prevent erosion.

In terms of biodiversity, no clear difference was observed in total species richness between vegetation types, except for a lower number in Type OZ. Typical grassland species were low overall (Table 2). In this regard, no special attention should be paid to a particular vegetation type in relation to natural processes. However, the occurrence of individual species differed among vegetation types. Type P was characterized by indigenous species. Thus, to sustain the abundance of indigenous species, Type P is valuable. Two of the representative species in Type P are grasses (i.e., *Luzula capitata* and *Bromus remotiflorus*), which are generally important food sources for several Orthoptera species (Wünsch et al. 2012). Pollination is important in grassland species (Sydenham et al. 2022). Representative species included several with entomophilous flowers (e.g., *Aster iinumae* in Type C and *Agrimonia pilosa* var. *japonica* in Type Sa). Indeed, among frequent typical grassland species, *Cirsium oligophyllum* has entomophilous flowers and is more frequent in Type P. Land managers should prioritize such natural processes, considering landscape perspectives (e.g., proportion of grasslands in surrounding areas in relation to dispersal availability and habitat uniqueness; Bátori et al. 2020).

Conclusion

Since the positive influences of greater plant species richness and functional diversity on preventing soil erosion in grasslands are still unclear (Scheres and Schüttrumpf 2020), developments in the engineering of embankments, at least, should investigate both at the same time for their more sustainable and adaptive design (Sasaki et al. 2000). We can identify a clear seasonal pattern in dominant species on a riverbank. The ecosystem properties are driven mainly by the traits of the dominant species in a community (the mass ratio hypothesis; Grime 1998). Dominant species in spring can be estimated from those in autumn. Thus, dominant species in autumn offer an effective indicator of the potential to control soil erosion on riverbanks. Vegetation dominated by *Imperata cylindrica* var. *koenigii* is superior for erosion control in terms of the persistence of its dominance throughout the year and the scarcity of *Lolium multiflorum* in spring. Vegetation dominated by *Pleioblastus chino* is also superior in terms of the scarcity of *L. multiflorum*. Since the root architecture of *P. chino* is unclear, further research is needed

to evaluate the potential of the vegetation type to control soil erosion.

Our plots featured generally species-poor grassland, without a clear difference in species richness between vegetation types. However, this vegetation classification is linked to species composition, which depends on the presence of representative species in each vegetation type. By this measure, the *P. chino* vegetation type is superior in terms of larger numbers of indigenous representative species and typical grassland species. Nevertheless, natural processes should be evaluated by multiple traits (e.g., support for pollinators and herbivores) (Petchey and Gaston 2006). The long flowering period and the presence of insect-pollinated plants in these secondary grasslands are favourable for pollinator assemblages and for palynivores in Europe (Bátori et al. 2020). Since such functional traits are not been generally assessed in Japan, further research is needed on this aspect.

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