

441

WILD-RICE AND SEDIMENTATION PROCESSES IN A LAKE SUPERIOR COASTAL WETLAND

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Abstract: Sedimentation rate and nutrient concentrations were assessed in 1989 at four sites of differing stream morphometry in the Kakagon Sloughs, a Lake Superior coastal wetland in northern Wisconsin dominated by northern wild-rice (*Zizania palustris*). Pre-weighed sediment traps were placed at each site along deep-to-shallow water zones. Accrued sediment was collected during five time periods corresponding to differing stages of growth in wild-rice stands. There were higher sedimentation rates at the river sites (straight sections and inside and outside curves) when compared to the backwater site. Differences were also observed among depths and at the different time periods, demonstrating the influence of vegetation on the sedimentation process in this wetland complex. Higher sedimentation rates took place closest to the vegetation-open water interface (deep zones). However, in shallow zones, a significant proportion of the annual sedimentation took place during the submersed and floating leaf stages, showing the importance of these time periods for providing an annual input of sediment to large areas of riverine habitat. Of nutrients tested, both TKN and NO₃-N had lower concentrations in the period following wild-rice stem elongation. These data suggest that the early growth habit of wild-rice (submersed and floating stages) promotes pulses of nutrient-rich sediment, which are necessary for the later nutrient-demanding stages of stem elongation and grain formation.

Key Words: Lake Superior wetland, sedimentation, wild-rice, *Zizania*, river dynamics, current velocity, sediment nutrients, vegetation, Kakagon Sloughs

INTRODUCTION

Traditionally, plant ecologists have explained spatial heterogeneity by studying the environmental factors that likely influence the observed patterns. Conversely, vegetation can exert a major control on the surrounding environment. This paper investigates the influence of wild-rice (*Zizania palustris* var. *palustris* L.) on the timing and abundance of sedimentation and nutrient availability in the Kakagon Sloughs, a coastal wetland on the southern shore of Lake Superior.

In general, wetland plants are known to influence many aspects of their abiotic environment. In the interface between sediment and the water column, aquatic macrophytes affect rates of nutrient cycling, eutrophication, and sedimentation (Sculthorpe 1967, Barko and Smart 1980, Carpenter and Lodge 1986) and also bring about shifts in community composition through these dynamics (Posey 1988). Aquatic macrophyte beds influence sedimentation rates by decreasing water velocity, resulting in increased particle deposition

(Kemp et al. 1984, Mitsch and Gosselink 1986, Richard 1987). Protection of shoreline vegetation has been used as a cost-effective means to maintain water quality because it reduces erosion and traps sediment (Dean 1979, Mitsch and Gosselink 1986, Brooks 1989). Among vegetation types, emergent plants are especially tolerant of sediment accumulation, whereas some floating-leaf and submerged species can be damaged by increased sedimentation (Brooks 1989).

Wild-rice stands are thought to benefit from increased sediment deposition by utilizing the nutrients associated with the sedimentation processes that they influence (Dore 1969, Lee and Stewart 1983). Like many annual species, wild-rice is efficient in the uptake of nutrients and is often limited to the more productive lakes and streams within its range (Dore 1969, Aiken et al. 1988). I hypothesized that a feedback loop exists whereby wild-rice decreases current velocity in areas where it grows, which increases the sedimentation rate and hence the availability of nutrients in that

immediate area. This trapping of nutrients then increases the productivity of the stand.

Both current velocity and rates of sediment deposition vary widely along a meandering river. In general, currents are greatest at the concave or outside of meanders (outside curves) and least at the convex or inside of meanders (inside curves). At stretches between two meander bends (straight sections) a cross-over occurs as the dominant flow shifts from one side of the river to the other; current velocities are more evenly distributed across the river at these straight sections (Leopold et al. 1964, Gordon et al. 1992). Sediment deposition takes place when the velocity of sediment-laden water decreases, as when it enters vegetation beds or as it approaches the inside meander bends (Richards 1982). Backwater areas are generally isolated from the sediment supply except at the flood stage, even though they may be open to the main river channel (Richards 1982).

The direct connection between reduced flow rates and increased sediment deposition has not yet been demonstrated with wild-rice. This study investigates four different flow regimes along a highly productive riverine wild-rice habitat in the Kakagon Sloughs. In particular, backwater areas, inside river bends, straight channel sections, and outside river bends were chosen to assess possible differences in sedimentation processes and nutrient availability at sites with differing water-flow characteristics.

Predictions

I tested five specific predictions suggested by the general feedback hypothesis discussed above, using natural differences in stream morphometry among four sites (backwater areas, inside river bends, straight sections, and outside river bends). In the following predictions, I am referring to the sedimentation rates during one growing season and not annual rates, which would address the fluxes after the growing season and prior to ice out in the following year.

1) River sites with increased flow will have a greater depositional rate than the backwater areas that lack through-flow and the associated sediment-laden water. Relative to sedimentation rate, this prediction simplifies to:

river sites > backwater

2) The inside bends will have the least current velocity (promoting sediment deposition) and the outside bends the greatest change in velocity (once moving water enters the wild-rice beds). Both of these conditions will promote increased sedimentation rates during the growing season. Relative to sedimentation rate, these predictions simplify to:

inside curve = outside curve > straight section

3) Sedimentation rates will differ according to the phenological stage of wild-rice. Depositional rates will be greater during the submerged-leaf stage when the plants form an underwater blanket of vegetation over the total sediment surface. Since flows during this time are more sediment-rich, this would create a more favorable deposition period. Sedimentation rates relative to wild-rice growth stages simplifies to:

submerged-leaf > emergent-leaf > senescent
> pre-seedling

4) For all times but the submerged-leaf stage, sedimentation rates will be greatest at the open water-emergent vegetation interface. During the lengthy emergent-leaf stage of wild-rice, this "wall" of vegetation will resist flow into the rice beds. Hence, sedimentation rates will be progressively less toward the near shoreline areas as:

open water/wild-rice interface > mid-profile
> near shore

5) Nutrient availability will be greater at river sites when compared to the backwater site, as sedimentation is expected to be greater along the river (prediction #1). Within river sites, nutrient availability will peak at the end of the submerged-leaf stage or immediately after the initial seasonal flush of sedimentation suggested by prediction #3. Because the submerged-leaf stage of wild-rice is followed by a period of stem elongation when 70% of the total annual biomass is added (Thomas and Stewart 1969), nutrient levels will decline during stem elongation due to nutrient uptake.

STUDY SITE

The Kakagon Sloughs are part of a vast 5,000 hectare tract of Lake Superior wetlands that are owned and managed by the Bad River Band of Lake Superior Chippewa (Figure 1). The majority of the area is lowland, supporting a complex mosaic of marsh, swamp forest, peatland, and emergent/floating/submerged aquatic communities (Meeker 1993). Only the Kakagon portion has substantial stands of wild-rice, and it is unique among all Lake Superior wetlands in its domination by wild-rice. The substrates of a major portion of the aquatic communities in the Kakagon are characterized by a veneer of organic muck overlaying stratified lake deposits with a high proportion of clay particles. Due to seiche activity in adjacent Chequamegon Bay, the water currents in the Kakagon River system fluctuate from downstream flow to upstream flow, with short periods of still water in between. These periodic seiches have amplitudes as great as 40

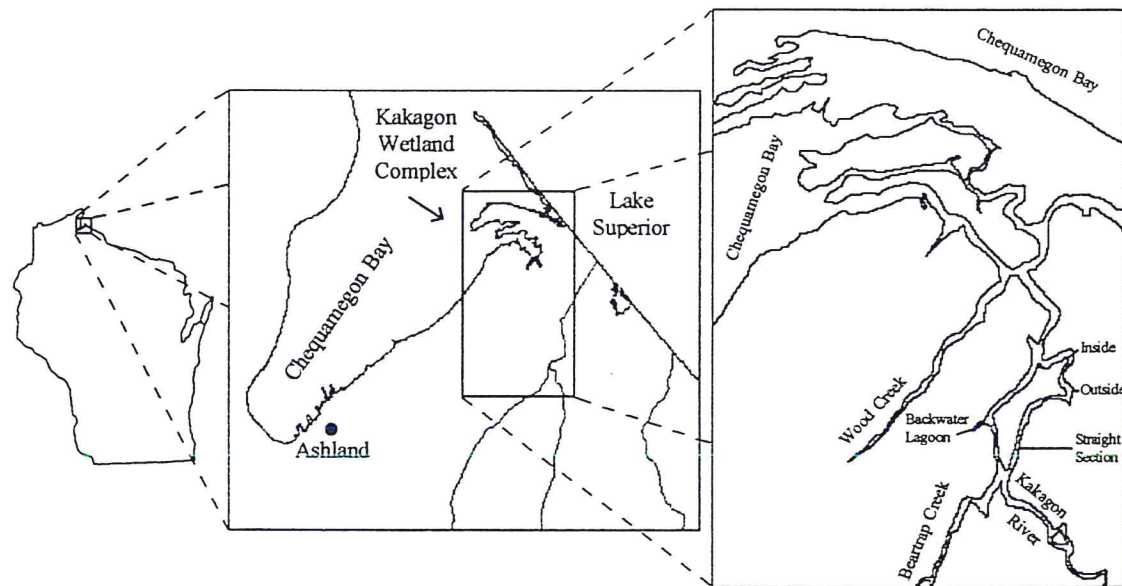


Figure 1. Map of the Kakagon Sloughs wetland complex showing the sampling areas. Latitude $46^{\circ} 38'$; Longitude $90^{\circ} 44'$.

cm and often ebb and flow in a regular fashion with six cycles in one 24-hour period (Meeker 1993). Specific conductivity ranges between 25 and $105 \mu\text{M s}^{-1}$, with a slight increase in conductance at the upstream locations. The pH ranges between 6.2 and 7.5 with no discernible pattern. Dissolved oxygen levels at the surface in mid-summer along the same riverine portions vary between 4.2 and 8.8 ppm. Secchi depth readings show acute differences in suspended sediments following major precipitation events, and these readings are generally greater as the season progresses, changing from average readings of 0.60 to 0.80 m in May and June to 0.90 to 1.10 m in July and August (Meeker 1993).

METHODS

Current Velocity

Due to seiche activity in the Kakagon River, currents were measured during the peaks of both downstream and upstream flows. The relative differences in current velocity among three time periods were assessed in areas annually dominated by dense wild-rice stands. These time periods represent three phenological stages in the life history of wild-rice and include 1) late April, immediately after ice-out and before the germination of the wild-rice seed, 2) early May, the submerged-leaf stage of wild-rice when the plants have grown to about 10 cm above the sediment surface, and 3) mid-July during the emergent-leaf stage, when all the leaves are fully expanded and as much as a meter above the water's surface. For consistency, current ve-

locities were measured only during non-flood conditions at least two days after major precipitation events.

Current velocities were measured by a hand-held, propeller-driven Beauvert current meter on cross-sectional profiles at only straight sections of the Kakagon River due to time constraints. Measurements throughout the river profiles were taken repeatedly (5–7 replicates per day) on five days within each of the three phenological periods. Each profile began near shore, and currents were measured at 2-m intervals to water depths of 1.5 m, which is slightly beyond the maximum depth for most of the vegetation in the Kakagon River. Current velocity readings were made at 25-cm intervals from near the water's surface to 5 cm above the sediment. The propeller revolutions were counted electronically, and the velocity was measured with accuracy to a lower limit of 0.025 m s^{-1} .

Sedimentation

Sedimentation rates were assessed from April 15 through October 1, 1989 in four different channel morphology types (sites) along the Kakagon River system, including 1) a backwater lagoon, 2) inside curves along the river, 3) straight sections along the river, and 4) outside curves along the river. Sites were chosen in areas known to be dominated by wild-rice in the previous three field seasons (Meeker pers. observation). One transect at each site extended from the interface of open water-vegetation to the limits of the wild-rice stands on the shallow end of the sampling profile. Along each sampling profile four Zones (deep, mid-

Table 1. Placement of sediment samples at the four sampling sites relative to their distance from open water and water depth (m).

	Deep		Mid-deep		Mid-shallow		Shallow	
	Distance from Open Water (m)	Depth	Distance from Open Water (m)	Depth	Distance from Open Water (m)	Depth	Distance from Open Water (m)	Depth
Backwater	1.5	(1.0)	4.0	(0.75)	12.0	(0.45)	18.0	(0.25)
Inside Curve	1.5	(1.0)	4.0	(0.75)	12.0	(0.45)	18.0	(0.25)
Straight Section	1.5	(1.0)	4.0	(0.75)	8.0	(0.45)	10.0	(0.25)
Outside Curve	1.5	(1.0)	4.0	(0.75)	6.0	(0.45)	8.0	(0.25)

deep, mid-shallow, and shallow) were located based on water depth and distance from open water through the use of a 50 m tape (Table 1).

At each of the 16 sampling stations listed in Table 1, four pre-weighed petri dishes (surface area of 65 cm²) were placed 50 cm apart on the surface of the river bed using a snorkel or SCUBA so as not to disturb the sediment. The petri dishes were placed at the beginning of and collected at the end of five time intervals, including the pre-emergent stage of wild-rice (April 15–May 1), the submerged-leaf stage (May 2–June 2), the emergent-leaf stage without full stem elongation (June 15–July 15), the flowering stage with full elongation of stem (July 16–August 16), and the senescent stage (September 1–October 1). To minimize sediment loss in the collection process, petri dish samples were first covered while under water and then brought to the surface. To estimate mean total sediment accrued during each time interval of the four replicate samples, sediment samples were dried to a constant mass in a drying oven, weighed, and a mean calculated. Dried sediment samples were then combusted at 290° C in a muffle furnace to estimate the percent organic matter due to loss of mass by ignition.

Nutrient Sampling

At the mid-shallow zone at each site (no closer than 10 m to petri samples to minimize disturbance) three replicate sediment samples were collected from the surface of the river bed at each of three time periods, including May 25 (late submerged-leaf stage for wild-rice), July 30 (stem elongation stage), and October 1 (senescent stage of wild-rice). Sediment was collected with a modified trowel and collecting can to a depth of 5 cm over an approximately 400 cm² area with dense wild-rice (approximately 80 stems m⁻² at the emergent stage).

Sediments were analyzed for nutrient levels at the University of Wisconsin's Soil and Plant Analysis Laboratory. Analyses included total sediment nitrogen by Kjeldahl digestion (TKN), inorganic nitrogen in the form of both ammonia (NH₄-N) and nitrate (NO₃-N)

by steam distillation, and available phosphorus (P) and available potassium (K) by the Bray P1 process. Results were reported on a dry weight basis in ppm (mg kg⁻¹ sediment).

Data Analysis

Current Velocity. Contours representing downstream flow patterns were drawn by hand from median values (Tukey 1977) measured at various locations. Each median value was based on 15–20 separate measurements.

Sedimentation. Sediment accrued was converted to gm dm⁻² month⁻¹ for comparative purposes by first calculating a per day value and multiplying by 30. Each main effect was analyzed separately by collapsing over the other two variables (e.g., site differences on sedimentation were compared by collapsing over both time and location on profile).

Nutrients. Two-way analyses of variance were conducted on all nutrients for the main factors (site and time), and means were compared by using Fisher's LSD tests (Systat[®] 1992).

RESULTS

Current Velocity

Downstream flows generally exceeded upstream flows (seiche activity) in the same areas by 30% in a given day, and only the downstream flow results will be discussed.

During the non-vegetated time period (Figure 2a), current velocities mostly exceeded 0.05 m s⁻¹ for most of the profile, and relatively still water (< 0.025 m s⁻¹) occurred only in the very near-shore environment (and during the times of current direction changes due to seiche activity). Low current velocities (< 0.025 m s⁻¹) occurred during the submerged-leaf stage (Figure 2b), when wild-rice forms a uniform blanket of 10- to 15-cm tall vegetation above the sediment surface. When the plants form their emergent leaves, a wall of vegetation separates areas where the currents are less

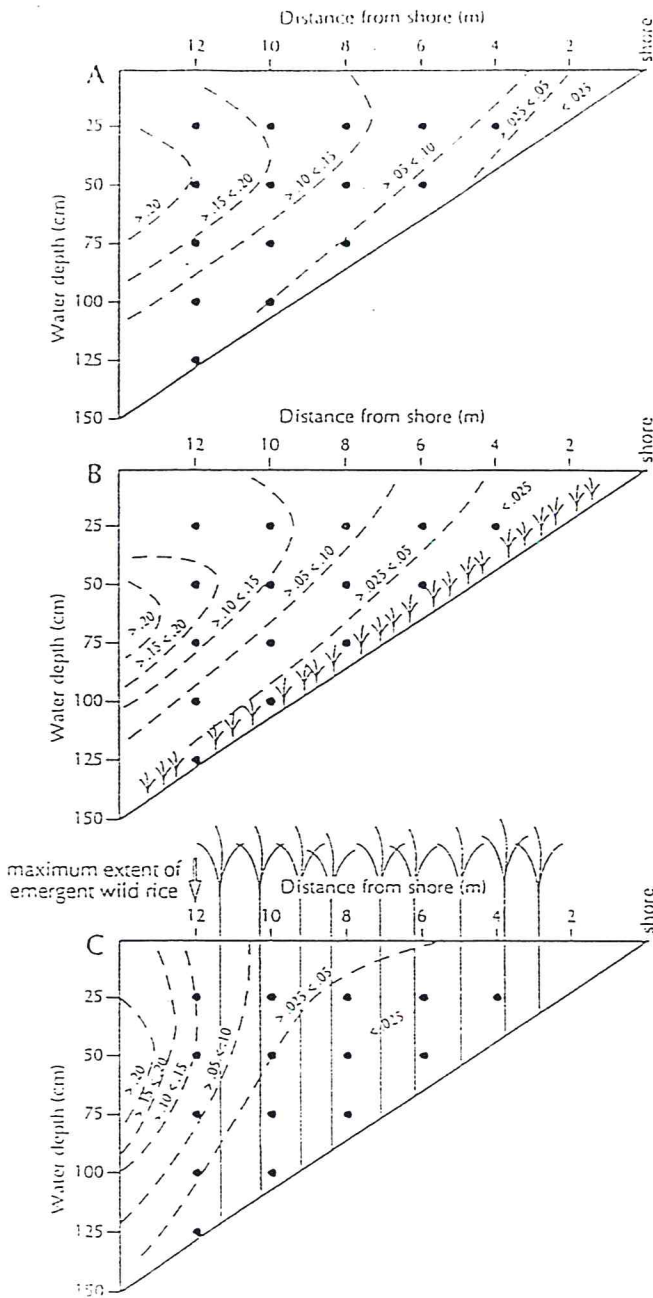


Figure 2. Current velocities (m s^{-1}) in a straight section of the Kakagon River from shore to the deep zone. Growth stages of wild-rice include a) pre-seed germination, b) submerged-leaf stage, and c) emergent-leaf stage. See text for dates of sampling in relation to growth stage.

than 0.05 m s^{-1} from the faster moving open water, while most of the vegetative profile experiences relatively still water ($< 0.025 \text{ m s}^{-1}$, Figure 2c).

Sedimentation

Main Effects. The backwater lagoon accrued less total sediment ($2.7 \text{ gm dm}^{-2} \text{ mo}^{-1}$) than the inside,

straight and outside sections of the river (10.2 , 10.6 , and $11.0 \text{ gm dm}^{-2} \text{ mo}^{-1}$), which were similar (Figure 3a). Additionally, mean percent organic matter of this sediment (shown in parentheses in Figure 3 along with the associated means for total sediment accrued) was higher in the backwater (28.1%) than that of the three river sites (16%–21%).

Sediment accrued varied during the growing season (Figure 3b). The middle three growth stages of wild-rice (submerged-leaf and the two emergent stages) had sedimentation rates of 11.2 , 10.2 and $11.3 \text{ gm dm}^{-2} \text{ mo}^{-1}$, higher than the senescent stage (6.5) which was in turn, higher than the pre-germination stage (3.7). Percent organic matter showed a general trend of increasing over time periods, with a maximum of 28.3% during the senescent stage.

The most sedimentation ($16.4 \text{ gm dm}^{-2} \text{ mo}^{-1}$) occurred in the open water/vegetation zone, followed by the mid-deep zone ($9.8 \text{ gm dm}^{-2} \text{ mo}^{-1}$), which were both higher than the two shallow zones (4.8 and $3.4 \text{ gm dm}^{-2} \text{ mo}^{-1}$, respectively, Figure 3c).

Interaction Effects. The three river locations show similar patterns in their sedimentation rates across the growing season, with less deposition occurring during the pre-seedling and senescent stages (Figure 4). This pattern is in contrast to the backwater location where deposition was much less and showed little change in the amount over time (Figure 4). Deposition patterns also varied among the zones across the growing season. On the inside curve (Figure 5a) with relatively slower water velocities, the submerged-leaf stage had the highest level of deposition in the mid-deep, mid shallow, and shallow zones. In the straight section (Figure 5b), the submerged-leaf stage had less deposition than both emergent stages in the mid-deep zone, and at the outside curve (Figure 5c), the submerged-leaf stage had less deposition than the emergent stages in the deep zone. Overall, higher amounts of sediment deposition occurred during the submerged-leaf stage, when contrasted to the other growth stages, at mid-shallow and shallow zones for all river sites combined (Figure 5d).

Nutrient Analysis

Both total nitrogen (TKN) and inorganic ammonia ($\text{NH}_4\text{-N}$) levels were higher at river sites compared to the backwater site (Figure 6a-b; Table 2, $F_{1,24} = 63.2$, $p < 0.01$ and $F_{3,24} = 20.9$, $p < 0.01$ for TKN and $\text{NH}_4\text{-N}$, respectively). The outside curve site had the highest levels of TKN ($p < 0.01$, Fisher LSD test), followed by no significant differences between the inside curve and the straight section, while the backwater had significantly less TKN ($p < 0.01$, Fisher

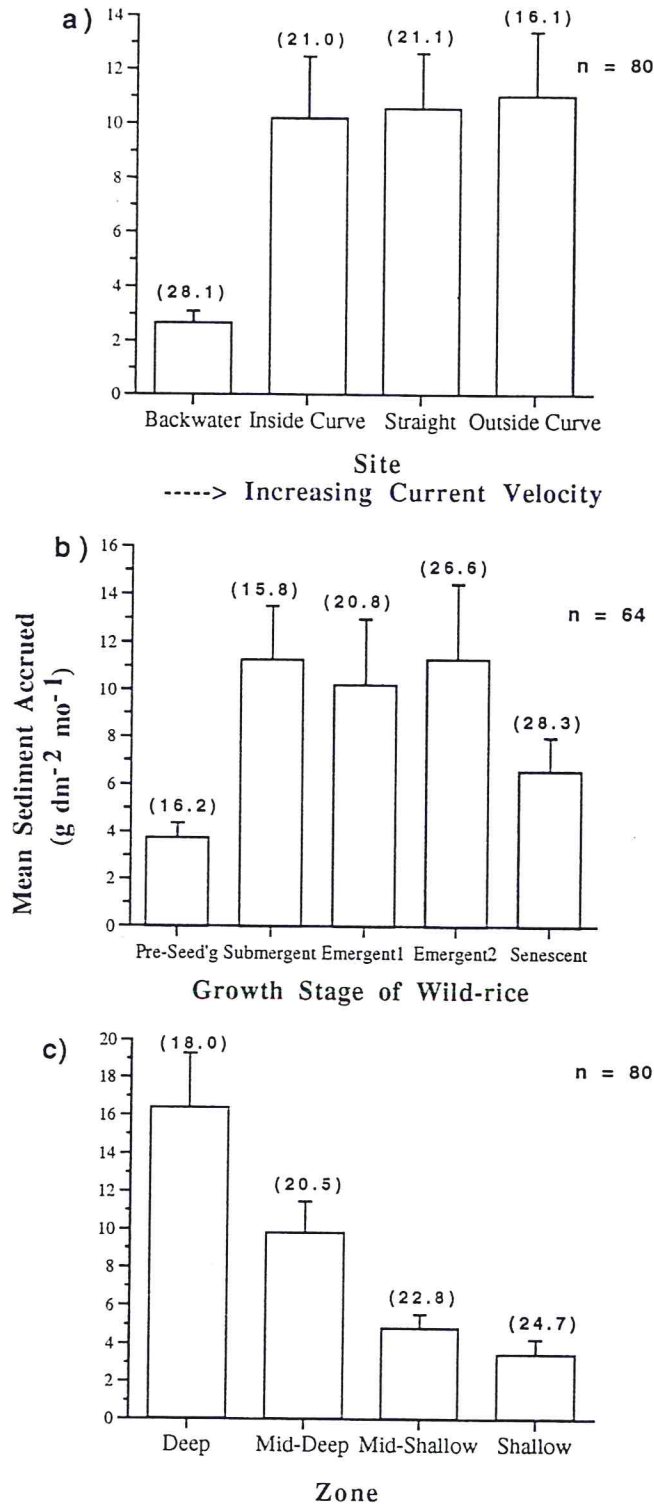


Figure 3. Mean sedimentation rates a) at four sites with differing current velocities, b) at five phenological stages of wild-rice, and c) at four depth zones. Numbers in parentheses indicate mean % organic matter. Error bars indicate two SE.

LSD test). Inorganic ammonia (NH₄-N) levels were also significantly greater at the river sites than the backwater site ($p < 0.01$, Fisher LSD test). Nitrate (NO₃-N) did not show site differences (Figure 6c, Table 2).

Nitrogen levels were not constant over growth stages at the three sampling times. Both TKN and NO₃-N showed a similar pattern at each of the sites, with lower levels during the period of culm emergence (Figure 6a and c; Table 2, $F_{2,24} = 11.1$, $p < 0.01$ and $F_{2,24} = 9.6$, $p < 0.01$ for TKN and NO₃-N, respectively). Time x site interactions were significant for both TKN and NH₄-N (Figures 6a and b; Table 2, $F_{6,24} = 5.9$; $p < 0.01$ and $F_{6,24} = 4.0$; $p < 0.01$ for TKN and NH₄-N, respectively). These interactions are most apparent in Figure 6b, comparing changes in NH₄-N levels over time between the outside curve site, where there were greater concentrations of NH₄-N during the culm elongation period compared to the straight section site that had the lowest NH₄-N levels at this time ($p < 0.01$, Fisher LSD test).

Results for available phosphorus (P) and potassium (K) were quite different from those of the nitrogen analyses. Phosphorus concentrations differed for both time and site (Table 3; $F_{2,24} = 53.2$, $p < 0.01$ and $F_{3,24} = 24.5$, $p < 0.01$, respectively). Less available P was present during the submerged-leaf stage of wild-rice when compared to the culm elongation and senescent stages ($p < 0.01$, Fisher LSD test, Figure 7a). Available K levels also differed among sampling times (Table 3; $F_{2,24} = 43.9$, $p < 0.01$), but in contrast to available P, the K levels were significantly greater during the submerged-leaf stage (Figure 7b). The patterns of potassium levels also vary at sites with regard to growth stage of plants (time) (Table 3; $F_{6,24} = 6.7$, $p < 0.01$).

DISCUSSION

Differences in the rates of sedimentation among the different phenological stages of wild-rice showed that vegetation can act as a sediment filter at river sites. Wild-rice also exerts a significant influence on the location of sediment deposition in the Kakagon Sloughs.

Prediction 1

As predicted, there were higher sedimentation rates at the river sites than in the backwater site. Backwater sites receive a smaller annual flush of sediment because the water entering them likely contains less, having already deposited the sediment moving through the vegetation that grows across the mouth of the backwater. The assessed low sedimentation rate in the backwater site during one growing season does not

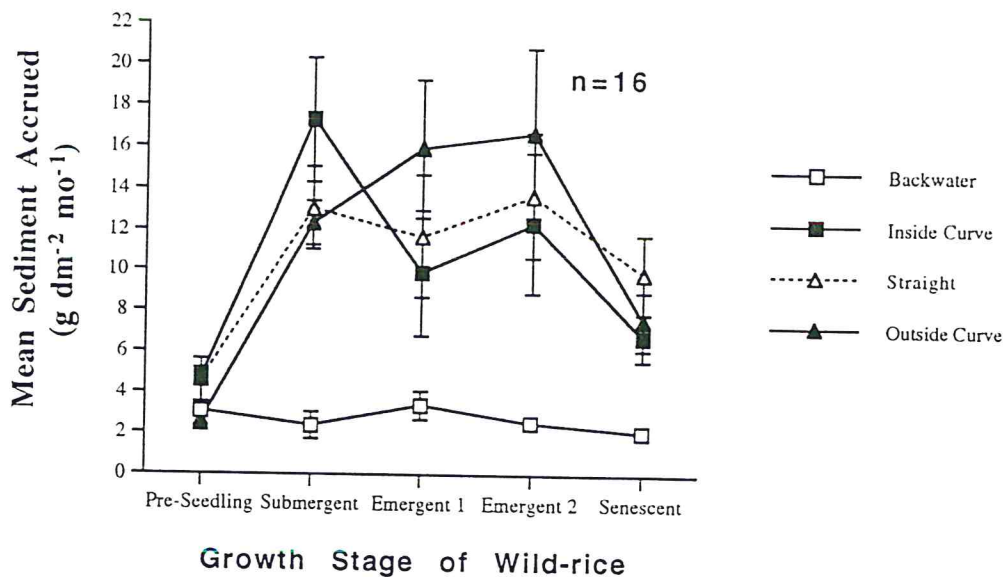


Figure 4. Mean sedimentation rates during five phenological stages of wild-rice growth for each of four sites with different channel morphometry. Error bars indicate one SE.

suggest that backwater basins fill at slower rates than river channels. Sediments at river sites are in constant flux due to the annual scouring and removal of sediment. Therefore, over many years, the unscoured backwater areas may accumulate sediment at an overall greater rate, especially considering the greater organic component of the sediment in these areas.

Prediction 2

Contrary to predictions, sedimentation rates on inside and outside curves were not higher than on straight sections of the river (Figure 3a). On the outside curve, a substantial amount of this deposition took place at deep zones during the second emergent-leaf stage (Figure 5c). Greater sedimentation during this growth stage apparently is due to the significant change in current velocity at outside bends as water enters rice beds. On the other hand, the outside curve received less sediment during the submerged-leaf stage when compared to the other river sites. These differences are probably due to the fact that outside curves have faster currents that limit sedimentation during the submerged-leaf stage. Again, it is important to note that sediment accrued during one growing season (May–October) is not the only determining factor for total accumulation. The sediment flux is probably greater at outside curves as scouring rates increase, resulting in the generally observed movement of river meanders over time (Jeffries and Mills 1990). Hence, inside bends act as sediment sinks over time, and the outside bends tend to be sources of sediment for other areas downstream (Richards 1982).

Prediction 3

Consistent with predictions, sedimentation rates during the senescent and pre-seedling stages were less than during the other three life stages when the vegetation was more dense. Contrary to this prediction, however, the submerged-leaf stage did not show the greatest rate (Figure 3b). These findings are consistent with studies that have demonstrated that submerged vascular plants act both to trap and reduce the resuspension of sediments after deposition (Kemp et al. 1984). Other studies have suggested that individual macrophytes are adapted to seasonal cycles in river environs by the ability of dislodged propagules to re-root and collect sediment during the summer growth cycle (Jeffries and Mills 1990). The results from this study have shown similar findings but through growth and decay of populations of annual plants, not merely the actions of individual plants.

The importance of the submerged-leaf stage is considerably greater than Figure 3b suggests. This is especially true considering that much of the area along the total river profile receives significant amounts of sediment *only* during the submerged stage. The deep and mid-deep zones, which receive ample sediment at all the vegetated time periods, actually account for a smaller part of the total area profile compared to the mid-shallow and shallow locations (Table 1). Figure 5d shows the timing of sedimentation at specific locations along the profile as a composite from all the river sites. The degree of sedimentation during the submerged-leaf stage is of particular importance, indicating that the areas shoreward from the mid-deep

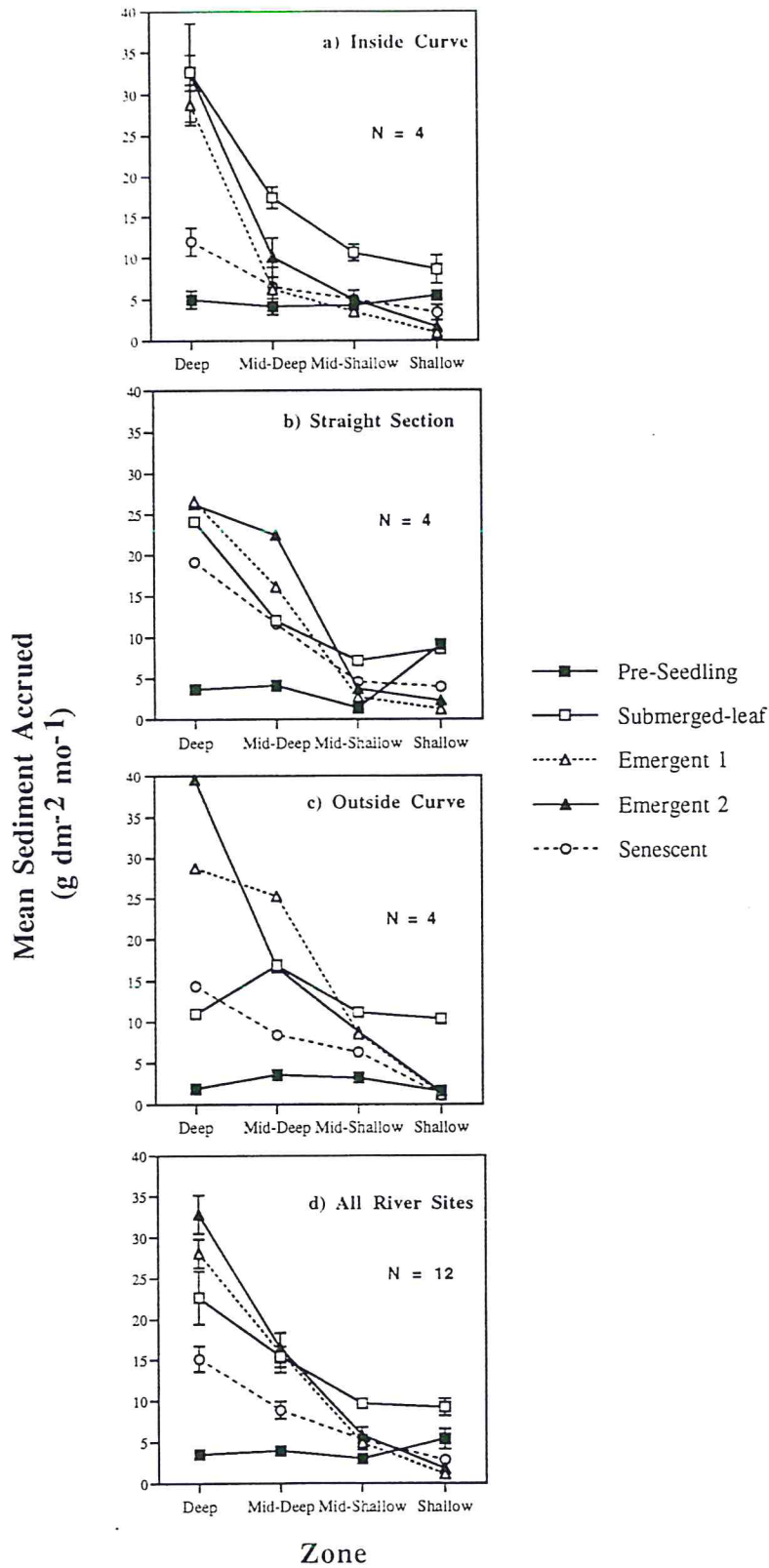


Figure 5. Mean sedimentation rates for river sites relative to zone and growth stage. See text for dates of sampling in relation to growth stage. Sites include (a) inside curves with relatively low current velocity, (b) straight sections with moderate velocities, (c) outside curves with high current velocities, and (d) all river sites combined. Error bars equal one SE.

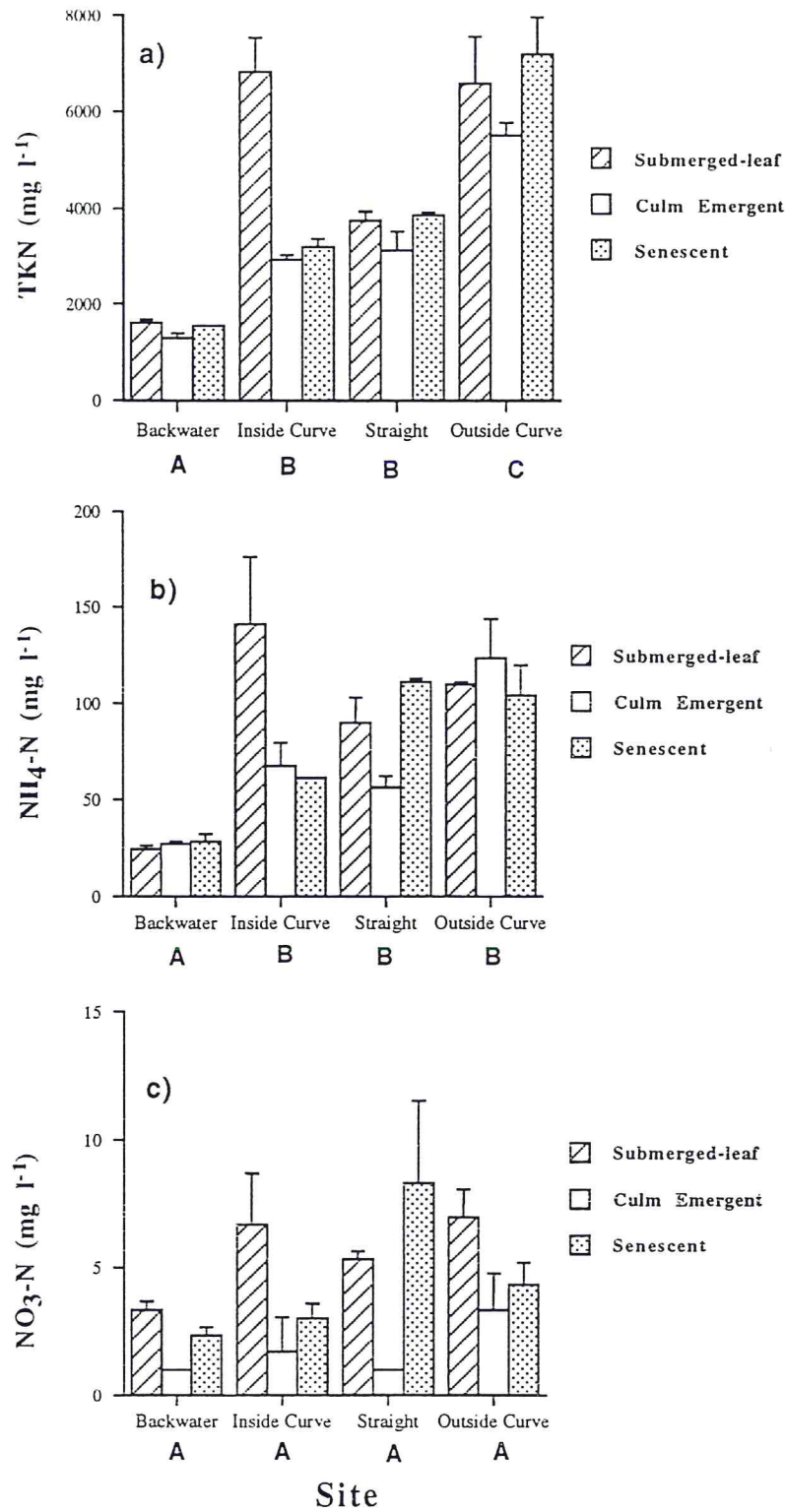


Figure 6. Nitrogen concentrations of mid-shallow zones as a) total Keldahl nitrogen (TKN), b) inorganic ammonia (NH₄-N), and c) inorganic nitrate (NO₃-N) across four sites with differing sedimentation dynamics at three different growth stages of wild-rice, including the submerged-leaf, culm emergent and senescent stages. See text for dates of sampling in relation to growth stage. Error bars indicate one SE. Different letters under sites indicate differences among means at p < 0.05.

ion
rate

Table 2. Two-way analyses of variance on the effects for site and growth stage (time) on concentrations of total nitrogen (TKN), ammonia ($\text{NH}_4\text{-N}$), and nitrate ($\text{NO}_3\text{-N}$) in the mid-shallow zone.

	df	F	P
TKN			
Time	2	11.1	0.01
Site	3	63.2	0.01
Time \times Site	6	5.9	0.01
Error	24		
$\text{NH}_4\text{-N}$			
Time	2	2.8	0.08
Site	3	20.9	0.00
Time \times Site	6	4.0	0.01
Error	24		
$\text{NO}_3\text{-N}$			
Time	2	9.6	0.01
Site	3	2.9	0.05
Time \times Site	6	2.0	0.11
Error	24		

location receive about half of their total annual sediment load during this short, four-week period.

Prediction 4

As expected, the seasonal accumulation of sediment varies across zones, with higher accumulations at deep locations (Figure 3c). This observed pattern suggests that, over years, there may be a zone of sediment accumulation at a specific depth contour. However, while sampling for sediment density along river profiles, I noticed not only the 1989 peak reported in this paper (Figure 3c), but two and sometimes three peaks of less dense, apparently newly deposited sediment slightly shoreward from the 1989 peak. Hence, zones of peak sedimentation shift shoreward and back toward open water from one season to the next, corresponding to differences in the Lake Superior water levels from year to year. In this manner and over a period of a few years, substantial sedimentation may be occurring across a wider zone than suggested by the 1989 sampling alone (Figure 3c), pointing to yet another important manifestation of periodic water-level fluctuation. This process of spreading out the zone of peak sedimentation may be added means whereby the wild-rice stands of the Kakagon maintain an overall high productivity.

Prediction 5

I predicted that river sites would have greater concentrations of available nutrients than backwater areas

Table 3. Two-way analyses of variance on the effects for site and growth stage (time) on concentrations of phosphorus (P) and potassium (K).

	df	F	P
Phosphorus (P)			
Time	2	53.2	0.01
Site	3	24.5	0.01
Time \times Site	6	2.2	0.08
Error	24		
Potassium (K)			
Time	2	43.9	0.01
Site	3	5.7	0.01
Time \times Site	6	6.7	0.01
Error	24		

and that nutrient levels would be greatest after sediment flush in late spring and least after the period of wild-rice stem elongation. These predictions seem to be true for some nutrients but not for others.

Generally, the backwater areas had lower nutrient concentrations, especially nitrogen levels. As would be expected, wild-rice productivity in the backwater areas within the Kakagon system is often lower than the riverine stretches (Meeker 1993). Others have noted evidence that lakes without annual flushes of nutrient-rich sediment become less productive over time (Dore 1969, Peden 1982, Keenan and Lee 1988). The concept that wild-rice, like an annual agricultural crop, eventually "mines" the sediment concurs with the widely held idea among the Bad River Chippewa that there is more year-to-year variability in wild-rice productivity in the backwater areas of the Kakagon system (Hillary Butler, pers. comm.).

Relative to the predictions about the temporal pattern of nutrient concentrations, both TKN and $\text{NO}_3\text{-N}$ have, as predicted, lower concentrations in the period during stem elongation (Figures 6a and c). Others have shown rather constant nitrogen levels in wetlands over a season (Klopatek 1978), as seasonal increases in organic matter in the sediment apparently balances the nitrogen uptake by macrophytes. (It is not clear whether the marsh soils in Klopatek's study were flooded throughout the whole season.) Consistent with the results presented here, Archibold et al. (1985) noted a similar seasonal decline in $\text{NO}_3\text{-N}$ concentration in wild-rice wetlands in Canada.

One difficulty with my general prediction on nutrient availability (prediction 5) is that it did not address differences *within* the three river sites, where nutrient concentration varied widely (Figures 6 and 7). Some of this variability may be explained, however, by again looking at the sedimentation data. For example, the proportion of total sedimentation that occurred during

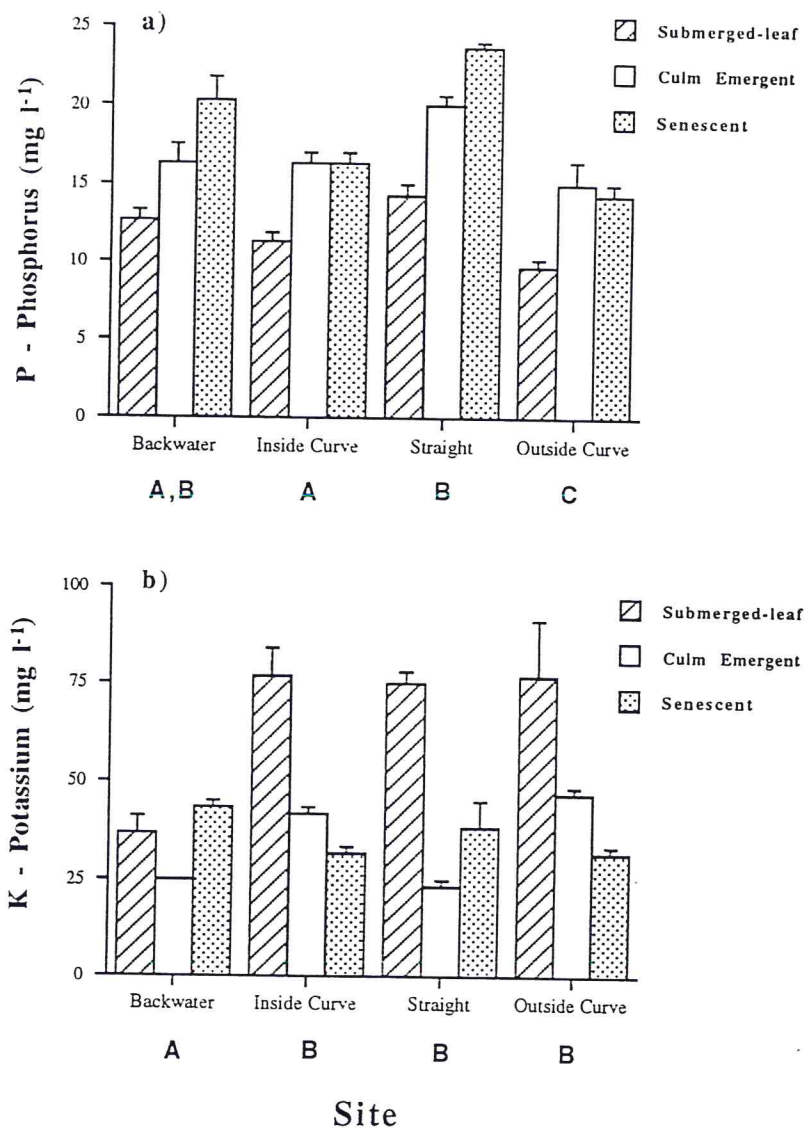


Figure 7. Phosphorus and potassium concentrations of mid-shallow zones as (a) total phosphorus, (b) total potassium across four sites with differing sedimentation dynamics at three different growth stages of wild-rice, including the submerged-leaf, culm emergent and senescent stages. See text for dates of sampling in relation to growth stage. Error bars indicate one SE. Different letters under sites indicate differences among means at $p < 0.05$.

the submerged-leaf stage was greatest for the inside curve site (Figure 4). This suggests that the inside curve is the site most likely to follow the general prediction stating that nutrient levels would be at their peaks toward the end of the submerged-leaf stage. This was the especially the case for both TKN and $\text{NH}_4\text{-N}$ (Figure 6a, b). At the outside bends, however, where the current velocity is strongest, sedimentation rates at the mid-shallow depths (where the nutrient samples were taken) were similar at all but the pre-seedling stage (Figure 5c). Predictably, outside curves also showed little difference in TKN and $\text{NH}_4\text{-N}$ concen-

trations among the three sampling times (Figures 6a and b). $\text{NH}_4\text{-N}$ is a more likely form of nitrogen to be taken up by higher plants in flooded conditions (Klopatek 1978), as well as being far more abundant than NO_3 . The seasonal changes in $\text{NH}_4\text{-N}$ concentrations seem to be explained by the sedimentation dynamics.

CONCLUSIONS

The results of this study suggest that wild-rice's stage of maximum growth immediately follows the import of nutrients that accompanies the first seasonal

flush of sediment deposition. Exactly how does this proposed adaptive strategy confer advantage to plants or populations of plants in riverine habitat? Wild-rice productivity, as measured in terms of biomass and mean seed yield, is greater in riverine areas when compared to backwater areas (Meeker 1993). In these riverine areas, productivity is also greater at moderate depths in locations just inside the vegetation-open water interface.

These findings are not surprising for the Kakagon, an area historically known to be a reliable source of grain sustenance for native peoples (Jenks 1901). However, questions arise as to how these results can be generalized outside this system. For example, how important is the seiche activity that operates in this coastal wetland in influencing these results? The upstream flow characteristics of a seiche logically increase the retention time of inputs to a lotic system and presumably increase both sedimentation rates and nutrient availability. The importance of seiche will most likely need to be addressed in comparative studies of other systems where this activity is absent.

Finally, it should be noted that deposition of sediment can also affect plants in negative ways and has been isolated as an important contributing factor in cultural eutrophication (Mitsch and Gosselink 1986). As an annual plant, the greatest sedimentation-related threat to wild-rice's survival would likely be excess seed burial that could reduce seedling emergence. In all of the sites sampled in this study, the amount of sediment accrued was not excessive, yet at what level does sediment burial begin to seriously impede wild-rice emergence? In experiments conducted concurrently with the research presented here, I have shown that while 4 cm of sediment and no sediment (a planted control) did not reduce wild-rice emergence and final stem density, placing an 8-cm-thick layer of sediment (of similar density and texture to that which accrued in this study) reduced wild-rice seedling emergence and final density to very low levels (Meeker 1993). Observations by Oelke (1982) concur with these findings, as they noted that the first internode of an individual wild-rice plant may elongate up to 5 cm, potentially allowing it to emerge through a like thickness of sediment. Overall, wild-rice's biology and annual pattern of development is well suited to a riverine environment.

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