agronomy

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Populations of *Ipomoea hederacea* var. *integriuscula* in Field Margins Are Maintained by Seed Production of Individuals from a Specific Cohort

Nozomi Ihara [1,2] and Hiroyuki Kobayashi [2,*]

[1] Institute for Plant Protection, National Agriculture and Food Research Organization, Tsukuba 305-8604, Japan
[2] Center for Weed and Wildlife Management, Utsunomiya University, Utsunomiya 321-8505, Japan
* Correspondence: kobah@cc.utsunomiya-u.ac.jp

Abstract: Entireleaf morning glory (*Ipomoea hederacea* Jacq. var. *integriuscula* A. Gray) is a difficult-to-control weed that causes severe yield loss in soybean (*Glycine max* L.). It invades fields from the field margins and contributes to maintenance of the populations in the fields. This study aimed to determine the optimal period to control the populations in field margins effectively. We identified the naturally emerging plants in field margins and adjacent fields. We recorded the number of invading vines and the timing of flowering and fruiting of several cohorts (each cohort comprised a group of individuals that emerged within a certain time frame). The main seed-producing cohort on the field margins was a cohort that emerged from early August to mid-September and flowered and fruited after mid-September. The weed formed seed banks in the field margins, maintained by repeated depletion and accumulation during the emergence and seed production stages. The weed control rate by weed management practices was higher in field margins (100%) than in the fields (76%). In conclusion, the entireleaf morning glory populations were maintained by specific cohorts in field margins and weed management practices from early August to mid-September can effectively reduce its population size in the field margins.

Keywords: population; cohort; weed management date; weed control rate; seed bank

Citation: Ihara, N.; Kobayashi, H. Populations of *Ipomoea hederacea* var. *integriuscula* in Field Margins Are Maintained by Seed Production of Individuals from a Specific Cohort. *Agronomy* **2022**, *12*, 2392. https://doi.org/10.3390/agronomy12102392

Academic Editor: Stephen J. Novak

Received: 12 July 2022
Accepted: 28 September 2022
Published: 3 October 2022

1. Introduction

Morning glories (*Ipomoea* spp.), are annual summer vine alien weeds that invade several crops, including soybean (*Glycine max* (L.) Merrill), sugarcane (*Saccharum officinarum* L.), cotton (*Gossypium hirsutum* L.), and other crops [1–3]. In Japan, the infestation of morning glories in soybean fields has been a major weed problem since the 1990s [4–6]. Vines of alien morning glories entwine soybean plants, which causes reduced harvesting efficiency and a substantial yield loss. Among the several species of *Ipomoea*, entireleaf morning glory (*I. hederacea* Jacq. var. *integriuscula* A.Gray) is considered the most difficult-to-control alien morning glory in Japan. Controlling these weeds by intertillage and earthing up, the conventional practices followed in soybean cultivation in Japan, is difficult [7]. Moreover, soil-applied herbicides are less effective on them [8,9]. Although foliar-applied herbicides, such as bentazon, fluthiacet-methyl, used in soybean demonstrated some efficacy against other *Ipomoea* species (e.g., red morning glory (*Ipomoea coccinea* L.)), they are less efficient for control of entireleaf morning glory [10–13]. A recent study has shown the efficacy of imazamox ammonium salt, a newly registered herbicide, in controlling entireleaf morning glory; however, the herbicide has been reported to damage soybean [14].

Entireleaf morning glory also invades the boundaries between fields, referred to as field margin ridges. The ridges are made by heaping up the soil in a trapezoidal shape, approximately 50 cm in height and 0.5–1 m in width. The field margins are used not only as boundaries but also to maintain flood water levels in paddy rice (*Oryza sativa* L.) cultivation and are maintained by remaking the soil before cultivation. Various weeds grow on field margins that may infest adjacent fields and facilitate the spread of pests and diseases [15]. For example, Canada thistle (*Cirsium arvense* (L.) Scop.) invades the adjacent field from the field margins by wind-dispersed seeds [16]. Similarly, Marsh dayflower (*Murdannia keisak* (Hassk.) Hand-Mazz.) that emerged on field margins invades the adjacent crop field by stems [17]. It has been reported that controlling the weed on field margins suppressed invasion rate in adjacent fields [17]. Therefore, it is necessary to control the weed populations of both fields and field margins to prevent them from invading each other. Several field margin management practices, such as mowing and herbicide applications, are used in Japan and other regions, including Europe and North America, to control these weeds [18–20]. In Japan, field margin management practices are conducted according to increase in height of the weeds [18] or cultivation calendar of the paddy rice (before transplanting and flowering), while in other regions, field margin management practices are often performed every season or fallow period [21]. However, in none of the regions, the emergence, flowering, and fruiting times of field margin weeds, which are the target of the control, are considered in determining the management time.

Weed control methods based on population dynamics in the field have long been proposed. Conley et al. [22] showed that individuals of giant foxtail (*Setaria faberi* R.A.W. Herrm.) that emerged at VE (emergence) and VC (cotyledon) soybean growth stages had high fecundity in soybean fields. In the study, the authors proposed the possibility of estimating seed production and biomass from the initial weed volume, leading to the development of economic weed management practices that consider the fecundity of giant foxtail in soybean fields. On the other hand, the ecology of field margin weeds, which is necessary for effective management practices, has not been investigated in many cases because field margins are not used for direct crop production. The same is true for entireleaf morning glory. In entireleaf morning glory, the populations in fields and their margins could invade each other and produce seeds, expand their distribution by their vines, and maintain each other's populations. However, phenology and population dynamics of the species in field margins have not been clarified. Our preliminary study found that these weeds emerged and flowered in a farmer's field margins (the same as this research site) from spring to autumn. The plants emerged in the bare field margins immediately after weed management practices. Thus, it is highly likely that the contribution of entireleaf morning glory in field margins to maintenance of the populations differs based on the cohort (individuals that emerged within a certain time frame), as one cohort of giant foxtail (emerged in the early growth stage of soybean) had high fecundity in soybean fields [22]. Determining the time of emergence, flowering, and fruiting for each cohort, evaluating the degree of contribution to population maintenance, and estimating the effective management time would better manage populations of entireleaf morning glory.

Therefore, in this study, we aimed to determine the period in which the populations in field margins can be efficiently controlled. We investigated occurrence and timing of flowering and fruiting in each cohort of entireleaf morning glory on field margins managed by a farmer. Our research identified that a cohort, which emerged from early August to mid-September, contributes the most to maintaining the populations in field margins.

2. Materials and Methods

2.1. Study Site

This study was conducted in 2016 and 2017 in Tsukuba, Ibaraki, Japan, in four rectangular fields and their margins, where entireleaf morning glory was dominant. These fields were managed by a single farmer and were located within a radius of 250 m from one point (36°0847.6″ N, 140°0556.1″ E). The studied fields followed one crop rotation system: rice, winter barley (*Hordeum vulgare* L.), and soybeans for two years. We classified four fields into two groups according to the kind of crop cultivated in the summer of 2016. The first group comprised two fields (3000 m^2 each) where rice was cultivated in the summer of 2016. The fields in this group were designated as RBS-1 (Rice–Barley–Soybean-1) and RBS-2 rotation. The second group comprised two fields (4000 m^2 each) where soybeans were cultivated. The fields in this group were designated as BSR-1 (Barley–Soybean–Rice-1) and BSR-2. In each field, we selected one field margin (out of the four margins), where entireleaf morning glory emerged, as the study site.

2.2. Agricultural Practices

Across the four fields, conventional tillage (eight times over two years) was carried out (Table S1). The following cultivars were used in this study: rice, 'Koshihikari' and 'Himegonomi'; barley, 'Kashimamugi'; soybean, 'Natto-Shoryu'. Planting and harvesting dates of the crops grown are shown in Table S1. Pest management practices for all crops were conducted following the guidelines provided by the Ibaraki prefectural government [23]. Weed management in the fields was performed up to four times per cultivation period. In rice fields, foliar- and soil-applied herbicides (combination product of ipfencarbazone (0.25 g a.i. ha^{-1}), bromobutide (0.9 g a.i. ha^{-1}), and bensulfuron methyl (0.51 g a.i. ha^{-1})) were added (Table S2). In barley fields, a soil-applied herbicide (combination product of pendimethalin (0.75 g a.i. ha^{-1}) and linuron (0.50 g a.i. ha^{-1})) was added in BSR-1 and -2. No herbicide was applied in barley in RBS-1 and -2. In soybean fields, a soil-applied herbicides (combination product of alachlor (1.6 kg a.i. ha^{-1}) and linuron (0.642 g a.i. ha^{-1})) and a foliar-applied herbicide, bentazon (0.708 g a.i. ha^{-1}), were added.

The field margins were maintained by heaping up the soil before flooding for puddling in rice cultivation year (levee plastering). The maintained margins were used for two years (one rice–barley–soybean rotation). Weed management in field margins was performed two to four times per year using glyphosate potassium salt solution (4.0 kg a.i. ha^{-1}, Table S2) or a shoulder-mounted mower. Weeds were cut to a height of approximately 10 cm above the ground by the mower. The farmer continued using his customary weed management practices. Details of weed management practices are summarized in Table S1.

2.3. Study Design and Field Survey of the Aboveground Parts of Entireleaf Morning Glory

We investigated the emergence and growth of entireleaf morning glory in fixed quadrats for two years in the fields and their margins to record the flowering time and the number of seeds produced. The quadrat size in fields was determined per the width of the crop row: 0.6 × 1 m and 0.5 × 1 m quadrats were used in fields during rice and barley cultivating periods, respectively (hereinafter called "rice fields" and "barley fields," respectively). During soybean cultivating periods (hereinafter called "soybean fields"), 1.2 × 1 m and 1.2 × 0.5 m quadrats were used in the fields during 2016 and 2017, respectively, because the density of the seedlings was markedly different between the two years. During the fallow periods, 1 × 1 m quadrats were used in the fields. For the field margins, we placed three quadrats (0.5 × 0.5 m), except in the field margins of BSR-1 and -2, where four quadrats were placed in 2017. In 2016, we placed three line transects per field at right angles to crop rows, starting from one selected field margin toward the center of each field. Each transect contained three quadrats. In RBS-1 and -2, each transect was placed 1, 10, and 15 m away from selected field margins (the position of 15 m was the center of the short-side of the fields). In BSR-1 and -2, each transect was placed 1, 10, and 20 m away from selected field margins (the position of 20 m was the center of the short-side of the fields). In 2017, we changed the number of transects to two and four in the RBS and BSR fields, respectively, because in 2016, some quadrats in fields RBS-1 and -2 had a high density, while some quadrats in fields BSR-1 and -2 had a low density of entireleaf morning glory seedlings.

All naturally emerged entireleaf morning glory seedlings in each quadrat were labeled by stapling plastic tape carrying a serial number to trace growth of the individual plants. The staples did not affect their growth because they joined both ends of each plastic tape, which loosely surrounded stems of the seedling. The dates of emergence, development of flower buds, flowering, fruiting, and death of each plant were recorded. The monitoring was conducted from 22 April to 15 December 2016, and from 20 April to 13 December 2017. In rice fields, we started the monitoring after the mid-summer drainage period in early July because flooded conditions almost completely inhibited the emergence of this species. To understand the relationship between the agricultural practices and the emergence and growth of the weed, the monitoring was conducted every week from April to August and every two weeks from September to December, depending on the frequency of the farmer's agricultural practices. We labeled seedlings that newly emerged until each investigation date (once every one or two weeks) as seedlings that emerged on the same emergence date. Individuals that emerged on the same investigation date were considered one subpopulation, and the subpopulations that reached the flowering and fruiting stage on a similar investigation date were considered one cohort.

According to our preliminary field investigation, only individuals that emerged from a place close to the ridge (approximately 1 m from the edge of the field, almost the same location as the first row of each crop) extended vines from the field to the field margin. Therefore, the number of vines that invaded field margins was evaluated by counting the number of invading vines of labeled individuals that emerged from a quadrat placed 1 m away from the field margin. The number of vines that invaded fields from the field margins was also determined using labeled individuals.

Each individual was considered to have reached fruiting when diameter of the ovary exceeded approximately 5 mm. The number of nodes of 10 or more plants which were labeled fruiting plants per quadrat and each node was counted to estimate the number of seeds that would be produced. We observed that entireleaf morning glory produced fruits at every node, except at the cotyledonary node. A single fruit of entireleaf morning glory usually contains 4–6 seeds [24]. Thus, the number of seeds produced was estimated as follows: number of produced seeds (m^{-2}) = number of fruiting plants in each quadrat (m^{-2}) $\times$ average number of nodes (except cotyledonary nodes) $\times$ 5. The number of seeds produced was calculated for each quadrat where the fruiting plants emerged.

The effect of farmer's agricultural practices (including cultivation management such as seeding and tillage) on the life and death of labeled plants was calculated using the following formula: weed control rate (%) = number of individuals that died at the time of the survey the week after management/number of individuals before management $\times$ 100. The weed control rate could not be calculated when there were no surviving individuals of entireleaf morning glory just before management, such as the date of the soybean harvest.

The day length at the study site was calculated using the data of the timings of sunrise and sunset in Tsukuba [25].

2.4. Survey of the Soil Seed Bank

To verify the population dynamics of the aboveground parts of entireleaf morning glory, we investigated the changes in the number of seeds buried in soil layers up to a depth of 15 cm from the ground surface in the same field margins. We placed quadrats for soil sampling next to those used for monitoring the emerging plants. The quadrat size was 0.5 (width of the upper base) $\times$ 2 m. Sampling dates were as follows: April 2016, September 2016, December 2016 to January 2017, April 2017, October 2017, and December 2017 to January 2018.

Soil samples were collected using a handheld split-core sampler (HS-25S; Fujiwara Scientific Company, Tokyo, Japan). We collected soil samples with a diameter of 5 cm and a depth of 15 cm. Five soil samples were collected from each quadrat and mixed as one sample. The collected soil samples were passed through a 1 mm sieve. The residue containing weed seeds that remained on the sieve was washed using well water and air-dried. The buried seeds of entireleaf morning glory were extracted manually from the residue and identified visually based on their shape, size, and color, as described in a previous study [26]. The seeds with water-impermeable seed coats were considered viable. The number of viable buried seeds was calculated based on the area of the handheld sampler.

2.5. Investigation of Buried Seed Longevity in Field Margins

The seeds of entireleaf morning glory collected from the fields and field margins of RBS-1 and -2 during December 2015 were buried in the surface (within 2–3 cm depth) and the lower layer (10 cm depth) of the same field margins. The seeds were placed in a polyester bag at 100 seeds bag^{-1}, mixed with sieved soil of the fields, and then buried within one month of the collection. The buried bags were dug up from February to November 2016 to determine the number of viable seeds. The seed viability was tested by germinating the seeds at a variable temperature of 20/30 °C for 14 d under dark conditions. The ungerminated seeds were judged to be dead or alive by applying gentle pressure to the seeds, and those that resisted the applied pressure were recorded as viable seeds [27].

2.6. Data Analysis

The crop types in the two RBS fields were one year ahead of the two BSR fields. The two fields where the same crop was cultivated in the same year were considered replicates. Thus, there were two pairs with two replicates. We traced the growth of the emerged individuals and recorded the dates of flowering and fruiting of each, as described above. For each emergence date, we counted the numbers of individuals who reached flowering and those who died before flowering. For each cohort, we counted the number of individuals who reached flowering on a particular flowering date. Because flowering dates varied among individuals in the same cohort, we determined the date of the first confirmed flowering, the last flowering, and the median.

A paired *t*-test was used to compare the number of newly emerged seedlings before and after every weed management practice in the field margins. The values consisted of the number of newly emerged seedlings within almost one week before a management practice and approximately two to three weeks after the management in the same quadrat since the herbicidal effects appeared after seven days of the application. The Tukey–Kramer test was used to analyze the effects of the distance between field margins and the quadrats used for monitoring the emerging plants (1, 10, and 15 m in RBS-1 and -2; 1, 10, and 20 m in BSR-1 and -2) on the cumulative number of emergences. All statistical analyses were performed using R 3.4.4 [28].

3. Results and Discussion

3.1. The Movement of Entireleaf Morning Glory Vines between the Field Margins and Fields

An average range of 0.5–13 vines m^{-1} had invaded the rice fields from their adjacent field margins (Table 1). The number was higher than the number of vines that had invaded the soybean fields from the field margins. The invasion distance from field margins to the fields was equal to the distance of the first row of crops from the edge, as the vines became entangled with crops in the fields. In contrast, there was no invasion of vines from the rice fields to the field margins, although a slight invasion from the soybean fields to the field margins was observed.

The Poaceae perennial weed *Leersia japonica* (Honda) Makino ex Honda, which grows in paddy field margins like entireleaf morning glory, had >220 cm-long stems and invaded fields from the field margins by the stems [29]. Similarly, knotgrass (*Paspalum distichum* L. var. *distichum*) with >230 cm long stems could enter fields from the field margins [30]. Compared with these species, the degree of invasion of the fields by entireleaf morning glory was minor because the upward elongation of the vines by entanglement with crops was prioritized over their lateral elongation. These findings indicate that the extent of invasion by the entireleaf morning glory vines between the field margins and the fields was small, and two populations at these places were relatively independent. In this study, field margin management practices, especially herbicide (glyphosate potassium salt solution) applications, had a high weed control rate (75–100%; Figure 1). The management practices were carried out at least twice a year. It has been reported that weed invasion of fields from the field margins is suppressed under appropriate field margin management practices [17]. In this study, individuals that emerged in the field margins from early August to mid-September, when the interval between field margin management practices was one month or more, invaded the fields with 13 vines m^{-1}. The number was the largest of vines of all cohorts in a year. If no field margin management practices were carried out, more vines might have invaded fields from the field margins, and the total invasion between the field margins and the fields increased.

Table 1. Number of reciprocally invading vines of entireleaf morning glory between fields and their margins.

Direction of Invasion	Field Name	Crop	Year	Invading Vines (m^{-2}) [a]	
Margin →Field	RBS-1	Rice	2016	13	(11)
		Soybean	2017	1.5	(1.9)
	RBS-2	Rice	2016	4.7	(5.0)
		Soybean	2017	0.5	(1.0)
	BSR-1	Soybean	2016	0.7	(1.2)
		Rice	2017	0.5	(1.0)
	BSR-2	Soybean	2016	-	-
		Rice	2017	1.5	(3.0)
Field →Margin	RBS-1	Rice	2016	-	-
		Soybean	2017	1.1	(3.0)
	RBS-2	Rice	2016	-	-
		Soybean	2017	0.6	(1.5)
	BSR-1	Soybean	2016	0.3	(0.8)
		Rice	2017	-	-
	BSR-2	Soybean	2016	-	-
		Rice	2017	-	-

[a] The number of vines from the fields to their margins is based on the number of vines of individuals that emerged in the quadrats 1 m away from the field edge. RBS-1, rice–barley–soybean-1; RBS-2, rice–barley–soybean-2; BSR-1, barley–soybean–rice-1; BSR-2, barley–soybean–rice-2; –, no vines invaded the other side. Values are presented as mean (standard deviation, SD).

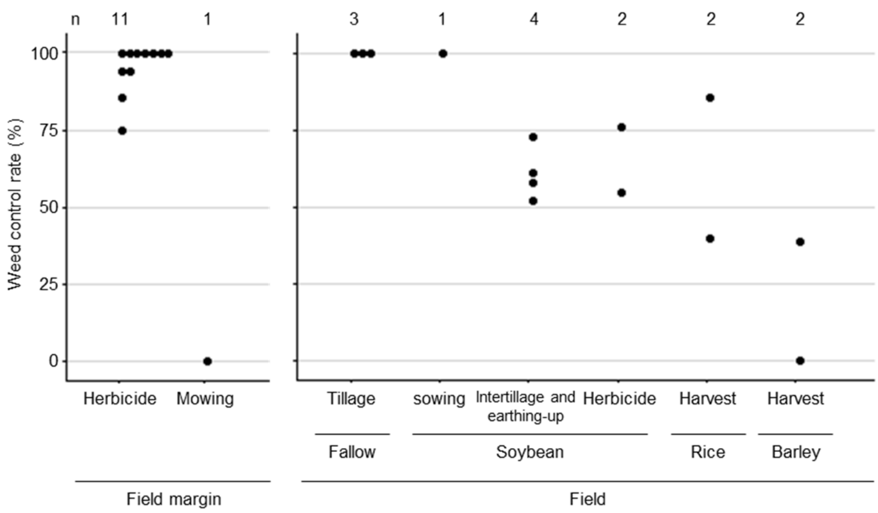

Figure 1. Weed control rate by agricultural practices in the fields and their margins. One bullet shows the weed control rate by one practice. Bullets are shown using a horizontal jitter display. Fields and survey years are not distinguished in this figure. Fallow refers to the post-harvest conditions for rice and barley. Weed control rates for practices such as puddling with a harrow, rice transplanting and herbicide treatment, soybean harvesting, and barley sowing and herbicide treatment are not shown because entireleaf morning glory did not exist just before the practice. Values at the top of the figure represent the number of practices in the two years.

3.2. Flowering and Fruiting Phenology of Entireleaf Morning Glory in Field Margins

In the field margins, entireleaf morning glory emerged from April to November (Figure 2a,c,e,g), regardless of the type of crop in the field. The annual cumulative number of seedlings varied widely depending on the field margin and year. In RBS-1 and -2, the maximum cumulative number of seedlings was 410 plants m^{-2} in 2016 and 440 plants m^{-2}

in 2017, and in BSR-1 and -2, it was 810 plants m^{-2} in 2016 and 25 plants m^{-2} in 2017. More newly emerged seedlings were observed after field margin management practices than before the practices (paired *t*-test; $p < 0.01$; data not shown) owing to environmental changes, such as light or temperature, under less weed coverage conditions on field margins.

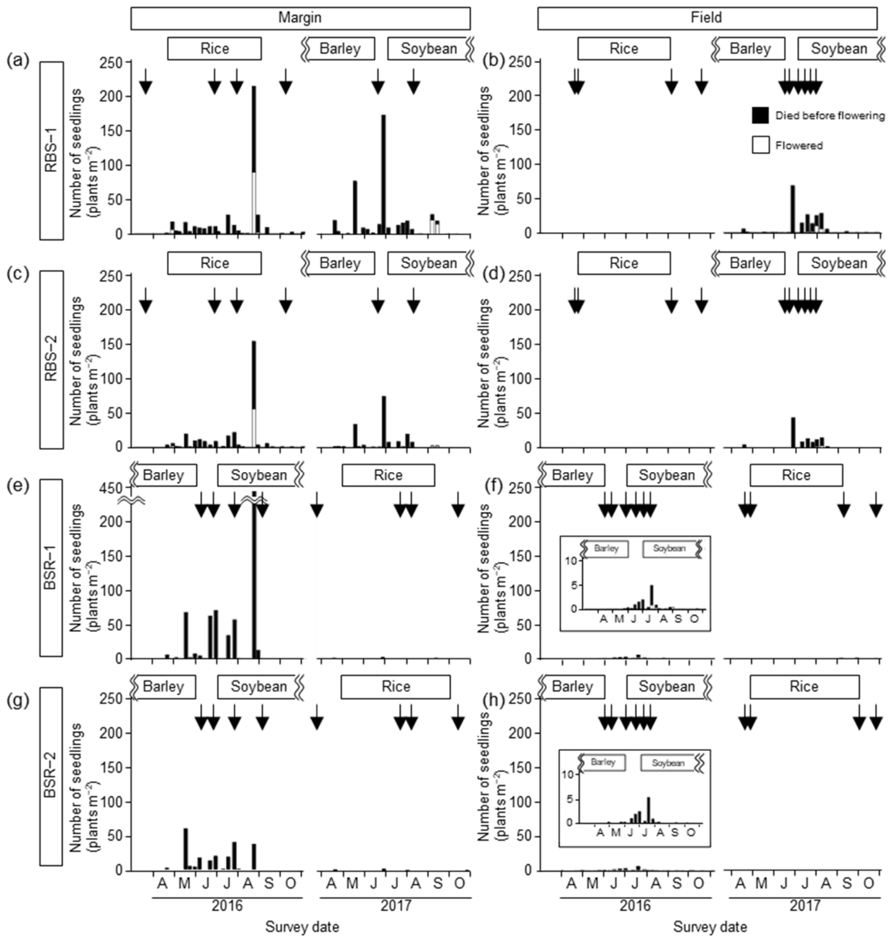

Figure 2. Number of seedlings of entireleaf morning glory at the time of each survey and the data of flowering success/failure of the seedlings. Field margin (**a**) and field (**b**) of RBS-1; field margin (**c**) and field (**d**) of RBS-2; field margin (**e**) and field (**f**) of BSR-1; field margin (**g**) and field (**h**) of BSR-2. The number of newly emerged seedlings at each survey is the sum of white and black areas (stacked bar chart). The white and black areas on the bars indicate the numbers of individuals with successful and failure of flowering (died before flowering); arrows indicate dates of weed management practices (including tillage); RBS-1, rice–barley–soybean-1; RBS-2, rice–barley–soybean-2; BSR-1, barley–soybean–rice-1; BSR-2, barley–soybean–rice-2. Values are presented as mean. The inset figures in panels (**f**,**h**) show an enlarged view of the results in 2016. The horizontal axis shows the survey months (April to October of each year).

Two cohorts reached flowering and fruiting at the field margins, regardless of the type of crop in the field: cohort-1 emerged in late April (Figure 2a,c,e,g), flowered in early July (Figure 3a,c,e,g), and fruited after mid-July (Table 2) and cohort-2 emerged from early August to mid-September (Figure 2a,c,e,g), flowered, and fruited after mid-September (Figure 3a,c,e,g; Table 2). The flowering rate of labeled individuals varied greatly depending on the date of emergence, even within the same cohorts. However, there were dates of emergence when individuals in field margins showed 100% successful flowering (emerged on April 22, 2016, in RBS-1, emerged on August 9 in RBS-2, emerged on October 5 in BSR-1, emerged on August 22, 2017, in RBS-1 and BSR-1, emerged on August 31 in BSR-2, emerged on September 7 in RBS-2, BSR-1 and -2, emerged on September 14 in RBS-2 and BSR-2;

Figure 2a,c,e,g). The estimated number of seeds produced by individuals in cohort-1 (up to 350 seeds m^{-2}, the date of emergence was 30 April 2016) was smaller than that in cohort-2 (up to 5000 seeds m^{-2}, the date of emergence was 25 August 2016; Table 2). All other cohorts had died before fruiting due to field margin management practices during early August and frost injury after autumn. Therefore, we determined that cohort-2 emerged from early August to mid-September and was the main seed-producing population. There are two possible reasons for a large amount of seed production in cohort-2. (1) The frequency of the field margin management practices by the farmer decreased after the beginning of August, and reproductive success was higher than in other cohorts. In 2017, many of the individuals that emerged after the end of August in RBS-1 and -2 reached flowering because no field margin management practice was carried out after August 9. (2) In this study, the day length during flower bud formation was approximately 13 h or less, regardless of the year, field margins, or cohorts (data not shown). Entireleaf morning glory is a qualitative short-day plant [31]. The day length during the emergence period of cohort-2 was especially long in August (12 h 59 min–13 h 58 min), suggesting that individuals in the cohort had a long vegetative growth period. Some alien morning glories have been reported as short-day plants; however, the photoperiod responses differ among species [31]. Red morning glory and pitted morning glory (*I. lacunosa* L.), sown in August in Ibaraki, Japan, flowered in mid-September and early to mid-September, respectively [32]. In addition, entireleaf morning glory, sown in early June in Tottori, Japan, flowered in late July and fruited in late August [4]. These findings suggest the photoperiod responses could be related to intraspecific variations.

3.3. Population Dynamics of Entireleaf Morning Glory in Field Margins

To verify the increase and decrease in the populations due to emergence and seed production, we investigated the seasonal changes in soil seed banks in the field margins. In RBS-1 and -2, where the number of buried seeds was sufficient to detect seasonal changes, more than 350 seeds m^{-2} were detected during the survey. The number of buried seeds decreased by up to 740 seeds m^{-2} from spring (1100 seeds m^{-2} in RBS-2) to summer (360 seeds m^{-2} in RBS-2) of 2017, regardless of the type of crop in the fields (Figure 4a,b). In BSR-1 and -2, the number of buried seeds decreased by up to 1200 seeds m^{-2} from spring (1500 seeds m^{-2} in BSR-1) to autumn (280 seeds m^{-2} in BSR-1) in 2016 (Figure 4c,d). Seed death is presumed to be due to premature death in the soil after germination or the decay of ungerminated seeds. In this study, artificially buried seeds of entireleaf morning glory in the field margins were depleted by up to 74% at depths of 2–3 cm and by up to 58% at depths of 10 cm within one year after burial, even those produced in the buried year (data not shown). This suggests that the depletion of buried seeds of entireleaf morning glory under natural conditions can occur within one year of seed production. Kobayashi and Oyanagi [33] found that the number of buried seeds in short-lived southern crabgrass (*Digitaria ciliaris* (Retz.) Koeler) decreased by approximately 80% by the spring of the subsequent year under no-tillage conditions. Morning glories have high seed longevity; 5% of seeds survived 17 years after burial for ivy leaf morning glory (*I. hederacea* (L.) Jacq.,) [34], and 33% and 13% survived 5.5 years after burial for purple moon-flower (*I. turbinata* Lag.) and pitted morning glory, respectively [35]. However, our study suggests that the seed longevity of this species was very short in the field margins under no-tillage conditions, similar to that of southern crabgrass. In RBS-1 and -2, the number of buried seeds in the natural condition of field margins increased by up to 640 seeds m^{-2} from late autumn to winter (Figure 4a,b). This period coincided with the fruiting time of the main seed-producing population, cohort-2, which emerged from early August to mid-September. In BSR-1 and -2, the total number of buried seeds was small, and no clear seasonal change in the buried seeds was detected (Figure 4c,d).

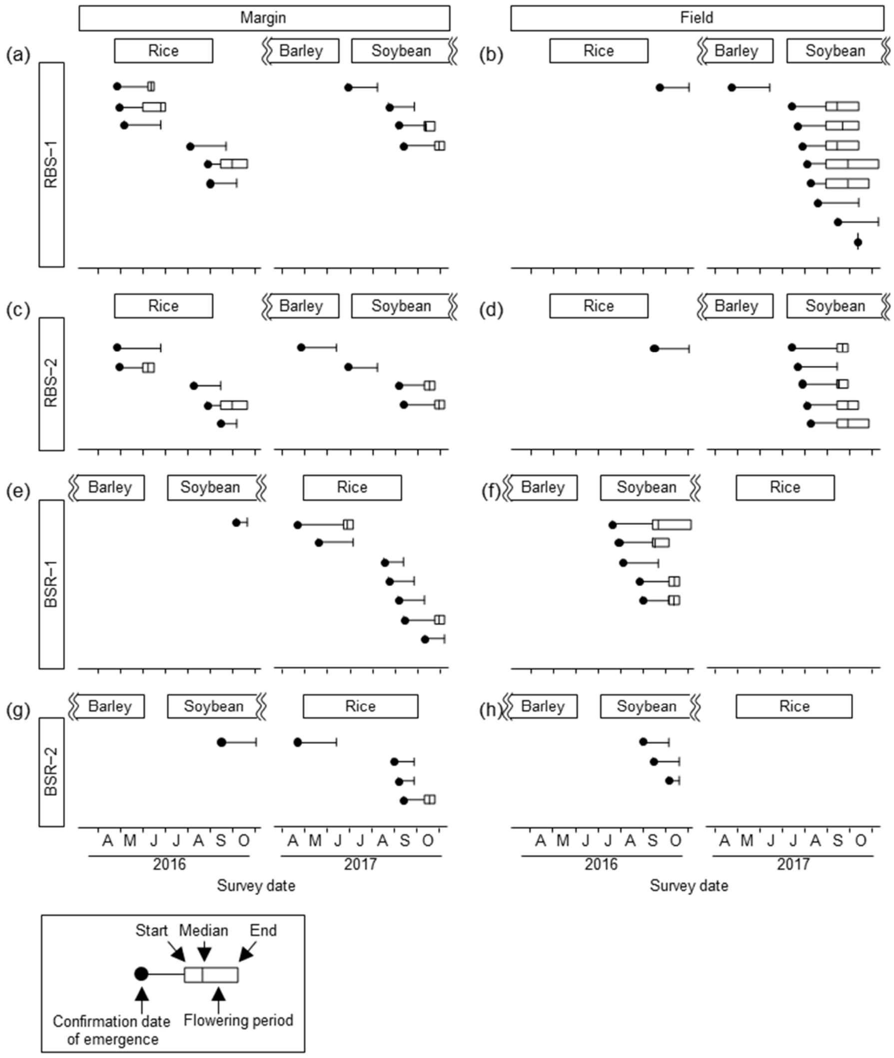

Figure 3. Relationship between confirmation date of emergence and flowering time of entireleaf morning glory. Field margin (**a**) and field (**b**) of RBS-1; field margin (**c**) and field (**d**) of RBS-2; field margin (**e**) and field (**f**) of BSR-1; field margin (**g**) and field (**h**) of BSR-2. The set of black circle(s), horizontal bar(s), and rectangle(s) within a bar represent the growth stage(s) of a subpopulation of one cohort (bottom left area bounded by a square). Black circle, confirmation date of emergence; horizontal bar between the black circle and the square, vegetative growth stage; left end of the rectangle, start of flowering; right end of the rectangle, end of flowering; bar inside the rectangle, median of the flowering period. RBS-1, rice–barley–soybean-1; RBS-2: rice–barley–soybean-2; BSR-1, barley–soybean–rice-1; BSR-2, barley–soybean–rice-2. Horizontal axis shows survey months (April to October of each year).

Our results clarified for the first time that the populations of entireleaf morning glory in the field margins are maintained by repeated depletion and accumulation. It is caused by the emergence from spring to autumn and new seed supply from late autumn to winter every year (Figure 5). Furthermore, cohort-2, which emerged from early August to mid-September, was a cohort with the highest contribution to population maintenance.

Table 2. Confirmation date of emergence and fruiting, and the estimated number of seeds of entireleaf morning glory produced in the fields and their margins.

Field	Site (Crop)	Year	Confirmation Date		Estimated Produced Seeds (Seeds m^{-2}) [a]	
			Emergence	Fruiting		
RBS-1	Margin	2016	22 April	15 June	99	(110)
			30 April	15 June	350	(340)
			5 May	24 June	49	(99)
			3 August	21 September	110	(220)
			25 August	21 September	5000	(3900)
			31 August	5 October	110	(130)
		2017	22 August	29 September	72	(120)
			7 September	12 October	610	(740)
			14 September	27 October	520	(900)
	Field (Rice)	2016	21 September	4 November	5.6	(17)
	Field (Soybean)	2017	12 July	31 August	260	(200)
			20 July	31 August	490	(550)
			Jul. 27	31 August	450	(420)
			2 August	14 September	1100	(600)
			9 August	14 September	600	(550)
			17 August	12 October	18	(44)
			14 September	9 November	6.1	(15)
			12 October	27 October	3.1	(7.5)
RBS-2	Margin	2016	22 April	24 June	66	(110)
			30 April	15 June	200	(340)
			9 August	13 September	150	(260)
			25 August	21 September	4000	(2900)
			13 September	5 October	76	(130)
		2017	7 September	12 October	87	(150)
			9 September	9 November	43	(75)
	Field (Rice)	2016	13 September	4 November	6.7	(20)
	Field (Soybean)	2017	12 July	14 September	160	(260)
			20 July	14 September	97	(160)
			27 July	14 September	230	(290)
			2 August	14 September	320	(70)
			9 August	14 September	360	(390)
BSR-1	Margin	2016	5 October	19 October	32	(55)
		2017	20 April	14 June	190	(380)
			19 May	20 July	140	(290)
			17 August	14 September	96	(190)
			22 August	29 September	48	(96)
			7 September	12 October	96	(190)
			14 September	27 October	96	(110)
			12 October	9 November	30	(60)
	Field (Soybean)	2016	19 July	25 August	140	(130)
			28 July	21 September	55	(91)
			3 August	21 September	14	(42)
			25 August	19 October	15	(46)
			31 August	5 October	38	(36)
	Field (Rice)	2017	NA	NA	-	(-)
SR-2	Margin	2016	13 September	14 November	64	(110)
		2017	20 April	14 June	280	(570)
			31 August	29 September	48	(96)
			7 September	26 September	96	(190)
			14 September	12 October	96	(190)
	Field (Soybean)	2016	31 August	5 October	7.6	(23)
			13 September	19 October	23	(49)
			5 October	29 November	2.8	(8.3)
	Field (Rice)	2017	NA	NA	-	(-)

[a] The number of seeds produced represents values estimated based on the number of fruiting plants and the average number of nodes. RBS-1, rice–barley–soybean-1; RBS-2, rice–barley–soybean-2; BSR-1, barley–soybean–rice-1; BSR-2, barley–soybean–rice-2; NA, not applicable; −, no seeds were produced. Values are presented as mean (SD).

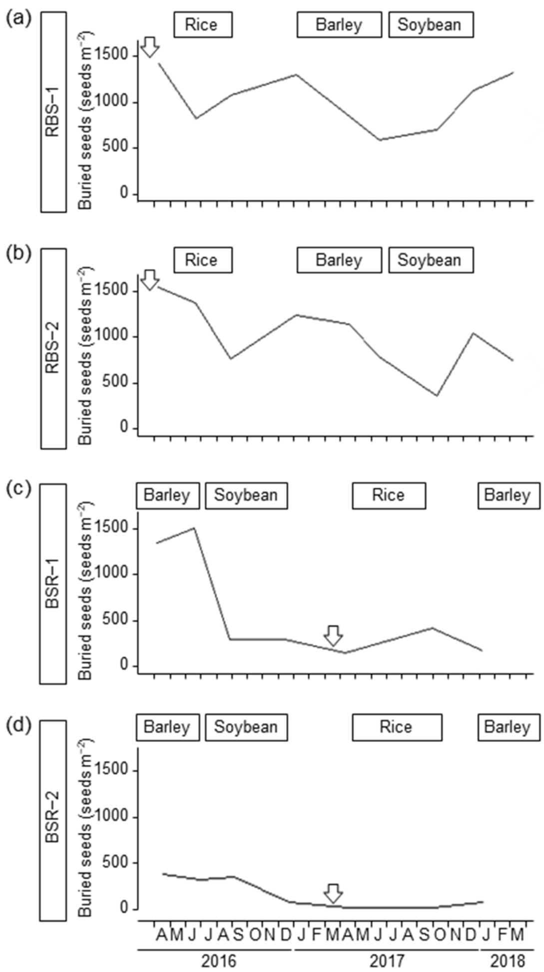

Figure 4. Numbers of buried seeds of entireleaf morning glory in the field margins. (**a**) RBS-1; (**b**) RBS-2; (**c**) BSR-1; (**d**) BSR-2. Arrows, the time of levee plastering. RBS-1, rice–barley–soybean-1; RBS-2, rice–barley–soybean-2; BSR-1, barley–soybean–rice-1; BSR-2, barley–soybean–rice-2. Values are presented as mean. The horizontal axis shows the survey months (April 2016 to March 2018).

3.4. Population Dynamics of Entireleaf Morning Glory in Fields

In the fields, the emergence period of entireleaf morning glory was from April to November. The emergence was especially concentrated within one month after soybean sowing or rice harvest (Figure 2b,d,f,h). In the same fields and year, locations of the quadrats (distance from the field margin) did not affect the cumulative number of seedlings (Tukey–Kramer test; $p = 0.77$, data not shown). The annual cumulative number of seedlings was 2.9 plants m^{-2} in 2016 (rice cultivation year) and 198 plants m^{-2} in 2017 (soybean cultivation year) for RBS-1 and -2, and 15 plants m^{-2} in 2016 (soybean cultivation year) and 1.9 plants m^{-2} in 2017 (rice cultivation year) for BSR-1 and -2.

In the soybean fields, individuals of entireleaf morning glory that emerged within one month after soybean sowing (mid-July to August) reached flowering and fruiting stages (Figure 2b,d,f,h) and flowered from late August to mid-September (Figure 3b,d,f,h) and fruited from late August to October (Table 2). In the rice fields, individuals that emerged after rice harvest reached flowering and fruiting stages in early November (Figure 2b,d,f,h, Table 2). The flowering rate of labeled individuals that emerged within one month after soybean sowing varied by date of emergence, up to 100% in 2016 (emerged on August 31: BSR-1 and -2) and up to 43% in 2017 (emerged on August 2: RBS-1) (Figure 2b,d,f,h). The total number of entireleaf morning glory seeds produced in soybean fields was up to 2900 seeds m^{-2}, which was higher than that of the field margins (up to 1200 seeds m^{-2}) during the same period (Table 2). During the soybean cultivation year in field RBS-1, some individuals that emerged during the barley cultivation period (April to June) also flowered (Figure 2b,d,f,h and Figure 3b,d,f,h). However, all the plants died before fruiting because of barley harvesting and subsequent tilling. In rice fields, fruiting individuals were observed only in RBS-1 and -2, and the total number of seeds produced was very small compared to that in soybean fields (Table 2).

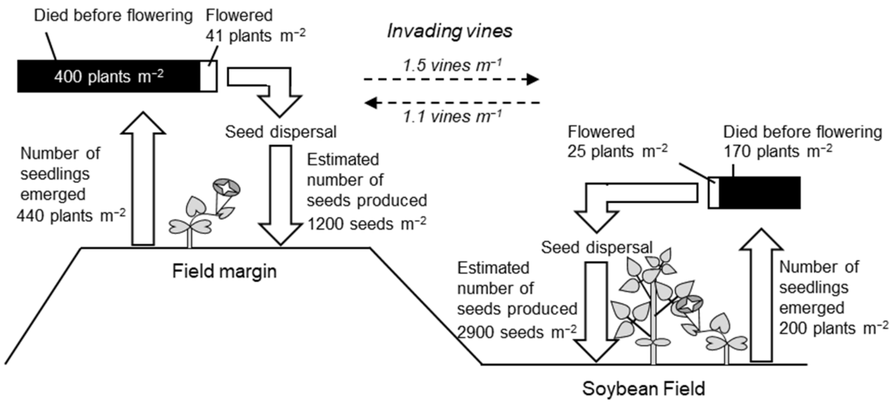

Figure 5. Population model of entireleaf morning glory in the field and margin of RBS-1 in 2017. The quantitative flow of the populations of entireleaf morning glory from the germination to seed dispersal in the field and their margins is indicated by arrows and values. The fate of the seedlings (successful flowering or death before flowering) is indicated by numbers in the white and black bars. The total number of flowering and dying plants differed from the total number of emerged plants because each value was rounded to two significant figures. Italics and dotted arrows indicate the number of invading vines and the direction of invasion, respectively. RBS-1 (rice–barley–soybean-1) in 2017 was selected because the number of plants that emerged was sufficient to illustrate a quantitative change in the population.

These results suggest that cohorts of entireleaf morning glory that emerged within one month after soybean sowing are the main seed-producing populations in the fields (Figure 5). This speculation could be explained by two reasons: (1) The environmental conditions were favorable for emergence, and the number of seedlings was large due to concentrated agricultural practices, such as soybean sowing and weeding. (2) The maximum weed control rate for entireleaf morning glory in the soybean fields was 76% (Figure 1), which was lower than that in the field margins, resulting in high reproductive success. In addition, the emerging individuals did not produce flower buds when the day length was approximately 13 h or longer, which was the same as in the field margins (data not shown). Therefore, the vegetative growth period was sufficient for individuals that emerged early after sowing to produce many seeds. Concordant with our findings, a previous study has shown that survival rates of entireleaf morning glory, which emerged until the V2 (second trifoliate) soybean growth stage were higher than those emerged in the V2 stage under similar management practices as in our study (a soil-applied herbicide in pre-emergence plus a foliar-applied herbicide in V2) [36].

3.5. Suggestions for Reducing the Population Size of Entireleaf Morning Glory

The populations that produced seeds in soybean fields were injured by weed management at least once before flowering. However, the weed control rate of intertillage and earthing up practices and foliar-applied herbicide applications were 52–73% and 55–76%, respectively (Figure 1), and individuals that survived weed management practices reached fruiting. In the fields, it is necessary to increase weed control rate during soybean cultivation to prevent weed seed production. Bentazon was used as a foliar-applied herbicide in the fields. The leaf age of entireleaf morning glory at the time of herbicide application was a maximum of seven leaves. In general, herbicide efficacy is high when applied to young weeds. Bentazon can control entireleaf morning glory with less than three leaves [11,37].

This difference in leaf stage is considered one of the reasons for the low weed control rate in soybean fields. Applying effective herbicides on plants with an appropriate leaf stage (less than three leaves) will increase weed control rate during soybean cultivation.

The weed control rate in the field margins was 75–100% (Figure 1). This rate was especially high when the non-selective herbicide was applied (100%). Mowing at a cutting height of 10 cm could not kill individuals because the blade could not cut the stem near the ground surface. The cohorts whose flowering rates were 100% were not subjected to herbicide applications until flowering (Figure 2a,c,e,g, Table S1). Although the weed control rate of each management practice was high, the farmer did not conduct weed management at the optimal time; thus, many seeds were produced in the field margins. Optimizing the weed management timing of the field margins is important to reduce population size and prevent seed production of entireleaf morning glory. In particular, additional weed management until mid-September, which is the flowering time of cohort-2, can effectively prevent seed production in the cohort.

We concluded that entireleaf morning glory populations in field margins are maintained by specific cohorts and applying an additional weed management practice from early August to mid-September could easily reduce the population size. Furthermore, our study revealed that the weed control rates of the farmer's weed management practices in soybean fields were low, whereas those in the field margins were extremely high. To reduce the population size of entireleaf morning glory, it is important to improve the weed control rate in soybean fields and to optimize the timing of weed management practices in field margins. Piskackova et al. [38] showed a model for optimizing timing of weed management for several crops. The model was developed for sicklepod (*Senna obtusifolia* (L.) H.S.Irwin et Barneby), considering its size and phenological stage. Our study will provide essential data for such models to control entireleaf morning glory in the future. However, the timing of weed management practices in field margins generally differs depending on countries, climate conditions, weed species, and individual farmers. Furthermore, differences among management practices induce variations in the emergence of entireleaf morning glory. Nevertheless, the present study identified an optimal period for weed management practices in field margins to prevent seed production by tracing the fate and seed production of individuals comprising each cohort. This concept can be applied to other countries or regions with different environments.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy12102392/s1, Table S1: Agricultural practice in study fields. Table S2: List of herbicides used in this study.

Author Contributions: Conceptualization, N.I. and H.K.; funding acquisition, H.K.; investigation, N.I.; visualization, N.I.; writing—original draft, N.I.; writing—review and editing, H.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Ministry of Agriculture, Forestry and Fisheries, Japan, and was carried out as part of the research project "Development of diagnostic methods and countermeasure techniques for overcoming high-yield inhibitory factors". This project has no grant number.

Data Availability Statement: All data related to this study are presented in the manuscript and the Supplementary Information.

Acknowledgments: The authors gratefully acknowledge the cooperation of farmers for allowing the use of their fields during this study. The authors would also like to thank the members of the weed control group, Institute for Plant Protection, National Agriculture and Food Research Organization (NARO), Japan, and members of the Center for Weed and Wildlife Management, Utsunomiya University, Japan, for assistance. The authors are grateful to the staff of the Technical Support Center of NARO for their support.

Conflicts of Interest: The authors declare no conflict of interest.

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