Invasive Alien Plant Species in Riparian Areas of Japan: The Contribution of Agricultural Weeds, Revegetation Species and Aquacultural Species

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Abstract

In Japanese riparian habitats, invasion by alien plants constitutes one of the most serious threats to biodiversity through the displacement of native plants. This paper presents a list of "invasive alien plant species" in Japanese riparian habitats. Invasive alien species, defined here as dominant or codominant species in certain plant communities, can be categorized as "agricultural weeds," "revegetation species," or "aquacultural species." In riparian areas, the category of agricultural weeds contains significantly more invasive alien species than would be expected by chance. The same result was found for introduced revegetation species. To prevent the introduction of new invaders into riparian areas, appropriate alien plant management is needed for both natural habitats and agricultural areas of the catchments. The use of alien pasture species for revegetation or control of soil erosion should be avoided in order to conserve biodiversity and native ecosystems.

Key words: biological invasion, geographical origin, plant families, propagule pressure, statistical trends

1. Introduction

Invasion by alien plants constitutes one of the most serious threats to biodiversity through the displacement of native plants (Coblentz, 1990; Vitousek *et al*., 1996; Simberloff *et al*., 1997). Owing to frequent disturbances, riparian areas are particularly vulnerable to invasion by alien vascular plants (Stohlgren *et al*., 1998; Hood & Naiman, 2000; Planty-Tabacchi *et al*., 2001; Washitani, 2001). In Japanese riparian habitats, the total area occupied by vegetation in which alien plants were dominant had reached 11,000 ha by 1999, which amounted to 15% of the total vegetation area of rivers administered by the Japanese Ministry of Land Infrastructure and Transport (Miyawaki & Washitani, 2004).

Riparian ecosystems are important for maintaining local biodiversity because of their environmental uniqueness. Riparian vegetation is established under the influences of unique environmental conditions such as flooding disturbance regimes. The vegetation thus established in turn influences the dynamics of water flow and the movement of sediments and nutrients into rivers (*e.g*., Peterjohn & Correll, 1984; Décamps, 1993; Nakatsubo, 1997), and it features high species diversity (Gould & Walker, 1997; Naiman *et al*., 1993; Ward *et al.,* 1999).

One explanation for the high species diversity of riparian ecosystems is that floods periodically destroy vegetation cover, create bare ground for recolonization, and produce a shifting mosaic of vegetation patterns and landforms that create diverse habitats (Malanson, 1993; Hood & Naiman, 2000). In addition, riparian areas serve as landscape corridors facilitating the dispersal of propagules by water flow, which is indispensable to range expansion and maintenance of metapopulation dynamics of riparian plants (*e.g*., Staniforth & Cavers, 1976; Schneider & Sharitz, 1988; Campbell *et al*., 2002).

The same factors that maintain a diversity of plant species may equally increase vulnerability to invasion by alien plants in riparian areas (Washitani, 2000). Disturbances to create unoccupied sites and dispersal of propagules by water flow in riparian areas may promote invasions by alien plant species for some of the same reasons that they sustain native species diversity.

In Japanese riparian habitats, approximately 40%

of invasive alien species belong to the largest plant families: Compositae, Gramineae, and Leguminosae (Washitani, 2002b). The Compositae contain a high number of widely distributed agricultural weeds (Heywood, 1989; Cronk & Fuller, 1995), and the Gramineae and the Leguminosae contain all the pasture species intentionally introduced into Japanese riparian areas for revegetation (Washitani, 2002a).

Most weeds of agricultural systems have competitive ruderal adaptations that are suitable for taking over disturbed habitats (Grime, 1977). Consequently, environments favoring these species include sparse meadows that are subject to seasonal disturbances such as floods, as well as roadsides and agricultural fields (Washitani & Morimoto, 1993). These characteristics of agricultural weeds make them potential invaders of riparian habitats.

Pasture grass species are a major source of plant invaders in many parts of the world (Heywood, 1989; Lonsdale, 1994). In Japanese riparian areas, there is a long tradition of introducing alien pasture grasses to prevent soil erosion or provide revegetation after construction work (Ecological Society of Japan, 2002; Imamoto *et al.,* 2003). It is not surprising, therefore, that these plants, which were chosen because of their rapid growth, adaptation to sunlit environments, and tenacity, have also shown markedly high invasiveness (Washitani, 2002a; Myers & Bazely, 2003).

Although the terrestrial habitats of riparian areas are diverse, the aquatic environment is relatively uniform (Ashton & Mitchell, 1989). Accordingly, many species, particularly submerged and floating plants, are widely distributed throughout the world. This holds for alien aquatic plant species such as water hyacinth (*Eichhornia crassipes* (Mart.)) Solms-Laub.) and water lettuce (*Pistia stratiotes* L.) introduced into Japanese riparian areas as ornamentals (Committee for Investigating the Effects of and Countermeasures against Riparian Exotic Species, 2003).

In response to the expanding ranges of and increasing damage caused by alien species, the control of invasive alien species has become a priority for environmental management and an integral component of many habitat conservation efforts in Japanese riparian areas (Committee for Investigating the Effects of and Countermeasures against Riparian Exotic Species, 2003). At least 444 alien species had been added to the Japanese riparian flora by 1999 (Committee for Investigating the Effects of and Countermeasures against Riparian Exotic Species, 2001). However, alien species do not always become invasive. To conserve native species and ecosystems appropriately, we must judge which alien species should be given the highest priority as "invasive alien species" in management programs. This paper presents a list of invasive alien plant species in Japanese riparian habitats for use in such a judgment process. Using the list, we tested the hypothesis that agricultural weeds and revegetation species contribute highly to the number of invasive alien plants. We also discuss desirable management strategies for suppressing the invasion of alien plant species in Japanese riparian habitats.

2. Terminology

We define "alien species" as those introduced after the mid-19th century, when Japan abandoned its national isolation policy (Washitani & Morimoto, 1993; Murakami & Washitani, 2002). Only about 20 alien species were identified up to the beginning of the Meiji era (1868), since international trade was restricted to only selected routes for many years during the Edo period by the feudal government (Enomoto, 1999). The Ecological Society of Japan (2002) has listed more than 1,500 species of alien plants recorded in Japan. It is not clear, however, how many of these species persist in Japan.

The categories "invasive alien species," "agricultural weeds," "revegetation species," and "aquacultural species" often overlap with each other, and consequently a species can belong to more than one category. An "invasive alien species" is an alien species whose introduction or spread threatens biological diversity (Ecological Society of Japan, 2002; UNEP, 2002). We define an "invasive alien plant" as a dominant or codominant species present in a certain vegetated riparian area. It can safely be assumed that these species are invasive since they often competitively exclude native plants (*e.g.*, Miyawaki & Washitani, 1996; Muranaka & Washitani, 2001). Therefore, alien plants that do not form the dominant vegetation should not be considered as "invasive." We also define the species that form the dominant vegetation along at least 12 of 123 investigated rivers as "widely invasive."

"Agricultural weeds" are undesirable plants that invade highly disturbed agricultural land, where they reduce the productive capacity of crops (Pimentel, 1986). Some agricultural weeds are native to Japan, but we consider only alien species, in this study.

We define "revegetation species" as species actively introduced to prevent soil erosion or to promote revegetation after various types of construction work. In Japan, many pasture grass species and several woody leguminous species have been introduced for this purpose (Washitani, 2002a).

"Aquacultural species" are defined as floating or submerged plants introduced as ornamentals. This group contains plants used for water purification such as *E. crassipes* and *P. stratiotes* (Fujita *et al.*, 2001).

3. Data Sets and Analyses

We assembled separate data sets on alien agricultural weeds, revegetation species, aquacultural species, alien species, and invasive alien species in Japanese riparian areas. The data on the last two categories came from the Committee for Investigating the Effects of and Countermeasures against Riparian Exotic Species (2001), which listed 444 alien species identified during National Censuses on River Environments (NCRE) that have been conducted by the Ministry of Land, Infrastructure and Transport (MLIT) of Japan since 1991 (Ministry of Construction, River Bureau, River Environment Division, 1996, 1997a, 1997b, 1998, 1999, 2000; MLIT, River Bureau, River Environment Division, 2001). The NCRE is a periodic survey of the fauna and flora of the 123 rivers (109 river systems) within the jurisdiction of the MLIT (Ikeuchi & Kanao, 2003). Life forms and origins of the alien species were given by the Ecological Society of Japan (2002) and Shimizu (2003).

We identified 87 invasive alien riparian species as dominant or codominant on the NCRE vegetation maps. We counted the number of rivers and total vegetation area dominated or codominated by each species. Twenty-two of these species were widely invasive (i.e., forming the dominant or codominant vegetation on at least 12 rivers).

Data on agricultural weeds came from the Livestock Technology Association (1994), which listed 172 major alien weed species in Japan. Of these species, 140 were listed in the alien flora of Japanese riparian habitats and were used in this analysis.

Data on revegetation species were obtained from Yano (1988), Enomoto (1999), and the Ecological Society of Japan (2002). Forty revegetation species were listed among the alien flora of Japanese riparian habitats and were used in this analysis.

Data on aquacultural species came from Kadono (1994). Nine aquacultural species were listed among the alien flora of Japanese riparian habitats and were used in this analysis.

We used a Monte Carlo simulation procedure described in Daehler (1998) to test for differences between the observed and expected numbers of invasive alien species, widely invasive alien species, and invasive agricultural weeds by life form, origin, and family. In testing invasive alien species of each life form, for example, each iteration of the simulation involved choosing 87 invasive alien species (the number of dominant or codominant species) at random, and without replacement, from all 444 alien species and summing the number of these randomly chosen species. We repeated the simulation 50,000 times for each test and used the average number of species as the expected number of invasive species. We also used these simulations to generate test statistics for each feature to judge two-tailed statistical significance. To produce test statistics for the right (or left) tail, we divided the number of simulations that produced a value as high (or as low) as, or higher (or lower) than, the observed value by 50,000 (i.e., the total number of simulations). These test statistics were compared with a sequentially derived Bonferroni critical value to judge statistical significance at the α = 0.05 level (Holm, 1979).

4. Results

4.1 Number of invasive alien species

We use Venn diagrams to show the overlap between sets of species by category in the flora of Japanese riparian habitats (Fig. 1(a)). Sixty-four percent of the riparian invasive alien species (56 of 87) are agricultural weeds (hereafter referred to as “invasive agricultural weeds”) or revegetation species (“invasive revegetation species”). Only 5% of the invasive alien species (4 of 87) are aquacultural species (“invasive aquacultural weeds”). Figure 1(b)

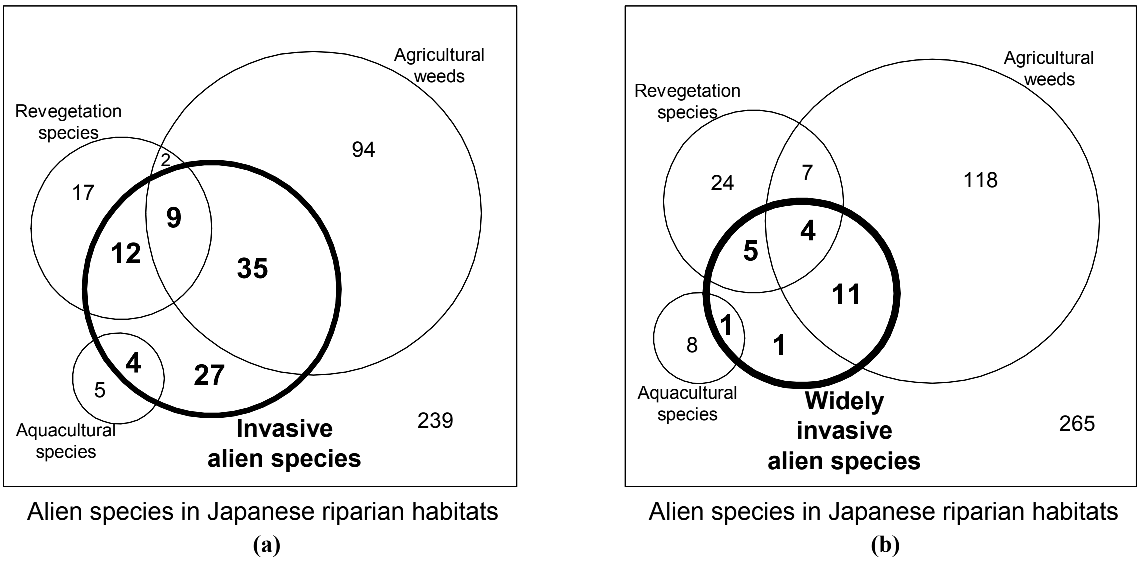

Fig. 1 Venn diagrams showing the overlap of the sets of (a) invasive alien species, agricultural weeds, revegetation species, and aquaculture species, and (b) widely invasive alien species, agricultural weeds, revegetation species, and aquaculture species in flora of Japanese riparian habitats. The numbers in each sector are the species counts. The total number of species is 444.

illustrates the overlap between sets of widely invasive species by category. Ninety-one percent of the widely invasive species (20 of 22) are agricultural weeds or revegetation species. Only 4.5% of the widely invasive alien species (1 of 22) are aquacultural species.

Thirty-one percent of agricultural weeds (44 of 140) and 52.5% of revegetation species (21 of 40) are riparian invasive alien species. The set of agricultural weeds contains significantly more invasive alien species than expected by chance (Fisher's exact test, $P < 0.001$; Table 1). The same result was found for revegetation species (Fisher's exact test, $P < 0.001$; Table 2). Although 44% of aquacultural species (4 of 9) are riparian invasive alien species, the difference from the expected number is not statistically significant (Fisher's exact test, $P = 0.08$).

Table 1 Numbers of invasive alien species versus agricultural weeds in Japanese riparian habitats.

		Agricultural weeds	
		Yes	No
Invasive alien species	Yes	44 (9.9%)	43 (9.7%)
	No	96 (21.6%)	261 (58.8%)

Fisher's exact test, $P < 0.0001$

Table 2 Numbers of invasive alien species versus revegetation species in Japanese riparian habitats.

		Revegetation species	
		Yes	No
Invasive alien species	Yes	21 (4.7%)	66 (14.9%)
	No	19 (4.3%)	338 (76.1%)

Fisher's exact test, $P < 0.0001$

Eleven percent of agricultural weeds (15 of 140) and 22.5% of revegetation species (9 of 40) are widely invasive species. The set of agricultural weeds contains far more invasive alien species than expected (Fisher's exact test, $P < 0.001$). The same result was found for revegetation species (Fisher's exact test, $P < 0.001$). Although 44% of aquacultural species (4 of 9) are invasive alien species, the difference from the expected number of widely invasive alien species is not statistically significant (Fisher's exact test, $P = 0.350$).

Invasive agricultural weeds, revegetation species, and aquacultural species dominated (or codominated) more rivers than did other invasive alien species (Fig. 2). Among these four categories, the number of rivers dominated (or codominated) by invasive alien species is significantly different (Kruskal-Wallis test, $P < 0.001$).

The majority (83 of 87, 95.4%) of the invasive alien plants in Japanese riparian areas are herbaceous (Table 3). Polycarpic herbaceous perennials are the most common (45 of 87, 51.7%), followed by annuals (35 of 87, 40.2%). The category of monocarpic herbaceous perennials has fewer invasive alien species than expected on the basis of our simulations ($P < 0.05$ after Bonferroni correction). Although only two widely invasive species are trees, this number is greater than expected ($P < 0.05$ after Bonferroni correction). The category of invasive agricultural weeds contains annuals (25 of 44, 56.8%) and poly-

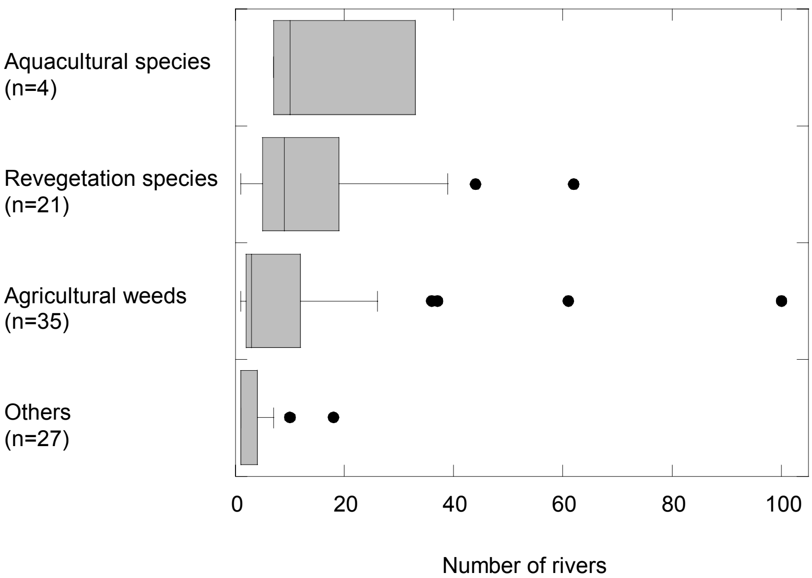

Fig. 2 Number of rivers invaded by invasive alien species (revegetation species, aquacultural species, agricultural species, and others) among 123 rivers up to 1999. The nine species contained in the overlap between invasive revegetation species and invasive agricultural weeds (Fig. 1(a)) are included in invasive revegetation species. Each box is bounded by the 25% and 75% quartiles and is divided at the median; the horizontal lines indicate the extreme values within 1.5 times the interquartile range from the upper and lower values of each box. The circles indicate values more than 1.5 interquartile ranges away from the upper values of each box.

carpic perennials (19 of 44, 43.2%). The category of monocarpic herbaceous perennials has fewer invasive agricultural weeds than expected ($P < 0.05$ after Bonferroni correction). Among invasive revegetation species, polycarpic herbaceous perennials are the most common (15 of 21, 71.4%), followed by annuals (3 of 21, 14.3%). All four aquacultural invasive species are polycarpic herbaceous perennials.

With regard to their origins, 36.8% of the invasive alien plants are native to North America (32 of 87; Table 3), followed by Eurasia (13 of 87, 14.9%), Europe (10 of 87, 11.5%), and South America (10 of 87, 11.5%). Temperate areas are especially important sources. The number of invasive species native to North America is greater than expected on the basis of our simulations ($P < 0.05$ after Bonferroni correction). In contrast, the number native to Europe is less than expected ($P < 0.05$ after Bonferroni correction). Among widely invasive alien species, 63.6% are native to North America (14 of 22), far more than expected ($P < 0.05$ after Bonferroni correction).

Many of the invasive alien plants come from families whose representatives are common invaders in temperate climates (Pyšek, 1998): Compositae (24 species), Gramineae (21), Leguminosae (9), Polygonaceae (5), and Onagraceae (4). Among widely invasive alien species, the Compositae (9), Gramineae (7), and Leguminosae (3) account for 86.4% (19 of 22). Of the invasive agricultural weeds, the largest number come from the Compositae (18 of 44, 40.9%; Table 3), followed by the Gramineae (9 of 44, 20.5%). The invasive revegetation species belong to either the Gramineae (14 of 21, 66.7%) or the Leguminosae (7 of 21, 33.3%).

Table 3 Comparison of numbers of invasive alien species, widely invasive alien species, agricultural weeds, revegetation species, and aquacultural species in Japanese riparian habitats. Numbers in parentheses indicate expected species numbers based on simulations. *$P < 0.05$; ** $P < 0.01$ (all P values are Bonferroni-corrected)

	Invasive alien species (n = 87)	Widely invasive alien species (n = 22)	Agricultural weeds (n = 44)	Revegetation species (n = 21)	Aqua-cultural species (n = 4)
Life form					
Herbaceous plants					
Polycarpic perennial	45 (38.2)	9 (9.6)	19 (16.9)	15 (14.2)	4 (4.0)
Monocarpic perennial	3 (11.2)**	0 (2.8)	0 (4.4)*	1 (2.6)	0 (0.0)
Annual	35 (34.9)	10 (8.8)	25 (22.7)	3 (3.1)	0 (0.0)
Woody plants					
Shrubs	1 (1.7)	1 (0.4)	0 (0.0)	1 (0.5)	0 (0.0)
Trees	3 (1.0)	2 (0.3)*	0 (0.0)	1 (0.5)	0 (0.0)
Origin					
North America	32 (19.8)**	14 (5.0)**	21 (14.8)	4 (2.6)	1 (1.3)
Eurasia	13 (13.1)	1 (3.3)	3 (5.3)	6 (7.3)	0 (0.0)
Europe	10 (19.6)*	1 (5.0)	5 (8.8)	3 (4.2)	0 (0.4)
South America	10 (6.6)	3 (1.7)	6 (4.1)	2 (1.1)	2 (0.9)
Tropical America	8 (7.1)	0 (1.8)	5 (5.3)	1 (1.0)	1 (0.4)
Eastern Asia	7 (7.1)	1 (1.8)	2 (1.2)	1 (0.5)	0 (0.0)
Mediterranean	4 (6.7)	1 (1.7)	1 (1.9)	2 (2.1)	0 (0.4)
Africa	1 (2.5)	1 (0.6)	0 (0.9)	1 (1.1)	0 (0.4)
Unknown	2 (4.5)	0 (1.1)	1 (1.6)	1 (1.0)	0 (0.0)
Family					
Compositae	24 (16.1)	9 (4.1)	18 (12.9)	0 (0.0)	0 (0.0)
Gramineae	21 (13.7)	7 (3.5)	9 (4.1)*	14 (14.2)	0 (0.0)
Leguminosae	9 (5.3)	3 (1.3)	3 (1.6)	7 (6.8)	0 (0.0)
Polygonaceae	5 (2.9)	0 (0.7)	4 (1.6)	0 (0.0)	0 (0.0)
Onagraceae	4 (2.0)	0 (0.5)	4 (1.9)	0 (0.0)	0 (0.0)
Scrophulariaceae	2 (2.8)	0 (0.7)	1 (2.8)	0 (0.0)	0 (0.0)
Rubiaceae	2 (0.6)	0 (0.2)	0 (0.0)	0 (0.0)	0 (0.0)
Iridaceae	2 (1.2)	0 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)
Hydrocharitaceae	2 (0.4)	1 (0.1)	0 (0.0)	0 (0.0)	2 (0.9)
Cruciferae	2 (5.5)	0 (1.4)	1 (2.8)	0 (0.0)	0 (0.0)
Chenopodiaceae	2 (1.0)	0 (0.3)	1 (1.3)	0 (0.0)	0 (0.0)
Amaranthaceae	2 (2.8)	0 (0.7)	1 (2.5)	0 (0.0)	0 (0.0)
Others	10 (32.9)**	2 (8.3)**	2 (12.6)**	0 (0.0)	2 (3.1)

4.2 Vegetation area dominated by invasive alien species

The total riparian area occupied by vegetation dominated (or codominated) by alien plant species (“total alien vegetation area”) reached approximately 11,900 ha by 1999 (Miyawaki & Washitani, 2004). Seventy-seven percent of the total alien vegetation area was occupied by widely invasive alien species (Table 4). Invasive agricultural weeds, invasive revegetation species, and invasive aquacultural species occupied 62.5%, 45.6%, and 1.1% of the area, respectively. Sixty percent of the area was occupied by polycarpic herbaceous perennials. Seventy-two percent of the area was occupied by species native to North America. Three large families, the Compositae, Gramineae, and Leguminosae, accounted for most of the invasive alien species (62.1%; Table 3), and amounted to 95.5% of the total alien vegetation area (Table 4).

Table 4 Percentage cover of invasive alien species, widely invasive alien species, agricultural weeds, revegetation species, and aquacultural species in vegetation dominated by alien plant species in Japanese riparian habitats

	Invasive alien species	Widely invasive alien species	Agricultural weeds	Revegetation species	Aquacultural species
Life form					
Herbaceous plants					
Polycarpic perennial	60.3	39.8	44.6	22.2	1.1
Monocarpic perennial	0.8	0.0	0.0	0.6	0.0
Annual	18.3	16.9	17.9	2.4	0.0
Woody plants					
Shrubs	1.9	1.9	0.0	1.9	0.0
Trees	18.7	18.7	0.0	18.5	0.0
Origin					
North America	72.3	65.2	51.1	22.7	<0.1
Eurasia	10.3	0.0	0.1	10.1	0.0
Europe	1.5	0.5	<0.1	1.3	0.0
South America	5.5	3.7	4.4	1.5	1.0
Tropical America	1.3	0.0	1.0	1.0	<0.1
Eastern Asia	0.8	0.2	0.6	0.5	0.0
Mediterranean	4.7	4.6	4.6	4.7	0.0
Africa	3.2	3.2	0.0	3.2	0.0
Unknown	0.5	0.0	0.5	0.5	0.0
Family					
Compositae	47.8	41.6	47.3	0.0	0.0
Gramineae	25.4	11.8	11.8	23.3	0.0
Leguminosae	22.3	20.9	0.6	22.3	0.0
Polygonaceae	0.2	0.0	0.2	0.0	0.0
Onagraceae	0.7	0.0	0.7	0.0	0.0
Scrophulariaceae	<0.1	0.0	<0.1	0.0	0.0
Rubiaceae	0.1	0.0	0.0	0.0	0.0
Iridaceae	<0.1	0.0	0.0	0.0	0.0
Hydrocharitaceae	1.1	1.0	0.0	0.0	0.0
Cruciferae	<0.1	0.0	<0.1	0.0	1.0
Chenopodiaceae	<0.1	0.0	<0.1	0.0	0.0
Amaranthaceae	0.3	0.0	<0.1	0.0	0.0
Others	2.1	2.0	1.8	0.0	<0.1
Total	100.0	77.3	62.4	45.6	1.1

5. Discussion

5.1 Taxonomic pattern of invasive alien species

In Japanese riparian areas, the set of invasive alien species contained 22 families and 87 species (Table 5), with strong representation by species of the Compositae (27.6%), Gramineae (24.1%), and Leguminosae (10.3%), which are typically well-represented in alien floras worldwide. In addition, alien plants belonging to these three families occupied 95.5% of the alien vegetation area of the investigated river systems. Several recent studies focused on the taxonomic pattern of plant invasions (*e.g.*, Daehler, 1998; Pyšek, 1998). The results of these studies led to the same conclusion: the largest plant families (Compositae, Gramineae, and Leguminosae) contribute most to the total number of alien species in local flora.

From an evolutionary point of view, the Compositae are considered one of the most advanced families, and it contains numerous agricultural weeds, many of which are remarkably successful and have become distributed extensively throughout temperate zones worldwide (Heywood, 1989; Cronk & Fuller, 1995). The presence of invasive alien plants of the Gramineae and Leguminosae in Japanese riparian areas is largely the result of deliberate introduction of revege-

Table 5 Invasive alien plant species identified along 123 rivers (109 river systems) in Japan.

Species	Family	Number of rivers[1]	Vegetation area[2] (ha)	Category[3]
Solidago altissima L.	Compositae	100	3370	W
Robinia pseudoacacia L.	Leguminosae	62	2197	R
Erigeron canadensis L.	Compositae	61	386	W
Paspalum distichum L.	Gramineae	44	59	RW
Sorghum halepense (L.) Pers.	Gramineae	44	549	RW
Panicum dichotomiflorum Michx.	Gramineae	39	216	RW
Ambrosia trifida L.	Compositae	37	603	W
Conyza sumatrensis (Retz.) Walker	Compositae	36	254	W
Egeria densa Planch.	Hydrocharitaceae	33	121	A
Eragrostis curvula (Schrad.) Nees	Gramineae	31	379	R
Xanthium occidentale Bertol.	Compositae	26	71	W
Sicyos angulatus L.	Cucurbitaceae	24	319	W
Amorpha fruticosa L.	Leguminosae	19	230	R
Trifolium repens L.	Leguminosae	18	57	R
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	18	20	
Andropogon virginicus L.	Gramineae	17	134	W
Paspalum dilatatum Poir.	Gramineae	16	59	RW
Ambrosia artemisiifolia var. *elatior* L.	Compositae	13	22	W
Aster subulatus Michx.	Compositae	12	12	W
Bidens pilosa L.	Compositae	12	151	W
Festuca arundinacea Sch.	Gramineae	12	37	R
Stenactis annuus (L.) Cass.	Compositae	11	76	W
Eichhornia crassipes (Mart.) Solms-Laub.	Pontederiaceae	11	9	A
Lolium multiflorum Lam.	Gramineae	11	77	R
Helianthus tuberosus L.	Compositae	10	22	
Myriophyllum brasiliense Cambess.	Haloragaceae	9	1	A
Bidens frondosa L.	Compositae	9	25	W
Dactylis glomerata L.	Gramineae	9	834	R
Aster subulatus Michx. var. *sandwicensis* A. G. Jones	Compositae	8	3	W
Agrostis alba L.	Gramineae	8	61	RW
Paspalum urvillei Steud.	Gramineae	8	124	RW
Oenothera biennis L.	Onagraceae	7	79	W
Diodia teres Walt.	Rubiaceae	7	14	
Verbena brasiliensis Vell.	Verbenaceae	7	2	
Solidago gigantea Aiton var. *leiophylla* Fernald	Compositae	7	579	W
Elodea nuttallii (Planch.) H. St. John	Hydrocharitaceae	7	5	A
Amaranthus patulus Bertol.	Amaranthaceae	6	8	W

Trifolium pratense L.	Leguminosae	6	91	
Paspalum distichum L.var. *indutum* Shinners	Gramineae	5	17	R
Phleum pratense L.	Gramineae	5	63	R
Poa pratensis L.	Gramineae	5	132	R
Rumex crispus L.	Polygonaceae	4	8	W
Nasturtium officinale R. Br.	Cruciferae	4	1	
Melilotus officinalis (L.) Pall. ssp. *alba* Medik.	Leguminosae	4	63	RW
Festuca pratensis Huds.	Gramineae	4	63	
Vulpia myuros C. C. Gmel.	Gramineae	4	16	
Diodia virginiana L.	Rubiaceae	3	3	
Cosmos bipinnatus Cav.	Compositae	3	4	W
Rudbeckia laciniata L.	Compositae	3	55	R
Paspalum notatum Flugge	Gramineae	3	115	RW
Persicaria pilosa (Roxb.) Kitag.	Polygonaceae	2	9	W
Rumex obtusifolius L.	Polygonaceae	2	4	W
Celosia argentea L.	Amaranthaceae	2	25	
Brassica juncea (L.) Czern.	Cruciferae	2	1	W
Trifolium dubium Sibth.	Leguminosae	2	<1	W
Sapium sebiferum (L.) Roxb.	Euphorbiaceae	2	2	
Oenothera erythrosepala Borbás	Onagraceae	2	<1	W
Oenothera laciniata Hill	Onagraceae	2	1	W
Lindernia dubia (L.) Pennell	Scrophulariaceae	2	<1	W
Aster novae-angliae L.	Compositae	2	28	
Coreopsis lanceolata L.	Compositae	2	11	W
Hypochoeris radicata L.	Compositae	2	2	W
Sisyrinchium atlanticum E. P. Bicknell	Iridaceae	2	<1	
Boehmeria nivea (L.) Gaud.	Urticaceae	1	1	
Fagopyrum cymosum Meisn.	Polygonaceae	1	<1	
Rumex acetosella L.	Polygonaceae	1	<1	W
Spergularia rubra (L.) J. Presl et C. Presl	Caryophyllaceae	1	<1	
Atriplex hastata L.	Chenopodiaceae	1	1	W
Chenopodium ambrosioides L. var. *ambrosioides*	Chenopodiaceae	1	1	
Sedum sarmentosum Bunge	Crassulaceae	1	<1	
Aeschynomene virginica (L.) Britton, Sterns et Poggenb.	Leguminosae	1	1	
Medicago polymorpha L.	Leguminosae	1	4	RW
Medicago sativa L.	Leguminosae	1	10	R
Ludwigia decurrens Walter	Onagraceae	1	<1	W
Ipomoea triloba L.	Convolvulaceae	1	<1	W
Veronica anagallis-aquatica L.	Scrophulariaceae	1	<1	
Artemisia annua L.	Compositae	1	1	
Aster pilosus Willd.	Compositae	1	<1	
Bidens pilosa L. var. *minor* (Blume) Sherff	Compositae	1	<1	W
Coreopsis tinctoria Nutt.	Compositae	1	2	
Erechtites hieracifolia (L.) Raf. ex DC.	Compositae	1	1	W
Galinsoga ciliata (Raf.) Blake	Compositae	1	<1	W
Iris pseudacorus L.	Iridaceae	1	<1	
Aira caryophyllea L.	Gramineae	1	<1	
Aira elegans Willd. ex Kunth	Gramineae	1	<1	
Briza maxima L.	Gramineae	1	<1	
Bromus catharticus Vahl	Gramineae	1	82	W

[1]Number of rivers invaded.
[2]Total area occupied by vegetation dominated by alien species up to 1999 (total investigated area is approximately 82,000 ha).
[3]W: agricultural weed; R: revegetation species; A: aquacultural species.

tation species. Many Gramineae spread by rapid growth of densely spaced tillers, sometimes accompanied by dense litter production, which promotes monocultures (Washitani, 2002a). The Leguminosae also appear to have a high number of invasive species, including serious invaders (Heywood, 1989). The nitrogen-fixing ability of leguminous species may help them to invade nutrient-poor habitats (Richardson *et al*., 2000). Many leguminous invasive species are rapidly growing shrubs or trees, with abundant production of seeds that often have the ability to survive long periods of dormancy (Heywood, 1989; Cronk & Fuller, 1995). These characteristics probably contribute to the success of these three families as riparian invaders.

We may have underestimated the invasiveness of some families, however, because we based our judgment of invasive alien species on NCRE vegetation maps. NCRE surveys are conducted between summer and fall (Ministry of Construction, River Bureau, River Environment Division, 1996, 1997a, 1997b, 1998, 1999, 2000; MLIT, River Bureau, River Environment Division, 2001), therefore, the invasiveness of families including species dominant or codominant in vegetation in spring (*e.g*., Cruciferae) may be undervalued in this study.

5.2 Origins of invasive alien species

One striking aspect of the invasive alien plants seen in the riparian areas of Japan is the surprisingly large contribution of species native to North America (invasive, 37%; widely invasive, 64%). The climatic similarity and intensive trade between Japan and the United States undoubtedly contribute to these findings (Washitani & Morimoto, 1993). In 2002, for example, most corn, soybeans, hay, and pasture seed consumed in Japan were imported from the United States (Fig. 3; Plant Protection Station, Ministry of Agriculture, Forestry and Fisheries of Japan, 2003). The large Japanese market share of U.S. seed exports has continued for a long period (Fig. 4). Despite the enactment of seed purity laws in many nations, alien plant seeds are still common contaminants in the international seed trade (Mack, 2003). Large amounts and a wide range of seeds of weed species have been found in imported fodder crops and hay (Enomoto, 1999). For example, at least 50 species were detected in shipments of crops (wheat, soybeans,

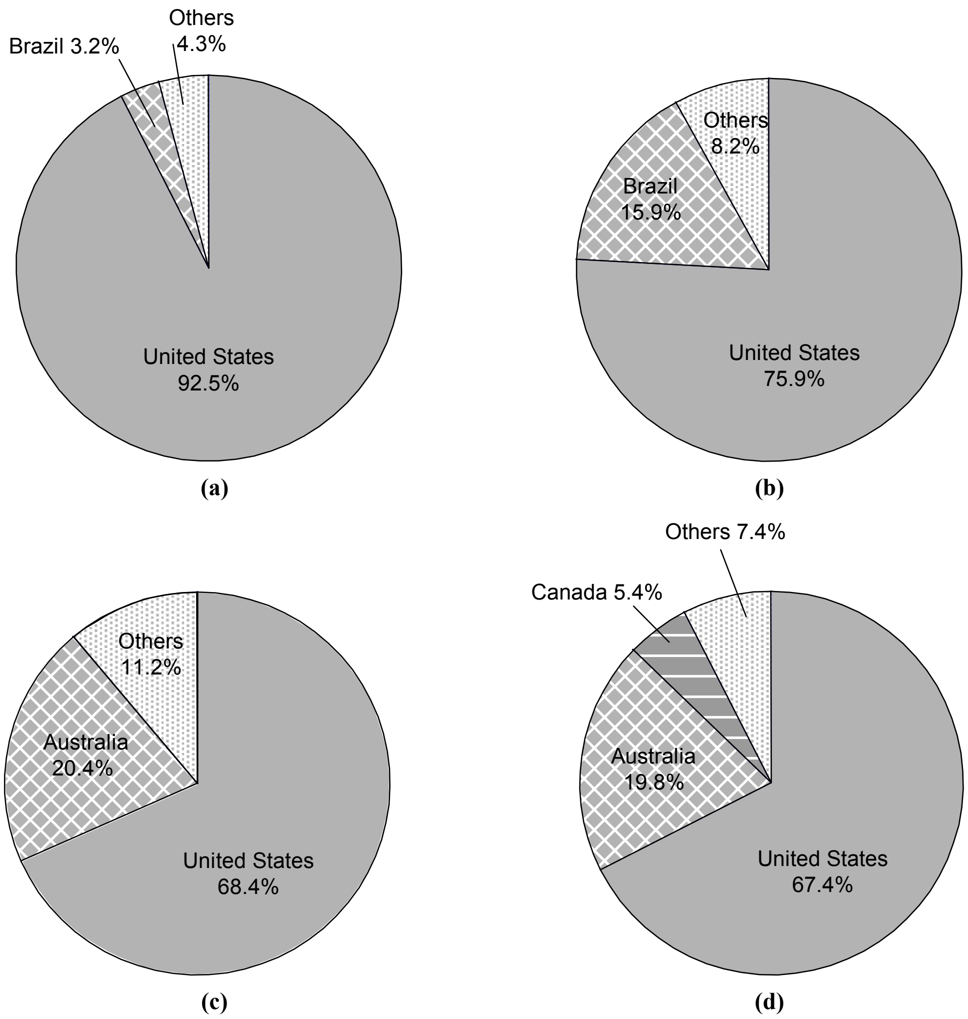

Fig. 3 Exporters of agricultural products to Japan in 2002: (a) corn, (b) soybean, (c) hay, and (d) pasture seed. Data from Plant Protection Station, the Ministry of Agriculture, Forestry and Fisheries of Japan (2003).

sorghum, and corn) from the United States to Japan in 1994-1995 (Enomoto, 1999). The importation of fodder crops grew rapidly until 1985 before leveling off (Nishida & Shimizu, 1999; Ministry of Agriculture, Forestry and Fisheries of Japan, 2002). It is clear that large numbers of alien plant seeds have been introduced into Japan in imported crops.

In addition, although most pasture seeds (67.4%) were imported from the United States in 2002 (Fig. 3(d)), the geographic origins of most are in fact Europe or Eurasia (Plant Protection Station, Ministry of Agriculture, Forestry and Fisheries of Japan, 2003). Consequently, the U.S. contribution to the number of and area occupied by invasive alien species spread through trade is actually greater than the contribution to origin shown in Table 3 and Table 4 (Fig. 5).

In spite of the large contribution of European plants to the alien flora of Japanese riparian areas (Washitani, 2002b), Europe contributed far less to the number and quantity of invasive alien species than the United States (Fig. 5). One reason may be that total European seed exports to Japan were much smaller than those from the United States. In 2002, for example, little of the corn (0.07%), soybeans (0.004%), or hay (0.1%) consumed in Japan was imported from the European Union (Plant Protection Station, Ministry of Agriculture, Forestry and Fisheries of Japan, 2003). It is clear that the European contribution to numbers of alien plant seeds introduced into Japan in imported crops is smaller than that from North America (the United States).

5.3 Invasiveness of agricultural weeds and revegetation species

More than half of the invasive alien species in Japanese riparian areas were either agricultural weeds (invasive, 51%; widely invasive, 68%) or revegetation species (invasive, 24%; widely invasive, 41%). Our statistical analyses suggest that in Japanese riparian habitats there is a greater tendency for alien agricultural weeds and introduced revegetation species to be

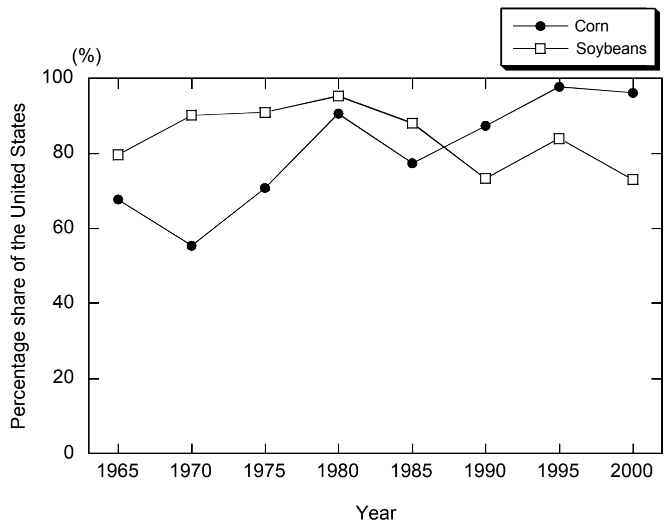

Fig. 4 Changes in the U.S.'s share of crops imported to Japan. Data from the Ministry of Agriculture, Forestry and Fisheries of Japan (2002).

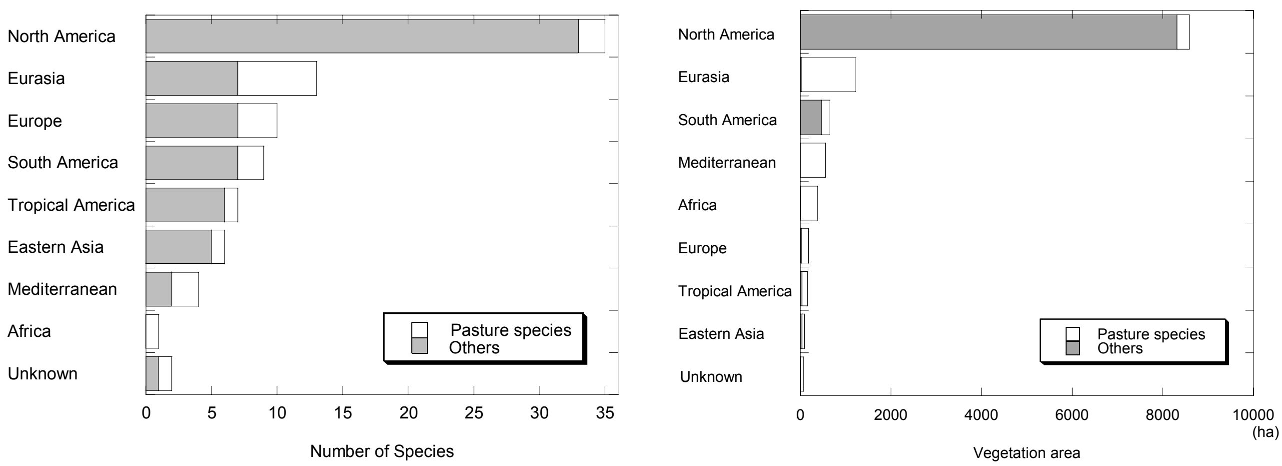

Fig. 5 Origins of the invasive alien species in Japanese riparian areas. (a) Number of invasive alien species (total number of pasture species = 19; total number of invasive alien species = 87). (b) Total vegetation area occupied by alien species among the 123 rivers (total alien vegetation area = 11,882 ha).

invaders than other alien species (Table 1 & 2) and for invasive agricultural species, invasive revegetation species and invasive aquacultural species to be distributed more widely than other invasive alien species (Fig. 2).

The availability of suitable habitats and the supply of propagules of alien agricultural weeds and revegetation species in riparian areas may account for their invasiveness. As we have mentioned, riparian habitats are subject to numerous and varied disturbances (*e.g.*, construction works, floods). These disturbances are likely to increase the creation of bare areas suitable for colonization by these species (Gregory *et al*., 1991; Pollock *et al*., 1998).

Propagule pressure is widely recognized as a fundamental driver of invasion (Williamson, 1996; Kolar & Lodge, 2001). Recent studies have shown a strong human influence on the characteristics and abundance of alien species (Lockwood, 1999; Kiritani & Yamamura, 2003). For birds, Lockwood (1999) explained that the taxonomic distribution of alien birds in relation to the probability of successful introduction could be explained by differences in the probability of deliberate introduction by humans. Birds actively transported as pets, food, or game species were much more likely to be traded, and thus dominate the lists of aliens (Lockwood, 1999). For insects, Kiritani and Yamamura (2003) showed that increases in plant material imports were associated with an increasing number of alien insects.

In Japanese riparian areas, propagule supply from adjacent invaded habitats (*e.g*., pastures, revegetated levees, agricultural fields, roadsides) is likely to contribute significantly to the further invasion of alien plants. In 1999, the total area of riparian pastures dominated by alien grasses had reached 18,000 ha, which amounted to 12% of the total river area administered by the Ministry of Land, Infrastructure and Transport (Miyawaki & Washitani, 2004; Fig. 6).

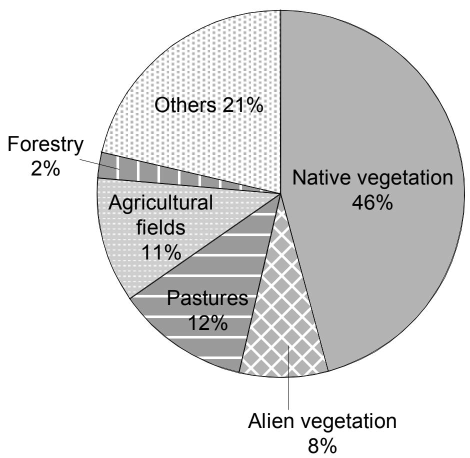

Fig. 6 Percentage of riparian area of Japan by land status or usage. Data from NCRE (Ministry of Construction, River Bureau, River Environment Division, 1996, 1997a, 1997b, 1998, 1999, 2000; MLIT, River Bureau, River Environment Division, 2001).

We estimated that more than half of the total levee area was occupied by revegetation species (*e.g*., *Lolium multiflorum* L., *Festuca arundinacea* Schreb.) from NCRE (Miyawaki & Washitani, unpublished). Furthermore, in the upper reaches of many rivers in Japan, woody leguminous species such as *Robinia pseudoacacia* L. and *Amorpha fruticosa* L. are often used for soil erosion control (Washitani, 2002a).

Similarly, in 1999 the total area of riparian agricultural fields had reached 17,000 ha, equivalent to 11% of the total river area (Fig. 6). In agricultural fields in Japan, the area invaded by alien agricultural weeds significantly increased since the 1980s (National Grassland Research Institute, 1998; Nishida & Shimizu, 1999). The majority of alien agricultural weeds were introduced as contaminants of imported agricultural produce (Nishida & Shimizu, 1999). Consequently, the agricultural weeds primarily invading agricultural fields would contribute to the total number of alien species in Japanese riparian habitats.

5.4 Control strategies for invasive alien plants in riparian areas

Alien species that form dominant (or codominant) communities are listed in Table 4. These species should be given the highest priority for management programs in Japanese riparian areas. Species that typically form dominant communities and are abundant in their respective communities have a much wider geographical distribution than those that occur as scattered or isolated individuals (Williamson & Fitter, 1996). Moreover, the fact that a species with a certain impact in one place has a similar impact in an ecologically similar place is widely thought to be the best predictor of its invasive character (Williamson, 1996; Reichard, 1997).

Active control of invasive alien species started along in some rivers before 2002 (Committee for Investigating the Effects of and Countermeasures against Riparian Exotic Species, 2003; Table 6). The examples given are much fewer than the number of rivers invaded and influenced by these alien species (Table 5), so to conserve biodiversity and ecosystems, more active management is needed in Japanese riparian areas.

In addition to discouraging the introduction of unstudied potentially invasive species, one strategy for reducing introductions of species that could invade riparian areas in the future would be to scrutinize extremely carefully any proposed introductions of primarily revegetation species. More than half of riparian invaders are agricultural weeds, so appropriate management of weeds in agricultural areas could be effective in restricting the introduction of new invaders to riparian areas. Therefore, alien plant management plans are needed for both natural habitats and agricultural areas. In addition, the use of alien pasture species for the purpose of revegetation or control of soil erosion should be restrained, firstly to conserve biodiversity and native ecosystems, but also

Table 6 Target species for control in Japanese riparian zones executed up to 2002. Data from the Committee for Investigating the Effects of and Countermeasures against Riparian Exotic Species (2003).

Target species	Number of cases
Solidago altissima	10
Eichhornia crassipes	9
Sicyos angulatus	6
Robinia pseudoacacia	4
Ambrosia trifida	3
Gramineae spp.	4

to avoid provoking grass pollen allergies.

There is a lack of information on the biological and ecological characteristics of alien plant species in Japanese riparian habitats (Miyawaki & Washitani, 2004). To enable the planning of appropriate management practices, more extensive studies of alien species are needed. Identifying the characteristics of invasive alien species is the first step in developing management strategies for Japanese riparian areas and will be a stepping-stone to further detailed studies on invasion biology and conservation ecology.

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