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Patterns in the secondary succession of a *Carex vesicaria* L. wetland following a permanent drawdown

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Abstract

The Myrkdalen Lake, western Norway, was subjected to a ca. 1.4 m permanent drawdown in June 1987. This left the original wetland vegetation belts “hanging” over the new water level. One year after the drawdown, a permanent transect with contiguous 1.0m × 0.5 m quadrats was established through a *Carex vesicaria* wetland belt, and was analysed annually through 2001. The transect was 17 m long and included the lower part of a *Phalaris arundinacea* vegetation and the upper part of an *Equisetum fluviatile* vegetation. All quadrats were located on the same type of substrate and extended through a 65-cm difference in elevation. During the study period, the transect was completely inundated for only 6 days. A secondary succession was initiated immediately after the drawdown. The main trend was a gradual decreased cover of *C. vesicaria* and an increase particularly in the cover of *P. arundinacea* and *Calamagrostis purpurea*. Regression analyses indicated that variation in the cover of the different species could be expressed as linear, quadratic, or exponential functions of the number of years since drawdown. Parallel with the decreased abundance of *C. vesicaria*, there was a linear decrease in the number of its fertile shoots. Very low numbers of flowering shoots were found after the mean cover of *P. arundinacea* exceeded the cover of *C. vesicaria*. The study indicates that the drawdown resulted in a hydrological regime that was not optimal for *C. vesicaria*. Despite this, a clonal wetland sedge may obviously survive a major drawdown for more than 14 years.

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1. Introduction

Lakes and rivers have frequently been subjected to regulation, especially in connection with hydroelectric constructions and agricultural development. Such regulations often result

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in either increased or decreased water level, but both cause major changes in wetland vegetation over time. Most helophytes bordering lakes are dependent on an excess of water, and if they do not require periods of inundation, they certainly tolerate flooding. Spatial and temporal patterns of flood are among the primary environmental factors influencing the distribution of vegetation wetland vegetation, particularly on floodplains (Hejný and Segal, 1998). Recent studies (e.g. Keddy, 2000; Townsend, 2001) indicate that amplitude of water level fluctuations and inundation during extremely wet years strongly controls species composition on floodplains. Any change in the hydrological regime of a lake should, therefore, cause major changes in the distribution of plants surrounding the lake, and also its wetland vegetation zonation (Keddy, 2000). In Boreal lakes, distinct vertical vegetation belts are often found. *Carex* species are most frequent from ca. 20 cm above to 50 cm below the mean summer water limit, while *Equisetum fluviatile* may dominate to a depth of more than 100 cm (Vaarama, 1938; Ruuhijärvi, 1974; Toivonen and Lappalainen, 1980).

Most studies of the effects of drawdown have concentrated on the establishment of vegetation on exposed soil or sediments (e.g. Rydin and Borgegård, 1988) and several models have been developed to predict wetland successions (Van der Valk, 1981; Noon, 1996; Prach et al., 1999). Floristic change in wetland vegetation as a result of a permanent drawdown is a typical example of secondary succession. Effects of species distribution on mires in Finland after drawdown were investigated by Jukaine and Laiho (1995). By comparing the vegetation on undrained pine-mire sites with that of sites drained 3–55 years earlier they found that tall sedges like *Carex lasiocarpa* and *C. rostrata* disappeared soon after drainage. Grootjans et al. (1996) studied changes in percentage cover, frequency, and half-life of species in permanent wetland plots over a 16-year period. They found that species responded differently to a 40–80 cm drop in water level. After 16 years, a species-poor vegetation type had evolved which was dominated by grass species such as *Phalaris arundinacea* and *Poa trivialis*. Other studies have also shown that tall clonal grasses like *Calamagrostis canescens* and *P. arundinacea* may penetrate into tall-sedge communities subjected to disturbance (Apfelbaum and Sams, 1987; Prach et al., 1990; Soukupová, 1992; Barnes, 1999). Such species can obviously be more competitive than sedges in sites with few days of inundation.

In many *Carex* species, flowering is controlled by external environmental factors (Bernard, 1975; Bernard and Gorham, 1978; Solander, 1983; Hultgren, 1989; Heide, 1997). If so, one may expect a variation in number of flowering *C. vesicaria* shoots after a drawdown. Variation in the number of fertile shoots may be a more accurate measure of species performance than cover in stressed environments.

The Myrkdalen Lake, western Norway, was subjected to a ca. 1.4 m permanent drawdown in June 1987 in order to increase the area of arable land. Primary succession on exposed sediments of a fluvial delta close to the lake has earlier been described (Odland, 1997; Odland and del Moral, 2002). These studies showed that *C. vesicaria*, *C. rostrata*, *P. arundinacea* and often *Salix* spp. established quickly. The drawdown left the original *P. arundinacea*, *C. vesicaria*, and *E. fluviatile* vegetation “hanging” above the new mean summer water level, and one would expect major floristic changes in these zones.

This paper deals with the fate of *C. vesicaria* in its original vegetation belt, and it focuses on changes in relation to time during a secondary succession. Based on distribution and autecology, it could be predicted that *C. vesicaria* should disappear from its original sites. The following main questions were addressed in this study. (a) What was the main pattern in

the secondary succession of the original *C. vesicaria* vegetation? (b) How was the pattern of establishment of other species during the secondary succession? (c) How long time would succession proceed before a new stable vegetation was developed? (d) How was the variation in the number of flowering shoots of *C. vesicaria* during the succession?

2. Material and methods

The investigated site (60°40'N 6°28'E, UTM-LN 6146) lies on the outermost part of a fluvial delta in the Myrkdalen Lake (229 m above sea level). The lake is a part of the northern branch of the Vosso River catchment in western Norway. A sediment surface sample from the transect consisted mainly of particles with a diameter between 250 and 125 μm . Loss-on-ignition was 5.3%, pH was 5.0, and base saturation was 25.3%. The delta originally had broad zones of wetland vegetation separated into three distinct vertical belts (Fig. 1). *E. fluviatile* dominated the lower part of the original littoral vegetation, with the middle belt dominated by *C. vesicaria* or *C. rostrata*. The original mean summer water level was positioned in the upper part of this belt. Most of the upper delta plain was dominated by either *P. arundinacea* or *Calamagrostis purpurea*. Stands with *Salix* spp. and *Alnus incana* occurred scattered. In this part, major areas were cultivated and used as hayfields.

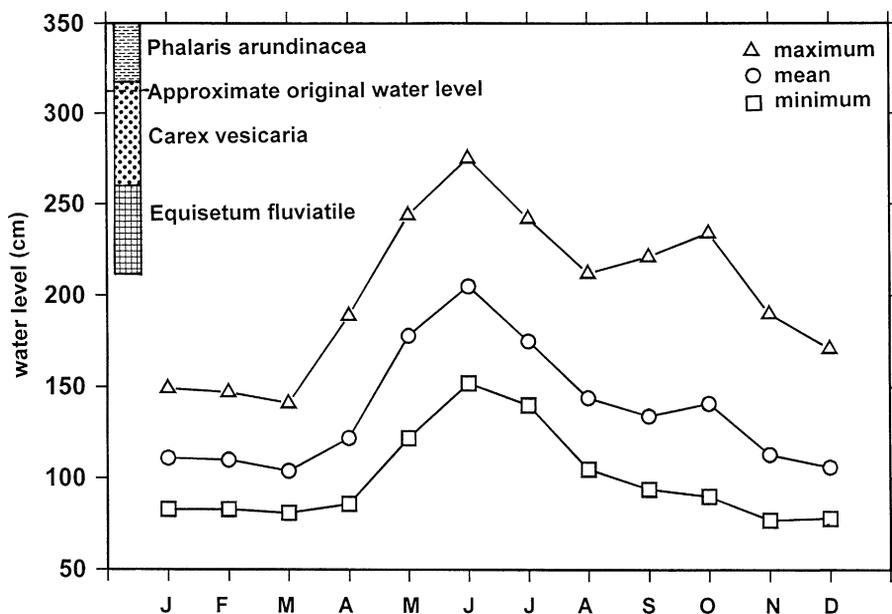


Fig. 1. Variation in the water level during the study period (1988–2000) as measured by the Myrkdalen water gauge. Mean monthly-, mean monthly maximum-, and mean monthly minimum-values are plotted. Inserted diagram in the upper left part shows the vertical distribution of the original vegetation belts. The studied transect and randomly selected quadrats lie mainly within the original *Carex vesicaria* belt (between 267 and 327 cm on the water gauge scale). Approximate position of the original mean summer water level is indicated.

A permanent transect was established through the original *C. vesicaria* vegetation in a gently sloping (ca. 5°) part of the delta. The transect was 17 m long, and included a 65 cm elevation gradient (vegetation belt) situated between 267 and 327 cm. Contiguous 1.0 m × 0.5 m quadrats were analysed along this transect from 1988 (1 year after the drawdown) until 2001.

The elevation of each quadrat was measured with a levelling instrument at its upper edge. All height measurements were given in relation to the elevation scale at the permanent water gauge in the lake (Fig. 1). The uppermost quadrat was placed in the lower part of the *P. arundinacea* belt and the lowermost in the upper part of the *E. fluviatile* belt. All three vegetation belts were monocultures with only some bryophytes in the bottom layer. Species cover was visually estimated in percentage. During the period 1993–2001, the number of flowering shoots of *C. vesicaria* within the quadrats was also counted.

Arithmetic mean cover (C) of the different species across the transect was calculated for each year. Linear and non-linear regression analyses were performed to estimate C as a function of time (Yr = years since drawdown).

In 2001, 17 quadrats selected at random from other parts of the original *C. vesicaria* belt were also analysed. This was done to test if the floristic composition within the transect was different from vegetation developed in other parts of the delta. The differences in cover of the species between transect and random quadrats were tested by t -tests.

3. Results

3.1. Variation in water level

A considerable variation in water level was observed during the investigation period (Fig. 1). Especially high water levels were recorded in 1989, 1990, and 1995, with extreme low levels in 1988 and 1996. Maximum amplitude during the study period was 400 cm, and the transect was fully inundated for 6 days only whereas the lowermost parts were so for 43 days.

3.2. Variation in species cover during the study period

The decrease in cover of *C. vesicaria* started from the edges (upper and lower part) of its original belt (Fig. 2). Quadrats in the centre of the transect retained a 100% cover until 8 years after the drawdown. In 2001, its abundance was highest (40%) in the middle part, and *C. vesicaria* had disappeared or had a cover less than 20% in the edges of the belt. As the cover of *C. vesicaria* decreased, *P. arundinacea* expanded in the upper part of the transect (Fig. 3). This species established in the lowermost part of the transect 1 year after the drawdown and since then spread from both edges into the *C. vesicaria* vegetation. During the first 9 years, the increase of *P. arundinacea* was rather slow, with a mean annual cover less than 13%, increasing from 27 to 82% during the last 5 years (Fig. 4). The cover had decreased both in the upper and the lower part during the last years.

C. purpurea appeared for the first time in the lowest part of the transect in 1991, and since then its mean annual cover increased from 1.5 to 24.7% (Fig. 4). In 2001, this grass

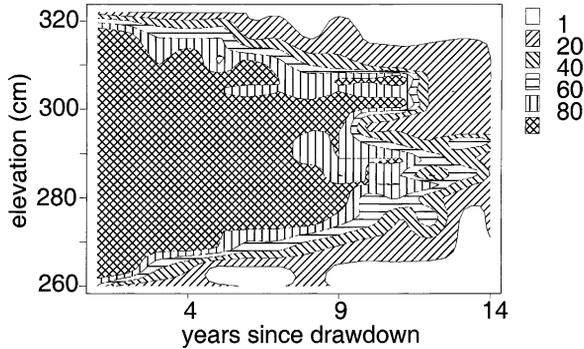


Fig. 2. Contour plots showing the variation in percent cover (divided into six cover levels) of *C. vesicaria* in relation to elevation and time (years after the drawdown in 1987). The elevation scale fits with the water level scale in Fig. 1.

was also recorded in the upper part of the transect, when it had reached a cover of 80% in the lower part.

Ranunculus repens appeared in the lowest part of the transect in 1988, and a few years later it was also found in the middle part, though sparse and scattered. The cover of this species increased with the decline in *C. vesicaria* and particularly high cover was recorded in 1999 and 2000 (Fig. 4). During the first 4 years after drawdown, *Galeopsis bifida* occurred scattered only with low abundance. In 1992, however, cover increased considerably in the central part, and the cover remained high for some 4 years. Later, however, the abundance of *G. bifida* declined again.

The lowest quadrat of the transects was in the upper part of the original *E. fluviatile* belt (Fig. 1), where this horsetail originally had a cover of 30–40%. After the drawdown, its abundance decreased gradually. During 1988–1993, *E. fluviatile* spread, probably by rhizome growth, 6 m upwards in the transect. In 2001, only a few shoots were recorded.

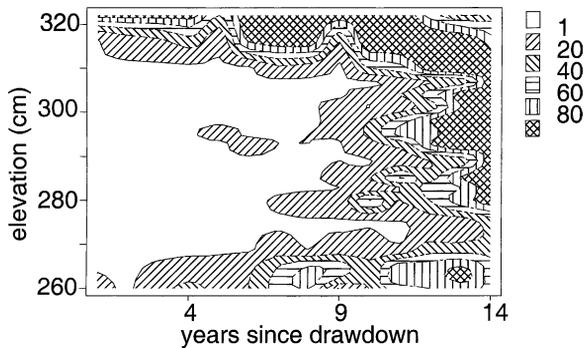


Fig. 3. Contour plots showing the variation in percent cover (divided into six cover levels) of *P. arundinacea* in relation to elevation and time (years after the drawdown in 1987). The elevation scale fits with the water level scale in Fig. 1.

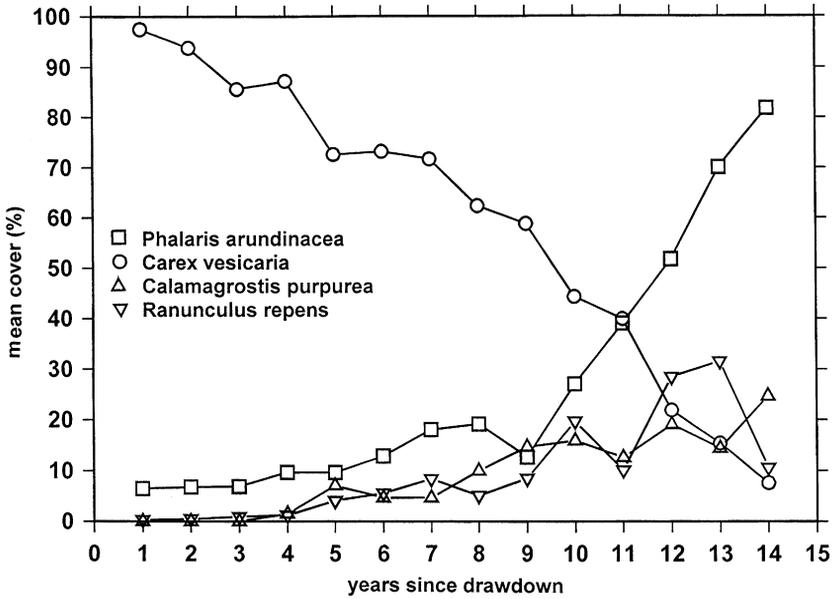


Fig. 4. Variation in mean annual percentage cover of *C. vesicaria*, *P. arundinacea*, *C. purpurea*, and *R. repens* in the permanent quadrats during the study period. The standard deviation (S.D.) varied between 38.5 and 10.2 for *C. vesicaria*, from 4.9 to 29.4 for *P. arundinacea*, from 4.9 to 30.0 for *C. purpurea*, and from 0.9 to 19.9 for *R. repens*. Results of regression analyses are given in Table 1.

This shows that its underground rhizomes have been alive for at least 14 years after the drawdown.

As soon as the cover of *C. vesicaria* had decreased below about 90%, *Deschampsia cespitosa* started to invade. *D. cespitosa* became first established in the lower part and later in the upper. Maximum cover (60%) was found between 6 and 10 years after the drawdown. When the cover of *P. arundinacea* exceeded some 50%, the cover of *D. cespitosa* began to

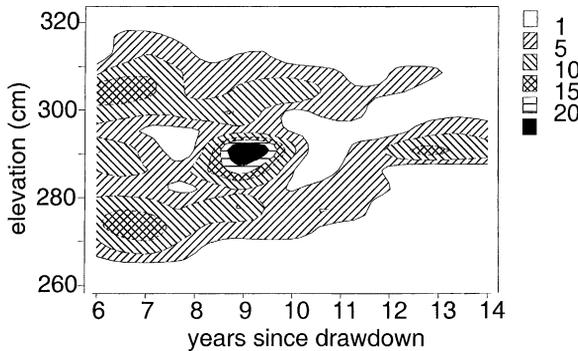


Fig. 5. Variation in number (divided into six levels) of *C. vesicaria* plants producing flowers within the 17 permanent quadrats during the period 1993–2001. The elevation scale fits with the water level scale in Fig. 1.

Table 1

Results of regression analyses with year since drawdown (Yr) as the independent variable and mean percentage cover for each year of the different species as dependent variables and mean cover values (%) \pm S.D. of the different species within the transect quadrats ($n = 17$) and in 17 random quadrats are given

Species	Succession pattern in the transect ^a			Differences in mean species cover (%) ^b		
	Regression equation	r	P	Transect	Random	P
<i>Carex vesicaria</i> L.	$-6.9 \times \text{Yr} + 111.0$	-0.98	<0.001	7.2 ± 10.2	2.1 ± 7.2	0.102
<i>Phalaris arundinacea</i> L.	$4.07 \times e^{0.20 \times \text{Yr}}$	0.96	<0.001	81.8 ± 25.1	82.4 ± 22.0	0.942
<i>Calamagrostis purpurea</i> (Trin.) Trin.	$1.78 \times \text{Yr} - 4.0$	0.94	<0.001	25.9 ± 28.7	17.7 ± 20.9	0.347
<i>Ranunculus repens</i> L.	$2.00 \times \text{Yr} - 4.8$	0.78	<0.001	10.6 ± 5.0	3.8 ± 6.4	0.002
<i>Galeopsis bifida</i> L.	$-0.29 \times \text{Yr}^2 + 4.4 \times \text{Yr} - 6.6$	0.66	<0.001	2.4 ± 7.2	2.3 ± 2.8	0.950
<i>Deschampsia cespitosa</i> (L.) Beauv.	$-0.17 \times \text{Yr}^2 + 2.65 \times \text{Yr} - 1.7$	0.90	<0.001	2.7 ± 6.1	0.9 ± 2.6	0.269
<i>Galium palustre</i> L.	$0.08 \times \text{Yr} - 0.1$	0.56	0.037	0.2 ± 0.4	1.4 ± 2.7	0.005
<i>Equisetum fluviatile</i> L.	$-0.15 \times \text{Yr} + 1.6$	-0.81	<0.001	0.1 ± 0.2	0.0	Not tested
<i>Caltha palustris</i> L.	(Only found in 2001)			0.4 ± 1.2	0.9 ± 2.6	0.461
Number of <i>Carex vesicaria</i> flowers	$-10.6 \times \text{Yr} + 151.8$	-0.79	0.012	0.7 ± 2.4	0.4 ± 1.5	0.610

^a Number of *C. vesicaria* flowers gives the linear decrease in the total number of fertile *C. vesicaria* shoots within the transect during the period 1993–2001. Yr = number of years since drawdown; r = correlation coefficient; P = significance level.

^b Differences between the mean values in the transect quadrats and in the random samples were tested by t -tests.

decrease. In 2001, the latter species was only found with a low cover in the uppermost quadrats. *Galium palustre* gradually invaded quadrats where the cover of *C. vesicaria* had declined. *G. palustre*, however, remained sparse and scattered during the whole study period, with a cover always below 10%. *Caltha palustris* was only found with low cover in the lowermost quadrats in 2001.

3.3. Variation in number of flowering shoots of *C. vesicaria* during an 8-year period

Flowering of *C. vesicaria* varied substantially both within the same quadrats and between the different quadrats (Fig. 5). The highest number of flowering shoots was recorded in 1996 (year 9), but the number was strongly reduced in 2001. The plants in the middle part of the transect produced flowers for a longer period than at the edges. In 2001, 10 flowering plants occurred in the middle quadrat, and almost none in the other quadrats.

3.4. Regression analyses

In regression analyses with year since drawdown as the predictor and mean cover of the species in the transect for each year as the response variable (Table 1, Fig. 4), *C. vesicaria* and *E. fluviatile* showed a significant linear decrease. *C. purpurea*, *R. repens*, and *G. palustre* showed a significant linear increase. *G. bifida* and *D. cespitosa* showed significant quadratic responses with maximum cover during intermediate stages of the succession. The increase in *P. arundinacea* with time was best explained by an exponential function.

The decrease in number of flowering *C. vesicaria* shoots (number of flowers) during the 9-year period could also be given as a function of its cover (C) and time (Yr). A multiple regression gave the following equation: number of flowers = $2.34 - 0.17 \times Yr + 0.05 \times C$, $r = 0.49$, $P < 0.001$.

Cover was significant ($P = 0.000$), while year was not ($P = 0.255$).

3.5. Comparisons between quadrats within the transect and in other parts of the floodplain

Mean elevation for the 17 quadrats in the transect was 323.6 ± 18.1 cm, and for the random quadrats it was 327.7 ± 19.5 cm. A t -test showed that the mean elevation of the transect quadrats and the random quadrats was not significantly different ($P = 0.534$).

All species except *G. palustre* and *R. repens* had similar occurrences in the transect and in the random quadrats (Table 1). This suggests that the main patterns found in the transect study were similar to the general secondary succession patterns of the original *C. vesicaria* wetland on this floodplain.

4. Discussion

Investigations on secondary succession initiated by direct human influences such as mowing, grazing, logging, and fertilization are numerous. Such impacts often cause changes

in multiple environmental variables, and a direct relation between cause and vegetation response on the different species may be difficult to establish. In a drawdown study like the present, there was change in only one major environmental variable, namely the water level fluctuation.

The new hydrological regime of the lake entailed a drastic decline in inundation after the drawdown. Under normal conditions, a sedge wetland should experience at least one month of flooding per year (Prach, 1992). An extinction of the original *C. vesicaria* belt should, therefore, be expected. The studied succession process was surprisingly slow, as after 14 years the sedge was still present. Extrapolation of the linear regression (Table 1) predicts that *C. vesicaria* will not produce flowers in 2002 (15 years after drawdown) and will probably come extinct after 16 years. The multiple regressions showed that the general decrease in flowering plants was mainly associated with the decrease in cover. However, there was a major variation in flowering plants from year to year. During the period 1993–1997, total number of flowering plants in the 17 quadrats varied between 35 and 106, while during the last 4 years the number varied between 12 and 20. Low flowering occurred, when the mean cover had decreased below 40%, and this coincided with the time when the cover of *P. arundinacea* exceeded the cover of *C. vesicaria* (Fig. 4). Flowering frequency was probably also influenced by annual variations in water level and temperature during the study period.

Similarly, Grootjans and Schipper (1987) found that *C. palustris* survived unfavourable conditions (a 40 cm drop in the water table) for at least 10 years as an adult, but sexual reproduction no longer occurred.

An increase in the abundance of grass species following changes in the hydrological regime has frequently been shown. Barnes (1999) reported an expansion of *P. arundinacea* on small river fluvial islands over a period of 15 years, where it had become the dominant species at elevations lower than 1 m above the normal water level (see also Prach, 1992). Soukupová (1992) found a similar response for *C. canescens*. *D. cespitosa* appears to be an important species at intermediate stages of both primary (Odland, 1997; Odland and del Moral, 2002) and secondary succession (this work).

4.1. Autecology and life history of *C. vesicaria* and *P. arundinacea*

The two main species included in this study, *C. vesicaria* and *P. arundinacea*, are generally confined to different vegetation belts along lakeshores, though the latter may also be growing close to the lake edge. Prach (1992) found that *C. vesicaria*, *D. cespitosa*, and *P. arundinacea* growing on a floodplain had their optima at different elevations relative to the water level. *C. vesicaria* was confined to the lowermost parts that were flooded more than 40 days a year during the study period.

The relatively slow development of *P. arundinacea* on the study site was quite consistent with its developmental pattern on exposed sediments on the floodplain (Odland and del Moral, 2002). This tall grass species obviously needed several years to develop underground rhizomes that eventually could develop dense aboveground stands. Another delaying factor may also be the low germination percentages of its seeds, which has been explained by seed dormancy (Berg, 1982). Good et al. (1978) and Lech (1996) reported that *P. arundinacea* responded with increased germination and growth to drawdown, and it has frequently been considered to be an aggressive invader in disturbed habitats, where the substrate was

favourable (Apfelbaum and Sams, 1987; Conchou and Pautou, 1987; Conchou and Fustec, 1988; Chester et al., 1995; Morrison and Molofsky, 1998; Prach et al., 1990). Its highly competitive ability in the studied transect may be partly due to its high biomass production and growth pattern (e.g. Kopecký, 1967; Ho, 1979; Conchou and Pautou, 1987; Lech and Simpson, 1994). *P. arundinacea* shows a rapid growth in spring, producing up to 2 m tall shoots that form dense, highly productive stands and spread by rhizomes that are about 50 cm long. New tillers that arise rhizome branching reportedly have a life span of 4 years and the below ground meristem dies after 5 years (Klimesová and Čížková, 1996).

Most *Carex* species have extensive underground biomasses and can produce both long spreading and short, clumping rhizomes. The different shoots have an estimated life span of less than 2 years (Bernard, 1990). According to Soukupová (1988), *C. vesicaria* can have an intensive long-term tillering. The major advantage of *P. arundinacea* has probably been its height and ability to produce dense stands that reduce the amount of light to the *C. vesicaria* shoots. Closer to the lake margin, the abundance of *P. arundinacea* may be reduced during long periods of inundation (Kopecký, 1967; Conchou and Pautou, 1987), but that did not occur in the studied site. On the exposed sediments, *C. vesicaria* and *P. arundinacea* had their optima at different elevations (below and above 205 cm, respectively) above the water level (Odland and del Moral, 2002). In that study, the development of dense *P. arundinacea* stands was also found to be relatively slow during the first 6–7 years. Consequently, its expansion on both exposed sediments and in the original *C. vesicaria* wetland zone followed the same exponential pattern.

4.2. Has new climax vegetation been established?

Can it be assumed that the developed *P. arundinacea* vegetation was in equilibrium with the new water level? The vegetation in the transect quadrats (and also in other parts of the floodplain) was very similar to *P. arundinacea* vegetation found elsewhere on the floodplain before the drawdown. However, the significant increase in *C. purpurea* suggests that this species will continue to increase in abundance. Both monospecific and mixed stands of *P. arundinacea* and *C. purpurea* were found on the floodplain before and after the drawdown (Odland and del Moral, 2002). Probably this will be the situation also after the drawdown. It cannot, however, be concluded that a completely stabilised vegetation has become established 14 years after the drawdown. *C. vesicaria* was still present, although it hardly experienced any inundation any more. In time, possibly also *Salix* spp. may become established within this site.

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