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Response of mid-water common reed stands to water level variations and winter conditions in Lake Poygan, Wisconsin, USA

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Abstract

Because of wetland recession, common reed (*Phragmites australis*) stands in the Upper Winnebago Pool Lakes, Wisconsin, now mark the former outer margins of destroyed cattail (*Typha* spp.) marshes, occurring off shore in water up to 1.5 m deep. These mid-water common reed stands have experienced fragmentation and losses in area. This study examined the relation between changes in characteristics of common reed stands and some key environmental factors that may affect their success, especially those related to seasonal patterns in water level management and exposure to wind and severe winter temperatures. Individual patches (28–26,598 m^2) within each common reed stand (6740–43,048 m^2) were characterized with regard to stem densities (1–245 m^{-2}) and water depths around the perimeter (0.10–1.52 m) and in the interior (0.22–1.30 m). Water-level cumulative frequency duration curves were used to quantify duration and continuity of exposure of common reed stands to various extreme water levels during 1986–1996, and we correlated these with annual percent changes in area derived from aerial photographs. Higher stem densities corresponded to larger patch size, greater historical stability, and less fragmentation. In addition, larger patches tended to be deeper, and covered a greater range of water depths. Conversely, more “ragged” patches tended to have lower maximum depths, both in the interior and on the perimeter, as well as smaller water level ranges. Overall, higher stem densities were associated with shallower water, though intermediate depths have experienced the greatest decline. Although combinations of extreme water levels and winter temperatures did not significantly predict annual changes in area of all common reed stands, these factors explained up to 75% of the variance in stands with the greatest loss.

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This indicates recent losses were caused by combined effects of extreme water levels and winter temperatures.

Keywords: Common reed; *Phragmites australis*; Water level; Stem density; Winter

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1. Introduction

Common reed (*Phragmites australis* (Cav.) Trin. ex Steud. is a widely distributed helophytic perennial, especially in the temperate mid-latitudes, that produces new shoots in the spring from rhizome buds formed primarily in the summer of the previous year (Tucker, 1990). In the Upper Winnebago Pool Lakes of Wisconsin, USA, the stems emerge above the water throughout May, when water temperatures reach 10–15 °C, and grow rapidly to mid-June. Maximum stem height is attained in mid to late June. Plants in shallower water develop sooner (Tucker, 1990; Kahl, 1993), whilst stem height may be affected by water depth and its fluctuations (Coops et al., 1996), nutrient availability, herbivory (Haslam, 1971a), and organic matter accumulation (Van der Putten et al., 1997; Rolletschek et al., 2000). Conditions are usually unfavorable for seed germination and establishment, which require shallow water (<5 cm) or mudflats (Haslam, 1971b; Tucker, 1990).

Prior to the creation of the 75,286 ha Upper Winnebago Pool Lakes (Lakes Butte des Morts, Winneconne, and Poygan) in east central Wisconsin by the damming of the Fox River in the 1850s, this watershed was dominated by fertile riverine marshes covered by dense emergent vegetation (Linde, 1975). Changes in water level regimes, increased sediment and nutrient loads due to agricultural practices and urbanization, and increasing exposure of formerly protected shorelines to wave attack and ice scour have contributed to the loss of tens of thousands of hectares of wetland habitat in this system, which once was amongst the most diverse in Wisconsin (NWWT, 1994). Now, the dense, monotypic common reed stands in the Upper Winnebago Pool Lakes mark the former outer margins of marshes, which consisted of a variety of emergent plants, but mostly cattails (*Typha* spp.), and have been destroyed over the last 150 years. Generally, marsh loss was initiated by higher water levels, which caused the interwoven root masses of cattails to float above the substrate. Wave action then fragmented the root masses, and the separated cattail “bogs” drifted away from shore and down the lower Fox River, transforming these areas into large, turbid, open-water lakes with concomittant loss of deep water and fish habitat, further exacerbated by common carp sediment disturbance (*Cyprinus carpio* Zimmerman, 1953; Sloey and Spangler, 1977; WDNR, 1989; Kahl, 1993). Because of water level increases and shoreline recession, many of the common reed stands now are situated off shore in water up to 1.5 m deep, whilst others remain in existing littoral marshes. The mid-water common reed stands have persisted despite imposed water level regimes with winter drawdowns, waves, boating, common carp activity, and algal overgrowth. However, recent evidence indicates that common reed stands have been rapidly diminishing in size and vigor over the past 10–15 years (Gabriel and Bodensteiner, 1998, 2002; A. Techlow, Wisconsin Department of Natural Resources, personal communication).

Given the potential significance of offshore stands of emergent macrophytes (Kahl, 1993) in a system that is already highly anthropogenically stressed, our goal was to assess the relationship between changes in the spatial configuration of common reed stands and environmental factors, particularly water levels and winter weather. Since current spatial patterns could yield clues to factors adversely affecting these stands, we collected information on the current status of common reed stands, including water depth, stem density and uniformity of stem distribution within stands.

2. Materials and methods

2.1. Study sites

Although the disappearance of common reed stands appears to be a system-wide phenomenon on the Upper Winnebago Pool Lakes, this study was limited to the four offshore stands in Lake Poygan: (1) East Channel; (2) Hindenburg Line; (3) Lone Willow Island; and (4) West Bay (Fig. 1). Lake Poygan (14,102 ha) is the uppermost of the Upper Winnebago Pool Lakes, and the mean depth (2.1 m) and maximum depth (3.4 m) are similar to the other lakes. All of the lakes are characterized as hyper-eutrophic and turbid (Lillie and Mason, 1983). The mean Secchi disk depth is 0.25 m, and the 5% photic zone during 1975 through 1981 fell between 1.4 and 2.2 m (WDNR, 1989; Kahl, 1993).

2.2. Biometric measurements

Within each stand, individual patches of common reed were distinguished as aggregations of live stems from multiple plants with a minimum dimension of 2 m, separated from the nearest adjacent patch by a minimum of 4 m of open water. Each common reed patch was characterized with regard to stem densities and water depths around the perimeter and in the interior. Both stem densities and interior water levels were measured along systematically spaced transects running perpendicularly through the long axis of each patch. The number of transect measurements reflected the spatial heterogeneity of each stand, ranging between two and five for each patch, depending on its size.

Stem densities were determined by counting live common reed stems within a floating, 1 m^2 quadrat. Stems were counted 1 m inside the perimeter of a patch at each end of a transect, as well as at two randomly determined points along a transect in the interior of the stand. Interior water depths were measured at the location of the quadrat samples and every 5 m along each transect, following a calibrated floating line and using a depth pole. In addition, perimeter water depth was measured at 5 m intervals along the perimeter of most patches in each stand; patches with a long axis of less than 20 m had four perimeter measurements taken at the cardinal compass points. Data collection required 2 months of fieldwork during the growing season, so stem heights were not measured since they would change with time. Water depths at each study site were standardized relative to Lake Poygan gauge levels.

In total, 40 different patches were identified and measured within the four stands, including 332 stem density measurements, 610 interior water depth measurements, and 1435 perimeter water depth measurements.

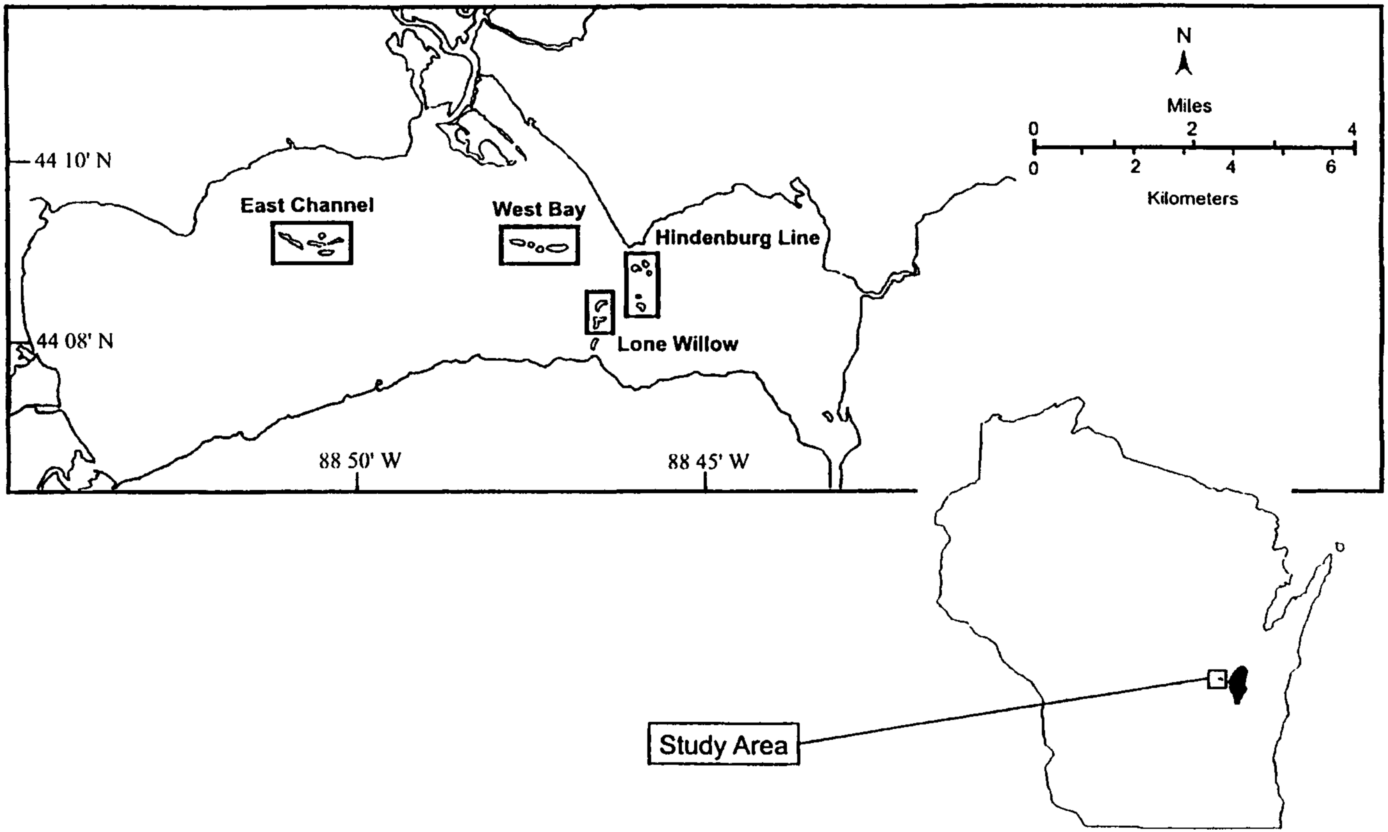

Fig. 1. Locations of the four common reed stands in Lake Poygan, Wisconsin.

Table 1
Number of patches, patch area, patch perimeter, and perimeter to area ratio in the four common reed stands in Lake Poygan

Patch characteristic	East Channel		Hindenburg Line		Lone Willow		West Bay	
	1937	1997	1937	1997	1937	1997	1937	1997
Number	10	11	16	12	2	2	11	15
Area (m^2)								
Total	110004	6740	85501	30247	43970	43048	40878	32734
Mean	11000	612	5343	2327	21985	21524	3405	2182
Maximum	21412	1933	33426	15818	27635	26598	13925	14523
Minimum	43	48	264	98	16235	16450	78	28
Loss (%)		94		65		2		20
Perimeter (m)								
Total	7522	1299	6237	2859	2218	2148	3645	3541
Mean	752	118	389	220	1109	1074	303	236
Maximum	1571	254	1323	673	1459	1351	821	995
Minimum	28	30	66	45	760	797	34	20
Loss (%)		83		54		3		2
Perimeter/area								
Total	0.07	0.19	0.07	0.09	0.05	0.05	0.09	0.11
Mean	0.16	0.33	0.16	0.23	0.05	0.05	0.18	0.32
Maximum	0.67	0.61	0.25	0.46	0.05	0.05	0.44	0.73
Minimum	0.05	0.09	0.04	0.04	0.05	0.05	0.06	0.07

2.3. History of spatial changes in the common reed stands

To relate changes in spatial characteristics of the common reed patches to environmental factors, we utilized a previously conducted analysis of a historical collection of aerial photographs (Gabriel and Bodensteiner, 1998, 2002). We determined spatial changes in patches of common reeds within each of the four stands based on common metrics used to identify landscape changes, including: (1) number of patches; (2) areal coverage; and (3) edge metrics, e.g. perimeter of stands, total perimeter, and perimeter to area ratio (Table 1; cf. Ritter et al., 1992; Ritters et al., 1995).

2.4. History of water levels and winter temperatures

The historical record of water levels was taken from data recorded at the Oshkosh, Wisconsin gauge (04082500) operated by the US Army Corps of Engineers. Daily water levels were compiled from 12:00 noon gauge readings from 1986 through summer 1997. This water level record coincides with an almost annual record of aerial photographs that were used to assess historical spatial changes in the common reed stands. This record period is subsequent to changes in the water level management regime instituted in 1982 that may be contributing to the deterioration of common reed stands.

Since most data demonstrated skewness and kurtosis, with the exception of the water depth data, non-parametric tests were used to analyze each environmental variable separately: Mann–Whitney *U*-test and Kruskal–Wallis test for analysis of differences and Spearman's rank order to measure correlation. However, multiple regression analysis was used for some comparisons since no analagous non-parametric test exists. Stem densities were related to water depth and to location within a patch within stands, and to these variables plus fetch distance of prevailing southwesterly winds in the summer with all interaction effects among all stands using regression analysis. Location was coded as +1 or −1 to reflect interior and perimeter locations since interior distances from the perimeter varied among patches. Actual water depth in meters was used. Fetch was simply ranked from 1 to 4, reflecting least to most, since both distance and exposure to wind varied among patches within a stand.

Water-level duration curves were created for 1986 through 1994 for the months during which critical life cycle stages occur, including winter dormancy (1 October–30 March), spring germination, sprouting, and emergence (1 April–30 May), and summer flowering (1 June–31 July), as identified for the Upper Winnebago Pool Lakes (Kahl, 1993). These curves were used to quantify duration and continuity of exposure to various water levels. Our goal was to identify a set of seasonal water levels that exhibited the greatest variability between years. These were determined empirically from cumulative frequency duration curves based on the 1986–1994 period, using the 10 and 25th percentiles for number of days at low winter and summer water levels, and the 75th and 90th percentiles for number of days at high spring and summer levels. Water level scenarios were related to annual changes in common reed areal coverage using linear regression. Scenarios were composed of number of days at extreme winter levels or combinations of high spring and summer levels and low winter levels versus percent annual change within and among stands from 1986 to 1994. Best models were selected based on the highest value of the square of Pearson's product moment correlation coefficient (r^2).

Each of four single-factor winter temperature-related scenarios was also related to annual changes in areal coverage by linear regression. Two scenarios addressed extreme temperatures, being the number of days and number of degree-days at or less than −18 °C (lower 5th percentile). The other two scenarios were number of days and number of degree-days at or less than 0 °C.

Finally, the water level scenarios and temperature scenarios that showed the strongest relations to changes in areal coverage were combined into single models with the interaction term.

3. Results

3.1. Spatial stand characteristics

Areal losses in stands varied widely from 1937 through 1997. All reed stands declined both in total area and total perimeter since 1937 (Table 1). The largest decrease was observed in the East Channel stand, which decreased by 94% in area and 83% in total perimeter since 1937. These large losses are followed closely by those of the Hindenburg Line stand, where a 65% loss in area and a 54% decrease in total perimeter have occurred since 1937. Decreases in the West Bay stand are less extensive, the stand having lost only 20% of its area and 2%

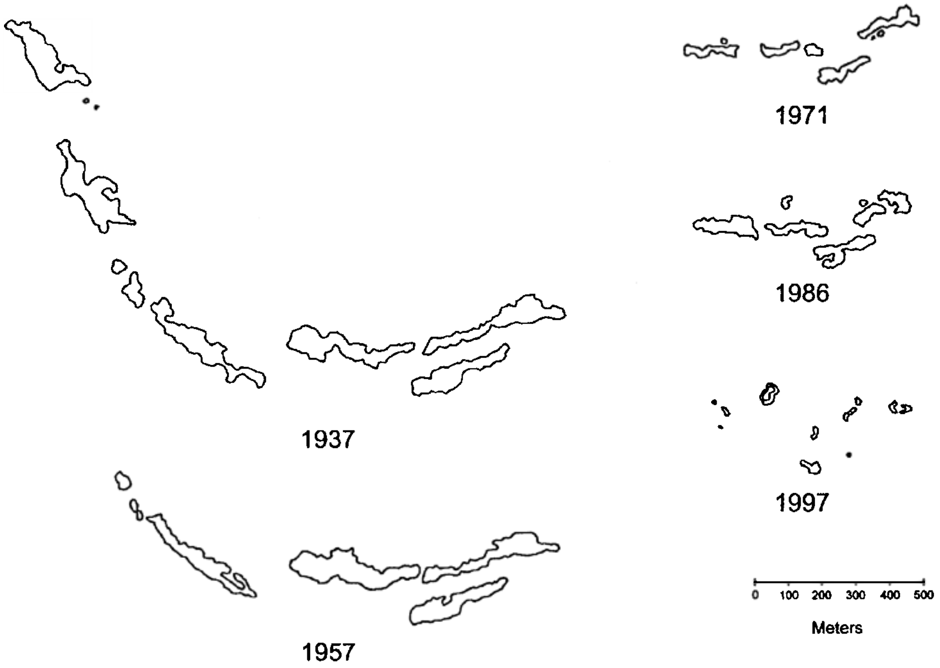

Fig. 2. Historical changes in common reed patches in the East Channel stand based on outlines drawn from aerial photographs.

of its perimeter since 1937. The Lone Willow stand has been the most stable of the of the common reed stands, having lost only 2% of its area and 3% of its perimeter since 1937.

Changes in perimeter to area ratios and numbers of patches indicated that stand loss is characterized by increased fragmentation and shrinking patch size (Table 1). The pattern of loss, most evident in stands with the greatest fetch and exposure to wind and wave attack from prevailing southwesterly winds in the summer (Fig. 1), appeared to proceed through an increase in irregularities along the perimeter, especially along edges facing the southwest as is exemplified by the East Channel stand (Fig. 2).

3.2. Biometric measurements

The spatial pattern of stem densities, as a measure of individual stand health, is consistent with the findings of our aerial photo analysis (Gabriel and Bodensteiner, 1998, 2002); we found the greatest densities in the least changed stands, with the largest historical area and stability. Various measures of stem densities correlated to patch size, stability, and fragmentation. The Lone Willow stand had the highest median stem density, while East Channel had the lowest median and maximum stem density and the lowest variability in stem density (Table 2). For the entire set of stands, we found that maximum stem density increased as the size of the common reed patch increased, both in terms of area and perimeter (Table 3). Conversely, minimum stem density decreased as area and perimeter increased.

Table 2
Median stem densities and mean water depths in patches of each of the four common reed stands in Lake Poygan

Stand characteristic	East Channel	Hindenburg Line	Lone Willow	West Bay
Stem density (N m^{-2})				
Median	59	60	76	63
Inter-quartile range	38	46	67	79
N	32	166	48	86
Maximum	117	245	171	193
Minimum	51	1	9	7
Interior water depth (m)				
Mean	0.93	0.74	0.73	0.56
S.D.	0.11	0.16	0.19	0.20
N	95	233	126	156
Maximum	1.25	1.18	1.30	1.08
Minimum	0.70	0.22	0.35	0.25
Perimeter water depth (m)				
Mean	1.06	0.88	1.06	0.81
S.D.	0.15	0.26	0.17	0.29
N	106	481	362	486
Maximum	1.30	1.52	1.48	1.30
Minimum	0.72	0.30	0.45	0.10

Also, the more “ragged” the edge of a common reed patch, as indicated by higher perimeter to area ratios, the lower the stem density. On a stand by stand basis, the significant relationships between spatial characteristics and stem densities were consistent with those of the entire set (Table 3). Median and minimum stem density relationships were strongest in West Bay,

Table 3
Statistically significant Spearman’s rank correlation coefficients (r) between spatial characteristics of common reed stands and stem densities in 1997 ($P < 0.05$)

Spatial characteristic	Stem density		
	Median	Maximum	Minimum
All stands ($N = 40$)			
Patch area		0.49	−0.46
Patch perimeter		0.47	−0.49
Perimeter/area		−0.50	0.40
East Channel ($N = 11$)			
Patch area		0.66	
Patch perimeter			
Perimeter/area	−0.65	−0.83	
West Bay ($N = 15$)			
Patch area	−0.61		−0.95
Patch perimeter	−0.56		−0.93
Perimeter/area			0.89

Insignificant results for the Hindenburg Line and Lone Willow stands were not included.

while maximum stem density relationships were strongest in the East Channel stand. Among all stands the rank of fetch was significantly and directly related to stem density, but only accounted for 14% of the variance. Based on measures of stem density, the Lone Willow stand was the healthiest while the East Channel stand was the least healthy of the Lake Poygan common reed stands.

The highest mean depths as well as the lowest minimum depths were found in the East Channel stand (Table 2). Hindenburg Line and West Bay stands had shallower mean, maximum and minimum interior and perimeter water depths, and Hindenburg Line stand's interior water depths were the shallowest of all the stands. In contrast, the Lone Willow stand had mean perimeter water depths as high as those of the East Channel stand, and its maximum perimeter and interior water depths exceeded those of East Channel. Perimeter water depths were more variable in both the Hindenburg Line and West Bay stands, as indicated both by the range and variability of water depths.

The differences in both perimeter and interior water depths between stands were significant (interior 0.66 m versus exterior 0.88 m; Kruskal–Wallis, $P < 0.05$). Perimeter depths were greater than interior depths, both for all the stands and for individual patches as well (Mann–Whitney U-test, $P < 0.05$). Finally, perimeter water depths varied by the cardinal direction of exposure (Kruskal–Wallis, $P < 0.05$), but the direction depended on the individual stand (Table 4). Maximum perimeter depth corresponded to the edge of the stand facing the maximum fetch and historical lakeward edge in two of the three stands. In the Lone Willow stand the deepest edge was directly adjacent to the former river channel.

Larger patches, indicated both by area and perimeter, tended to be deeper, but also had a greater range of water depths (Table 5). Conversely, more "ragged" patches tended to have lower maximum depths, both in the interior and on the perimeter, as well as smaller water level ranges.

3.3. Effects of water depths and fluctuations

Overall, higher stem densities were associated with shallower water (Table 6). However, examination of individual stands produced mixed results. While this relationship was consistent in the West Bay and Lone Willow stands, it was considerably weaker for the Hindenburg

Table 4
Mean perimeter water depths (m) by cardinal direction

Stand	Cardinal direction of perimeter			
	East	North	South	West[a]
All stands ($N = 1329$)	0.89	0.94	0.94	0.85
Hindenburg Line ($N = 481$)	0.85	0.87	0.82	0.95[b,c]
Lone Willow ($N = 362$)	1.07	1.14[c]	1.04	0.94[b]
West Bay ($N = 486$)	0.75	0.83	0.94[b,c]	0.62

Due to the high degree of fragmentation, no distinction was made for perimeter directions for the East Channel stand.

[a] Predominant wind direction.

[b] Direction of maximum fetch.

[c] Direction of historical lakeward perimeter.

Table 5
Statistically significant Spearman's rank correlation coefficients (r) between water depths of common reed stands and area, perimeter, and perimeter to area ratio (P/A) ($P < 0.05$)

Water depth	Patch characteristic		
	Area	Perimeter	P/A
All stands ($N = 40$)			
Interior maximum	0.78	0.76	−0.67
Interior range	0.74	0.81	−0.48
Perimeter mean	0.66	0.54	−0.76
Perimeter median	0.67	0.55	−0.77
Perimeter maximum	0.90	0.86	−0.77
Perimeter range	0.79	0.83	−0.56
Hindenburg Line ($N = 12$)			
Interior maximum	0.90	0.92	−0.76
Interior range	0.87	0.89	−0.67
Perimeter mean	0.77	0.60	−0.89
Perimeter median	0.78	0.61	−0.94
Perimeter maximum	0.93	0.96	−0.80
Perimeter range	0.90	0.93	−0.68
West Bay ($N = 15$)			
Interior maximum	0.82		
Interior range	0.76	0.80	
Perimeter maximum	0.95	0.87	−0.80
Perimeter range	0.76		

Insignificant results for the East Channel and Lone Willow stands were not included.

Line stand and was not significant for the East Channel stand. Our observations in the field and the analysis of field data indicate that this relationship is likely complicated by other factors. Both shallower and deeper areas did not seem to experience the same decline. Intermediate depths, especially those near 0.30 m on the Oshkosh gauge, appear to be subject to the greatest decline within patches.

Although we found a significant difference between interior and perimeter water depths for all the stands, the implications of these differences for spatial characteristics and stem densities is less clear. For example, we found significant differences in stem counts between

Table 6
Statistically significant regression models predicting stem density from water depth and location relative to the perimeter of a stand (r^2 is Pearson product-moment correlation coefficient)

Site	Parameter				Statistics		
	Depth	Location	Depth location[a]	Intercept	r^2	P	n
Hindenburg Line	−53.0	−7.1	[a]	106.3	0.12	0.0001	165
Lone Willow	−71.6	−13.6	[a]	139.9	0.43	0.0001	48
West Bay	−66.6	−5.0	[a]	108.9	0.19	0.0005	75
All stands	−57.3	−34.9	35.4	107.7	0.19	0.0001	288

[a] Interaction was not significant.

deeper perimeter locations and shallower interior locations in all the stands (interior 81 m^{-2} versus perimeter 55 m^{-2}; Mann–Whitney *U*-test, $P < 0.05$). Although we did find a significant variation in perimeter water depths depending on the cardinal direction of the perimeter (Kruskal–Wallis, $P < 0.05$), we did not find a similar significant relationship between cardinal direction of the nearest perimeter and stem densities in all the stands. Perimeter stem density was only significantly related to direction of exposure in the West Bay stand (Kruskal–Wallis, $P < 0.05$). The occurrence of this relation for only one stand of the four could be related to fetch: the West Bay stand has by far the greatest exposure to summer prevailing wind and waves from the southwest, being 6.1 km, while the corresponding distances are 3.5 km for the East Channel stand, 1.3 km for the Lone Willow stand, and 2.1 km for the Hindenburg Line stand.

The regression model including both variables for individual stands indicated that both factors were significant (Table 6). The regression model for all stands including all three variables and all interaction effects indicated that only water depth, location, and the interaction of water depth with location were significant. Removing the non-significant variable, fetch, reduced the r^2 from 0.20 to 0.19. Apparently, fetch did not explain additional variance next to the factor location.

3.4. Impact of extreme water levels

For the two single-factor water level scenarios, only the Lone Willow stand showed a significant relation between annual changes in areal coverage and water level extremes, using winter days less than the 10th percentile ($r^2 = 0.65$, $P = 0.02$). For all stands combined or for sets of three of the four individual stands, we failed to detect any significant pattern.

Although the best-fitting scenarios with multiple seasonal levels incorporated the winter 25th percentile level and days at spring levels above the 75th percentile, none of these were statistically significant. As expected, changes in areal coverage of Hindenburg Line stand and East Channel stand were the most closely correlated among the four stands ($r^2 = 0.62$; $P < 0.05$), and this was the only significant relationship.

Among the four temperature criteria, the number of degree-days at or less than 0 °C showed the strongest relation to changes in areal coverage for three of the four stands and for all stands combined (r^2 East Channel: 0.32, $P = 0.14$; r^2 Lone Willow: 0.29, $P = 0.17$; r^2 West Bay: 0.05, $P = 0.59$; r^2 all stands: 0.33, $P = 0.14$). The exception was Hindenburg Line stand, which showed the strongest relation to days at or below −18 °C ($r^2 = 0.35$, $P = 0.12$). Therefore, both the number of days and the number of degree-days below the temperature criteria were included in multiple regression models to determine which combination of temperature criterion and water level scenario formed the best model. The two single-factor water level scenarios of low winter water levels alone (10 and 25th percentiles) resulted in better models than any scenario that used a combination of multiple seasonal water levels. So models using all possible pairwise combinations of number of days below the 10th or 25th percentile water levels and number of days or degree-days at or below 0 and −18 °C along with the interaction effects were tested for each stand and for all stands combined.

Number of winter days at or below the 10th percentile water level during the study period showed a stronger relationship to change in stand area for three of the four individual stands

Table 7
Water level and temperature parameters in regression models that best predicted annual change in individual and combined stand areas, 1986–1994

Site	Parameter		Statistics	
	Days < water level percentile	Temperature (°C)	r^2	P^a
East Channel	10th	Days < 0	0.86	0.0367[a]
Hindenburg Line	25th	Days < −18	0.58	0.2831
Lone Willow	10th	Degree-days < −18	0.95	0.0043[a]
West Bay	10th	Days < −18	0.64	0.2094
All stands	10th	Days < 0	0.78	0.0812

[a] Significant at $P < 0.05$.

and all stands combined than winter days at or below the 25th percentile (Table 7). Strongest relationships to winter temperature criteria varied, with the best predictor for three stands being days or degree-days at or less than −18 °C. Areal change in the remaining stand as well as all stands combined was better predicted by days at or less than 0 °C.

4. Discussion

Although most of the best-fit models incorporating winter water levels and temperatures did not significantly explain changes in reed stand expansion, they do demonstrate two important points. First, these relationships were better than those testing either water levels or temperature alone. Second, they all generally indicate that as the duration of low water levels and cold temperatures increases, reed stands decrease in area. Furthermore, the ability to achieve statistical significance is limited by the sample size, i.e. the number of years of aerial photographs that we had available. Nonetheless, the amount of variance in annual changes that is accounted for by this relationship is still considerable, as exemplified by the East Channel stand, which has demonstrated the greatest losses since 1986 (Fig. 3).

Conceptually, under the current water level management scheme for these lakes, autumn drawdown exposes successively deeper portions of a particular stand to increasing wave action at the perimeter (Krug, 1981). Low water during the winter exposes parts of the rhizome mat to sub-freezing temperatures, while ice movement physically disrupts senesced plants, dead culms and root masses, depending on the particular bathymetry of a stand. Rhizomes below the winter water line may be protected and less susceptible to damage, and higher elevations in the stands are less susceptible to ice encasement as the water level falls below the rhizome mat. Subsequently, the characteristic higher spring and early summer water levels coupled with high turbidity from spring runoff reduce light availability and rate of warming, which effectively shortens the growing season (Haslam, 1969; Kahl, 1993). These winter stressors coupled with long-term inundation in the spring could then have caused the observed decreases in some of the common reed stands.

Deterioration caused by unprecedented, long-term inundation is probably accelerated by other factors. Even as the East Channel stand has almost completely disappeared and has the lowest mean and the maximum stem densities, the Lone Willow stand, in comparable

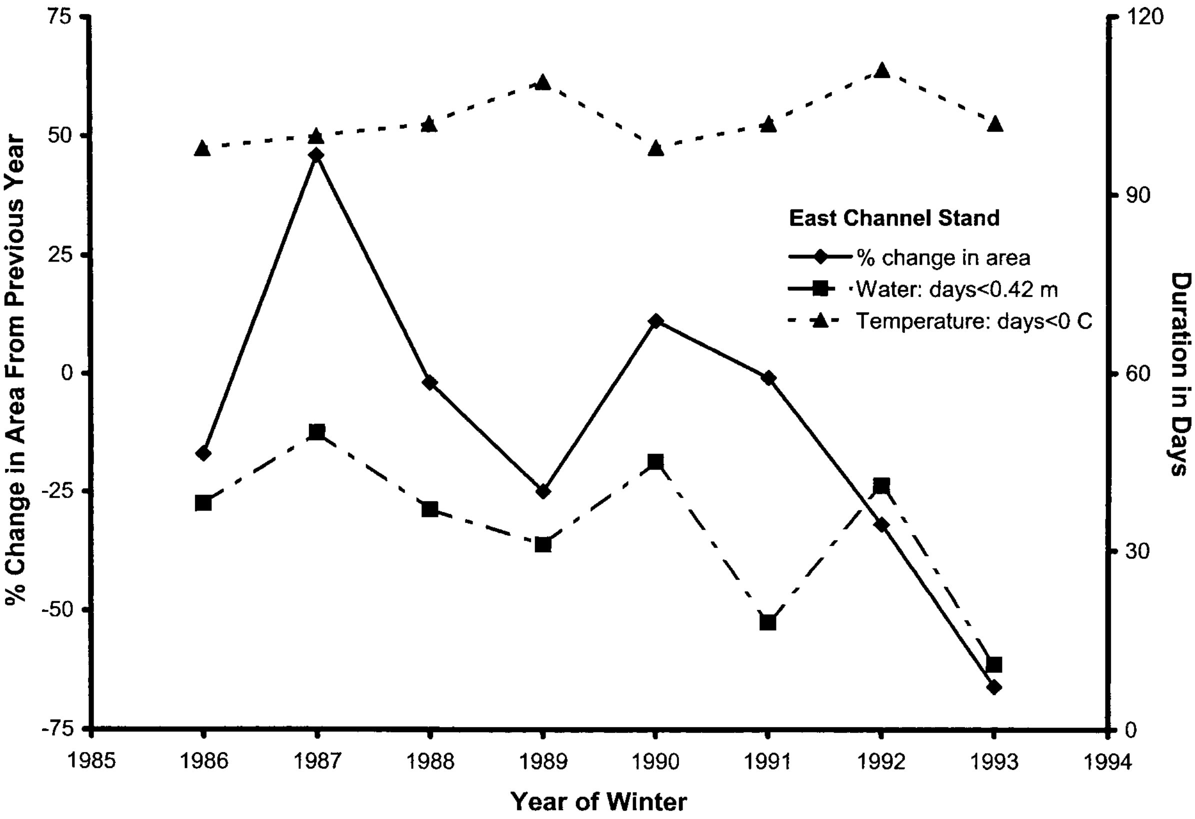

Fig. 3. Annual changes in area of the East Channel common reed stand in relation to extreme low winter water levels (lower 10th percentile) and extreme low winter temperatures (lower 5th percentile) from 1986 through 1994. (Stand area is plotted against the year of the previous winter.)

depths, is much more vigorous. Studies in Europe indicate that dying stands have less than 100 stems m^{-2} and healthy stands more than 200 stems m^{-2} (Hara et al., 1993; Van der Putten, 1997). Even though all four stands have less than a median value of 100 stems m^{-2}, this criterion may not apply to our Wisconsin stands, either because of geography or mid-water location. Water level regulation could interact with individual stand characteristics, particularly bathymetry, to result in different losses among stands. Based on bathymetric locations of the persistent dead rhizome mat, initial losses were notably concentrated in areas 25–50 cm deep in July. These areas are almost devoid of living plants, while areas 75–120 cm deep remain thickly populated. Luxuriant growth also occurs in areas less than 25 cm deep. Excavations through the rhizome mat in both perimeter and interior areas of some stands did not indicate that shallower waters were due to accumulation of organic matter. In the East Channel stand the now decades-old extensive mat of dead rhizomes has become pitted by erosion, unlike the areas of more limited and recent loss in the other three stands, so that both interior and perimeter water depths are the highest among the stands. Also, East Channel has the smallest range of depths where patches persist. These deeper, more restricted water depths appear to represent conditions still suitable to common reed plants and are likely the culmination of long-term stresses inflicted on both the deeper and shallower plants.

Water level regimes during the growing season are implicated in stand losses because long-term losses in areal coverage concur with peaks in water levels during the growing season. Summer water levels have been regulated 1 m higher and winter levels 10 to 30 cm higher following management changes enacted in 1982. This change was followed by a net loss of total stand area, although on a year to year basis both increases and decreases occurred (Fig. 3). Flooding rhizomes to 1 m deep during the growing season has been used as a control measure for common reeds (Marks et al., 1994). Changes in water level management and variations around target levels could have caused plants within stands to shift to depths more conducive to growth, thus increasing the area susceptible to loss through time. However, our historical analyses indicate that when common reed stands declined in area, they did not show simultaneous areas of new growth (Gabriel and Bodensteiner, 1998, 2002).

The range of losses among the four common reed stands provides insight into potential causes for the declines. The mid-lake locations, the proximity of the stands to each other, and the open water circulation within patches (Gabriel and Bodensteiner, 1998), indicate that a singular lake-wide impact has not caused the spatially non-uniform pattern of decline. We could not attribute stand losses to direct destruction through land reclamation, mowing, and other intrusive activities; mechanical damage caused by impingement of woody debris, trash, and filamentous algae on live plants; and grazing by terrestrial wildlife, herbivorous fish, and livestock (Graneli, 1989; Ostendorp, 1989; Van der Putten, 1997). We observed recreational boaters aggregated around the Lone Willow stand, but this has been the least affected area. Smaller losses may have occurred through destruction of dead culms and loss of air transport to the rhizomes, since snowmobile paths have corresponded to lines of no growth the following spring (Haslam, 1970; Brix, 1989; Weisner and Graneli, 1989; Kahl, 1993; Armstrong et al., 1996a; Fürtig et al., 1996). Eutrophication and accumulation of phytotoxins could have more generally affected stand health (Armstrong et al., 1996b), if these interacted with other factors that varied by stand. For example, substrate differed among the stands with the firmest substrate at Lone Willow and East Channel stands, but these also represented the extremes of changes in stand area.

Regardless of the amount of change, stand loss appears to follow a consistent pattern. Loss occurs from the outside of each patch inward, with most of the loss either in proximity to the historical lakeward edges or aligned to the direction of prevailing summer winds (Fig. 2). The patch edge assumes an irregular outline, as indicated by changes in perimeter and perimeter to area ratios. Eventually, a larger patch is broken into smaller patches. Loss then proceeds through the progressive elimination of the smallest, and apparently most vulnerable patches, reducing the overall area of the stand, and exposing more of a patch to wind and wave action (Gabriel and Bodensteiner, 1998, 2002). This pattern of loss is also reflected in the inverse relation of mean stem densities to proportion of loss since 1937. In larger patches a greater proportion of individual plants occur inside the less dense margin, whereas irregularly shaped and small patches have a higher proportion of plants located on the margin. Areas of low stem density appear to be eliminated in smaller patches, resulting in higher minimum stem densities. As patches decrease in size and overall stem density declines, the susceptibility to additional damage likely increases (Haslam, 1970; Ostendorp, 1992; Coops and van der Velde, 1996).

Given the overall trend of loss during the 60-year period of photographic records, we expect that stand loss will continue under current water level management and climatic conditions. Although the current water level management regime concurs with the most recent period of loss, alterations to that regime to facilitate preservation and restoration of common reed stands must be carefully considered. One potential outcome to changing the magnitude or timing of water levels is the exposure of common reeds in previously less affected depths to additional stress.

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