



Similar germination but dissimilar flood tolerance behaviour of seeds of two weed species (*Ludwigia*) inhabiting rice fields in Rajgir, India

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ABSTRACT: We aimed to determine seed germination responses and flood tolerance of *Ludwigia hyssopifolia* and *L. perennis* that grow in rice fields in Rajgir, India. Freshly-matured seeds were incubated in 12 hr / 12 hr light / dark and complete darkness at constant 25 °C and natural daily fluctuating temperatures. Seeds exposed to different light durations were then incubated in complete darkness. Seeds exposed to different flooding durations were incubated in continuously flooded or non-flooded environments. Seeds of both species germinated within four days in light/dark but failed to germinate in complete darkness, revealing their nondormant and positive photoblastic behavior. Some seeds of both species (10 – 20 %) germinated in complete darkness after exposure to light for 24h. Seeds failed to produce normal seedlings in a continuously flooded environment. Seeds of the two studied species tolerate at least one week of flood. Seeds of *L. perennis* have a higher tolerance to flooding than those of *L. hyssopifolia*, which survived four weeks in a flooded environment. The two species have the same germination behaviour but differ in ability to tolerate flooding. Since seeds of both species are nondormant, positively photoblastic, and have different degrees of flood tolerance, a flooding regime of rice fields will not be sufficient to control these weeds.

KEY WORDS: flooding tolerance, hypoxic conditions, nondormant seeds, photoblastic seeds, weed control.

INTRODUCTION

Ludwigia (Onagraceae) is an aquatic plant genus native to Central and South America (Mabberley, 2017) and is now distributed not only in many other tropical countries but also in some temperate countries (Dandelot *et al.*, 2005; Hussner, 2010; Nehring and Kolthoff, 2011). Many *Ludwigia* spp. are invasive in aquatic ecosystems and also occur as weeds in many croplands, especially in rice fields (Moody, 1989; Holm *et al.*, 1997; Chauhan *et al.*, 2011). Invasive *Ludwigia* spp. adversely affect aquatic ecosystems by replacing the native diverse vegetation (Dandelot *et al.*, 2008; Pivari *et al.*, 2008; Stiers *et al.*, 2011; Grewell *et al.*, 2016), blocking the water runaways (Thouvenot *et al.*, 2013; Gallardo *et al.*, 2016; Sarat *et al.* 2019) and enhancing sedimentation (Brusati, 2009; Gallardo *et al.*, 2016). Some *Ludwigia* spp. have been reported to produce allelopathic chemicals, which suppress the growth of other plants (Dandelot *et al.*, 2008; Sakpere *et al.*, 2010; Roy *et al.*, 2011; Mukherjee and Barik, 2013). As a weed in rice fields, *Ludwigia* causes significant decreases in yield through competition (Dandelot *et al.*, 2008; Chauhan and Johnson, 2010a; Chauhan *et al.*, 2011; Mukherjee and Barik, 2013), and high economic costs are involved in controlling *Ludwigia* infestations (EPPO, 2011).

Among the weedy *Ludwigia* species, *L. hyssopifolia* and *L. perennis* are widely distributed weeds with high invasive potential (Holm *et al.*, 1997). *Ludwigia hyssopifolia* is native to tropical America and Northern

Australia (POWO, 2023), while it occurs as a rice field weed in many rice-growing countries, including India (Panda *et al.*, 2019), Sri Lanka (Chandrasena, 1987), Malaysia (Begum *et al.*, 2008), Thailand, and Indonesia (Holm *et al.*, 1997). On the contrary, *L. perennis* is a native species in tropical Africa, South and Southeast Asia, and Northern Australia (POWO, 2023). In India, these two species have been recorded in direct seedings (Panda *et al.*, 2019; Jannu and Narender, 2023) and transplanted rice fields (Sreemadhavan, 1966). Mutakin *et al.* (2021) reported that even under the new rice growing technology 'System of Rice Intensification (SRI)', *L. hyssopifolia* became the dominant weed in rice fields in Indonesia.

Rice is the staple food in Asia, including India, and much effort has been put into improving the efficiency of rice farming systems and production. Weeds are one of the significant factors causing the yield reduction in rice farming systems. Thus, many approaches have been used to control them. Using herbicides is the easiest and most effective method among weed control techniques (Chauhan *et al.* 2014). However, emerging evidence of the harmful effects of herbicides on human health and environmental risks is promoting a trend toward using eco-friendly, less hazardous weed control methods (Zimdahl, 2018).

Furthermore, evidence on the development of herbicide-resistant weed varieties (Kaur *et al.*, 2022) has also discouraged the use of herbicides alone for weed control (Kayeke *et al.*, 2017). Integrated weed



management is the current trend in rice cultivation (Sangramsingh *et al.*, 2022; Jannu and Marender, 2023); however, much scientific information is required to plan integrated weed management properly (Janu and Marender, 2023). The biology and physiology of the crop species, hydrology and soil conditions of the cropland, and biology and physiology of weed species are of utmost importance in an adequately integrated weed management plan (Mortensen *et al.*, 2000; Cherry and Gough, 2006; Rao and Nagamani, 2010; Chauhan and Johnson, 2010b; Ibáñez *et al.*, 2014; Grewell *et al.*, 2016). Although seedling and adult plant biology and physiology are often considered, seed biological information about weeds is seldom used in planning integrated weed management (Mortensen *et al.*, 2000; Chauhan and Johnson, 2010b; Chauhan, 2012a). Lacking the necessary seed biological information on weeds is one of the reasons why this information is not considered in proper planning (Chauhan, 2012a; Thapa and Bhatt, 2014; Grewell *et al.*, 2016).

Seed germination requirements, specifically, light and temperature and the ability of seeds to germinate under hypoxic (flooded) conditions, should be considered in planning proper weed management in rice farming systems. In particular, flooding is used as a weed control strategy in rice fields (Yamauchi, 1996). However, the prior exposure of seeds of mudflat plants (also common in rice fields) to flooded environments strongly interferes with their germination process both positively and negatively once the non-flooded environment is regained (Phartyal *et al.*, 2020 and reference therein). Therefore, it is essential to consider the ability of rice field weed seeds to germinate and survive under flooded (hypoxic) conditions. Although some information is available in the scientific literature on the seed germination of some *Ludwigia* species, no information is available on *L. hyssopifolia* or *L. perennis*. Available information suggests that seeds of *Ludwigia* spp. have either no dormancy (Oziegbe *et al.*, 2010; Sumudunie and Jayasuriya, 2019) or physiological dormancy (Wulff and Briceno, 1976; Chul and Moody, 1989; Wogu and Ugborogho, 2000; Sumudunie and Jayasuriya, 2019). Further, germination studies suggested that *Ludwigia* seeds are photoblastic, and only a few seeds germinate under complete darkness (Salisbury, 1972; Wulff and Briceno, 1976; Gillard *et al.*, 2017; Sumudunie and Jayasuriya, 2019). However, no information is available on the effect of flooding on the germinability of *Ludwigia* species.

Therefore, research was conducted to evaluate the germination behaviour of two weedy *Ludwigia* species, *Ludwigia hyssopifolia* (G. Don) Exell. and *Ludwigia perennis* L. widely inhabit rice fields in Rajgir, Bihar, India. Special attention was given to evaluating how different durations of prior exposure of their seeds to light and flooding affect seed germination in complete darkness and non-flooding conditions. The findings of our study will be valuable information for better

understanding the seed germination behaviour of these two weed species and planning effective measures for integrated weed management in rice fields.

MATERIALS AND METHODS

Fruit collection and seed extraction

The fruits were collected from more than five individuals of *Ludwigia hyssopifolia* and *L. perennis* plants grown on a lower bank of a water canal around a rice field in Rajgir (25.019964N, 85.405461E), Bihar, India. Care was taken to collect only mature dried fruits directly from the plants. The fruit collection was carried out in February 2019. The fruits were collected in brown paper bags, brought to the Seed Biology Laboratory of Nalanda University, Rajgir, India, and stored for two days until they were used for laboratory experiments. The seeds were extracted by crushing the fruits and cleaning out the debris.

Seed germination

Four replicates of about 250 seeds each of both species were placed separately in 9-cm diameter Petri dishes on filter papers moistened with distilled water. Ungerminated seeds at the termination of the experiment were counted for each replicate to determine the total number of seeds shown for calculating the final germination percentage. Seed samples were incubated at constant 25 °C under both 12 hr / 12 hr light / dark and complete dark conditions in a temperature-controlled incubator. A cool white fluorescent lamp provided the light (1000 lumens). The darkness was provided by wrapping Petri dishes with three layers of aluminium foil. The same experiment was repeated by keeping Petri dishes on a laboratory bench to expose seeds to natural, fluctuating temperature conditions. Seeds incubated in light / dark were observed for germination at 2-day intervals for 14 days or until all the seeds germinated. Seeds kept in the dark were observed for germination after 14 days at the end of the experiment. The emergence of the visible shoot was considered the criterion for germination.

Effect of prior light exposure on seed germination in darkness

Six sets containing four replicates of approximately 250 seeds each of both species were incubated on filter papers moistened with distilled water at 25 °C under light conditions for 1, 2, 4, 8, 12, and 24 hours (for prior light exposure treatments). After that, each set of seeds was moved for incubation under completely dark conditions at the same incubation temperature for 14 days, and the seeds were observed for germination. The emergence of the visible shoot was the criterion for germination. Ungerminated seeds at the termination of the experiment were counted for each replicate to determine the total number of seeds shown for calculating the final germination percentage.



Effect of hypoxic (flooded) environments on seed germination

In the first set of experiments, four replicates of about 250 seeds of both species were placed between two filter papers on the bottom of eight 250 ml beakers to avoid floatation of seeds and ensure they were always under flooded conditions throughout the experimental period. Subsequently, the beakers were filled with 200 ml of water (to maintain a water depth of approximately 10 cm and create hypoxic environments) and incubated at 25 °C in the 12 hr / 12 hr light / dark regime. The light was provided from the side to ensure that all the seeds received enough light. Filter papers were taken out from the beaker, and seeds were observed for germination at 2-day intervals for 14 days. After observations, which took about 10 min per replicate, filter papers with seeds were returned to the bottom of the beaker. This experiment aimed to determine whether continuously flooded seeds had normal germination (root and shoot emergence).

In the second set of experiments, as described above, three subsets of four replicates of about 250 seeds for each species were exposed to hypoxic (flooded) environments under full dark conditions. However, after 2, 3, or 4 weeks of flooding, one set of seeds for each species was retrieved and incubated on filter papers moistened with distilled water at 25 °C in light / dark (12 hr / 12 hr) under oxic (unflooded) environments. Seeds were observed for germination in 2-day intervals for 14 days or until all the seeds germinated. The emergence of the visible shoot was the criterion for germination. This experiment aimed to evaluate the effect of prior exposure to flooding on seed germination under non-flooding conditions. As described above, the total number of seeds shown and the final germination percentage were counted.

Statistical analysis

All the germination percentage data were arcsine transformed. Transformed data were analyzed with a two-way ANOVA procedure in PAST 4.1 statistical software. The analysis used species and germination treatments as the two factors. When ANOVA was significant, Dunnett's Mean separation procedure was conducted to determine the treatment combinations that differed significantly from others. Non-transformed data were used in all graphs.

RESULTS

Seed germination

Seeds of two *Ludwigia* species germinated to 80 – 90 % under light / dark conditions within 14 days regardless of the temperature (constant 25 °C vs. natural daily fluctuating outside temperature) (Figure 1). However, only an insignificant number of seeds germinated when incubated in complete darkness. There were no significant differences in germination between species ($F = 0.169, P = 0.69$) or between temperature conditions ($F = 0.005, P = 0.9413$).

Seed germination under light / dark conditions was significantly higher than under complete darkness ($F = 113.4, P < 0.001$).

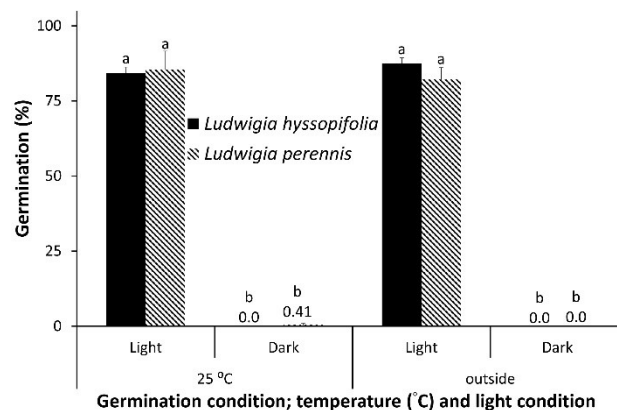


Fig. 1. Germination of *Ludwigia hyssopifolia* and *L. perennis* seeds in 12hr / 12hr light / dark and complete dark conditions at constant 25 °C and at natural daily temperature fluctuation of outside environmental conditions. Error bars are + SE. Different lowercase letters indicate significant differences between treatments within a species. There are no significant differences in germination between species.

Effect of prior light exposure on seed germination in darkness

The germination percentage increased with increased prior light exposure time (Figure 2, $F = 839, P < 0.001$). Even after 24 hrs. prior light exposure, seeds of *L. hyssopifolia* and *L. perennis* germinated only to 11.3 ± 1.9 and 20.6 ± 2.4 %, respectively. The germination percentage of *L. perennis* was significantly higher than that of *L. hyssopifolia* after 12 and 24 hours of prior light exposure ($F = 16.42, P < 0.001$). However, they germinated to 80 – 90 % in light / dark (12 hr / 12 hr) within ~4 days at their standard germination test.

Effect of hypoxic (flooded) environments on seed germination

In the first experiment, 80 – 90 % of the seeds of both species had radicle emergence under continuously flooded conditions (data not shown). However, no shoot emergence occurred from radicle-emerged seeds in a flooded environment; instead, they all rotted and died.

In the second experiment, the germination percentage of *L. hyssopifolia* incubated in the non-flooded environment (seed kept on filter papers moistened with distilled water after flooded treatment) was significantly reduced with increased duration of flooding (Figure 3, $F = 350.7, P < 0.001$). However, all radicle-emergent seeds had produced a normal and healthy shoot. In contrast, the germination percentage of *L. perennis* seeds incubated in a non-flooded environment after being moved from flooding was approximately 75 % for all the tested flooding durations. The germination percentage of *L.*



perennis seeds was not significantly different among exposure treatments or from the control (Figure 3, $F=3.49$, $P=0.048$). Like *L. hyssopifolia*, all radicle-emergent seeds of *L. perennis* also produced a normal and healthy shoot.

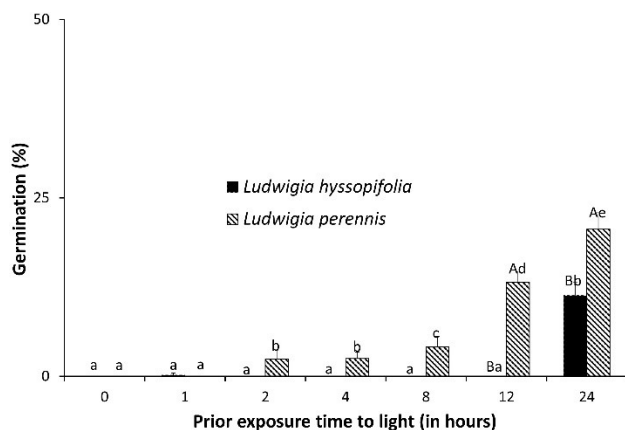


Fig. 2. Germination of *Ludwigia hyssopifolia* and *L. perennis* seeds at 25 °C in complete darkness after prior exposure to light for different periods (0, 1, 2, 4, 8, 12 and 24 h). Error bars are + SE. Different uppercase letters indicate significant differences between species within the same exposure time. Different lowercase letters indicate significant differences between different exposure times within the same species.

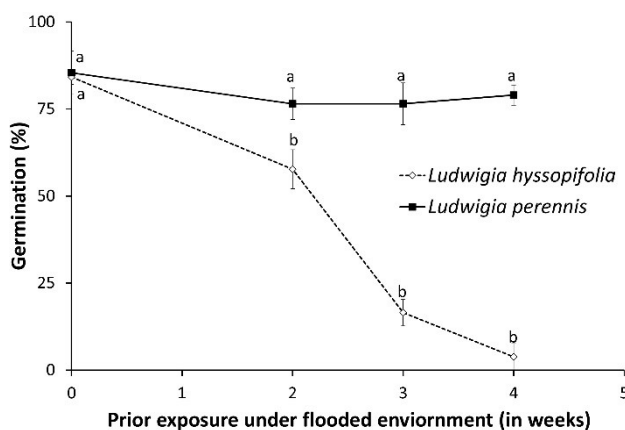


Fig. 3. Germination of *Ludwigia hyssopifolia* and *L. perennis* seeds after prior exposure for different duration (0, 2, 3 and 4 weeks) under flooded (hypoxic) environments in complete darkness and then moved to non-flooded environments (on filter papers moistened with distilled water at 25 °C in 12 hr / 12 hr light / dark conditions). Error bars are ± SE. Different lowercase letters indicate significant differences between different immersion times within the same species.

DISCUSSION

The seeds of the two study species were nondormant, as 80 – 90 % germinated within four days. This conclusion agrees with the observations of Oziegbe *et al.* (2010) and Sumudunie and Jayasuriya (2019), who reported that seeds of *L. abyssinica*, *L. adscendens*, *L. erecta*, *L. leptocarpa* and *L. octovalvis* and *L. peruviana*

are nondormant. However, some species of *Ludwigia* have been reported to produce seeds with physiological dormancy (Salisbury, 1972; Wulff and Briceno, 1976; Gillard *et al.*, 2017; Sumudunie and Jayasuriya, 2019). Interestingly, Sumudunie and Jayasuriya (2019) reported that *L. peruviana* and *L. decurrens* in the same habitat produce nondormant and physiologically dormant seeds, respectively. Moreover, our experiments showed that the seeds of *L. hyssopifolia* and *L. perennis* are photoblastic as observed for many other *Ludwigia* species (Salisbury, 1972; Wulff and Briceno, 1976; Gillard *et al.*, 2017; Sumudunie and Jayasuriya, 2019). Thus, *L. hyssopifolia* and *L. perennis* seeds can also form a soil seed bank. Seeds of the two species are tiny (diameter < 0.5 mm) and thus have a high potential to be incorporated into the soil. Tiny seeds can always be remarkably incorporated into the soil seed bank and move into deeper soil layers (Thompson *et al.*, 1993; Metzner *et al.*, 2017; and Shiferaw *et al.*, 2018). Further, when they were incorporated into the soil, seeds would not receive the required light conditions for germination and, thus, stay in the soil seed bank until brought to the soil surface, where they would be exposed to the light conditions required for germination. Since *L. perennis* seeds (0.00001 mg) were reported to be 14 times smaller than those of *L. hyssopifolia* seeds (0.00014 mg) (SNR, INSR and RBGK, 2023), *L. perennis* seeds have a higher potential to be incorporated into the deeper layers of the soil seed bank than *L. hyssopifolia*. Furthermore, both species are known to produce orthodox seeds (SNR, INSR and RBGK, 2023), an additional trait that plays a crucial role in seed persistence in the soil.

The ability to form a soil seed bank is an essential characteristic of a successful weed (Holzner, 1982; Grundy and Jones, 2002). Further, it is a problematic character for controlling the weeds. Thus, taking necessary precautions to deplete the soil seed banks is crucial when planning to eradicate these two species. Weed plants are recommended to be removed before they reach the stage of seed production and dispersal maturity. A pre-tillage (before crop sowing tillage) can expose buried weed seeds in the soil seed bank to light. When nondormant seeds of both species are exposed to light, and a sufficient amount of moisture is present, they would germinate. The emerging seedlings could be removed using physical or chemical eradication techniques for weed control.

Prior exposure to light causes the seeds of both species to germinate in completely dark conditions. However, only < 25 % of the seeds germinated in complete darkness, even after 24 hours of exposure to prior light. Thus, most seeds require > 48 hrs exposure to light for germination to progress. However, a gradual increase of germination with an increased exposure time reveals that seeds of *L. hyssopifolia* and *L. perennis* have a varying degree of sensitivity to light exposure, i.e., 12 hrs



exposure is enough to trigger the germination of ~ 10 % of the seeds, while another 15 % of the seeds require ~ 24 hrs exposure to light. Different sensitivities to light by the seeds could be a bet-hedging adaptation of these seeds (Venable, 2007). Soon after dispersal, some portion of the seeds potentially can germinate before they are incorporated into the soil seed bank.

As shown in our experiment, if seeds of both species experience continuously flooded environments and are exposed to light, they germinate (radicle emerge). However, no shoot emergence occurs, and germinated seeds fail to produce normal mature plants in a flooded environment. On the other hand, our experiments showed that if the flooded seeds were not exposed to light, they would not germinate. Further, 60 % of the *L. perennis* seeds and > 75 % of the *L. hyssopifolia* seeds germinated when they were moved from 2 weeks of exposure to a flooded environment to a non-flooded environment (on filter papers moistened with distilled water). That is, most of the seeds do not lose viability when they remain immersed in water for two weeks. Furthermore, even after being immersed in water for four weeks, > 75 % of the *L. perennis* seeds germinated, demonstrating that these seeds withstand hypoxic (flooded) conditions and overhydration stress and regain the germination ability soon after water withdrawal. Phartyal *et al.* (2020) noted similar seed germination behaviour in several species of mudflat plants.

Ludwigia perennis produces dust seeds, while *L. hyssopifolia* produces seeds that are about 0.5 mm in diameter. Thus, the seeds of *L. hyssopifolia* are many times larger than those of *L. perennis*. Since large seeds are said to be more vigorous than small ones (Roy *et al.*, 1996; Cookson *et al.*, 2001) and more tolerant of stress conditions (Donaldson, 1996; Canak *et al.*, 2020), it could be assumed that large seeds of *L. hyssopifolia* survive better under hypoxic conditions compared to smaller seeds of *L. perennis*. However, the opposite was observed, where smaller seeds of *L. perennis* tolerated hypoxic conditions better than *L. hyssopifolia* seeds. This may be due to the adaptation of these two species to their habitat conditions. Both species disperse seeds during the dry period when the mudflats and streams are dry. Since *L. perennis* seeds are tiny, they have a higher ability to be incorporated into the deep layers in the soil seed bank than those of *L. hyssopifolia* (Thompson *et al.*, 1993; Metzner *et al.*, 2017; Shiferaw *et al.*, 2018), where they are susceptible to more extended periods of flood and hypoxic conditions than seeds on the surface. As a result, *L. perennis* seeds must tolerate hypoxic conditions longer than *L. hyssopifolia* seeds to survive in habitats with these conditions. Thus, although these two species are in the same habitat, they have contrasting seed germination responses to similar flooding (hypoxic) environmental conditions. *Ludwigia hyssopifolia* produces large seeds that stay in the top layers of the soil and germinate as soon as conditions are favourable for germination. Since *L.*

hyssopifolia seedlings are produced from somewhat large seeds, their competitiveness will probably be higher than that of *L. perennis* (Coomes and Grubb, 2003; Wu and Du, 2008). However, *L. perennis* produces many tiny seeds capable of being incorporated into the deep layers of the soil seed bank, and seeds have developed a greater tolerance to flooding conditions than those of *L. hyssopifolia*. Therefore, they seem to have developed a greater tolerance to flooding conditions.

Flooding before rice seed sowing is often recommended as a method to control weeds, especially in integrated weed management planning (Hill *et al.*, 1994, 2001; Yan *et al.*, 2007; Chauhan, 2012b). Flooding the field is supposed to kill the existing weed community in the field (Hill *et al.*, 1994, 2001; Yan *et al.*, 2007; Chauhan, 2012b) as well as kill many seeds in the soil seed bank (Chauhan, 2012b). However, our results indicated that more than two weeks of flooding is required to kill *L. hyssopifolia* seeds, while flooding may not kill *L. perennis* seeds in the soil seed bank. Thus, to eradicate *L. perennis*, it is vital to promote most of the seeds to germinate before practising flooding. This can be quickly done because *L. perennis* seeds are nondormant but photoblastic; therefore, it is only necessary to expose the buried seeds to light. Thus, presowing tillage can be practised several times to expose the buried seeds. This method will expose both *L. perennis* and *L. hyssopifolia* seeds to light and promote germination. Then, subsequent flooding can eliminate the seedlings that were produced.

CONCLUSIONS

Seeds of *L. perennis* and *L. hyssopifolia* are nondormant but photoblastic. In addition, seeds of both species can tolerate flood for one week, while the flooding tolerance of *L. perennis* is more than four weeks. Although the two study species share the same habitat and have a phylogenetically close relationship, *L. perennis* and *L. hyssopifolia* have adopted two contrasting germination strategies with regard to flooding environmental conditions of their habitat. To control these two troublesome weeds in rice fields, we recommend that fields be given several rounds of presowing tillage and then flooded for one week.

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