

## SHRUB SPECIES AS INDICATORS OF WETLAND SEDIMENTATION

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**Abstract:** Shrub cover was quantified by species for a 1.9-ha shrub carr adjacent to White Clay Lake near Shawano, WI, USA and related to soil properties and sedimentation rates. Principal components analysis of soil characteristics distinguished two distinct groups: alluvial surface soils having organic matter contents less than 30 g/100g and histic surface soils having organic matter contents averaging 56 g/100g. The alluvial surface soils were on slightly elevated natural levees along a relict stream bed that had received 1.3 cm/yr of silty sediments from agricultural runoff. Alluvial surface soils had twice the bulk density and organic P concentrations, nearly three times the reactive P, and 4.5 times the NO<sub>3</sub>-N concentrations of histic surface soils. Total shrub cover and shrub overlap was significantly greater on the alluvial surface soils, but there was no difference between the two soil groups in proportion of open space, suggesting that the increased total shrub cover on alluvial surface soils was due to increased shrub layering rather than infilling of canopy gaps. Shrub diversity was greater on the alluvial surface soils: average shrub species richness per 30.5 m line segment was five species on alluvial surface soils as opposed to three species on histic surface soils. Four willow species were strongly associated with the alluvial surface soils and may serve as indicators of sediment deposition: *Salix discolor*, *S. eriocephala*, *S. interior*, and *S. lucida*. The most common shrub species present, *Cornus sericea* spp. *sericea* and *Salix petiolaris*, were poor indicators of soil conditions within the wetland.

**Key Words:** shrub carr, *Salix* spp., *Cornus* spp., woody cover, alluvial, histic, sedimentation, Wisconsin

### INTRODUCTION

Shrub carrs are wetlands dominated by shrubs other than *Alnus*, and are one of the most common wetland types in the upper Great Lakes region of the United States (Frolik 1941, Curtis 1959, White 1965, Vogl 1969, Mensing et al. 1998). Unlike upland shrub communities in humid temperate climates, which are short-lived seres in the secondary succession of old fields to forests, shrub carrs are dominated by tall shrub species that do not become trees at maturity, persisting for decades in that growth form (Curtis 1959).

Despite recognition that shrub carrs are naturally occurring ecosystems, the encroachment of shrubs into wet meadows is viewed negatively by most conservationists, and wetlands are actively managed to reduce shrub density to favor desired plant assemblages and wildlife species (Hanowski et al. 1999). Shrub encroachment can occur rapidly with the invasion of exotic species, such as *Rhamnus frangula* L. (Taft and Solecki 1990), but more commonly results from the addition and densification of native shrub stands within wetlands. Reported causes of native shrub encroachment include ditching (Frolik 1941, Fisher et al. 1996), drainage (Thibodeau 1985), moderate burning (Frolik 1941), grazing by livestock and feral animals (Cook

et al. 1996, Dobkin et al. 1998, Vulink et al. 2000), abandonment of wetland cultivation (Vogl 1969), and abandonment of mowing for marsh hay (Frolik 1941).

In addition to these direct sources of disturbance, the intensification of upland agriculture can affect shrub carrs indirectly. In a study of anthropogenic disturbances in landscapes surrounding shrub carrs in central Minnesota, Mensing et al. (1998) found that shrub carr diversity was highly correlated with land use, the best single predictor being the percentage of cultivated land within the watershed draining to the wetland. Similarly, pollen studies of a lakeside wetland in southern Ontario showed an increase in abundance of *Alnus incana* (L.) Moench and *Salix* associated with elevated soil silicates and sediment-accumulation rate (0.25 cm/yr) that was due to erosion from land clearance and agriculture in the early 19<sup>th</sup> century (Yu et al. 1996). In the absence of these anthropogenic disturbances, the pollen record indicated a successional trend from herbaceous marsh directly to cedar swamp without the shrub-marsh or alder-thicket stages.

Although initial land clearing for agriculture took place during the 19<sup>th</sup> century in the upper Great Lakes states, a second wave of agricultural intensification occurred during the late 20<sup>th</sup> century when short growing-

season corn strains were introduced that enabled farmers to plant corn for the first time in northern areas with colder climates. The corn crops displaced crops such as oats and hay that provide greater soil cover. Conventional corn tillage is much more erosive than small grains or hay, accelerating the transport of sediment and nutrients from farm fields (Wischmeier and Smith 1978). The rate of wetland sedimentation simultaneously increased with this shift in agricultural practice as a result of increased downslope transport of eroded soil materials in watersheds (Persson et al. 1983, Johnston 1993).

Ecological indicators are designed to provide clear signals about status or trends with the most efficient use of resources (National Research Council 2000). Certain plants grow under specific edaphic conditions, such that their presence is a reliable indicator of soil or bedrock characteristics. This principle is the basis for the use of hydrophytes as indicators of wetlands (Reed 1988). There has been mixed success in developing plant indicators of wetland biotic integrity or soil characteristics (Ehrenfeld et al. 1997, Wilcox et al. 2002).

The purpose of this study was to assess shrubs as indicators of wetland sedimentation. The study was conducted in a shrub carr adjacent to White Clay Lake in northeastern Wisconsin, selected because its sedimentation rates are well quantified using  $^{137}\text{Cs}$  dating (Johnston et al. 1984a). The site was selected because its soils and chemistry have been mapped in detail (Johnston et al. 1984b, Johnston 1993), providing important information about soil characteristics that could influence shrub biomass and species composition. The objectives of the study were to (1) quantify woody plant cover by species, (2) relate shrub species, cover, and biodiversity to soil properties, and (3) use the results to suggest plant indicators of wetland sedimentation.

## METHODS

### Study Site

The 1.9-ha shrub carr study site adjoins White Clay Lake, located 60 km northwest of Green Bay, Wisconsin, USA. It is part of a larger wetland complex, currently bounded by green ash (*Fraxinus pennsylvanica* Marsh.) swamp to the north and east, northern white cedar (*Thuja occidentalis* L.) swamp to the south, and sedge meadow to the west. Inspection of 1938 aerial photos showed that the wetland vegetation was primarily herbaceous at that time, indicating that shrub encroachment was relatively recent (Figure 1). The presence of an old barbed wire fence post remaining in the shrub carr suggests that the area was

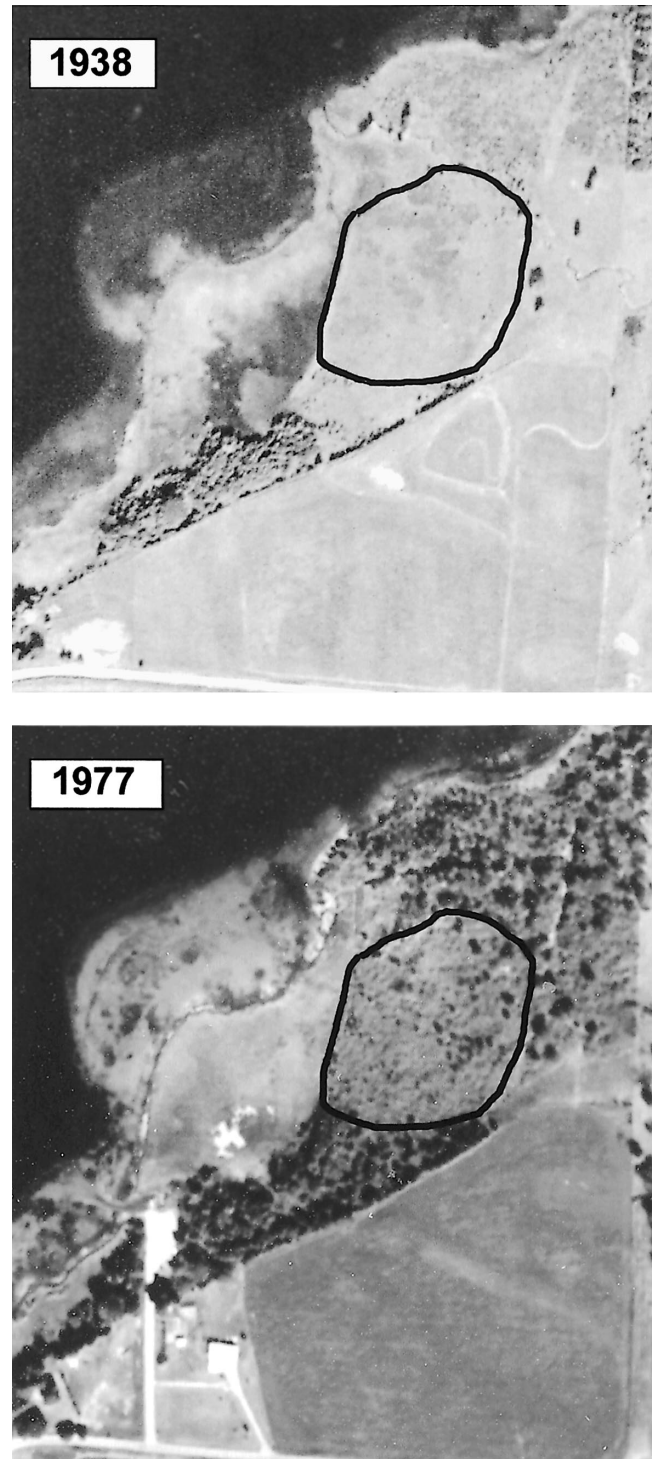


Figure 1. Aerial photos of study site taken in 1938 and 1977, with 1.9-ha shrub carr area delineated in black.

formerly used as pasture. Grazing of wetlands was a common land-use practice in the White Clay Lake watershed (Persson et al. 1983).

The shrub carr normally lacks surface water except during seasonal flooding; the water table is at or near

the soil surface most of the year (Johnston 1993). The shrub carr receives surface-water input from an unnamed, second-order stream that drains the land from several dairy farms. The stream overtops its banks and floods the wetland during early spring and major runoff events but follows a defined channel during normal and low flow periods. The current stream path loops north of the shrub carr, but inspection of historical aerial photos showed that it formerly flowed through the northeast corner of the shrub carr in the same approximate location from 1938 (the earliest aerial photo date) to 1966 (Johnston et al. 1984b). This location is called the relict stream path.

The Shawano County Soil Survey identifies the entire wetland complex as Fordum loam (coarse-loamy, mixed, nonacid, frigid Mollic Fluvaquents), a poorly to very poorly drained soil found on nearly level flood plains and drainageways (Gundlach et al. 1982). Soils within the wetland complex that includes the shrub carr were mapped and described in detail by Johnston et al. (1984b) and include Aquents, Aquepts, and Saprists overlying glacial deposits. Soils within the shrub carr portion of the wetland are primarily Endoaquepts, with an 18-cm histic (organic) O horizon overlying glaciolacustrine deposits (Johnston et al. 1984b). Soils along the northeast edge of the shrub carr are Thapto-Histic Fluvaquents, with up to 60 cm of alluvium deposited over the O horizon.

Dating of soils within the shrub carr provided evidence of their recent sedimentation history. Soil surface deposits had been dated at multiple locations throughout the wetland using  $^{137}\text{Cs}$ , a method that uses decay of radionuclear fall-out products from atmospheric weapons testing during the 1960s to determine sediment age (Johnston et al. 1984a). This dating showed that the overlying alluvial layer of the Thapto-Histic Fluvaquents had been deposited primarily during the latter half of the 20<sup>th</sup> century, a period of agricultural intensification in the region. Also, recent sediments were not uniformly distributed across the shrub carr surface but were thickest in low natural levees adjacent to the relict stream path (maximum deposition rate = 2.4 cm/yr, average deposition rate = 1.3 cm/yr), the location of the Thapto-Histic Fluvaquents. The Endoaquepts were soils more than 40 m away from the relict stream bed that lacked surficial alluvium. Coupled with a detailed elevation survey conducted within the wetland, these data indicated that the wetland surface had been level (with some micro-relief) prior to the deposition of these new alluvial deposits over the pre-agricultural soil surface, but that the alluvium created low natural levees adjacent to the channel of the relict stream that deposited them (Johnston et al. 1984a). In this paper, the Endoaquepts are henceforth referred to as "histice surface soils" and the

Thapto-Histic Fluvaquents are termed "alluvial surface soils."

### Soil Sampling

A systematic sampling grid of 14 points spaced at regular 30.5-m intervals was established within the shrub carr, and soil samples were collected at each grid point. Samples of the surface soil were collected to a depth of 15 cm at each point on the sampling grid. The samples were analyzed for inorganic P (Murphy and Riley 1962) following extraction with HCl and NaOH, and total P following perchloric acid digestion (Mehta et al. 1954). Nitrogen concentrations were determined by Kjeldahl distillation following extraction with 2M KCl for ammonium- and nitrate-N, and digestion with sulfuric acid, potassium sulfate, and selenium for organic-N (Black et al. 1965). Organic matter content was determined by loss on ignition in a muffle furnace at 400°C for 6 hr. Soil bulk density was determined by volumetric sampling. All nutrient concentrations were multiplied by bulk density to convert to per-volume units. Details of soil sampling and analysis methods are described in Johnston et al. (1984a).

The location of a relict stream channel within the shrub carr had been previously mapped from 1966 historical aerial photos using a Bausch and Lomb Stereo Zoom Transferscope (Johnston et al. 1984a); this map was used to compute distances between the soil sample points and the relict stream. A detailed topographic map of the shrub carr (15-cm contour intervals) had been compiled using standard surveying and drafting techniques (Johnston et al. 1984b) and was used to determine the elevation of sample points.

Because many of the soil variables were correlated with each other, a principal components analysis was used to reduce the soil variables to a smaller number of independent factors. Analysis of variance was used to compare soil and vegetation characteristics between the two groups of sample points distinguished by the principal components analysis.

### Woody Plant Cover

Because the objective of the research was to relate vegetation and soil characteristics, the sample design for characterizing woody plant cover was established to coincide with the pre-existing grid of soil sample points. Woody plant cover was measured using the line-intercept method (Canfield 1941), in which the vertical projection of the plant canopy onto a length of fiberglass survey tape was recorded by species. Methods of transect establishment, transect segmentation, and data analysis followed Buell and Cantlon (1950). Similar to the methods of Buell and Cantlon,

Table 1. Synonymy of shrub taxa in the White Clay Lake wetland. Original taxon = species listed in Johnston 1982, ITIS = Integrated Taxonomic Information System, BONAP = Biology of North America Program (Kartesz 1994).

Original Taxon	Accepted by ITIS?	Accepted by		Synonymous Taxon	Common Name
		BONAP?			
<i>Cornus obliqua</i> Raf.	Yes	No		<i>Cornus amomum</i> Mill.	silky dogwood
<i>Cornus stolonifera</i> Michx.	No	No		<i>Cornus sericea</i> spp. <i>sericea</i> L.	redosier dogwood
<i>Salix bebbiana</i> Sarg.	Yes	Yes		—	Bebb's willow
<i>Salix discolor</i> Muhl.	Yes	Yes		—	pussy willow
<i>Salix interior</i> Rowlee	Yes	No		<i>Salix exigua</i> Nutt.	sandbar willow
<i>Salix lucida</i> Muhl.	Yes	Yes		—	shining willow
<i>Salix petiolaris</i> Sm.	Yes	Yes		—	slender willow
<i>Salix rigida</i> Muhl.	No	No		<i>Salix eriocephala</i> Michx.	Missouri willow

who were trying to relate shrub and tree layer data, data were collected in a series of parallel transects spaced a uniform distance apart, and data were analyzed by dividing the transects into a series of end-to-end segments. In this study, woody plant cover data were collected along four parallel north-south transects (i.e., four north-south rows of grid points) spaced 30.5 meters apart from each other. Each transect spanned the length of the shrub carr and was 91 or 122 meters in length. Plant data were analyzed by dividing the transects into three to four 30.5-m end-to-end segments, each segment centered over a soil sample point, for a total of 14 segments. Transects were used as means of segment placement only; no data were summarized by transect.

Data computed for each segment included length of cover by individual woody species, cumulative cover by all shrub species, length of shrub overlap (i.e., one shrub species overlapping another), length of open space, and shrub richness (i.e., number of species per segment). In addition, the following data were summarized for the entire length of line measured: cover by any shrub, cover by any tree, total cover by any tree or shrub, species proportion of total cover, percent frequency by species (i.e., proportion of segments in which the species occurred), open space, cumulative cover by all shrub species, cumulative cover of all woody species, overlap of trees over shrubs, and overlap of shrubs over shrubs. Due to species overlap, the length of "total cover by any tree or shrub" was less than "cumulative cover of all woody species" because species differences were ignored in the former but not in the latter. This is consistent with established vegetation analysis conventions, in which stratification or multiple layering of vegetation can cause total cover for all species in a community to exceed 100 per cent (Grieg-Smith 1957, Kent and Coker 1992).

In addition to line-intercept data, the height of each shrub clump (i.e., a contiguous patch of shrub stems of the same species) was measured using a surveying

rod. Mean shrub height per clump was computed by species.

Woody plants were identified to species using flower, fruit, and vegetative characteristics. Identification of willow species was based on Argus (1964), but taxa were updated (Table 1) to nomenclature currently accepted by the Integrated Taxonomic Information System (ITIS: [www.itis.usda.gov](http://www.itis.usda.gov)). Species identified by vegetative characters were confirmed using flowering material from voucher specimens in the Wisconsin State Herbarium that had been collected in a comprehensive plant survey conducted the previous growing season (Johnston 1982). Wetland indicator status for each plant species was determined from the "National List of Vascular Plant Species That Occur in Wetlands" (1996 update of Reed 1988, downloaded from <http://www.nwi.fws.gov/bha/>), using indices for the North Central region. The "Coefficient of Conservatism" (C) assigned by a committee of Wisconsin botanists (<http://www.botany.wisc.edu/wisflora/WFQA.html>) was also compiled for each woody plant species. The C value ranges from 0 to 10 and represents an estimated probability that a native plant is likely to occur in a landscape relatively unaltered from pre-settlement conditions, with higher values assigned to plants with demonstrated fidelity to a remnant natural community (Swink and Wilhelm 1994).

## RESULTS

### Vegetation

Eight shrub taxa were encountered along the line transects (Table 1). Unaccepted names for the shrub species originally identified as *Cornus stolonifera* Michx. and *Salix rigida* Muhl. were corrected to their ITIS-accepted names, *Cornus sericea* spp. *sericea* L. and *Salix eriocephala* Michx., respectively. Synonyms are also listed in Table 1 for two ITIS-accepted species (*Cornus obliqua* Raf. and *Salix interior* Rowlee) that

Table 2. Summary of total values for woody plant cover, expressed as length of line intercepted and percent of total line length. Note that "total cover by any tree or shrub" is less than the sum of "cover by any shrub" plus "cover by any tree" due to overlap by trees over shrubs and that "cumulative cover, all woody species" exceeds 100% due to species overlap (trees over shrubs, shrubs over shrubs).

Measurement	Length, m	% of Total Line Length
Cover by any shrub	315	73.2%
Cover by any tree	55	12.8%
Total cover by any tree or shrub	323	75.2%
Open space	106	24.8%
Total line length	429	100.0%
Cumulative cover, all shrub species	393	91.6%
Cumulative cover, all woody species (= cover by any tree + cumulative cover, all shrub species)	448	104.4%
Overlap, trees over shrubs	47	10.9%
Overlap, shrubs over shrubs	79	18.3%

are not accepted by the Biology of North America Program (BONAP: Kartesz 1994), which is the basis for the "National List of Vascular Plant Species That Occur in Wetlands."

Shrubs covered 73% of the 429 m of line transect measured (Table 2). Trees covered 55 m of line but overlapped the shrub layer for all but 8 m, so that cover by any woody plant was only slightly greater (75%) than cover by shrubs alone. Portions of open transect (i.e., not covered by woody plants) were mostly sedge meadow. Adding the cumulative cover by all woody species (448.4 m) to the length of open space (106.4 m) yielded a total of 555 m, which due to spe-

cies overlap was 126 m longer than the 429 m of transect measured.

Redosier dogwood (*Cornus sericea* ssp. *sericea*) was by far the most abundant shrub species, occurring in all transect segments and constituting 62% of total cover (Table 3). Another dogwood species, *Cornus obliqua* Raf., was uncommon. Six species of willow shrubs (*Salix* spp.) were present in the shrub carr, with slender willow (*Salix petiolaris* Sm.) and pussy willow (*Salix discolor* Muhl.) occurring in >71% of all line segments and providing 10% and 7% of total cover, respectively. Average shrub height was ~2 m for the *Cornus* species, ~3 m for *Salix petiolaris*, *S. interior*, and *S. lucida* Muhl., and >4 m for *Salix discolor*, *Salix eriocephala*, and *Salix bebbiana* Sarg. In addition to the six willow species in the shrub carr, there were three willow species found elsewhere in the White Clay Lake wetland: *Salix amygdaloides* Anderss., *S. candida* Fluegge, and *S. nigra* Marsh (Johnston 1982).

The four species of trees present were paper birch (*Betula papyrifera* Marsh.), green ash (*Fraxinus pennsylvanica* Marsh.), white cedar (*Thuja occidentalis* L.), and American elm (*Ulmus americana* L.) The high percent frequency of *Fraxinus pennsylvanica* (43%) was not surprising given its dominance in a green ash swamp immediately north of the shrub carr, but its proportion of total cover in the shrub carr was only 5% because the individual trees were young and had small canopies.

All of the woody plant species present were wetland indicators (Table 3). All of the shrub species were either FACW or FACW+. Of the tree species, *Betula papyrifera* was classified as FACU+, *Ulmus americana* was classified as FACW-, and *Fraxinus penn-*

Table 3. Measurements and indices for woody species present. "% of cumulative woody cover" = cover by an individual species ÷ cumulative cover of all woody species, expressed as a percentage. \* = wetland indicator status of synonymous species shown.

Species	% of Cumulative Woody Cover	% Frequency	Mean Shrub ht./clump, m	Coefficient of Conservatism	Wetland Indicator
<i>Cornus obliqua</i> *	0.1%	7%	1.8	4	FACW+
<i>Cornus sericea</i> ssp. <i>sericea</i>	62.2%	100%	2.2	3	FACW
<i>Salix bebbiana</i>	4.1%	57%	4.3	7	FACW+
<i>Salix discolor</i>	7.4%	79%	4.1	2	FACW
<i>Salix interior</i> *	0.1%	7%	3.2	2	FACW+
<i>Salix lucida</i>	0.5%	7%	3.4	5	FACW+
<i>Salix petiolaris</i>	10.3%	71%	3.1	6	FACW+
<i>Salix eriocephala</i>	2.9%	14%	4.6	4	FACW
<i>Betula papyrifera</i> Marsh.	1.7%	14%	—	3	FACU+
<i>Fraxinus pennsylvanica</i> Marsh.	4.8%	43%	—	2	FACW
<i>Thuja occidentalis</i> L.	3.8%	29%	—	9	FACW
<i>Ulmus americana</i> L.	2.0%	21%	—	3	FACW-
Total	100.0%				

Table 4. Principal components (PC) analysis of soil physical and chemical characteristics. Numbers in bold are  $\geq|0.5|$ .

	PC 1	PC 2	PC 3
Eigenvalue	5.47	1.36	1.17
Variance explained	0.608	0.151	0.130
Variable loadings:			
Reactive P	<b>-0.968</b>	0.120	-0.121
Bulk density	<b>-0.967</b>	-0.043	0.035
Organic P	<b>-0.930</b>	-0.106	-0.270
Elevation	<b>-0.927</b>	-0.194	0.067
Organic matter %	<b>0.868</b>	-0.293	-0.244
NO <sub>3</sub> -N	<b>-0.729</b>	-0.071	0.228
Distance from relict stream	<b>0.638</b>	<b>-0.609</b>	0.134
Organic N	-0.317	<b>-0.669</b>	<b>-0.563</b>
NH <sub>4</sub> -N	0.283	<b>0.623</b>	<b>-0.561</b>

*sylvanica* and *Thuja occidentalis* were classified as FACW.

Coefficients of conservatism (Table 3) for the woody species ranged from 2 (occurring in a broad range of habitats) to 9 (narrow habitat fidelity). Species with high coefficients of conservatism (C) were *Thuja occidentalis* (C = 9), *Salix bebbiana* (C = 7), *Salix petiolaris* (C = 6), and *Salix lucida* (C = 5). Species with coefficients of conservatism of 2 or 3 included both the most and least abundant species in the shrub carr: *Cornus sericea* spp. *sericea* and *Salix interior*, respectively.

#### Soil-Plant Relationships

Principal components analysis of nine soil and physiographic parameters yielded three principal components with eigenvalues  $>1.0$ , which cumulatively explained 89% of the variance in the soil data (Table 4). The first principal component explained 61% of the variance and was negatively related to soil bulk density, phosphorus (reactive P and organic P concentra-

tions), elevation, and NO<sub>3</sub>-N and positively related to soil organic matter content and distance from the relict streambed. The second and third principal components were related primarily to organic N and NH<sub>4</sub>-N concentrations but explained much less of the variance in the soil data (15% and 13%, respectively).

The first principal component distinguished two distinct groups of sample points: alluvial surface soils having organic matter contents less than 30 g/100g and histic surface soils having organic matter contents averaging 56 g/100g (Table 5). The alluvial soils were on slightly elevated natural levees close to the relict stream bed, which had received substantial deposition of silty sediments rich in phosphorus.

Soil properties of the two groups were distinctly different (Table 5). Alluvial surface soils had twice the bulk density and organic P concentrations, nearly three times the reactive P, and 4.5 times the NO<sub>3</sub>-N concentrations of histic surface soils. Analysis of variance comparing mean values for soil and physiographic parameters in the two groups revealed significant differences for all of the parameters that were highly loaded to principal component 1: bulk density, organic matter content, elevation, distance to stream, reactive P, organic P, and NO<sub>3</sub>-N. There were no significant differences between the two groups in soil organic N or NH<sub>4</sub>-N concentrations. Previous research indicated average sedimentation rates of 1.3 cm/yr for alluvial soils and 0.5 cm/yr for soils with histic surfaces (Johnston et al. 1984a).

Comparison of the vegetation characteristics associated with the alluvial surface vs. histic surface soils showed that total shrub cover and overlap was significantly greater on the alluvial soils (Table 6). Shrub overlap averaged 48% on alluvial surface soils vs. only 10% on histic surface soils. Shrub diversity was also greater on the alluvial soils: average shrub species richness was five species on alluvial surface soils as opposed to three species on histic surface soils. This is counterintuitive, given that disturbance is often associated with a decrease in plant diversity.

Table 5. ANOVA comparison of average physical and chemical characteristics of soils by surface type. d.f. = 12, \*\* P < 0.01, \* P < 0.05, ns = not significant.

	Histic	Alluvial	F-value	Significance
Bulk density, Mg/m <sup>3</sup>	0.25	0.57	154.6	**
Organic matter, g/100 g	55.9	23.2	32.8	**
Elevation, m above benchmark	27.1	27.4	136.1	**
Distance to relict stream, m	87	42	4.8	*
Reactive P, mg/L	137	375	99.3	**
Organic P, mg/L	245	511	55.9	**
NO <sub>3</sub> -N, mg/L	1.7	7.5	7.1	*
NH <sub>4</sub> -N, mg/L	15.4	9.6	0.8	ns
Organic N, mg/L	5850	6745	1.2	ns

Table 6. ANOVA comparison of average cover per segment by shrub species on histic surface vs. alluvial surface soils ( $\bar{x} \pm SD$ ). All values except shrub richness expressed as percent cover per segment length. "Other *Salix*" includes *Salix interior*, *S. eriocephala*, and *S. lucida*. Note that average cumulative cover for alluvial surface soils exceeds 100% due to shrub species overlap. d.f. = 12, \*\* P < 0.01, \* P < 0.05, ns = not significant.

	Histic	Alluvial	F-value	Significance
<i>Cornus sericea</i> spp. <i>sericea</i>	64.1 ± 22	67.8 ± 15	0.1	ns
<i>Salix petiolaris</i>	8.4 ± 13	19.1 ± 19	1.4	ns
<i>Salix bebbiana</i>	3.6 ± 4	6.7 ± 6	1.2	ns
<i>Salix discolor</i>	5.3 ± 6	16.9 ± 4	11.3	**
Other <i>Salix</i>	0	17.4 ± 15	18.5	**
Cumulative cover, all shrub species	81.6 ± 28	128.0 ± 40	5.6	*
Shrub overlap	10.3 ± 11	47.9 ± 36	10.5	**
Open space	28.6 ± 21	20.0 ± 15	0.4	ns
Shrub richness, no. of species/segment	3 ± 1	5 ± 2	5.1	*

Three willow species, *Salix interior*, *S. eriocephala*, and *S. lucida*, occurred only on the alluvial surface soils. *Salix discolor* was also significantly associated with, but not restricted to, alluvial surface soils. There was no significant difference between the groups in the cover of *Cornus sericea* spp. *sericea* or *Salix petiolaris*, the two most abundant shrub species. Tree cover and open space were also unrelated to the soil groupings.

## DISCUSSION

Shrub species composition and abundance in the White Clay Lake shrub carr were typical of those in shrub carrs studied elsewhere in Wisconsin. White (1965) measured 122 m of line intercept in each of 76 shrub carrs in southeastern Wisconsin and found shrub covers ranging from 18 to 100% (average cover = 65%). *Salix petiolaris* and redosier dogwood the most common species, present in >88% of the stands, and had respective average percentage intercepts of 33% and 23% (White 1965). *Salix bebbiana* and *S. discolor* occurred in about 70% of White's 76 stands, but their average percentage intercept was only 7.2% and 5.4%, respectively. *Salix lucida* and *S. interior* occurred in <4% of the 76 stands. White (1965) distinguished fen-carrs from other shrub carrs based on an ordination of the stands; fen-carrs were the least disturbed and were dominated by redosier dogwood.

There was a substantial amount of shrub species overlap at White Clay Lake, such that cumulative cover by any woody species was 104% of the total line length, and open space was an additional 25% of total line length. In their study of shrub cover in wetlands of the New Jersey Pine Barrens, Buell and Cantlon (1950) similarly reported that "total shrubby cover is 93 per cent with 30 per cent open space . . . [t]hus 23 per cent of the shrub cover is due to overlap of shrub canopies." In another New Jersey Pine Barrens study,

mean total shrub cover was 102%, with unoccupied space of 18% (Stevenson and Buell 1965). In contrast to the 18.4% shrub overlap in the White Clay Lake shrub carr, White (1965) reported an average shrub overlap of only 5.6%, and he concluded that "one shrub rarely grows beneath another in the shrub-carr." This difference may be due to the relative lack of tall shrubs such as *Salix eriocephala* in White's study. In upland shrub communities of arid regions, where shrub cover is much sparser and vegetation patches are clumped in a matrix of bare ground and litter (e.g., Floyd and Anderson 1987), shrub species overlap is less common to non-existent.

The similarity in open space between histic surface and alluvial surface soils in the White Clay Lake shrub carr suggests that the greater average cumulative shrub cover on alluvial surface soils (Table 6) was due to increased shrub layering, rather than infilling of canopy gaps. The *Salix* species associated with the alluvial surface soils are generally taller in stature than redosier dogwood or *Salix petiolaris*, allowing the latter species to be overtopped. Redosier dogwood has been demonstrated to tolerate experimental shading without substantial loss of biomass (Sheppard and Pellett 1976), so its overgrowth by other shrubs would not be expected to diminish its abundance.

The two most abundant taxa in the White Clay Lake shrub carr, *Cornus sericea* ssp. *sericea* and *Salix petiolaris*, were poor indicators of environmental condition. They were ubiquitous throughout the shrub carr and were equally abundant on histic surface and alluvial surface soils. The best indicators of shrub carr sedimentation were the willow species associated with the alluvial surface soils: *Salix interior*, *S. eriocephala*, *S. lucida*, and *S. discolor*. A number of species in the Salicaceae are known to occur in riparian areas (Krasny et al. 1988a,b, Bendix and Hupp 2000, Hughes et al. 2000, Johnson 2000, Shaw et al. 2001, Karrenburg et al. 2002), but anecdotal reports of soil preferences

are much more common than quantitative studies. White (1965) found redosier dogwood and *Salix petiolaris* growing on mineral soils along streams as well as on histic soils in fen-carrs. Mosseler et al. (1988) reported that “*S. eriocephala* and *S. exigua* Nutt. were most often associated with moist but better-drained sites on floodplains and along fast-flowing streams, while *S. amygdaloides* and *S. lucida* were most commonly associated with poorly drained or permanently inundated wetlands.” Orians et al. (1999) observed that “*S. eriocephala* is most common along rivers, while *S. sericea* is more common in marsh habitats.”

Due to interest in the potential use of willows as biofuels (Ranney et al. 1987), recent research has provided insight into the biology and ecology of *Salix* species that helps explain some of the patterns observed in this study. A field test of biomass production by four *Salix* species on a fertile silty clay loam upland site showed that *S. eriocephala* was most productive, followed by *S. lucida* and *S. exigua*; *S. amygdaloides* was least productive (Mosseler et al. 1988). Fertilization experiments with three of the same *Salix* species showed differences in efficiency of nutrient use: *S. eriocephala* produced 35.1% and 22.5% more plant weight per unit N uptake than *S. exigua* and *S. lucida*, respectively (Simon et al. 1990). These findings are consistent with the findings of this study that *S. eriocephala* was the tallest shrub present and was restricted to nitrate-rich soils.

Although this study did not investigate ecological mechanisms of species segregation, possibilities include differences in the spatial distribution of soil moisture or aeration conditions, germination conditions, soil fertility, and soil mycorrhizae. Distribution patterns of several Salicaceae were observed by Krasny et al. (1988a) within river floodplains in Alaska. They reported that only *Populus balsamifera* L. and *Salix interior* were commonly found on sandy (xeric) sites, *Salix interior* and *Salix alaxensis* (Anderss.) Cov. were more common than *P. balsamifera* on frequently inundated sites, and all three species were found on silty (mesic) sites. Germination studies showed that vegetative reproduction differences related to soil moisture and texture provided the best explanation of these field-observed patterns: colonization of dry sandy sites by *Populus balsamifera* and *Salix interior* was almost exclusively by root suckering, whereas *Salix alaxensis* did not invade these sites due to its inability to root sucker. Colonization of mesic silty sites was almost exclusively by seed, but there were few significant differences among the species in number of germinants on mesic silty soils (Krasny et al. 1988a). In the White Clay Lake shrub carr, sediment deposition events may provide a litter-free soil surface more conducive to *Salix* germination; the histic surface soils

were covered by grass and leaf litter that might inhibit germination.

Available nutrients (reactive P, NO<sub>3</sub>-N) were greatest in the alluvial surface soil at the White Clay Lake shrub carr, suggesting that better plant nutrition promotes increased shrub productivity and diversity. Willow phosphorus uptake on the slightly elevated alluvial surface soils may also be enhanced by the presence of soil mycorrhizae. Mycorrhizal associations are known to be important to plant diversity in general (Bever et al. 2001) and *Salix* phosphorus uptake in particular (Marshall and Pattullo 1981), but mycorrhizal survival is poor in constantly waterlogged soils (Koslowski 2002).

Woody plants have several advantages as indicators. Woody biomass is persistent, in contrast to herbaceous species that are annuals or lack persistent identifiable detritus, so that their presence is ephemeral. Many woody species can be identified from flower, fruit, or leaf characteristics, so that a single visit to a wetland sometime during the growing season is sufficient to make a reliable determination. Some woody plants are distinctive enough to be detected from a distance, providing the potential for using remote sensing for identification.

The use of *Salix* species as indicators is complicated by several factors, however. First, *Salix* species are somewhat difficult to distinguish, particularly if sampled during the summer after dehiscence of flowers and fruits that are the basis of most taxonomic keys. In this study, *Salix* species were observed throughout the growing season to ensure their correct identification, but the use of leaf keys such as the key prepared by Argus (1964) provided fairly reliable taxonomic identification. Second, *Salix* taxonomy has evolved, so that nomenclature used in early studies may differ from currently accepted taxa. Even now, two widely accepted taxonomic authorities (ITIS and BONAP) differ in their acceptance of *Salix* nomenclature (Table 1). Finally, *Salix* species can hybridize in nature, complicating their identification. Viable hybrids have been reported for *S. bebbiana* & *S. petiolaris* (Mosseler 1990), *S. eriocephala* & *S. sericea* (Orians and Floyd 1997, Fritz et al. 1998, Orians et al. 1999), and *S. eriocephala* & *S. petiolaris* (Salick and Pfeffer 1999).

Sedimentation of wetlands alters their ecology and can be irreversibly detrimental to systems not adapted to sedimentation (Werner and Zedler 2002). Direct measurement of wetland sedimentation rates is costly and labor-intensive, requiring repeat visits to a wetland (sediment traps), soil excavation (diagnostic soil horizons), or laboratory analysis of soil samples (radioisotope dating) or tree cores (tree-ring analysis) (DeLaune et al. 1978, Johnston et al. 1984a, Hupp and Morris 1990, Kleiss 1996). The ability to identify sed-

imentation problems before they become widespread would benefit wetland conservation. This research suggests four key *Salix* species that could indicate accelerated sedimentation rates in shrub carrs, based on the research presented and evidence from literature sources. Although studies at other sites would be needed to verify the reliability of these shrub species as indicators of wetland sedimentation, the results appear promising.

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