The role of weed seed contamination in grain commodities as propagule pressure

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Abstract The international grain trade is a major pathway for the introduction of alien plants because grain commodities can be contaminated with various weed seeds. To evaluate how alien weed seeds derived from imported grain commodities affect the local flora in international trading ports, we conducted a floristic survey at each of the 10 grain landing ports and non-grain landing ports throughout Japan to compare the flora between these two types of ports. We also surveyed weed seed contamination of wheat imported into Japan, and the contamination rate was calculated for each species based on our survey and previous studies on weed seed contamination. The flora clearly differed between the grain landing ports and the non-grain ports. In the grain landing ports, alien species were more abundant than in non-grain landing ports. There was a tendency for the more abundant species at the grain landing ports to show higher contamination levels in grain commodities. These results indicate that contaminant seeds spill from imported grain in grain landing ports and the most common contaminant species are likely to become established. We clearly show that weed seed contamination in grain commodities plays an important role in propagule pressure. Gathering information about the prevalence of weeds in grain-exporting countries and monitoring the weed species composition in imported grain commodities is becoming increasingly important for predicting the unintentional introduction of troublesome weeds and identifying effective weed management options.

Keywords Establishment success · International grain trade · Residence time · Unintentional introduction

Introduction

The expansion of international trade has promoted the introduction and spread of alien species. Biological invasion has received considerable attention because invasive alien species often cause biodiversity losses,
ecosystem modifications, and deleterious impacts on the economy (Mack et al. 2000; Pimentel et al. 2001). Potential alien species must go through several stages to become naturalized and invasive (Williamson and Fitter 1996; Blackburn et al. 2011). The first stage is introduction: species are brought into new locations beyond the limits of their native range. The second is establishment: species can survive in a new environment and establish self-sustaining populations in locations where they are introduced. The third is spread: species expand their distribution in new locations away from the point of introduction and they can become widespread and a threat to biodiversity, economy, and human health.

Many studies have focused on the establishment and spread stages to identify species traits associated with invasiveness or habitat characteristics associated with susceptibility to invasion (Burke and Grime 1996; Pyšek and Richardson 2007; Divíšek et al. 2018; Van Boheemen et al. 2019). During the last decade however, propagule pressure (the number of individuals released into a region where they are not native and the number of introduction events per unit time) has been recognized as one of the most important factors for successful establishment and spread in alien species invasions (Holle and Simberloff 2005; Lockwood et al. 2005; Simberloff 2009). Colautti et al. (2006) proposed that propagule pressure should form the basis of a null model for invasive studies. Although some studies have evaluated the role of propagule pressure in the case of intentional introductions for tree plantations (Pyšek et al. 2009), ornamental plants (Lavoie et al. 2016), or pet birds (Cassey et al. 2004), few researchers have examined the empirical relationships between propagule pressure and successful establishment for unintentional introductions (see Lee and Chown 2009; Lawrence and Cordell 2010).

The international grain trade is a major pathway of unintentional introductions (Hulme 2009) because various weed seeds contaminate grain commodities (Asai et al. 2007; Shimono and Konuma, 2008; Michael et al. 2010; Wilson et al. 2016; Gervill et al. 2019). Japan is a global leader among grain-importing countries; approximately 25 million tons of grain are imported each year (Ministry of Agriculture, Forestry, and Fisheries 2020). Consequently, a large number of weed seeds are estimated to be unintentionally introduced into Japan. These weed seeds can spill out of grain commodities during unloading, transportation, and usage, and some of them establish successfully (Shimono et al. 2015). Moreover, some species, such as *Abutilon theophrasti* Medik., *Aegilops cylindrica* Host, and *Lolium* L. spp., derived from grain commodities have become problematic weeds in farmlands and natural habitats (Donald and Ogg 1991; Kurokawa et al. 2004; Lehan et al. 2013; Higuchi et al. 2017). Therefore, the assessment of weed seeds in imported grain commodities and their role in exerting propagule pressure can provide basic information for effective weed management practices and prevention measures against the further introduction of alien species.

International trading ports, as primary introduction sites for contaminant weed seeds in imported grain, can be considered a valuable model system to compare the stages between the introduction and establishment of alien species. In this study, we surveyed the weed seed contamination of wheat imported into Japan, and the contamination rate was calculated for each species based on our survey and previous studies on weed seed contamination (Asai et al. 2007; Wilson et al. 2016). We also conducted a floristic survey at the 10 grain landing ports, where relatively large amounts of grain commodities were imported every year, and 10 non-grain landing ports where cargos other than grain are imported. Then, we compared the flora between grain landing ports and non-grain landing ports to confirm whether there was a difference in the flora between the two types of ports. Furthermore, we evaluated the relationship between the distribution pattern of each species at each type of port and the contamination rate of each species in grain commodities to confirm whether the species typical of grain landing ports were likely to be derived from seed contaminants in grain commodities. We also assessed the relationship between residence time (time since the introduction) and abundance of each alien species because not only propagule pressure but also residence time are crucial for determining the likelihood of establishment of the species (Richardson and Pyšek 2006; Pyšek et al. 2009). We evaluated the role of grain trade as propagule pressure, and our results will be useful for risk assessment of the alien species introduction pathways to avoid further ecological and economic losses.
Methods

Study sites

We selected 20 international trading ports in Japan, including 10 grain landing ports and 10 non-grain landing ports (Fig. 1). The grain included cereals, rice, corn, pulses, and millet. We defined grain landing ports as those where an average of two hundred thousand tons or more of grain were imported annually (Ministry of Land, Infrastructure and Transport 2020). Non-grain landing ports were those where less than approximately ten thousand tons of grain were imported annually, and were chosen as close as possible to each grain landing port to reduce geographical bias. We classified the two ports of Mikawa and Kitakyusyu as non-grain landing ports, although more than ten thousand tons of grain are imported annually. These ports are divided into multiple geographically separate districts, and different types of cargo are handled in different districts. We chose study sites far from grain handling districts in the two ports (supplementary material Fig. 1).

Fig. 1 Locations of 20 study ports and the import volumes of grain at each port. The volume of grain is the sum of those imported directly from overseas and those transferred from other ports in Japan. The volume is the average from 2007 to 2016. Grain includes cereals, rice, corn, pulses, and millet.
Floristic survey

From 2016 to 2018, we surveyed the flora at each port twice a year: spring (from May to June) and fall (from September to October). Twenty 100 m transects were set along the roads in each port. For grain landing ports, we selected the roads near silos and the entrances used by fodder companies, or the main roads used to carry cargo away from the ports. For non-grain landing ports where there are no silos and fodder companies, we selected the roads near the landing places or the main roads. We focused on species that have reproduced successfully to evaluate the establishment stage and identify the species correctly. All flowering or fruiting herbaceous plants were recorded along each transect within a width of 1 m from both road edges. Moss, woody plants, and planted horticultural plants were excluded from the records. The species were identified according to Satake et al. (1981, 1982a,b), Osada (1989), Shimizu et al. (2001), Shimizu (2003), Umezawa (2007), Yashiro (2007), Uemura et al. (2010), and Flora-Kanagawa Association (2018). The nomenclature followed Yonekura and Kajita (2003). The species were classified as native to Japan or alien, and the introduction year (the earliest record in Japan) of each alien species was identified according to Shimizu et al. (2001), Muranaka (2008), Uemura et al. (2010), and Flora-Kanagawa Association (2018).

Identification of propagules in wheat imported into Japan

We investigated the propagules derived from imported wheat. Japan imports wheat from the USA, Canada, and Australia, which, when combined, account for 99% of all wheat imports to Japan (Ministry of Finance 2020). We obtained three 20 kg samples of five wheat classes imported between 2006 and 2007, three classes of the US wheat (Hard Red Winter wheat: HRW, Western White wheat: WW and Dark Northern Spring wheat: DNS), one class of Canadian wheat (No.1 Canada Western Red Spring wheat: CW) and two classes of Australian wheat (Australian Standard White wheat: ASW and Prime Hard wheat: PH). Each sample was obtained from a different shipment. Seeds other than wheat were picked out from each wheat sample following the method described by Shimono and Konuma (2008). The seeds were identified on the basis of the shape, size, color, and texture of the surface (Martin and Barkley 1961; Davis 1993; Ishikawa 1994; Guo 1998), and the number of each type was counted. To verify seed identification, some of the seeds were germinated and grown in an isolated garden to maturity, and then the plants were identified (Osada 1989; Flora of North America Editorial Committee 1993+; Flora-Kanagawa Association 2018). The seeds were stored in an airtight container with silica gel at room temperature (20–28 °C).

Calculation of the contamination rate of each species detected from imported grain

The contamination rate of each species detected from imported grains was calculated using the data from our survey and previous studies (Asai et al. 2007; Wilson et al. 2016). Asai et al. (2007) studied weed seed contamination in imported small grain crops (wheat, barley, rye, oats, and canola) in Japan, mainly from the USA, Canada, and Australia, from 1993 to 1995. Although the top three imported grains in Japan are corn, soybean, and wheat, we could not obtain corn and soybean (or other crop) samples imported into Japan. Therefore, we used data from Wilson et al. (2016). They have published a list of weed seed contaminant species reported in 947 samples of 10 imported grain crops (corn, rice, soybean, cereals, pulse, canola, sunflower, flax, millet, and sorghum) in Canada from 2007 to 2015. More than 75% of these crops, except rice, were imported from the USA. Japan also imports 70% of corn and 70% of soybean from the USA (Ministry of Finance 2020). Therefore, the list in Wilson et al. (2016) can be substituted for propagules in Japan. In Wilson et al. (2016), the data of corn, soybean, cereals, and sorghum were used because the import volumes of the other grains from the USA into Japan were small (less than 1 million tons).

Using data from our survey and Asai et al. (2007), the relative frequency of each contaminant species was calculated by dividing the number of seeds of each contaminant species by the total number of seeds. Wilson et al. (2016) showed the number of lots in which seeds of each weed species had been detected. Therefore, the relative frequency of each species was calculated by dividing the number of lots in which seeds for each species were detected by the
total number of lots. These values were weighted by multiplying the relative quantity of each crop import for 10 years from 2007 to 2016 (Ministry of Finance 2020; supplementary material Table 1). Then, we calculated the total value of each species for all grains, and this value was considered the contamination rate of each weed species in each study. The contamination rate was divided into 40 ranks. The ranks were calculated by dividing the value into 40 equal parts and ranking them from 40 to 1 in the order of increasing numbers; next, the ranks of the three studies were averaged.

Statistical analyses

Plants identified at the species or genus level were used for analysis. To compare the number of native and alien species between the grain landing ports and the non-grain landing ports, we used a generalized linear model (GLM) assuming a negative binomial distribution using the log-link function including the port type (grain landing port or non-grain landing port) as an independent variable. Shannon’s index of diversity was calculated for each port to assess species diversity among ports. A non-metric multidimensional scaling (NMDS) analysis based on Bray–Curtis distances was conducted using the number of transects that each species was recorded in at each port to assess the floristic similarities among ports. We also performed an indicator species analysis (INSPAN) to identify representative species that can characterize each port type. Indicator species are defined as the most characteristic species of each group, found mostly in a single group of the typology and present in the majority of the sites belonging to that group (Dufrene and Legendre 1997). The indicator value (IV) index is based on within-species abundance and occurrence comparisons, without any comparison among species. The IV is maximum when all individuals of a species are found in a single group of sites and when the species occurs in all sites of that group. We selected species with IV > 0.25 and significance level (P-value) < 0.05 as the indicator species (Dufrene and Legendre 1997). We checked whether these indicator species were reported to be contaminants in imported grain using the data from our survey and previous studies (Shimizu et al. 1995; Asai et al. 2007; Wilson et al. 2016).

To assess whether the most common contaminant species were more common at the grain landing ports, we examined the relationship between the average contamination rate and the distribution pattern for each species. Since the above-mentioned NMDS analysis separated 20 study ports into the grain landing ports and the non-grain landing ports by axis-2 in both spring and fall, we used the NMDS score of axis-2 of each species as an index of how the species tended to be distributed according to the port types.

To evaluate whether high propagule pressure and long residence time are associated with the establishment success of alien species in port areas, we calculated Kendall’s rank correlation coefficients between the average contamination rates or the introduction year and the abundance (total number of transects that each alien species was recorded in at each port type). Six species whose introduction years were not identified, 11 species introduced before 1800, and 11 crops were excluded from the analysis.

Differences in contaminant species composition among grain samples were also assessed using the NMDS analysis based on the data of relative frequency of each species for each grain sample. First, we compared species composition among wheat classes in our survey at the species level. Second, we compared the species composition of cereals (wheat, barley, oats, and rye) among three studies at the genus level (our survey, Asai et al. (2007) and Wilson et al. (2016)).

Statistical analyses were performed using R version 4.0.0 (R Core Team 2020).

Results

Comparison of flora between grain and non-grain landing ports

In total, 612 species were recorded within 64 families; 601 species were identified to the species level and 11 to the genus level (supplementary material Table 2). Poaceae was the dominant family (123 species), followed by Asteraceae (96 species) in both spring and fall (Fig. 2). In grain landing ports, Brassicaceae and Amaranthaceae (including Chenopodiaceae) were the third most dominant families in spring and fall, respectively. In the non-grain landing ports, Caryophyllaceae and Fabaceae were the third
most dominant families in spring and fall, respectively. A total of 238 alien species and 141 native species were recorded in spring, and 220 alien species and 223 native species were recorded in fall. The numbers of alien species per port in spring and fall were significantly higher in the grain landing ports (mean ± standard error: 66.4 ± 6.22 and 50.0 ± 2.39) than in the non-grain landing ports (49.5 ± 4.60 and 40.4 ± 2.83) (spring: \( P = 0.024 \), fall: \( P = 0.007 \)), but the number of native species did not differ significantly between the port types in both seasons (Fig. 3).

As a result, Shannon’s indices of diversity for the grain landing ports (6.05 ± 0.14 and 5.95 ± 0.06) were slightly higher than those of non-grain landing ports (5.79 ± 0.13 and 5.87 ± 0.10) in both seasons.

The NMDS analysis showed that the 20 study ports were separated along the latitudinal gradient, Hokkaido, Tohoku, and the western area from Kanto by axis-1 and were separated into the grain landing ports and the non-grain landing ports by axis-2 in both spring and fall (Fig. 4). This indicated that the flora was not only strongly affected by climate but also by port types.

According to the INSPAN, 16 indicator species were identified for the grain landing ports in spring (Table 1a). Among them, three species (wheat, barley, and rapeseed) were crops. All the remaining 13 weed species were reported to be contaminants in imported grains. Only three indicator species, *Trifolium repens* L., *Juncus tenuis* Willd., and *Sisyrinchium*
*Micranthum* Cav., were identified for the non-grain landing ports in spring (Table 1a) and *T. repens* was reported to be a contaminant in imported grains. In the fall, all six indicator species of the grain landing ports and one of five indicator species of non-grain landing ports were reported as contaminant species (Table 1b). The indicator species of the grain landing ports were recorded in almost all the grain landing ports, while the indicator species of the non-grain landing ports were also frequently recorded in the grain landing ports (supplementary material Fig. 2).

**Contaminant seed composition in wheat**

A total of 59,229 contaminant seeds were detected from the wheat samples, belonging to 92 types from 15 families (supplementary material Table 3). Seventy-three were identified at the species level, 17 to the genus level, and two to the family level. Poaceae was the most dominant family, with 25 types, followed by Brassicaceae (17), Polygonaceae (12), Asteraceae (8), and Amaranthaceae (6). The number of contaminant seeds per 20 kg of the wheat samples ranged from 371 to 6,975.

The species composition was different among the wheat classes (Fig. 5). Two classes of winter wheat from the USA (HRW and WW) contained many seeds of *Bromus tectorum* L., *Avena fatua* L., and *Aegilops cylindrica*. One class of spring wheat from the USA (DNS) contained many seeds of *Setaria* P. Beauv. species and *A. fatua*. Seeds of *Brassica* L. spp. (oilseed rape) were the most abundant in Canadian wheat (CW). Seeds of *Lolium* spp. accounted for 75% of all contaminants in one class of Australian wheat (ASW). Another class of Australian wheat (PH) was characterized by seeds of *Erucastrum australonectum* Al-Shehbaz & Warwick, which were detected only in this wheat class.

The NMDS analysis of the contaminant seed composition in wheat showed remarkable differences between imported grains from North America and Australia and between eastern and western Australia.
(Fig. 6a). There was a moderate difference between winter and spring wheat in North America. The differences in the contaminant seed composition of cereals among grain-exporting countries also appeared even if the studies were analyzed together (Fig. 6b). The composition of the 2010s cereals, mainly from the USA (Wilson et al. 2016), was similar to that of the 2000s DNS USA wheat. However, there were some differences in the composition of wheat imported from the USA in the 1990s (Asai et al. 2007) and the 2000s (our survey). The 1990s wheat from the USA in Asai et al. (2007) had a higher proportion of seeds of Bassia scoparia (L.) A.J.Scott, Echinochloa crus-galli (L.) P.Beauv. var. crus-galli, Rumex L. spp., but no seeds of A. cylindrica, which were abundant in the 2000s winter wheat from the USA in our survey. The weed seed compositions of Canadian grains were roughly similar between the 1990s (Asai et al. 2007) and the 2000s (our survey), although the Canadian grain in Asai et al. (2007) had a high proportion of seeds of Stellaria media (L.) Vill.; however, the seeds were scarce in CW in our survey.

The top 20 contaminant species (22 taxa with the highest rankings averaged over three studies) are shown in Table 2, along with the total number of transects in which they were recorded in each port type (the grain and the non-grain landing ports). The contaminant species included 7 crops, 10 alien to Japan,
and 5 native to Japan. The native species, which were cosmopolitan and abundant throughout Japan, were found in both port types. Except for two species (*Setaria pumila* (Poir.) Roem. & Schult. and *Persicaria* Mill. spp.); these native species were found more often in the grain landing ports. Similarly, the alien species were found more often in the grain landing ports; however, one alien species (*Panicum* L. spp.) was recorded more often in the non-grain landing ports. *Bassia scoparia* and *A. cylindrica* were barely recorded at any ports despite their high rankings as contaminants. About half of the indicator species were high ranking contaminants (Table 1).

**Relationship between the distribution pattern and the contamination rate**

The NMDS analysis based on the flora at each port separated 20 ports into the grain landing ports and the non-grain landing ports by axis-2 in both spring and fall (Fig. 4). Therefore, we used the NMDS score of axis-2 of each species as an index of how the species tended to be distributed according to port types; species with positive scores were distributed more in the grain landing ports, and species with negative scores were distributed more in the non-grain landing ports. The scatter plots between the NMDS scores of axis-2 and the average contamination rankings showed that species with positive scores tended to have higher contamination rankings than species with negative scores in both seasons, indicating that species whose distribution was biased in the grain landing ports tended to show high contamination rankings (Fig. 7). There was only one species, *Setaria pumila*, with a negative score and a high contamination ranking of more than 10.

**Factors affecting the abundance of alien species at ports**

The contamination ranking was positively correlated with the abundance of alien species recorded at grain landing ports, but not with the abundance of alien species recorded at non-grain landing ports in both seasons (Fig. 8a). The introduction year was negatively correlated with the abundance regardless of the port type and season (Fig. 8b). Most of the highly abundant species were first recorded before 1950. These results indicated that weed seed contamination plays a role as a propagule pressure only at the grain landing ports, while a longer residence time is associated with the establishment of alien species at both ports.

**Discussion**

Our study revealed that the flora was clearly different between the grain landing ports and the non-grain landing ports throughout Japan (Fig. 4). Alien species were more abundant in the grain landing ports than in the non-grain landing ports in spring and fall (Fig. 3). Furthermore, all the indicator species at the
grain landing ports in both seasons were reported to be contaminants in imported grain (Table 1), and there was a tendency for the more abundant species at the grain landing ports to show high contamination rankings (Fig. 7). These results indicated that species formed naturalized populations from the seeds of contaminant species spilled from imported grains, and consequently, species diversity increased at the grain landing ports.

Poaceae and Asteraceae were the dominant families in grain and non-grain landing ports (Fig. 2), and it has been reported that both families contribute most to the total number of global naturalized alien species based on the Global Naturalized Alien Flora (GloNAF) database (Pyšek et al. 2017). In contrast, the Brassicaceae and Amaranthaceae were recorded more frequently in the grain landing ports than in the non-grain ones (Fig. 2). As shown in the indicator species of the grain landing ports, Brassicaceae and Amaranthaceae characterize the flora of the grain landing ports in spring and fall, respectively (Table 1). Consistent with these findings, the majority of contaminant species in imported grains reported in previous studies belonged to these two families (Asai et al. 2007; Shimono and Konuma 2008; Wilson et al. 2016). For example, based on the number of seeds or lots, Brassicaceae was the second most common family among contaminants in wheat (our survey, Shimono and Konuma 2008) and cereals (Wilson et al. 2016), and Amaranthaceae in corn, soybean, and sorghum (Wilson et al. 2016). These families were the second and third most common families found as contaminants in small grain crops (Asai et al. 2007). In addition to grains, the Amaranthaceae was the most frequently identified weed family detected in commercial pet food for birds or small rodents in the USA (Oseland et al. 2020) and Italy (Cossu et al. 2020). The researchers claimed that the contamination of *Amaranthus* L. species in bird feed mixes could have originated from contaminants in proso millet, grain sorghum, and corn, which were the raw materials used to make bird feed (Oseland et al. 2020).

The top 20 weed species with the highest contamination rankings shown in Table 2 are also known to be common, and troublesome weeds in fields of cereals, corn, or sorghum in the USA and Canada (Lee-son et al. 2005; Van Wychen 2020). This is consistent with a previous study showing that weed abundance in fields was the most significant factor affecting the number of seeds contaminating grains (Shimono and Konuma 2008). All native weeds and four alien weeds (*Lolium* spp., *Avena fatua*, *Amaranthus* spp., and *Panicum* spp.) are also common in Japan. The other one alien weed (*Thlaspi arvense* L.) has become a problematic weed in wheat fields in a limited area (Aoki and Asai 2016). However, the remaining five alien weeds (*Bromus tectorum*, *Fallopia convolvulus* (L.) Á.Löve, *Bassia scoparia*, *Aegilops cylindrica*, *Raphanus raphanistrum* L.) are not commonly found in Japan. In particular, *B. scoparia* and *A. cylindrica* are rarely seen in Japan despite their high contamination level. These species may not be able to adapt to wild environments in Japan and, thus, fail to establish.
In general, identifying the causes of a failed invasion is a challenging task because invasions are complex processes with multiple stages, occurring at different spatial and temporal scales (van Kleunen et al. 2015). However, the comparison of life-history traits between species that failed to establish and those that succeeded in establishing could provide important insights in which traits might be important for establishment (Catford et al. 2019). For example, multispecies introduction experiments at grasslands suggested that high seed mass was an important factor increasing establishment success (Kempel et al. 2013; Catford et al. 2019). This framework is invaluable for understanding the process of biological invasion because few studies have considered the effect of different life-history syndromes on the relationship between establishment success and the numbers introduced (Cassey et al. 2014). Another factor affecting the abundance of alien species could be the residence time (Richardson and Pyšek 2006; Pyšek et al. 2009). Many successful colonizers were introduced to Japan before 1950 (Fig. 8b). *Aegilops cylindrica* was first recorded in Japan in 1973 (Shimizu 2003). Therefore, the unsuccessful establishment may be related to shorter residence time, and it is necessary to investigate carefully whether these species will establish and become more abundant in Japan in the future.

The contaminant seed composition in wheat showed notable differences between the production areas (Fig. 6a). Our survey of contaminant seed composition in wheat is based on a small number of lots over a short period. However, because the species composition was characteristic of each wheat class and the differences in the species composition of cereals from different countries also appeared even if the individual studies were analyzed together (Fig. 6b), we believe that we obtained sufficient information on the contaminants in each wheat class. Our results showed that the contaminant species in grain could be partially predicted from the production areas.

We calculated the contamination level based on three studies (our survey, Asai et al. (2007), and Wilson et al. (2016)). We used the data reported by Wilson et al. (2016), comprising a list of weed seed contaminant species of imported grains in Canada, as a substitute for propagules entering Japan because Canada and Japan import more than 70% of corn and soybean from the USA. Data from Wilson et al. (2016)
Table 1  Indicator species for the grain landing ports and the non-grain landing ports in spring (a) and fall (b) according to an indicator species analysis (INSPAN)

(a)

| Port type          | Family    | Scientific name                        | Indicator value | P-value | Category | Contamination |
|--------------------|-----------|----------------------------------------|-----------------|---------|----------|--------------|
| Grain landing port | Poaceae   | *Triticum aestivum*                    | 0.900           | 0.001   | C        | ✓            |
|                    | Brassicaceae | *Brassica napus*                     | 0.854           | 0.003   | C        | ✓            |
|                    | Brassicaceae | *Sisymbrium orientale*                | 0.773           | 0.002   | A        | ✓            |
|                    | Caryophyllaceae | *Stellaria media*                  | 0.773           | 0.001   | N        | ✓            |
|                    | Brassicaceae | *Capsella bursa-pastoris*             | 0.767           | 0.007   | N        | ✓            |
|                    | Rubiaceae   | *Galium aparine*                      | 0.756           | 0.002   | A        | ✓            |
|                    | Poaceae     | *Hordeum vulgare*                     | 0.700           | 0.002   | C        | ✓            |
|                    | Rubiaceae   | *Galium spurium* var. echinospermon   | 0.700           | 0.016   | N        | ✓            |
|                    | Poaceae     | *Bromus diandrus*                     | 0.687           | 0.014   | A        | ✓            |
|                    | Malvaceae   | *Malva parviflora*                    | 0.600           | 0.010   | A        | ✓            |
|                    | Poaceae     | *Poa annua*                           | 0.571           | 0.001   | N        | ✓            |
|                    | Polygonaceae| *Polygonum aviculare*                 | 0.562           | 0.043   | N        | ✓            |
|                    | Poaceae     | *Avena fatua*                         | 0.547           | 0.027   | A        | ✓            |
|                    | Brassicaceae| *Brassica tournefortii*               | 0.500           | 0.032   | A        | ✓            |
|                    | Brassicaceae| *Raphanus raphanistrum*              | 0.500           | 0.030   | A        | ✓            |
|                    | Amaranthaceae| *Amaranthus viridis*             | 0.470           | 0.046   | A        | ✓            |
| Non-grain landing port | Fabaceae | *Trifolium repens*                   | 0.726           | 0.011   | A        | ✓            |
|                    | Juncaceae  | *Juncus tenuis*                      | 0.588           | 0.033   | N        |             |
|                    | Iridaceae  | *Sisyrinchium micranthum*             | 0.501           | 0.048   | A        |             |

(b)

| Port type          | Family    | Scientific name                        | Indicator value | P-value | Category | Contamination |
|--------------------|-----------|----------------------------------------|-----------------|---------|----------|--------------|
| Grain landing port | Convolvulaceae | *Ipomoea hederacea*               | 0.767           | 0.002   | A        | ✓            |
|                    | Amaranthaceae | *Amaranthus hybridus*             | 0.756           | 0.003   | A        | ✓            |
|                    | Portulacaceae | *Portulaca oleracea*              | 0.704           | 0.022   | N        | ✓            |
|                    | Amaranthaceae | *Amaranthus viridis*              | 0.667           | 0.015   | A        | ✓            |
|                    | Phytolaccaceae| *Phytolacca americana*            | 0.659           | 0.018   | A        | ✓            |
|                    | Malvaceae   | *Sida spinosa*                      | 0.600           | 0.015   | A        | ✓            |
| Non-grain landing port | Poaceae | *Phragmites australis*          | 0.748           | 0.011   | N        |             |
|                    | Poaceae     | *Digitaria violascens*             | 0.746           | 0.022   | N        |             |
|                    | Poaceae     | *Miscanthus sinensis*              | 0.731           | 0.020   | N        |             |
|                    | Fabaceae    | *Lespedeza cuneata*                | 0.614           | 0.026   | N        |             |
|                    | Asteraceae  | *Erigeron canadensis*              | 0.601           | 0.003   | A        | ✓            |

Indicator species are classified into three categories; C: crop species, A: alien species and N: native species. Species with records of contamination in imported grain are checked in the last column.
Table 2 Top 20 species with the highest contamination ranks averaged over three studies. The contamination rate and corresponding rank for each study as well as the average of the rank over three studies are shown. The rank was calculated by dividing the values into 40 equal parts and ranking them from 40 to 1 in the order of increasing numbers

| Family          | Scientific name          | Category*1 | Rate   | Rank  | Rate   | Rank  | Average | Order | Number of transects |
|-----------------|--------------------------|------------|--------|-------|--------|-------|---------|-------|---------------------|
| Amaranthaceae   | Chenopodium album        | N          | 0.0045 | 2     | 0.1122 | 40    | 0.3634  | 40    | 27.33               |
| Brassicaceae    | Brassica spp.*2          | C          | 0.0818 | 21    | 0.0934 | 34    | 0.1675  | 19    | 24.67               |
| Poaceae         | Lolium spp.*3            | A          | 0.1495 | 38    | 0.0756 | 27    | 0.0101  | 2     | 22.33               |
| Poaceae         | Avena fatua              | A          | 0.1307 | 33    | 0.0506 | 19    | 0.0760  | 9     | 20.33               |
| Poaceae         | Bromus tectorum          | A          | 0.1615 | 40    | 0.0226 | 9     | 0.0990  | 11    | 20.00               |
| Polygonaceae    | Fallopia convolvulus     | A          | 0.0442 | 11    | 0.0754 | 27    | 0.1208  | 14    | 17.33               |
| Poaceae         | Setaria viridis          | N          | 0.0382 | 10    | 0.0652 | 24    | 0.1482  | 17    | 17.00               |
| Amaranthaceae   | Amaranthus spp.*4        | A          | 0.0050 | 2     | 0.0205 | 8     | 0.3235  | 36    | 15.33               |
| Amaranthaceae   | Bassia scoparia          | A          | 0.0109 | 3     | 0.0652 | 24    | 0.1435  | 16    | 14.33               |
| Poaceae         | Setaria pumila           | N          | 0.0515 | 13    | 0.0344 | 13    | 0.1286  | 15    | 13.67               |
| Poaceae         | Hordeum vulgare          | C          | 0.0850 | 22    | 0.0013 | 1     | 0.1218  | 14    | 12.33               |
| Poaceae         | Triticum aestivum        | C          | 0.0000 | 0     | 0.0047 | 2     | 0.3024  | 34    | 12.00               |
| Brassicaceae    | Thlaspi arvense          | A          | 0.0058 | 2     | 0.0611 | 22    | 0.0414  | 5     | 9.67                |
| Poaceae         | Echinochloa crus-galli   | N          | 0.0172 | 5     | 0.0231 | 9     | 0.1186  | 14    | 9.33                |
| Fabaceae        | Glycine max subsp. max   | C          | 0.0033 | 1     | 0.0099 | 4     | 0.2024  | 23    | 9.33                |
| Polygonaceae    | Persicaria spp.*5        | N          | 0.0018 | 1     | 0.0466 | 17    | 0.0789  | 9     | 9.00                |
| Linaceae        | Linum usitatissimum      | C          | 0.0097 | 3     | 0.0231 | 9     | 0.0472  | 6     | 6.00                |
| Poaceae         | Panicum spp.*6           | A          | 0.0061 | 6     | 0.0252 | 9     | 0.0673  | 8     | 6.00                |
| Poaceae         | Aegilops cylindrica      | A          | 0.0416 | 11    | 0.0000 | 0     | 0.0440  | 5     | 5.33                |
| Poaceae         | Avena sativa             | A          | 0.0062 | 2     | 0.0028 | 2     | 0.0894  | 10    | 4.67                |
| Brassicaceae    | Raphanus raphanistrum    | A          | 0.0173 | 5     | 0.0136 | 5     | 0.0208  | 3     | 4.33                |
| Asteraceae      | Helianthus annuus        | C          | 0.0017 | 1     | 0.0023 | 1     | 0.0902  | 10    | 4.00                |

*1A: alien species; C: crop species; N: native species

*2 includes B. juncea, B. kaber, B. napus, or B. rapa

*3 includes L. multiformor or L. rigidum

*4 includes A. albus, A. caudatus, A. hybridus, A. retroflexus, A. palmeri, or A. viridis

*5 includes P. hydropiper, P. lapathifolia, P. maculosa subsp. hirticaulis, or P. pensylvanica. Only P. pensylvanica is an alien species but not recorded in the flora survey

*6 includes P. capillare or P. dichotomiflorum

Our survey

The last four columns show the total number of transects that each species was recorded in each port type (GP: grain landing port, NGP: non-grain landing port)

and the present study share the same major contaminant species but not minor species (supplementary material Table 4). The minor species in the previous study may be derived from regions that have limited trade with Japan. Since they are all minor species, we believe that they did not significantly affect our results. The survey years varied from 1993 to 2015 according to the particular study and this is notable as weed species composition may have changed over the past 20 years. As the NMDS analysis demonstrated, the contaminant seed composition of cereals was different between grain-exporting countries, even when the studies were analyzed together (Fig. 6b); thus, it can be said that there has been no major change in 20 years. However, there were some differences in the contaminants in wheat imported from the USA in the 1990s (Asai et al. 2007) and in the 2000s (our survey). This may indicate a change in weed flora in the agricultural fields in grain-exporting countries, or it may be due to different sampling methods. For example, although the seeds of A. cylindrica were abundant in winter wheat imported from the USA in the 2000s in our survey, they were not detected in wheat imported from the USA in the 1990s (Asai et al. 2007). However, A. cylindrica became a troublesome weed with changes in wheat production practices.
after the 1970s in the USA (Donald and Ogg 1991); thus, the abundance of this species in wheat fields may have increased rapidly over the last few decades.

There are many cosmopolitan species contained in imported grains, such as *Chenopodium album* L., *E. crus-galli* var. *crus-gall*, *Setaria viridis* (L.) P. Beauv., and *Capsella bursa-pastoris* (L.) Medik. Various lineages, which have different genetic compositions from the strains native to Japan, have been introduced from foreign countries because some of them, such as *Arabidopsis thaliana* (L.) Heynh. (Platt et al. 2010) and *C. bursa-pastoris* (Cornille et al. 2016), show geographically structured genetic variation. Therefore, non-native lineages with high reproduction capabilities may expand and displace native lineages, as has occurred in *Phragmites australis* (Cav.) Trin. ex Steud. (Saltonstall 2002; Pyšek et al. 2018). Given a lack of reproductive barriers between native and non-native lineages, there is a risk of hybridization between them, and heterosis achieved by hybridization enhances invasiveness (Ellstrand and Schierenbeck 2000).

Moreover, herbicide-resistant weeds such as *Amaranthus palmeri* S. Watson have been increasing in recent years worldwide (Gaines et al. 2010). Highly contaminating species are known as major weeds in farmlands, and these species are often reported to be herbicide-resistant (Owen et al. 2014). Herbicide-resistant weed seeds have been reported as contaminants in commercial grains (Michael et al. 2010; Shimono et al. 2010), and the establishment of herbicide-resistant weed species is common at major grain landing ports in Japan (Shimono et al. 2015, 2020). Gene flow via pollen or seed movement from resistant plants could promote the rapid expansion of resistance alleles to previously herbicide-susceptible populations (Busi et al. 2011).

Thus, it is becoming increasingly important to monitor the occurrence of weeds in grain-exporting countries and the weed species composition in imported grain commodities to predict the contamination of grains by troublesome weeds and identify effective weed management options.

**Conclusion**

Although it has long been recognized that various weed seeds are contained in imported grains, the relationship between establishment and propagule pressure has not previously been evaluated. We have demonstrated that weed seed contamination in grain commodities plays an important role in propagule pressure by showing a positive relationship between contamination levels and successful establishment. Our findings support previous studies showing that propagule pressure is one of the best predictors for the establishment success of alien species (Lockwood et al. 2005; Simberloff 2009). The management of pathways represents the frontline in the prevention of biological invasions. Knowledge of the goods traded and their origin and destination should enable reasonable estimates of the risk of alien species introduction (Hulme 2009).

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**Authors’ contributions** YS conceived the ideas; MI, TN, MA and YS collected data; MI, TN, and YS analyzed the data; TM prepared the alien plant information list; AK prepared wheat samples; MA and TT gave useful advice; MI and YS wrote the paper.

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**Availability of data and material** All data used herein are included in this manuscript and its supplementary information files.

**Code availability** Non-applicable.

**Declarations**

**Conflicts of interest** There are no conflicts of interest to declare.

**Additional declarations for articles in life science journals that report the results of studies involving humans and/or animals** Non-applicable.

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**Consent to participate** All authors have consented to participate in this study.
References

Aoki M, Asai M (2016) Emergence and control of naturalized weeds, Camelina microcarpa Andr. ex DC., Descurainia sophia (L.) Webb ex Prantl, and Thlaspi arvense L., in wheat fields in Nagano Prefecture. J Weed Sci Technol 61:139–148

Asai M, Kurokawa S, Shimizu N, Enomoto T (2007) Exotic weed seeds detected from imported small cereal grains into Japan during 1990s’. J Weed Sci Technol 52:1–10

Blackburn TM, Pyšek P, Bacher S, Carlson JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Burke MJW, Grime JP (1996) An experimental study of plant community invasibility. Ecol 77:776–790

Busi R, Michel S, Powles SB, Delye C (2011) Gene flow increases the initial frequency of herbicide resistance alleles in unselected Lolium rigidum populations. Agri Ecosyst Environ 142:403–409

Cassey P, Blackburn TM, Sol D, Duncan RP, Lockwood JL (2004) Global patterns of introduction effort and establishment success in birds. P Roy Soc B-Biol Sci 271:405–408

Cassey P, Prowse TAA, Blackburn TM (2014) A population model for predicting the successful establishment of introduced bird species. Oecologia 175:417–428

Catford JA, Smith AL, Wragg PD, Clark AT, Kosmala M, Cavender-Bares J, Reich PB, Tilman D (2019) Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. Ecol Let 22:593–604

Colautti RI, Grigorov Ia, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037

Cornille A, Salcedo A, Kryvokhyzha D, Glémin S, Holm K, Wright SI, Lacours M (2016) Genomic signature of successful colonization of Eurasia by the allopolyploid shepherd’s purse (Capsella bursa-pastoris). Mol Ecol 25:616–629

Cossu TA, Lozano V, Stuppy W, Brundu G (2020) Seed contaminants: an overlooked pathway for the introduction of non-native plants in Sardinia (Italy). Plant Biot Syst 154:843–850

Davis LW (1993) Weed seeds of the great plains: A handbook for identification. University Press of Kansas, Lawrence, KS

Divišek J, Chytrý M, Beckage B, Gotelli NJ, Lososová Z, Pyšek P, Richardson DM, Molofsky J (2018) Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nat Commun 9:1–10

Donald WW, Ogg AG (1991) Biology and control of jointed goatgrass (Aegilops cylindrica), a review. Weed Technol 5:3–17

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? Euphytica 148:35–46

Flora of North America Editorial Committee (1993+) Flora of North America North of Mexico. 12+ vols. New York and Oxford, USA. vol. 1, 1993; vol. 2, 1993; vol. 3, 1997; vol. 4, 2003; vol. 5, 2005; vol. 19, 2006; vol. 20, 2006; vol. 21, 2006; vol. 22, 2000; vol. 23, 2002; vol. 25, 2003; vol. 26, 2002

Flora-Kanagawa Association (2018) Flora of Kanagawa 2018. Kanagawa Prefectural Museum of Natural History, Kanagawa

Gaines TA, Zhang W, Wang D, Bukan B, Chisholm ST, Shaner DL, Nissen SJ, Patzoldt WL, Tranel PJ, Culpepper AS, Grey TL, Webster TM, Vencill WK, Douglas Sammons R, Jiang J, Preston C, Leach JE, Westra P (2010) Gene amplification confers glyphosate resistance in Amaranthus palmeri. PNAS 107:1029–1034

Gervilla C, Rita J, Cursach J (2019) Contaminant seeds in imported crop seed lots: a non-negligible human-mediated pathway for introduction of plant species to islands. Weed Res 59:245–253

Guo QX (1998) Identification of weed seeds with colored pictures. China Agricultural Press, Beijing

Higuchi Y, Shimono Y, Tominaga T (2017) The expansion route of ryegrasses (Lolium Spp.) into sandy coasts in Japan. Invasive Plant Sci Manag 10:61–71

Holle BV, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecol 86:3212–3218

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Ishikawa S (1994) Seeds / Fruits of Japan. Ishikawa Shigeo Zukan Kanko Iinkai, Tokyo

Kempel A, Chrobock T, Fischer M, Rohr RP, Van Kleunen M (2013) Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. PNAS 110:12727–12732

Kurokawa S, Shibatake H, Akiyama H, Yoshimura Y (2004) Molecular and morphological differentiation between the crop and weedy types in Velvetleaf (Abutilon theophrasti Medik.) using a chloroplast DNA marker: seed source of the present invasive Velvetleaf in Japan. Heredity 93:603–609

Lavoie C, Joly S, Bergeron A, Guay G, Groeneveld E (2016) Explaining naturalization and invasiveness: new insights from historical ornamental plant catalogs. Ecol Evol 6:7188–7198

Lawrence DJ, Cordell JR (2010) Relative contributions of domestic and foreign sourced ballast water to propagule pressure in Puget Sound, Washington, USA. Biol Conserv 143:700–709

Lee JE, Chown SL (2009) Breaching the dispersal barrier to invasion: quantification and management. Ecol Appl 19:1944–1959

Leeson JY, Thomas AG, Hall LM, Brenzil CA, Andrews T, Brown KR, Van Acker RC (2005) Prairie Weed Surveys...
of Cereal, Oilseed and Pulse Crops from the 1970s to the 2000s. Agriculture and Agri-Food Canada, Saskatoon Research Centre, Saskatchewan, Canada

Lehan NE, Murphy JR, Thorburn LP, Bradley BA (2013) Accidental introductions are an important source of invasive species in the continental United States. Ame J Bot 100:1287–1293

Lockwood JL, Caspey P, Blackburn T (2005) The role of propague pressure in explaining species invasions. Trends Ecol Evol 20:223–228

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Martin AC, Barkley WD (1961) Seed Identification Manual. Blackburn Press, NJ

Michael PJ, Owen MJ, Powles SB (2010) Herbicide-resistant weed seeds contaminate grain sown in the Western Australian grainbelt. Weed Sci 58:466–472

Ministry of Agriculture, Forestry, and Fisheries (2020) Related statistics of Japan. https://www.maff.go.jp/j/zyukyu/fbs/. Accessed 18 Jan 2021

Ministry of Finance (2020) Trade statistics of Japan. https://www.mlit.go.jp/k-toukei/ Accessed 18 Jan 2021

Ministry of Finance (2020) Supply and demand of food in Japan. https://www.mlit.go.jp/j/zyukyu/fbs/. Accessed 18 Jan 2021

Ministry of Land, Infrastructure and Transport (2020) Traffic-related statistics of Japan. https://www.mlit.go.jp/j/toukei/saishintoukeithyou.html. Accessed 18 Jan 2021

Muranaka T (2008) Naturalization and invasion of alien plants in Japan: relationships among their origin of use and time of introduction. Japanese J Conserv Ecol 13:89–101

Osada T (1989) Picture book of Poaceae in Japan. Heibonsha, Tokyo

Osland E, Bish M, Spinka C, Bradley K (2020) Examination of commercially available bird feed for weed seed contaminants. Invasive Plant Sci Manag 13:14–22

Owen MJ, Martinez NJ, Powles SB (2014) Multiple herbicide-resistant Lolium rigidum (annual ryegrass) now dominates across the Western Australian grain belt. Weed Res 54:314–324

Pimentel D, McNair S, Janecka J, Simmonds C, O’Connell C, Wong E, Russel L, Zern J, Aquino T, Tsunoda E (2000) Economic and environmental threats of alien plant, animal, and microbe invasions. Agric Ecosyst Environ 84:1–20

Platt A, Horton M, Huahg YS, Li Y, Anastasio AE, Mulyati NW, Agren J, Bossdorf O, Byers D, Donohue K, Dunning M, Holub EB, Hudson A, Corre VL, Loutet O, Roux F, Warthmann N, Weigel D, Rivero L, Scholl R, Nordborg M, Bergelson J, Borevitz JO (2010) The scale of population structure in Arabidopsis thaliana. PLoS Genet 6:e1000843

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological invasions, Ecological Studies 193. Springer-Verlag, Berlin, pp 97–125

Pyšek P, Křivánek M, Jarošík V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecol 90:2734–2744

Pyšek P, Pergl J, Essl F, Lenzner B, Dawson W, Kreft H, Weigelt P, Winter M, Kartesz J, Nishino M et al (2017) Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia 89:203–274

Pyšek P, Škalová H, Čuda J, Guo WY, Suda J, Doležal J, Kauzál O, Lambertini C, Lučanová M, Mandáková T, Moravcová L, Pyšková K, Brix H, Meyerson LA (2018) Small genome separates native and invasive populations in an ecologically important cosmopolitan grass. Ecol 99:79–90

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 18 Jan 2021

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431

Saltonstall K (2002) Cryptic invasion by a non-native genotype of the Common reed, Phragmites australis, into North America. PNAS 99:2445–2449

Satake Y, Ohwi J, Kitamura S, Watari S, Tominari T (1981) Wild flowers of Japan III. Heibonsha, Tokyo

Satake Y, Ohwi j, Kitamura S, Watari S, Tominari T (1982a) Wild flowers of Japan I. Heibonsha, Tokyo

Satake Y, Ohwi j, Kitamura S, Watari S, Tominari T (1982b) Wild flowers of Japan II. Heibonsha, Tokyo

Shimizu N, Uozumi S (1995) Establishment and diffusion mechanisms of alien weeds invading grasslands and forage crop fields (II). J Weed Sci Technol 40:178–179

Shimizu N, Morita H, Hirota S (2001) Flora of Alien Species in Japan. Plant Invader 600 species. Zenkoku Noson Kyoiku Kyokai, Tokyo

Shimizu T (2003) Naturalized plants of Japan. Heibonsha, Tokyo

Shimono Y, Konuma A (2008) Effects of human-mediated processes on weed species composition in internationally traded grain commodities. Weed Res 48:10–18

Shimono Y, Takiguchi Y, Konuma A (2010) Contamination of internationally traded wheat by herbicide-resistant Lolium rigidum. Weed Biol Manag 10:219–228

Shimono Y, Shimo A, Oguma H, Konuma A, Tomina T (2015) Establishment of Lolium species resistant to acetolactate synthase-inhibiting herbicide in and around grain-importation ports in Japan. Weed Res 55:101–111

Shimono A, Kanbe H, Nakamura S, Ueno S, Yamashita J, Asai M (2020) Initial invasion of glyphosate-resistant Amaranthus palmeri around grain-import ports in Japan. Plants People Planet 2:640–648

Smirhloff D (2009) The role of propague pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102

Uemura S, Shimizu N, Mizuta M, Hirota S, Morita H, Katsuyama T, Ikehara N (2010) Flora of Alien Species in Japan. Volume 2. Plant Invader 500 species. Zenkoku Noson Kyoiku Kyokai, Tokyo

Umezawa S (2007) Flora of Hokkaido. Hokkaido University Kyoiku Kyokai, Tokyo

Van Boheemen LA, Atwater DZ, Hodgins KA (2019) Rapid and repeated local adaptation to climate in an invasive plant. New Phytol 222:614–627

Van Kleunen M, Dawson W, Maurel N (2015) Characteristics of successful alien plants. Mol Ecol 24:1954–1968
The role of weed seed contamination in grain commodities as propagule pressure

Williamson M, Fitter A (1996) The Varying Success of Invaders. Ecol 77:1661–1666

Wilson CE, Castro KL, Thurston GB, Sissons A (2016) Pathway risk analysis of weed seeds in imported grain: a Canadian perspective. NeoBiota 30:49–74

Van Wychen L (2020) 2020 Survey of the Most Common and Troublesome Weeds in Grass Crops, Pasture & Turf in the United States and Canada. Weed Science Society of America National Weed Survey Dataset. Available: https://wssa.net/wp-content/uploads/2020-Weed-Survey_grass-crops.xlsx

Yashiro K (2007) Picture Book of Cyperaceae. Zenkoku Noukou Kyoiku Kyokai, Tokyo

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