Agriculture, Ecosystems and Environment

Type of paper

Original paper

Title

Quantifying the ecosystem service of non-native weed seed predation provided by invertebrates and vertebrates in upland wheat fields converted from paddy fields

Author names and affiliations

Minoru Ichihara [a,b,*,1], Keisuke Maruyama [b], Masayuki Yamashita [b], Hitoshi Sawada [b], Hidehiro Inagaki [c], Yoshiki Ishida [c], Motoaki Asai [d]

[a] The United Graduate School of Agricultural Science, Gifu University, 1-1 Yanagido, Gifu-shi, Gifu 501-1193, Japan

[b] Faculty of Agriculture, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka-shi, Shizuoka 422-8529, Japan

[c] Shizuoka Prefectural Research Institute of Agriculture and Forestry, 678-1 Tomigaoka, Iwata-shi, Shizuoka 438-0803, Japan

[d] National Agricultural Research Center, 3-1-1 Kannondai, Tsukuba-shi, Ibaraki 305-8666, Japan

[1] Present address: Shizuoka Prefectural Research Institute of Agriculture and Forestry, 678-1 Tomigaoka, Iwata-shi, Shizuoka 438-0803, Japan

E-mail addresses

minoru1_ichihara@pref.shizuoka.lg.jp (M. Ichihara)

nrd32734@yahoo.co.jp (K. Maruyama)

abmyama@agr.shizuoka.ac.jp (M. Yamashita)

abhsawa@agr.shizuoka.ac.jp (H. Sawada)

hidehiro1_inagaki@pref.shizuoka.lg.jp (H. Inagaki)

yoshiki1_ishida@pref.shizuoka.lg.jp (Y. Ishida)

masai@affrc.go.jp (M. Asai)

***Corresponding author**

Tel.: +81-538-36-1553

Fax: +81-538-37-8466

E-mail : minoru1_ichihara@pref.shizuoka.lg.jp (Minoru Ichihara)

Postal address:
Shizuoka Prefectural Research Institute of Agriculture and Forestry, 678-1 Tomigaoka, Iwata-shi, Shizuoka 438-0803, Japan

Abstract

The extent of post-dispersal weed seed predation in upland wheat fields converted from paddy fields was quantified in Shizuoka Prefecture, central Japan. We investigated the temporal variability in seed predation of Italian ryegrass (*Lolium multiflorum* Lam.), a non-native winter annual weed in Japan, during summer after the seed shed in both the field interior areas and boundary strips, and estimated the total seed loss due to predation during the summer. Furthermore, the contribution of invertebrates and vertebrates to seed predation was estimated by using exclosures. The total seed loss due to predation during four months (from late June to late October) in the field interior areas and boundary strips was estimated to be 35-43% (the maximum proportion of seed predation per two weeks = 27%) and 42% (25%), respectively. The seed predators in the field interior areas were vertebrates (rodents or birds) and invertebrates (crickets and ground beetles). In contrast, seed predators in the boundary strips were mainly invertebrates (crickets and ground beetles). The results of this study suggest that predators make a substantial contribution in the depletion of post-dispersal seeds of Italian ryegrass in converted paddy fields.

Keywords

Post-dispersal seed predation; Converted paddy fields; Seed predators;
Weed population dynamics; Italian ryegrass

1. Introduction

Post-dispersal seed predation is one of the main causes of weed seed mortality and could contribute to biological weed control (Zhang et al., 1997; Davis et al., 2003; Westerman et al., 2003a, 2003b, 2005; Gallandt et al., 2005; Heggenstaller et al., 2006; Baraibar et al., 2009). Tillage systems (Baraibar et al., 2009) and cropping systems (Davis et al., 2003; Westerman et al., 2005; Heggenstaller et al., 2006) largely influence seed predation, and the contribution of seed predation to weed control varies according to these conditions. Westerman et al. (2005) reported that improvement of cropping systems enhances seed predation and could effectively contribute to reducing herbicide use. Furthermore, agricultural landscape structure can influence seed predation in fields because non-crop areas such as field boundaries are important habitats for seed predators, and these areas play an important role in supporting seed predators (Menalled et al., 2000; Saska et al., 2007). Although quantitative studies on seed predation at the field and landscape levels have increased mainly in Europe and the United States, the extent of post-dispersal weed seed predation in monsoon Asia, including Japan, has rarely been examined (Chauhan et al., 2010). Before post-dispersal weed seed predation can be implemented as a form of weed control in this area, the degree of seed predation and the identity of predators needed to be investigated because these factors may be different depending on the cropping system, climate, and field conditions.

The climate of monsoon Asia is characterized by relatively high temperatures and abundant rainfall during summer. In central Japan, the summer is hot and humid (average temperature > 25 °C, average rainfall > 200 mm/month). Such conditions are ideal for rice production; however, since rice consumption in Japan is declining, the government has promoted growing other crops. Thus, conversion of paddy fields to upland fields is increasing, and many paddy fields are now producing wheat and soybeans.

In wheat fields, infestation of Italian ryegrass (*Lolium multiflorum* Lam.), a non-native winter annual weed, is often one of the most serious weed problems, causing economically important yield losses of wheat (Asai and Yogo, 2005; Suzuki et al., 2010). The lack of effective registered herbicides for this weed, as well as the scarcity of labor for weeding with the trend toward large-scale farming, are thought to contribute to the increased infestation in Japan (Asai and Yogo, 2005). To control Italian ryegrass effectively, integrated weed management (IWM) based on knowledge of the plant’s population ecology must be developed. In particular, a better understanding of the factors for reducing Italian ryegrass populations is essential.

The population dynamics of Italian ryegrass may be largely influenced by post-dispersal seed predation during the summer because all seeds are shed in the early summer when wheat is harvested. Particularly in no-till fields**,** seeds may be subject to relatively high predation because many Italian ryegrass seeds in tilled fields are buried deeper in the soil by tillage, whereas seeds in the no-till fields are more prevalent near the soil surface (Ichihara et al., 2010). Ichihara et al. (2009) compared the fate of seeds stored in pots filled with soil with that of seeds placed on the soil surface during three months in summer, and observed that the proportion of missing seeds on the soil surface was 13-29% higher than those distributed in the soil. Furthermore, Ichihara et al. (2010) investigated the seedbank dynamics of Italian ryegrass in wheat-soybean double-cropped fields under both tilled and no-till systems, suggesting that seed predation may strongly influence seedbank depletion in the no-till fields.

During summer in converted paddy fields, soybeans are usually cultivated after the wheat is harvested; however, soybeans are often damaged by excess moisture because the converted paddy fields tend to be waterlogged by heavy rains. Therefore, weeds are often dominant in the fields during summer. Weedy vegetation can be an attractive habitat for insect seed predators by providing food and refuge (Saska et al., 2007), whereas frequent waterlogging can reduce these insects. Therefore, we cannot predict the potential dynamics of seed predation in converted paddy fields from previous studies conducted in Europe and the United States.

The contribution of seed predators to seed predation may vary according to the climate and field conditions. Westerman et al. (2003a, 2003b) reported that predominant post-dispersal seed predators in agricultural lands in the temperate climate of the Netherlands were rodents and ground beetles, whereas the main seed predators in semi-arid regions of Spain (Baraibar et al., 2009) and in tropical climate of Philippines (Chauhan et al., 2010) were ants. In central Japan, the insect seed predators in agricultural lands are mainly crickets and ground beetles. Field crickets including *Teleogryllus emma* (Ohmachi et Matsuura) are often observed in converted paddy fields in central Japan (Ichihara, unpublished data), and crickets are known to be one of the main seed predators in agricultural ecosystems (Carmona et al., 1999; O'Rourke et al., 2006). Ground beetles of the genus *Harpalus*, *Amara* and *Anisodactylus* are often observed in boundary strips of paddy fields (Yahiro et al., 1992; Kagawa et al., 2008; Lee et al., 2008), vegetable fields (Hiramatsu, 2004) and fallow vegetable fields (Yamazaki et al., 2003) in Japan. Particularly, *Harpalus sinicus* Hope heavily feed on the seeds of *Echinochloa crus-galli* (L.) P. Beauv. var. *crus-galli* in Japan (Yamashita and Kobayashi 2007). Furthermore, birds and rodents may also feed on weed seeds; however, the contributions of invertebrates and vertebrates to seed predation in converted paddy fields are unknown.

To quantify post-dispersal seed predation, two lines of investigations are important. (1) The temporal variability in seed predation and total seed loss due to predation (proportion of all seeds consumed to all seeds produced) must be precisely determined. Although the proportion of seed predation during a few days to several weeks has often been reported, the total seed loss has rarely been assessed (Westerman et al., 2003a). The total seed loss must be determined in order to understand the effects of seed predation on weed population dynamics. Particularly for Italian ryegrass, it is important to estimate the total seed loss due to predation during summer because all seeds are shed in early summer, and seedling emergence starts in autumn. (2) Seed predation not only in the field interior areas but also in the field boundaries must be quantified because non-crop areas such as field boundaries in agricultural landscapes are important habitats for seed predators and can serve as population sources for field colonization (Menalled et al., 2000; Saska et al., 2007). Particularly in converted paddy fields, the boundary strips that are slightly elevated trails can be important refuges for seed predators to escape waterlogging.

In this study, we investigated the temporal variability in post-dispersal seed predation of Italian ryegrass and the contribution of invertebrates and vertebrates to predation in both the interior areas and boundary strips of converted paddy fields where weeds were dominant during the summer. Furthermore, the total seed loss due to predation during summer was estimated.

2. Materials and methods

2.1. Experimental sites

Experiments were conducted at converted paddy fields in 2006 (field A: 22 a) and 2007 (field B: 29 a), in which wheat and soybeans had been double-cropped for 20 years since the conversion. These fields were located in a simple landscape after farmland consolidation in Fukuroi City, Shizuoka Prefecture, Japan (34° 42’ N, 137° 55’ E, 1 m above sea level), and the proportion of non-cropped areas was extremely low. The soil type of these fields was poorly drained heavy clay. Portions of field A (3 a) and field B (7 a) were managed under a no-till system from July 2005 and July 2004, respectively. These fields were separated by a 0.5 m wide ditch, and each field was surrounded by 1-3 m wide boundary strips. The climate of this region during summer is characterized by relatively high temperatures (average temperature > 25 °C) and abundant rainfall (average rainfall > 200 mm/month).

Wheat was sown on December 1, 2005 (field A) and December 7, 2006 (field B) and harvested on June 6, 2006 and June 13, 2007, respectively. In the wheat cropping period for both years, Italian ryegrass infested both the field interior areas and boundary strips. After harvest, wheat stubble and residual straw were burnt in the fields, and soybeans were sown on July 15, 2006 (field A) and July 25, 2007 (field B), respectively. However, the soybeans barely emerged and soybean cropping was immediately abandoned in both years. After soybean sowing, the field interior areas were dominated by *Physalis angulata* L. var. *angulata*, and the boundary strips were dominated by *Physalis angulata* L. var. *angulata*, *Ipomoea* spp. and *Equisetum arvense* L. The boundary strips were mowed at 1 cm height using a weed cutter on May (before wheat harvest), July (before soybean sowing) and October in both years.

In the wheat and soybean cropping, glyphosate (2.05 kg ai/ha) was applied pre-planting in both years. In the wheat cropping, thiobencarb+pendimethalin+linuron (3.50+0.35+0.53 kg ai/ha) and diflufenican+trifluralin (0.09+0.93 kg ai/ha) was applied pre-emergence in 2005-2006 and in 2006-2007, respectively. In the soybean cropping, dimethenamid+linuron (0.70+0.60 kg ai/ha) was applied pre-emergence only in 2007. No insecticide was applied to any of the experimental fields in this study.

2.2. Seed predation and seed predators

Temporal variability in post-dispersal seed predation of Italian ryegrass was monitored after ryegrass shed its seed during four months from late June to late October in the interior areas of no-till fields and boundary strips. Furthermore, seed predation was monitored during May (before seed dispersal) in both the field interior areas and boundary strips in 2007. The proportion of seed predation was measured using “seed cards” (Westerman et al., 2003a, 2003b) that were prepared using sand cloth (6×7 cm, grain size 60, BELL STAR ABRASIVE MFG, Nara, Japan) sprayed with repositionable glue (Spray Adhesive 55, Sumitomo 3M, Tokyo, Japan), to which 50 ryegrass seeds were applied. The remaining glue was covered with fine sand. The density of seeds on the cards corresponded to approximately the maximum density of the seedbank observed in these experimental fields.

To evaluate the type of animals removing the seeds, three exclosure treatments were employed: (1) no exclosures, (2) vertebrates exclosures, and (3) vertebrates and invertebrates (except for ants) exclosures. For the no exclosure treatment, the seed card was placed in the study area without a mesh cage, allowing all seed predators (invertebrates and vertebrates) to remove the seeds. For the vertebrates exclosure treatment, the seed card was placed inside a cubic cage (side length: 15 cm) of metal wire mesh (mesh size: 1.27 cm^2), allowing invertebrates such as crickets, ground beetles and ants to remove the seeds. For the vertebrates and invertebrates (except for ants) exclosure treatment, the seed card was placed inside a cubic cage (side length: 15 cm) of metal wire mesh (mesh size: 0.25 cm^2), allowing only small invertebrates such as ants to remove the seeds. This latter treatment was used only in 2007. Furthermore, a control treatment was employed to assess seed loss due to rain, wind, or loss of adhesive power. For the control treatment, the seed card was placed at the bottom of a cubic cage (side length: 15 cm) of metal wire mesh (mesh size: 0.25 cm^2), and the cage was supported about 10cm above the ground with four metallic poles. The upper part of each pole was lined with double-sided adhesive to keep seed predators out of the cage. All treatments had 5 replicates, except for the control treatment (3 replicates), in the field interior areas and boundary strips.

The seed cards for all treatments were placed randomly in the field interior areas and boundary strips. Each seed card was separated by at least 1 m from other cards. In the field interior areas, all seed cards were placed at least 5 m from the field edge, and in the boundary strips, seed cards were placed at least 1 m from the edge. All seed cards were simultaneously replaced about every 2 weeks during the monitoring periods. From late June to early August, the seed cards could not be placed due to cultural operations including wheat harvest, burning, herbicide application and soybean sowing. The sampling periods for the seed cards are presented in Table 1.

Crickets and ground beetles, which were assumed to be the major insect seed predators in these experimental fields, were captured by hand in the field interior areas and boundary strips during summer. These insects could not be sampled quantitatively by pitfall traps because these fields were often waterlogged by heavy rains, and such traps would float away. A feeding study of the captured insects was conducted to determine whether these insects would feed on the seeds of Italian ryegrass. The individual insects were placed in Petri dishes (diameter 9 cm or 12 cm) containing Italian ryegrass seeds in an incubator (M-210FN, TAITEC, Saitama, Japan) at 25 °C and a 12-h photoperiod. Insects that fed on the seeds were identified to the species level.

2.3. Data analysis

The number of seeds remaining on the seed cards for all three exclosure treatments were converted into the proportion of seed predation relative to the number of seeds remaining on the control cards using Abbott's correction formula: $Mi = (Ci - Ri)/Ci$, where Mi is the proportion of seed predation during each sampling period, i, Ri is the number of seeds remaining on the cards for each treatment, and Ci is the number of seeds remaining on the control cards (Abbott, 1925).

The effects of exclosure treatments on Mi were tested with analysis of variance (ANOVA) using R (R Development Core Team, 2008) for each sampling period. In order to satisfy assumptions of normality and equality of variance in ANOVA models, proportion data were arcsine-transformed before the tests. If these tests indicated that Mi were significantly different among the treatments, Tukey's multiple comparison tests were carried out to determine which of the treatments were significantly different from the others.

2.4. Total seed loss due to predation

We assumed that Italian ryegrass seeds are consumed when they are lying on the soil surface, particularly in the wheat-soybean double-cropped fields, after Italian ryegrass seed shedding (late June) to the start of emergence (late October) (Ichihara et al., 2010). Therefore, we regarded the proportion of seed predation throughout this period as the total proportion of seed loss due to predation during summer, M, and calculated it as:

$$M = 1 - \prod_{i=1}^{n}(1 - Mi)$$

Here, $\prod_{i=1}^{n}(1 - Mi)$ is the total proportion of seeds that survive predation. *M* was estimated using *Mi* during the period between late June to late October. However, because *Mi* during the period of late June to early August in 2007 was not investigated, we substituted *Mi* in the field interior areas during this period in 2006 (*Mi*=0) for those data to estimate *M* in 2007. *M* in the boundary strips in 2006 was not estimated because the start of the investigation was delayed.

3. Results

The total seed loss due to predation for Italian ryegrass during summer (*M*) in the field interior areas tended to be higher in the no exclosure treatment than in the vertebrates exclosure (Table 2). *M* in the field interior areas in 2006 was 0.43 (no exclosure) and 0.34 (vertebrates exclosure), and values in 2007 were 0.35 and 0.13, respectively. In contrast, *M* in the vertebrates and invertebrates exclosure (except for ants) was very low (0.07) in 2007.

In the field interior areas, the proportion of seed predation (*Mi*) in the no exclosure treatment tended to be more variable in time than that in the vertebrates exclosure, although *Mi* was not significantly different between the treatments (Fig. 1). In 2006, *Mi* in the no exclosure treatment increased in mid August (0.16) and mid September (0.20), and was less than 0.06 in the other periods. In 2007, *Mi* in the no exclosure treatment increased in early June (0.14), mid September (0.14) and early October (0.11) and was less than 0.07 in the other periods. In contrast, *Mi* in the vertebrates exclosure treatment was the highest in mid September, 2006 (0.27) and less than 0.06 in the other periods throughout both years.

The total seed loss due to predation during summer (*M*) in the boundary strips tended to be higher in the no exclosure treatment than in the vertebrates exclosure, as was the case in the field interior areas (Table 2). *M* in the boundary strips in 2007 was 0.42 (no exclosure) and 0.33 (vertebrates exclosure). In contrast, *M* in the vertebrates and invertebrates exclosure (except for ants) was very low (0.05) in 2007.

In the boundary strips, a seasonal pattern of *Mi* in the no exclosure and vertebrates exclosure treatment was almost similar (Fig. 2). *Mi* in both treatments increased in mid September for both 2006 (0.15-0.16) and 2007 (0.17-0.23). In 2006, *Mi* in the vertebrates exclosure treatment increased again in late October (0.25).

The proportion of seed loss in the control treatment was less than 0.09 for both the field interior areas and boundary strips, except for the field interior areas in mid August, 2006 (0.15) that was likely due to heavy rainfall from 8 to 9 August (Fig. 3).

In these experimental fields, crickets (*Teleogryllus emma* (Ohmachi et Matsuura) (body length: 32.9 mm), *Modicogryllus siamensis* Chopard (14.8 mm)) and ground beetles (*Anisodactylus punctatipennis* Morawitz (11.2 mm), *Anisodactylus signatus* (Panzer) (12.5 mm), *Harpalus chalcentus* Bates (13.8 mm), *Harpalus niigatanus* Schauberger (11.6 mm), *Harpalus sinicus* Hope (12.9 mm)) were often observed, and all captured insects of these species fed on Italian ryegrass seeds.

4. Discussion

This study revealed the extent of post-dispersal seed predation of Italian ryegrass in both the interior areas and boundary strips of converted paddy fields, in which weeds were dominant during summer. The total seed loss due to predation for Italian ryegrass during summer (*M*) in the field interior areas was estimated to be 35-43% (Table 2). To our knowledge, this is the first study to quantify the total seed loss due to predation in agricultural lands in monsoon Asia. Westerman et al. (2003a) measured the total seed loss due to predation for the most abundant weed species in organic wheat fields in the Netherlands to be 32-70% during three months in summer, a result consistent with the results of our study. These results suggest that predators make a substantial contribution in depleting the supply of post-dispersal seeds of Italian ryegrass in converted paddy fields.

However, the maximum proportion of seed predation per two weeks was 14-27% in these fields (Fig. 1), a value that is very low in comparison with the results (60-90%/2 weeks) of Westerman et al. (2003a). One of the reasons why the total seed loss due to predation in this study was similar to the results of Westerman et al. (2003a) in spite of the lower proportion of seed predation per two weeks is that the pattern of seed shed of Italian ryegrass and the weeds (*Chenopodium album* L. and *Stellaria media* (L.) Vill. etc.) investigated in Westerman et al. (2003a) is different. Italian ryegrass seeds are all shed in early summer, and all the seeds are exposed to predation during summer. In contrast, the duration of seed shed of *Chenopodium album* and *Stellaria media* overlaps with the period for seed predation, in which case the seeds shed after the peak of seed predation are barely consumed. Therefore, the total seed loss due to predation for Italian ryegrass is likely to be estimated higher than for *Chenopodium album* and *Stellaria media*.

The lower proportion of seed predation per two weeks in this study is attributable to the following two reasons. Firstly, these experimental fields are burnt after the wheat harvest (late June) every year, and the soil surface is exposed to extremely high temperatures. It is possible that the seed predators (in particular, insects with low mobility such as ground beetles) were killed by the heat or fire. Secondly, summer precipitation in this area is high (>200 mm/month), and the poorly drained converted paddy fields are often waterlogged by heavy rains. The number of insect seed predators decreased due to irrigation in cereal fields in the semi-arid region of Spain, and the proportion of seed predation also decreased (Baraibar et al., 2009). Therefore, the converted paddy fields where excess rainfall can accumulate are an unsuitable habitat for most seed predators, even if weeds are dominant during summer.

The total seed loss due to predation (*M*) for Italian ryegrass in the boundary strips was estimated to be 42%, a value similar to that in the field interior areas (Table 2). Although we predicted that the degree of seed predation would be higher in the boundary strips than in the field interior areas because the boundary strips could be an important habitat and refuge for seed predators to escape waterlogging and burning, this prediction was not supported by our results. This finding was probably due to the following three reasons. Firstly, the width of the boundary strips in these experimental fields was narrow (1-3 m) as a result of farmland consolidation, and the proportion of boundary strips in the fields was very low. Recently, the non-crop habitats such as boundary strips in the agricultural landscape are declining in area due to farmland consolidation in Japan. Secondly, weeds were dominant in both the field interior areas and the boundary strips. Thirdly, the boundary strips were severely disturbed by mowing to 1 cm height three times during the summer. Therefore, the boundary strips in these experimental fields might not be a particularly attractive habitat for seed predators in comparison with the field interior areas.

We estimated the total seed loss due to predation (*M*), assuming that seeds were not buried during the monitoring periods. In fact, seeds on the soil surface may be gradually buried by natural causes such as rain and escape from predation. Westerman et al. (2009) investigated seed burial rates using different sized (1-3 mm) beads as surrogate seeds, and indicated that smaller seeds were incorporated into the soil more easily than larger seeds. Although the relatively large (6-7 mm) Italian ryegrass seeds are not easily buried, it is possible that the total seed loss due to predation is overestimated in this study. It is also possible that the total seed loss was underestimated because seed predation during the period immediately after the shedding of Italian ryegrass seed (from June to July) was exceedingly difficult to monitor due to cultural operations, and we assumed no losses (M_i=0) in that period. In future studies, it will be necessary to consider seed burial due to natural causes, and to clearly evaluate seed predation during the period just after the seeds are shed.

Our results suggest that seed predators in the field interior areas and boundary strips were slightly different. In the field interior areas, the proportion of seed predation (M_i) was numerically higher in the no exclosure treatment than in the vertebrates exclosure treatment particularly in 2007, although the difference was not statistically significant (Fig. 1). Therefore, the seed predators in the field interior areas are probably both vertebrates (rodents or birds) and invertebrates (crickets and ground beetles). In contrast, the main seed predators in the boundary strips are likely to be invertebrates (crickets and ground beetles) because seasonal patterns of the proportion of seed predation in the no exclosure and vertebrates exclosure treatments was almost similar (Fig. 2). The field interior areas were dominated by high densities of *Physalis angulata* var. *angulata* (plant height

>50cm) during summer, and the vegetation in the interior areas of the fields was more dense than in the boundary strips. It is well known that rodents remove fewer seeds from open areas (Hulme 1994; Hulme 1998). Holmes and Froud-Williams (2005) reported that seed removal by birds was greater in the interior regions of wheat fields than in the boundaries. Although the proportion of seed predation in the vertebrates and invertebrates (except for ants) exclosure treatments was very low in both the field interior areas and boundary strips (Fig. 1, 2), we observed ants removing the seeds of Italian ryegrass from the soil surface. Because it was likely difficult for small invertebrates to remove seeds glued to seed cards (Shuler et al., 2008), it is possible that the proportion of seed predation by ants is underestimated in this study.

To quantify post-dispersal seed predation, it is necessary to consider the presence of seeds of non-target species in the fields because ground beetles (Jorgensen and Toft 1997; Honek et al., 2003, 2007) and crickets (Carmona et al., 1999) preferentially consume seeds on the basis of seed traits. Particularly for ground beetles, preferred seed size increases with the body mass (Honek et al. 2007). The average body mass of ground beetles that were observed in these experimental fields was 23 mg (dry body mass calculated from average body length (Jarosik, 1989)) and ground beetles of this size were estimated to prefer 0.6 mg seeds from the results of Honek et al. (2007). Compared to the preferred seed size, the seeds of Italian ryegrass are large (3.0 mg). However, in these experimental fields, the seedbank was dominated by high densities of Italian ryegrass during summer (seedbank density of this species on the soil surface in August and November was 4400 and 2130 /m^2, respectively, Ichihara, unpublished data), and the presence of seeds of non-target species might have little influence on the seed predation of Italian ryegrass. If there are many seeds of non-target species that are more preferred by seed predators than Italian ryegrass, predation of Italian ryegrass seed may decrease more than the results of this study have indicated.

Although the results of this study suggest that the seed predation is an important depletion factor for post-dispersal seeds of Italian ryegrass, predation may not be sufficient to strongly suppress the population growth of this weed. In July after the ryegrass seed was shed, the seedbank density of this weed was extremely high (4000-5000 m^{-2}) in these experimental fields (Ichihara et al., 2010). Even if 40% of these seeds were consumed, the seedbank density would still be very high (2400-3000 m^{-2}). The degree of Italian ryegrass occurrence in the following year was similar to the previous year (Ichihara, unpublished data). Therefore, to suppress the growth of Italian ryegrass populations effectively, greater seed predation may be needed.

Agricultural biodiversity can play an important role in enhancing seed predation in the interior regions of fields (Kromp 1999; Menalled et al., 2000; Saska et al., 2007; Tscharntke et al., 2007). The experimental fields in this study were, however, located in a simple landscape after farmland consolidation, and the proportion of non-crop habitats such as boundary strips in this area was very low. Furthermore, the converted paddy fields may be unsuitable habitats for seed predators due to waterlogging and burning. To conserve the seed predators, the creation or augmentation of refuge habitats including field margins and set-aside areas is necessary. Seed predation in the field interior areas may be largely influenced by the proportion, shape and spatial distribution of non-crop habitats in the agricultural landscape (Menalled et al., 2000; Booman et al., 2009). We plan to investigate the influence of landscape structure on seed predation and weed population dynamics in future studies.

5. Conclusions

The results of this study suggest that seed predators make a substantial contribution in the depletion of post-dispersal seeds of a non-native weed, Italian ryegrass in converted paddy fields, although these fields seem to be unsuitable habitats for the predators due to waterlogging and burning. The seed predators in the field interior areas are both vertebrates (rodents or birds) and invertebrates (crickets and ground beetles), whereas seed predators in the boundary strips are mainly invertebrates (crickets and ground beetles). Although the boundary strips are predicted to be important refuges for seed predators and exhibit higher seed predation, the degree of seed predation in the boundary strips in our study site is similar to that in the field interior areas. This is probably because the boundary strips may not be a particularly attractive habitat for the predators due to the low proportion of boundary strips in the fields as a result of farmland consolidation and severe disturbance in the boundary strips. To conserve the seed predators and enhance the ecosystem service of weed seed predation in the field interior areas, it is necessary to create or augment suitable refuge habitats including field margins and set-aside areas.

Acknowledgements

This research was supported in part by a Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (no. 20580012). We gratefully acknowledge Dr. M. Ishitani for his invaluable assistance in identifying ground beetles. We thank the farmer H. Ochiai for allowing us to use his fields. We also thank T. Suzuki, K. Kato, S. Wada, Y. Adachi and Dr. H. Tobina for their invaluable advice and assistance.

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Figure and Table legends

Fig. 1. Proportion of seed predation per 2 weeks in no exclosure, vertebrates exclosure, and vertebrates and invertebrates (except for ants) exclosure treatments in the field interior areas in (a) 2006 and (b) 2007. Error bars represent the standard errors of the means. Asterisks indicate significant differences during that period (*$P < 0{\cdot}05$ **$P < 0{\cdot}01$). The means significantly different at $P < 0{\cdot}05$ based on Tukey's multiple comparison test are identified by different letters. Cultural operations (wheat harvest, burning, herbicide application and soybean sowing) were conducted during the periods from June to July (gray areas). Details for the sampling periods of the seed cards are presented in Table 1.

Fig. 2. Proportion of seed predation per 2 weeks in no exclosure, vertebrates exclosure, and vertebrates and invertebrates (except for ants) exclosure treatments in the boundary strips in (a) 2006 and (b) 2007. Error bars represent the standard errors of the means. Asterisks indicate significant differences during that period (*$P < 0{\cdot}05$ **$P < 0{\cdot}01$). The means significantly different at $P < 0{\cdot}05$ based on Tukey's multiple comparison test are identified by different letters. Cultural operations (wheat harvest, burning, herbicide application and soybean sowing) were conducted during the periods from June to July (gray areas). Details for the sampling periods of the seed cards are presented in Table 1.

Fig. 3. Proportion of background seed loss per 2 weeks in the field interior areas and boundary strips in (a) 2006 and (b) 2007. Error bars represent the standard errors of the means. Cultural operations (wheat harvest, burning, herbicide application and soybean sowing) were conducted during the periods from June to July (gray areas). Details for the sampling periods of the seed cards are presented in Table 1.

Table 1. Sampling periods of seed cards in no exclosure (circle), vertebrates exclosure (black circle), and vertebrates and invertebrates (except for ants) exclosure (double circle) treatments in the field interior areas and boundary strips. The seed cards were not placed during part of the period (dash) due to cultural operations.

Table 2. Estimates of total seed loss due to predation for Italian ryegrass in the field interior areas and boundary strips in 2006 and 2007.

Table 1. Sampling periods of seed cards in no exclosure (circle), vertebrates exclosure (black circle), and vertebrates and invertebrates (except for ants) exclosure (double circle) treatments in the field interior areas and boundary strips. The seed cards were not placed during part of the period (dash) due to cultural operations.

	periods		field interior areas	boundary strips
2006	28 Jun-4 Jul	(7 days)	○●	-
	5 Jul-23 Jul		-	-
	24 Jul-7 Aug	(15 days)	○●	-
	7-23 Aug	(17 days)	○●	-
	23 Aug-6 Sep	(15 days)	○●	○●
	6-20 Sep	(15 days)	○●	○●
	20 Sep-4 Oct	(15 days)	○●	○●
	4-18 Oct	(15 days)	○●	○●
	18-30 Oct	(13 days)	○●	○●
2007	2-16 May	(15 days)	○●	○●
	16-28 May	(13 days)	○●◎	○●◎
	28 May-13 Jun	(17 days)	○●◎	○●◎
	14 Jun-5 Aug		-	-
	6-20 Aug	(15 days)	○●◎	○●◎
	20 Aug-3 Sep	(15 days)	○●◎	○●◎
	3 Sep-19 Sep	(17 days)	○●◎	○●◎
	19 Sep-3 Oct	(15 days)	○●◎	○●◎
	3-17 Oct	(15 days)	○●◎	○●◎
	17-31 Oct	(15 days)	○●◎	○●◎

Table 2. Estimates of total seed loss due to predation for Italian ryegrass in the field interior areas and boundary strips in 2006 and 2007.

	2006		2007	
treatment	field interior areas	boundary strips	field interior areas	boundary strips
no exclosure	0.43	–	0.35	0.42
vertebrates exclosure	0.34	–	0.13	0.33
vertebrates and invertebrates (except for ants) exclosure	–	–	0.07	0.05

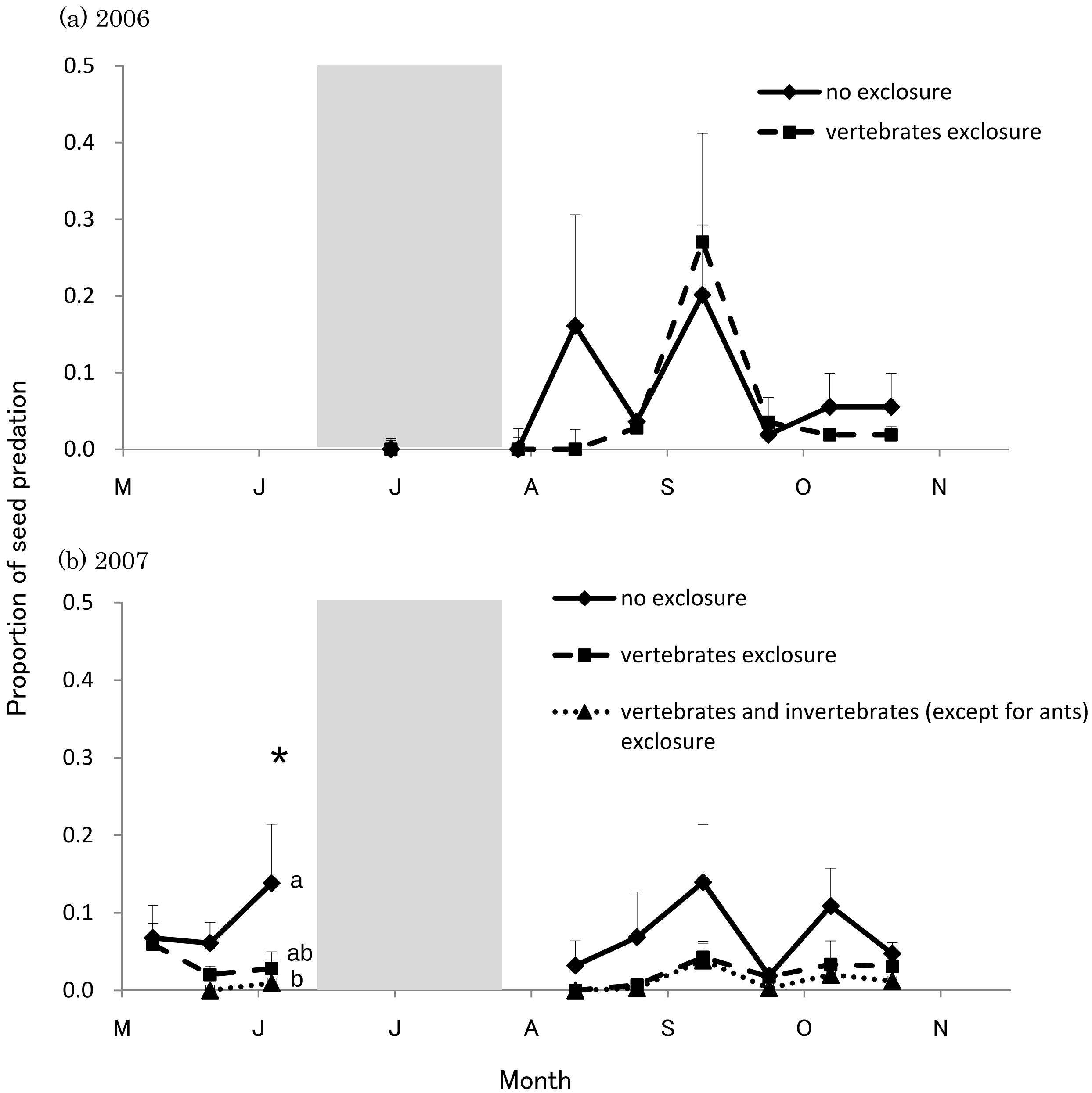
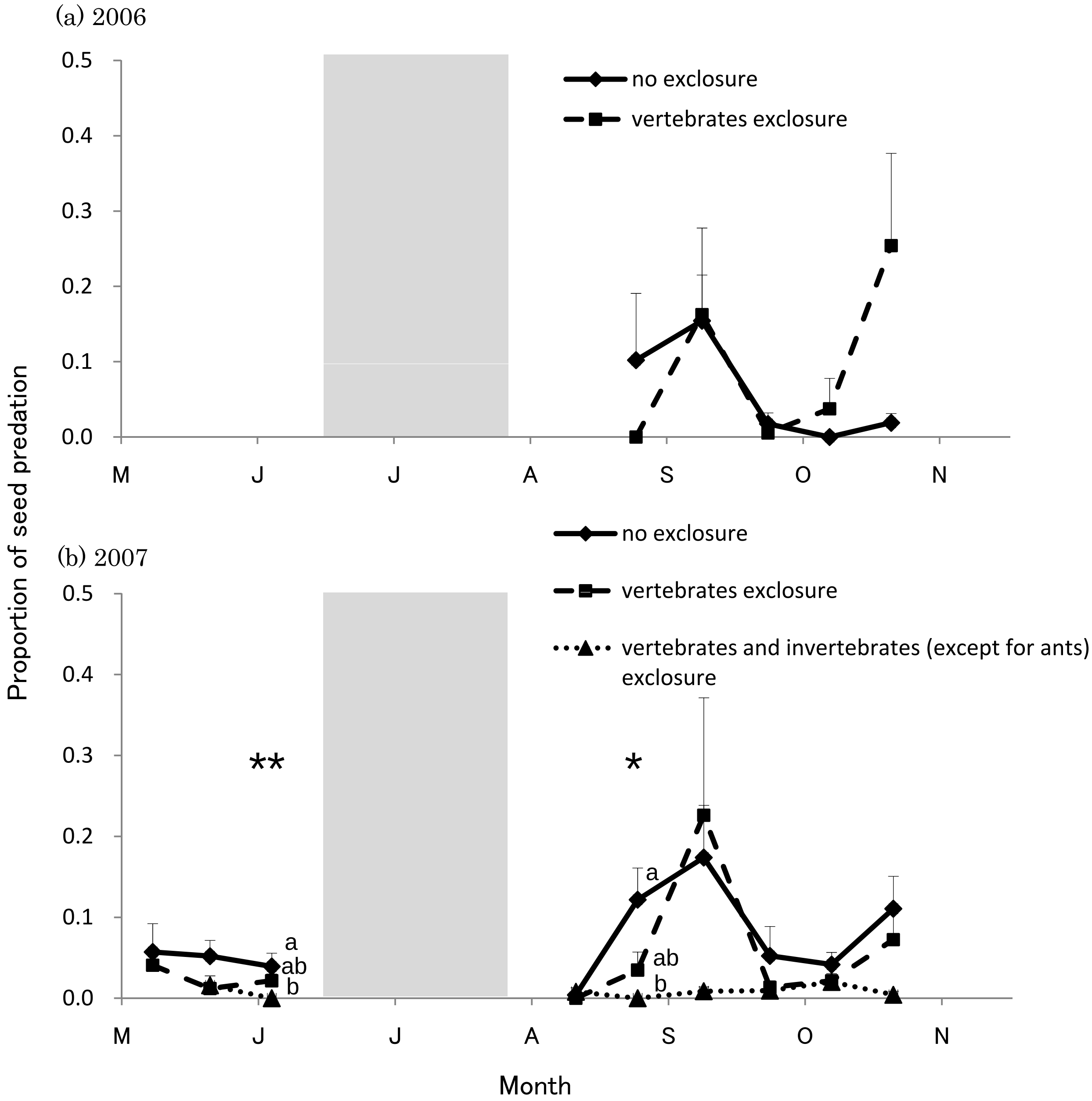

(a) 2006
0.5
0.4
0.3
0.2
0.1
0.0
no exclosure
vertebrates exclosure
M
J
J
A
S
O
N
(b) 2007
0.5
0.4
0.3
0.2
0.1
0.0
no exclosure
vertebrates exclosure
vertebrates and invertebrates (except for ants) exclosure
*
a
ab
b
M
J
J
A
S
O
N
Proportion of seed predation
Month

Fig. 1.



(a) 2006
no exclosure
vertebrates exclosure
0.5
0.4
0.3
0.2
0.1
0.0
M
J
J
A
S
O
N
Proportion of seed predation
(b) 2007
no exclosure
vertebrates exclosure
vertebrates and invertebrates (except for ants) exclosure
**
*
a
ab
b
a
ab
b
0.5
0.4
0.3
0.2
0.1
0.0
M
J
J
A
S
O
N
Month

Fig. 2.

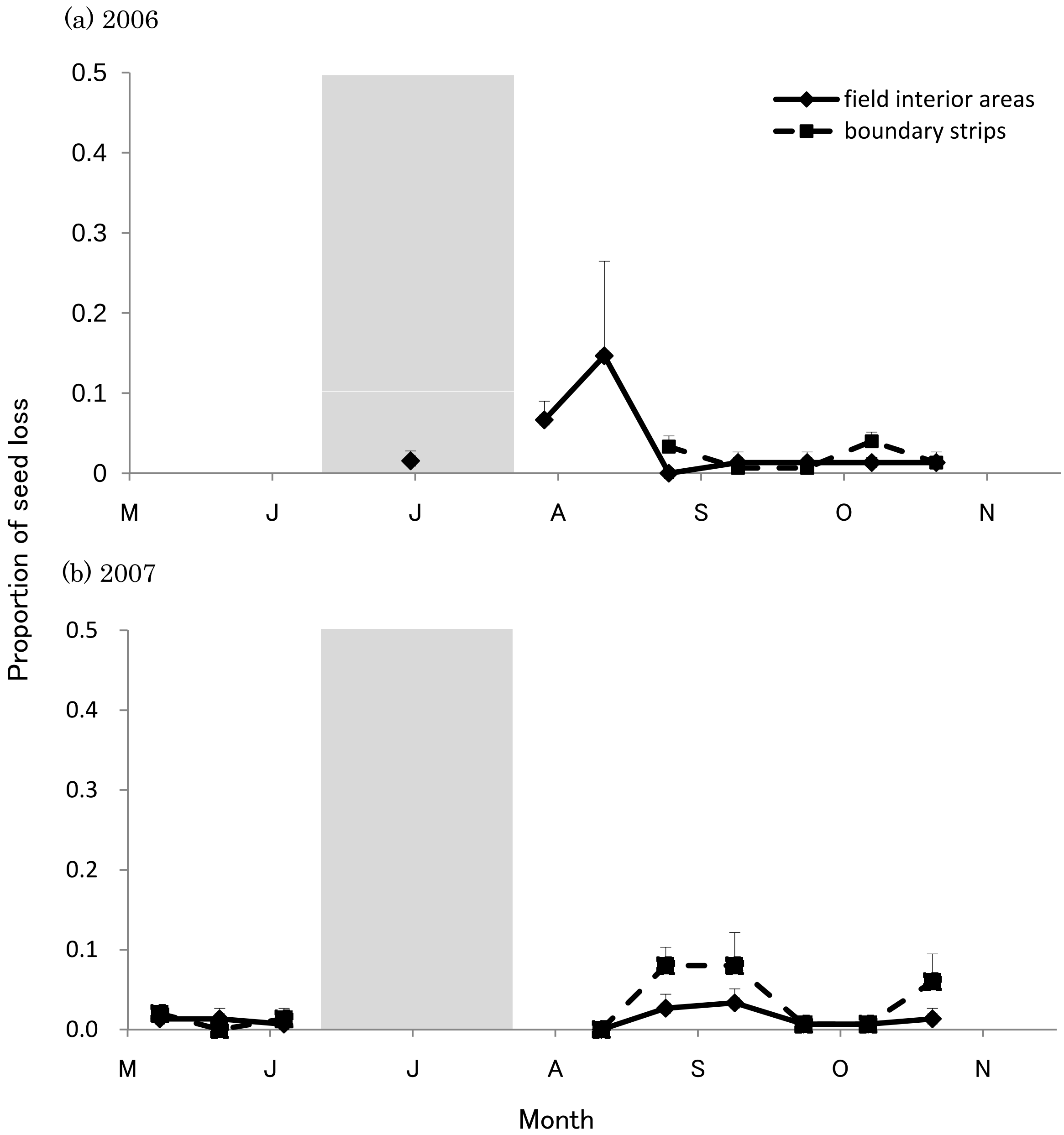

(a) 2006
0.5
0.4
0.3
0.2
0.1
0
M
J
J
A
S
O
N
field interior areas
boundary strips
Proportion of seed loss
(b) 2007
0.5
0.4
0.3
0.2
0.1
0.0
M
J
J
A
S
O
N
Month

Fig. 3.