Seasonal changes in the germination of buried seeds of *Monochoria vaginalis*

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Summary

This study investigates the seasonal variation of germination ability of buried seeds of *Monochoria vaginalis* (Burm.f.) Presl var. *plantaginea* Solms. The field-collected seeds were buried in a flooded or an upland field and then exhumed monthly. The exhumed seeds were germinated under four temperature regimes. The seeds exhumed from the flooded soil were dormant at the beginning of burial and proceeded into a conditional dormancy/non-dormancy/conditional dormancy cycle throughout the remaining period of the experiment. The seeds exhumed monthly from the non-flooded soil exhibited an annual dormant cycle, which is dormancy/conditional dormancy/non-dormancy/conditional dormancy/dormancy. At day and night temperatures of 25/20 °C, the exhumed seeds from both the flooded and the upland soil resembled each other in terms of seasonal variation of the germination percentage. In September and October, more seeds exhumed from upland soil failed to germinate under higher temperature than from flooded soil. Strictly avoiding exposure to light during seed exhuming and seed testing prevented the seeds from germinating. A short exposure of the exhumed seeds to light during preparation promoted dark germination when the seeds were at the non-dormant stage. The potential implications of our results for weed management strategies in rice production are discussed.

Keywords: buried seed, dormancy, germination, *Monochoria vaginalis*, rice.

Introduction

Monochoria vaginalis has been listed as a serious weed in six countries, including Borneo, Indonesia, Japan, Korea and Taiwan (Holm *et al.*, 1979). A recent investigation rated *M. vaginalis* as the worst weed in South-east Asia next to *Echinochloa colonum* (L.) Link (Waterhouse, 1993). In Taiwan, it is one of the five most serious weeds in paddy fields (Chiang & Leu, 1982). Although easily killed by butachlor during the seedling stage (Liu & Tsai, 1986), *M. vaginalis* remains a serious weed. In light of this predicament, further knowledge of seed germination biology is required if effective management strategies are to be proposed.

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Elucidating the dormancy cycle of *M. vaginalis* is a prerequisite for understanding the year-round behaviour of the seeds in the soil. According to Baskin & Baskin (1985), dormant seeds are defined as seeds not germinating at any temperature regime. In the soil, these seeds gradually become conditionally dormant, capable of germinating at relatively narrow temperature regimes. In undisturbed soils, the conditionally dormant seeds may enter into a non-dormant state. The non-dormant seeds germinate at a wider range of temperatures. Other soil factors, e.g. allelopathic inhibitors, lack of light or oxygen, or extreme temperatures may inhibit the germination of the non-dormant or conditionally dormant seeds in the soil. Non-germinated seeds may proceed into conditional dormancy and then back into the dormant state again.

The germination characteristics of seeds of temperate species have received extensive interest (Baskin & Baskin, 1988, 1989a; Probert, 1992). Although seed ecology of paddy weeds has gained less attention, the ecology of wetland seedbanks has been thoroughly reviewed (Leck, 1989). This study surveys the changes in dormant states of buried seeds of *M. vaginalis*.

Materials and methods

Seeds

The seeds of *M. vaginalis* (Burm.f.) Persil var. *plantaginea* Solms. were collected on the experimental farm of the National Taiwan University in Taipei in October 1993 and May 1994. Empty and underdeveloped seeds were discarded by floating in tapwater. The remaining seeds were air dried to about 8.5% moisture content (wet basis) and hermetically stored in a −20 °C chest cabinet to keep the seeds fresh. At the time of collection, the seeds were dormant, and storage at −20 °C was therefore assumed not to influence the dormancy status of the seeds.

Burial experiment I (BE I)

In November 1993, after 1 month of storage at −20 °C, the seeds collected in October 1993 were divided into 48 samples and packed separately in 4 cm × 6 cm bags of fine-mesh nylon gauze (≈2000 seeds per bag). Half of the bags were buried horizontally in a loam soil under non-irrigated upland conditions. The other 24 bags were buried in a loam soil under water-logged conditions. The water level was maintained 5–10 cm above the soil surface throughout the experiment. The depth of burial was ≈10 cm.

Burial experiment II (BE II)

In June 1994, the seeds collected in May 1994 were divided into 24 samples and packed and buried as in BE I, except that the envelopes were buried in sandy loam in black plastic pots that were lined with gauze to prevent loss of soil. The pots were then buried in upland or a paddy field at a depth so that the envelopes were ≈10 cm below soil surface. This procedure prevented light from reaching the seeds during exhuming and when preparing the seeds for the germination test.

Germination tests

One bag of seeds was exhumed monthly from each experiment. No light-preventing procedure was adopted in BE I during transportation and processing of the seeds and when counting the numbers of germinated seeds. In contrast, in BE II, the exhumed pots were covered with a black polyethylene bag and then moved into a dark room that was equipped with a dim green light (< 0.01 µmol m^{-2} s^{-1}). All the seed-handling procedures were performed in the dark room.

The exhumed seeds were water washed and air dried for 1 day in the laboratory (BE I) or in a dark room (BE II). Thirty-two Petri dishes each with 50 seeds were prepared for each bag. The seeds were placed on two sheets of filter paper and 10 mL of distilled water was added. Petri dishes were wrapped with parafilm to prevent loss of water. Half of the Petri dishes were subjected to a 16-h dark period and 8-h light period daily. Light was provided by fluorescent tubes at an intensity of about 30 µmol m^{-2} s^{-1} at the water surface (4 mm above the seed surface). To create a completely dark condition the other half of the Petri dishes was sealed by two layers of aluminium bag. This test method maintained the seeds under partially anaerobic conditions, which promoted germination (Momonoki, 1992; Chen & Kuo, 1995). Germination tests were performed in incubators at the following day/night temperature regimes: 30/25, 30/20, 25/20 and 23/13 °C.

A seed was considered germinated if the embryo axes protruded more than 2 mm. The time of the first count depended on the germination temperature; the final count was made at the 14th day of incubation. The mean germination time at 16 °C has previously been found to be 7 days for non-dormant seeds (Chen & Kuo, 1995).

Field emergence

Monthly, 400 exhumed seeds from both BE I and BE II were sown on a water-logged field 0.5 cm below the soil surface. The topsoil had been autoclaved to kill all seeds. Burial at 0.5 cm did not significantly reduce germination compared with unburied *M. vaginalis* seeds (Chen & Kuo, 1995). Seedling counting was terminated 1 month after sowing.

Meteorological data

The daily mean soil temperature at 10 cm below the soil surface was calculated from the data recorded at 30-min intervals by a data logger.

Results

The daily mean soil temperature in the paddy fields (10 cm below the surface) in Taipei during the experiments is shown in Fig. 1. The mean soil temperature exhibited a typical annual fluctuation: the highest mean temperature ranging from 28 to 30 °C occurred during June and September, whereas in the winter it was as low as 12–14 °C. The mean upland soil temperature at 10 cm below the surface did not significantly differ from that of the paddy field, although the amplitudes of daily alternating temperature always exceeded that of the paddy field (data not shown). During autumn and early winter, precipitation was less than during spring and summer. Nevertheless, the soils always remained wet during autumn and winter because of lower radiation and temperatures. In contrast, during the summer, the topsoil dried out on a few sunny days.

The results of BE I showed that all *M. vaginalis* seeds collected in October 1993 and stored at −20 °C for 1 month were dormant at all four temperature regimes. Although still very high after 1 month of burial in water-logged soil (Fig. 2a), the dormancy level was greatly reduced after 2 months of burial. Thereafter, 60–90% of the seeds germinated at 30/25 °C, except those exhumed in October 1995. At 30/20 °C, the germination percentage was 30–80%. Comparing

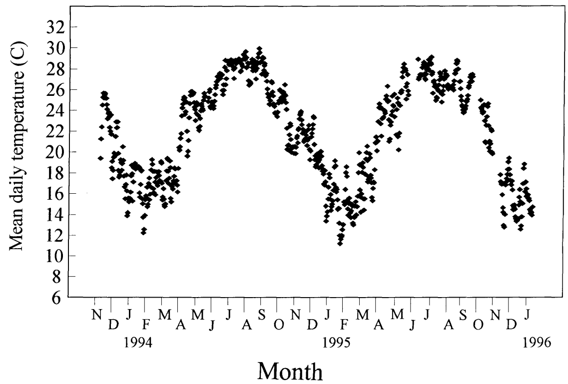

Fig. 1 Daily mean temperature at 10 cm below a flooded soil surface at Taipei during the experiments.

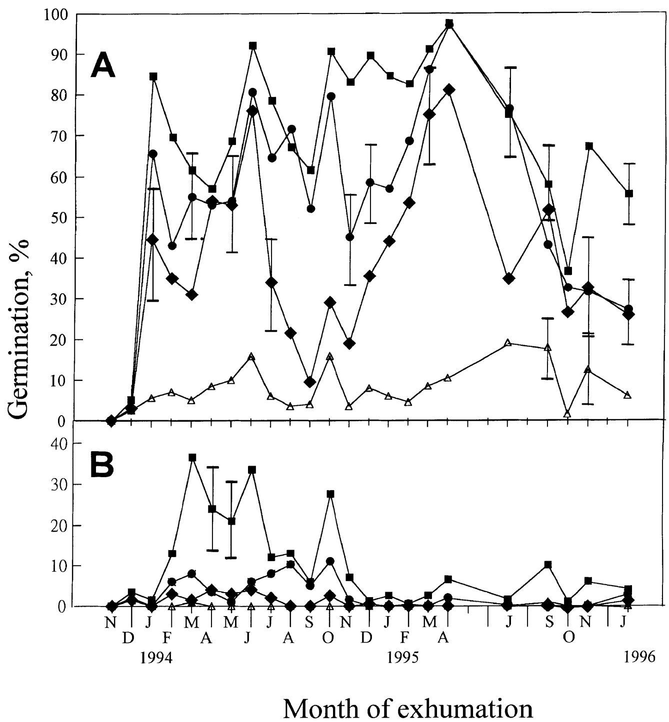

Fig. 2 Percentage germination under light (A) and dark (B) conditions of *Monochoria vaginalis* seeds exhumed monthly from a flooded soil (BE I). Vertical bars indicate ±standard error if greater than 5%. Germination tests were performed at 30/25 (■), 30/20 (●), 25/20 (◆) and 23/13 °C (Δ). No exhumation was made in May, June, August and December 1995. During exhuming, the seeds were not strictly prevented from exposure to light.

these two temperature regimes revealed a greater difference in germination during winter than during summer. At 25/20 °C, the germination pattern revealed a seasonal fluctuation. Germination increased from winter until early summer, and then decreased again until autumn. At 23/13 °C germination never exceeded 20% throughout the experiment.

From March to June of the first year of paddy-field burial, 20–40% of the seeds germinated at 30/25 °C under the dark condition (Fig. 2b). The lower germination percentage under the dark condition indicated that these seeds were very sensitive to light exposure during exhumation. One year after the burial, a short exposure to light did not stimulate germination.

At 25/20 °C the annual fluctuation in percentage germination of the exhumed seeds buried in upland soil (Fig. 3a) resembled those buried in the paddy fields (Fig. 2a). However, in the upland soil, the seeds became completely dormant during summer, as revealed by a low germination percentage at 30/25 °C. The seeds gradually proceeded into conditional dormancy during autumn and winter and became non-dormant in the spring of the next year. According to dark germination tests (Fig. 3b), up to 30% of the seeds lost their light requirement in the first spring.

Although the BE II experiments did not last long enough to reveal any dormancy cycle, our results nevertheless indicated that the seeds buried in summer maintained a longer dormancy period (Figs 4 and 5) than those buried in winter (Figs 2 and 3). Again, the seeds acquired the ability to germinate quicker when buried in the paddy field than in upland soil. In contrast to BE I, in BE II no seeds germinated under the dark condition (Figs 4b and 5b).

The seeds that were exhumed from water-logged soil did not germinate in the field at the beginning (Fig. 6a). In the 2-year survey, the percentage emergence of the exhumed seeds gradually increased up to 90% during spring. The percentage then decreased during summer and was lowest in winters, with the exception of October and November 1994. Seeds exhumed from upland soil also displayed an annual change in percentage field emergence (Fig. 6b) but were generally more dormant, except from April to June 1994 and in April 1995.

Discussion

The seeds of *M. vaginalis* are easily separated from the fruits, the average length is less than 2 mm, and the mean seed weight is around 0.17 mg. According to Grime (1989), these characteristics imply that the seeds constitute a persistent seedbank in the soil. Similar to other

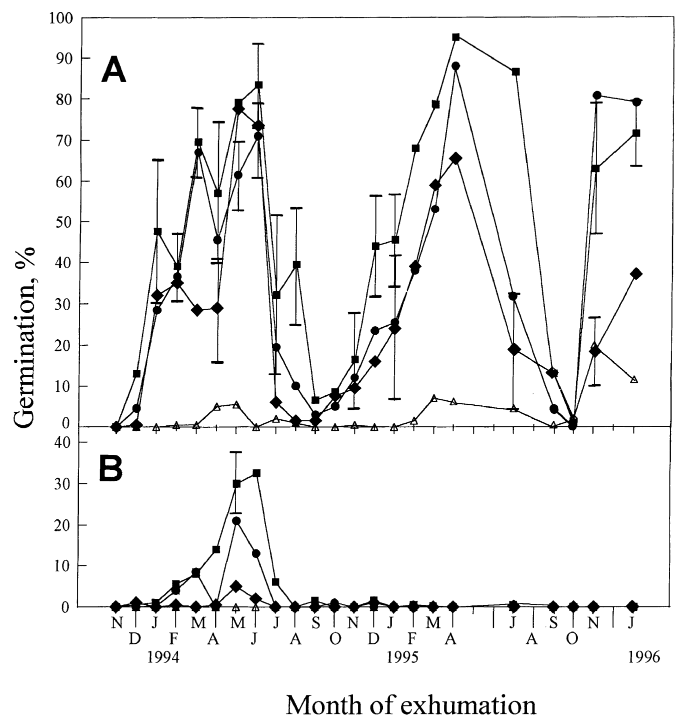

Fig. 3 Percentage germination of *Monochoria vaginalis* seeds exhumed monthly from upland soil (BE I). Legends as in Fig. 2.

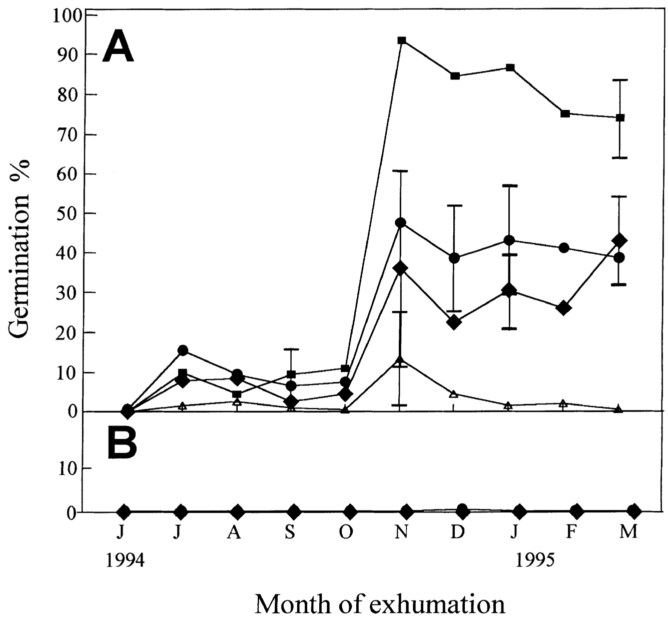

Fig. 4 Percentage germination of *Monochoria vaginalis* seeds exhumed monthly from a flooded soil (BE II). The seeds were protected from light during exhumation and the seeds for the dark germination test were prepared under green safe light. Legends as in Fig. 2.

tiny persistent seeds, the non-dormant seeds of *M. vaginalis* failed to germinate in the dark. However, the seeds are highly sensitive to dim light. Two days of 1 min of exposure to light at an intensity of 4×10^{-4} mol m^{-2} were sufficient for 50% of the dormant *M. vaginalis* seeds to germinate (Chen & Kuo, 1995). This low level of light intensity has also been shown to promote the emergence of some dicotyledonous weed seeds, which were subjected to a single tillage at night under artificial light and then buried again (Scopel *et al.*, 1994).

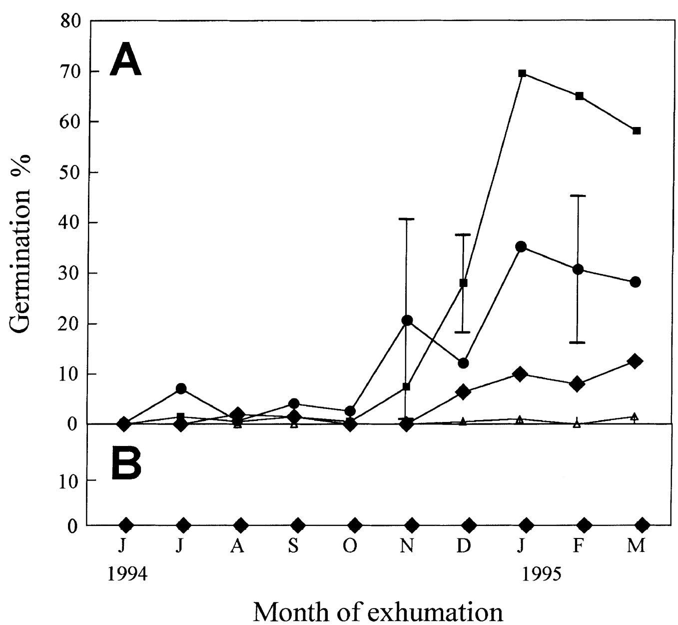

Fig. 5 Percentage germination of *Monochoria vaginalis* seeds exhumed monthly from upland soil (BE II). The seeds were kept from light during exhumation and the seeds for the dark germination test were prepared under green safe light. Legends as in Fig. 2.

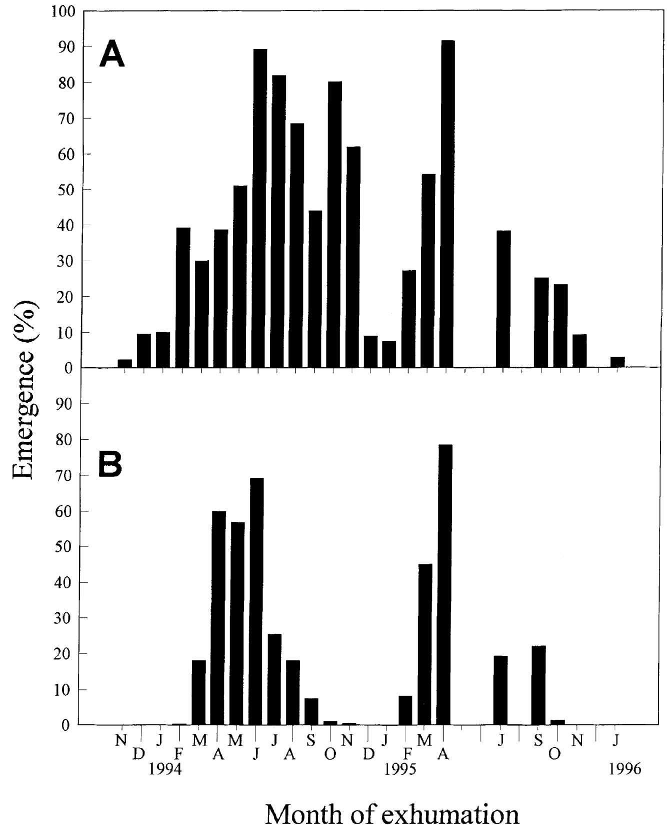

Fig. 6 Percentage emergence of *Monochoria vaginalis* seeds exhumed monthly from a flooded (A) and an upland (B) soil and then replanted into a water-logged field. No exhumation was made in May, June, August and December 1995.

Some seeds exhibit a fluctuation in light requirement during burial, e.g. *Capsella bursa-pastoris* (L.) Medik (Baskin & Baskin, 1989b), *Polygonum aviculare* L. (Baskin & Baskin, 1990), *Oenothera biennis* L. (Baskin & Baskin, 1994) and *Carex stricta* Lam. (Baskin *et al.*, 1996). On the other hand, some species maintain light requirement during the entire period of burial, such as the seeds of the wetland plants *Cyperus erythrorhizos* Muhl., *Cyperus flavicomus* Michx., *Fimbristylis autumnalis* (L.) Roem. & Schult. (Baskin *et al.*, 1993), as well as *Carex comosa* F. Bott seeds buried in non-flooded conditions (Baskin *et al.*, 1996). Exhumed seeds of these species did not germinate in darkness.

The *M. vaginalis* seeds did not lose their light requirement for germination during burial (Figs 4b and 5b). However, up to 30% of the buried seeds responded to a short period of light exposure during exhumation in the spring and early summer of 1994 (Figs 2b and 3b). Thereafter, the seeds required more light for germination. Flooding somewhat decreased the light requirement of *M. vaginalis* seeds. In contrast, the effect of flooding on overcoming seed dormancy of *C. comosa* was much more significant (Baskin *et al.*, 1996).

Our results clearly indicated that the buried seeds of *M. vaginalis* in paddy fields experienced annual changes in the dormant state (Fig. 2a). The seeds were dormant at the beginning of the burial, became conditionally dormant in January, went into the non-dormant state in April, became conditionally dormant again in July, and remained so until March 1995. This annual dormancy cycle was not perfectly repeated during 1995. Only 40% of the seeds germinated at 30/25 °C around August 1995, whereas in 1994 the germination percentage was 60–90%. The germination percentage at the lowest temperature regime (25/20 °C) fluctuated throughout the experiment in contrast to 30/25 °C, when the germination percentage remained high for most of the burial period. This fluctuation pattern reflects the characteristic of a strictly summer annual species (Karssen, 1982; Baskin & Baskin, 1989a). Notably, the conditional dormancy/non-dormancy/conditional dormancy cycle of *M. vaginalis* resembled that of the seeds of the wetland perennials *Gratiola viscidula* Pennell and *Scirpus lineatus* Michx. (Baskin *et al.*, 1989) as well as that of facultative winter annual or spring- and summer-germinating summer annuals (Baskin & Baskin, 1989a).

Seeds performed differently when buried in the upland soil (Fig. 3a), exhibiting a dormancy/conditional dormancy/non-dormancy/conditional dormancy/dormancy cycle, resembling that of the spring-germinating summer annual *P. aviculare* (Baskin & Baskin, 1990). Interestingly, most of the *M. vaginalis* seeds that were exhumed in September and October from upland soil failed to germinate at 30/25 °C, whereas those from the paddy field germinated under the same conditions. It suggests that the drying condition of the soil during summer may induce complete dormancy of the buried seeds.

Although the seeds of *Carex* species were less dormant in flooded than in non-flooded soil, the basic dormant cycle did not differ much (Baskin *et al.*, 1996). According to their results, the seeds of some other *Cyperaceae* species entered conditional dormancy under non-flooded conditions, but not when buried in flooded soil (Baskin *et al.*, 1993). The above findings suggest that drying may induce dormancy in buried seeds of aquatic species, which may be of ecological significance. Dormancy of the non-dormant *M. vaginalis* seeds can be partially induced by drying in the laboratory. However, up to 80% of the artificially dried seeds germinated when tested at 30/25 °C (data not shown). The cause of the drastic decrease in percentage germination at 30/25 °C of the non-flooded seeds that were exhumed in September or October remains unexplained.

In Taiwan there are two rice (*Oryza sativa* L.) crops per year. In the northern part of the island, the first crop is grown from March to July and the second crop from August to November. In practice, the seed behaviour of *M. vaginalis* more resembles that of a spring- and summer-germinating summer annual weed, because *M. vaginalis* emerges from the field in late spring when temperature regimes are around 30/25 °C. The weed plants will produce mature seeds and then be killed at the time of rice harvesting and subsequent land preparation. During the summer rice season, the seeds germinate at the beginning of transplanting. The weed plants will again be killed at harvest. On the other hand, field observations have shown that the plant can survive the winter climate, behaving like a perennial or at least a biennial species as long as the paddy field remains water-logged all year round (Zimdahl *et al.*, 1989). Consequently, *M. vaginalis* closely resembles *G. viscidula* and *S. lineatus* and, incidentally, the seeds of the last two species are also small and light dependent (Baskin *et al.*, 1989).

A large portion of the *M. vaginalis* seeds in the soil loses its dormancy after March. These seeds would germinate promptly after land preparation provided that the soil is well flooded and the seeds had been exposed to light for a short time. These characteristics render the weed easy to control, but hard to eliminate. However, our data indicate that several times of tillage in late spring would minimize the weed population efficiently. The germination pattern also reveals a promising means of controlling this weed in the second rice crop; in order to induce completely dormancy of the *M. vaginalis* seeds, the soil should be allowed to be completely dried out for a short period between the two rice crops. Incorporating land preparation and desiccation procedures in the cropping practice could contribute to a more effective weed control strategy.

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