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# The influence of time on the soil seed bank and vegetation across a landscape-scale wetland restoration project

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**Abstract**

Wicken Fen National Nature Reserve (NNR) in Cambridgeshire, UK, is a wetland of international importance, but is isolated in a landscape now dominated by arable farming on drained fen peats. The prospect of species extinctions within the NNR led to the creation of the Wicken Fen Vision, an ambitious project expanding the reserve boundary by the purchase and restoration, through natural regeneration, of c.50km² of arable land. We sampled three fields from each of three distinct age-categories of restoration land (5, 15 and 60 years post-arable), and three fields within the adjacent, undrained NNR, to determine (1) changes in seed bank composition across the study area, (2) relationships between restoration age, the seed bank and standing vegetation, and (3) the contribution of the seed bank to restoring wetland vegetation. Historic arable management contributed to a ‘vertical mixing’ effect in the seed bank of the youngest two age-categories, with associated and significant differences in species functional traits across the study area. Plants associated with the NNR were absent from all restoration age-categories. Seed bank species common to all ages-categories exhibited a bias towards moderate to high Ellenberg F (moisture) values, persistent seed banks, and lateral vegetative spread. Relatively short (c.6 years) periods of drainage and ploughing impact heavily upon seed bank diversity and soils, resulting in a lack of pre-drainage vegetation, even after decades of restoration adjacent to intact, species-rich habitat. However, the seed banks of highly degraded fields can contribute towards the creation of novel wetland vegetation assemblages over time and under suitable environmental conditions.

**Keywords**

fen; landscape-scale; lateral vegetative spread; natural regeneration; restoration; seed bank; standing vegetation; wetland; Wicken Fen

## Introduction

In Britain, as in other parts of Europe, fen meadow and lowland wet grassland habitats have declined dramatically in the past century due to land drainage and agricultural intensification (Anon. 1998, Manchester et al. 1999). This trend has been particularly marked in the Fens of East Anglia (UK) where a huge expanse of topogenous and ombrogenous mire habitat once covering an area of 3,850km² now totals only 7.13km². Here rapid habitat loss began in the 17$^{th}$ century with drainage and considerable re-alignment of river courses to create grazing pastures. Technological advances from the mid-19th century onward led to suitable conditions for crop production and ultimately the dominant intensive arable land use that is prevalent today. The remaining undrained habitat is now located within a few isolated nature reserves on the southern fringes of the original Fen basin (Moore 1997).

The dramatic decline in undrained habitat has promoted research into the potential for the restoration of fen and wet grassland vegetation alliances through the utilisation of the soil seed bank (Thompson & Grime 1979; Grootjans & van Diggelen 1995; Bekker et al. 1998a; Jensen 1998; Wagner et al. 2003). The composition and resilience of the seed bank is known to play an important role in the process of habitat restoration (Roberts 1981, Bekker et al. 1997, Thompson et al. 1997; Pakeman & Small 2005), although the value of the seed bank to restoration varies greatly according to the type and duration of degradation activities.

Investigations examining fen meadow and wet grassland have generally concluded that the seeds of the main constituent species of undrained habitats are transient in nature and are not viable in the seed bank after a relatively short time period (Jansen et al. 2000; Matus et al. 2003; Blomqvist et al 2003; but see Jensen 2004). Under this scenario, re-establishing species based on pre-degradation assemblages must initially rely upon the restoration of dispersal vectors which were historically present (Middleton 1999) or upon artificial introduction through direct seeding, transplanting donor hay (Klimkowska et al. 2009) or the planting of propagated plants (Wells 1983; McDonald et al. 1996; Galatowitsch & van der Valk 1994). However, these approaches, even if successful in restoring wetland function, cannot restore the former wetland ecosystem because peat wastage/degradation of soils, hydrological fragmentation and habitat isolation have all combined to create a novel starting point for restoration (Hughes et al. 2005).

Increasingly, wetland restoration projects are being designed at a landscape scale (e.g. Oostvaardersplassen, The Netherlands; Wicken Fen Vision, UK www.wicken.org.uk/vision; Great Fen Project UK www.greatfen.org.uk) and often include management based on the concept of "re-naturation"; allowing ecosystem change to a future natural state through minimal anthropogenic intervention (Pfadenhauer & Klötzli 1996). Such a future natural state incorporates the historic changes that will have occurred in the hydrology and soils as well as the biota of highly degraded systems. Consequently, restoration in this context does not imply replicating complex species assemblages that were present historically. As a result, novel assemblages may be established through a combination of the availability of viable seeds in the soil, natural dispersal of seed and plant material, and suitable conditions for germination and establishment. It follows that knowledge of the composition and functional traits of viable seeds in restoration soils is a necessary step in helping to predict future natural states.

The main purpose of this study was to evaluate the influence of the seed bank on wetland habitat development across a project area containing land in three distinct restoration age-categories, located adjacent to Wicken Fen National Nature Reserve (NNR) in East Anglia, U.K. Through the collection of seed bank and standing vegetation data from within a landscape-scale restoration project and the bordering NNR, the following three research questions were addressed:

- How does the seed bank of highly degraded fields change with time under a wetland restoration regime characterised by natural regeneration and extensive grazing?

- How does the relationship between the seed bank and standing vegetation change with restoration age?
- Can the seed bank contribute to the restoration of wetland vegetation?

## Material and Methods

*Location of study site*

The study site was situated 16 miles north of Cambridge (UK) (52.3°N, 0.3°E) and encompasses both Wicken Fen National Nature Reserve and the 'Wicken Fen Vision', a landscape-scale wetland restoration initiative set up by the National Trust (the NGO that owns the site) adjacent to Wicken Fen NNR. The area receives an average annual rainfall of 530mm. Average annual potential evapotranspiration rates in the area are 594mm, and exceed rainfall during much of the growing season (McCartney & de la Hera 2004; McCartney et al. 2001).

*Wicken Fen NNR and the Wicken Vision*

Wicken Fen NNR, one of the oldest nature reserves in the UK, comprises 159 ha of undrained alkaline peat and supports nationally scarce fen grassland and tall herb communities associated with moderate to low fertility floodplain fens with moderate to high pH (McCartney & de la Hera 2004). The site is of European importance for its *Molinia caerulea-Cirsium dissectum* community, and it has a remarkably diverse flora and fauna, with close to 8,000 species recorded (Warrington et al. 2009). For the past century, the reserve has been surrounded by drained and intensively farmed arable land, effectively isolating the NNR and its associated species and habitats. It is now perched 2-3 metres above the agricultural land due to peat drainage and wastage.

The Wicken Fen Vision aims to purchase *ca* 53km² of predominantly arable land, stretching from the boundary of Wicken Fen NNR to the northern boundary of the city of Cambridge. The project has so far purchased 9.3km² (17.5%) of the proposed project area. It was initiated as a response to the prospect of potential species extinctions within the relatively small area of Wicken Fen NNR. The expansion of the nature reserve boundary was seen as a possible solution to this problem by providing additional habitats in which species might complete their life cycles. As the project evolved, it became clear that large areas of restoration land could also have the potential to accommodate new species not known from the NNR, as well as acting as refuges and stepping stones in the wider landscape for a variety of migratory species. The restoration area, located on former intensively farmed arable land, is now managed by natural regeneration, hydrological manipulation where practicable, and an extensive grazing regime employing hardy breeds of Highland cattle and Konik ponies. This low-intensity management strategy allows for the potential formation of a constantly changing mosaic of habitats rather than a targeted set of habitats and vegetation alliances in fixed locations, and may be viewed as a more natural, cost-effective (Primack 1996) and adaptable form of landscape-scale conservation management.

*Seed bank and vegetation sampling*

As a result of the staggered nature of land purchase, it was possible to select three distinct restoration age-categories for sampling across the project area: 5, 15 and 60 years post-arable. The oldest restoration area (60 years) was drained and ploughed during the early 1940s under the Ministry of Agriculture's 'Dig for Victory' campaign (Ennion 1949), before being restored by natural regeneration in the late 1940s and early 1950s by the National Trust. The 5 and 15 year age-categories were in an arable regime for considerably longer, with available information suggesting a period of degradation of not less than seventy years. In addition to these three age-categories, a fourth area was sampled from within the undrained Wicken Fen NNR to provide a reference area. Although the remnant soils in all the restoration areas consist of shallow, highly degraded peats, the historical variations in duration, location and intensity of arable farming have contributed to differences in soil profiles for each of the three age-categories (see Table 1). Three fields were sampled within each age-category.

Soil seed banks were sampled in November 2007 using an auger of 6cm diameter and 10cm depth. Three compartments (fields surrounded by wet ditches) were sampled within each of the three age-categories of restoration land and the reference area. In each compartment a transect of 50m length was established parallel with and 2m distant from a chosen ditch edge, with a second transect 32m from the ditch edge. Two bulk samples (each consisting of 10 soil cores taken at regular intervals from each transect), were divided into two depths (0-5 cm; 5-10 cm) to investigate the vertical distribution of seeds. This generated four samples (i.e. 2 depths for each bulk sample) for each transect, eight samples for each compartment, and 24 samples for each age-category and the reference area. The soil volume for each pooled sample was 1411cm$^3$, which exceeds the volumes of 400-600 cm$^3$ (Hayashi & Numata 1971) and 1-1.2 litres (Hutchings & Booth 1996) recommended to accurately detect species composition in a grassland seed bank. Immediately following collection, samples were stored in the dark at a constant 3°C for four weeks to mimic natural stratification, and then passed through a 10mm diameter wire sieve to extract plant debris. Each sample was then mixed thoroughly before being spread to an even depth of 4cm above a 1cm layer of sterilised sharp sand in a germination tray. Trays were randomly placed in an unheated greenhouse on January 5th 2008 and watered from below using an automated system. Preset light controls allowed for a daily constant of 16 hours light and 8 hours darkness. Germination was recorded for a 12 month period, with seedlings identified, counted and extracted every three weeks. Disturbance of the samples took place every three months to promote germination in potentially buried seed. Species that were not readily identifiable at an early stage were removed and grown on until diagnostic features were visible. Five control trays filled with sterilised peat were included to test for possible contamination of samples by airborne seeds.

Standing vegetation was recorded in July 2007 using five 4-m² quadrats randomly placed along each 50m seed bank transect, with species (nomenclature follows Stace 1997) and percentage abundance recorded.

*Data analysis*

For the examination of seed bank and standing vegetation composition Detrended Correspondence Analysis (DCA) was performed using the package CANOCO for Windows 4.5 (ter Braak & Ŝmilauer 1997-2002). Data were log (x+1) transformed and rare species downweighted to prevent both very common and rare species from unduly influencing the ordination. For both vegetation and seed bank data, hierarchical analysis of variance (ANOVA) was used to test for differences between 1) age-categories, 2) distances from the ditch and 3) soil layer (seed bank only) on the first and second DCA axes. “Treatment” effects were tested against the appropriate error term; age in the field stratum, distance in the transect stratum, and depth at the soil core stratum, followed by Tukey's HSD to compare categories when tests were significant.

The potential for the seed bank to influence standing vegetation under a range of biophysical conditions (for example different hydroperiods) was addressed through identifying species functional traits. Species were classified to C-S-R and Regeneration Strategy types according to Grime et al. (2007) and were categorised for their tolerance to varying hydrological conditions using Ellenberg's F (moisture) values (Hill et al. 2004). In the C-S-R analysis, C = Competitor, S = Stress-tolerant, R = Ruderal (with CR, CS, SR and CSR employed as intermediate strategies). Four main Regeneration Strategy types were present in the seed bank and standing vegetation; V = vegetative expansion; S = seasonal regeneration; W = numerous widely dispersed seeds; $B_s$ = persistent seed bank, with many species having more than one association to a strategy type. Comparison of C-S-R strategy types across restoration age-categories and between core depths was made for seed bank species by calculating a cover-weighted mean for each bulked soil core sample, with one-way ANOVA used to test for differences between age and depth categories. Regeneration Strategies for each restoration age were calculated for seed bank species and standing vegetation using a cover-weighted mean at the field scale. Ellenberg values for F (moisture) were calculated for seed bank and standing vegetation following the same procedure.

Sørenson's similarity coefficient [$S_s = 2c / (a + b)$, where a = number of species in seed bank, b = number of species in vegetation, and c = number of species common to both seed bank and vegetation] was used to determine the similarity of the seed bank and standing vegetation for each restoration age-category based on presence-absence data using the statistical package MVSP (Kovach 1993).

Predictions on the potential for the seed bank to influence vegetation assemblages incorporated pooling species which were present across all age-categories sampled (termed 'constant species') and those which were specific to one of the age-categories (termed 'exclusive species').

## Results

### *Seed bank composition in different age-categories of restoration land*

A total of 9,882 seedlings from 135 species emerged from the soil samples. Monocotyledons accounted for 31 species (23.0%) and 39.8 % of seed bank seedlings, whilst dicotyledons accounted for 104 species (77.0%) and 61.24% of the total number of seedlings. The most common species in the seed bank were *Poa trivialis* (11.7%), *Urtica dioica* (8.3%), *Eupatorium cannabinum* (6.9%), *Juncus inflexus* (6.6%), *Samolus valerandi* (6.2%), *Carex hirta* (3.2%) and *Agrostis stolonifera* (3.4%). The mean number of species, as determined by the Tukey HSD, did not vary significantly with depth between the 5 and 15 year age-categories (P=0.245). Depth was significant between the 15 and 60 year age-categories (P<0.001) and the 60 year and reference categories (P<0.001), with the upper soil layer (0-5cm) containing more species on average than the lower soil layer (5-10cm).

In the seed bank ordination, there were highly significant differences between age-categories on both the first ($F_{3,8}$= 70.51, P<0.001) and second ($F_{3,8}$= 62.74, P<0.001) DCA axes. The ordination (Figure 1) displays a separation of the age-categories, and an apparent progression from the early stages of restoration through to the oldest of the restoration ages sampled. The reference seed bank category is quite separate from the apparent trajectory of the restoration age-categories.

The standing vegetation ordination (Figure 2) also produced clear distinctions between restoration age-categories, with highly significant differences between all four ages on the first ($F_{3,8}$=71.89, P<0.001) but not the second ($F_{3,8}$= 0.70, P=0.58) DCA axes.

***Comparisons between seed banks and standing vegetation***

<u>I. Differences between age-categories</u>

Sørenson's similarity coefficient ($S_s$) for the standing vegetation and seed bank (Table 2) increases through the sampled age-categories, leading to a high value for the reference fen category compared to seed bank studies in similar habitats (LaDeau & Ellison 1999; Matus et al. 2001). Within the three age-categories of restoration land, seed bank diversity remained fairly static, whilst recruitment of species into the standing vegetation and shared species within the seed bank and vegetation increased over time (Table 2).



<u>II. Proximity to ditch edge</u>

Examination of the proximity to ditch edge showed significant differences between the 2m and 32 m from ditch transects on DCA axis 2 but not on DCA axis 1 in both seed bank species ($F_{1,24}$= 7.47, P=0.026) and standing vegetation ($F_{1,24}$= 29.96, P<0.001) ordinations.

*Standing vegetation*

The mean standing vegetation DCA axis 2 scores for the 5 year (1.502 at 2m; 2.326 at 32m) and 15 year (1.084 at 2m; 2.949 at 32m) age-categories indicated a separation in vegetation assemblages with distance from the ditch; species associated with a disturbed, wetter environment predominating at 2m (e.g. *Calystegia sepium, Holcus lanatus* and *Phragmites australis*) and species suited to a drier, disturbed habitat prevalent at 32m (e.g. *Anisantha sterilis, Cirsium arvense, Arrhenatherum elatius*). There was no clear separation between distance from ditch within the 60 year and reference age-categories.

*Seed bank*

The effect of distance from ditch on the seed bank was subtle, and was most apparent in the mean DCA axis 2 scores for 5 year (-0.199 at 2m; 0.022 at 32m) and 15 year (-0.146 at 2m; 0.177 at 32m) age-categories, with the 60 year and reference age-categories displaying no discernable distinction between distance to ditch in vegetation communities. In the 5 year and 15 year seed bank, species associated with disturbed arable habitats dominated at 32m (e.g. *Chenopodium ficifolium, Alopecurus myosuroides* and *Urtica urens*), whilst a mixture of rank grasses and weedy wetland species dominated at 2m (e.g. *Arrhenatherum elatius, Dactylis glomerata* and *Ranunculus sceleratus*).

***Functional traits***

Ellenberg F ($E_F$) values displayed differences in the standing vegetation across the restoration areas, with the 5 year (average $E_F$ = 5.255) and 15 year (average $E_F$ = 5.795) age-categories indicating significantly drier conditions ($P = 0.003$ and $P<0.001$ respectively) than those in the 60 year habitat (average $E_F$ = 7.353). There was no significant difference between the 60 year and the reference habitat. In the seed bank, the 5 year category (average $E_F$ = 5.762) comprised species indicating significantly drier conditions than in the 60 year age category ($P = 0.017$; average $E_F = 7.694$), but the 15 year age category was not significantly different from the 60 year age category. As in the standing vegetation, there was no significant difference in the seed bank between the 60 year age-category and the reference habitat ($P= 0.596$).

Only one Regenerative Strategy (S) showed a significant difference between age-categories within the seed bank (Table 3). The 15 year category significantly differed from the 60 year ($P = 0.042$) and reference ($P = 0.041$) ages, but not from the 5 year age category ($P = 0.947$). Four regenerative strategies (S, VBs, VW, WBs) showed significant differences between age-categories for standing vegetation. The reference age category was significantly different from all restoration ages for two of these strategies (VW and WBs); the 5 year age category showed a significant difference from all other age-categories for the S regeneration strategy, and the 60 year age-category was significantly different from all other age-categories for the VBs regeneration strategy.

The seed bank C-S-R analysis revealed marked differences in early (≤15 years) and later (60years) stages of restoration when examining stress-tolerators (S) and ruderals (R) (Table 4), although all categories (C,S,R) were significantly different between age classes.

***Exclusive & constant species***

The clear separation of seed bank restoration age-categories demonstrated in Figure 1 can be illustrated further by examining the seed bank species present within each age class. Species which were specific to a restoration age category (‘exclusive species’) are shown in Table 5. Plants characterised as ruderal, weedy species with an annual life history and a therophytic life form are prevalent in the exclusive species identified in the five-year and 15-year age-categories, whereas the 60 year age category is characterised by a suite of species more associated with wet grassland or a weedy-wet vegetation, a perennial life history and a hemicryptophytic life form. The exclusive species found in the reference seed bank all have affinities to a fen/degraded fen grassland vegetation, but follow much the same outline of life history, form and regeneration as the 60 year age-category. The standing vegetation ordination displayed a similar pattern to the seed bank *i.e.* species associated with dry, fertile, disturbed sites occur to the left of DCA axis 1 (5yrs; 15yrs) and those of wet, intact infertile sites were located to the right of axis 1 (60yrs; reference vegetation).

Species which were common to all age classes (termed 'constant species') in the seed bank are shown in Table 6. All constant species have an Ellenberg F (moisture) score of between 6 and 9, and all apart from one species (*Festuca rubra*) have a persistent seed bank type. It is notable that of the 16 species common to all age classes in the seed bank, nine (including *Juncus articulatus, J. subnodulosus, J. inflexus, Agrostis stolonifera* and *Epilobium parviflorum*) appear in the standing vegetation in the 60 year age category. Of these nine species, seven have a lateral spread (as defined in Grime et al. 2007) of ≥4 (highlighted in bold in Table 6) and thus have the potential, if established in the standing vegetation, to appreciably contribute towards the restoration of a wet grassland/rush pasture community type. Two of the seven laterally spreading species are perceived as aggressive weed species (*Cirsium arvense* and *Urtica dioica*), although of all the constant species present they are amongst the least tolerant of wet (periodically waterlogged) conditions (e.g. Silvertown et al. 1999), and make up a small component of the standing vegetation in the 60 year age category (2.4% and 0.9% respectively).

## *Discussion*

### *Seed bank composition in different age-categories of restoration land*

The trend of greater species diversity in the upper (0-5cm) soil depth is consistent with previous seed bank studies (Maas & Schopp-Guth 1995; Bekker et al. 1998b; Matus et al. 2003). However, the lack of significance between upper and lower soil depths in the 5 and 15 year age-categories is notable, and may be attributed to land management practices prior to restoration when the regular ploughing of the soils created a 'vertical mixing' effect within the seed bank. This has led to the loss of differentiation in both species number and seed bank type between depths, even after a period of 15 years**.**

Results from the seed bank study clearly demonstrate that after >5 years of continuous ploughing and drainage the restoration of a reference-type fen vegetation through utilisation of the seed bank is not possible, even after many subsequent decades in sympathetic management, with plants that are considered constituent species associated with target UK fen vegetation communities (see Rodwell 1991) remaining absent from the seed bank and standing vegetation. This is in agreement with other investigations into the restoration of target wetland vegetation (Brown 1998; Matus et al 2003; Bossuyt & Olivier 2008), and confirms the high priority attached to the retention and protection of undrained habitat.

### *Comparisons between seed banks and standing vegetation*

Habitats which have a high level of disturbance are more likely to have a high Sørenson similarity coefficient ($S_s$) score (*e.g.* Bekker et al. 1999). However, an $S_s$ score of 0.41 after 5 years in restoration suggests that recruitment from the seed bank declines rapidly following cessation of high levels of disturbance (see Dölle & Schmidt 2009). The increase in Sørenson similarity scores relate to a very gradual recruitment of species into the standing vegetation from the seed bank (Table 1). This recruitment is likely to be linked to various environmental filters including a) more naturalised hydroperiods and associated b) increase in Ellenberg F (moisture) scores; c) disturbance events and d) the germination strategies of the buried seed bank. In a re-naturation management regime, the recruitment of additional species not present within the standing vegetation is most likely to be linked to seed dispersal vectors such as zoochory, hydrochory and anemochory and/or by sporadic disturbance events promoting germination of species in the seed bank (but see Pakeman & Small 2005). On the Wicken Vision project area, the self-reliant herds of grazing animals are capable of creating disturbance at a local scale through trampling but at present do not move between the NNR and the restoration land and therefore cannot yet act as agents for zoochory between the two sites.

The differences in the seed bank and standing vegetation when examining the proximity to drainage ditches implies that in the previous arable regime, the ditch banks were not as heavily affected by cultivation as in-field areas, and retained an impoverished wetland flora. The ditch system would have been managed and kept open to assist drainage and would have retained a reservoir of wetland species. Hence proximity to the ditch network provides an opportunity for colonisation of the fields following reversion to restoration management. This process may be further facilitated by ditch management activities (e.g. 'slubbing') which may bring propagules onto the field edge and are carried out in some parts of the Wicken Vision land. The similarity between mean DCA axis 2 scores in the 60 year and reference age-categories, examination of the Ellenberg moisture scores and species present together indicate that some wetland hydrological function has been restored in the older restoration areas, with wetland species present both near to and further away from the ditches.

***Functional Traits***

The lack of significant differences in Regenerative Strategies is marked across seed bank age-categories, and highlights the heterogeneous nature of the seed bank at all stages of habitat restoration. The bias towards species with a primary regeneration strategy of seasonal regeneration (S) in the 5 and 15 year age-categories for both the seed bank and standing vegetation is strongly associated with the recent history of agricultural land management and the developing nature of the standing vegetation. By the oldest restoration age (60 years), species which combine strategies of lateral vegetative spread and a persistent seed bank have established in the standing vegetation. This grouping of regenerative strategies is typically associated with meadows which have been severely drained in the past (Grime 1979; Grime 2002). Such habitats are frequently dominated by a few aggressive species, and must rely on temporally unpredictable disturbance events such as poaching and grazing by livestock in order to promote the germination and recruitment of new species (see Isselstein et al. 2002).

This pattern of vegetation Regeneration Strategies is also evident in the C-S-R results (Table 4). As expected, after prolonged periods of annual disturbance by ploughing, species that can tolerate periods of intense, frequent disturbance (as represented by the high R score) are much more abundant in the early stages of arable reversion. As the habitat begins to stabilise, so the plants adapted as stress tolerators (S) increase. The similarity between the S scores for the 60 year restoration age and the reference habitat and their reduced R scores indicate the diminishing influence of the intense, regular and widespread mechanical disturbance maintained during the previous arable regime.

Ellenberg moisture scores for the standing vegetation in part reflect the gradual restoration of a wetland hydroperiod after decades of drainage, but may also relate to the differences in soil type following agricultural intensification (see Table 1). The Ellenberg F results for the seed bank strongly suggest a change in environmental conditions between the 15 and 60 year age-categories. This change has allowed some species associated with a wetter environment, which were present within the seed bank, to establish in the vegetation within 60 years.

***Seed Bank Exclusive and Constant Species***

The clear differences in exclusive species functional traits found in each age category (Table 4) reflects the impact of the previous arable regime and the subsequent length of time in which the seed bank has been able to recover since restoration commenced. The presence of only three exclusive species in the 15 year age category compared to the eight species found in the 5 year age category and the ten species found in the 60 year category suggests a merging of categories at the mid-way point of the restoration timeline, clearly illustrated in Figure 1. The appearance of so many new exclusive species associated with a wetland-type of vegetation (e.g. *Carex otrubae, Equisetum arvense* and *Galium palustre*) in the 60 year age-category, along with the evidence of increased Ellenberg moisture scores, suggest a partial restoration of hydrological function and an increased potential for the establishment of wetland vegetation (albeit a species-poor type) through natural regeneration under suitable conditions.

The connection with hydrological control, land management and the potential for the restoration of wetland vegetation through the seed bank is perhaps most clearly demonstrated when examining the Constant species and their respective functional traits. All ages sampled have the potential to contribute towards a wetland vegetation type, but it is not until the oldest of the restoration ages that the majority of the Constant seed bank species appear in the standing vegetation. Restoration relies upon numerous environmental factors promoting germination and establishment (see Middleton 1999), including substrate, disturbance, fluctuation in temperature and hydrology. The frequency and timing of disturbance events also contribute to the successful recruitment and retention of vulnerable seedlings (e.g. Croft et al. 1997). The functional traits exhibited by the Constant species suggest that hydrological control coupled with managed disturbance (through flooding, drawdown or grazing) will best promote the early establishment of species-poor wetland vegetation through natural regeneration following commencement of restoration.



***Conclusion***

Following six decades spent under sympathetic conservation management, preceded by just six years of degradation through regular ploughing and drainage of the peat soils, even the oldest and most intact of the restoration age-categories is lacking the constituent plant species which are present within the adjacent undrained vegetation of the NNR. The transient nature of undrained fen and wet grassland seed banks coupled with the rapid loss of peat through drainage and oxidation suggests that under natural regeneration, hundreds of years will need to elapse before vegetation diversity returns to pre-drainage levels. Even then it is likely that historic biotic changes, particularly in the soils, will result in novel vegetation assemblages, with the loss of peat depth and quality having a direct impact on the ability of the soils to store and slowly release water over dry periods in the late spring and summer months (Gillman 1994).

However, if the desired outcome of a project is not the replication of historic habitat but rather the development through natural regeneration of potentially novel wet grassland assemblages, then the seed bank can help to achieve this goal provided suitable conditions are present to facilitate the germination of seed bank species and subsequent establishment of seedlings. The vegetation is still species-poor relative to undrained habitats, but if structural diversity can be sustained through extensive grazing by herbivores and fluctuating water tables, opportunities will be presented for the recruitment of flora and fauna over time and through a variety of dispersal mechanisms.

*Implications for Practice*

- It is not possible to restore historic undrained fen grassland vegetation alliances from the seed bank even after only relatively short time periods of severe habitat degradation (≥6 consecutive years). Consequently, high priority must be given to the preservation of existing undrained fen grassland communities.
- A seed bank of highly degraded fields can contribute towards the creation of novel wetland vegetation assemblages over time but is dependent upon suitable environmental conditions. Such novel assemblages are likely to be botanically species-poor and dominated by laterally spreading, aggressive species.

- Hydrological restoration (and the associated promotion of flooding; poaching and grazing by livestock; drawdown) should be prioritised when attempting to create or restore wetland habitat by natural regeneration.
- Land managers involved in restoration projects led by natural regeneration should investigate opportunities for increasing species diversity through natural dispersal mechanisms such as zoochory and hydrochory.

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**Table 1**: Description of pre-restoration management and *in situ* soil profiles for each age-category

| years in restoration | historical management | soil profile |
|---|---|---|
| 5 | drainage and intensive agricultural management regime for a continuous period of >70 years, leading to substantial peat wastage | peat depth ≤46cm, directly overlying Gault clay bedrock |
| 15 | drainage and intensive agricultural management regime for a continuous period of >70 years, leading to substantial peat wastage | peat depth ≤34cm, with silt and gravel deposits above the Gault clay |
| 60 | drainage and agricultural management for a continuous period of 6 years, leading to peat wastage | peat depth ≤70cm, overlying silty loam and gravel deposits on Gault clay |
| reference habitat | intact peat within undrained habitat under nature conservation management for >100 years | Continuous sedge peat to depths of ≥200cm |

**Table 2:** Similarity of the seed bank and standing vegetation

| age-category | Veg | Sb | Veg + Sb | $S_s$veg-sb |
|---|---|---|---|---|
| 5 | 43 | 82 | 29 | 0.41 |
| 15 | 44 | 81 | 32 | 0.51 |
| 60 | 61 | 85 | 42 | 0.57 |
| reference | 69 | 63 | 43 | 0.65 |

Columns display number of species common to the standing vegetation (Veg), the seed bank (Sb), species common to the vegetation and seed bank (Veg + Sb) and the Sørenson coefficient score ($S_s$veg-sb) for each age-category sampled.

**Table 3**: Regeneration strategies for the seed bank ($S_b$) and standing vegetation ($S_v$)

| $S_b$ age-categories | Bs | S | SBs | V | VBs | VS | VSBs | VW | VWBs |
|---|---|---|---|---|---|---|---|---|---|
| **5** | 17.36 | $3.50_{ab}$ | 3.04 | 2.85 | 18.54 | 4.42 | 3.51 | 0 | 13.65 |
| **15** | 8.71 | $4.16_{b}$ | 10.83 | 1.4 | 11.57 | 2.32 | 10.68 | 2.82 | 35.73 |
| **60** | 4.78 | $0.08_{a}$ | 3.26 | 3.86 | 25.86 | 10.42 | 10.84 | 0.801 | 26.1 |
| **reference** | 8.45 | $0.06_{a}$ | 0.98 | 6.44 | 12.37 | 3.69 | 5.69 | 3.68 | 18.29 |
| **F value** | 1.8 | 6.36 | 1.29 | 0.84 | 3.69 | 1.69 | 1.12 | 3.09 | 3.03 |
| **P value** | 0.22 | **0.02** | 0.34 | 0.51 | 0.06 | 0.25 | 0.4 | 0.09 | 0.09 |
| **$S_v$ age-categories** | **Bs** | **S** | **SBs** | **V** | **VBs** | **VS** | **VSBs** | **VW** | **VWBs** |
| **5** | 0.31 | $40.39_{b}$ | 0.54 | 20.63 | $4.51_{a}$ | 25.41 | 1.08 | $0.02_{a}$ | 7.1 |
| **15** | 0 | $6.71_{a}$ | 0.38 | 19.92 | $3.96_{a}$ | 12.24 | 16.7 | $5.66_{a}$ | 34.43 |
| **60** | 0.13 | $0.39_{a}$ | 0.81 | 10.85 | $23.57_{b}$ | 7.07 | 17.49 | $17.21_{a}$ | 17.96 |
| **reference** | 0.12 | $0.67_{a}$ | 0.26 | 13.49 | $8.16_{a}$ | 2.17 | 8.39 | $49.02_{b}$ | 6.1 |
| **F value** | 1.24 | 14.28 | 0.36 | 1.03 | 13.92 | 2.72 | 3.69 | 24.6 | 2.44 |
| **P value** | 0.36 | **<0.01** | 0.78 | 0.43 | **<0.01** | 0.12 | 0.06 | ***<0.01*** | 0.14 |

Columns contain the mean score for each age-category for each strategy. For individual columns differences between age-category means were tested using Tukey's HSD if there was a significant ANOVA F-value. Means that do not share a common superscript letter can be considered significantly different. Regeneration Strategies: V = vegetative expansion; S = seasonal regeneration; W = numerous widely dispersed seeds; $B_s$ = persistent seed bank. Bold type denotes significant P values <0.05.

**Table 4**: The relative proportions of seed bank species identified as Competitors (C), Stress Tolerators (S) or Ruderals (R).

| age-categories | mean C | mean S | mean R |
|---|---|---|---|
| 5 | $0.4^{a}$ | $0.1^{ab}$ | $0.51^{ab}$ |
| 15 | $0.4^{a}$ | $0.1^{b}$ | $0.51^{b}$ |
| 60 | $0.46^{a}$ | $0.26^{a}$ | $0.29^{a}$ |
| reference | $0.51^{b}$ | $0.22^{a}$ | $0.27^{a}$ |
| F value | 4.54 | 56.48 | 38.65 |
| P value | **<0.01** | **<0.01** | **<0.01** |

Columns contain the mean score for each age-category for each C-S-R strategy type. For individual columns differences between age-category means were tested using Tukey's HSD if there was a significant ANOVA F-value. Means that do not share a common superscript letter can be considered significantly different. C = competitor, S = stress-tolerator, R = ruderal. Bold type denotes significant P values <0.05.

**Table 5**: Exclusive species: species specific to a seed bank age-category

| species | restoration age | n upper | n lower | life history | C-S-R strategy | life form | SbT | regen strategy |
|---|---|---|---|---|---|---|---|---|
| *Alopecurus myosuroides* | *5* | 14 | 3 | Aws | R | Th | 3 | Bs |
| *Lolium perenne* | *5* | 7 | 1 | P | CR/CSR | H | 1 | S |
| *Papaver dubium* | *5* | 5 | 9 | As | R | Th | 3 | Bs |
| *Papaver rhoeas* | *5* | 6 | 3 | Asw | R | Th | 3 | Bs |
| *Persicaria maculosa* | *5* | 2 | 4 | As | R/CR | Th | 4 | Bs |
| *Polygonum aviculare* | *5* | 8 | 10 | As | R | Th | 3 | Bs |
| *Rumex acetosa* | *5* | 1 | 19 | P | CSR | H | 2 | V, S |
| *Veronica hederifolia* | *5* | 13 | 3 | As | R/SR | Th | 3 | Bs |
| *Chaenorhinum minus* | *15* | 3 | 4 | As | R/SR | Th | 3 | S, ?Bs |
| *Conium maculatum* | *15* | 2 | 3 | ?B | CR | H | 2 | S |
| *Stellaria media* | *15* | 2 | 3 | Aws | R | Th | 3 | Bs |
| *Carex hirta* | *60* | 204 | 151 | P | C/CSR | H | ? | V, ?Bs |
| *Carex otrubae* | *60* | 83 | 9 | P | CR/CSR | H | 2 | V, ?Bs |
| *Equisetum arvense* | *60* | 6 | 12 | P | CR | G/Hel | 1 | V, W, S |
| *Festuca pratensis* | *60* | 6 | 1 | P | CSR | H/Ch | 1 | V, S |
| *Galium palustre* | *60* | 24 | 12 | P | CR/CSR | H | 3 | V, Bs |
| *Poa pratensis* | *60* | 8 | 3 | P | CSR | H | 3 | V, Bs |
| *Potentilla anserina* | *60* | 3 | 4 | P | CR/CSR | H | 2 | V |
| *Potentilla reptans* | *60* | 5 | 2 | P | CR/CSR | H | 3 | V, Bs |
| *Ranunculus repens* | *60* | 11 | 21 | P | CR | H | 3 | (V), Bs |
| *Trifolium repens* | *60* | 4 | 5 | P | CR/CSR | H/Ch | 3 | (V), Bs |
| *Calamagrostis canescens* | *reference* | 8 | 10 | P | C/SC | H/Hel | ?2 | V, W |
| *Cladium mariscus* | *reference* | 26 | 9 | P | SC | Wet | ? | V, ? |
| *Galium uliginosum* | *reference* | 9 | 1 | P | S/CSR | Hel | ?1 | V, ?Bs |
| *Hydrocotyle vulgaris* | *reference* | 2 | 5 | P | CSR | H | 2 | V, ?Bs |
| *Molinia caerulea* | *reference* | 4 | 2 | P | SC | H | 2 | V, ?Bs |
| *Salix caprea* | *reference* | 1 | 1 | P | C/SC | Ph | 1 | (V), W, S |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Scutellaria galericulata* | *reference* | 6 | 1 | P | CR/CSR | H | ? | V, ? |

Species found within the soil seed bank which were exclusive to one of the four age-categories used in the study

- n upper refers to the number of emergent seedlings of a species in the 0-5cm half of the soil core;
- n lower refers to the number of emergent seedlings of a species in the 5-10cm half of the soil cores.

Interpretations for all abbreviations are taken from Grime et al. (2007) *i.e.*:

- **Life History**: Aws *annual winter/summer*, P *polycarpic perennial*, As *summer annual*, Asw *annual summer/winter*, ?B *usually biennial*.
- **C-S-R-Strategy**: C *competitor*, S *stress-tolerator*, R *ruderal*, CR *competitive ruderal*, SR *stress tolerant ruderal*, SC *stress tolerant competitor*, CSR *'CSR strategist'*.
- **Life-form:** Th *Therophyte* [plant passing unfavourable season as seeds] H *Hemicryptophyte* [herb with buds at soil level], G *geophyte* [herb with buds below soil surface], Hel *Helophyte* [marsh plant], Ph *Phanerophyte* [woody plant with buds >250mm above soil surface], Ch *herbaceous Chamaephyte* [plant with buds not in contact but <250mm above the soil surface].
- **SbT** corresponds to Thompson et al. 1997 and Grime et al. 2007 seed bank type *i.e.* 1,transient seed bank present during the summer and germinating synchronously in autumn; 2, transient seed bank present during winter and germinating synchronously in winter/spring; 3, small quantity of seed persists in the soil for >5 years, but concentration of seed is only high after seed has just been shed; 4,a large bank of long persistent seeds in the soil throughout the year.
- **Regenerative strategy for species:** V *lateral vegetative spread*, S *seasonal regeneration by seed in vegetation gaps*, W *numerous small, wind-dispersed seeds or spores*, Bs *persistent bank of seeds or spores*, ? *strategies of regeneration by seed uncertain.*.

**Table 6:** Constant species: species present in all seed bank age-categories

| species | $5_u$ | $5_l$ | SV | $15_u$ | $15_l$ | SV | $60_u$ | $60_l$ | SV | $ref_u$ | $ref_l$ | SV | SbT | Lat spread | regen strategy |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Agrostis stolonifera*** | 52 | 22 | √ | 7 | 8 | √ | 93 | 24 | √ | 88 | 27 | √ | 3 | **5** | V,Bs |
| *Chenopodium rubrum* | 5 | 4 | | 3 | 7 | | 1 | 8 | | 2 | 1 | | 3 | 1 | Bs |
| ***Cirsium arvense*** | 67 | 41 | √ | 20 | 6 | √ | 84 | 35 | √ | 1 | 2 | √ | 3 | **5** | V,W,Bs |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Epilobium hirsutum*** | 7 | 6 | | 9 | 6 | | 42 | 13 | | 144 | 22 | | 3 | **5** | V,W,Bs | |
| *Epilobium montanum* | 18 | 14 | | 18 | 54 | | 33 | 56 | | 46 | 25 | | 3 | 2 | (V),W,Bs | |
| *Epilobium parviflora* | 16 | 6 | | 9 | 4 | | 34 | 7 | √ | 33 | 3 | | 3 | 2 | (V),W,Bs | |
| ***Festuca rubra*** | 7 | 10 | √ | 3 | 6 | √ | 124 | 16 | √ | 48 | 5 | √ | 1 | **4** | V,S | |
| *Geranium dissectum* | 8 | 6 | √ | 5 | 6 | √ | 4 | 1 | | 2 | 4 | | 2 | 1 | S | |
| ***Juncus articulatus*** | 1 | 2 | | 2 | 12 | | 45 | 43 | √ | 63 | 24 | √ | 3 | **4** | V,Bs | |
| *Juncus bufonius* | 21 | 10 | | 0 | 4 | | 18 | 13 | | 70 | 8 | | 3 | 1 | Bs | |
| ***Juncus inflexus*** | 13 | 7 | | 9 | 4 | | 372 | 213 | √ | 1 | 0 | √ | 3 | **4** | V,Bs | |
| ***Juncus subnodulosus*** | 3 | 7 | | 4 | 12 | | 26 | 28 | √ | 72 | 60 | √ | 3 | **5** | V,Bs | |
| *Poa trivialis* | 168 | 80 | √ | 323 | 78 | √ | 219 | 46 | √ | 89 | 4 | √ | 3 | 2 | V,Bs | |
| ***Samolus valerandi*** | 16 | 15 | | 28 | 24 | | 114 | 106 | | 165 | 125 | √ | 3 | **4** | ?V,Bs | |
| ***Urtica dioica*** | 127 | 23 | √ | 126 | 63 | √ | 68 | 22 | √ | 95 | 93 | √ | 3 | **4** | V,Bs | |
| *Veronica catenata* | 2 | 2 | | 1 | 4 | | 9 | 7 | | 4 | 1 | | 3 | 2 | (V),Bs | 1 |

Species found within the soil seed bank which were present in all of the four age-categories used in the study.

- **SV** indicates if the species is found in the standing vegetation.
- **Age-categories** are numerically represented, where 5=5 years since restoration, 15=15 years since restoration, 60=60 years since restoration, ref=reference habitat. Ages are suffixed by either 'u', denoting 'upper ' soil core depth, or 'l' denoting 'lower' soil core depth.
- **Sb type** (defined as in Table 5)
- **Lateral spread** (Grime et al. 2007) is interpreted as 1: therophyte (very limited lateral spread in extent and duration); 2: perennials with small, compact and unbranched rhizomes or forming small tussocks ≤100mm in diameter; 3: perennials with rhizomatous systems or tussocks attaining 100-250mm; 4: perennials attaining diameter of 250-1000mm; 5; perennials attaining diameter of >1000mm. Values ≥4 in bold.
- **Regenerative strategy** (Grime et al. 2007 – defined as in Table 5)
- **Ellenberg F (moisture) value** for each of the constant species, where 5=Moist-site indicator, mainly on fresh soils of average dampness; 7= Dampness indicator, mainly on constantly moist or damp, but not on wet soils; 9= Wet-site indicator, often on water-saturated, badly aerated soils (Hill et al. 2004).

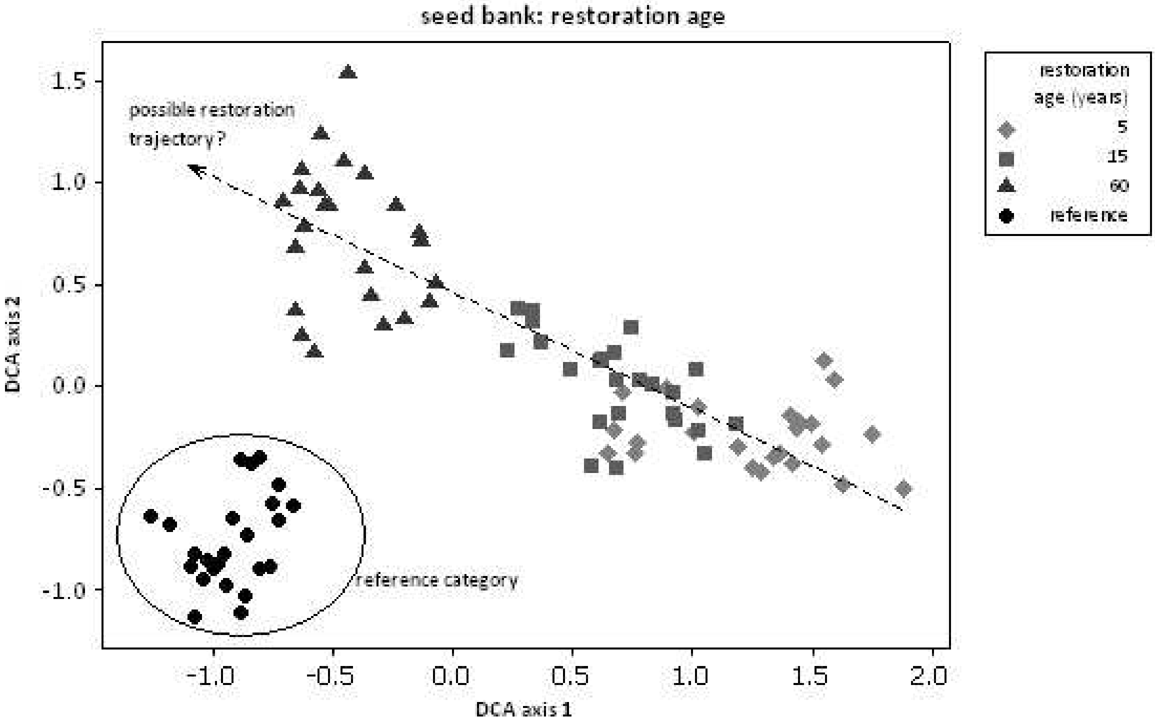
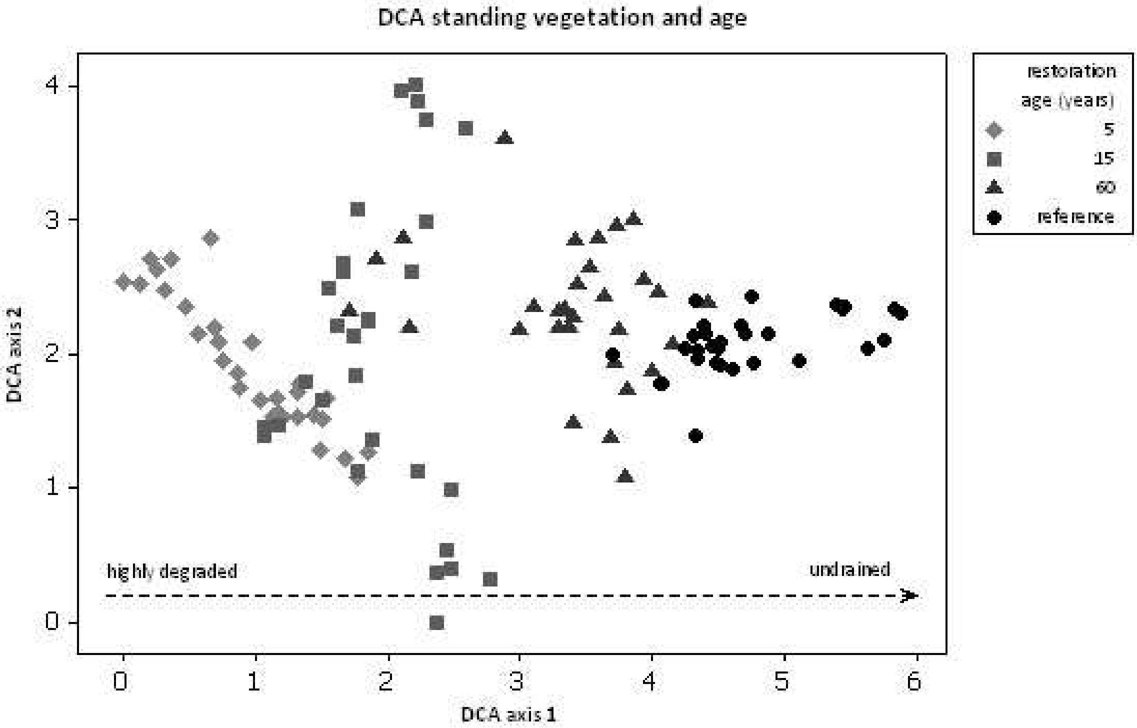



**Figure 1**: Sample scores of individual seed bank samples on the first and second axes of the Detrended Correspondence Analysis of the seed bank data. Symbols used to differentiate the four age-categories. The two axes explained 19.6% and 8.9% of the variation in the data. Possible restoration trajectory superimposed

33




731

732 **Figure 2**: Sample scores of individual samples on the first and second axes of the Detrended
733 Correspondence Analysis of the vegetation data. Symbols used to differentiate the four age-categories.
734 The two axes explained 26.5% and 7.0% of the variation in the data. Possible restoration trajectory
735 superimposed.