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THE EFFECT OF THE GREAT DROUGHT OF 1934 ON THE LEAF STRUCTURE OF CERTAIN IOWA PLANTS

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By August, 1934, it was evident that the Middle West had been through the greatest drought in its recorded weather history. This drought, which began in June, 1933, was the driest twelve-month period ever recorded for Indiana, Illinois, Wisconsin, Minnesota, Iowa, Missouri, Nebraska, and the Dakotas (Kincer, 1934b).

The moisture shortage in Iowa, from June, 1933, to August, 1934, was 13.14 inches (Kincer, 1934b). Deficient rainfall was accompanied by record-breaking temperatures. Kincer (1934a), in comparing the record-breaking temperatures of 1934 with those of 1901, states that, in Des Moines, the maximum temperature was 108 degrees, or 22 degrees above normal, in July, 1934, while the maximum was 109 degrees, or 23 degrees above normal, in July, 1901. During this same month in 1934, Des Moines had 12 days with temperatures of 100 degrees or higher; 9 of these days were successive. In 1901, there were the same number of high-temperature days, but only six were in succession. The two successive hottest weeks had average maxima of 102 degrees in 1934, and 101 degrees in 1901. The mean temperature in June, 1934, was 8.4 degrees above normal and in July about 7 degrees above normal, while in 1901 it was 2.6 degrees and 8.4 degrees above normal for the same periods. Ward (1936) records correlative action in dust storms, floods, tornadoes, and hurricanes during this period.

In the northern half of Iowa, the vegetation was green all summer during 1934; but, in the southern half of the state, the pastures were brown, all grasses had succumbed to the drought, and the common roadside flora had died, with the exception of the hardier weeds. Surviving weeds included *Amaranthus retroflexus, Ambrosia trifida, Ambrosia artemisiifolia, Arctium minus, Asclepias verticillata, Asparagus officinalis, Baptisia tinctoria, Cassia Chamaecrista, Chenopodium album, Cirsium* spp., *Convolvulus sepium, Datura Stromonium, Eupatorium* spp., *Euphorbia corollata, Euphorbia Cyparissias, Euphorbia marginata, Helianthus* spp., *Melilotus alba, Polygonum* spp., *Silphium integrifolium, Silphium laciniatum, Solidago* spp., *Verbena* spp. Of the crop plants, sorghum and soybeans seemed to have withstood the drought conditions fairly well. Many woody plants, as well as herbaceous plants, in the southwestern and south central portions of the state died during the drought.

During the summer of 1935, woody and herbaceous plants throughout the state were green as normally.

According to Maximov (1929), Zalenski showed "that the network of veins in the leaves of plants growing in dry, open habitats is better developed than in plants growing in woodland shade or, in general, under conditions of low evaporation." Leaves inserted high on the plant stem were shown to have a more xeromorphic structure than leaves inserted low on the stem, that is, the upper leaves had: (1) a greater total length of the vascular bundles per unit area of leaf surface, (2) more typical development of palisade parenchyma, and (3) less typical development of spongy parenchyma, etc.

Alexandrov, Alexandrov, and Timofeev (1921) state that restricted ground-water supply induced xeromorphic structure in the leaves of *Bryonia* and *Ipomoea.* Eberhardt (1903) showed that when the moisture content of the atmosphere was low, leaves developed a more xeromorphic structure than when the moisture content of the atmosphere was high. Stahl (1883) and many investigators since have shown that sun leaves are more xeromorphic in structure than shade leaves. Tumanov (1927) showed that periodic wilting induced xeromorphic structure in the mesomorphic leaves of the sunflower.

Temperature is known to be more effective than degree of moisture in the air in causing water loss in plants, according to Curtis,[1] and high temperatures should therefore induce greater xeromorphy in leaves than low temperatures.

Nordhausen (1903) found that the structure of the leaves of trees and shrubs was predetermined by the conditions of illumination and transpiration under which the buds were formed during the previous year.

Wylie (1939) showed that the correlation between the dimensions of the intervascular interval and leaf thickness in the leaves of certain Iowa plants is high, significant and positive ($r = +0.735 \pm 0.0597$.)

Maximov (1929) further states that "all influences which result in a greatly increased loss of water by the plant, or a restricted supply of water to the developing leaves, lead to essentially similar changes of leaf structure. These . . . . . structural changes may be termed 'xeromorphic'."

The summer of 1934 was the severest test of survival characteristics to which Iowa plants had been subjected in more than thirty years. The response of the leaves of surviving plants in specified areas forms the basis of this study.

MATERIALS AND METHODS

Leaves from nine woody and from six herbaceous plants (see table I), including two monocotyledonous and thirteen dicotyledonous plants, were collected in sunny locations, between August 25 and August 30, 1934. Leaves of woody plants were selected as near 8 feet from the ground as possible. These plants were tagged, and leaves from the same branch were sampled again in the summer of 1935. The leaves of herbaceous plants were selected from as near the midsection of the plant as possible, in 1934. In 1935, because of the death of the original plants during the winter, different plants had to be selected, but collections were made within a few yards of the original plants, August 19 to 23.

[1] O. F. Curtis, in a lecture entitled "Leaf Temperatures and Transpiration," presented at the 276th meeting of the Synapsis Club, University of California Citrus Experiment Station, Riverside, California, April 6, 1942.

Collections were made at the following four locations in the state of Iowa: Fort Atkinson State Park in the northeastern corner, Gitchie Manitou State Park in the northwestern corner, Waubonsie State Park in the southwestern corner, and Farmington State Park in the southeastern corner of the state. Fort Atkinson State Park is on an elevated, dry piece of ground near the Turkey River. Gitchie Manitou lies along the Big Sioux River, and though it can not be said to be very high it is somewhat higher than the two southern locations. Waubonsie State Park is located on low ground approximately 3 miles west of the Nishnabotna River and 5 miles east of the Missouri River. Farmington State Park lies on fairly high ground above Farmington Lake, about 1 mile from the Des Moines River.

No *Polygonum pennsylvanicum* was available in or near Fort Atkinson State Park in 1934. No *Abutilon Theophrasti, Acer saccharum* or *Juglans nigra* was found in or near Gitchie Manitou State Park in 1934, but quantities of *Iva xanthifolia* were available. At Waubonsie State Park, *Abutilon Theophrasti, Fraxinus americana, Juglans nigra,* and *Quercus* spp. were plentiful in 1934, but no *Acer saccharum* or *Polygonum pennsylvanicum* could be found, though *Polygonum pennsylvanicum* was present in 1935. At Farmington State Park, *Abutilon Theophrasti* was scarce, as was *Fraxinus americana* and *Tilia americana,* though *Juglans nigra* and *Quercus* spp. were plentiful.

The central portions of the blades of five leaves of each plant used in this study were placed in a bottle of killing solution of formalin, acetic acid, and alcohol immediately on collection, and the intercellular spaces were evacuated of air by means of a bicycle pump. The leaves were prepared for sectioning by the paraffin method, sectioned transversely and tangentially 10μ thick, and stained with Delafield's haematoxylon and safranin. All measurements were made from permanent microscope slides so prepared.

For comparisons of xeromorphic structure, leaf thickness and the length and width of the intervascular interval were measured directly from the prepared slides with a microscope fitted with an ocular micrometer. The intervascular interval was measured from vein edge to vein edge and included the border parenchyma. Thirty measurements were made of each item in each leaf sample.

RESULTS

Herbaceous Plants. Examination of table I will show that at Fort Atkinson State Park, the leaf thickness of herbaceous plants in three genera out of four was greater in 1935 than in 1934. The same condition was found at Waubonsie State Park, in four genera out of five, and at Farmington State Park, in four genera out of six. At Gitchie Manitou State Park, in three genera out of five, the leaf thickness was greater in 1934 than in 1935.

At Fort Atkinson, in three genera out of four, the intervascular interval was larger in 1935 than in 1934. The same condition was found at Gitchie Manitou, in four genera out of five; at Waubonsie, in two genera out of four; and at Farmington, in five genera out of six.

TABLE I. LEAF THICKNESS AND DIMENSIONS OF INTERVASCULAR INTERVAL (EXPRESSED IN MICRONS) OF LEAVES OF HERBACEOUS AND WOODY PLANTS AT WIDELY SEPARATED LOCATIONS IN IOWA, SUMMER, 1934 AND 1935

Species	Year	Fort Atkinson State Park			Gitchie Manitou State Park			Waubonsie State Park			Farmington State Park		
		Leaf thickness	Intervascular interval		Leaf thickness	Intervascular interval		Leaf thickness	Intervascular interval		Leaf thickness	Intervascular interval	
			Length	Width		Length	Width		Length	Width		Length	Width
Herbaceous Plants													
Abutilon Theophrasti	1934	129.0	213	125	…*	…	…	100.5	175	109	134.8	180	131
	1935	…	240	166	…	…	…	128.7	214	119	146.3	215	132
Amaranthus retroflexus	1934	208.4	104	59	182.6	193	120	174.9	117	72	146.9	81	51
	1935	198.5	118	66	184.0	242	128	196.2	147	70	157.3	85	56
Ambrosia artemisiifolia	1934	130.0	105	55	149.4	68	46	151.0	97	62	99.1	104	66
	1935	168.0	83	50	146.1	93	55	87.7	95	59	100.8	143	79
Polygonum pennsylvanicum	1934	…	…	…	166.9	201	122	…	…	…	174.5	208	137
	1935	190.2	178	108	153.4	174	122	174.0	225	130	143.7	228	140
Setaria glauca	1934	116.8	464	82	108.7	307	73	177.6	…	…	176.2	509	70
	1935	145.1	…	…	112.5	381	63	197.6	…	…	81.1	520	72
Zea mays (Yellow Dent)	1934	151.2	523	130	175.6	437	97	142.2	602	99	180.9	634	101
	1935	171.6	598	104	173.9	500	98	147.3	383	105	207.6	532	135

TABLE 1—Continued

Species	Year	Fort Atkinson State Park			Gitchie Manitou State Park			Waubonsie State Park			Farmington State Park		
		Leaf thick-ness	Intervascular interval		Leaf thick-ness	Intervascular interval		Leaf thick-ness	Intervascular interval		Leaf thick-ness	Intervascular interval	
			Length	Width		Length	Width		Length	Width		Length	Width
Woody Plants													
Acer negundo	1934	143.0	244	172	154.4	247	165	130.6	251	179	142.3	263	186
	1935	165.6	266	202	163.0	246	164	141.9	269	180	151.3	317	220
Acer saccharum	1934	124.1	250	173	....	....	....	....	....	....	....	....	....
	1935	147.7	231	155	....	....	....	....	....	....	150.6	293	191
Fraxinus americana	1934	164.5	266	171	212.8	246	136	82.5	206	144	154.0	232	139
	1935	185.2	275	169	180.5	266	144	127.7	255	167	....	....	....
Juglans nigra	1934	182.8	203	150	....	....	....	137.7	213	143	123.0	231	149
	1935	109.7	221	158	....	....	....	135.1	245	169	123.4	276	175
Populus deltoides	1934	....	....	....	284.9	261	164	218.8	286	180	210.6	297	194
	1935	194.1	296	197	225.5	292	198	305.0	333	223	273.1	303	242
Quercus macrocarpa	1934	148.7	201	152	151.9	231	147	153.0	229	174	105.1	272	168
	1935	148.4	252	177	165.2	242	155	104.0	268	181	158.7	281	193
Rhus glabra	1934	150.2	150	79	194.8	151	89	90.8	162	95	158.3	178	90
	1935	103.0	150	101	186.6	176	96	145.4	181	96	144.1	165	99
Tilia americana	1934	....	....	....	171.3	273	154	147.0	243	167	102.5	256	163
	1935	....	....	....	157.0	293	191	150.6	289	173	....	....	....
Ulmus americana	1934	158.3	311	207	162.7	241	153	170.2	268	196	202.3	315	219
	1935	184.5	250	142	183.0	311	202	175.5	299	198	168.4	311	243

* Dashes indicate that material was not available.

TABLE II. CLIMATOLOGICAL DATA* FOR CHARLES CITY, IA., SIOUX CITY, IA, OMAHA, NEB., AND KEOKUK IA., NEAREST WEATHER STATIONS TO FORT ATKINSON, GITCHIE MANITOU, WAUBONSIE, AND FARMINGTON STATE PARKS, RESPECTIVELY

Date	Charles City (Fort Atkinson State Park)				Sioux City (Gitchie Manitou State Park)				Omaha (Waubonsie State Park)				Keokuk (Farmington State Park)			
	Mean maximum temperature degrees F.	Mean relative humidity percent	Precipitation (Inches)		Mean maximum temperature degrees F.	Mean relative humidity percent	Precipitation (Inches)		Mean maximum temperature degrees F.	Mean relative humidity percent	Precipitation (Inches)		Mean maximum temperature degrees F.	Mean relative humidity percent	Precipitation (Inches)	
			Total	Departure from normal			Total	Departure from normal			Total	Departure from normal			Total	Departure from normal
1934—																
April	59	57	0.96	−1.6	64	48	0.55	−2.2	67	45	0.28	−2.2	64	55	2.64	−0.4
May	83	41	0.54	−3.8	86	51	1.34	−3.4	86	41	0.60	−3.2	81	40	0.60	−2.6
June	89	53	1.25	−3.4	87	56	6.27	+2.3	91	53	2.97	−1.6	93	56	3.01	−1.1
July	88	64	3.91	+0.1	92	56	4.93	+1.4	97	44	0.52	−3.0	96	51	0.95	−2.5
August	80	69	3.86	+0.4	87	56	1.12	−2.0	90	51	1.11	−1.9	89	60	2.66	−0.5
Total or Mean	79.8	56.7	10.52	−8.3	83.4	53.4	14.21	−3.9	86.1	46.8	5.48	−11.9	84.5	52.4	9.86	−7.1
1935—																
April	54	72	2.91	+0.4	56	69	4.31	+1.6	59	61	0.80	−1.7	58	68	2.48	−0.5
May	64	65	2.72	−1.6	63	72	2.75	−1.3	64	73	3.57	−0.2	65	75	7.28	+3.4
June	74	72	6.91	+2.3	77	66	2.16	−1.8	78	74	5.25	+0.7	78	73	6.40	+2.3
July	88	72	1.10	−2.7	94	62	2.02	−1.5	95	68	1.11	−2.4	90	69	4.85	+1.4
August	82	74	4.29	+0.8	86	65	2.00	−1.1	88	72	2.15	−0.9	85	70	1.90	−1.3
Total or Mean	72.4	71.1	17.93	−0.8	75.2	66.8	13.24	−4.1	76.8	69.6	12.88	−4.5	75.3	71.0	22.91	+5.3

* Source of data: From Small (1934, 1935).

Examination of the climatological data in table II shows that Gitchie Manitou had the heaviest rainfall, and that in June the rainfall was 2.3 inches above normal. No other station had this luxury rainfall in June, 1934. However, all the other stations had a luxury water supply in June, 1935, except Gitchie Manitou, where it was drier in 1935 than in 1934. The reciprocal quantitative morphology, with respect to leaf thickness, of the leaves at Gitchie Manitou seems attributable to the luxury water supply in June, 1934, at the period when the expanded leaf blades begin to thicken, and the water deficiency in June and in other spring and summer months in 1935, as contrasted with the drought at other stations in 1934 and luxury water supply in June, 1935. The similar response of the intervascular interval of leaves of the various species at Gitchie Manitou to that at other locations, in 1935, is perhaps explained by the fact that there was a luxury rainfall at Gitchie Manitou in April, 1935, and ample ground water was supplied for the expanding leaves. The drought condition which followed in May and June affected only the thickening process.

Woody Plants. The response of the woody plants of Iowa was, in general, similar to that of the herbaceous plants. At Fort Atkinson, in four genera out of seven, the leaf thickness was greater in 1935 than in 1934. At Gitchie Manitou, in only three genera out of seven was the leaf thickness greater in 1935 than in 1934. At Waubonsie, the leaf thickness was greater in six genera out of eight in 1935, while at Farmington in four genera out of six, the leaf thickness was greater in 1935. As in the case of herbaceous plants, woody plants at Gitchie Manitou, where a luxury water supply existed in June, had the larger proportion of genera with thicker leaves in 1934.

The intervascular interval was larger in 1935 than in 1934, in four of the seven genera sampled at Fort Atkinson. The same condition was found at Gitchie Manitou in six genera out of seven; at Waubonsie, in all eight genera sampled; and at Farmington, in four genera out of six.

DISCUSSION

The majority of plant genera surviving the 1934 drought responded in a way contrary to expectations based on the literature. When drought conditions existed at Fort Atkinson, Waubonsie, and Farmington State Parks, leaves were thinner and the intervascular intervals were smaller, in most genera, whether herbaceous or woody. Plants at Gitchie Manitou enjoyed a luxury water supply in June and July, 1934, and the leaves of the majority of genera were thicker than in 1935, when drought conditions existed through May, June, and July. However, intervascular intervals were greater at Gitchie Manitou in 1935, than in 1934, which corresponds to the greater water supply in April, 1935, and the drought in April and May, 1934.

The fact that a positive correlation existed between mean leaf thickness in the four areas of Iowa, and the total precipitation from April through August, in each of these areas ($r = + 0.39$), and that a positive correlation existed between the mean intervascular interval and the total precipitation ($r = + 0.61$), are of doubtful significance, since the period of adequate water supply seems to control more specifically leaf expansion and intervascular interval, and the later occurring process of leaf thickening.

An explanation of the mechanism operating in the production of the diverse leaf anatomy during 1934 and 1935 may be as follows: In general leaf expansion precedes leaf thickening. If adequate water is available prior to and during the expansion period, leaves will expand normally, developing average-sized intervascular intervals. If water supply is limited at this time, leaf expansion is limited, and intervascular intervals are reduced in size. If adequate water supply is available during the leaf thickening period, leaves will thicken normally. If adequate water supply is not available leaves will be thinner than normal.

Adequate water supply during the leaf thickening period permits adequate carbohydrate synthesis for building cellular material needed in leaf thickening, and provides water for cellular expansion. However, other factors are perhaps involved in leaf thickening. For instance, leaf thickening probably takes place at a period of high light intensity.

It was shown by Turrell (1939) that the structure of leaves of two morphologically different plants responded to increased light intensity in different degrees, the higher light intensity inducing the greater xeromorphy with adequate water supply. The induction of leaf thickening was postulated by Turrell and Bauguess (1942) to be due to the diffusion of the leaf growth hormone to the lower sides of the leaf lamina. Thus it seems plausible that high light intensity in late spring may cause the diffusion of the leaf hormone to greater depths of the leaf tissues, and brings about leaf thickening at this time if adequate photosynthate and water are available. If adequate water is not available at the time high light intensities are supplied to the developing leaf, the action of the growth hormone diffusion is without effect, due to the limitation of carbohydrates for cellular addition, and water for cell expansion.

This explanation seems to account for the irregular and unanticipated response of the leaves of Iowa plants to the great drought of 1934, as compared with the year 1935. However, it should be recognized that interpretation of data obtained in the field is extremely difficult where the interaction of a number of factors influences the growth of the plant.

The dynamic account of Weaver *et al* (1935) should be consulted for the effect of the great drought of 1934 on the soil and plants of Nebraska.

SUMMARY

Leaves of herbaceous and woody species from three widely separated Iowa State Parks developed smaller leaf thicknesses and intervascular intervals in the summer of 1934, when drought conditions existed at

three of the locations (Fort Atkinson, Waubonsie, and Farmington State Parks), than at the same locations in the summer of 1935, when rainfall was nearly normal. At Gitchie Manitou State Park, leaf thickness of herbaceous and woody species was greater in 1934 than in 1935; this difference may be explained by the nearly normal water supply which was available in this area in June, 1934, while drought conditions existed in 1935. The greater intervascular intervals of 1935 in this area correspond to adequate water supply in April, and smaller intervascular intervals correspond to drought in April, 1934.

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