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Some ecological factors in secondary succession: upland hardwood. II. Soil reaction and plant distribution in the Sycamore creek region

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SOME ECOLOGICAL FACTORS IN SECONDARY SUCCESSION: UPLAND HARDWOODS

II. SOIL REACTION AND PLANT DISTRIBUTION IN THE SYCAMORE CREEK REGION

By STANLEY A. CAIN *and* RAY C. FRIESNER

An examination of the vegetation of the Sycamore Creek region would certainly warrant the assumption that the soils of many of the ridge tops are decidedly acid, for there are a number of plant communities made up of notoriously acid-tolerant species. Conspicuous members of these communities are *Vaccinium vacillans*[1], *V. stamineum*, *Gaylussacia baccata*, *Populus grandidentata*, and various mosses, as *Polytrichum juniperinum*, *Catherinea angustata*, *Leucobryum*, *Dicranum*, etc. Since these communities are exclusively on the tops and upper slopes of the characteristically narrow ridges, it was thought desirable to investigate the extent of the hydrogen-ion concentration of these soils and to ascertain any relations existing between the pH and the topography, and, inevitably, of course, the vegetation.

The existence of a correlation between the reaction of the substratum and the nature of the plant cover was suggested by Pfeffer in the last part of last century; but it was not until the technique of soil reaction determination was worked out, about 1915-16, that any activity was seen along this line. Since that time there has appeared a voluminous literature. It is not within the scope of this paper to go into the principles underlying the technique, Clark (7), or the purpose of such investigations, Christopherson (6). It will be sufficient to note a few facts which have stimulated the present studies.

First, Salisbury (11) in 1922, published on the stratification of hydrogen-ion concentration of the soil in relation to leaching and plant succession. He came to the conclusion that, due to leaching action, the surface soil is poorest in bases which increase in amount with increasing depth. The organic content decreases rapidly with increasing depth, associated with which there is a gradient of hydrogen-ion concentration attaining its maximum at the surface. The view is advanced that woodlands in general and probably all types of undisturbed plant com-

[1]Nomenclature: Gray's New Manual of Botany, 7th Ed.

munities are tending to become progressively more acid, with consequent changes in the character of the vegetation. This he summarizes in two fundamental principles, viz.:

(a) A progressive increase in the acidity, resulting in corresponding changes in the character of the vegetation;

(b) A more rapid leaching on high than on low ground, resulting in a depression of the upper limits of the zones as the summit vegetation extends with the extension of higher acidity.

Second, when the formations are not too poor in species, we can, according to Olsen (10), conclude from the composition of the vegetation to the hydrogen-ion concentration of the soil.

Lastly, this problem was made desirable because of an idea derived from a paper by Miss Braun (1) on certain relic colonies in southern Ohio. The plant communities considered by her were prairie relics. It was thought that the Sycamore Creek communities here considered are also relic colonies, but in this case xerophytic-acid-boreal relics. Bog-plant communities along the southern limits of their present distribution are well-known hydrophytic-acid-boreal relics. Transeau (12); Cain (3). It is believed that the xerophytic communities are much more common, although not so well known. Topography and stream erosion are conducive to the development and maintenance of these xerophytic relics, whereas the process of plantation tends toward the elimination of bog-plant habitats.

PROCEDURE—Three ridges were selected for the present investigation. In the case of series AB and series C, the ridges present north and south slopes, the crest of the ridge being about one hundred feet above the base. Series D represents a continuation of C to the northward, but runs up onto ridge D lengthwise. The symbols A, B, C, D, correspond to the atmometer stations. Cain and Friesner (4). Station A was on the north slope and Station B was on the top of the ridge here indicated as AB. Atmometer Station C was on the top of the ridge where the pH series C was located. Series D was an extension of line C in the direction of Station D, but was not actually to its location. The direction of the line for each series was selected and then run out by the use of a surveyor's tape and an Abney clinometer. Notes were kept of the angles and the length of each slope, so that it was an easy matter to indicate the location of the samples and plot the topography of the ridges in the graphs.

Soil samples of about two hundred grams each were collected in paper bags. Those samples indicated as surface soil were taken immediately beneath the litter in the soil layer of highest organic content. Subsoil samples were taken at a depth of approximately six inches, which was sufficient to pass the humus layer in all cases. In series AB, samples 30 and 32 were taken at three inches depth, which was the bottom of the soil due to the sandstone outcropping. As indicated in the tables, these samples were in pairs, surface and subsoils taken in a vertical line.

The hydrogen-ion concentration of these samples was determined electrometrically by the use of the Youden portable apparatus developed at the Boyce Thompson Institute, 1928. All readings were completed within a few days after collecting. The samples were procured on November 10 and November 16. Gustafson (9) has shown that soil samples do not undergo any appreciable change on storage. Three or more separate readings were made from each sample collected. The present data include about 250 readings for the establishment of three curves.

Results and Discussion—From an examination of the tables and curves for the three series of pH readings, it will be seen that there is a general tendency for the subsoil to be more acid than the surface soil. Of the forty-one sets of surface and subsoil samples, only seven showed the surface to be more acid than the subsoil. These seven instances were:

Sample No.		Surface Soil pH	Subsoil pH
AB	1	4.756	4.926
	7	4.196	4.569
	13	5.286	5.789
C	9	5.891	6.474
D	11	4.903	5.596
	13	5.027	5.136
	15	5.212	5.636

It will be seen that these samples are among the more acid. On referring them to their topographical positions, one finds that these samples were taken on the ridge tops except for AB 13 and C 9, which were on lower slopes. These surface soils contain very little organic matter, the humus baving been greatly reduced, apparently by fire. The differences in pH between the surface and the subsoils in some cases are of about the same order as the differences between different tests of the same sample, but in most cases there is a much greater difference between the averages for surface and subsoil than between different tests of the same sample. It should be noted that the former occur mainly in samples which are of the more acid type for this region.

In view of these results, it must be concluded that the stratification of soil reaction in this region results in a gradient reaching a maximum pH in the subsoil. This result is directly opposed to part of the conclusion reached by Salisbury (11), which he states as follows: "The organic content decreases rapidly with increasing depth, associated with which, and in some cases with increasing base content, there is a gradient of hydrogen-ion concentration attaining its maximum at the surface." In some previous work, Cain (2), the type of gradient observed by Salisbury was found to exist for lowland forest soils and probably will be found in some upland soils of this region when a more extensive study is made. A number of soil reaction profiles and transects of high ridges and mountains in the Great Smoky mountains of Tennessee indicate gradients entirely in harmony with Salisbury's observations, where, despite a naturally acid subsoil, the surface soils reach extreme hydrogen-ion concentrations as a result of upland peat formation, Cain (5).

The conclusion reached by Salisbury is an entirely reasonable one. The inversion of the gradient in the soils of the Sycamore Creek region is probably explained by the following facts. The vegetation of these ridges has been greatly disturbed by cutting and fires, resulting in a reduction of the organic content of the surface soils. Second, the underlying sandstone and shale rocks, upon decomposition, produce an inorganic acid soil. Christopherson (6) and others have noticed that the composition of the parent rock influences the hydrogen-ion concentration of the soils, granites and amphibolites producing soils of high acidity, while schists produce soils near the neutral point.

The Wisconsin ice sheet covered that part of Morgan county here under study. The hills are topped with a heavy clay known as the Miami Clay Loam, which is probably of this glacial origin, though in many places it is very difficult to be certain that it is not residual soil from the underlying sandstone (knobstone) and shale. This clay varies from zero to several feet in thickness. Where the clay is absent, such as on the slopes, the soil is very shallow and is clearly the residual product of underlying sandy shale which in turn seems to be but local shaleimpurities of the knobstone. Reaction studies of these soils seem to indicate no correlation between soil reaction and relative amounts of sand, shale and clay in any particular soil sample.

TABLE I—pH OF SOIL SAMPLES, RIDGE TRANSECT AB, SYCAMORE CREEK

SURFACE SOIL			SUBSOIL			SURFACE SOIL			SUBSOIL		
No.	pH	Aver.	No.	pH	Aver.	No.	pH	Aver.	No.	pH	Aver.
1a	4.796		2a	4.893		3a	5.398		4a	5.000	
1b	4.779	4.756	2b	4.949	4.926	3b	5.483	5.379	4b	4.915	4.938
1c	4.694		2c	4.847		3c	5.255		4c	4.898	
5a	4.983		6a	4.592		7a	4.235		8a	4.541	
5b	4.813	4.853	6b	4.558	4.575	7b	4.320	4.196	8b	4.541	4.569
5c	4.762		6c	4.575		7c	4.033		8c	4.626	
9a	4.507		10a	4.439		11a	5.034		12a	4.694	
9b	4.711	4.575	10b	4.405	4.442	11b	4.813	5.051	12b	4.626	4.660
9c	4.507		10c	4.483		11c	5.306		12c	4.660	
13a	5.170		14a	5.704		15a	6.180		16a	6.486	
13b	5.272	5.286	14b	5.925	5.789	15b	6.367	6.378	16b	6.486	6.356
13c	5.415		14c	5.738		15c	6.588		16c	6.095	
17a	7.285		18a	7.530		19a	7.530		20a	7.506	
17b	7.666	7.566	18b	7.598	7.528	19b	7.770	7.690	20b	7.353	7.432
17c	7.717		18c	7.455		19c	7.770		20c	7.438	
21a	6.469		22a	5.085		23a	6.367		24a	5.755	
21b	6.741	6.560	22b	4.830	4.955	23b	6.299	6.367	24b	5.670	5.721
21c	6.469		22c	4.949		23c	6.435		24c	5.738	
25a	5.272		26a	4.745		27a	4.898		28a	4.728	
25b	5.119	5.315	26b	4.762	4.773	27b	4.983	4.955	28b	4.864	4.853
25c	5.255		26c	4.813		27c	4.983		28c	4.966	
29a	5.857		30a	5.153		31a	5.636		32a	5.069	
29b	5.925	5.857	30b	5.017	5.096	31b	5.676	5.647	32b	5.085	5.074
29c	5.789		30c	5.119		31c	5.636		32c	5.068	
33a	6.452		34a	4.609		35a	6.333		36a	5.102	
33b	6.452	6.486	34b	4.643	4.654	35b	6.486	6.435	36b	5.051	5.051
33c	6.554		34c	4.711		35c	6.486		36c	5.000	
37a	6.435		38a	5.670		39a	6.486		40a	5.187	
37b	6.707	6.323	38b	5.318	5.447	39b	6.588	6.418	40b	5.238	5.227
37c	6.826		38c	5.289		39c	6.180		40c	5.255	

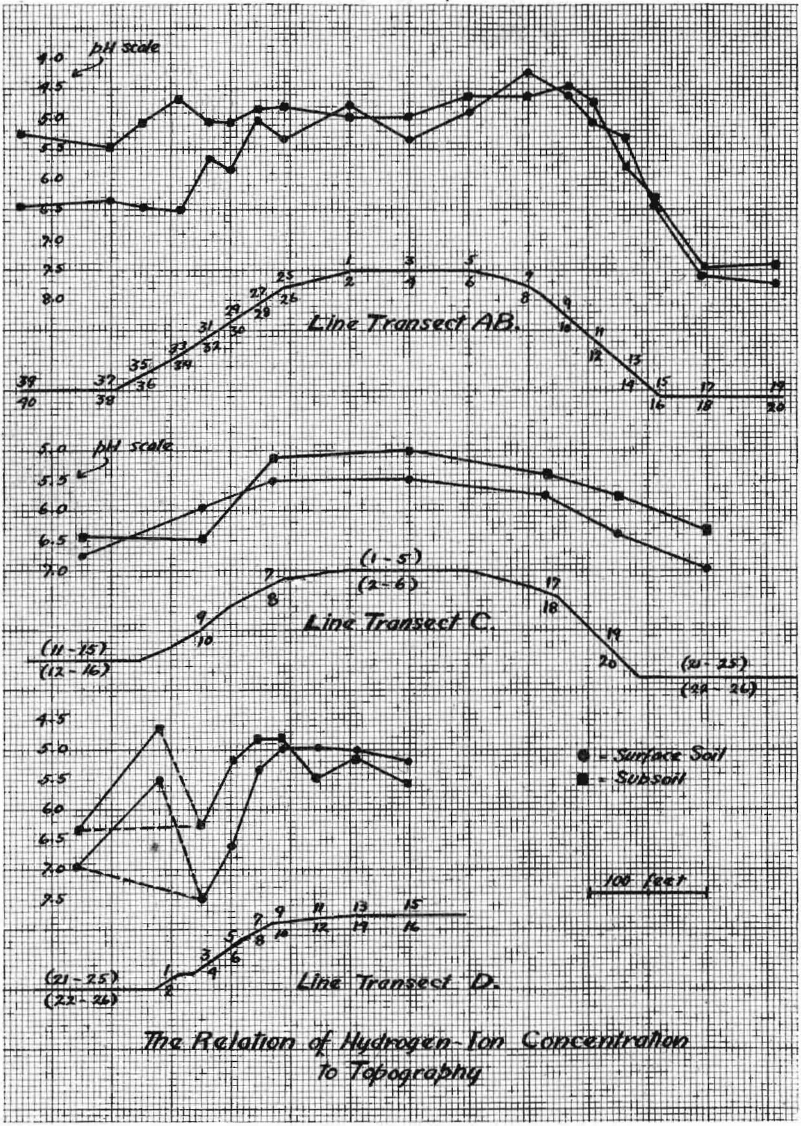

Figure 1. The relation of hydrogen-ion concentration to topography
Series AB, C, D

TABLE II—pH OF SOIL SAMPLES, RIDGE TRANSECT C, SYCAMORE CREEK

SURFACE SOIL			SUBSOIL			SURFACE SOIL			SUBSOIL		
No.	pH	Aver.	No.	pH	Aver.	No.	pH	Aver.	No.	pH	Aver.
1a	5.772		2a	5.170		3a	4.983		4a	4.949	
1b	5.721	5.743	2b	5.187	5.204	3b	5.085	5.218	4b	4.966	4.972
1c	5.738		2c	5.255		3c	5.585		4c	5.000	
5a	5.432		6a	4.864		7a	5.381		8a	4.949	
5b	5.398	5.485	6b	4.762	4.830	7b	5.364	5.495	8b	5.136	5.113
5c	5.534		6c	4.864		7c	5.466		8c	5.255	
						7d	5.772				
9a	5.602		10a	6.537		11a	6.945		12a	6.520	
9b	5.959	5.891	10b	6.537	6.474	11b	6.401	6.764	12b	6.520	6.560
9c	6.112		10c	6.350		11c	6.945		12c	6.639	
13a	6.707		14a	6.265		15a	6.571		16a	6.588	
13b	7.030	6.888	14b	6.265	6.146	15b	6.826	6.718	16b	6.656	6.599
13c	6.928		14c	5.908		15c	6.758		16c	6.554	
17a	5.755		18a	5.415		19a	6.435		20a	5.974	
17b	5.721	5.749	18b	5.449	5.432	19b	6.367	6.401	20b	5.636	5.778
17c	5.772		18c	5.432		19c	6.401		20c	5.832	
21a	6.571		22a	5.942		23a	6.637		24a	6.214	
21b	6.775	6.707	22b	5.806	5.840	23b	7.047	6.911	24b	6.248	6.288
21c	6.775		22c	5.772		23c	7.013		24c	6.410	
25a	7.183		26a	7.047							
25b	7.370	7.308	26b	6.860	6.951						
25c	7.370		26c	6.945							

TABLE III—pH OF SOIL SAMPLES, RIDGE TRANSECT D, SYCAMORE CREEK

SURFACE SOIL			SUBSOIL			SURFACE SOIL			SUBSOIL		
No.	pH	Aver.	No.	pH	Aver.	No.	pH	Aver.	No.	pH	Aver.
1a	5.670		2a	4.864		3a	7.564		4a	6.282	
1b	5.449	5.551	2b	4.422	4.626	3b	7.387	7.539	4b	6.044	6.203
1c	5.534		2c	4.592		3c	7.666		4c	6.282	
5a	6.911		6a	5.344		7a	5.415		8a	4.864	
5b	6.350	6.639	6b	5.000	5.115	7b	5.221	5.314	8b	4.864	4.869
5c	6.656		6c	5.000		7c	5.306		8c	4.881	
9a	4.830		10a	4.881		11a	4.966		12a	5.653	
9b	4.966	4.920	10b	4.830	4.852	11b	4.915	4.903	12b	5.806	5.596
9c	4.966		10c	4.874		11c	4.830		12c	5.330	
13a	5.221		14a	5.136		15a	5.068		16a	5.704	
13b	5.204	5.027	14b	5.272	5.136	15b	5.330	5.212	16b	5.806	5.636
13c	4.864		14c	5.000		15c	5.238		16c	5.398	
13d	4.847										

The soils of the Sycamore Creek region, from these observations, are found to range from pH 4.0 in series AB, sample 7, to pH 7.77 in sample 19 of that same series. By far the majority of the samples are acid in reaction. The most acid soils are characteristic of the ridge tops and upper slopes, while the soils of the bottoms are much less acid, many of them, in fact, being circumneutral. It can be seen from plotting the pH with the contour of the ridges that there is a general agreement of the three curves; that is, the line of the topography and the curves of the surface soil pH and the subsoil pH, plotted in continuous lines as they were collected, show conformity (Figure 1).

As has previously been mentioned, Salisbury noticed that "woodlands occupying valley slopes tend to exhibit less marked surface leaching as we descend, and the chief differences between upland and lowland woods are regarded as related to this factor." The present work is in complete agreement with that couclusion in so far as it expresses the relation of hydrogen-ion concentration to topography. There is sufficient evidence of the effect of more extensive leaching out of bases on the ridge tops and upper slopes. However, it is not believed that the conclusion is warranted that this difference in soil reaction constitutes the chief cause of the differences between upland and lowland vegetation. It must be remembered that, although soil reaction is an important factor, there are other factors, edaphic and climatic, contributing to the upland-lowland differences in vegetation. For example, differences in soil moisture and the physical and chemical nature of the soil (other than pH) are frequently important. Then there are the atmospheric factors summed up in the evaporating power of the air. Fuller (8) has shown that the differences in ratios between evaporation and growth-water in various plant associations are sufficient to be efficient factors in causing succession. Further, it must be noted that considerable fluctuations occur within different vegetation types, so that soil reaction becomes a factor capable of interpretation only in cases of considerable differences in the respective pH ranges of related plant associations. It is not desired, then, to deny soil reaction as a factor, but merely to emphasize the following points: (a) soil reaction alone is probably not often a limiting factor; (b) it is possible to determine soil reaction to a much finer degree than it can be interpreted in terms of vegetation. Therefore, the pH of plant associations should be expressed in terms of comparative ranges and averages of reaction. This is particularly desirable in view of local variations which occur in the soil reaction. Christopherson (6) comments on this point as follows: "Variation in the soil reaction may take place from one locality to another within short distances. The soil of one particular stand may thus vary considerably from place to place, and the soil of different stands of the same association may vary still more. In spite of this, however, the associations may be limited to a relatively narrow range of soil reactions, which are characteristic for each association."

TABLE IV—COMPARISON OF SOILS FROM RIDGES AB, C AND D

SURFACE SOIL			SUBSOIL		
Series AB					
Ridge top	pH 5.583	15 tests	Ridge top	pH 5.023	15 tests
Upper slope	pH 4.979	15 tests	Upper slope	pH 4.746	15 tests
Lower slope	pH 5.880	18 tests	Lower slope	pH 5.264	18 tests
Bottom	pH 6.996	12 tests	Bottom	pH 6.408	12 tests
Series C					
Ridge top	pH 5.473	9 tests	Ridge top	pH 5.002	9 tests
Upper slope	pH 5.622	7 tests	Upper slope	pH 5.272	6 tests
Lower slope	pH 6.146	6 tests	Lower slope	pH 6.126	6 tests
Bottom	pH 6.882	18 tests	Bottom	pH 6.347	18 tests
Series D					
Ridge top	pH 5.044	10 tests	Ridge top	pH 5.589	9 tests
Upper slope	pH 5.624	9 tests	Upper slope	pH 5.945	9 tests
Lower slope	pH 6.545	6 tests	Lower slope	pH 5.414	6 tests
Bottom	same as C		Bottom	same as C	
Averages					
Ridge top	pH 5.366	34 tests	Ridge top	pH 5.122	33 tests
Upper slope	pH 5.408	31 tests	Upper slope	pH 4.988	30 tests
Lower slope	pH 6.190	30 tests	Lower slope	pH 5.601	30 tests
Bottom	pH 6.939	30 tests	Bottom	pH 6.377	30 tests
		125			123

Table IV sums up the results of the relation of soil reaction to topography, while the relation of the reaction to the vegetation is found to be as follows: The ridge tops and upper slopes are the location of the xerophytic-acid-boreal relics. It can therefore be said that these colonies are to be found in the Sycamore Creek region where the soil reaction averages around pH 5.3 to 5.4 for the surface and pH 4.9 to 5.1 for the subsoil. The relation of the various plant associations characteristic of the secondary succession in this region, to the soil reaction, is not fully investigated, but it would seem that all the stages are capable of development within the region. So, the climax beech-maple association is to be expected, even on the ridge tops. As a matter of fact, the ridge top in series D, although now open and occupied by *Vaccinium* and the like, bears remnants of a former climax forest. Two possible explanations occur for the presence of the ericads as a characteristic part of the early stages in secondary succession after cut-over and fire. First, they get a start after deforestation from seeds brought in by migrating birds. This has been shown by Darwin, Wallace, and many since their time, to be a common means of wide distribution for plants with edible fruits. The other possibility is that some of these plants have survived in the less favorable habitats (where competition is less severe) since early postglacial times, and are to be considered then as true boreal relics. It would not seem possible to determine at the present time which is the true explanation.

One or two facts remain to be pointed out as to differences in soil reactions. In the first place, the differences between the pH averages of the surface and the subsoil (Table IV) are greater at the bottom than they are at the top of the ridges; viz:

Ridge top—Average difference	.244
Upper slope—Average difference	.420
Lower slope—Average difference	.489
Bottom—Average difference	.449

TABLE V—SOIL REACTION DIFFERENCES, THREE TESTS PER SAMPLE, BASED ON 250 READINGS

Surface soil—Greatest difference	.602
Least difference	.040
Average difference	.264
Subsoil—Greatest difference	.442
Least difference	.017
Average difference	.236
ph 4 Range—Average difference	.125
pH 6-7 Range—Average difference	.288

Second, the tables reveal something of the amount of fluctuation to be expected in the soil reaction of different parts of the same locality. Table V brings out these points. The average deviation, based on three tests per sample, is .264 for the surface soils and slightly less, .236, for the subsoils. It will also be seen that the more acid the soil the less the fluctuations are likely to be, since the soils within the range of pH 4 show an average deviation of .125, while the circumneutral soils show a deviation of .288 in pH.

SUMMARY

1. Floristic studies of the ridges of the Sycamore Creek region reveal the presence of a number of acid-tolerant plants which make up xerophytic-acid-boreal relic colonies.

2. Soil reaction studies indicate that the soils in which these plants grow are decidedly acid, reaching a maximum on the ridge tops where the relic colonies are more abundant.

3. Hydrogen-ion curves parallel profile curves of the ridges, the former ascending with the latter.

4. The subsoil is more acid than the surface soil in most places, though a few samples were taken in which the reverse was true.

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