Landscape Ecology vol. 4 no. 1 pp 5-19 (1990)
SPB Academic Publishing bv, The Hague

The use of a geographic information system to analyze long-term landscape alteration by beaver

Carol A. Johnston and Robert J. Naiman[1]
Natural Resources Research Institute, University of Minnesota, Duluth, MN 55811, USA

Keywords: geographic information systems, GIS, *Castor canadensis*, impoundments, hydrology, vegetation, transitions

Abstract

A Geographic Information System (GIS) was used to analyze how beaver *(Castor canadensis)* have altered the hydrology and vegetation of Voyageurs National Park, Minnesota over a 46-year period. Maps of beaver ponds prepared from 1940, 1948, 1961, 1972, 1981, and 1986 aerial photographs were analyzed with a raster-based GIS to determine impoundment hydrology and vegetation distributions for each map date. Overlay and classification techniques were used to qdantify hydrologic and vegetation changes between map dates. The GIS was superior to manual methods for some analyses (*e.g.*, area measurement), and indispensible for others (*e.g.*, transition analysis). Total area impounded increased from 1% to 13% of the landscape between 1940 and 1986, as the beaver population increased from near extirpation to a density of 1 colony/km^2. Most of the impoundment area increase occurred during the first two decades, when 77% of cumulative impoundment area was flooded. Once impounded > 60% of the area maintained the same water depth or vegetation during any decade. GIS procedures were combined with field data to show that available nitrogen stocks nearly tripled between 1940 and 1986 as a result of beaver impoundment.

Introduction

Temporal change is an integral part of community, ecosystem, and landscape functioning: pioneer plant communities are succeeded by secondary plant communities, nutrient availability is affected by litter accumulation, landscape patchiness is altered by disturbance, and ecotone locations are affected by climatic change. While conventional research methods are suitable for quantifying such changes in small areas (*i.e.*, 0.1 to 10 ha) over short periods of time (*i.e.*, < 3 yr), they are inadequate for studying longer-term ecological change over large heterogeneous areas.

Geographic Information System (GIS), coupled with field studies and historical aerial photography, provide a means of researching the magnitude and consequences of temporal change for large areas over the half-century record of available air photo coverage. We have used this technique to study long-term landscape alteration by beaver *(Castor canadensis)*. By changing the flow of water in the landscape, beaver impoundments convert terrestrial to aquatic ecosystems, alter plant communities, and effect pathways and rates of nutrient cycling (Johnston and Naiman 1987; Naiman *et al.* 1986, 1988a). Beaver ponds increase landscape heterogeneity by creating a spatial mosaic of aquatic and

[1] *Present* address: Center for Streamside Studies, AR-10, University of Washington, Seattle, WA 98195, USA.

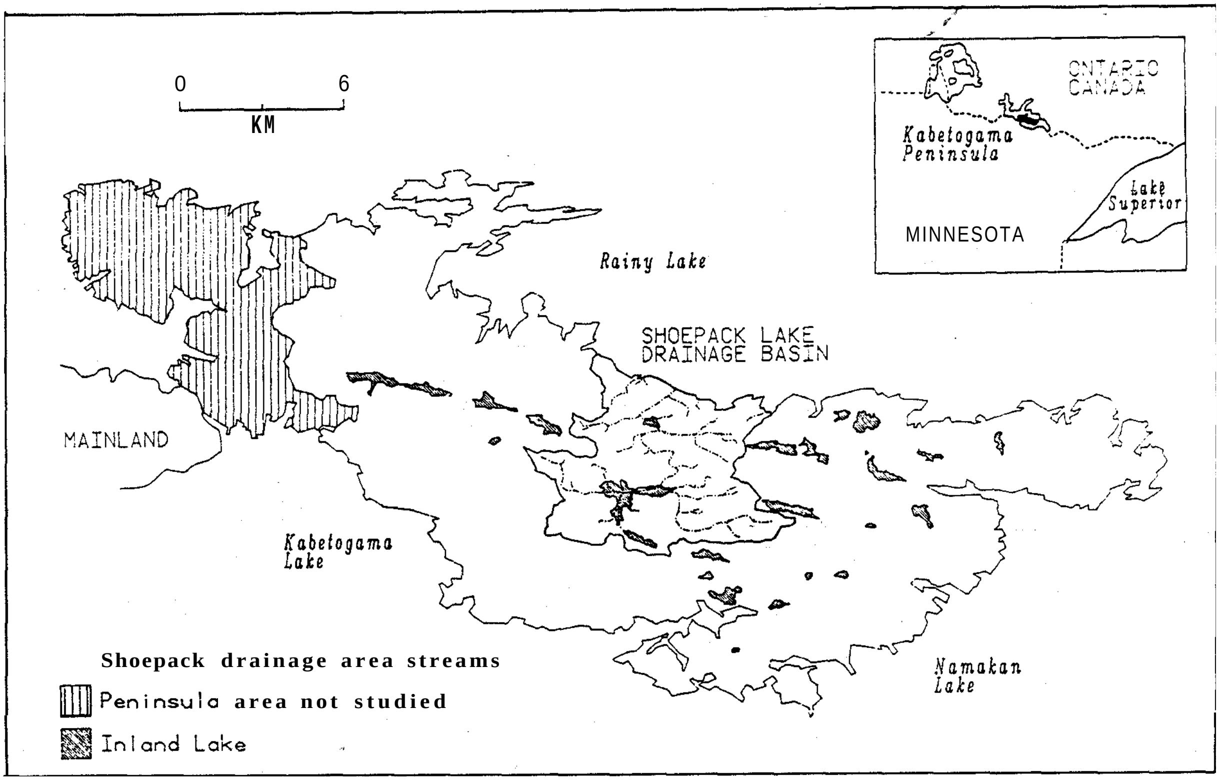

Fig. 1. **Study site. The Shoepack Lake drainage basin was used to develop the empirical relationship between measured and GIS-estimated stream lengths (Table 4).**

semi-aquatic patches in an otherwise forested matrix. This mosaic has been an integral part of the landscape for thousands of years, and only in the last 200–300 yrs has it been reduced in extent due to trapping pressure by man.

Because they are created and maintained by living organisms, beaver ponds are themselves dynamic, changing as they are colonized, flooded, and abandoned by beaver. Beaver act as agents of disturbance, setting back terrestrial vegetation succession by flooding forested areas. The ponding of water creates anaerobic conditions in beaver impoundment sediments, altering the form and abundance of compounds affected by redox reactions. When beaver leave and the pond drains, vegetation succession resumes and the sediments revert to aerobic conditions. In this way, beaver ponds constitute a rapidly shifting mosaic of hydrological and vegetatively diverse landscape patches.

The relatively large size (> 0.5 ha) of most beaver ponds, and their sharp contrast with the surrounding forest, makes it possible to accurately map the ponds using current and historical aerial photography. The GIS makes it possible to analyze the aerial extent, distribution, and characteristics of beaver ponds from these maps. Not only can GIS be used to determine spatial relationships at a given point in time, it can also be used to rapidly analyze temporal changes in the spatial mosaic.

All data presented here, with the exception of nutrient and precipitation data, were derived from GIS analysis of air photo-derived maps, and illustrate how GIS techniques can be used for ecological research. By combining GIS capabilities with air photo interpretation and field studies, we have: (1) measured the length of streams impounded by beaver, (2) determined the location, areal extent hydrology, and vegetation distributions of areas altered by beaver impoundment, (3) analyzed how the hydrology and vegetation of those areas have changed over time as a result of beaver disturbance and vegetation succession, and (4) related the spa-

Table 1. Aerial photography used to map beaver impoundments of the Kabetogama Peninsula.

Year	Scale	Film type	Commissioning agency
1940	1:20,000	Black & white panchromatic	U.S. Agric. Stabilization & Conservation Service
1948	1:15,840	Black & white infra-red	Boise-Cascade Company, International Falls, MN
1961	1:15,840	Black & white infra-red	St. Louis County Duluth, MN
1972	1:15,840	Black & white infra-red	Voyageurs National Park, International Falls, MN
1981	1:24,000	Color	Superior National Forest, Duluth, MN
1986	1:24,000	Color infra-red	this study

tial mosaic of beaver impoundments to landscape nutrient retention. The objective of this paper is to describe our use of a GIS for these purposes, and demonstrate its importance as a tool for analyzing spatial and temporal ecological change.

Methods

A 250 km^2 area, constituting 85% of the Kabetogama Peninsula of Voyageurs National Park and encompassing 741 beaver ponds, was chosen for study (Fig. 1). Voyageurs National Park, established in 1971, is part of an extensive boreal forest on the U.S.-Canada border approximately 25 km east of International Falls, Minnesota (48°34′N, 93’23′W), Shallow upland soils, derived from loamy to clayey glacial deposits, overlie metasedimentary and granitic bedrock. Although the topography ranges from steep cliff faces to flat glaciolacustrine plains, maximum topographic relief within the study area is only 80 m. Average annual precipitation is 63 cm, based on U.S. National Climatic Data Center records for the International Falls Station taken between 1940 and 1986. The summer months are the wettest, with two-thirds of the average annual precipitation falling between May and September.

Aerial photography was obtained for 6 different years spanning 1940–1986 (Table 1). The aerial photographs were stereoscopically interpreted (3 x magnification) using well-established methods to identify areas altered by past and present ponding of water by beaver (Dickinson 1971; Parsons and Brown 1978; Bogucki *et al.* 1986; Remillard *et al.* 1987). These beaver impoundments ranged from open water ponds to ‘beaver meadows,’ formerly ponded areas revegetated by grasses and sedges. Vegetation and hydrologic zones within each impoundment having an area of 0.5 ha or more were delineated and classified using the U.S. Fish and Wildlife Service’s (USFWS) *Classification of Wetlands and Deepwater Habitats of the United States*, a standardized classification system in widespread use (Cowardin *et al.* 1979; Table 2). Beaver ponds representing the range of types occuring on the peninsula were examined in the field concurrently with 1986 air photo acquisition to determined how air photo signatures matched ground conditions.

The interpreted information was transferred from the aerial photography to 1:24,000 U.S.G.S. topographic maps using a Stereo Zoom Transferscope to correct for distortion and scale variation. The topographic maps were also used for delineating the drainage basins of each primary impoundment. Primary impoundments are those which contain a beaver lodge, as opposed to secondary impoundments constructed adjacent to primary ponds for dam protection and forage access.

An ERDAS Geographic Information System run on an IBM PC/AT was used for data entry and analysis (Table 3). The following GIS data layers were manually digitized from the topographic and beaver pond maps using a Calcomp 91480 digitizing table: peninsula outline, permanent lakes within the peninsula, beaver pond outlines, wetland types

Table 2. U.S. Fish & Wildlife Service (Cowardin *et al.* 1979) wetland classes associated with beaver impoundments of the Kabetogama Peninsula. All wetlands are in the Palustrine system. * = special modifier (m) used to designate floating mat. # = includes deciduous and evergreen needle-leaved conifers, typically tamarack (*Larix laricina*) and black spruce (*Picea mariana*).

Class	Subclass	Water regime	Code
Aquatic bed	Rooted vascular	Semipermanently flooded	AB3F
Emergent	Persistent	Temporarily flooded	EM1A
		Saturated	EM1B
		Seasonally flooded	EM1E
		Semipermanently flooded	EM1F
		Semipermanently flooded	EM1Fm *
Shrub/scrub	Broad-leaved deciduous	Saturated	SS1B
		Seasonally flooded	SS1E
		Semipermanently flooded	SS1F
		Semipermanently flooded	SS1Fm *
	Broad-leaved deciduous	Saturated	SS3B
		Seasonally flooded	SS3E
		Semipermanently flooded	SS3Fm *
	Dead	Seasonally flooded	SSSE
		Semipermanently flooded	**SSSF**
		Semipermanently flooded	SS5Fm *
	Needle-leaved	Saturated	SSSB #
		Seasonally flooded	SS8E #
		Semipermanently flooded	SS8Fm *#
Forested	Broad-leaved deciduous	Temporarily flooded	FO1A
		Seasonally flooded	FO1E
		Semipermanently flooded	FO1F
	Dead	Saturated	FO5B
		Seasonally flooded	FO5E
		Semipermanently flooded	FO5F
		Semipermanently flooded	FO5Fm *
	Needle-leaved	Saturated	FOSB #
		Semipermanently flooded	FO8F #
		Semipermanently flooded	FO8Fm *#
Unconsolidated bottom (open water)	–	Semipermanently flooded	UBF
	–	Permanently flooded	UBH
Unconsolidated shore	Silt	Temporarily flooded	US4A

within beaver ponds for each data of photography, drainage basins of primary ponds, and streams. Since **ERDAS** is a raster-type GIS, the digitized polygons were gridded into a matrix of **7** $\times$ **7** m picture elements (*i.e.*, pixels), a pixel size determined experimentally to be appropriate for the data resolution. GIs-derived data from each of the six air photo dates were exported to a spreadsheet program (LOTUS **123),** which was used to compute summary statistics for each date and trends for four time periods between aerial photo dates: **1940–1948, 1948–1961, 1961–1972, 1972–1981,** which approximate decadal intervals.

Stream drainageways were classified by stream order (Morisawa **1968)** for the Shoepack Lake drainage basin, a **38** km^2 portion of the study area (Fig. 1). Comparison of the topographic maps with the interpreted aerial photographs revealed that beaver had impounded many drainageways not mapped as streams. When these areas were checked in the field, small (< 1 m wide) streams were found to occur at the pond outlets. Therefore, any beaver

Table 3. GIS procedure used to characterize beaver impoundments and measure transition rates.

Step	Description	ERDAS programs used
A.	Measure beaver impoundment area by vegetation and hydrologic type:	
	1. Digitize peninsula outline, lakes, and impoundment types	DIGPOL
	2. Create background file of the peninsula and its permanent lakes	MAKEFIL, GRDPOL, CUT ER
	3. Create beaver impoundment file, detailed classification	MAKEFIL, GRDPOL, CUT ER
	4. Overlay beaver impoundment file on peninsula background	OVERLAY
	5. Recode file to generalized landscape types	RECODE
	6. Measure total area of each landscape type	BSTATS
	7. Export area data to ASCII file	EXPTRL
B.	Compute transition rates and error check maps:	
	1. Compute transition rates for each possible change, and recode output	MATRIX
	2. Execute error-checking routine to locate illogical transitions	CLUMP, SIEVE
	3. Make corrections to maps as needed, repeat steps A.1. through B.1., export data	EXPTRL
C.	Define and measure individual impoundments and impoundment clusters:	
	1. Digitize primary pond watersheds	DIGPOL
	2. Define individual ponds by intersecting watershed and impoundment files, export data	RECODE, MATRIX, EXPTRL
	3. Define and number impoundment clusters, export data	RECODE, CLUMP, SIEVE, EXPTRL
D.	Measure length of streams impounded by beaver:	
	1. Digitize streams by stream order	DIGPOL
	2. Create raster file of streams	MAKEFIL, GRDPOL
	3. Overlay impoundment and stream files, export data	RECODE, OVERLAY, EXPTRL
	4. Multiply number of pixels in impounded stream by conversion coefficient	(see text)

impoundment which occurred at the headwaters of a draingeway as of **1986** was considered to be the source of a first order stream. These drainageways and all permanent and intermittent streams shown on the topographic maps were digitized as line segments by stream order. The line segment files were then rasterized into *7* x *7* m pixels for overlay onto the impoundment file (Table **3).**

A simple computer program was written to measure stream lengths from the unrasterized line segment files (*i.e.*, **ERDAS** files with a .DIG extension), based on the formula for computing the distance between two points:

$$d = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2},$$

where **d** is distance

x_1 and y_1 are the x,y coordinates of the first point, and
x_2 and y_2 are the x,y coordinates of the second point.

Table 4. Length of streams (beaver-impounded and total) within a 38 km^2 portion of the Kabetogama Peninsula, 1986. Estimated lengths calculated by multiplying number of pixels x 0.00761 km/pixel.

Stream order	Total number of pixels	Total measured length (km)	Total estimated length (km)	% Error estimated vs. measured	Impounded number of pixels	Impounded estimated length (km)	% Of length impounded
1st	3015	–	22.95	–	1599	12.17	53.0
2nd	1937	14.63	14.75	0.8	1068	8.13	55.1
3rd	384	2.83	2.92	3.2	0	0	0
4th	828	6.51	6.30	−3.2	723	5.50	87.3
Total, 1st–4th order streams	6164	–	46.92	–	3390	25.80	55.0

This program could not be used with rasterized files, such as the GIS file created by overlaying the stream and impoundment files, so a method for estimating stream length from rasterized files was developed empirically using data from the 38 km^2 drainage basin. A conversion coefficient (stream length/pixel) was calculated by dividing the total number of pixels in second, third, and fourth order streams by the total length of those streams as measured from the unrasterized line segment files. The coefficient was used with GIS-generated data (Table 3) to estimate the total length of streams impounded by beaver.

Field sampling was conducted at nine beaver ponds representing the range of hydrologic conditions observed. Soil samples were taken along a hydrologic gradient extending from dry conditions (forest) through progressively wetter beaver pond sediments (moist, wet, and pond). Ground reconnaisance was used to relate these categories to the mapped vegetation classes (Naiman *et al.* 1988a). Samples were collected monthly between April and October, and analyzed for plant-available N (KCI extractable nitrogen plus dissolved nitrogen in the soil solution) and total N (Naiman *et al.* 1988a).

Results

Stream length impounded

The stream length conversion coefficient was 7.61 m/pixel, 9% higher than the 7 m pixel dimension which would have been obtained for a straight stream paralleling the grid structure. Estimated stream lengths obtained using this coefficient were within **3.2%** of measured stream lengths (Table 4). **As** of 1986, beaver had impounded 53% of the first order streams, ***55%*** of the second order streams, and 87% of the fourth order streams within the Shoepack Lake drainage basin. The third order 'streams' were two lobes of Shoepack Lake (Fig. 1), and were therefore not impoundable (Table 4).

Impoundment vegetation and hydrology

A total of **32 USFWS** wetland classes were mapped within the Kabetogama Peninsula (Table **2).** However, some were uncommon (*e.g.*, US4A), functionally similar (*e.g.*, SS3B and SS8B), difficult to reliably distinguish (*e.g.*, SS1B vs. **SS1E),** or difficult to map consistenty with aerial photos taken at different times of year (*e.g.*, AB3F does not appear on spring aerial photography), Therefore, the ERDAS RECODE program was used to reassign the original impoundment categories to one of 13 generalized landscape types: 11 impoundment types, land not impounded, and permanent lakes (Table ***5).*** The impoundment types were further aggregated into 4 vegetation groups and **3** hydrology groups (Table 5).

The GIS-generated data showed that the majority of land hydrologically affected by beaver had wetland vegetation (Table ***5).*** Open water areas

Table 5. Area of permanent lakes, unimpounded land, and beaver impoundments within a 250 km^2 portion of the Kabetogama Peninsula, 1940–1986, by generalized landscape type. Vegetation and hydrology group summaries are shown in Fig. 2.

Generalized landscape types	USFWS wetland classes (Table 2)	Impoundment vegetation group	Impoundment hydrology group	Area (Ha)					
				1940	1948	1961	1972	1981	1986
Lakes not impounded	–	–	–	700	679	678	680	678	678
Land not impounded	–	–	–	24050	23292	21879	21614	21416	21134
Beaver impoundments:									
Wet meadow	EM1A, EM1B, EM1E, FO5B US4A	herbaceous	moist	101	121	447	661	**542**	616
Wet deciduous shrubs	SS1B, SS1E	deciduous	moist	45	165	402	412	383	301
Saturated bog	SS3B, SS8B, FO8B	bog	moist	67	138	231	220	219	235
Saturated decid. forest	FOIA, FO1E	deciduous	moist	1	33	69	84	91	60
Shallow marsh	EM1F	herbaceous	wet	17	99	281	424	558	476
Flooded bog	SS3E, SS8E, FO8E	bog	wet	2	34	63	53	37	24
Flooded deciduous	SS1F, FO1F	deciduous	wet	4	17	5	2	9	62
Pond, aquatic macrophytes	AB3F, UBF, UBH	open water	pond	13	191	686	599	693	873
Floating meadow	EM1Fm	herbaceous	pond	1	14	103	107	162	164
Dead woody	SS5E, SSSF, FO5E, FO5F	deciduous	pond	3	189	89	48	98	245
Floating woody mat	SS1Fm, SS3Fm, SS5Fm, SS8Fm, FO5Fm, FO5Fm, FO8Fm	bog	pond	3	34	75	104	121	140
	Total impoundment area			257	1035	2451	2714	2913	-3196

constituted only **27%** of the area impounded in 1986 (Fig. 2). In 1940, when many of the impoundments appeared to be abandoned, open water ponds constituted an even smaller percentage (5%) of total impoundment area (Table *5)*. Wet meadow and shallow marsh were the second and third most abundant wetland types in beaver impoundments as of 1986 (Fig. 2).

The GIS results also revealed a dramatic increase in total area impounded by beaver between 1940 and 1986 (Table 5, Fig. 3), a period of beaver population growth (Broschart *et al.* 1989). Despite temporary abandonment and drainage, none of the impoundments established during the 46-year study period reverted to the forest cover which beaver had impounded to create the ponds (Naiman *et al.* 1988a). Therefore, all areas which had been impounded at any time during the study period were still distinct patches, and the total area affected by impoundment was cumulative over time. **As** the beaver population increased from near extirpation during the 1930s (Broschart *et al.* 1989) to a 1984 density of 0.92 colony/km^2 (Smith and Peterson 1988), the area impounded increased from 1% to 13% of the peninsula area (Fig. **3).** The fastest rate of new impoundment occurred between 1940 and 1961, when the proportion of the landscape impounded increased by an order of magnitude. The rate of new impoundment was much less after 1961 (Fig. 3).

There were shifts in the predominant vegetation of the total impounded area as beaver activity changed and impoundments matured. Most of the peninsula was forested in the 1940s (Rakestraw *et al.* 1979), so flooded deciduous trees and bogs initially constituted about half of the total area impounded. Their total area has been relatively constant since 1961 (Fig. 3a), ***so*** that by 1986 woody deciduous and bog types constituted only **29%** of all impounded area (Fig. 2). Herbaceous impoundment area continuously increased, however, as impounded woody vegetation died and was replaced

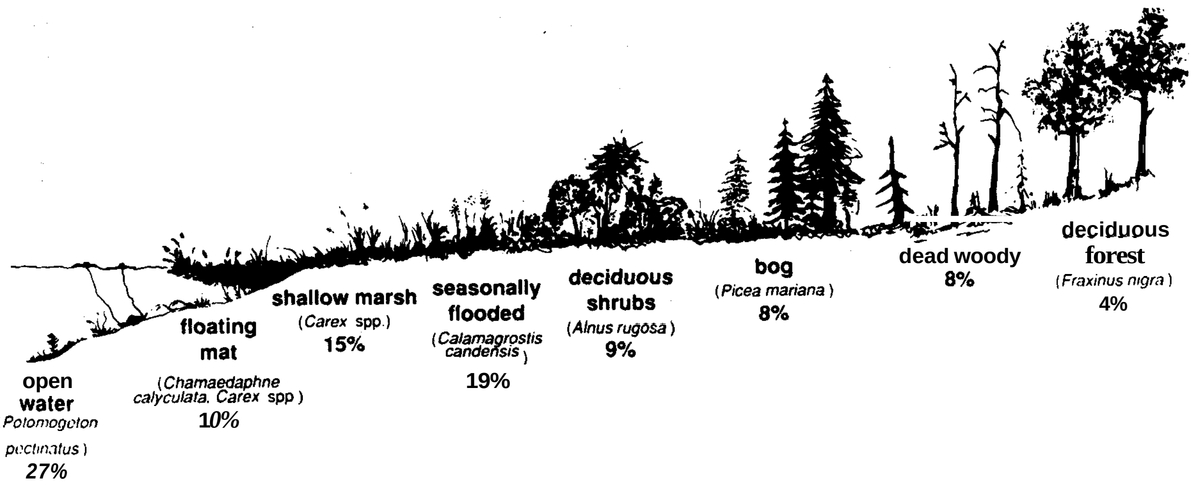

Fig. 2. **Proportion of beaver impoundments in major vegetation types, 1986. Representative species shown in parentheses. 'Floating mat' includes floating meadow and floating woody mat.** 'Bog' **includes saturated and flooded bog. 'Deciduous forest' includes flooded deciduous and saturated deciduous forest.**

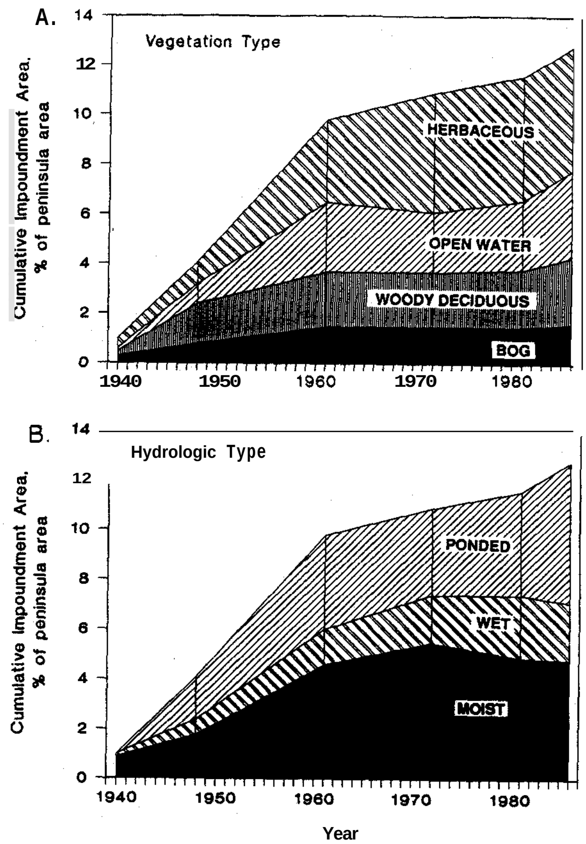

Fig. 3. **Cumulative impoundment area, by (a) vegetation type, and (b) hydrologic type. Vegetation and hydrologic groupings are listed** in **Table 5.**

by m'ore water-tolerant grasses and sedges (*e.g.*, ***Carex*** spp., ***Calamagrostis canadensis, Scirpus cyperinus}.*** Herbaceous impoundments were the major vegetation type in every year except 1948, when beaver were rapidly expanding into areas of deciduous forest (Fig. 3a). Herbaceous plant communities were rare outside of beaver impoundments, occurring primarily in the form of marshes adjacent to the surrounding large lakes (Kurmis *et al.* 1986).

The predominant hydrology of impounded areas has also changed over time. 'Moist' impoundment areas, those with saturated soils or a seasonally high water table, dominated from 1940 to 1972. 'Ponded' impoundments, those with water too deep to support emergent vegetation, dominated thereafter. 'Wet' impoundments, wetlands with shallow standing water, were intermediate in areal extent. The sharp increase in ponded area between 1981 and 1986 was not related to precipitation nor beaver population trends (Johnston and Naiman, in press), and may be an indication that beaver were creating more impoundments in search of new food supplies.

Table 6. Transition classes used to analyze vegetation and hydrologic changes of previously impounded areas.

Transition class	Class at beginning of time period	Class at end of time period
	Vegetation transitions:	
Woody death	Bog	Open water or herbaceous
	Deciduous	Open water or herbaceous
Woody invasion	Open water	Deciduous or bog
	Herbaceous	Deciduous or bog
Emergent to water	Emergent	Open water
Water to emergent	Open water	Emergent
No vegetation change	Open water	Open water
	Herbaceous	Herbaceous
	Bog	Bog
	Deciduous	Deciduous
	Hydrologic transitions:	
Water level up	Moist	Wet or ponded
	Wet	Ponded
Water level down	Wet	Moist
	Ponded	Wet or Moist
No hydrology change	Moist	Moist
	Wet	Wet
	Ponded	Ponded

Vegetation and hydrologic transitions

Although the above results describe cumulative vegetation and hydrologic trends, additional analysis was needed to characterize the transitions within beaver impounded areas which caused those trends. The ERDAS MATRIX program was used to analyze these transitions for each of the 5,103,561 individual 7 x 7 m pixels within the study area by comparing beaver impoundment maps from the onset versus the end of each decadal period (Table 3). The 169 possible transition classes (13 initial classes x 13 final classes) were grouped by recoding the output from the MATRIX analysis. Any pixel (*i.e.*, 7 x 7 m area) which changed from 'not impounded' to any of the 11 impoundment types, either due to construction of new ponds or expansion of old ones, was considered 'newly impounded.' Changes which occurred in previously impounded pixels were grouped into vegetation and hydrologic transition classes (Table 6, Fig. 4).

The major change in the 1940s and 1950s was the creation of new beaver impoundments (Fig. 5), consistent with the rapid rate of increase in total area impounded (Table 5). More than 60% of all pixels impounded as of 1948 and 1961 had been newly flooded during the previous decade (*i.e.*, 1940–1948 and 1948–1961: Fig. 5). As the rate of pond establishment declined in the 1960s and 1970s, however, less than 12% of the impounded pixels existing at the end of each decade were newly impounded. Although the increase in beaver population undoubtedly contributed to the increase in new impoundment area, the rate of new pond creation per beaver colony was much higher in the 1940s and 1950s than it was subsequently (Johnston and Naiman, in press).

Previously impounded pixels tended to have relatively stable hydrology, a trend which was consistent throughout the four decades studied (Fig. 6a). About 60% of the pixels impounded at the onset of each decade had the same water depth at the end of the decade. This indicates that changes occur within 40% of the pre-existing spatial mosaic during any decade, despite variations in precipitation and the rate of new impoundment creation. Further study is needed to determine if this proportion holds during periods of beaver population decline, as well.

There was some evidence that precipitation during the year preceding air photo acquisition influenced hydrologic trends, but the relationships were not consistent. About 35% of all impoundments existing in 1940 (an extremely dry year: Table 7) had higher water levels in 1948 (a year of above normal precipitation), while only 7% of impoundments had lower water levels (Fig. 6a). The trend reversed between 1948 and 1961, when water depth increased in 13% and decreased in 29% of pre-existing impoundments. This coincided with a change from precipitation surplus in 1948 to deficit in 1961 (Table 7). These relationships did not hold for the 1961–72 and 1972–81 time periods, however. Therefore, additional factors, such as impoundment recolonization rates, may have affected the hydrologic changes observed.

The vegetation in existing impoundments tended to be even more stable than water depth. With the exception of 1948–61, about 70% of the im-

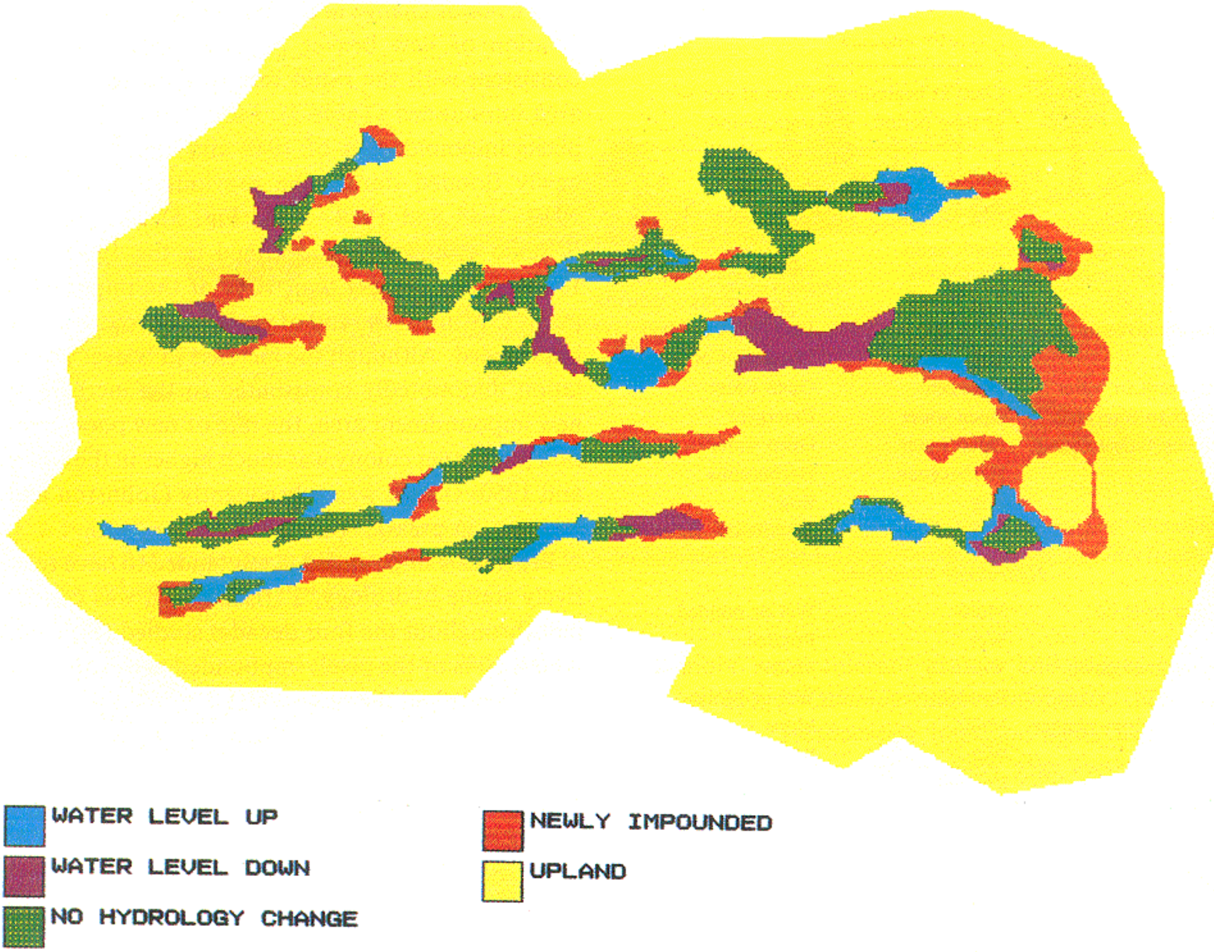

Fig. 4a. GIS image of hydrologic changes in beaver impoundments within a 5.6 km^2 portion of the 250 km^2 study area, 1981 to 1986. Transition classes are described in Table 6.

pounded pixels had the same vegetation class at the beginning and end of each decade. In the 1950s, the trees and shrubs which had been killed by flooding the previous decade (Table 5) fell to the ground, resulting in a high proportion of woody die-back (Fig. 6b). Given the large area of dead woody vegetation observed on the 1986 aerial photos (Table 5), we expect to see a similar trend by the end of the 1980s as that dead vegetation topples.

An unexpected finding was the lack of woody reinvasion in drained impoundments, which was observed in the field as well as in the GIS-derived data. Although other authors have reported shrub and sapling encroachment into drained beaver ponds (Remillard *et al.* 1987), our data showed this to be a small percentage of the total change over the decadal periods analyzed (Fig. 6b). This is surprising given the predominance of forest adjacent to the impoundments (Kurmis *et al.* 1986).

Hydrology and vegetation showed similar trends over time (Fig. 4), indicating the influence of edaphic conditions on vegetation; when hydrology changed, the dominant vegetation type changed as well. Exchanges between open water and emergent classes were consistent with the hydrologic trends observed (Fig. 6). When the proportion of water level increases exceeded decreases, the proportion of emergent-to-water changes exceeded water-to-emergent changes. The fact that vegetation was more resistent to change than was hydrology (Fig.

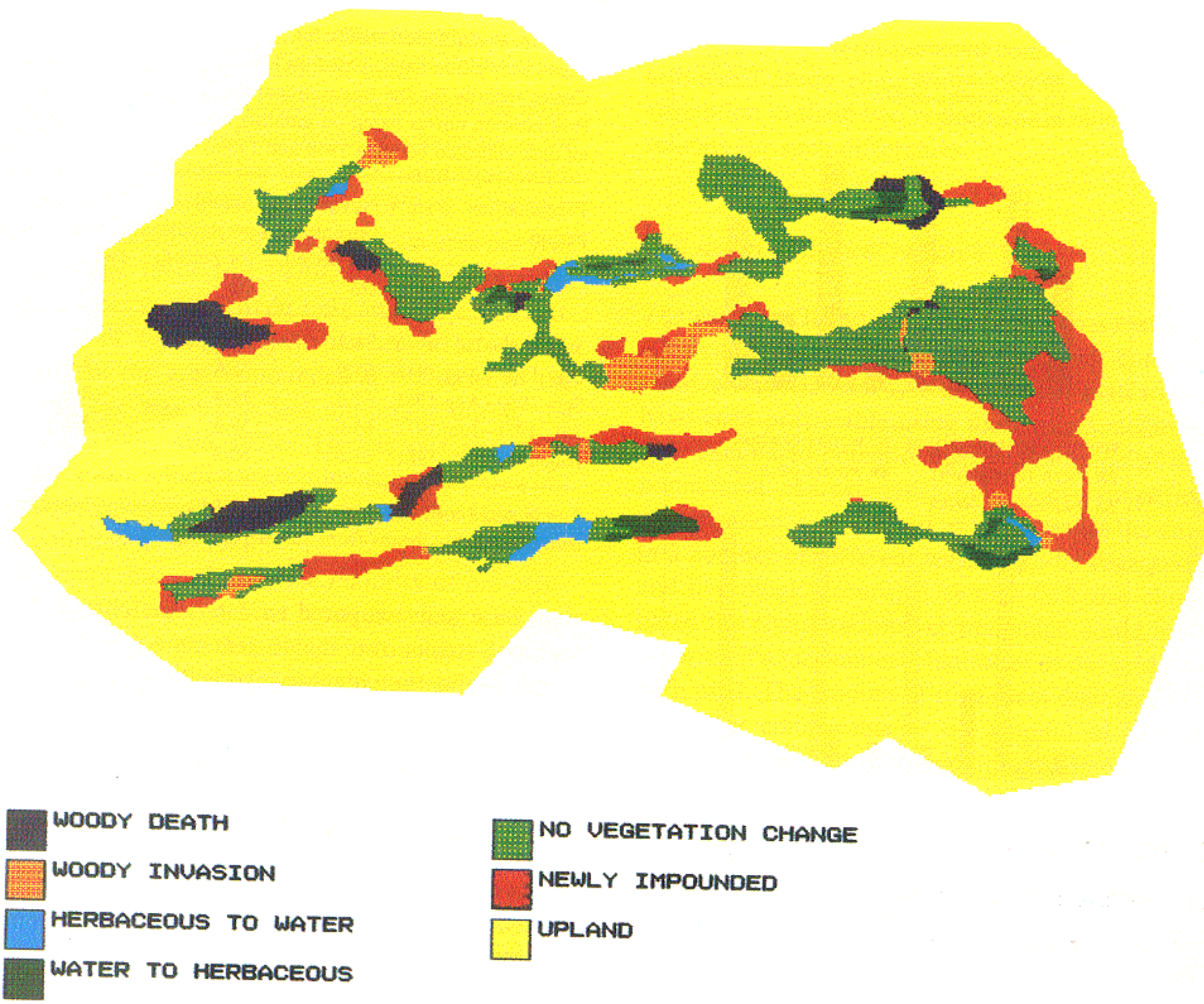

Fig. 4b. GIS image of vegetation changes in beaver impoundments within a 5.6 km² portion of the 250 km² study area, 1981 to 1986. Transition classes are described in Table 6.

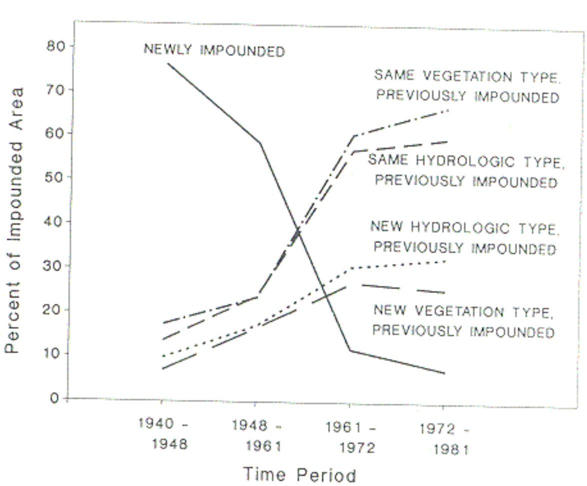

Fig. 5. Hydrologic and vegetation changes, impoundments existing at end of decadal period (newly established and existing impoundments).

6) is probably due to the adaptation of emergent vegetation forms commonly found in beaver impoundments to hydrologic fluctuations (*e.g.*, mat- and tussock-forming sedges: Johnston and Naiman 1987).

Linking ecosystem processes with spatial data

Nitrogen dynamics in beaver-impounded areas are strongly tied to hydrology because of the interac-

←

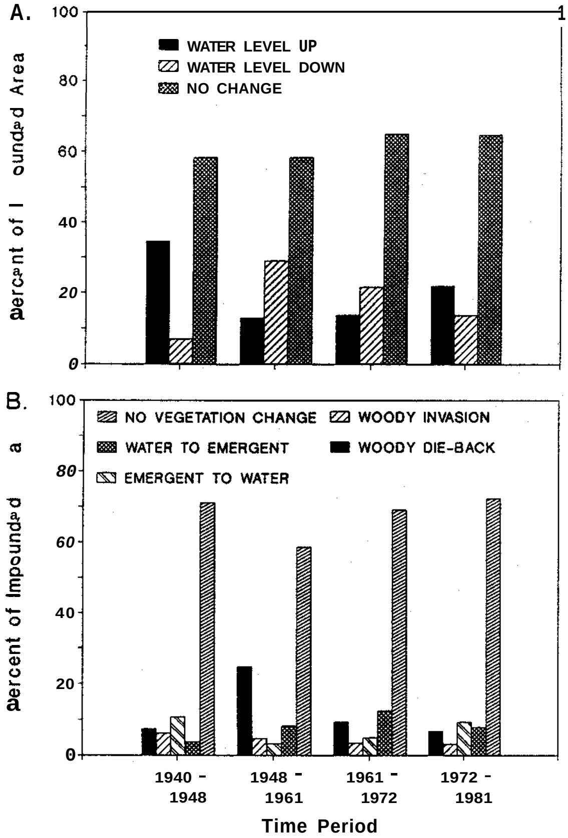

Fig. 6. Transitions in existing impoundments, as percent of impounded area, by time period. (a) Hydrologic transitions. (b) Vegetation transitions. Transition classes are described in Table 6.

tions between redox potential and the microbial processes affecting nitrogen availability in wetlands (Gambrell and Patrick 1978). To determine how beaver impoundments have affected nutrient availability in the landscape, we measured total N and plant-available N (kg/ha) in sediment cores collected from 9 impoundment areas representing the 4 hydrologic types (land not impounded, moist, wet, and pond: Naiman *et al.* 1988a). These concentrations were extrapolated to the peninsula as a whole by assigning them to each pixel in the GIS data base having a corresponding hydrologic type. The data for the subset of pixels which had been impounded by beaver as of 1986 were summarized to determine the absolute amounts (kg) of total N and plant available N. The same procedure was applied to the same subset of pixels extracted from the 1940 GIS

Table 7. Precipitation trends for the 12 months preceeding air photo acquisition dates, based on U.S. National Climatic Data Center records for the International Falls, Minnesota station. Precipitation norms based on monthly and annual averages of all data collected between 1940 and 1986.

Precipitation period	Normal precipitation for period, cm	Actual precipitation for period, cm	Deviation from norm, cm
Jan 1940–Jul 1940*	36.3	22.0	−14.3
Sep 1947–Aug 1948	63.0	71.6	8.6
Sep 1960–Aug 1961	63.0	54.4	−8.6
Jul 1971–Jun 1972	63.0	59.8	−3.2
Aug 1980–Jul 1981	63.0	60.4	−2.7

* = No data collected prior to January 1940; deviation based on sum of monthly means from January through July.

data base and compared to determine changes in standing stocks over the 46 year time period.

We found that plant-available N stocks nearly tripled as a result of beaver impoundments, increasing from 13.2 x 10^3 kg in 1940 to 34.0 x 10^3 kg in 1986 (Naiman *et al.* 1988a). Total N stocks also increased slightly, from 5.76 x 10^6 kg N in 1940 to 6.12 x 10^6 kg N in 1986. Thus, while beaver have only a small influence on total N distribution in the landscape over a half-century period of time, they substantially increase N availability over large areas.

Discussion

Beaver/landscape linkages

GIS analysis showed that beaver are important agents of change, altering vegetation and hydrology over a substantial portion of the landscape through impoundment construction, abandonment, and recolonization. During the 1940s and 1950s, beaver impounded new areas at the rate of 0.42% of the landscape per year. By comparison, the rate of urban encroachment into agricultural land around Milwaukee, Wisconsin between 1937 and 1963 was 0.64% per year (Sharpe *et al.* 1981), and the rate of cropland abandonment in Oglethorpe County, Georgia between 1955 and 1980 was 0.8% per year

(Turner **1987).** Clearly, the influence of beaver on landscapes approaches that of man.

The magnitude and type of beaver-induced landscape alteration has been dynamic, changing as the beaver population has increased and impoundments have matured. The rate of new impoundment decreased to **0.09%** of peninsula area per year during the **1960s** and **1970s,** but increased again **(0.23%** per year) between **1981** and **1986.** The conversion of forest to open patches affected one-fourth of the area impounded at the onset of the 1950s, but was much less important during the 1940s, 1960s, and **1970s.** Herbaceous and open water areas, which were a minority of the area impounded prior to **1961,** constituted **71%** of the area impounded as of **1986.**

Despite this variation, the majority of pre-existing impoundments did not change in water level nor vegetation over the decadal periods analyzed. Once impounded ≥60% of the area maintained the same water depth or vegetation during any decade. The fact that this percentage was so constant over time implies an underlying mechanism not influenced by changes in beaver population nor climate.

A possible cause of this stability may be the large pools of water, carbon, and nutrients sequestered by beaver impoundments (*i.e.*, patch bodies: Johnston and Naiman **1987).** By promoting the growth of peat-forming vegetation resistant to water level fluctuations (*e.g.*, sedge tussocks and floating peat mats), wetland conditions may be perpetuated even after the beaver colony departs (Naiman ***et al.*** **1988a). GIS** analysis of beaver-landscape linkages could be used to test this hypothesis.

GIS may also help determine why vegetative alterations caused by beaver impoundments on the Kabetogama Peninsula differed quantitatively from those observed in other areas, despite similarities in forest and impoundment species. For example, shrub re-invasion was common in abandoned beaver ponds in the Adirondack Mountains at New York State (Remillard ***et al.*** **1987),** while it was virtually non-existent on the Kabetogama Peninsula. It is possible that abandoned beaver ponds were wetter, or that the cycle of beaver pond flooding and abandonment was shorter in Minnesota than in New York, either of which would retard shrub re-invastion (Remillard, personal communication). A GIS-aided study comparing edaphic factors and vegetation in these two regions could elucidate the reasons for such differences.

GIS use in ecological research

The use of a **GIS** to automate areal measurements allowed us to use a much more detailed, comprehensive classification system (Table **2)** than would have been practicable using mechanical methods. This eliminated potential misrepresentation of impoundment characteristics due to oversimplified classification, and allowed us to generalize the data in a number of different ways (*e.g.*, by vegetation and hydrologic groups). Use of a GIS also eliminated the computational errors which could have occurred if a mechanical planimeter or dot grid had been used. The amount of time spent digitizing the maps was comparable to the amount of time it would have taken to measure impoundment areas using a planimeter, but resulted in much more versatile data base that could be used for further spatial analysis and/or map production.

Use of a **GIS** was essential to the analysis of impoundment change. Over **20.4** million individual transitions were computed **(4** time periods × **5.1** million pixels per scene). Manual trend analysis methods (*e.g.*, Tiner ***et al.*** **1984)** could not have duplicated this level of detail, and data would have been the only result. The **GIS** generated not only the transition data, but a database which can be used with other data layers to explore spatial relationships affecting these transition rates.

Because of the close relationship between hydrology and the abundance of compounds affected by redox reactions, it was possible to use aerial photography and **GIS** analysis to infer historical nutrient standing stocks. In addition, the **GIS** could be used to determine areas where a sequence of environmental changes would affect nutrient cycling processes. For example, denitrification rates would be highest in areas with fluctuating water levels: aerobic conditions promote the production of nitrate, which is subsequently denitrified when rising water levels generate anaerobic conditions (Patrick and Wyatt 1964). The GIS could also be used to determine the spatial distribution of nutrient stocks relative to vectors of nutrient flux in the landscape, such as stream networks.

Use of a raster-based GIS did not pose methodological limitations on measurements of cumulative areas and transitions. Each pixel was analyzed as an independent entity with a single numerical code representing its wetland type, just as a satellite image would classify the landscape into a matrix of individual reflectance values (*e.g.*, Hall *et al.* 1988), and the results were automatically summarized. However, unlike polygons in vector-based GISs which may be assigned multiple attributes (*e.g.*, vegetation type, pond number), each pixel in a raster GIS data layer may have one and only one data value assigned to it. To uniquely identify each pixel in our rasterized data layer by both wetland type and pond number would have required a prohibitively complex classification system (741 ponds * 13 landscape types = 9,633 unique combinations). This disadvantage was overcome through the use of GIS techniques based on Boolean algebra (Burrough 1986). The watershed of each primary pond was identified by a unique number, so the pond identity of each impoundment pixel was determined by intersecting the watershed data layer with a simplified beaver impoundment data layer (1 = impounded, 0 = not impounded). The result was a map identifying all 741 beaver ponds, which is currently being used to analyze the size, shape, growth, and hydrologic transitions of individual beaver ponds (Johnston and Naiman, unpublished manuscript).

While vector-based GISs are more convenient for making linear measurements, we have demonstrated that accurate linear measurements can be obtained by developing empirical relationships between measured length and number of pixels in a linear feature. The linearity of ecosystem features such as streams and ecotones (Naiman *et al.* 1988b), and landscape features, such as patch perimeter, shape, accessibility, dispersion, and fractal dimension (Forman and Godron 1986; Gardner *et al.* 1987) make this an important capability for ecological applications.

The increased availability of reasonably priced microcomputer-based Geographic Information Systems has occurred at an opportune time in the development of landscape ecology, with its emphasis on spatial and temporal relationships over large areas and long time periods. While the lack of digital data bases poses problems for some types of ecological research, aerial photos and satellite imagery provide excellent sources of information at the landscape scale. What is needed now are techniques for measuring ecological processes over similarity large areas, such as long-path Fourier Transform infrared spectroscopy (Gosz *et al.* 1987), so that remotely sensed information can be related to ecosystem function.

While the use of a raster-based GIS had some disadvantages, such as the inability to assign multiple attributes to ponds, the ERDAS system used was user-friendly, relatively easy to leam, and provided accurate results. Unlike GIS applications for natural resource management, we made little use of the system's graphics and map generation capabilities. We used the GIS not as an ends in itself, but as an essential tool for the analysis of spatial and temporal change.

Acknowledgements

John Bonde, Michael Broschart, Lucinda Johnson, Mark Springan, and Mark Stensaas were involved with various aspects of air photo interpretation, data entry, and GIS analysis. Nutrient sampling and analysis was done by James Kelley and Tom Manning. Research support from the National Science Foundation (BSR-8516284 and BSR-8817665). We thank H.G. Merriam, J. Pastor, and M.M. Remillard for constructive comments on drafts of this manuscript. This is contribution 37 of the Center for Water and Environment and contribution number 4 of the Natural Resources Research Institute GIS Laboratory (NSF DIR-8805437).

Literature cited

Bogucki, D.J., Gruendling, G.K., Allen, E.B., Adams, K.B. and Remillard, M.M. **1986.** Photointerpretation of historical **(1948–1985)** beaver activity in the Adirondacks. Technical Papers; ASPRS-ACSM Fall Convention, Anchorage, Alaska. 23 Sept.–3 Oct. **1986.**

Broschart, M.R., Johnston, C.A. and Naiman, R.J. **1989.** Predicting beaver colony density in boreal landscapes. J. Wildl. Manage. **53: 929–934.**

Burrough, P.A. **1986.** Principles of geographical information systems for land resources assessment. Oxford Univ. Press, Oxford.

Cowardin, L.M., Carter, V., Golet, F.C. and LaRoe, E.T. **1979.** Classification of wetlands and freshwater habitats of the United States. U.S. Fish and Wildlife Serv., Office of Biol. Serv. **(FWS/OBS-79/3** 1). U.S. Govt. Printing Office, Washington, D.C.

Dickinson, N.R. **1971.** Aerial photographs as an aid in beaver management. New York Fish & Game J. **18: 57–61.**

Forman, R.T.T. and Godron, M. **1986.** Landscape Ecology. John Wiley & Sons, New York.

Gambrell, R.P. and Patrick, W.H. Jr. **1978.** Chemical and microbiological properties of anaerobic soils and sediments. *In* Plant life in aerobic environments. pp. **375–423.** Edited by D.D. Hook and R.M.M. Crawford. Ann Arbor Science Publishing, Ann Arbor, Michigan.

Gardner, R.H., Milne, B.T., Turner, M.G. and O'Neill, R.V. **1987.** Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology **1: 19–28.**

Gosz, J., Dahm, C. and Risser, P. **1987.** Long-path length FTIR analysis of ecosystem processes over varying landscapes and spatial scales (abstract). Bull. Ecological Soc. Amer. **68: 313.**

Hohn, F.E. **1960.** Applied Boolean algebra: an elementary introduction. Macmillan, New York.

Hall, F.G., Strebel, D.E., Goetz, S.J. and Sellers, P.J. **1988.** Linking knowledge among spatial and temporal scales: vegetation, atmosphere, climate, and remote sensing. Landscape Ecology **2: 3–22.**

Johnston, C.A. and Naiman, **R.J. 1987.** Boundary dynamics at the aquatic- terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology **1: 47–57.**

Johnston, C.A. and Naiman, R.J. In press. Aquatic patch creation in relation to beaver population trends. Ecology.

Kurmis, V., Webb, S. and Merriam, L. Jr. **1986.** Plant communities of Voyageurs National Park, Minnesota, U.S.A. Can. J. Botany **64: 531–540.**

Morisawa, M. **1968.** Streams: their dynamics and morphology. McGraw-Hill, New York.

Naiman, R.J., Melillo, J.M. and Hobbie, J.E. **1986.** Ecosystem alteration of boreal forest streams by beaver (***Castor canadensis***). Ecology **67: 1254–1269.**

Naiman, R.J., Johnston, C.A. and Kelley, J.C. 1988a. Alteration of North American streams by beaver. BioScience **38: 753–762.**

Naiman, R.J., Decamps, H., Pastor, J. and Johnston, C.A. 1988b. Potential importance of boundaries to fluvial ecosystems. Jour. N. Amer. Benthological Soc. **7: 289–306.**

Parsons, G.P. and Brown, M.K. **1978.** An assessment of aerial photograph interpretation for recognizing potential beaver colony sites. New York Fish & Game J. **25: 175–177.**

Patrick, W.H., Jr. and Wyatt, R. **1964.** Soil nitrogen loss as a result of alternate submergence and drying. Soil Sci. Soc. Amer. Proc. **28: 647–653.**

Rakestraw, L., Coffman, M. and Ferns, J. **1979.** Fire and logging history of Voyageurs National Park. Second Conference on Scientific Research in the National Parks. **26–30** November **1979.** San Francisco, California.

Remillard, M.M., Gruendling, G.K. and Bogucki, D.J. **1987.** Disturbance by beaver ***(Castor canadensis*** Kuhl) and increased landscape heterogeneity. ***In*** Landscape Heterogeneity and Disturbance. pp. **103–123.** Edited by **M.G.** Turner. Springer Verlag, New York.

Sharpe, D.M., Stearns, F.W., Burgess, R.L. and Johnson, W.C. **1981.** Spatio-temporal patterns of forest ecosystems in man-dominated landscapes of the eastern United States. *In* Perspectives in Landscape Ecology. pp. **109–116.** Edited by S.P. Tjallingii and A.A. de Veer. Centre for Agricultural Publication and Documentation, Wageningen.

Smith, D.W. and Peterson, R.O. **1988.** The effects of regulated lake levels on beaver at Voyageurs National Park, Minnesota. U.S. Dep. of Interior, National Park Service, Research/ Resources Management Report MWR-11. Midwest Regional Office, Omaha, Nebraska.

Tiner, R.W., Jr. **1984.** Wetlands of the United States: current status and recent trends. U.S. Dept. of Interior, Fish & Wildlife Service, Washington, D.C.

Turner, M.G. **1987.** Spatial simulation of landscape changes in Georgia: a comparison of **3** transition models. Landscape Ecology **1: 29–36.**