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ECOLOGICAL FACTORS IN REGION OF STARVED ROCK, ILLINOIS

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BY

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ECOLOGICAL FACTORS IN REGION OF STARVED ROCK, ILLINOIS

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FRANK THONE

(WITH FIVE FIGURES)

Introduction

The work of COWLES (5) in calling the attention of the then newly differentiated science of plant ecology to the concept of plant associations as stages in successions, not as entities complete and final in themselves, but rather as steps in the evolution of social life in the plant world, was of far reaching influence in determining the development of ecology in America as a dynamic science, as the study of a progress rather than as a mere set of methods for the description of states. COWLES was also the first to emphasize the importance of topography as a general control over other factors that directly influence the activities of plants.

The earlier work in this field contented itself with pointing out the general effects of topography as a modifier, within a given region, of the climatic factors. It indicated the direction of such modifications, but only estimated their extent; it was qualitative rather than quantitative. It was, however, only natural that as time passed students of ecology should desire to gain a more exact knowledge of the factors controlling plant communities and their development, and a good share of the work now being done in American and British ecology concerns itself with the measurement of such factors as soil moisture, soil chemistry, temperature of both soil and air, evaporating power of the air, and intensity of sunlight. With the cooperation of ecological plant physiologists, a number of more or less satisfactory methods for the measurement of these factors have been evolved. Among the many workers on the problems of soil moisture, BRIGGS and SHANTZ (3) may be cited for their development of the wilting coefficient concept, BRIGGS and McLANE (2) for the moisture equivalent idea, ALWAY (1) for the hygroscopic coefficient, and LIVINGSTON and KOKETSU (11) for the invention of the so-called soil points. Thermometric data were among the earliest to be gathered, although they are still among the least satisfactorily interpreted; special citations appear to be superfluous. Exception might be claimed for the "life zone" idea best developed by MERRIAM (15), but this is regional-climatic rather than local and topographic.

Modern ecological work in the measurement of the evaporating power of the air dates chiefly from the re-invention and popularization by LIVINGSTON (8, 9) of the porous cup atmometer. From time to time numerous attempts have been made to develop photographic and other methods for a field study of sunlight intensity, but none of them has been very satisfactory to students of plant activities. PULLING (16) gives a concise review of the work in this field. About the only instrument at present used by anyone except its own inventor is LIVINGSTON'S radio-atmometer (10), which obtains an approximate measurement of the effect of direct solar radiation on evaporation from a free water surface. Other methods for the measurement of ecological factors have some local vogue, but those here outlined are the ones most frequently used.

So widespread has been the practice of factor measurement, and so many the workers, that a complete review of the literature would be impossible in this connection, and in view of the extensive literature cited in such standard works as those of LIVINGSTON and SHREVE (12), and of CLEMENTS (14), may well be omitted.

An important consideration in the development of a successional series, but one that is not always given the prominence it deserves, is the fact that the determining conditions that permit or bar the entrance of new species in a given area are operative first on the seedling. Liminal conditions act on the infant of the race, practically always. The operation of this principle may be seen in the cultivation of adult plants outside of their natural habitats. These often thrive, but do not produce offspring. By the simple law of chance, propagules of all sorts are constantly falling into every area within the range of flight or carriage from the parent, but only where conditions are such as to permit their germination and initial growth do they become established. Once established they may weather an unfavorable season, but they cannot gain a foothold at all in a place where the conditions are unfavorable all the time. This principle recognized, it becomes at once apparent that any measurements undertaken with a view to their bearing upon succession should be made with special reference to seedling seasons and places. The first worker to use this idea as a definite basis for his investigations was FULLER (7), who made a study of the water relations of several plant associations on and near the Indiana dunes. His results indicated that the water supplying power of the soil was fairly uniform, or at least adequate for growth, throughout the season at all of his stations. On the other hand, the evaporating power of the air varied markedly, showing a pronounced correlation with the type of vegetation. The rate of evaporation bore an inverse relation to the density of the vegetation, being greatest on the cottonwood dune and least in the beech-maple forest. FULLER concluded that the differences in evaporation rates were sufficient to account for the successional range between the relative xerophytism of the cottonwood dune and the mesophytism of the climax forest.

The present problem

TERRAIN

Conditions rivalling those of the dunes in diversity of vegetational associations to be found within narrowly restricted limits exist in numerous steep-sided river gorges and their associated canyons scattered across the whole Mississippi Valley, along the edges of the various glacial drift areas, and in the unglaciated areas adjoining them. These cliffs and canyons are invariably the habitats of disjunct groups of various kinds: glacial relicts left behind by the northern retreat of the first post-Pleistocene flora, outliers from the mesophytic southeastern forests, forerunners of western and southwestern plains, and desert types. This contact of outposts of such different plant hosts is in itself an argument for the existence of notably different environmental complexes in close juxtaposition, and hence for the advantageousness of such locations as critical points in the study of the physical factors of ecology.

The data for the present study were obtained at the Illinois State Park at Starved Rock, in La Salle County, Illinois. Here, during early post-glacial times, the Illinois River cut a steep-sided trench through the St. Peter sandstone (which at this point is thrust to the surface by the La Salle anticline), and through its overlying strata of Pottsville shales and clays and blanket of glacial till. The geography of this region has been treated in detail by SAUER, and the geology by CADY (6). The sides of the trench still remain as lines of steep cliff, about a mile apart, facing each other across the floodplain of the now much shrunken river. The cliff on the south side of the river, from a point opposite the village of Utica eastward for about seven miles, is unusually precipitous and high, reaching a maximum of 157 feet from crest to mean low water level at the Starved Rock itself. It is furthermore cut into by a series of remarkable box canyons made by small tributary streams. Their sides are as precipitous as those of the cliff itself, and for the most part their bottoms are either at or near base level. Since the recession of the river (which now washes the base of the cliff only in a few limited spots, notably Starved Rock, Lovers' Leap, and Pulpit Rock) erosional débris has collected in places as talus slopes at the foot of the cliff, both within and outside the canyons. In addition, there are at the top of the cliffs the steep slopes from the top of the sandstone caprock to the general level of the upland till, and at the base a number of fragmentary river terraces of varying age, including oxbows in various stages of filling, and finally the present juvenile (and largely treeless) floodplain. A cross-section through a typical location either over the cliff side or into a canyon, therefore, would reveal the following types of terrain: (1) level upland of glacial or Pottsville clay; (2) more or less steep slope toward the edge of the sandstone cliff, also clayey; (3) exposed edge of cliff, sandy or sand mixed with clay and shale; (4) precipitous cliff, usually with weathered crevices and shelves; (5) talus slope, generally very sandy, with much humus and some clay; (6) canyon bottom (alluvial), or river terrace (alluvial to sandy), or juvenile floodplain (alluvial).

VEGETATION

With so varied a terrain as that just outlined, presenting such widely diverse types of habitat, it is only natural to expect a very widely diversified vegetational development. This expectation is well realized, for within the limits of the scant thousand acres of the Starved Rock State Park there is a collection of plants that for floristic and ecological interest can hardly be matched. All the orthodox successional stages between *Quercus macrocarpa* of the prairie edges and *Q. velutina* of the upland woods, to *Q. bicolor* of the sloughs and the *Populus-Salix* thickets of the river edge are there as a matter of course; but the region offers all the groups of disjuncts mentioned in a preceding paragraph as well. There are places in this park where one can stand beside a white pine and throw a stone through the top of a pawpaw!

No attempt can be made in this place even to outline the vegetational types to be found in this region. This has been presented briefly by COWLES (6), and a more detailed description by the present writer is now in preparation. The present study concerns itself more with the physical factors of the environment, especially as they affect seedling growth and hence succession, in a number of typical locations in the park. Ideally these determinations should have been made in a considerable number of places, at least three for each clearly distinguishable type of association, but this was beyond the available resources in time and apparatus. In all, seven stations were maintained throughout the major portion of one growing season, two on the upland, three on talus slopes, and two at the bottom. In locating these, some diversity was possible, overcoming in at least a slight degree the unavoidable inadequacy of data. Stations 7 and 6 were located on the upland, no. 7 on the upland proper, in a second growth *Quercus velutina-Q. alba-Carya ovata* association, and no. 6 on a gentle slope from this toward the edge of the cliff (but away from the exposed sandy terrain), in a second growth *Quercus rubra-Q. alba* association, with considerable undergrowth of *Cornus*, *Viburnum*, and seedlings of *Prunus*, etc. Stations 5, 3, and 2 were located on talus slopes, no. 5 about one-third of the way down one, on the face of the cliff, and nos. 3 and 2 near the tops of slopes on opposite sides of Hennepin Canyon. The tree growth at station 5 was predominantly *Quercus rubra*, with some *Q. alba*, *Juglans cinerea*, and *Tilia americana*, and a scattering of other mesophytic hardwood species. The shrubby undergrowth consisted mostly of *Hamamelis virginiana*, and the herbaceous situation was dominated by a magnificent "fernery" of *Osmunda claytoniana*. The soil here was a sand rich in humus, but with little clay. Station 3, within the canyon, was on a rather newer slope, the soil containing a considerable proportion of clay. The tree growth consisted largely of *Prunus serotina*, and there was a dense undergrowth of *Psedera quinquefolia*, *Ribes cynosbati*, *Lonicera Sullivantii*, and *Hydrangea arborescens*. There was also a fair development of mesophytic herbs. Station 2 was on a slope that was newer still. The soil was sandier than on station 3, but raw and poor in humus. It was full of stones, with large, moss-covered rocks protruding. There were fewer trees, and these were mostly young and small. A very considerable growth of *Hamamelis virginiana* was present, but few other shrubs, and almost no herbs. These three stations represented fairly well the state of the more mesophytic talus slopes. Stations 4 and 1 were on representative bottomlands, no. 4 being on the river floodplain and no. 1 on the floor of the canyon. The soil in both places was a black alluvium. The association at station 4 was dominated by *Acer saccharinum* and *Ulmus americana*, with many seedlings and saplings. Other undergrowth was mostly herbaceous, with *Laportea canadensis*, *Boehmeria cylindrica*, and *Campanula americana* as the conspicuous species. The alluvial floor of the canyon, where station 1 was located, bore an association of *Ulmus*, with some admixture of *Juglans*, *Fraxinus*, *Populus*, *Salix*, etc. Seedlings and young trees were numerous, and there was a fair amount of undergrowth, consisting largely of *Sambucus canadensis*, and at one place a notable thicket of *Euonymus*. There was an exceedingly rich, moistmesophytic herbaceous flora, typified by *Impatiens pallida*, *Pilea pumila*, *Campanula americana*, and *Lobelia syphilitica*. Lianas were abundant, more so than at station 4. In general, this was by far the most mesophytic of all the stations. These three groups of stations were thus fairly typical of upland, slope, and bottomland respectively, and represented the principal plant associations reasonably well.

Instruments and methods

An effort was made at each station to secure some measurement of each of the following physical factors: soil moisture, evaporating power of the air, intensity of solar radiation (in terms of its effect on evaporation from a free water surface), and temperature of soil and air.

SOIL MOISTURE.—Soil moisture data were obtained by (1) the usual determination of the oven-dry weight percentage in samples of about 200 gm. each, compared with the wilting coefficients, as derived by the indirect method of BRIGGS and SHANTZ; and (2) the "soil point" method of LIVINGSTON and KOKETSU. All data were obtained for a level of approximately 7.5 cm. below the soil surface. This was the shallower of the two depths used by FULLER in his dune studies, and represents the level at which most seedlings begin their adventures. The soil points were used in sets of four, and results recorded as the average, to eliminate as far as possible the errors due to variability in instruments and soil. Holes were dug to the proper depth with a trowel, care being taken that none of them was within one-half meter of any hole in the same set or any previous set. As a rule, soil from the holes into which the points were set was taken for use in the moisture percentage determinations. From April 30 until July 1 it was possible to visit the stations only three or four times a month. From July 1 until September 20 determinations were made every forty-eight hours, except when rain intervened.

EVAPORATING POWER OF AIR AND SUNLIGHT INTENSITY.—Data on the evaporating power of the air and on the effect of direct solar radiation on evaporation rate were obtained by means of a pair of standard Livingston spherical atmometer cups at each station.

These were equipped with the rainproofing valves described by LIVINGSTON and THONE (13). Their reservoir bottles were partly buried, so that the cups were about 20 cm. above the ground level. From April 30 until July 1 readings were made weekly or fortnightly, during the month of July they were made daily, and from August 6 until September 20 they were made every two days. All readings, after correction, were reduced to mean daily rates for ten-day periods.

TEMPERATURE.—Air temperatures were obtained from a Sixe-type minimax thermometer at each station. The thermometers were placed at the same level as the atmometers. No artificial shelter was used except at station 1, since there was sufficient natural cover to protect the instruments from direct insolation at all the other stations, and even at the latter place the growth of the *Impatiens* thicket soon made artificial shelter unnecessary. Readings were made on the same schedule as that used in the atmometer observations. The stations were visited each day just before the period of maximum temperature, so that the maxima and minima for the preceding twenty-four or forty-eight hour period were obtained.

Soil temperatures were obtained by means of test-tubes sunk into the soil to a depth of 10 cm. The lower end was kept filled with water, and the tube kept stoppered. When an observation was to be made, a thermometer was lowered into the tube until the bulb was immersed in the water, and read after sufficient time had been allowed for an equilibrium to be reached. Since the readings were always made shortly before the period of maximum air temperature, it may be assumed that the soil temperatures thus obtained were a little below the maximum for the day. Since, however, the total diurnal fluctuations in soil temperatures are known to be small, and especially since in the present study they seemed in the end to have no particular significance, this source of inaccuracy, as well as the rather crude method employed for obtaining the data, may be overlooked.

For both air and soil temperatures, it may be remarked that the figures up to July 1 can have but little significance, since they apply to periods of seven or fourteen days. During July, of course, true diurnal data were obtained. From August 6 until September 20 readings were made every forty-eight hours.

Discussion

Soil moisture (figs. 1, 2).—It is obvious that topography cannot affect the availability of soil water for plant growth until two other factors have operated. The first of these, the amount and distribution of precipitation, is climatic, and thus affects all locations about equally. The second factor (or more properly group of factors) is strictly edaphic, having to do with the effect of the mechanical makeup of the soil (size, arrangement, and packing of soil particles) upon the capacity of the soil to absorb and hold precipitation water, and to deliver it to the roots of the plants when they demand it. Finally, the topography is of importance in its effect upon such factors as run-off, subsurface drainage, and exposure to factors that influence evaporation, both from the surface of the soil itself and through plant transpiration.

The effects of the climatic factors are plainly evident in the general conformity of all the curves in the soil moisture graphs, both those representing the growth water (fig. 1) and those representing the results of the operation of the Livingston-Koketsu soil points (fig. 2). After the cessation of the spring rains in early June, and until their resumption in early September, the season was one of the hottest and driest summers on record in recent years. There was but one brief period of precipitation, heavy rains occurring during the first few days of August. The soil water percentages show a notable correlation between the rainfall distribution and the water content of the soil at all the stations. Beginning with moderate but varying amounts during the late spring rains, all stations showed a falling off throughout June, increasing in amount and rate of loss through the July drought, and ending in a sudden increase at the time of the early August rain. Following this was another sharp decrease throughout August, until a period of rains in early September brought a rise, somewhat resembling that of early August, but less in amount. Fair weather during the last observation period of the season brought the beginning of another decrease. The ready responses of the curve to both drought and rain are very notable features.

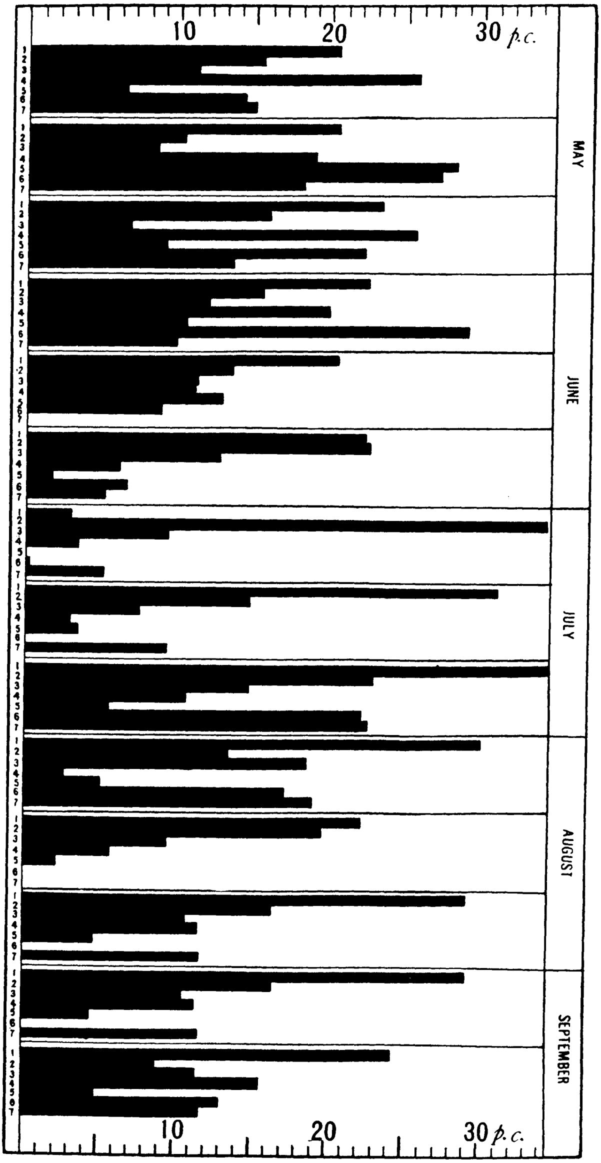

FIG. 1.—Percentages of growth water present in soil at seven representative stations, during ten-day periods from May 1 to September 20.

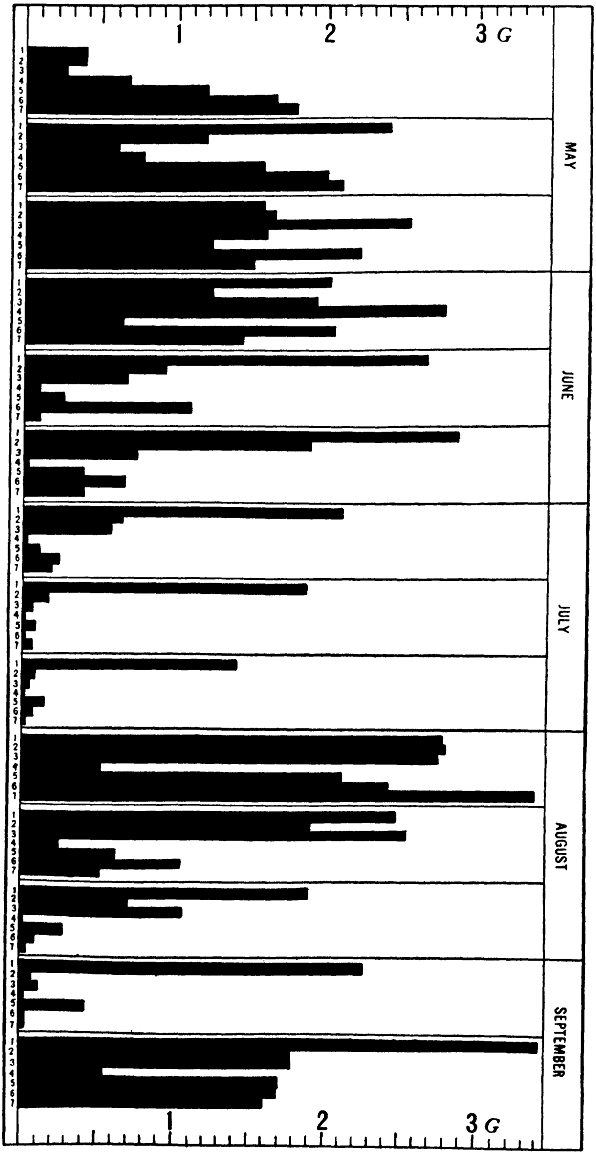

FIG. 2.—Amount of absorption in gm. per two-hour period by Livingston-Koketsu soil points at seven representative stations, during ten-day periods from May 1 to September 20.

The same fluctuation in the water-supplying power of the soil, as shown by the Livingston-Koketsu soil points (fig. 2), is even more marked. Both the individual determinations and their ten-day means show fluctuations closely parallel to those of the growth water percentage data. The close "bunching" of the ten-day means during July and the period ending September 8 is especially suggestive. Since the soil point method was devised in an effort to determine directly the water-supplying power of any kind of soil, independently of its wilting coefficient or any other physical constant, this shows clearly that during such periods of drought all the soils in the locations studied, save one, dropped to a very critical water-delivering power. In the Livingston-Koketsu experiments with wheat and *Coleus* under winter greenhouse conditions, permanent wilting ensued when the water-delivering power of a soil had fallen to a point between 0.04 and 0.11 gm. per two-hour period (as compared with about 15.0 gm. for the same period in a nearly saturated soil). The soil points used in the present determinations, however, have a somewhat greater absorbing power. According to data as yet unpublished, obtained by H. C. DIEHL, the new points have 1.25 times the absorptive power of those used by LIVINGSTON and KOKETSU. The water-delivering power of the soil at the permanent wilting point should therefore be between 0.05 and 0.14 gm. for a two-hour period. This is the case, at least, if we do not take into account the evaporating power of the air at permanent wilting. Since, however, the evaporating power of the air throughout the droughty periods was greater at the stations considered than it was in LIVINGSTON's greenhouses, we are safe in doing so, and in taking as an approximate water-supplying power at wilting point 0.15 gm. for the two-hour period. It will be seen that during the drought periods all of the stations save one either approached or passed this critical point, and that several of them were well beneath it for a period of thirty days during July and one of twenty during August, with an interval of only ten days between these two prolonged droughts. Further, a comparison with figs. 3 and 5 will show that these were the periods of greatest stress from extremes of temperature and evaporation. It is fairly evident, therefore, that seedlings that are to survive throughout most of the park must be of species able to get an early start or make sufficiently rapid growth to have well established root systems before the advent of the usual summer droughts.

A more detailed examination of individual stations serves to emphasize the facts already noted in general, and also brings out several edaphic phenomena of considerable interest. It is here that topograph factors appear to function. Thus, station 1 is the least exposed, and also the least well drained, being on the flat floor of a canyon. It is also subject to flooding when there is heavy rain, and the run-off from the tributary gullies comes over the canyon falls. It is not surprising, therefore, to find that it is constantly well above both the wilting coefficient and the Livingston-Koketsu wilting point. It is not surprising, either, to find here the largest number of young seedlings, and a herbaceous vegetation dominated by annuals. On the other hand, the highest upland station, no. 7, is both well drained and quite exposed; in correlation therewith it rapidly loses what water it gains, and persistently holds a place near the bottom of the column during the droughty periods. Few seedlings develop, and the herbaceous vegetation consists largely of grasses and sedges and of perennating prairie plants. The stations on the more or less sloping terrain (no. 6 on the upland and nos. 5, 3, and 2 on talus slopes) present phenomena intermediate between these extremes.

Station 4, on an alluvial flat beside the river, in a maple-elm-ash association, presents an anomalous situation. Starting in the spring with a moderate amount of soil water, it loses rapidly and fails to recover, during the summer rains, to anything like the degree displayed by the other stations. The soil point data confirm its bankruptcy. After it has lost its water during June, it falls to the bottom of the heap during the droughty periods and stays there more persistently than any other station. During the rains, when the others rapidly increased in their water-supplying power, this station rose but little, and then quickly dropped to the bottom again. This behavior may be accounted for in several ways. The soil here is a heavy, silty alluvium, very tenacious of the water it gets. It does not receive the benefit of periodic flooding, as does station 1. The thicket of saplings is so dense that only the heaviest rains ever penetrate the foliage sufficiently to wet more than the surface of the ground. A large proportion of the soil surface is bare, puddling easily, and thus facilitating direct evaporation. These, and possibly other unnoted factors, can account for the condition here.

EVAPORATING POWER OF AIR (fig. 3).—The effect of the climatic factors that influenced soil moisture conditions is plainly evident in the atmometric data also. There was more rainy and cloudy weather during May than during June, and the rates of evaporation show a corresponding decline during the latter month. Then, with the beginning of the hot, dry weather of July the rates increased suddenly and enormously. There was a sudden drop after the oncoming of the early August rainy period. Throughout August the daily temperatures were markedly lower than those for July (fig. 4), with much cloudy weather, although actual precipitation was confined to brief local showers; with this was correlated a reduction in the transpiration curves to one-half or less of their July heights. A short heated period at the beginning of September brought an increase in the rate, but the ensuing cool, humid days that closed the period of observation brought the curve down, and the season came to an end with a period of very low transpiration rates.

A feature of some interest in the set of atmometric curves is presented by the deep "dip" during the month of June. It was natural that evaporation rates should be higher during July, as already pointed out, but the sharp decrease from the May rates seems at first somewhat anomalous. One possible reason suggests itself in the comparative amounts of general exposure due to the foliation of the trees. The spring of 1921 was late and cool, and during May the trees, especially the oaks, were still nearly naked. As the foliation increased, changes in three of the four main factors controlling evaporation might naturally be expected; direct insolation and air movement would be reduced, and relative humidity probably increased. All of these changes would be in favor of reduced evaporation. The fourth main factor, temperature, increased somewhat during this time. This would have worked in the opposite direction, but presumably the operation of the other three had the greater effect.

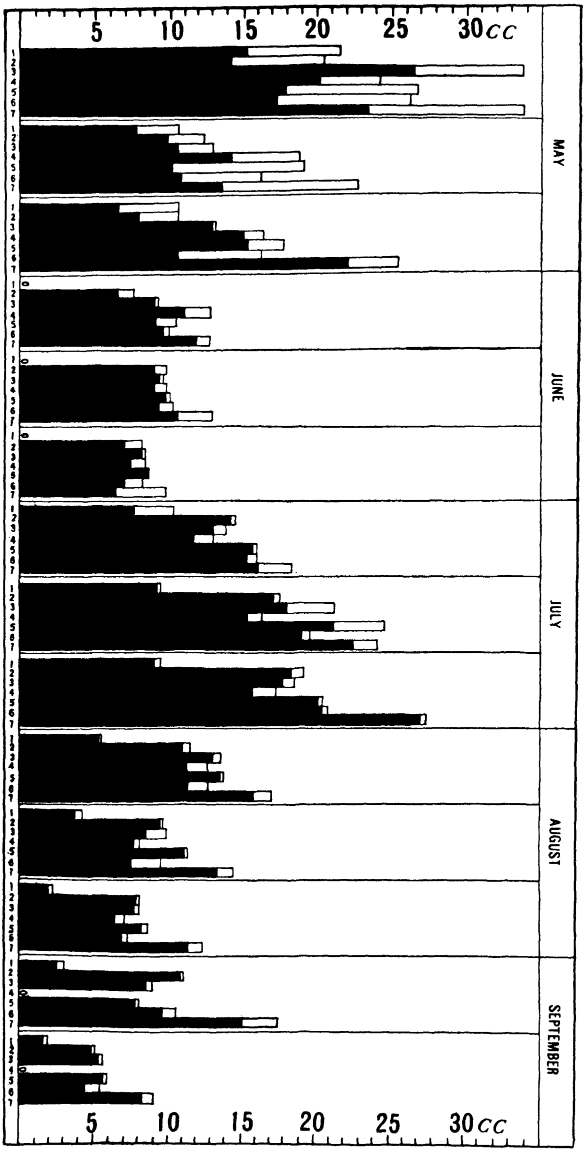

FIG. 3.—Mean daily amounts of evaporation in cubic centimeters from standard spherical black and white atmometers; black columns indicate simple atmometric effect; white extensions, increased evaporation due to direct insolation; a zero at base of column signifies data lacking for the period.

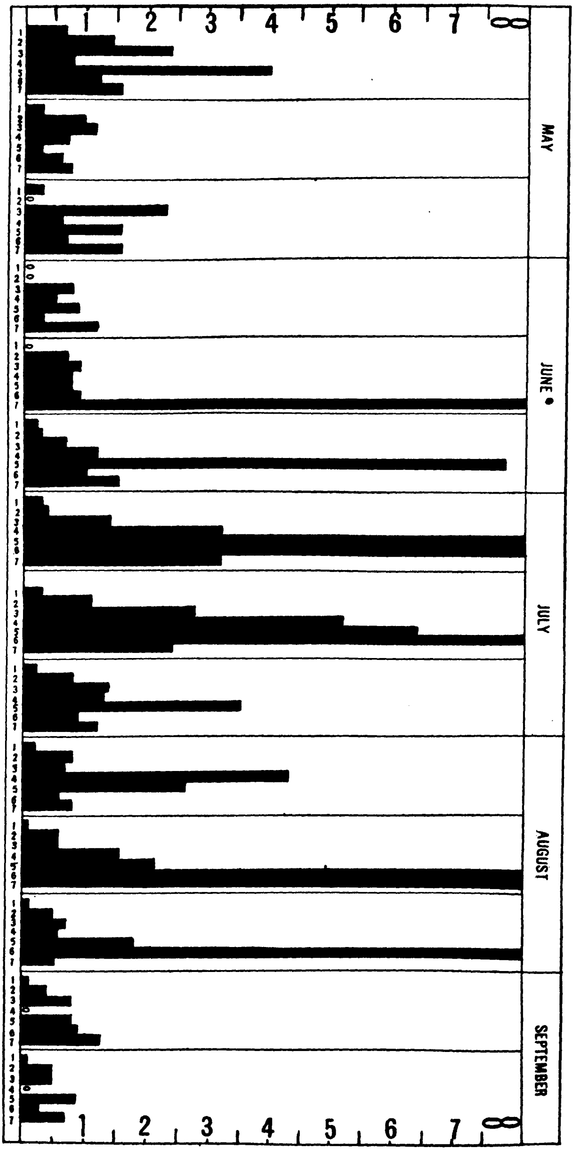

FIG. 4.—Relative xerophytism (ratio of evaporation rate to growth water) at the seven stations; a zero at base of column signifies data lacking for the period.

An examination of the differences between the curves of the separate stations brings to light certain topographical correlations. In the first place, there was a general correlation between the exposure of a station and its evaporation rate. Thus, station 7, the most exposed of the set, shows consistently the highest evaporation rates, while station 1, the least exposed, shows consistently the lowest. Even between these extremes the correlation holds, for of the three talus slope stations, no. 5, the most exposed, shows higher rates than nos. 3 and 2, which were partly sheltered within the canyon.

Again, the more exposed stations showed much more marked variation, both seasonal and diurnal, than did the more sheltered stations. The highest mean daily rate for a ten-day period (26.9 cc. per day, July 21–30) exceeded the lowest mean daily rate (8.1 cc. per day, September 9–20) by 18.8 cc. This may be compared with the excess of the maximum mean daily rate at station 1 (9.2 cc., July 21–30) over the minimum mean daily rate (1.3 cc., September 9–20), which is 7.9 cc. The excess at station 7 is 10.9 cc. greater than the excess at station 1, or a ratio of 2.4. Another notable thing is the relative stability of the daily rates at the more sheltered stations as compared with the greater fluctuation at the more exposed stations. Thus, at the two stations and for the two periods noted, the greatest mean daily rate at station 7 (26.9 cc.) exceeds the greatest mean daily rate at station 1 (9.2 cc.) by 17.7 cc., whereas the least mean daily rate at station 7 (8.1 cc.) exceeds the least mean daily rate at station 1 (1.3 cc.) by only 6.8 cc. The difference during the period of highest evaporation rate is 2.6 times as great as the difference during the period of lowest evaporation rate. The general effect of this factor is strikingly brought out by the "bunching" of the curves during June and September, the low evaporation periods. This greater variability displays itself even more markedly, of course, in the diurnal variations than in the variations of mean daily rates. During the period of high evaporation just cited, for example, the readings at station 7 on three successive days (July 14, 15, and 16) were 31.8 cc., 8.9 cc., and 19.1 cc. respectively, while on the same days readings at station 1 were 9.8 cc., 3.8 cc., and 10.4 cc. Similarly, even during a period of low evaporation, three successive readings at station 7 give 15.3 cc., 5.5 cc., and 11.6 cc., while at station 1 the corresponding readings are 4.0 cc., 1.4 cc., and 1.8 cc. Examination of the data from stations of intermediate exposure will show correlated results.

The ratios between growth water and evaporation rates, presented in fig. 4, serve to emphasize and render definite the ideas in the foregoing paragraphs. Of course, as FULLER (7) has pointed out, this ratio is a more or less artificial and arbitrary one, yet it is as good a method as we have at present for a quantitative statement of the relative xerophytism of different habitats, and inasmuch as it brings out strongly the cumulative effect of two factors operating in the same direction, it is of value.

The foregoing considerations of the atmometric and soil moisture data suggest strongly the essentially prairie-like summer conditions, even in this woodland island in the prairie, and the intensification of the summer xerophytism of the soil by the summer xerophytism of the air. The greatest evaporating power of the air prevails precisely during those periods when the plants are least able to obtain water from the soil to satisfy it. Summer rains relieve the tension, to be sure, but even after heavy rains the relief is short-lived, and slighter in degree than might be supposed. Only in places at once well endowed with a supply of water and at least fairly well sheltered from extreme transpirational conditions (represented in the present study by station 1) is there any chance for germination and growth of seedlings during the middle of the growing season. This theoretical conclusion is borne out by the existence in such places of annuals as the dominant herbaceous vegetation, and by the presence of large numbers of tree seedlings. Furthermore, it is here also that one finds "superclimax" trees, like *Acer saccharum* and *Asimina triloba*, belonging normally to more mesophytic regions. In the more exposed stations (the extreme being no. 7) the unfavorable summer conditions set in so early and become so severe as to discourage seedling growth. The canyon bottoms therefore receive strangers hospitably and permit of relatively rapid succession, while the exposed uplands conservatively cling to the climax vegetation they have, and permit, in places too xerophytic even for this, the survival of relict communities, like the conifers on the edges of the cliffs.

INSOLATION EFFECTS.—An examination of the radio-atmometric data serves to emphasize the atmometric phenomena already noted, in addition to its main purpose of getting some idea of the sunlight intensity as this affects evaporation. The evaporation from the black cups of course follows the same general seasonal curve as that from the white, the excess varying according to seasonal and local conditions. The radio-atmometric effect, as one might expect, was greatest during the season of greatest exposure, that is, during the month of May, before the leaves were on the trees. After the first of June the effect was much less marked. Even during the hot weather of July the evaporation rate from the black cups exceeded that from the white by but little.

The general differentiation in the radio-atmometric effect with the development of the foliar screen was accentuated by local variations. Thus, the tendency throughout the season was for a greater difference at station 7, the most exposed of the set, located in an open stand of second growth oak. Station 1, located on a treeless portion of the canyon bottom, in a stand of *Impatiens pallida*, showed a most notable radio-atmometric effect during May, before the surrounding herbage was well grown; after July 1 the effect fell almost to zero, and remained so throughout the rest of the season.

Of course it is not possible to take the radio-atmometric effect as a measure of solar radiation in all its effects on plants. It is intended only as an approximate determination of direct solar radiation on the evaporation of water from a free surface. Taking it as a rough index of the total illumination received, however, we find that during the season when other ecological factors are favorable for the growth of seedlings on the forest floor it is at its maximum, and that it falls off notably after the leafing out of the trees. Presumably then, sunlight conditions conspire with the ecological factors already discussed to make late spring the optimum season for seedling growth, and that at places like station 1, where other conditions are favorable even when they are most unfavorable elsewhere, sunlight intensity falls to an unfavorable level after about July 1, or possibly even earlier. It must be emphasized again, however, that so little is known about the sunlight relations of plants that attempts at close correlation are for the present unprofitable.

TEMPERATURE (fig. 5).—Temperatures of both air and soil show similar seasonal variations, with high points in July, and a falling off in August and September, interrupted by a brief period of high temperatures during the first few days of the latter month. The figures up to July 1 can be accepted only as approximations, since they are absolute maxima and minima for periods of more than a week, instead of mean daily maxima and minima. For this reason too much significance must not be attached to the greater spread between maxima and minima. Although a greater spread did undoubtedly exist, it probably was not so great as the thermometer readings at the ends of the periods would indicate.

So far as any significance may be attached to the figures before the period of daily readings began, the influence of the diminution of general exposure through the leafing of the trees seems to be at work here also, for during May the maxima both for air and soil show as marked a spread as that shown for the warmer months of July and August. This spread is especially noticeable in the data for soil maxima,[1] inasmuch as it amounts to eight or ten degrees throughout May, falls to a point at one of the June readings, and for the rest of the season never exceeds three degrees. These results agree fairly well with those of McDOUGALL (14), who found a consistent seasonal variation of about 4° F. between the soil temperatures of typical upland and lowland stations in Illinois forests.

Topographical differences seem to have some influence also, although the correlation is not so clear here as it is in the case of the atmometric and radio-atmometric data. It may be remarked, however, that the high lying stations (typified by no. 7) show the highest maxima both for air and soil, and the low lying stations the lowest maxima. On the other hand, the lowest minima for the air are obtained at the high lying stations and the highest minima at the lower ones. This may be due, among other things, to the denser leaf covering and the greater amount of underbrush at the

[1] Because of the close agreement between the readings for all the stations after July 1, it is not thought worth while to present the soil temperature data in detail.

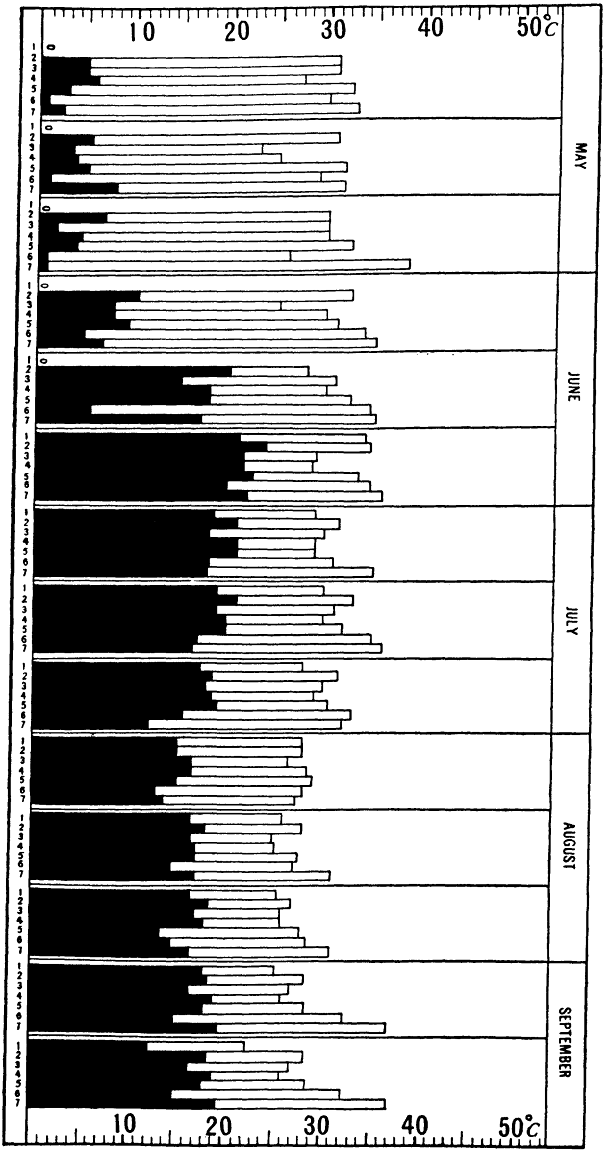

FIG. 5.—Mean daily maximum and minimum air temperatures at the seven stations; a zero at base of column signifies data lacking for the period.

lower stations, holding the lower stratum of air to a certain extent against displacement by air drainage.

One object in obtaining these temperature data was to ascertain whether temperature differences might be correlated with the invasion of lower latitude plants, like *Asimina triloba*, into the lower levels. The data obtained, however, are contradictory. The mean temperatures are undoubtedly higher at the higher lying stations, the last points of invasion, and also the last points of cession by relict northern species. On the other hand, the consistent higher minima at the lower levels might well permit a slightly longer growing period, and perhaps even milder winter conditions. Otherwise stated, the temperature optimum for southern species might not be so nearly approximated on the lower stations as at the higher, but a point above the minimum might be maintained throughout a longer period each year. The main reason for the confinement of southern invaders to the bottom lands, however, must probably be sought in the more favorable moisture conditions at these levels. The writer does not feel that attempts at close correlations between temperature and vegetation over such small differences in altitude would be very profitable at the present stage of development in ecological science. It is interesting to find, however, that fairly consistent small differences in temperature do coexist with small topographical differences.

Summary

1. This paper is a study of the ecological factors at seven representative topographical points in the Illinois State Park at Starved Rock, during the growing season of 1921. The factors studied were (*a*) soil moisture, (*b*) evaporating power of the air, (*c*) evaporating power of solar radiation, and (*d*) temperature of air and soil.

2. Observations were taken with special reference to their influence on seedling growth, because of the importance of the latter as a factor in succession.

3. Soil moisture was found to vary (*a*) seasonally, falling off after the close of the spring rains and reaching a point below the minimum necessary for plant growth during a considerable portion

of the summer, and rising again with the beginning of the fall rains; (*b*) according to the mechanical composition (and therefore retentivity) of the soil; (*c*) to a minor extent according to topography; and (*d*) according to the density of the foliage canopy.

4. The evaporating power of the air was found to vary (*a*) seasonally, increasing until midsummer and falling off afterward; (*b*) according to the state of tree foliation, declining after the forest had become completely clothed; and (*c*) topographically, being greatest for the same period in exposed stations and least in sheltered ones.

5. The evaporating power of solar radiation was found to vary in the same manner as the evaporating power of the air, complementing and emphasizing the data under the latter head.

6. Maximum temperatures were found to vary in much the same manner as the evaporating power of the air. Minimum temperatures of the air were found to be affected by topography in a mode inverse to that of the maxima, being highest at the low lying stations and lowest at the higher lying ones.

7. Certain vegetational phenomena showed a general correlation with the instrumental observations: (*a*) the density of ground cover, number of tree seedlings, and proportion of annuals in the total vegetation of any given association bore an inverse relation to the relative xerophytism; (*b*) in all but one of the stations, conditions were favorable for the development of seedlings only in spring and fall; (*c*) in the climax forest for the region (upland oak woods) the water-supplying power of the soil consistently fell nearly or quite to zero during the summer drought period; (*d*) the location of "subclimax" and "superclimax" associations showed closer correlation with water relations than with temperature.

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