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Thirteen years of wetland vegetation succession following a permanent drawdown, Myrkdalen Lake, Norway

Arvid Odland[1,3,*] and Roger del Moral[2]
*[1]Telemark University College, N-3800 Bø, Telemark, Norway; [2]Department of Botany, University of Washington, Box 355325, Seattle, WA 98195-5325, USA; [3]Current address: Department of Botany, University of Washington, Box 355325, Seattle, WA 98195-5325, USA; *Author for correspondence*

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Abstract

Myrkdalen Lake in Western Norway was subjected to a 1.4 m drawdown in June 1987. Plant establishment and vegetation succession on the exposed sediments of a fluvial delta plain was monitored through 2000. The investigated area extended from the original *Equisetum fluviatile* zone to the new lake edge. The substrate was homogeneous and consisted mainly of minerogenous fluvial sediments. Vegetation data were sampled within continuous quadrats along transects perpendicular to the shore, and they dropped 93 cm in elevation. Detrended Correspondence Analysis and Canonical Correspondence Analysis confirmed that "time since drawdown" and "elevation of the quadrats" appeared to be of nearly equal importance in explaining succession. Plant establishment was rapid on the exposed sediments due to a seed bank and to rapid invasion of plants. The succession includes both floristic change as a function of time and a spatial separation in relation to the water level. The species succession was marked by a growth form progression: mosses and annuals → non-clonal perennials → clonal perennials. After one month, the annual *Subularia aquatica* and small acrocarpous mosses dominated the site. Dominance then shifted to *Deschampsia cespitosa, Juncus filiformis, Blasia pusilla* and *Polytrichum commune*. Subsequently there was an increase of *Carex vesicaria* in the lower zone and *Calamagrostis purpurea* in the upper zone, while *Phalaris arundinacea* was common over most of the elevational gradient. *Equisetum* declined where it had dominated before drawdown, but it expanded gradually towards the new shoreline. The vegetation remained dynamic after 13 years and it is not considered to be in equilibrium with the new environmental gradient yet. However, annual changes measured by DCA scores have slowed and two vegetation zones have developed. The major vegetational differences along the elevational gradient can be explained by the height of the mean June water limit. This example of species turnover in space and time may be a model for other successions that occur along a strong gradient.

Introduction

In any wetland, plants are distributed according to their tolerances to flooding or saturation. How these patterns develop remains poorly understood despite intense efforts (e.g. van der Valk (1987); Weiher and Keddy (1995)). Wetlands often experience natural water level fluctuations that result in cyclic vegetation changes. Many experimental studies have demonstrated the importance of interspecific competition in establishing wetland zonation (Wilson and Keddy 1985; Shipley et al. 1989), which suggests that competitive displacement affects species patterns along wetland gradients. Many cases of wetland succession have been studied, but there remain few long-term permanent plot studies (Hejný and Segal 1998; del Moral 2000).

A traditional view of succession is that assemblages slowly and progressively occupy a site until a homogeneous, sustainable community develops. Recent studies of marshes and slack dunes suggest that communities are as likely to diverge or proceed on parallel trajectories (e.g. Olff et al. (1997); Lammerts and Grootjans (1998)). Little is known about the time scales of wetland succession. Many studies deal with wetland patterns and succession (e.g. van der Valk (1981); Noon (1996)), but few have measured rates. Rates can be estimated in several ways, including using changes in species cover (Prach et al. 1993; Oksanen and Tonteri 1995) and species turnover (beta diversity; Rydin and Borgegård (1988)). A simple method to calculate turnover is detrended correspondence analysis (DCA) scores, which are measured in half-change units (Eilertsen et al. 1990).

Primary succession normally involves recovery on newly created substrates or those that have been sterilized by a major perturbation. Secondary succession occurs after disturbances that left survivors, or some biological legacy. McCook (1994); Grishin et al. (1996) demonstrated that there is a continuum of disturbance intensity from mere damage, through some surviving species (secondary succession) to complete obliteration of any biological remnant (primary succession). A permanent drawdown will alter the ecological conditions drastically for the original vegetation on the shoreline by exposing sediments formerly under water. However, a seed bank in sediments containing some organic matter may improve the conditions for vegetation establishment. In such a case, neither a pure primary succession, neither or a typical secondary succession would be initiated. This may be then be considered as a special case of primary succession since all sites were colonized by species not originally present.

Permanent plots have been used in many studies, but a comparison of the simultaneous rate of succession along gradients and time has not been conducted on lake margins. Bakker et al. (1996) stressed that permanent plot studies permit both internal and external driving forces to be explored. Such studies can lead to new hypotheses and offer clues to appropriate experiments to test these hypotheses. This paper describes colonization, extinction and apparent competitive abilities of species colonizing exposed sediments. We will quantify and compare trajectories in space and time to determine whether extant vegetation has converged to that found before drawdown. We compare annual changes over 13 years (time) across 40 quadrats along transects (space) through the new shore, explore vegetation turnover rates, and life history and diversity changes.

Study area

The site (60°40′ N, 6°28′ E) lies on the outer edge of a fluvial delta in the Myrkdalen Lake (229 m a.s.l.). The lake is a part of the northern branch of the Vosso River basin in Western Norway, draining 157 km^2. The climate is sub-oceanic, with a mean July temperature of 14.5 °C, a mean January temperature of −3.0 °C. Mean annual precipitation is about 1500 mm. In 1987, the mean summer water level was permanently lowered resulting in a water level being 1.2 to 1.4 m lower than before. The drawdown was intended to increase the area of arable farmland on the delta. Nearby, within the lake, there are several artificial islands constructed from deep sediments. Odland (1997) described vegetation on these excavated islands and provided a basis for comparing rates in the sere to be described.

Sediments and hydrology

The transects crossed fine-grained fluvial sediments. Particle size analyses and chemical composition from the fluvial delta were given by Odland (1992, 1997). The transect sediments were mainly particles < 125 μm. Chemical analyses indicated that the sediments were low in nitrogen and that loss on ignition was $<$ 7%. The excavated sediments used to create the nearby islands were coarser, very low in organic content and derived from deeper lake layers probably lacking a seed bank. There is a water gauge in the lake that monitored the daily water-level fluctuations automatically. By the use of a leveling instrument, the elevation of all quadrats within the transects were given according to the scale of this water gauge (Figure 1).

Vegetation

Before drawdown, the littoral vegetation consisted of a broad zone dominated by *Equisetum fluviatile*, *Carex rostrata* and *C. vesicaria*. These helophytes dominated the lower delta, sometimes extending 200 m inland. *Phalaris arundinacea* and *Calamagrostis purpurea* stands were frequent at higher elevations, often forming a transition between the *Carex* belt and the cultivated parts of the delta. Scattered thickets of *Betula pubescens*, *Alnus incana* and *Salix nigricans* were also present (Odland 1992; Eie et al. 1995). Most of the original *Phalaris* vegetation has been transformed into hayfields after the drawdown.

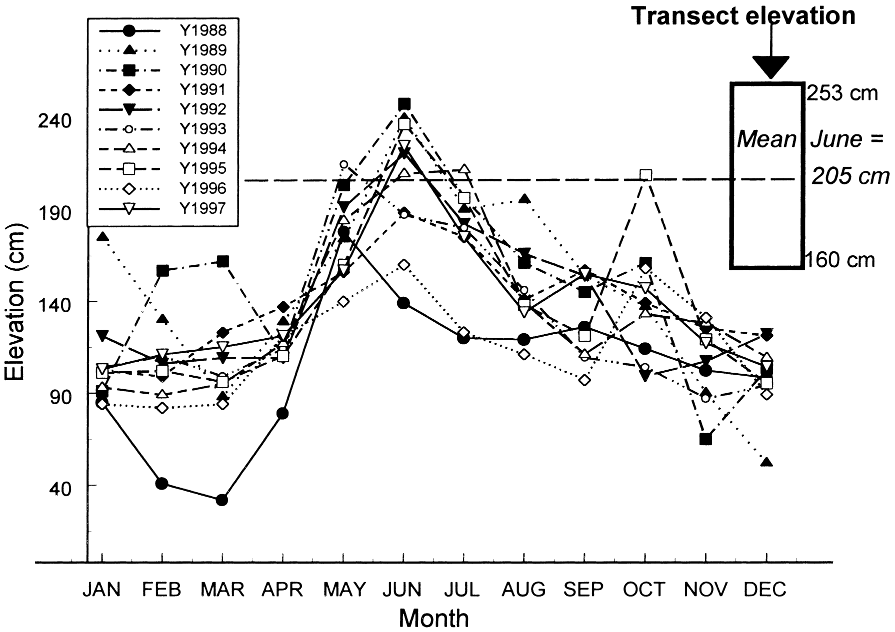

Figure 1. Mean monthly water levels from 1988 to 1997 measured at the Myrkdalen lake water gauge. Rectangle at top right shows the elevation range of the transect and the mean June water level.

Taxonomy and life histories

Vascular plant nomenclature follows Lid and Lid (1994). Nonvascular plant nomenclature follows Frisvoll et al. (1995). Immature plants caused identification problem, leading to a conservative treatment of taxa. *Salix nigricans*, *S. phylicifolia* and their hybrid are all named *S. nigricans*. *Drepanocladus* species (mainly *D. exannulatus*, but including *D. fluitans* and *D. aduncus* are named *Drepanocladus* spp. Dense mats of small acrocarpous mosses (including *Bryum* spp., *Funaria hygrometrica*, *Pohlia* spp. and *Pleuridium subulatum*) were lumped and named "acrocarpous mosses". We divided wetland vascular plants into five groups based on their potential life spans: annuals, non-clonal perennials, clonal (vegetatively expanding) perennials, bryophytes, and woody species. The most frequent species with their author names, and abbreviations (letters in bold) used in ordination diagrams are: Mosses: **Acr**ocarpous **sp**ecies, ***Bla**sia **pus**illa* L., ***Cal**liergon **sar**mentosum* (Wahlenb.) Kindb., ***Dic**ranella **pal**ustris* (Dicks.) E. Warb., ***Dre**panocladus* **spp.**, ***Mar**chantia **pol**ymorpha* L., ***Phi**lonotis **tom**entella* Mol., ***Pol**ytrichum **com**mune* Hedw., ***Rhy**tidiadelphus **squ**arrosus* Warnst., and ***Sca**pania* **spp**. Annuals: ***Ran**unculus **rep**tans* L., ***Cal**litriche **pal**ustris* L., and ***Sub**ularia **aqu**atica* L., ***Jun**cus **buf**onius* L. Clonal perennials: ***Agr**ostis **sto**lonifera* L., ***Alo**pecurus **gen**iculatus* L., ***Jun**cus **fil**iformis* L., ***Cal**amagrostis **pur**purea* (Trin.) Trin., ***Car**ex **nig**ra* (L.) Reich., ***Car**ex **ros**trata* Stokes, ***Car**ex **ves**icaria* L., ***Equ**isetum **flu**viatile* L., ***Pha**laris **aru**ndinacea* L., ***Ran**unculus **rep**tans* L., and ***Ran**unculus **rep**ens* L. Non-clonal perennials: ***Cal**tha **pal**ustris* L., ***Car**ex **can**escens* L., ***Car**ex **ova**lis* Good, ***De**schampsia **ces**pitosa* (L.) Beauv., ***Spa**rganium **ang**ustifolium* Michx. ***Gal**ium **pal**ustre* L., and ***Jun**cus **fil**iformis* L. Woody: ***Bet**ula **pub**escens* Ehrh.

Methods

Sampling

We established a transect on the exposed sediments perpendicular to the shore one month after drawdown (June 1987). Species cover percentages were determined by visual estimates in continuous 1 m by 0.5 m quadrats. For some analyses, the data were reduced to 10 elevational zones by calculating the mean of four consecutive quadrats. We conducted sampling annually during late July or early August between 1987 and 1997, and in 2000. Three different permanent transects (separated by 5 – 10 m) have been established and analyzed during the study period: the first lasted from 1987 to 1992, the second from 1993–

Table 1. Summary of the DCA ordination. Sum of all unconstrained eigenvalues (total inertia) was 3.741 and the sum of all canonical eigenvalues was 0.673. Elevation and time were passive variables and then compared to the DCA ordination.

Properties	AXIS 1	AXIS 2	AXIS 3	AXIS 4
Eigenvalues	0.472	0.385	0.170	0.123
Gradient Length	4.771	3.326	2.945	2.293
Species-Environment Correlation	0.985	0.822	0.235	0.060
Cumulative percent variation				
Of species data	12.6	22.9	27.5	30.8
Of species-environment relation	52.6	94.2	0	0

1997, and the last in 2000. All transects lied on the same substrate, had the same number of quadrats, and they covered the same elevational gradient. The transects were 40 m long and covered an elevational gradient of 93 cm. On the water gauge scale, the quadrats ranged from 160 to 253 cm (Figure 1). The upper quadrat would have been about 45 cm below the mean June water level prior to draw down.

Data analyses

The data were analyzed with CANOCO (ter Braak and Šmilauer 1998). Both indirect gradient analyses (Detrended Correspondence Analysis, DCA) and direct (Canonical Correspondence Analysis, CCA) were performed. Cover data were square root transformed and species with fewer than four occurrences were omitted in both analyses. DCA used the standard options. Elevation and time were introduced as passive variables, which allowed a direct comparison of ordination axes with these variables. The effects of years, and thereby the position of the different transects also, were tested by CCA using years as nominal environmental variables and time as a quantitative variable. CCA analyses were run with default settings. Stepwise forward selection and Monte Carlo permutations (n = 150) were run for all variables to determine their significance.

Cover percentages were averaged in four consecutive quadrats to clarify patterns and cover changes were expressed in three-dimensional plots (12 sample dates over 10 elevations). The mean DCA scores of four quadrats were calculated from the individual plot analysis and plotted against year and elevation. Graphs were prepared using AXUM5.0 (Mathsoft 1996).

Data from 1994 to 2000 were clustered using TWINSPAN (Hill 1979) in order to evaluate recent zonation. There were 40 quadrats in each of the five years, and if no change had occurred, each quadrat would be in the same class in each year. Pseudospecies cut levels (Hill 1979) of 0, 5, 10, 20, 40 and 60 were used to match the spread of cover. *Equisetum* was present before the drawdown, so it was treated as a passive variable (not used to create the classification, but retained in summaries).

Results

Hydrology

Mean monthly water level during the study period is shown in Figure 1. Mean water level for the period between 1988 and 2000 was 2.05 m in June. The extreme high water event occurred in June 1989 (4.13 m), the extreme low was in March 1988 (0.28 m). These extremes are transient and resulted from the narrow lake outlet and large discharge during snowmelt periods. Particularly high summer water levels occurred in 1989, 1990 and 1995 while, with extreme lows occurred in 1988 and 1996. Quadrats at the lower end of the transect experienced an average of over 80 days annual inundation, while the upper transect experienced only an average of 20 days inundation. In a wet year such as 1995, the entire transect remained submerged for at least one month.

Ordinations

Elevation and time (0.1 to 13 years) since drawdown were used as passive environmental variables in DCA and each was highly correlated with the first two axes (Table 1). Combined, they accounted for 94.2% of the species-environment correlation. The species-environment correlation with DCA-1 is 0.98 and that with DCA-2 is 0.82, showing that factors correlated with elevation and time since drawdown account for most of the species variation. The inter-set correlations of environmental variables (Table 2) showed that Eleva-

Table 2. Correlations between environmental variables and species ordination axes. DCA was run with two passive environmental factors (time since drawdown and transect elevation) and CCA with elevation and the different years (n = 12) as nominal environmental variables.

	DCA -1	DCA -2	CCA -1	CCA -2	CCA –3
Elevation	**0.68**	**0.50**	**–0.60**	**0.66**	0.14
Time	**0.58**	**–0.66**			
Year 1987			**0.43**	0.27	**0.64**
Year 1988			**0.31**	0.42	–0.36
Year 1989			0.17	0.20	–0.13
Year 1990			0.10	0.03	–0.04
Year 1991			0.03	–0.02	–0.11
Year 1992			–0.03	–0.07	–0.15
Year 1993			–0.07	–0.12	–0.07
Year 1994			–0.14	–0.13	0.08
Year 1995			–0.18	–0.12	0.09
Year 1996			–0.16	–0.15	0.09
Year 1997			–0.20	–0.17	0.10
Year 2000			**–0.27**	–0.19	0.19

tion was slightly more correlated to DCA-1, while Time was slightly more important along DCA-2.

Figure 2 shows the position of the species in relation to DCA-axis 1 and 2. The first axis is weighted by annuals (e.g. *Subularia* and *Callitriche*) and small acrocarpous moss species. Higher DCA-1 scores are weighted by rhizomatous species such as *Ranunculus repens*, *Phalaris* and *Calamagrostis*. Mosses had low DCA-2 scores (e.g., *Polytrichum commune, Blasia* and *Dicranella*). Graminoids (e.g., *Carex* spp. and *Alopecurus*) had high DCA-2 scores.

There was a dramatic change in DCA scores over both space and time. DCA-1 and DCA-2 quadrat scores were similar below approximately 200 cm (close to the height of the mean June water level) of the transect. The quadrat scores gradually diverged at higher elevations, and became separated by 2.8 SD units (Figure 3a). Scores along both axes increased steadily with time, though the rate of increase slowed the last years (Figure 3b). There was no indication that the succession had stabilized, but annual changes have slowed. From 1988 to 1997, there was a nearly perfect linear increase in the mean DCA-1 score ($r = 0.98$). The regression equation demonstrated that there had been a mean annual increase of 0.126 SD units per year along DCA-1 during these years. The variation in DCA-2 scores was smaller, and after 1995, there had been little directional change. Combined changes along the transect during representative years is shown in Figure 3c, when vector traces the DCA position of composite plots (from low to high position along the quadrats) in a given year.

The mean 2-D Euclidean distances between high and low elevations in each year was 2.2 units, while that between years, averaged over the 10 elevations, was 2.9 units. The difference was highly significant (t-test, $P < 0.0001$). Species turnover through time was greater than that along the elevational gradient.

We also analyzed the data by a stepwise-constrained ordination with “Elevation” as a quantitative variable and “Years” as nominal variables (Figure 4, Table 2). A forward selection multiple regression analysis of the CCA showed that elevation explained the most variation (eigenvalue = 0.35). Years 1987 (0.23), 1988 (0.19) and 2000 (0.09) were significant, while adding the remaining years improved the fit only slightly. Each year was significant (Monte Carlo test) except 1994 to 1996. This analysis showed that species patterns changed with both elevation and time, but because correlations with latter years were low, recent variation was reduced. The analysis indicated that the shift in transect in 1994 did not contribute significantly to explain the vegetation succession. The transect analyzed in 2000 was statistically significant ($r = -0.27$) to explain the species distribution along CCA axis 1, but it also included two years of succession compared to the other years which included only one year of succession.

Pattern of vegetation development

Mean cover percentages of representative species in composite quadrats are shown for each elevation band and year (Figure 5). Three different patterns were evident: an increase, a decrease after the rapid establishment, and a Gaussian response with an optimum at various times and elevations on the transects.

The upper eight quadrats were dominated initially by *Equisetum* where it had 40% cover in 1987. It showed little response to drawdown for two years, but since 1990, it had declined to less than 10% in these quadrats. *Equisetum* migrated downward by rhizome growth, and in 2000, it was within 9 m of the water (i.e. 19 cm below the mean June water level), which gives an average vegetative horizontal spread of about 1.8 m per year. Small acrocarpous mosses and the liverwort *Blasia* dominated the sediments in 1987. *Blasia* became abundant in the upper transect, but has since disappeared. Between 1989 and 1993, *Drepanocladus* spp. and *Polytrichum commune* were com-

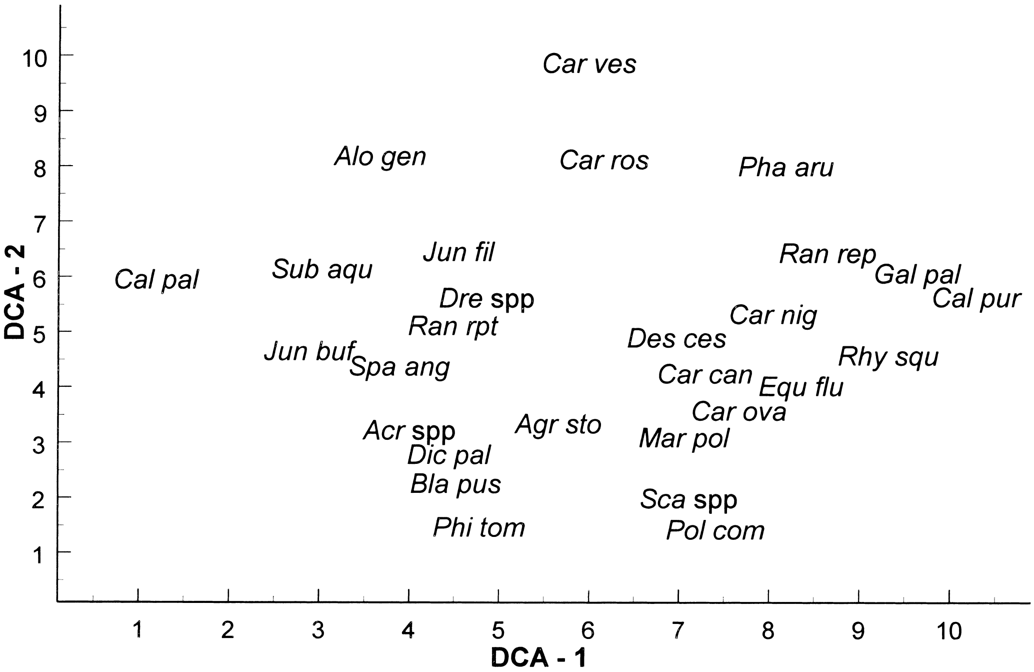

Figure 2. Position of the most common taxa in relation to DCA axes 1 and 2. Both DCA-1 and DCA-2 were positively correlated with elevation. DCA-1 was positively correlated with time and DCA – 2 was negatively correlated with time (See Table 2).

mon, but they too became rare. Annuals such as *Subularia*, and *Callitriche* were also initially abundant in the upper transect. *Subularia* shifted downward, reached a peak in 1989 to 1991, then became rare. *Ranunculus reptans* was abundant at low elevations until 1992; thereafter it became sparse. During the first few years, several other rare species occurred sporadically. These included *Eleocharis acicularis*, *Agrostis, Philonotis*, *Sparganium*, and juvenile plants of *Betula*.

Deschampsia became dominant along most of the transect in 1988. After 1994 it decreased, and was confined to the upper transect by 2000. *Juncus filiformis* peaked in 1988, and then it decreased rapidly. *Carex rostrata* and *C. vesicaria* were rare in 1987, but they became gradually abundant. By 2000, both were confined to lower elevations. There have been large annual fluctuations in the abundance of *Phalaris* and it often had a patchy distribution. Later invaders included *Calamagrostis, Ranunculus repens, Alopecurus, Carex ovalis, C. canescens, Galium* and *Rhytidiadelphus*. By summer 2000, the upper 20 quadrats were dominated by *Phalaris, Deschampsia*, and *Calamagrostis*, reflecting the uppermost lake margin in 1987. The lowermost 20 quadrats were dominated by *Carex vesicaria*, with *C. rostrata*, *Phalaris*, and some *Calamagrostis* consistently present.

Vegetation zonation

The TWINSPAN classification of the 200 quadrats from the last five sample years (1994–2000) revealed little change after 1995, strong zonation and correlation with elevation. The first two TWINSPAN divisions and their associated indicator species are shown in Figure 6. Numbers in parentheses refer to the “pseudospecies” cut-level of the indicator species. *Phalaris* was abundant in all groups, while *Deschampsia* and *Calamagrostis* together with *Rhytidiadelphus squarrosus* were associated with Groups A and B. *Ranunculus repens*, *Juncus filiformis*, and *Carex rostrata* were affiliated with Groups B and C, while *C. vesicaria* was completely dominant in Group D. Mean elevation for all quadrats included in the four different TWINSPAN groups are given in Figure 6 (cf. also Figure 1). This indicates that the groups are confined to different elevations along the transects. In 2000, Group A included the 20 lowest quadrats and Group D included the 20 upper quadrats. Groups B and C had disappeared, leaving only two zones. The mean elevation values for the different groups are almost perfectly equally distributed around the mean June water level.

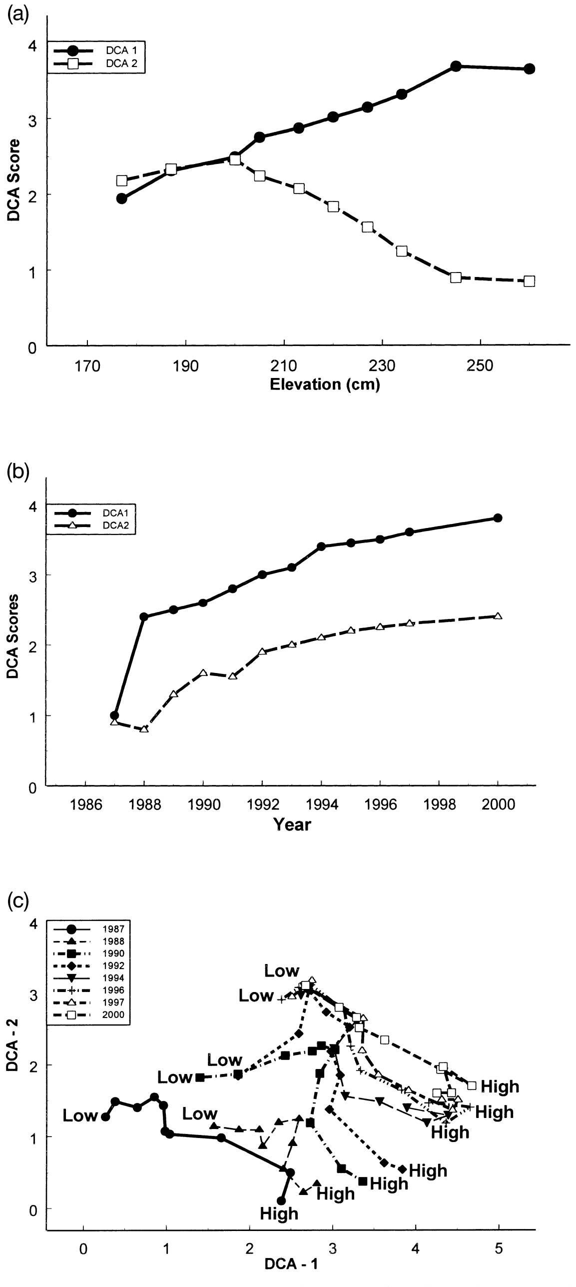

Figure 3. a. Mean DCA axes 1 and 2 scores for all quadrats at each elevation (mean of 4 consecutive quadrats), calculated over the 13 years of this study.; b. Annual changes in mean DCA axis 1 and 2 score for all quadrats of the transect in each year.; c. Mean (of four consecutive quadrats) DCA axis 1 and 2 sample scores of the transect during the study period. Lines are drawn from low (quadrats close to the water) to high (quadrats in the upper part of the transects).

Variation in life histories and species richness

Figure 7 shows the relative importance of four species life history groups over time. Bryophytes were initially abundant though annuals were common one month after drawdown and during 1988 (Figure 5). They were followed by the perennial herbs. Since then, clonal species had become dominant throughout the transects. Their abundances steadily increased over time.

Woody species establishment was poor. Juvenile *Betula* were initially frequent in the upper part of the transect, but none were recorded since 1991. A few *Salix* were recorded since 1989, but their total cover was always less than 25%. In 2000, they occurred near the upper quadrats (ca 220 cm). In comparison, *Salix* was abundant at higher elevations on the adjacent artificial islands.

There have been major changes in species (taxa) richness with time (Figure 8). Richness within the 0.5-m^2 quadrats varied from 1 to 28. Immediately after drawdown, number of taxa ranged from 1 to 12 per quadrat (mean = 4.5). After one year, richness reached its highest level (mean = 13.9), and varied from 7 to 24. Richness was similar in the third year, but afterwards it decreased by about one taxon per year.

There were also changes in richness in relation to elevation. In the lower parts, species richness varied between 2 and 12, while in the upper part it varied between 6 and 25. Since 1996, richness stabilized between two and four taxa in the lower zone and between 5 and 10 taxa in the upper zone.

Discussion

This study shows that two major processes have occurred simultaneously: temporal species turnover and spatial separation in relation to water level. Plants arrived and developed at different time after the drawdown. The exposed sediments could be colonized from a persistent seed or spore bank, from seeds or spores invading after drawdown or by vegetative expansion. Over time, species became confined to particular elevations. A typical example of such change in elevational distribution with time is shown by *Subularia* (Figure 5).

Both DCA and CCA showed that time since drawdown and elevation are significant for explaining the pattern in the data (Figure 4). However, DCA dem-

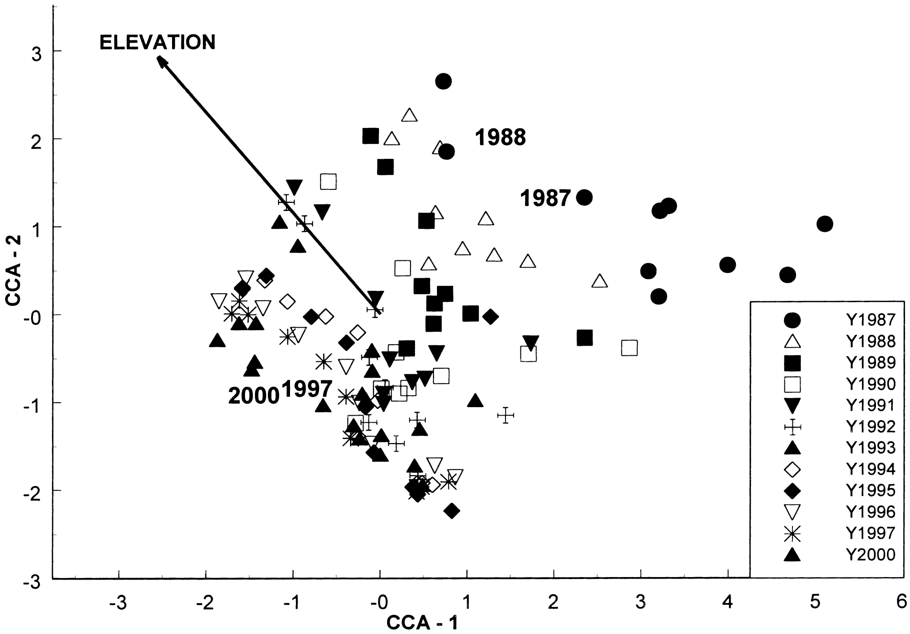

Figure 4. Mean position of quadrats plotted in CCA space. Each point is the mean of four consecutive quadrats in each year. CCA-1 is negatively correlated with quadrate elevation; CCA-2 is positively correlated with quadrat elevation. The positions of some of the nominal variables (sample years) are indicated.

onstrated that species turnover in time was 30% greater than turnover in space in any year. It was evident that the floristic turnover decreased with time, that is, the rate of succession slowed. The largest changes occurred between 1 month and 1 year after drawdown. An elevational zonation had developed since 1994 (Figure 6). Shifts in species growth forms suggest that competitive interactions are governing floristic change, with long-lived perennials maintaining an advantage.

The eigenvalues for the DCA were only slightly higher than for the CCA, indicating that the Time and Elevation captured most of the floristic variation within the data. Both DCA and CCA ordinations indicate that the vegetation was poorly differentiated during the first year of succession, but that zonation had developed.

The pattern of taxon richness on the transects (Figure 8) follow patterns often found during succession. Richness peaked one and two years after the drawdown, then the number of species on the transect declined, then stabilized. By 2000, there were in average only six species compared to 14 one year after drawdown. This may be an effect of increasing competition. *Phalaris* and *Calamagrostis* established dense populations relatively late in the upper zone once dominated by *Equisetum* while *Carex* spp. dominated the lower zone.

Change in life history features

The study suggested that the floristic change was driven by the development of dominance by persistent clonal species. Bryophytes were major pioneers on exposed fluvial sediments, but after five years, most had disappeared or were rare. The successional pattern here differed from what was found on nearby created islands (Odland 1997). *Marchantia* and *Polytrichum commune* were more common early in that succession and establishment and peak abundances of bryophytes was delayed by one year on the artificial islands. The rapid disappearance of bryophytes in both cases was associated with dense cover of the helophytes. The variable mean bryophyte cover during the succession (Figure 7) was due to the change in dominance of different bryophytes occurring at different elevations along the transect (Figure 5).

The rapid vegetation establishment of vascular plants on exposed sediments was certainly due in part to persistent seed banks. Seed banks are important for rapid recovery of marsh vegetation after natural drawdown (Keddy and Reznicek 1986; Smith and Kadlec 1983). They therefore play an important role in early

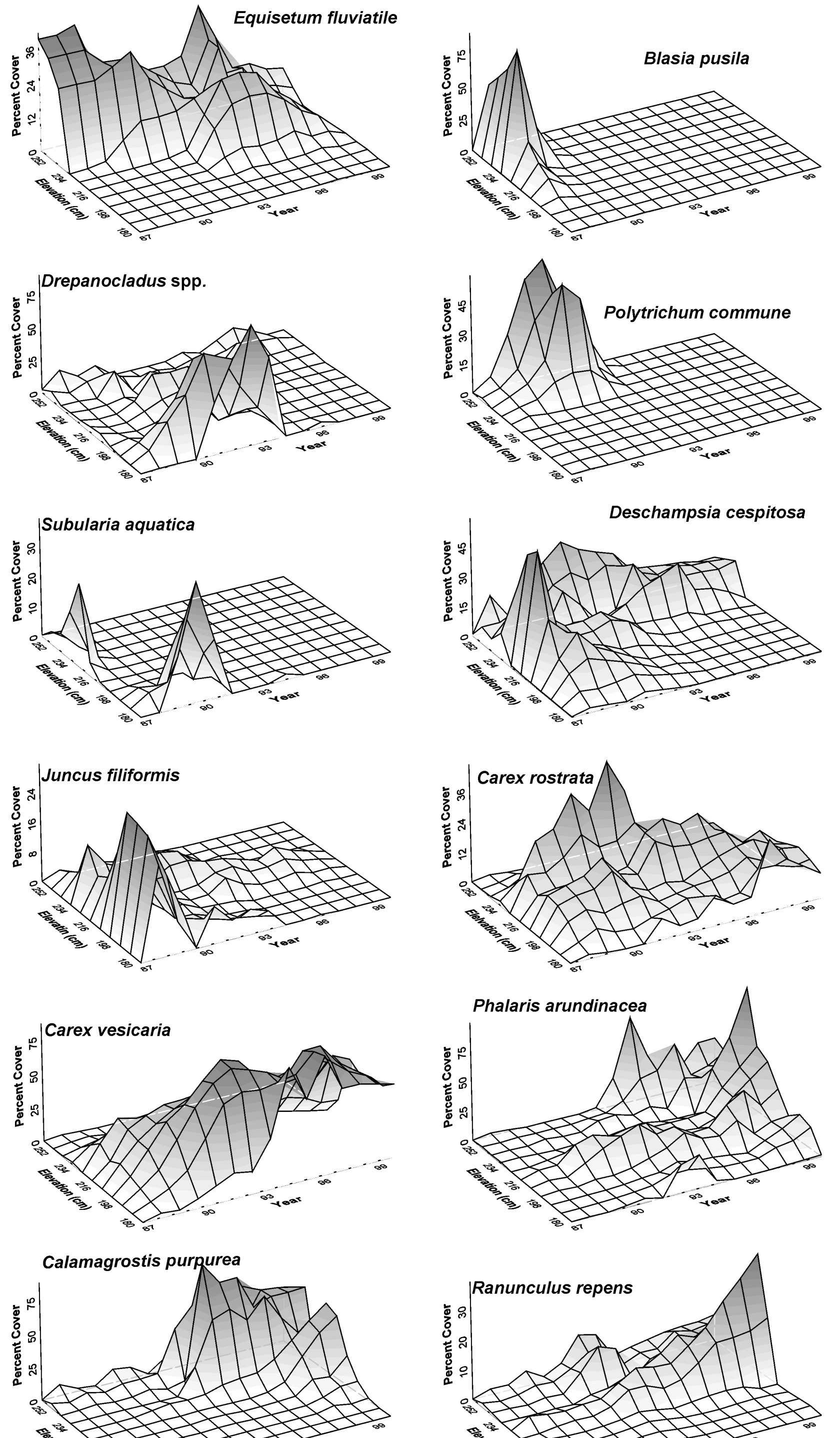

Figure 5. Percent cover response surfaces for 12 common species. Each graph shows variation in mean cover (of four sequential quadrats in a year) in response to Year and Elevation. Shading is based on five increments within the range of each species, which are noted on each graph.

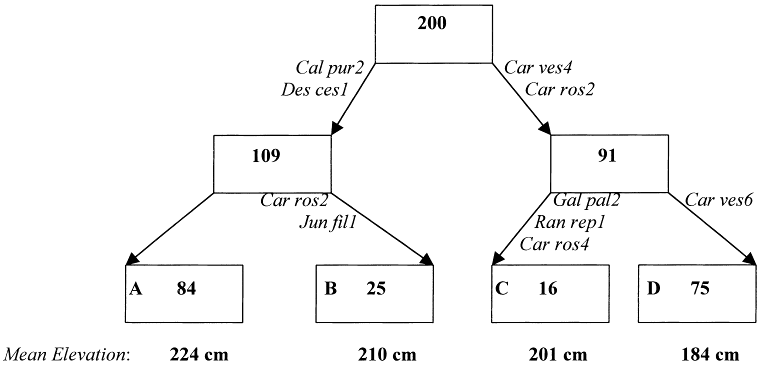

Figure 6. Results of TWINSPAN (four groups) classification of 40 quadrats over 5 sample years (1994 to 2000). Number of quadrats in each group is given in the boxes. Indicator species and their pseudospecies cut-levels are indicated. Cal pur = *Calamagrostis purpurea*, Des ces = *Deschampsia cespitosa*, Car ves = *Carex vesicaria*, Car ros = *Carex rostrata*, Jun fil = *Juncus filiformis*, Gal pal = *Galium palustre*, Ran rep = *Ranunculus repens*. Mean elevation of all quadrats in each of the four groups (A – D) is given.

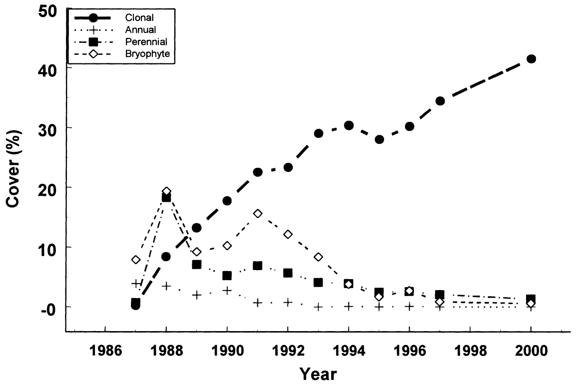

Figure 7. Variation in the mean percent cover from 1987 to 2000 of species classified to different growth forms.

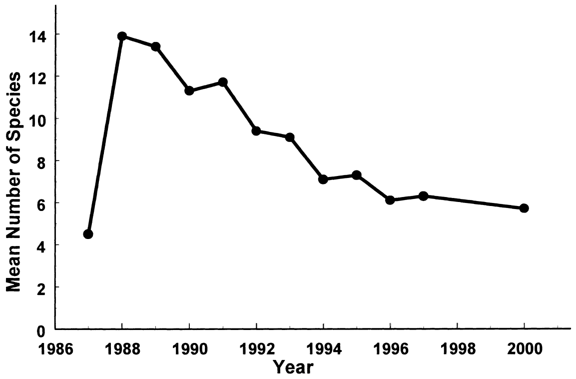

Figure 8. Mean species richness along the entire transect during the course of the study.

succession. The pool of seeds in wetland soil is important where water levels fluctuate markedly between years (van der Valk and Davies 1978; Haag 1983).

Wetland species can be dispersal dependent with short-lived propagules or seed bank species with long-lived seeds (van der Valk 1981). The abundance of annuals and non-clonal herbs immediately after drawdown suggests that these groups have a persistent seed bank. Species such as *Callitriche, Subularia, Juncus bufonius* and *Deschampsia* exemplify these species. Clonal species such as *Carex rostrata, C. vesicaria, Agrostis* and *Phalaris* were also found early in succession, though with low frequency. *Ranunculus reptans* was not found until one year after drawdown, suggesting that it lacked a seed bank or its seeds did not germinate promptly. *Calamagrostis* was not found until one year after drawdown and *Salix* did not occur before 1990. Such tardy arrivals strongly argue against their presence in a viable seed bank.

The perennial, non-clonal grass *Deschampsia* initially dominated most quadrats along the transect. Its seedlings grow rapidly and it was an excellent competitor on newly exposed sediments. It remained common until 1993, but thereafter it retreated upward (cf. Figure 6). *Carex* species initially dominated the upper transects, but they were replaced by grasses such as *Phalaris* and *Calamagrostis* (Figure 5) and the sediments were dominated by clonal herbs since 1989. Mature *Phalaris* plants spread rapidly by rhizomes (Klimešová and Čižková 1996) and individual shoots can persist for four years. It can tolerate substantial hydrological variation (Morrison and Molofsky 1998), thus providing potential competitive advantages over other clonal species (Prach and Pyšek 1994, 1999). Shoot production depends on inundation, and 50 days of flooding adversely affects biomass production in *Phalaris* (Kopecký 1967). This agrees with the low *Phalaris* abundance in the lowermost quadrats. Bernhard (1973) noted that *Carex* wetlands are less productive than grass wetlands and that under most conditions, dominance by grasses should be expected unless conditions are too stressful. This situation appears to reflect a gradient from upper sites suitable for grasses to lower sites that are inundated too frequently to permit grass dominance.

Development of an Equisetum fluviatile *vegetation belt*

The original *Equisetum* zone degraded gradually, but the decay process was slow despite strong competition from other tall and abundant invading species. This study reveals that *Equisetum* can spread downward by growth of rhizomes, despite dense cover of other species. We expect the eventual reestablishment of an *Equisetum* zone along the lake margin. The original population has yet to reach the new edge. A similar slow establishment of *Equisetum* was also found on the created wetland sites (Odland 1997). Gametophytes have not established beyond vegetative shoots, probably due to inhibition by dense vegetation. However, some *Equisetum* plants have been established nearby on the lake margin.

Species turnover and zonation

The study of wetland succession has emphasized zonation, but this may be erroneous (Hejný and Segal 1998). Our study shows that vegetation changes occurring within the transect can be divided into species turnover and species zonation. The first is most pronounced during the first years after drawdown, and since 1994, there was only minor variation in species composition within the quadrats. Wetland zonation involves processes that lead to a spatial separation of species along an inundation gradient. It is assumed that driving forces that cause zonation reflect the plant tolerances to different soil moisture and periods of inundation (plant morphology and physiology) and their competitive abilities. Competitive interactions reduce the breadth of distribution from what is possible to that which actually occurs (realized). Zonation is perceived when a few dominant species interact intensely, mutually narrowing their responses to the gradient.

Many studies of wetland zonation in boreal areas (e.g. Jensén (1979); Toivonen and Lappalainen (1980)) demonstrate this sequence in oligotrophic to mesotrophic habitats: *Equisetum fluviatile* → *Carex rostrata-C. vesicaria* → *Phalaris- Calamagrostis* → *Salix* spp. In this study, the middle part of this zonation has been established, but the extremes (*Equisetum* and *Salix*) have not yet returned.

The main dominants within the studied transects have been *Carex vesicaria*, *C. rostrata*, *Phalaris, Deschampsia*, and *Calamagrostis*. All have been recorded with cover over 80% in many quadrats. During the last seven years, competitive sorting appears to have occurred, leading to a spatial separation of these species. *C. vesicaria* dominated in the lower part, but there appeared to be a strong competition between *Calamagrostis* and *Phalaris* in the upper part where *Phalaris* became increasingly dominant. After earlier dominance, *C. rostrata* and *Deschampsia* (Figure 5) became subordinate species.

In most studies dealing with wetland vegetation zonation, plant distribution are related to "the mean summer water limit", presumably the mean June water limit. This study also indicates the importance of the mean June water level for the vegetation zonation. The first TWINSPAN division (Figure 6), which separates quadrats confined to each side of the centroid of a Correspondence Analysis (Hill 1979), separated mainly quadrats above and below the mean June water level. The 109 quadrats (group A and B) had a mean elevation of 2.208 m, 15.8 cm above the mean June water level, and the 91 quadrats (group C and D) had a mean altitude of 1.87 m, 18.0 cm below the mean June water level. The lower limit for vegetation development on the delta coincides with the mean maximum water level for January, February, and March (at approximately 1.50 m on the water gauge).

Has the succession been completed?

Wetland species can adjust their population spread to both changes in annual fluctuations and to directional changes in environmental conditions. Figure 3b and Figure 3c indicate that there had been long-term directional change, while Figure 7 shows that clonal herbs achieved dominance. Fluctuation in environmental conditions caused ephemeral fluctuations in species abundances around a directional mean. Although each basic type of change can occur independently, directional change and fluctuations usually occur together. This makes it difficult to separate between long-term directional succession patterns from fluctuations, especially in short-term studies. Was the coexistence of grasses and sedges found the middle part of the transect an equilibrium, or only a transient stage leading to discrete zonation? These two groups had different optima in relation to water level. Wetland grasses usually occur at higher elevations along lake margins (Klimešová and Čižková 1996) and *Phalaris* usually out competes *Deschampsia* (Prach et al. 1990). *Calamagrostis canescens*, *Carex gracilis* and *C. vesicaria* compete in Central European marshes, and their associations were unstable (Soukupová 1994). These results imply that the developing grass and sedge zones may become sharper, before equilibrium. However, continued lake fluctuation and the narrow elevation of current overlap (25 cm) suggest that a dynamic equilibrium zone could be maintained. Studies where the major controlling gradient may fluctuate require longer-term studies of permanent plots to separate succession from fluctuation (del Moral and Jones 2001).

The species that in time would dominate the zonation were abundant within one year after drawdown, but they had not invaded all their potential ecological ranges. *Equisetum* had yet to develop along the new shore. The potential upper zone dominants (woody shrubs) had yet to invade. This was in contrast to the created islands where *Salix* spp. established quickly and became dominant within few years in sites well above the mean June water level (Odland 1997). On the transect, mosses and perennial clonal species seemed to have precluded *Salix* establishment. The contrast with artificial islands suggested that species turnover patterns were strongly affected by priority effects, in which early occupancy of a site by alternative species leaded to different trajectories (cf., Eriksson and Eriksson (1998); Belyea and Lancaster (1999)).

The lack of *Salix* establishment on natural sediments probably resulted because they were not represented in the seed bank (cf., Tu et al. (1998)). By the time seeds dispersed onto the sediments, the existing species inhibited their establishment. There were, however, some *Salix* plants near the transect, and one could assume that they will eventually create a dense canopy that will reduce the abundance of grasses and sedges. del Moral (1999) noted a similar effect of *Salix* on subordinate vegetation in developing wetlands on Mount St. Helens.

Conclusions

This study revealed a rapid development of vegetation on exposed sediments after a permanent drawdown. The succession was facilitated by favorable substrates with fine textured silts and clays, a persistent seed bank, adequate water and rapid vegetative spread of some wetland species.

The vegetation development described here is in accordance with the general model of Gleasonian wetland succession proposed by van der Valk (1981). Most can be explained by individualistic replacements of species with contrasting life histories. Most species turnover occurred within 3 years of drawdown. The first phase was dominated by annuals, but perennial herbs soon invaded and came to dominate. Clonal species such as *Carex vesicaria* and *C. rostrata* quickly developed dense stands. *Phalaris* and *Calamagrostis* required over five years to dominate. *Equisetum*, present from the start, immediately commenced to move downward by rhizome expansion. Annual variation in clonal species through time has been dramatic, not gradual, but the longer-term pattern resulted in a spatial separation among these species. After 1994, it appears that a strong zonation had developed, but it is unclear that these zones will persist in place. The driving force in both processes was the new hydrological regime that combines annual fluctuations with periodic extreme events. The results of the vegetation classification indicate the importance of the mean June water limit for the vegetation zonation. Each species has a different tolerance to the duration and extent of inundation leading to changes in productivity and to differential competitive ability at each elevation. However, bryophytes may have altered subsequent development by their influence on vascular plants establishment. According to results from neighboring areas, one should expect a willow shrub to develop at the highest parts of the study site. Negative interactions from the earliest plants to establish on the germination of *Salix* seeds can have occurred.

Two zones with modest overlap now share the transect. We conclude that biotic interactions are sharpening zonal distinctions and that further zonation may possible if *Salix* invades the upper edge of the transect and *Equisetum* becomes dominant in the lower end.

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