

## SUCCESSIONAL CHANGES IN A SALIX NIGRA (SALICACEAE) FOREST IN SOUTH-CENTRAL OKLAHOMA

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### ABSTRACT

Periodic samplings of the vegetation of a 30-year-old, 2.02 ha, black willow (*Salix nigra*) forest on the north shore of Lake Texoma in south-central Oklahoma revealed the gradual replacement of *S. nigra* by a mixture of shade-tolerant bottomland hardwoods. Between 1960 and 1976, total tree density (trees/ha) decreased from 882 to 840, and *S. nigra* density decreased from 882 to 544. Mixed bottomland hardwood tree density increased from 0 to 296. Concomitantly, total basal area (m<sup>2</sup>/ha) increased from 25.8 to 53.2, with black willow being the sole contributor to basal area in 1960 and the primary contributor in 1976. The decreased density of *S. nigra* was due to its inability to reproduce in the willow forest. Little change was observed in the species composition of the vine, shrub, and herbaceous stratum, but marked changes were noted for various species.

## INTRODUCTION

Willow Flats is a 30-year-old, 2.02 ha, black willow (*Salix nigra* Marsh.) forest located on the north shore of Lake Texoma approximately 1.7 km west of the University of Oklahoma Biological Station; Marshall County, Oklahoma (R5E, T8S, Sec.7). The forest occurs on Quaternary river-terrace sands at an elevation of 189 m, and, because it lies between the minimum pool elevation (188 m) and flood control levels of the reservoir, periodically floods. Stands of *S. nigra* or *Populus deltoides* are locally common along waterways and around impoundments. Both species are recognized as representative of the pioneer stage of succession in newly exposed areas with fluctuating water levels; the successional changes that occur after their establishment have been described (Shull 1922 and 1944, Barclay 1924, Shelford 1954, Hosner and Minckler 1963, Wilson 1970).

According to local residents, the land on which the forest exists was cultivated, and few willows were present prior to impoundment of the Red River by the U.S. Army Corps of Engineers to form Lake Texoma in 1944-45. The first ecological studies of Willow Flats were conducted in 1960 (Prophet 1960, Penfound 1961). The forest consisted of a pure stand of *Salix nigra*. Subsequent sampling was conducted in 1964 and 1965 (Penfound 1965, Dent 1965, Parks and Barclay 1966), and revealed that *S. nigra* still dominated the canopy, although several other trees were also present. Impenetrable vine growth prevented sampling some areas in the forest.

In the summer of 1976 additional sampling of Willow Flats was conducted. The objective of our study was to describe the vegetation, compare results with previous studies, and document successional changes that had occurred in the intervening years. Johnson (1984) investigated a nearby area and reported that a black willow forest was being replaced primarily by *Celtis laevigata* and *Diospyros virginiana*.

## METHODS

In order to obtain data comparable to that of previous studies, the same sampling methods were employed with minor modifications. The boundaries of the original 0.75 ha rectangular sampling area were established by marking each corner tree with a broad red-painted band (Dent 1965). Three of the four corner trees were relocated, and the position of the fourth was deduced. The sampling area was divided into 186 quadrats (2.0 × 20.24 m each), from which 30 quadrats were randomly selected for sampling.

Trees (≥7.62 cm DBH) and tree saplings (<7.62 cm DBH) were sampled in each quadrat by the arms-length rectangle method of Penfound and Rice (1957). Their method was modified slightly due to the almost impenetrable growth of shrubs and vines in the study area. A 20.24 m cord was used to establish quadrat length and a meter stick to establish width. Species, number of individuals, and diameter-at-breast-height (DBH) were determined for each quadrat. Shrub, vine, and herbaceous species were sampled in a 2.0 × 2.0 m nested quadrat located at the west end of each of the 30 larger quadrats. Species, number of individuals, and percent aerial cover were determined. Aerial cover was estimated using the Braun-Blanquet system, with each cover class being assigned a numerical value (Oosting 1956). The five cover classes and their assigned values were: 0-5% = 1; 5-25% = 3; 25-50% = 5; 50-75% = 7; and 75-100% = 9. Where aerial cover is listed in the tabular

material, the numbers represent the additive values of the cover classes. From these data, density, basal area, and relative importance for trees, and density, aerial cover, frequency, and relative importance for shrubs, vines, and herbs were calculated for each species. Voucher specimens were deposited in the University of Oklahoma Biological Station herbarium. Nomenclature follows Kartesz and Kartesz (1980).

## RESULTS

In 1960 Willow Flats was a forest composed entirely of black willow trees of approximately 15 years of age and averaged 16.5 m (12.5-21.0 m) in height (Prophet 1960, Penfound 1961). Seedlings were absent, and saplings were rare. Seedlings of *Diospyros virginiana* and *Morus rubra* were present. In addition, two other unspecified tree species were observed in the area. In 1965 the canopy still consisted entirely of *S. nigra* (Dent 1965). However, five additional tree-stature species were observed in 1965 (*Morus rubra*, *Zanthoxylum clava-herculis*, *Melia azedarach*, *Celtis laevigata*, and *Ulmus americana*). Saplings of these species, with the exception of *M. azedarach*, plus those of *Maclura pomifera*, *Gleditsia triacanthos*, *Rhamnus caroliniana*, and *Juniperus virginiana* were also found in the quadrats with saplings of *S. nigra*. The black willow saplings were primarily stump sprouts.

In the present study thirteen tree species were found (Tables 1 and 2), and, of these, three occurred only as saplings (*Carya illinoensis*, *C. triacanthos*, and *Z. clava-herculis*). *Salix nigra*, the sole constituent of the canopy for the previous studies, was joined by eight additional tree species as well as several large *Cephalanthus occidentalis* shrubs (Table 1). In general, these additional species coincided with those reported as saplings or seedlings when the forest was in an earlier successional stage (Prophet 1960, Penfound 1961, Dent 1965, Parks and Barclay 1966).

Between 1960 (Prophet 1960) and 1976 total tree density (trees/ha) decreased from 882 to 840 and total basal area ( $m^2/ha$ ) increased from 26 to 53. The density of black willow decreased from 882 to 544 trees/ha, while that of mixed hardwoods increased from 0 to 296 trees/ha. Large dead willows were found in 23.3% (7 out of 30) of the quadrats, explaining, in part, the decrease in willow density. The black willow basal area increased from 26 to 50  $m^2/ha$  during the same time period.

Observed changes in the tree component of Willow Flats are expected if the ecological requirements of resident species are considered. Differences in germination requirements, shade tolerance, and competitive ability have resulted in the succession to a more rich forest than existed in 1960. Species of willow are considered to be very intolerant of shade, while the species that increased in density and/or basal area, i.e., *Diospyros virginiana*, *Celtis laevigata*, and *Ulmus americana* are tolerant to intermediate in their ability to compete in light-limited forests (Baker 1949). In addition, *Salix* species have long been recognized as floodplain pioneers (Shull 1922 and 1944, Barclay 1924, Shelford 1954, Weaver 1960, Lindsay *et al.* 1961, Hosner and Minckler 1963, Wilson 1970.). Germination and seedling establishment of *S. nigra* are dependent upon the availability of open, wet, porous soils directly exposed to the sun (McLeod and McPherson 1973). Germination and establishment involve a release of seeds in the late spring or early summer, dispersal onto muddy shores or into water, a slow retreat of the water after spring rains, and the persist-

tence of a band of very wet, open soil (McLeod and McPherson 1973). Conditions of exposed sites, open soils, and fluctuating water levels existed immediately after the creation of Lake Texoma, according to local residents, and persisted on a smaller scale during the present survey. The uniform size of the black willow trees and the lack of seedlings suggest that *Salix nigra* became quickly established in the Willow Flats area over a period of a few years. Shading by the canopy and subsequent establishment of ground-covering shrub, vine, and herbaceous species prevented the establishment of younger willows.

Detailed comparisons of the shrub and vine communities with previous studies are difficult due to lack of comparable data. In 1960 the shrub stratum was sparse (Prophet 1960, Penfound 1961), consisting primarily of *Cephalanthus occidentalis*. By 1965, *C. occidentalis* was reported (Dent 1965) to be "unusually dense", although its relative frequency (10.4) had decreased considerably from Prophet's (1960) value of 30.2. By 1976, the shrub's relative aerial cover and frequency were low especially when compared to those of various vine species. Oosting (1942) noted a similar decline in *C. occidentalis* concomitant with canopy closure.

In 1960, three vine species (*Rubus trivialis*, *Ampelopsis arborea*, and *Parthenocissus quinquefolia*) were found in the understory of Willow Flats with a total relative frequency of 51.1 (Prophet 1960). By 1965 vines composed 80.9% of the relative aerial cover (Penfound 1965; Table 3). Dense vine growth was also noted in 1965 (Dent 1965, Parks and Barclay 1966). Willow trees were "draped" with *Ampelopsis arborea*, *Smilax bona-nox*, and *Vitis cinerea*, and the understory consisted of a dense cover of *Rubus* spp. and *Toxicodendron radicans* (Parks and Barclay 1966). In 1976 this same phenomenon was observed; thickets and tangles of those species still provided 77.7% of the relative cover for vine and shrub species (Table 4) and were oftentimes impenetrable. Although species composition apparently did not change between 1960 and 1976, vine cover increased dramatically. Illustrative of this change was the growth of *T. radicans* (Table 3). Prophet (1960) and Penfound (1961) made no mention of this species; however, four years later Penfound (1965) reported a relative aerial cover of 9.5%. Dent (1965) noted that dense growth of this species precluded sampling. Its relative aerial cover in 1976 was 21.9%. *Ampelopsis arborea* and *Parthenocissus quinquefolia* also increased in aerial cover and frequency. All of the vine and shrub species encountered are common in bottomland forests of Oklahoma (Rice 1965).

Abundance of vine growth in black willow communities is well documented (Shull 1922, Oosting 1942, Weaver 1960, Wilson 1970), and the vigorous growth of vines in the vicinity of Willow Flats was previously described (Penfound *et al.* 1965a, Penfound *et al.* 1965b, Parks and Barclay 1966). The last study addressed the ecological role that vines play on the north shore of Lake Texoma and suggested that heavy vine growth with concomitant light reduction limits the next successional stage to shade tolerant species. The presence of *Diospyros virginiana*, *MacLura pomifera*, and *Celtis laevigata* in the seedling component of Willow Flats supports their interpretation. During the present study we observed vines bending over and breaking tree seedlings, stems, and branches. Similar observations have been reported from northern (Weaver 1960, Wilson 1970) and southeastern (Oosting 1942) bottomlands. This phenomenon may be important in delaying successional changes.

Twenty-five herbaceous species were sampled in 1976 (Table 5), indicating a

decrease in species richness from 1960, when thirty-six herbs were sampled (Prophet 1960, Penfound 1961). As noted with shrubs and vines, lack of historical data precludes detailed comparisons. Only five taxa were identified in 1960; the remaining 31 species were grouped as "other species". In subsequent studies little or no herbaceous data were collected.

When all species except the five identified in the 1960 study are grouped as "other species", it is clear that herbs had increased in both relative cover and frequency (Table 3). *Hydrocotyle verticillata* and *Polygonum hydropiperoides*, both present in 1960, were still dominant herbs in 1976, along with *Boehmeria cylindrica* and *Leersia oryzoides* (Table 5). These species are characteristic of wetlands and moist bottomland forest habitats.

The relative cover and frequency values of *Diodia virginiana* decreased over the years (Table 3). Two other species, *Panicum hians* and *Eupatorium serotinum*, were not found in samples from the herbaceous stratum in 1976. These three species are typical of more open sites than were present in Willow Flats in 1976; their decrease or disappearance was expected, given the increasingly shady conditions of the forest floor.

A pronounced zonation of *Hydrocotyle verticillata*, *Diodia virginiana*, and *Eupatorium serotinum* along a moisture gradient from wet to dry was noted by Prophet (1960) and Penfound (1961). Distinct zonation was not apparent in 1976, although a distribution of plants along a weak moisture gradient was noted. *Hydrocotyle verticillata*, *Leersia oryzoides*, *Polygonum hydropiperoides*, and *Ptilimnium capillaceum* were most abundant in the lower, wetter areas. Species such as *Teucrium canadense*, *Boehmeria cylindrica*, *Solanum* sp., and *Ipomoea* sp. occurred in higher, drier areas.

## DISCUSSION

Successional changes and the temporal pattern observed in Willow Flats are similar to those described for other floodplain forests (Shelford 1954, Hosner and Minckler 1963, Crites and Ebinger 1969, Wilson 1970, Johnson 1984). Furthermore, the tree and tree-sapling communities include species found in other bottomland forests in south-central Oklahoma (Brumer 1931, Penfound 1948, Rice and Penfound 1956, Rice 1965). As Shelford (1954), Hosner and Minckler (1963), Wilson (1970), and Robertson *et al.* (1978) noted, the pioneer willow community begins to be replaced by other bottomland hardwood species some 30 to 50 years after establishment. Willow Flats was approximately 30 years old at the time of this study.

The changes observed in the vegetation of Willow Flats between 1960 and 1976 suggest the demise of the black willow forest and the development of a bottomland forest similar to others in the vicinity. The inevitable and increasingly rapid disappearance of *Salix nigra* is indicated by the gradual decline in the density of mature trees; the absence of *S. nigra* seedlings or saplings; the lack of open habitats required for seedling establishment; and the appearance and increasing importance of other tree species in the forest canopy. As bottomland forest succession proceeds, species capable of growth in extremely wet soils will eventually dominate. A gradual change in the shrub, vine, and herbaceous components of Willow Flats is also expected as the canopy cover increases and light becomes increasingly limiting.

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Table 1. Tree species ( $\geq 7.62$  cm DBH) encountered in 1976 ranked according to decreasing relative importance.

Species	Density (stems/ha)	Basal area (m <sup>2</sup> /ha)	Relative Importance
<i>Salix nigra</i> Marsh.	543.6	49.97	79.36
<i>Diospyros virginiana</i> L.	164.8	0.95	10.70
<i>Morus rubra</i> L.	24.7	1.14	2.54
<i>Cephalanthus occidentalis</i> L. <sup>a</sup>	32.9	0.14	2.09
<i>Maclura pomifera</i> (Raf.) Schneid.	24.7	0.30	1.75
<i>Celtis laevigata</i> Willd.	16.6	0.24	1.21
<i>Melia azedarach</i> L.	8.2	0.15	0.63
<i>Ulmus americana</i> L.	8.2	0.12	0.60
<i>Juglans nigra</i> L.	8.2	0.07	0.55
<i>Populus deltoides</i> Bartr. ex Marsh.	8.2	0.07	0.55
Totals	840.1	53.15	99.98

<sup>a</sup>Taxon represented by four small trees; other individuals were typical shrubs (see Table 4).

Table 2. Tree seedlings ( $< 7.62$  cm DBH) encountered in 1976 ranked according to decreasing relative importance.

Species	Density (stems/ha)	Basal area (m <sup>2</sup> /ha)	Relative Importance
<i>Diospyros virginiana</i> L.	255.3	81.92	56.03
<i>Celtis laevigata</i> Willd.	57.6	17.04	12.13
<i>Maclura pomifera</i> (Raf.) Schneid.	49.4	19.21	12.05
<i>Carya illinoensis</i> (Wang.) K. Koch	49.4	6.42	7.47
<i>Ulmus americana</i> L.	16.6	3.89	3.13
<i>Melia azedarach</i> L.	16.6	2.69	2.70
<i>Morus rubra</i> L.	16.6	2.39	2.59
<i>Gleditsia triacanthos</i> L.	8.2	3.74	2.20
<i>Zanthoxylum clava-herculis</i> L.	8.2	2.39	1.72
Totals	477.9	139.69	100.02

Table 3. Comparison of relative aerial cover and relative frequency values for vine, shrub, and herbaceous species in 1960 (Prophet), 1965 (Penfound), and 1976 (Phillippi *et al.*), ranked according to decreasing values from 1976.

Species	Relative Aerial Cover			Relative Frequency	
	1960	1965	1976	1960	1976
Vine species:					
<i>Rubus</i> spp.	a	62.9	31.4	27.9 <sup>b</sup>	23.3
<i>Toxicodendron radicans</i> (L.) Kuntz	a	9.5	21.9	a	16.6
<i>Ampelopsis arborea</i> (L.) Koehne	a	8.5	14.2	13.9	19.9
<i>Parthenocissus quinquefolia</i> (L.) Planch.	a	a	8.8	9.3	13.3
Shrub species:					
<i>Cephalanthus occidentalis</i> L.	a	8.3	6.2	30.2	9.0
Herbaceous species:					
"Other species"	20.0	a	68.4	42.8	75.8
<i>Hydrocotyle verticillata</i> Thunb.	29.4	0.0	22.6	16.0	11.1
<i>Polygonum hydropiperoides</i> Michx.	6.1	a	7.9	5.3	10.3
<i>Diodia virginiana</i> L.	25.3	1.0	1.1	13.3	2.8
<i>Eupatorium serotinum</i> Michaux	10.4	1.0	0.0	9.3	0.0
<i>Panicum hians</i> Ell.	8.8	a	0.0	13.3	0.0

<sup>a</sup> Data not available

<sup>b</sup> *Rubus trivialis* according to Prophet (1960).

Table 4. Vine and shrub species encountered in 1976 arranged according to decreasing relative importance.

Species	Density (stems/m <sup>2</sup> )	Aerial Cover	Frequency	Relative Importance
Vine species				
<i>Rubus</i> spp.	3.46	86	0.70	29.53
<i>Toxicodendron radicans</i> (L.) Kuntze	4.26	60	0.50	26.72
<i>Ampelopsis arborea</i> (L.) Koehne	0.43	39	0.60	12.79
<i>Parthenocissus quinquefolia</i> (L.) Planch.	1.17	24	0.40	11.16
<i>Vitis</i> spp.	0.06	26	0.20	5.57
<i>Berchemia scandens</i> (Hill) K. Koch	0.48	13	0.17	5.03
<i>Smilax bona-nox</i> L.	0.17	2	0.07	1.57
Shrub species:				
<i>Cephalanthus occidentalis</i> L.	0.11	17	0.27	5.42
<i>Rosa</i> sp.	0.05	4	0.07	1.43
<i>Cornus drummondii</i> C. A. Mey.	0.025	3	0.03	0.78
Totals	10.215	274	3.01	100.00

Table 5. Herbaceous species encountered in 1976 arranged according to decreasing relative importance.

Species	Density (stems/m <sup>2</sup> )	Aerial Cover	Frequency	Relative Importance
<i>Hydrocotyle verticillata</i> Thunb.	17.62	60	0.40	28.97
<i>Boehmeria cylindrica</i> (L.) Sw.	3.83	61	0.63	17.35
<i>Leersia oryzoides</i> (L.) Sw.	3.93	35	0.23	10.48
<i>Polygonum hydropiperoides</i> Michx.	2.69	21	0.37	8.76
<i>Ptilimnium capillaceum</i> (Michx.) Raf.	0.76	16	0.20	4.62
<i>Teucrium canadense</i> L.	0.56	10	0.23	3.94
<i>Cynodon dactylon</i> (L.) Pers.	1.51	9	0.10	3.58
<i>Cocculus carolinus</i> (L.) DC.	0.14	9	0.17	2.84
<i>Verbesina</i> sp.	0.33	7	0.17	2.78
<sup>a</sup>	a	a	a	a
Totals	33.13	265	3.61	99.99

<sup>a</sup>Other species found with densities <0.33 stems/m<sup>2</sup>, cover <7, frequency <0.17, and relative importances <2.78 were: *Carex* sp., *Solanum* sp., Unidentified umbellifer, *Commelina erecta* L., *Diodia virginiana* L., *Ipomoea* sp., *Conyza canadensis* (L.) Cronq., *Samolus valerandi* L., Unidentified composite, *Panicum* sp., *Lactuca* sp., *Physalis* sp., *Acalypha* sp., Unidentified composite, *Scirpus* sp., *Juncus* sp.