

Impact of ploughing on soil seed bank dynamics in temporary pools

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Abstract We examined the impact of ploughing on soil seed banks of plant communities living in temporary marshes located in agricultural fields. The quantity, quality and vertical distribution of seeds were quantified under ploughed or unploughed treatment at community level. We also focussed on a typical semi-aquatic species, *Damasonium alisma*, to investigate the impact of ploughing at population level. We used two complementary techniques to study seed banks: hand sorting and seedling emergence. We found that species richness of seeds, seed abundance and germination ability were strongly affected by ploughing at community level. Concerning *D. alisma*, most of the seeds (56%) were stored in the two deepest soil layers among the four considered in ploughed pools. Moreover, the germination rate was higher for buried seeds (84%) than for seeds collected at the surface (33.6%). These patterns were almost inverted in

unploughed pools. Our results agree with the temporal storage effect generally suggested to describe the seed bank property of plant communities. But in addition, we showed that ploughing induces a spatial storage effect in accumulating species and individuals in the seed banks that favourably influence community dynamics. We conclude that, in contrast to what is usually thought, ploughing disturbance can be of benefit for such ephemeral wetland vegetation.

Keywords Agricultural practices · Community · *Damasonium alisma* · Ephemeral vegetation · Storage effect · Wetland

Introduction

Several species have evolved with human activities, and many of them can even be threatened by the abandonment of anthropogenic practices. This link has been primarily studied in agricultural landscapes, where biodiversity and human practices are strongly related (Stoate et al. 2001). Through their impact on population dynamics, agricultural practices have contributed to shape species richness and distribution of uncultivated plants. Temporary pools located in arable fields provide a good illustration of this relationship between agricultural practices and plant communities. Their drainage was

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recently undertaken, inducing the decline of such pools (Gallego-Fernández et al. 1999; Le-feuvre et al. 2000). Consequently, the flora adapted to this type of environment, composed mainly of small annual plants, is considered to be threatened, and many of such species are legally protected.

Among agricultural practices affecting plant communities, ploughing is one of the most deleterious since it physically removes seeds and seedlings from the soil surface (Ghersa and Martínez-Ghersa 2000; Tørresen and Skuterud 2002). On the other hand, seeds play a key role on individual's and species' survival (Shaukat and Siddiqui 2004; Adams et al. 2005). Soil seed bank was therefore usually seen as a basic way to momentarily escape unfavourable environmental conditions as severe drought or frost (Cohen 1966). More recently, Stöcklin and Fisher (1999) showed that species with high seed longevity had lower extinction rates. On an evolutionary scale, seed bank and dormancy were also presented as a way to face unpredictable environmental changes (Pacala 1986; Thrall et al. 1989), to maintain genetic polymorphism or to promote species diversity (Templeton and Levin 1979; Hedrick 1995; Vitalis et al. 2004). These considerations have been mainly theoretical and rarely tested in natural populations through experimental approaches (but see Kalisz 1991; Bliss and Zedler 1998; Bonis 1998). At the community level, the positive effects of seed bank properties have also been used as a relevant tool in conservation and restoration programmes (Miller and Cummins 2003) or ecosystem management (Wienhold and van der Valk 1989; Warr et al. 1993; Jalili et al. 2003; Middleton 2003). However, none of these previous studies was done on wetland communities affected by ploughing.

In natural wetland communities, seedling emergence is usually shown to be strongly related to the fluctuating water level (van der Valk 1978). But in cultivated fields, the seed bank dynamics may completely differ from what was found in uncultivated lands since ploughing may have a deep impact on seed distribution and viability. Indeed, the main role of ploughing is precisely to

kill weed seeds and seedlings before cultivated plants are sowed (Roberts 1981; Beuret 1989). However, the consequences of this agricultural practice on community dynamics in wetland communities are not clearly established. For wetland species affected by ploughing, a seed bank is likely to act as an effective source of colonising species and to determine the above-ground species composition even after deep ploughing (Luzuriaga et al. 2005).

To study seed banks, two techniques have been commonly used: hand sorting and seedling emergence (Standifer 1980). Usually, each of these two techniques appears to be insufficient by itself. Seedling emergence gives information about the plant community; it reveals a large part of the species contained in the soil samples and their interactions during germination are more or less preserved. However, many seeds cannot germinate in ex situ conditions, and some of the species are not detected with this technique. Consequently, seed hand sorting is often more accurate. Unfortunately, this method of direct counting gives no information on the ability of seeds to grow in their natural conditions, and it breaks the natural vertical structure of the seed bank. Furthermore, very small seed species can remain undetected or unidentified with this technique. The cultivation of the seeds is thus often necessary afterwards. In fact, these two techniques are complementary although in most cases they are not utilised together.

The aim of this paper is to understand the impact of ploughing on seed banks of temporary pools located in arable fields at community and population levels using both seedling emergence and soil sieving. An experimental approach was used to compare the quantity, the vertical distribution and the quality of seeds between ploughed and unploughed areas. We addressed two specific objectives: (1) What is the impact of ploughing on the seed banks' viability for plant communities living in temporary pools? (2) What is the impact of ploughing on a typical ephemeral threatened wetland species, *Damasonium alisma*, at the population level?

Methods

Pool description

Clay layers induce the formation of temporary pools in arable fields. Such pools generally fill up during the winter period (for a 30 cm maximum depth during the study) and progressively dry up during spring. Two of these pools located in the agricultural neighborhoods of Paris (France) were studied: one near the city of Echarcon (E) and the other near the city of Fleury-Merogis (F). Both pools E and F were round and had approximately the same size of 50 m² in March 2003. The E pool was located exactly at the edge of a cultivated field and consequently one half was located in the cultivated area (called Ec for E cultivated) and the other half was located in an uncultivated area (called Ew for E wild area). This pool was located in a typical intensive farmland landscape of annual arable crops. The land-use past of this pool remained similar for a period longer than 5 years, but the annual species grown in the cultivated area may have changed each year. The F pool was located in a wild area, which had not been cultivated for at least 5 years. The F pool was situated 5 km away from the E pool. The three pools had the same type of soils (uniformity of edaphic conditions) and provided our natural experimental framework to test the influence of ploughing on temporary wetland communities.

Species description

All ephemeral semi-aquatic species growing in temporary pools were studied. Among all species, *Damasonium alisma* Miller (*Alismataceae*), the star fruit, was more specifically considered for some experiments. This species is a rare annual plant growing in the muddy margins of pools with seasonal fluctuating water levels. It is a small (5–30 cm high) white flowered plant. Seeds germinate in early spring only under water, and the plant finishes its cycle before the pools have completely dried during summer. Its mating system is presumably facultative autogamous (Vuille 1987). Its distribution has

decreased during the twentieth century because of the disappearance of wet zones in Europe (Wheeler 2000). This semi-aquatic herb is found in England, France, Italy, Spain and possibly south-western Asia (Birkinshaw 1994). It is legally protected in France (Danton and Baffray 1995).

Seed bank study

Our sampling method was strongly influenced by the fact that we worked on protected species (seed samples had to be few). However, the small size of the pools allowed us to get sufficient information with few samples. Ten replicate soil samples (cylinders of 7-cm-diameter and 15-cm-depth) were cored in each pool. This sampling was performed in March 2003, i.e. after fall ploughing and before 2003 seed production. Each sample was then divided into 5 depth layers of 3-cm-thickness each, from the top to the bottom (0–3, 3–6, 6–9, 9–12, and 12–15 cm). Such division was limited in unploughed pools (F and Ew), in which the soil was so compact that the deepest layer (12–15 cm) was hardly reached and therefore not considered. Finally, the soil of each layer was sieved through 500- and 250- μ m-aperture meshes. All seeds of each species collected by this technique were hand sorted and identified.

One hundred and fifty *D. alisma* seeds were isolated from each layer and cultivated. Cultivation was performed in waterproof pots placed in incubators (12 h of light at 15°C and 12 h of obscurity at 10°C), filled with sterilized pool soil. Since *D. alisma* seeds were shown to germinate only below water and not just in damp conditions (Birkinshaw 1994), each pot was identically watered (i.e. the soil was kept under 1 cm of distilled water, pH = 7), and randomly positioned. Seedlings were numbered after 40 days.

To study seedling dynamics for the whole community, 15 other soil cores (cylinders of 20-cm-depth and 5-cm-diameter) were randomly extracted from each part of the E pool (Ec and Ew) and from the F pool in March 2003. Each sample was then divided in two layers: an upper stratum (U) and a lower stratum (L) of 10-cm-

thickness each (0–10 and 10–20 cm). After adjustment of their weight, each layer was spread out in large waterproof plastic pots and placed in the garden of the National Botanical Conservatory of the Parisian Basin. Each layer was watered regularly to keep the soil surface under 1 cm of water. The location of each pot in the garden was regularly randomised. Pots with sterile soil were also cultivated to check for seed contamination from the garden. Emergence of seedlings was assessed weekly during 6 weeks.

Data analysis

First, we wanted to test the effect of ploughing on seeds distribution along the vertical. The number of seeds collected from each depth layer obtained from Ec, Ew and F after hand sorting, was compared in each pool and between pools. Since each depth layer was not independent from one another but was grouped according to the core sample, we performed a linear mixed model. Mixed-effect models extend linear models by incorporating random effect to account for correlation among observations within the same group (Pinhero and Douglas 2000). Therefore, we incorporated “Depth”, “Pool”, and interaction between “Pool” and “Depth” as fixed effects and “Core” as a random effect. We used the same method with number of seeds of *D. alisma* only. The number of seeds was log transformed for these analyses. To test the effect of ploughing on *D. alisma* seed quality, we performed a regression analysis on the germination percentage of the 150 seeds we had cultivated, according to depth layers.

To quantify seedling dynamics, the cumulative number of seedlings found in each pot for each species recorded among the 6 week sampling assessments was considered as a dependent variable. To identify distribution trends of number of seedlings and species richness across the upper (U) and the lower (L) sediment layer within each pool (Ec, Ew and F), we performed *t*-test for paired comparisons. For these analyses, the numbers of seedlings and species richness were log transformed. We used S-PLUS (Math Soft 1999) for all our statistical analysis and considered a test as statistically significant at 5% level.

Table 1 Effects of pool, depth and interaction between pool and depth on the number of seeds found in the core samples by hand sorting (log transformed)

| Source | DF | F | Prob > F |
|--------------|----|-------|----------|
| Pool | 2 | 2.67 | 0.0705 |
| Depth | 1 | 93.63 | <0.001 |
| Pool × depth | 2 | 46.00 | <0.001 |

Pool and depth were considered as fixed effects and core as a random effect of the mixed model (LME S-PLUS)

Results

Impact of ploughing on wetland community

The number of seeds was not markedly different among pools ($P = 0.07$) but depended strongly on the depth at which they had been cored ($P < 0.001$) (Table 1). Moreover, the effect of depth was contrasted among pools (interaction Pool × Depth, $P < 0.001$). In particular, more seeds were found in the upper soil layers (i.e. near the surface) in the fallow parts of the pools, whereas in the cultivated parts of the pools, more seeds were found in lower layers (Fig. 1).

Seedling emergence

No germination occurred in the sterilised soil pots. In the E pool, all the species that emerged from the cores extracted from the cultivated pool (Ec) were also present in the cores coming from Ew: *Lythrum hyssopifolia* L., *Lythrum portula* L., *Juncus tenageia* L., *Polygonum persicaria* L., *Gnaphalium uliginosum* L., *Damasonium alisma* Mill. (Table 2). Four species were only found in the wild part of the pool: *Juncus bufonius* L., *Echinochloa crus-galli* L., *Ranunculus sardous* C., *Elatine alsinastrum* L. Seedlings abundance of a given species present in both parts of the pool differed (e.g. *P. persicaria* was more abundant in the cultivated part while *J. tenageia* was more abundant in the wild part).

All together, more seedlings emerged from the lower layers of the fallow pools ($t = -5.46$, d.f. = 14, $P < 0.001$ for Ew and $t = -3.13$, d.f. = 14, $P = 0.007$ for F). But no difference was found between layers in the cultivated part ($t = -0.08$, d.f. = 14, $P = 0.93$) of the pool (Fig. 2a). With regards to the number of different

Fig. 1 Relationship between number of seeds of the whole community (log transformed) and depth in each pool. Seeds were directly counted after the sieving of each depth layer from (a) the unploughed F pool, (b) the uncultivated area Ew and (c) the cultivated area Ec

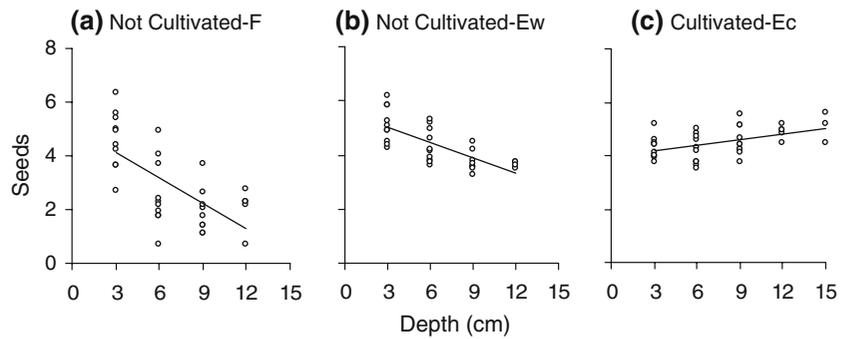


Table 2 Total number of seedlings of each wetland taxum counted in all pots during the direct seedling experiment

| Species | Ec | Ew | F |
|-------------------------------|------|------|------|
| <i>Lythrum hyssopifolia</i> | 347 | 576 | 534 |
| <i>Lythrum portula</i> | 2733 | 2735 | 20 |
| <i>Juncus tenageia</i> | 62 | 1045 | 62 |
| <i>Polygonum persicaria</i> | 170 | 15 | 36 |
| <i>Damasonium alisma</i> | 527 | 598 | 355 |
| <i>Gnaphalium uliginosum</i> | 2 | 19 | 74 |
| <i>Juncus bufonius</i> | 0 | 60 | 34 |
| <i>Echinochloa crus-galli</i> | 0 | 6 | 1380 |
| <i>Ranunculus sardous</i> | 0 | 8 | 36 |
| <i>Elatine alsinastrum</i> | 0 | 3 | 0 |

d.f. = 14, $P = 0.0115$), but no difference between layers in fallow pools was detected ($t = -1.97$, d.f. = 14, $P = 0.068$ for Ew and $t = -0.12$, d.f. = 14, $P = 0.90$ for F) (Fig. 2b).

Focus on *Damasonium alisma*

The number of *D. alisma* seeds per soil sample from sieved seed bank differed among pools ($P = 0.005$) (Table 3). In particular, the number of seeds showed an exponential decrease with depth in the uncultivated pools whereas there was a slight linear increase of seed quantity with depth in the ploughed pool (Fig. 3). Germination percentage was also different among pools according to the depth at which they were extracted. In the cultivated pool, seeds from the deeper layers had

species of seeds that germinated in the pots, more species in the lower layer compared to the upper one were found in the cultivated pool ($t = 2.90$,

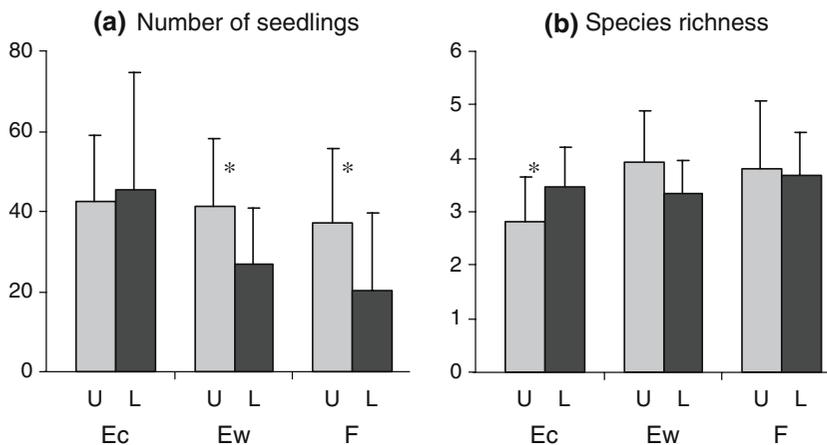


Fig. 2 (a) Seedlings distribution among layers revealed by direct seedling emergence experiment. Each sample was divided into two layers: U (the upper layer) in grey bars and L (the lower layer) in black bars. Each bar represents the mean cumulative data (log transformed) with its

standard deviation. An asterisk (*) denotes significant differences ($P < 0.05$) between U and L (t -test for paired data S-PLUS 2000). (b) Relative distribution of species richness recorded during seedling emergence for U and L in each pool

Table 3 Comparison of *D. alisma* seed numbers between pools including the effect of pool (Ew, Ec and F), depth (five layers) and interaction between pool and depth

| Source | DF | F | Prob > F |
|--------------|----|-------|----------|
| Pool | 2 | 5.50 | 0.005 |
| Depth | 1 | 70.53 | <0.001 |
| Pool × depth | 2 | 32.89 | <0.001 |

Core was considered as a random effect in the mixed model (LME S-PLUS). Number of seeds was log transformed for this analysis

a higher germination percentage than those of the upper layers. Conversely, in the wild pools, the seeds from the upper layers had a higher germination rate than the seeds from the deeper layers (Fig. 4).

Discussion

Impact of ploughing on plant community

Seed banks distribution was strongly affected by ploughing and differed between cultivated and wild pools. In the wild pools, more seeds were counted from the samples cored at the surface of the soil than from deeper layers. An opposite trend was found in the cultivated pool. Concerning the number of seeds that germinated from the soil samples (seedling emergence), no germination occurred in the sterilized soil pots. Therefore, we could assume that all the seedlings found in the pots during the experiment were the result of seeds germinating from samples cored in the pools. Again, more seedlings emerged from the upper layers of the wild pools whereas no difference was observed among layers in the cultivated pool. These first results were expected.

Fig. 3 Relationship between number of seeds of *D. alisma* (log transformed) and depth in each pool. Seeds were counted directly after the sieving of each depth layer from (a) the unploughed F pool, (b) the uncultivated area Ew and (c) the cultivated area Ec

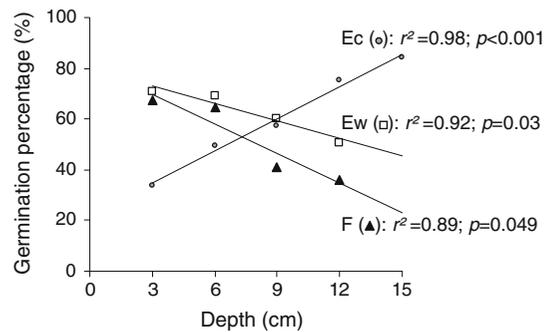
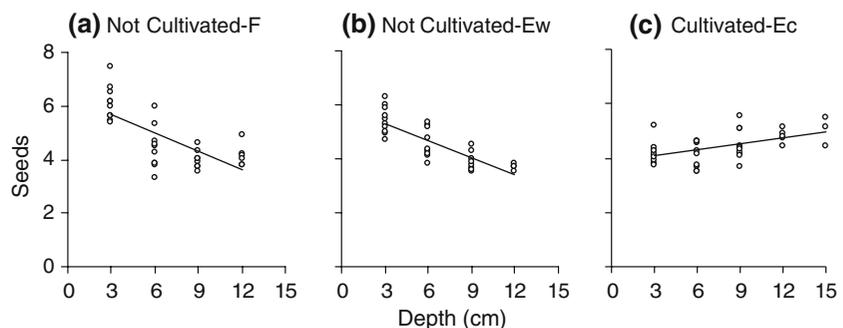


Fig. 4 Germination percentage of *D. alisma* seeds as a function of the depth layer in each pool. Each value represents, for a given depth, the percentage of seeds (among 150) that germinated in the incubator room. Square, triangle and ring symbol represent respectively results for Ew, F and Ec

Since one of the aims of ploughing is to turn over the soil, the quantitative distribution of soil seed banks was deeply affected and seeds were mostly buried by ploughing in cultivated pools.

We also found that the relative abundance of species among pools in the seedling emergence was contrasted: some species were more abundant in the cultivated part of the E pool while other species were mainly present in the wild part. For any given seed bank, the resulting emerging flora can be very different between pools because for each species, a particular set of conditions needs to be fulfilled in order to ensure successful germination and growth. In particular, in temporary pools, the fluctuating level of water was pointed out as a major factor influencing seedling recruitment from the seed bank (van der Valk 1978). This seed bank property was seen as a temporal storage effect because variable conditions will lead to the recruitment of some species only, excluding the others (Bonis 1998; Bliss and

Zedler 1998; Nicol et al. 2003; Warwick and Brock 2003). This property induces a contrast between species' abundance in the seed banks and species abundance observed in the field among adult plants (Jutila 2003). Other agricultural practices such as the use of herbicide or fertilisers may contribute to shape the seedlings' recruitment as well, and therefore certainly contribute to the selection of a different community from the seed bank (Tørresen and Skuterud 2002; Shaukat and Siddiqui 2004).

Interestingly, we found not only that more species were located deep in the soil in the cultivated pool, but also that most of their seeds were actually still viable. This highlights that many species of these wetland communities are able to bear a certain period of burying. In fact, a relatively large proportion of rare and endangered species living in temporary pools are expected to form long-term persistent seed banks, because this trait is susceptible to be selected in unpredictable environmental changes (Hölzel et al. 2004). Consequently, for this kind of ephemeral wetland community, most seeds are not killed by ploughing. Instead, a large part of the seed bank is stored in deep soil layers. As these results suggest, in storing seeds in the deep layers of the soil, ploughing induces a spatial storage effect on the seed banks of such communities.

Impact of ploughing on *Damasonium alisma*

We also focussed on a rare threatened species, *D. alisma*, that is typically found in temporary wetlands. As for community results, the vertical distribution of seeds was strongly affected by ploughing; for the wild pools, the seed distribution showed an exponential decrease with depth, whereas a slight linear increase of seed abundance with depth was observed in the cultivated pool. Moreover, our results concerning germination percentage showed that, in the wild pools, the seeds located in the upper layers (the first 3 cm) had a higher germination rate than the seeds in the deeper layers (from 3 to 15 cm). This result is consistent with other seed bank studies of other species performed in temporary pools, though uncultivated (Grillas et al. 1993;

Bonis and Lepart 1994; De Winton et al. 2000). But more interestingly, for the pool located in the cultivated field, we showed that the opposite tendency was produced: seeds were more abundant and had a better germination rate in the deeper soil layers. This is probably partly due to the interaction between the life cycle of the species and the timing of ploughing. Plants release seeds in late spring and the soil is ploughed during fall, burying the seeds that have been produced a few months before, and bringing up old seeds that had been produced formerly (one or more years before). Since soil samples were cored during early springtime, the best seeds (the youngest ones) were located deep in the soil. Therefore, ploughing had not only accumulated most of the seeds in deep layers, but had also concentrated the best seeds. Beyond this temporal aspect, which likely explains the inversion of the seed quality pattern in ploughed pool, the moist conditions probably also enhance seed survival in deep layers. Indeed, for this semi-aquatic species, dormant seeds remain dormant as long as they are either constantly damp or constantly submerged (Birkenshaw 1994). These first results concerning *D. alisma* are consistent with the spatial storage effect we have mentioned for the community results.

Birkenshaw (1994) showed that for *D. alisma*, seeds can germinate only when situated in the first 3 cm of the soil. Consequently, seeds that were actually able to germinate in our study were those of the first layer (i.e the first 3 cm). As our results suggested, these seeds were more abundant and had a better germination rate in the wild pools. Therefore, one should expect to find more adult plants in the wild pools, than in ploughed ones. Yet the botanical inventory performed in 2002 showed that *D. alisma* adult plants were about three times more abundant in the cultivated part than in the wild part of the pool (Decencière 2002). Moreover, this species is known for being chiefly present in disturbed pools (Arnal 1996). At first sight, these field results could be surprising according to our seed bank investigation, since we expected to find more adult plants in the wild pools. Thus, the quantity and quality of the seeds are not the only

factors that influence the relative abundance of the species among pools. It is likely that in wild pools, post germination obstacles such as competition with other species affect seedlings growth. In cultivated pools, perennial herbs were removed by ploughing, competition was probably lower and thus the viability of *D. alisma* seedlings was enhanced.

D. alisma seeds seemed to tolerate the burying conditions since the seeds deeply cored had a higher germination ability. When buried, seeds are protected from unfavourable environmental conditions while in the wild pools, most of the seeds germinate at the same time. Such conclusions agree with demographic models showing that seed survival is crucial for population viability of wetland plants (Adams 2005). During a drought, for example, most of the seedlings would be killed in wild pools, whereas seeds are largely protected in deep layers in cultivated fields and are able to give birth to new seedlings the following season, after the next ploughing. In addition, seedlings will face lower competition. In that manner, as for the whole community, seed banks constitute a spatial protected stock of individuals at the population level for *D. alisma*.

In conclusion, we showed that ploughing had a strong effect on species distribution and abundance of temporary wetland communities. Moreover, in allowing constitution and preservation of seed banks and in removing perennial species, rare annual species such as *D. alisma* can be protected in the long run. In this particular case, we believe that agricultural practices could have a beneficial effect for the preservation of rare species. Further investigations are needed, however, to understand the effects of other agricultural practices (Hölzel et al. 2004). The understanding of the processes that maintain this specific flora in the pools should be taken into account in order to develop more sustainable management policies.

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