AN AUTECOLOGICAL STUDY OF *SALIX NIGRA*, ESPECIALLY FACTORS THAT MIGHT LIMIT ITS DISTRIBUTION

By

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CHAPTER I

INTRODUCTION

Since 1899 when Cowles reported on sand dune succession around Lake Michigan, willows[1] have been known to be pioneer plants in succession around bodies of water. For this reason it has been supposed that the willow requires large quantities of water which are only available around permanent bodies of water. Cowles (1899) reported *Salix* as a pioneer in Michigan sand dune succession, but also noted that the willow shows an unexpected independence of soil moisture. Other studies of succession have placed the willow around man-made reservoirs (Hall and Smith, 1955), on flood plains of meandering rivers (Hosner and Minckler, 1963; Ware and Penfound, 1949; and Hefley, 1937), and beginning erosion channels (Weaver, 1960). In studies by Weaver (1960) and Hosner and Minckler (1963) it was noted that willows were found on newly formed land consisting of soil deposited by water, implying willows required high soil moisture levels. Also associating willows further with high water requirements were reports of high willow mortality during severe drought. Albertson and Weaver (1945) reported on an extended drought in Kansas and Nebraska which killed

[1]In this paper "willow" is used as a common name for any member of the genus *Salix*. "Black willow" refers to *Salix nigra*, the species under study here.

89% of all willows present. Brink (1954) in British Columbia reported that old willows were not able to survive severe flooding although the younger trees survived. All this seems to indicate that willows do indeed require high levels of water.

Byer (1969) recently found that some bog plants do not require bog conditions, thus calling into question the concept of assuming that conditions associated with a species are required by it.

In this study, environmental factors associated with the moisture regimen were examined to determine the degree to which this factor might limit the distribution of Salix nigra Marsh.[2] Characteristics of the soil in and near black willow stands were also examined, since they may be a factor in limiting the distribution.

Voucher specimens are deposited in the Oklahoma State University Herbarium (OKLA.).

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[2]Scientific nomenclature according to Waterfall, 1966.

CHAPTER II

LITERATURE REVIEW

Salix nigra is commonly found on the wet or moist soils along the banks of lakes and streams. It is shade intolerant and is usually found in almost pure stands on exposed sites. Young stands have no understory vegetation but with increasing age a dense vegetation develops. Reproduction of black willows is entirely by seeds. The most common growth form is a tree about thirty feet tall with multiple stems. The main branches are about fifteen feet above the forest floor and no "weeping" occurs.

The roots of black willow are able to survive in water saturated soil (Cannon and Free, 1917; Cannon, 1920; and Hosner and Boyce, 1962). Cannon and Free (1917) suggested that the roots were conductiong anaerobic respiration. Leyton and Rousseau (1958), in a study of *Salix atrocinera*, concluded that the roots were receiving an internal source of oxygen either pumped from above through the stem or by oxidation of some compound in the roots. Although the roots can grow in saturated soil, they respond to the lack of soil atmosphere by changing their growth habit. Kramer (1951) in a paper on injury to plants by flooding, noted that plants which can produce adventitious roots quickly were least subject to injury. Weaver and Himmel (1930) showed that production of adventitious roots from cuttings of *Salix pendula* occurred at oxygen levels as low as 1 ppm. Below this no rooting occurred. In its natural habitat the willow frequently has portions of its stem covered by newly deposited soil. Cowles (1899) noted that when this occurs the newly buried portion of the stem produced adventitious roots.

The seeds of wet habitat plants and their germination requirements have been studied by many people. Bedish (1967) and Sifton (1959) have shown that the cattail, Typha latifolia, was dependent on inundated soils for germination. Wilson (1970) has shown seeds of Populus deltoides, cottonwood, to germinate only on wet, recently stabilized soil. Moss (1938), Nakajima (1921,1926), Mayer and Poljakoff-Mayber (1963), and Ware and Penfound (1949) have shown that various other willows have a short viability period of one to three weeks and require very special conditions for germination. Nakajima (1921,1926) showed that storage conditions of moderately dry air below 25°C increased the length of viability of willow seeds greatly. Yanchevsky (1904), as reported by Moss (1938), described the early morphology of the seedling of some species of Salix and Populus. He reported the presence of long delicate hairs between the root and hypocotyl, and indicated that this was the primary absorptive organ for the young seedling. The cotyledons and hypocotyl develop rapidly, but the root develops very slowly. Therefore, these absorptive hairs were very critical in seedling survival. He also reported that the soil must be moist for at least one week following germination for survival of the seedling. If the soil dried or was disturbed, the hairs were injured and the seedling died. This appeared to be a critical stage in the survival of the young seedling.

Once the critical stage was past, the seedling becomes very tolerant. Hosner (1958, 1960) reported that a high percent of willow seedlings survived thirty-two and thirty days of complete inundation, and following these treatments, recovered rapidly to assume normal growth. Hosner and Boyce (1962) classified the black willow seedling as tolerant of saturated soil conditions. They listed three mechanisms of tolerance by seedlings. They were: "1) ability of established roots to continue to grow and function under poor aeration, 2) formation of adventitious roots at and above the root collar, and 3) drought resistance of stems and leaves". This drought resistance was also noted noted by Cowles (1899). Hosner and Minckler (1960) noted that the seedlings only occurred on open areas directly exposed to the sunlight and devoid of vegetation and litter. When these conditions have been lost due to successional changes, no seedlings were found (Penfound, 1960; Hefley, 1937).

CHAPTER III

DESCRIPTION OF STUDY AREA

A stand of black willows on the the margin of a pond in the northeast corner of the Oklahoma State University Ecology Preserve was used for this study. The Preserve is located nine miles west of Stillwater, Payne County, Oklahoma on the south side of State Highway 51. The pond was formed by construction of a dam in 1935. Since that time the north end of the pond has been "silting in" due to a small stream entering the pond from the north. The stand is on the north end of the pond on sandy loam alluvial soils.

Running through the middle of the willow stand is a small intermittent stream. This retains some water throughout the year, but only flows after heavy rains. Bordering the willow stand on the east and west are similar streams, but these only contain water when the pond is at spillway level. The water inundates the lowest part of the willow stand but recedes in dry periods, leaving an area of mud flats below the trees. The study area is shown in Figures 1 and 2.

On the west bank of the pond and bordering the willow stand is a Quercus marilandica-Quercus stellata forest. Higher above the pond the forest diminishes, giving way to prairie. On the east bank, bordering the willow stand is low shrubby vegetation. Above this, prairie vegetation dominates the small knoll. Across a small inlet, prairie vegetation begins almost at the bank and continues up the

Figure 1. AERIAL DIAGRAM OF THE STUDY AREA
Elevational stations are marked with an x.

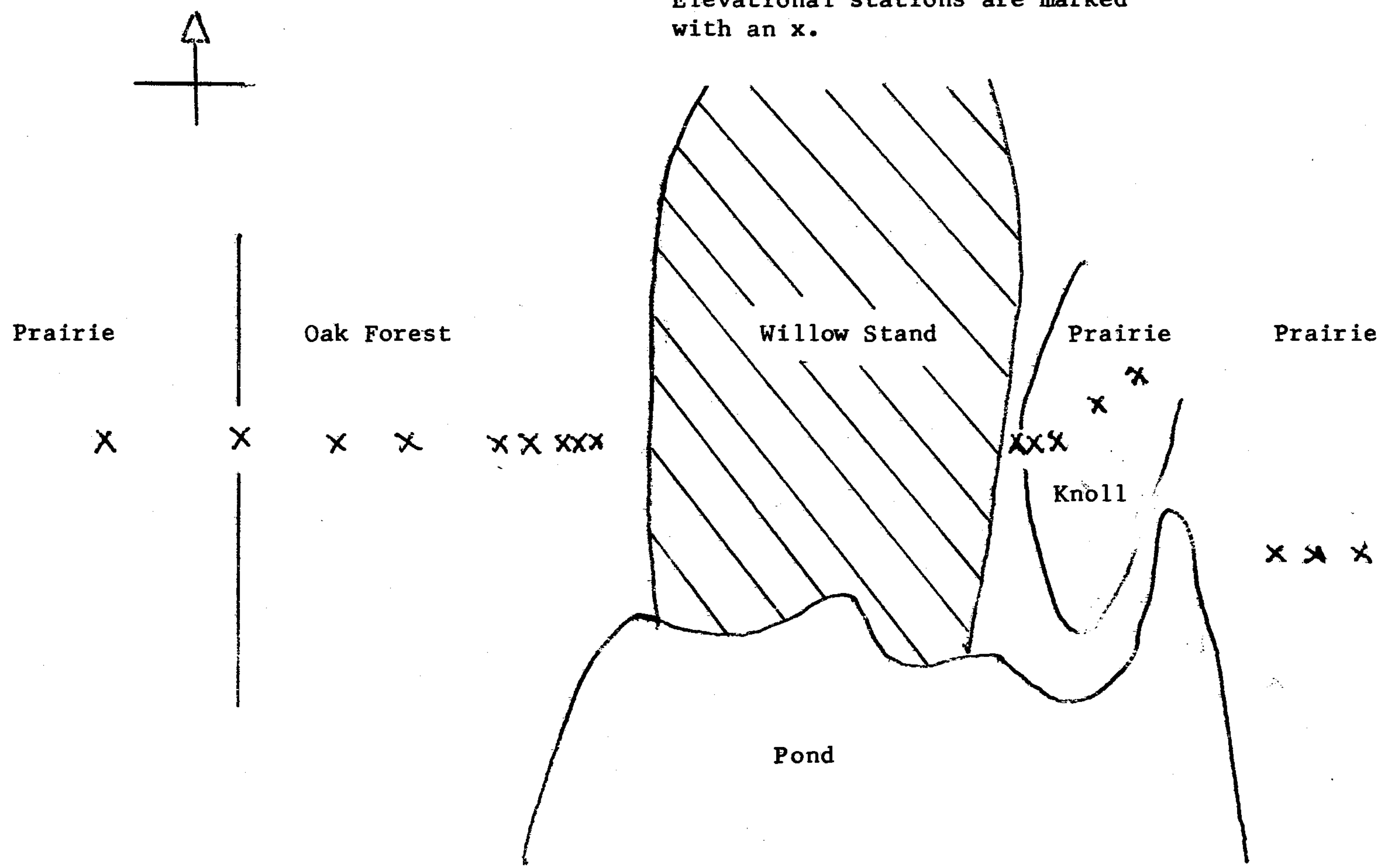
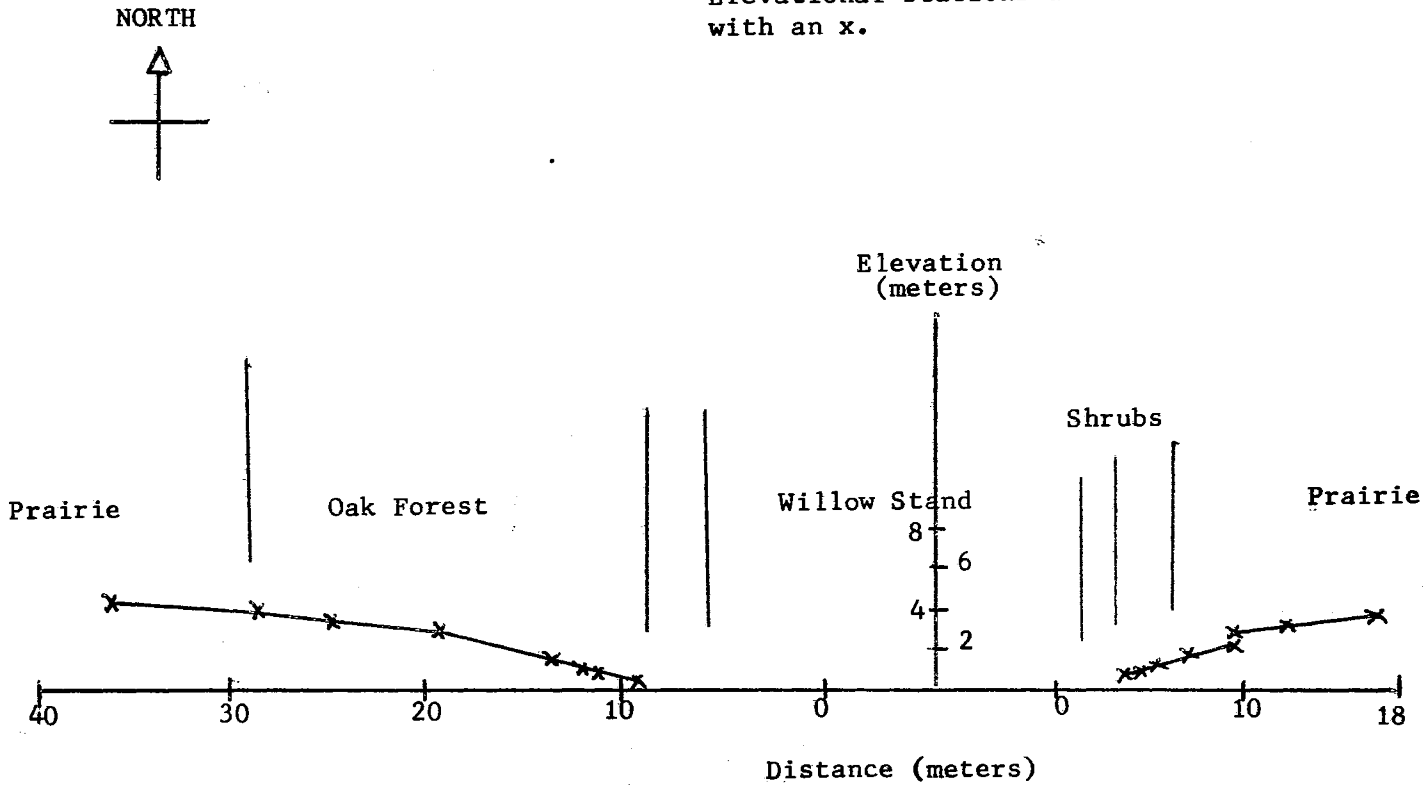


Figure 2. ELEVATIONAL DIAGRAM OF THE STUDY AREA
Elevational stations are marked
with an x.



eastern slope.

The rainfall and temperature data were obtained from the United States Weather Bureau Climatological Data, 1970. The rainfall is summarized in Table I. In the year of the study, 1970, May, June, and August had below average precipitation with July, September, and October above average precipitation. Annual average rainfall is 32.18 inches. The average temperature was below average in June, July, September, and October and above average in May and August. Average annual temperature is 60.8°F.

TABLE I

MONTHLY PRECIPITATION FOR 1970 GROWING SEASON AND

70 YEAR AVERAGE MONTHLY PRECIPITATION

	Precipitation (inches)		Departure
Time	Average	1970	from Average
May	4.62	0.60	-4.02
June	4.24	1.83	-2.41
July	3.53	4.78	+1.25
August	3.21	1.39	-1.82
September	3.38	6.57	+3.19
October	2.78	4.24	+1.46

Elevational transects were established on the slopes on opposite sides of the willow stand. These were measured with a transit and stations placed at 0.0 m, 0.25 m, 0.50 m, 0.75 m, 1.0 m, 1.5 m, 3.0 m, 3.5 m, 4.0 m, and 4.5 m elevations on the west slope. High water level is just below the 0.50 m station. The gap in elevations is due to a rocky outcrop which rises between 1.8 m and 2.8 m. The elevations on the east slope are 0.0 m, 0.25 m, 0.50 m, 0.75 m, 1.0 m, 1.5 m, 2.0 m, 2.5 m, 3.0 m, and 3.5 m. On both transects, the lowest station is within the willow stand, and the highest station in the prairie.

CHAPTER IV

METHODS AND MATERIALS

Soil Analysis

Soil moisture was measured by the gravimetric method. Weekly samples were taken for soil moisture at two depths, 2-12 and 12-22 cm, at each of 20 stations on the transects. This was done through the growing season, 8 May to 20 November, 1970. It was felt that water content by volume would add to the usefulness of the soil moisture information. Therefore the bulk densities of the soils were determined. This is a measure of the compaction or closeness of the soil particles. High values are associated with sandy soils and low values would indicate soils with more silt and clay. By multiplying the bulk density by the water content by weight, the water content by volume is obtained. This represents the volume percentage of water in the soil compared to a unit volume of soil.

The mineral nutrient content of field collected prairie and bottomland soil was determined by the Soil and Water Service Laboratory, Oklahoma State University Extension, by methods described by the Oklahoma State University Agronomy Department (1969).

A mechanical analysis of the soil at the lower depth, 12-22 cm, at each field station was conducted to determine percentages of sand, silt, and clay sized particles. The hydrometer method was utilized as described by Bouyoucos (1927). The lower depths were determined because this is where the greatest root growth would occur.

In the pot experiments, soil was collected from the field and sieved to remove all particles larger than 1/8 inch in diameter.

Propagation of Cuttings

Cuttings were used for all the experiments involving living black willow plants. These were obtained by collecting branches of naturally occurring black willow. In the laboratory these were trimmed to a single stem about 4x40 mm, stripped of all leaves, and placed in aerated water.

After rooting occurred, usually one to three weeks, they were potted in the desired media. Frequently the cuttings would produce leaves and sometimes flowers while producing roots.

Experiment 1 - Field Survival

After the stations were determined, two 50x50 cm plots were established that were equal in elevation to each reference station. One plot of the two was left vegetated, and the other had all vegetation removed and the soil to a depth of 25 cm was sieved to remove any plant parts and particles larger than 0.5 inch in diameter. This method is very similar to one used by Byer (1969). Black willow plants, grown from cuttings, which had been allowed to grow in good conditions for several weeks were transplanted to these plots on 7 May, 1971. The 0.0 and 0.25 m plots in each gradient were under water, and willows were not planted in these plots. Two plants per plot were used and these watered for two weeks to allow them to establish themselves.

Plants that died before the two weeks were over were replaced and watered for two weeks from the date of transplanting. In the vegetated plots, care was taken to avoid disturbance as much as possible. All transplants were observed over the growing season to determine health and survival.

Experiment 2 - Soil-Water Test

In this test, there were two types of field collected soil used, prairie and bottomland. The prairie soil was collected in the upland prairie near the west end of the west transect. The bottomland soil was collected from within the willow stand. Cuttings were potted in approximately equal volumes of soil. These pots which had drainage holes were placed in shorter, wider sealed pots so that water could be added to this reservoir pot and watering be accomplished from the bottom.

These pots were watered every five days with a particular increment of water designed to produce situations from barely moistened to flooded soil. The water increments were 0.25 inch, 0.50 inch, 1.0 inch, 2.0 inch, and 2.75 inch. The two soil types and five water levels gave ten different treatments, each with seven replicates. This and all other laboratory experiments were conducted under banks of lights with illumination varying from 400 to 550 footcandles with a photoperiod of sixteen hours and with temperature ranging from 21 to 23.5°C. This test ran to 79 days. At this time, the soil was washed from the roots and the roots separated from the shoots. Oven dry weight was determined for both the roots and shoots.

Experiment 3 - Soil-Water-Aeration-Nutrient Test

This duplicates experiment 2 and adds to it. All cuttings were potted in 425 grams of prairie or bottomland soil. The soil type and water level treatments were the same as those used in experiment 2. In addition, two new variables were added. In one, bottomland soil and all water levels were used but alternate waterings were with half strength Hoaglands solution. In the other, a sixth water treatment was added to each set. This was 2.75 inches of water with aeration of the wet soil provided by a buried air stone and a pump. This yielded six water level treatments and three soil treatments or eighteen different treatments. There were at least four replicates in each treatment with a maximum of nine. The duration of this experiment was 64 days. The soil was washed from the roots, and the leaves, roots, and stems bagged separately and oven dry weight determined for each.

Experiment 4 - Leaf-Water Relations

Leaves from experiment 3 were used to determine leaf water saturation deficit and percent water content for each of the eighteen treatments. Leaves were from extra plants set up for this purpose. Leaf water saturation deficit was determined by the equation

$$WSD = \frac{\text{Turgid Weight} - \text{Fresh Weight}}{\text{Turgid Weight} - \text{Dry Weight}} \quad X\ 100.$$

Percent water content was determined by

$$\%WC = \frac{\text{Fresh Weight} - \text{Dry Weight}}{\text{Fresh Weight}} \quad X\ 100.$$

These measures were determined twice during the course of the experiment with one leaf from three separate plants used as a sample. The third leaf down from the apex was collected and the fresh weight determined by weighing it immediately. The leaves were then soaked in distilled water for five hours, blotted, and the turgid weight determined. Leaves were then placed in an 105°C oven and dried and the dry weight taken. Techniques and formulas used in this portion of the work were those recommended by Barrs (1968).

Experiment 5 - Seed Germination

This was designed to see if there were viable willow seeds in the soil and where they might be found. On 24 October 1970 at twelve sites within the willow stand and six outside the stand, three 8.5x12 x3 inch blocks of intact soil were collected. The soil from three sites within the stand and three sites outside the stand were put into flats and brought to the greenhouse. Here the flats were placed in larger reservoir tanks where particular water levels could be maintained. Three replicates of each soil type were maintained at each of three water depths; 1 inch, 2 inches, and 3 inches. The 3 inch depth was equal in height to the soil sample.

The remaining flats, constituting an identical set, were placed in wire baskets suspended from a floating frame that was in the pond during the winter. The wire baskets were adjusted to immerse the flats in 1 inch, 2 inch, and 3 inch depths of water. This frame was anchored away from the bank to avoid possible tampering. These were observed for any evidence of viable willow seeds being present.

CHAPTER V

RESULTS AND DISCUSSION

Soil Analysis

It was felt that soil tests were required to discover any differences that might occur between the growing media of the black willow stand and adjacent sites where it does not grow. Soil moisture, bulk density, and mechanical analysis test are shown.

Soil Moisture

The elevational transects did indeed reflect a soil moisture gradient as shown by the summarized values shown in Table II. Complete weekly soil moisture data are given in Appendix A.

TABLE II

SUMMARIZED PERCENT SOIL MOISTURE BY VOLUME VALUES WITHIN FIELD STUDY AREA

Location	May	Time June	July	August
Average of Stations 7 through 12*	19.9	18.9	8.6	
Average of Stations 3 through 6*	25.9	22.9	20.6	19.2
Within willow stand*	34.0	32.7	22.4	15.1

*duplicate samples per station.

Bulk Density

Bulk density of the soil was determined to measure the tightness of the soil. Similar elevational stations were averaged and the results are summarized in Table III. Complete bulk density values are given in Appendix B.

TABLE III

SUMMARIZED BULK DENSITY MEASUREMENTS

Depth(cm)	Location	Stations	Bulk Density (g/cm^3)	Significance*
2-12	Upper west	9-12	1.45 (4)	abcd
2-12	Lower west	3-6	1.34 (4)	a
2-12	Within stand		1.49 (4)	cd
2-12	Lower east	3-7	1.44 (5)	abcd
2-12	Upper east	8-10	1.37 (3)	ab
12-22	Upper west	9-12	1.57 (4)	d
12-22	Lower west	3-6	1.54 (4)	cd
12-22	Within stand		1.62 (4)	e
12-22	Lower east	3-7	1.52 (5)	cd
12-22	Upper east	8-10	1.41 (3)	abc

*Like letters are not significantly different at 5% level.
Parenthesis indicates number of stations averaged.

The values within the stand were higher, indicating that the soil there was less structured than the soil in the transects. There appears to be no differences between transects in the top depth, but in the lower depth the west transect is slightly less structured than the east transect.

Mechanical Analysis

As a further measure of the soil texture, a mechanical analysis was conducted on the soils. Again similar elevational stations were averaged and the results shown in Figure 3. Complete data are given in Appendix C. Only the lower depths were done as this is where most root growth would occur.

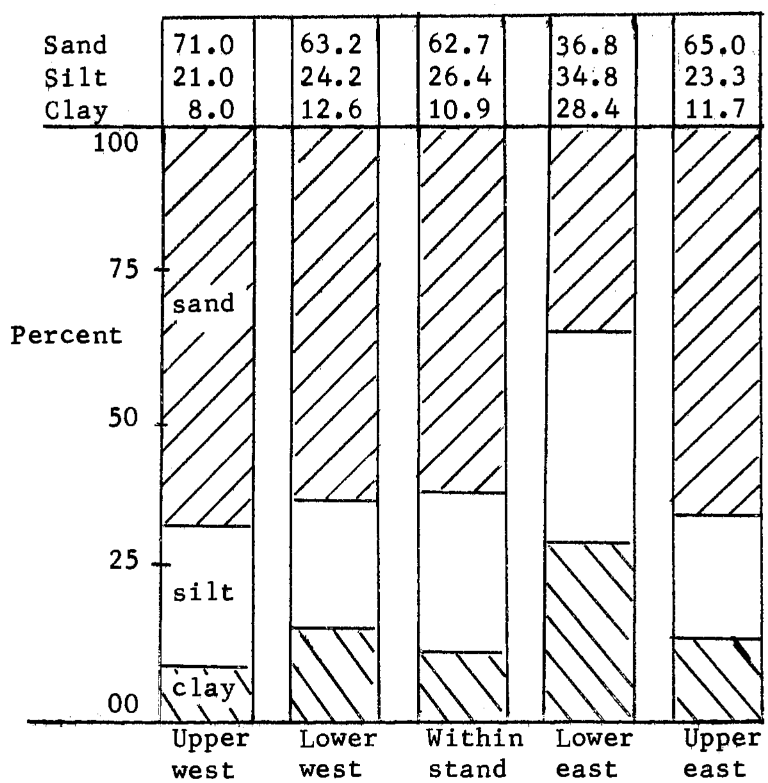


Figure 3. SUMMARIZED SOIL PARTICLE SIZE ANALYSIS FOR 12-22 CM DEPTH, TRIPLICATE SAMPLES

As can be seen from Figure 3, all the soils are similar except the lower east transect, which is higher in clay and silt, and lower in sand content. This increase in clay content is also shown by lower bulk density values for this location shown in Table III. This means that this soil would be much tighter, but it also would hold more water and retain it longer. This is reflected in the soil moisture values in Appendix A.

Experiment 1 - Field Survival

This experiment was designed to test the ability of black willow to survive at various levels of soil moisture under field conditions. The vegetated and unvegetated plots were used to determine if survival was affected by any plant interaction present.

The plants were placed in the field plots on 7 May 1970 and observed to determine length of survival. Table IV shows a monthly summary of the deaths of the willows.

TABLE IV

MONTHLY DEATHS OF FIELD PLANTED BLACK WILLOWS

		Month				Never	
	Stations	May	J	J	A	established	Survivors
Vegetated	3-6(lower)	4	2	7	1	2	0
	7-12(upper)	8	4	2	0	2	0
Cleared	3-6(lower)	1	1	11	1	1	1
	7-12(upper)	0	6	8	0	2	0

As shown in Table IV, survival of black willow was longest in the cleared plots below station 6 and shortest in the vegetated plots above station 6. Generally, lower elevations and the accompanying higher soil moisture were advantageous to survival. Also the plants in the cleared plots survived longer, either because of the mechanical treatment of the soil or lack of interference from other plants.

No physical differences in the soil within the transects were found that might limit black willow distribution. One soil factor that has not been investigated was mineral nutrient content.

Mineral Nutrient Content

Soil was collected from within the black willow stand and on the upland prairie. The soil was sieved to remove any particles larger than 1/8 inch in diameter. This soil was then taken to the Soil and Water Service Laboratory for analysis. The results are shown in Table V.

TABLE V

MINERAL NUTRIENT ANALYSIS OF PRAIRIE AND BOTTOMALND SOIL*

	Soil type			
	Bottomland		Prairie	
Test	value	level	value	level
pH	7.77	-	6.7	-
Organic Matter(%)	0.866	very low	1.43	low
Phosphorus(ppm)	3.66	very low	48.50	high
Potassium(ppm)	73.30	medium	400	very high
NO_3-Nitrogen(ppm)	5	-	5	-

*Analysis performed by the Oklahoma State University Extension Soil and Water Service Laboratory, Values represent average of three samples.

The mineral nutrient content data shows a difference in the bottomland and prairie, but it was difficult to conceive of black willow being limited to the bottomland soil, which has low nutrient levels.

Experiment 2 - Soil-Water Test

This experiment was designed to measure the growth response of black willows under varying water levels in two types of naturally occurring soil. These plants were grown in the laboratory in two soils and five watering regimes for 79 days. They were then harvested and oven dry weight determined for the roots and shoots. The roots are the best indicator of response because they represent all new growth occurring during treatment. Average per plant weights are given in Table VI. Graphic illustration of root growth is seen in Figure 4.

The willows grew significantly better in prairie soil than in bottomland soil, in which they occur naturally. In the prairie soil growth continued to increase as the water level increased. In the bottomland soil, growth was maximum in one inch depth (intermediate) and decreased in wetter or drier treatments. The reason for the difference in growth between the prairie and bottomland soils was thought to be the mineral nutrient content of the two soils. These differences are shown in Table V.

Growth of the black willow was best in prairie soil, which is richer in nutrients, and increasing levels of water. Cannon and Free (1917), Cannon (1920), and Leyton and Rousseau (1958) all report that willow roots are able to respire anaerboically through various postulated mechanisms. This would then explain the good growth which occurred in completely saturated soil.

TABLE VI

AVERAGE WEIGHT IN GRAMS OF BLACK WILLOWS GROWN IN PRAIRIE AND BOTTOMLAND SOIL AT FIVE WATER LEVELS

Soil	Plant part	Water level (inches) (dry) 0.25	0.50	1.0	(flooded) 2.0	2.75	Average for soil type
	Roots	.143	.259	.341	.346	.544	.327 A
Prairie	Shoots	.544	.793	1.126	.913	.949	.867 B
	Total	.697	1.052	1.467	1.259	1.493	1.194 C
	Roots	.103	.076	.163	.137	.091	.114 A
Bottomland	Shoots	.376	.514	.620	.557	.379	.489 B
	Total	.479	.590	.783	.694	.470	.603 C
Average for water level	Roots D	.123	.167	.252	.241	.318	
	Shoots e	.465	.654	.873	.735	.664	
	Total f	.588	.821	1.125	.976	.982	

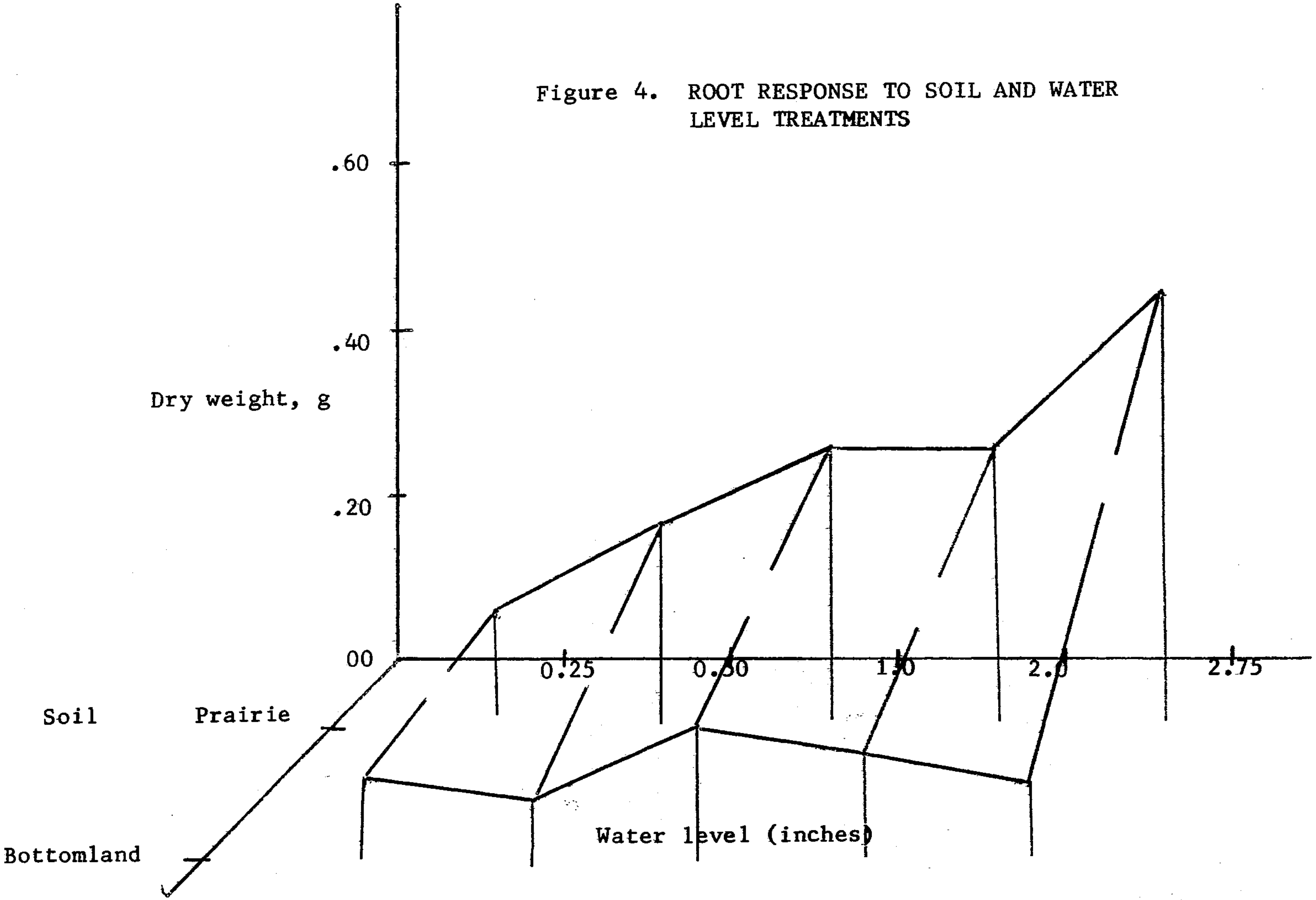
Upper case letters = differences significant at 1% level present.
Lower case letters = differences significant at 5% level present.
Values are averages of seven replicates.

Experiment 3 - Soil-Water-Aeration-Nutrient Test

To further elucidate some of the factors studied in experiment 2, this test was conducted to duplicate the previous experiment and add the new features, nutrition and aeration.

One group of plants potted in bottomland soil had nutrients in the form of half-strength Hoagland's solution added to the soil. Using this third soil type, nutrition and texture of the soil can be examined

Figure 4. ROOT RESPONSE TO SOIL AND WATER LEVEL TREATMENTS



for relative importance in black willow growth. The other factor added to this test was aeration. For most plants, growth in completely saturated soil for a long period would result in poor growth or death of the plant because of lack of oxygen for root respiration. In the previous experiment however, the black willow survived and even did well in completely saturated soil with limited aerobic root respiration. It was decided to see how the plant would respond to completely saturated soil with and without a soil atmosphere being present. The results of this experiment are found in Table VII with graphic illustrations in Figures 5 and 6. Root and leaf weights are shown in the figures because these represent new growth that occurred during the experiment. Stem size was extremely diverse due to the method of propagation and felt not to be an indicator of treatment growth response. Since the stem was a large percent of the total plant, this was reflected in total plant weights, making them not significant.

As in the previous experiment, the prairie soil and high water levels provided the best conditions for growth. The new soil type with bottomland texture and prairie nutrition showed a growth response very similar to that of the prairie soil. This indicates that the nutrient level of the soil was responsible for differences in growth between the two soil types in experiment 2. The black willow was more dependent on a soil nutrient supply than on the texture of the soil.

When air was supplied to the roots under complete water saturation, an increase in growth was found. Although black willow grew when the roots were flooded, even greater growth was achieved when there was an abundance of water and air to assure aerobic respiration of the roots.

TABLE VII

AVERAGE WEIGHT IN GRAMS OF BLACK WILLOW AT THREE SOIL TYPES AND

SIX LEVELS OF WATER INCLUDING ONE THAT WAS AERATED

Soil	Plant part	Water level (inches) 0.25	0.50	1.0	2.0	2.75	2.75*	Average for soil type
	Roots	.08	.15	.13	.14	.24	.07	.14 A
Bottomland	Stems	1.15	1.22	1.21	1.07	.70	.68	.99 x
	Leaves	.05	.10	.18	.13	.20	.05	.12 B
	Total	1.27	1.48	1.53	1.34	1.14	.80	1.25 x
Bottomland	Roots	.08	.13	.16	.35	.21	.33	.22
with	Stems	.59	1.05	1.13	1.00	1.43	1.55	1.11
nutrients	Leaves	.06	.18	.16	.19	.14	.22	.16
added	Total	.73	1.37	1.45	1.55	1.78	2.12	1.49
	Roots	.15	.03	.31	.47	.60	.63	.37 A
Prairie	Stems	.78	.46	.72	.70	.79	1.50	.81 x
	Leaves	.09	.08	.31	.29	.43	.59	.30 B
	Total	1.02	.57	1.34	1.46	1.84	2.74	1.48 x
Average	Roots C	.12	.11	.21	.33	.36	.35	
for	Stems x	.84	.91	1.02	.92	.98	1.24	
water	Leaves D	.07	.13	.22	.21	.26	.30	
level	Total x	1.03	1.15	1.45	1.46	1.60	1.90	

*with aeration. Values are averages of four to nine replicates.
F-Test used for statistical analysis, compare values sharing the same letter.
Upper case letters = differences significant at 1% level present.
Lower case letters = differences significant at 5% level present. x = not significant.

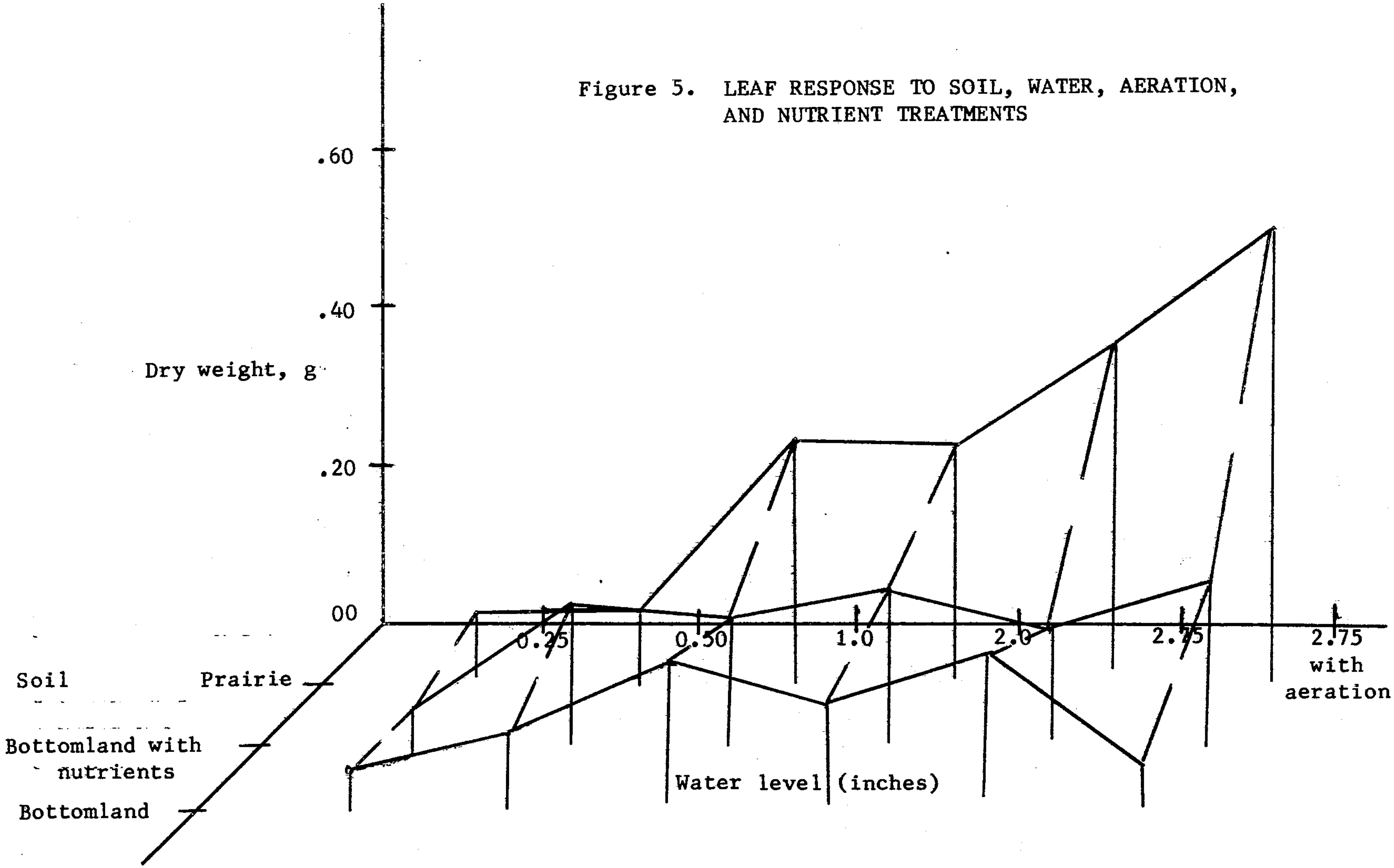
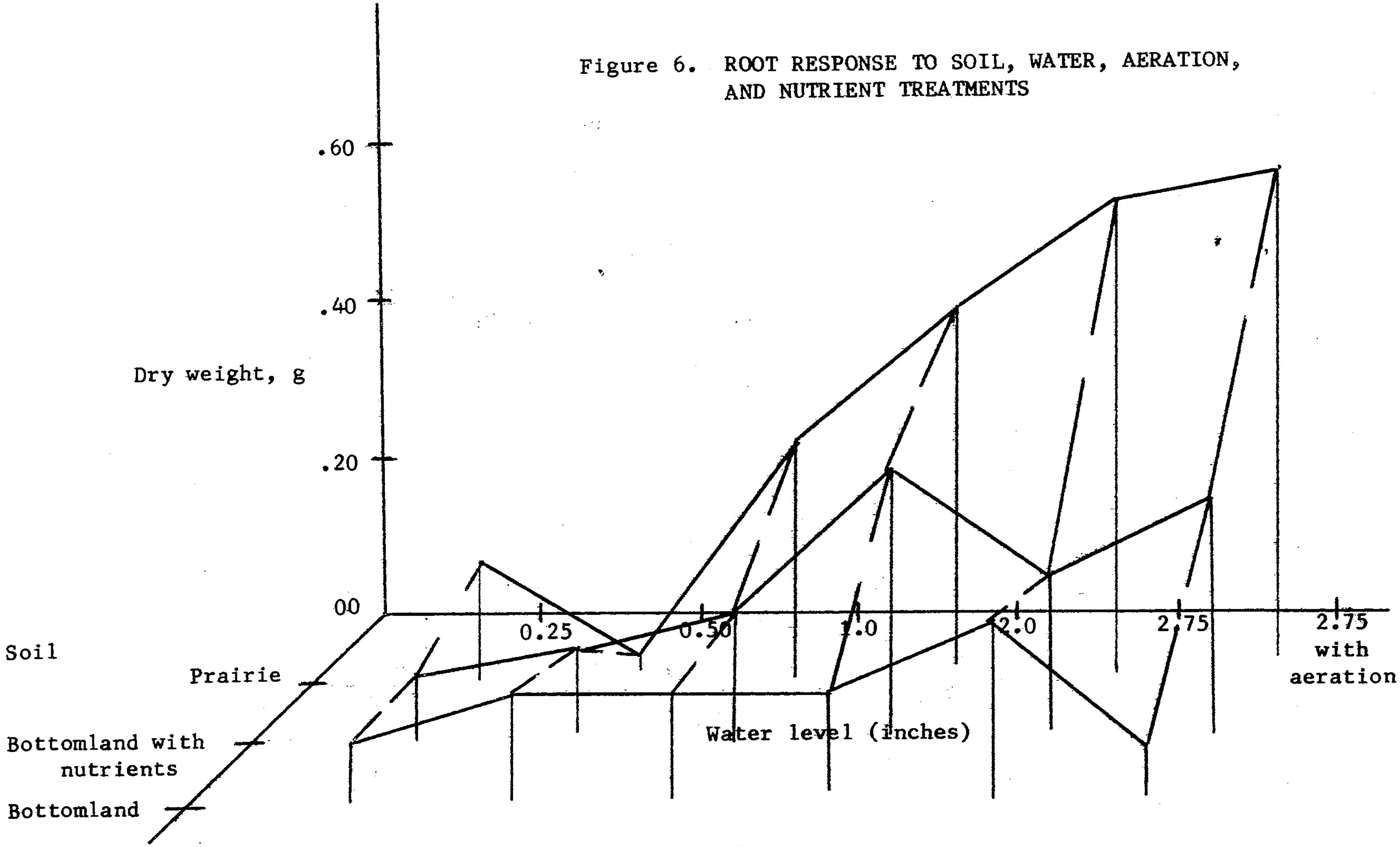


Figure 5. LEAF RESPONSE TO SOIL, WATER, AERATION, AND NUTRIENT TREATMENTS

Figure 6. ROOT RESPONSE TO SOIL, WATER, AERATION, AND NUTRIENT TREATMENTS



This experiment shows that the black willow grows greater in nutrient supplemented soil under complete saturation with aeration.

Experiment 4 - Leaf-Water Relations

The leaf water saturation deficit (WSD) and percent water content (WC) were determined by use of leaves from experiment 3. This was done to determine how the leaves were being affected by the various treatments.

The WSD data, which are shown in Table VIII, indicate that the leaves did not show any treatment effect. Thw WSD for the leaves was essentially the same for all treatments. There were occasional very large WSD values which probably result from poor determination techniques. Although the WSD in the leaves did not vary significantly, the treatment effect may be seen in the amount of leaf tissue maintained on the plant, expressed by leaf weight as shown in Tables VI and VII.

Table VIII also shows that the WC did not vary with the treatment. It should be noted that aeration increased the percent water content in the leaves, probably by increasing water absorption.

Experiment 5 - Seed Germination

This was designed to test for the presence of willow seeds within and outside the willow stand. The flats brought into the greenhouse produced no willow seedlings, although many other seedlings were found. In the field flats, again no willow seedlings were found, but seedlings of woody plants such as elm were found along with many other seedlings. There were no differences in the average number of species and individuals in the soil types or depth of water. The water levels

TABLE VIII

LEAF-WATER RELATION RESPONSE TO THREE SOIL TYPES AND SIX LEVELS OF WATER

Soil	Water level in inches	Water Saturation Deficit, %		Percent water content	
		Date of Test			
		3/29/71	4/29/71	3/29/71	4/29/71
	0.25	8.0	8.44	76	74
Bottomland	0.50	0.55	2.20	86	82
with	1.00	13.10	7.73	87	75
nutrients	2.00	21.69	5.91	82	72
added	2.75	12.69	20.63	86	68
	2.75*	17.56	16.30	86	74
	0.25	18.36	5.41	88	76
	0.50	41.16	3.26	92	69
Bottomland	1.00	14.06	3.69	88	75
	2.00	3.38	7.72	99	77
	2.75	-	8.61	82	69
	2.75*	-	4.14	91	75
	0.25	10.08	0.00	89	74
	0.50	5.69	3.60	94	72
Prairie	1.00	3.24	7.90	93	76
	2.00	-	8.17	93	73
	2.75	13.26	5.61	90	77
	2.75*	-	7.10	91	78

*with aeration
Values are averages of three replicates

maintained should have been favorable for willow seed germination, therefore either there were no seeds in the soil or they were no longer viable. Since an abundant seed fall was observed, this suggests that by the time of year that this experiment was conducted, fall, winter, and early spring, the seeds were no longer viable. Apparently black willow seeds have a rather short viability period, since growing conditions similar to the plant's natural habitat were provided by this experiment.

CHAPTER VI

CONCLUSIONS

Established plants are able to survive in a much broader range of environmental conditions than those in which they are naturally found. For years such plants as Babylon weeping willow and bald cypress, which have been thought to require high levels of water, have been used as ornamentals in landscaping. These plants once they have become established do not show a high water requirement. Black willow is similar to the ornamentals in its ability to survive if artifically established outside its natural habitat. The present research deals with the mechanisms that produce this phenomenon in this wild species.

The bottomland soil had no characteristic that was specifically required by black willow after the seedling stage. The soil texture, as measured by the bulk density and mechanical analysis, was not significantly different from the soil found in adjacent plant communities where black willow was absent. The only soil difference, apart from moisture content, is the mineral nutrient content. The richer prairie soil promoted greater growth than the bottomland soil in experimental plantings. Certainly black willow would not be limited by this poor soil nutrient condition to the bottomland soil.

The growth of black willow was strongly affected by the soil moisture. When grown in dry soil, it produces little leaf and root tissue, but when grown in saturated soil, rapid abundant growth occurs.

Although the greatest growth was attained in very wet soil, it can survives and grow in relatively dry soil. It appears that black willow is capable of surviving saturated soil conditions but does not require these conditions. Since it can tolerate very high soil moisture it can survive in places where inundation occurs often, and at times for prolonged periods.

Soil aeration was also important for growth but when saturated soil conditions exist, black willow was still capable of considerable growth. None of the experimental conditions reported here would restrict the distribution of established plants.

Nakajima (1921,1926), Mayer and Poljakoff-Mayber (1963), and Moss (1938) all found very short viability periods for Salix seeds, although none of them worked with Salix nigra. If these findings and the report of Yanchevsky (1904) on seedling morphology are applicable to Salix nigra, then the length of seed viability and special germination conditions (exposed wet soil for a long period of time) must be the factor that limit its distribution. Black willow does not root sprout and depends entirely on seeds and stem cuttings for reproduction. Since it is dependent on seeds, and the seeds have very critical environmental requirements for germination, black willow is limited to moist or wet environments.

In summary, none of the factors studied here, soil moisture, nutrient content, structure, and aeration of the soil appear to limit the local distribution of black willow. Instead black willow appears to be limited by its seed germination and seedling establishment requirements, which are met on moist or wet soil. These conditions are usually only met around a permanent source of water whose banks would remain wet for an extended period. Thus black willow is found in these places normally. Established plants do not have a high moisture requirement and hence could live in a much broader range of environmental conditions than restricted to by the seedlings.

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APPENDIX A

PERCENT SOIL MOISTURE VALUES BY WEEKS WITHIN THE FIELD STUDY AREA

Slope	Station	Depth	May 8	May 15	May 22	May 29	June 5	June 12
east	A	Bottom	30.1	39.9	39.2	33.0	37.3	35.3
	A	Top	32.0	29.8	32.6	35.5	39.2	32.3
	B	B	36.1	35.5	32.6	35.6	36.8	34.0
	B	T	51.1	30.1	32.2	36.0	37.6	34.0
west	A	B	34.5	29.6	34.2	38.1	40.8	33.7
	A	T	31.0	37.7	38.4	33.8	35.6	33.2
	B	B	33.8	32.6	35.5	41.1	32.1	30.5
	B	T	31.4	29.4	41.3	39.5	33.7	28.8
east	3	B	31.0	30.4	27.7	39.2	31.8	27.4
	3	T	30.2	35.6	26.4	34.6	42.8	26.6
	4	B	29.9	22.5	22.2	22.6	30.9	29.9
	4	T	27.1	23.6	20.6	24.6	31.4	26.6
	5	B	----	21.9	24.2	25.5	28.0	26.6
	5	T	22.8	22.8	24.0	25.1	31.2	30.4
	6	B	26.3	24.3	21.9	26.1	27.5	28.1
	6	T	24.5	22.5	22.8	22.0	29.2	26.4
	7	B	24.4	21.2	17.5	19.3	25.7	25.4
	7	T	20.8	18.2	16.3	18.6	29.0	22.9
	8	B	24.1	20.3	17.1	9.3	31.4	19.9
	8	T	17.8	13.3	10.3	16.7	29.0	17.9
	9	B	27.6	23.0	22.4	10.4	29.8	21.0
	9	T	22.3	14.8	11.2	19.3	29.0	13.8
	10	B	24.1	17.1	16.2	17.3	25.7	20.6
	10	T	20.8	17.0	10.8	21.4	27.4	20.1
west	3	B	38.5	34.7	35.1	33.6	21.9	22.0
	3	T	32.2	30.7	31.5	41.1	24.9	16.3
	4	B	27.0	22.5	21.4	19.1	16.3	17.9
	4	T	30.6	19.6	18.4	23.0	21.6	11.3
	5	B	25.9	27.7	22.9	23.1	31.0	23.9
	5	T	26.1	18.5	13.7	24.3	37.7	25.1
	6	B	27.9	20.5	15.9	12.2	13.2	9.4
	6	T	26.9	18.4	19.6	20.5	28.0	13.9
	9	B	27.6	21.0	14.1	16.6	27.0	19.9
	9	T	22.5	14.8	9.6	25.7	32.0	23.6
	10	B	54.3	25.6	14.8	9.9	22.0	14.9
	10	T	26.2	19.6	16.1	16.1	38.3	18.9
	11	B	22.8	21.2	12.6	13.0	15.2	16.8
	11	T	16.5	14.2	9.0	9.1	25.5	16.2
	12	B	26.7	22.9	13.2	9.3	23.4	13.0
	12	T	25.1	17.8	7.4	14.4	24.7	12.0

APPENDIX A (Continued)

SOIL MOISTURE

Site	June 19	June 26	July 3	July 10	July 17	July 24	July 31	August 7	August 14	August 21
EAB	28.4		21.4	18.3	30.9	27.7	22.2	20.4	14.7	16.0
EAT	25.4		25.6	14.2	32.2	26.2	24.9	18.5	13.1	15.9
EBB	29.0		20.1	20.7	33.5	24.8	23.8	18.0	17.3	13.9
EBT	22.2		16.7	11.6	26.7	19.7	20.1	16.5	13.6	10.4
WAB	30.9		18.5	20.3	28.7	28.4	21.9	11.8	11.7	11.7
WAT	35.0		16.4	19.0	28.9	14.8	20.0	13.3	8.6	10.1
WBB	23.8		19.3	13.4	22.7	17.3	13.4	9.9	12.3	10.4
WBT	24.3		17.6	12.8	25.9	20.0	17.4	10.4	8.6	10.4
E3B	25.1		19.9	20.2	23.6	22.2	21.6	18.5	21.3	
E3T	24.3		19.9	17.4	25.1	27.4	23.0	16.8	13.2	
E4B	20.5		20.1	17.2	43.9	25.2	20.8	17.2	19.3	
E4T	20.4		19.0	15.8	27.1	24.0	27.1	17.0	15.6	
E5B	27.4		19.6							
E5T	21.7		17.6							
E6B	28.6		18.1	18.5	30.6	24.6	25.4	21.0	18.1	18.7
E6T	24.6		18.0	14.0	30.2	26.1	31.0	18.1	17.1	15.7
E7B	21.3									
E7T	18.8									
E8B	14.1									
E8T	14.2									
E9B	11.7									
E9T	9.2									
E10B	15.9		10.2							
E10T	13.7		8.8							
W3B	13.4		17.1							
W3T	12.3		12.1							
W4B	15.2									
W4T	11.3									
W5B	22.6		16.3							
W5T	13.9		13.7							
W6B	10.9									
W6T	18.8									
W9B	13.0									
W9T	13.2									
W10B	9.4		8.0							
W10T	10.7		9.1							
W11B	10.7		7.7	7.5						
W11T	8.6		5.7	6.7						
W12B	6.4									
W12T	5.9									

APPENDIX A (Continued)

SOIL MOISTURE

	August	September				October		November	
Site	28	4	11	18	25	2	9	13	20
EAB	20.6	22.0	13.9	17.7	31.3	30.6			35.3
EAT	18.0	13.9	7.9	20.4	31.9	25.8			42.6
EBB	21.9	17.5	15.1	20.4	34.7	28.0			35.0
EBT	15.0	14.8	10.1	23.4	27.9	24.9			--
WAB	14.1	10.4	11.3	15.7	29.6	32.1	Submerged		--
WAT	13.7	11.2	13.0	20.1	31.4	26.4			36.5
WBB	16.7	12.8	9.6	13.8	29.8	30.6			43.0
WBT	13.3	11.5	7.7	19.8	32.6	27.1			41.4
E6B	19.9								
E6T	21.2								

A = six feet within willow stand.
B = three feet within willow stand.
Values represent average of duplicate samples.

APPENDIX B

BULK DENSITY VALUES FOR FIELD STATIONS

Slope	Station	Depth	$P_b (g/cm^3)$
east	A	Bottom	1.65
	A	Top	1.49
	B	B	1.62
	B	T	1.62
west	A	B	1.61
	A	T	1.36
	B	B	1.62
	B	T	1.49
east	3	B	1.44
	3	T	1.24
	4	B	1.54
	4	T	1.44
	5	B	1.56
	5	T	1.57
	6	B	1.55
	6	T	1.51
	7	B	1.52
	7	T	1.31
	8	B	1.41
	8	T	1.40
	9	B	1.29
	9	T	1.39
	10	B	1.40
	10	T	1.36
west	3	B	1.58
	3	T	1.24
	4	B	1.74
	4	T	1.40
	5	B	1.58
	5	T	1.26
	6	B	1.45
	6	T	1.46
	9	B	1.64
	9	T	1.41
	10	B	1.57
	10	T	1.48
	11	B	1.52
	11	T	1.50
	12	B	1.55
	12	T	1.41

A = six feet within willow stand.
B= three feet within willow stand.

APPENDIX C

SOIL PARTICLE SIZE ANALYSIS FOR 12-22 CM DEPTH

		Percent		
Slope	Station	Sand	Silt	Clay
west	12	69	24	7
	11	73	18	9
	10	67	21	12
	9	62	25	13
	6	71	18	11
	5	55	28	17
	4	63	26	11
	3	61	27	12
	B	68	22	10
	A	74	17	9
east	A	50	37	13
	B	59	30	11
	3	39	36	25
	4	35	35	30
	5	44	35	21
	6	35	34	31
	7	31	34	35
	8	60	25	15
	9	74	16	10
	10	61	29	10

A = six feet within willow stand.
B = three feet within willow stand.
Each value represents the average of three samples.

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VITA

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Candidate for the Degree of

Master of Science

Thesis: AN AUTECOLOGICAL STUDY OF SALIX NIGRA, ESPECIALLY FACTORS THAT MIGHT LIMIT ITS DISTRIBUTION

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