THE RELATION OF pH TO PLANT DISTRIBUTION IN NATURE[1]

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INTRODUCTION

FOURTEEN years have elapsed since Dr. E. T. Wherry (1916) first applied the modern method of measuring soil acidity towards the solution of plant distribution problems. Since this classical work Wherry and many others have produced hydrogen-ion papers in almost colossal proportions. Mevius (1927) writes a comprehensive review of soil reaction as it affects both cultivated and wild plants and gives 759 titles. Arrhenius (1926) in his review uses 403 titles. The author, however, will use and cite only such works as seem pertinent for the purpose of this paper. Although the attack has been concentrated on the higher plants, the lower, green ones, at least, do not remain unscathed, so that we have soil acidity studies from algae to orchids. By virtue of his sustained and vigorous activity Wherry is still the leading pH investigator among plant ecologists in America. Ironically enough, if we except his work, soil acidity investigations though begun in America have attained their fullest expression in Europe. Some of the European workers, as we shall soon see, have been singularly precise in their determinations and thought provoking in their carefully prepared presentations.

The once apparently narrow and novel subject of soil reaction has by this time developed into a very broad field. Without necessarily ignoring the perfectly patent influence of soil acidity on plant distribution, most investigators soon realized that other factors were opera-

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tive. More and more species found outside of their so-called natural ranges have quite necessarily generated many points of view regarding the whole subject of soil acidity. Some still consider pH *the* factor; others, *a* factor; and there are those who consider its influence unimportant in their particular studied species. Some consider its influence direct; others, indirect. Some say it is hydrogen-ion *per se*. Also, some writers lay much stress on attending factors. The latter view complicates the matter uncomfortably, for it forces us to recognize an abstruse triangular interrelationship among hydrogen-ion concentration, plants and attending factors, or what Clements calls concomitants. In the following pages we can only suggest the present status of pH work. In doing so we might first make a preliminary survey of the whole plant kingdom by beginning with the higher plants and ending with the algae.

Members of Plant Kingdom Investigated

Seed plants.—Following Coville's (1913) lead, Wherry has shown that the ericads are, with few exceptions, notably acid-loving species. The reader is referred to his summary of 1920 for his thought and work to that date. Only a few species are found to reach over into alkaline soils. Wherry (1920) has also shown a very restricted range for the orchids, nearly all of them being confined to decidedly acid habitats. If the reader consults the work of Arrhenius (1920), Olsen (1921), Salisbury (1921), Atkins (1922), Chodat (1924), Kelley (1923) and Christophersen (1925), he will find many other seed plants with high correlation between pH and distribution. On the other hand, it must be brought out that trees, as a group, are notably indifferent. See Kotilainen (1927), Geisler (1926), Salisbury (1921) and Kurz (1923). Miss Geisler also points out that a number of the herbaceous flowering plants of the forests tolerate a wide range.

Ferns.—Wherry (1920), Steagall (1926) and Robinove and La Rue (1928) have given special consideration to the ferns and present their findings in convenient tables. The results of all three investigators indicate that most species of ferns for which the data are at all comprehensive tolerate a wide range of acidity. Wherry, however, assigns optimum reactions to nearly all his species. Most of Robinove and La Rue's species show a wide range of tolerance extending from definitely acid to alkaline habitats. Only a few, where the number of tests was limited, proved the exception, as Robinove and La Rue expected. But the data of Steagall and Wherry extended even their range considerably: consult Table I, which is an adaptation from Robinove and La Rue, Wherry and Steagall.

Table 1.

	Species	No of tests	pH range	Optimum reaction
Robinove and La Rue	Cystopteris bulbifera	3	7.4-8.2	7.0
Wherry	" "	30	5.5-8.5	7.0
Steagall	" "	12	6.0-8.0	7.0
R and L R	Aspidium spinulosum	8	4.8-6.4	
W	Var intermedium	20	4.5-8.0	
S.	" "	10	5.5-7.0	6.0
R. and L.R	Pteris aquilina	3	4.6-6.8	
W	" "	30	4.5-6.5	5.5
S.	" "	6	5.5-6.0	5.5
W.	(Southern) Camptosorus rhizophyllus	50	5.5-8.5	7.0
S.	" " "	10	4.5-6.5	5.5
W.	" Asplenium platyneuron	50	4.5-8.5	4.5
S	" " "	13	5.0-6.5	6.0
W.	(Northern) Polypodium vulgare	50	5.0-8.5	6.0
S.	" " "	12	4.5-5.0	5.0
W.	(Southern) Polypodium polypodioides	15	4.5-7.0	4.5
S.	" " "	10	4.5-7.0	6.5
W	" Pellaea atropurpurea	30	5.5-8.5	7.0
S.	" " "	15	7.5-8.0	8.0

In the second part of the table the writer advisedly pits a part of Wherry's data against Steagall's. As expected, Wherry's individuals, because of the greater number of tests, show in the main wider ranges than Steagall's. Both investigators assign an optimum reaction to their species. In accord with Wherry's practice, the reaction most frequently encountered is called the optimum reaction. The optimum thus roughly conforms with the frequency mode of the statisticians. Wherry sees a relationship between "soil reaction and geographic range." The writer can do no better than quote him in part from pages 262–264 (1920):

It is noteworthy, however, that the peculiar relations found to exist among rock ferns—the favoring of acid soils by southern species and of circumneutral soils by northern ones—is likewise well marked in the present series of plants. As the same sort of relation appears also with other plants than the ferns, in particular with the native orchids, it is sufficiently definite to justify inquiry into its probable origin. . . .

The territory left bare by the retreat of the great ice-sheet must at first have presented an almost unbroken expanse of circumneutral soils, and the vegetation which first occupied it accordingly comprised only plants which thrive best in such soils. Although acid soils have developed subsequently in many places, and permitted invasion by plants adapted to growth under acid conditions, a considerable number of the original occupants still persist, and are to-day classed as ''northern'' species.

In more southern regions, on the other hand, decomposition usually outstrips disintegration, so that soils containing undecomposed carbonate minerals are relatively rare. Except where limestone outcrops or where leaf mold accumulates, therefore, the dominant soil reactions are inclined to be acid, and the plants, established there since long before the glacial period, have become adapted to growth in such soils. The favoring of circumneutral soils by northern species, and of acid soils by southern ones, is thus connected with the geological history of the respective regions.

If we refer to the table we will notice that the optima of Wherry and Steagall do not always coincide. In making a meteorological study of southern Illinois, Miss Steagall finds that the latter differs very little from Virginia (southern limit of Wherry's fern study) except that the summer temperature in July may average 20° F. higher than in Virginia. According to Miss Steagall, this extremely high July temperature, together with the low rainfall—sometimes less than one half inch in July—rather than soil reaction, accounts for the distribution of rock ferns in southern Illinois. Here, too, we shall rely on quotations from pages 134–135, Miss Steagall (1926):

Polypodium polypodioides, a southern fern, in Wherry's tests run into maximum specific acidity 300 [pH 4.5]; *Polypodium vulgare* found its maximum at 10 [pH 6.0]. In southern Illinois tests *P. polypodioides* had its maximum at specific acidity 3 [pH 6.5], although it showed itself capable of living in higher acidities; *P. vulgare* had its maximum at 100 [pH 5.0], and did not run lower anywhere. What is the factor that reverses these fern habitats between Virginia and southern Illinois? As has been shown, the striking difference between the Virginia and the southern Illinois climate is the intense heat of summer. Since *P. polypodioides* is better adapted by its structure to endure these conditions, it runs ten to fifty feet higher on the sandstone, where there is little soil but its own frond mold. As a consequence its soil tests run the gamut of acidities from one [pH 7.0] to 300 [pH 4.5], only with the difference that here its maximum runs at acidity 3 [pH 6.5]. *P. vulgare,* on the contrary, less xerophytic in structure, adheres to the lower rocks where there is more soil, even when this soil be weathered to acidity 100 [pH 5.0].

Camptosorus rhizophyllus in a cooler climate grows on calcareous rock, and there finds the right amount of moisture when specific acidity is one, but in southern Illinois that it may get sufficient moisture it must resort to sandstone with maximum 30 [pH 5.5].

The distinguishing factor between north and south, as far as the plant is concerned, is not the presence or absence of calcareous rock, as has been suggested. These are abundant in both regions. Temperature has changed, and this factor affects the amount of soil water and the amount of transpiration. This factor then has driven the semi-xerophytic forms from the dry limestone to a medium where moisture is available.

Even while we hold this judgment in abeyance we can not keep from seeing that Dr. Wherry has opened up a highly suggestive train of thought which Miss Steagall has met in a highly interesting manner.

Mosses and liverworts.—The almost universal correlation between Sphagnums and acid substrata is well known. But Robinove and La Rue (1928), already quoted, have recently given us some data for thirty-two species of liverworts and sixty-two of true mosses. Of the ninety-four species, thirty-eight were tested in less than five situations each, and only twelve species in ten or more habitats. They worked in a region having chiefly sandy soils so that naturally most habitats are of acid reactions. In such a region one would not expect many species or individuals in alkaline substrata; yet 34 per cent. show a wide range, twelve of the thirty-two of the so-called indifferents growing in soils all the way from definitely acid to those having a pH of 7.0 or more. The indications are that mosses and liverworts are not sensitive to reactions; however, they realize that their data do not warrant any general conclusions concerning the reaction preference of Bryophytes.

Algae.—Wehrle (1927) has given us a fascinating account regarding the reaction and distribution of algae. His studies comprise many species found in brooks, pools, ponds and moors. He classifies his algal habitats into four categories as to hydrogen-ion concentration, each type being characterized by its own algal flora. In the highly acid waters of the moors the reaction is relatively constant, being regulated by humus acid buffers. In such waters the species are few but the number of individuals enormous. Strongly alkaline waters are also few in species and rich in individuals. The latter waters are also relatively constant as to reaction because of the buffer action of the lime content. By far the greatest number of species were found in weakly acid waters (pH 5.0–7.0). Most of these species tolerate a wide range. Some of his alkaline waters are rich in lime and some almost lime free. Yet 85 per cent. of the species of the former habitat are also found in the latter. He concludes, therefore, that the pH must be the factor.

If the waters are not strongly buffered he finds pronounced vacillation in pH. Much of the acidity of such habitats is due to carbon dioxide. In one pool containing *Nitella* in the upper strata of water the pH would rise (acidity increase) as the day progressed. *Nitella* carrying on photosynthesis consumed the carbon dioxide accumulated from the respiration of water organisms. In the lower strata the pH also increases but after noon decreases again. Presumably the respiration of mud organisms liberates more carbon dioxide than is consumed in the lower strata where light radiation is weaker, except at midday (see Fig. 1). If the water was quiet he found pH 7.9 at the surface where the light was strongest; about 25 cm deeper he obtained pH 6.5, and at the bottom where the light was weakest, pH 6.0. This rather nice stratification was often obliterated by convection currents set up by jumping frogs as the investigator approached the pool. We have here a beautiful example of the nicety of balance in nature.

Wehrle gives the ranges for over three hundred species. Some species show very restricted and others very wide ranges, seemingly independent of pH. Interest-

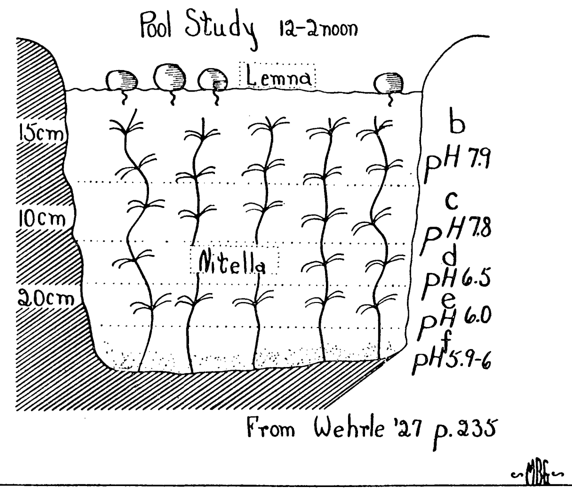


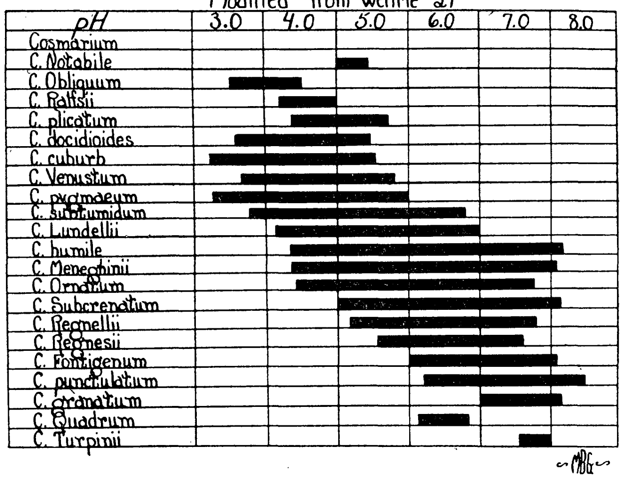
Fig. 1

ingly enough we find all degrees of tolerance in a genus if only it have a large enough number of species. The writer has tabulated just enough of his *Cosmariums* to show the enormous variation of tolerance among species of the same genus (refer to Table II).

Ulehla (1923) illustrates the importance of reactions on the growth of algae in a neat experiment. It seems that one of the Oedogoniums (*O. psychohormium*) has specialized cells called psychohormia. These cells are incrusted with calcium salts, usually calcium carbonate. Ulehla submerged this *Oedogonium* in water acidulated with carbonic acid. If subjected to sunlight for thiry minutes the reactions of the water changed from pH 6.90 to pH 7.05 because the photosynthetic action of the alga used the carbon dioxide introduced into the water. He repeated the experiment but placed the culture in darkness for thirty minutes. The reaction again changed from pH 5.85 to pH 6.18. This time, Ulehla explains, the calcium carbonate incrustations on the alga neutral-

Table 2

Modified from Wehrle '27



ized the reaction of the water to the point most favorable for the alga. If kept in darkness for a day or two the alga died, because after all the calcium was exhausted the reaction of the water became acid by the plant's liberation of carbon dioxide during its respiration. This *Oedogonium,* presumably a calciphyte, dies in acid reactions. He often finds this and other calciphytic algae on shell animals where the buffer reaction of the calcareous shells keeps the water locally neutralized.

In nature he finds that species of *Cladophora* and *Oedogonium* are covered with the iron bacteria *Sideromonas confervarum* whose iron and calcium carbonate incrustations work as a buffer. As carbon dioxide accumulates in the water by respiration calcium bicarbonate is formed. This compound liberates hydroxyl-ions which neutralize the hydrogen-ions. Without the iron bacteria the *Cladophoras* and *Oedogoniums* referred to occur in alkaline waters attached to limestone and sandstone which furnish local buffering.

Lichens.—Trümpener (1926), dealing with species of tree lichens, finds that most of them are grouped around certain pH values (see Table III). He considers pH an

Table 3

Table I. Frequency of Lichens in pH-Intervals of the Substratum.

PH	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9	7.0
Xanthoria parieteina							2	2	1	7	8	2	4	5	4	1	9	1	1	3
Physica grisea								1	1	2	2		2	1		1		1		
Physica pulverulenta							1	2	1	10	1	1	2	2		1	3			
Anaptychia ciliaris			2		1		1	1		1	1		1	1		2				
Parmelia acetabulum			1	1	3	2		2	1	1	2		2	2	1	2				
Xanth. candalaria					1	2	1	5	1	3	1		1	1	1					
Lecanora varia			4	5	6	3	2	3	3	3	4	3	5	4						
Physcia ascendens			1		1		3	3	2	4	2	1	2	1						
Physcia tenella				1	2		3	3	1	7	3		1							
Ramalina pollinaria				1	1		2	2		2	2	1								
Ramalina fraxinea			1		1	1	2	2	1	3	1									
Ramalina farinacea		2		1	1		2	1	1	1	1									
Parmelia subaurifera		1	2	2	1	2	4	1	1	2										
Parmelia sulcata		1	2	1	2	1	3	1	1	1										
Parmelia saxatilis		1	1	1	3	1	8	1	2	1										
Parmelia physodes		1	7	1	7	1	6	1	1	1										
Pertusaria communis	2	1	1	1	1	1	2	1	1											
Evernia prunastri	3	4	7	1	1	1	6	1												
Lecanora Subfusca						1	1	3	2	3	3	3	4	3	5	4				
Trümpener '26																				

—MBG—

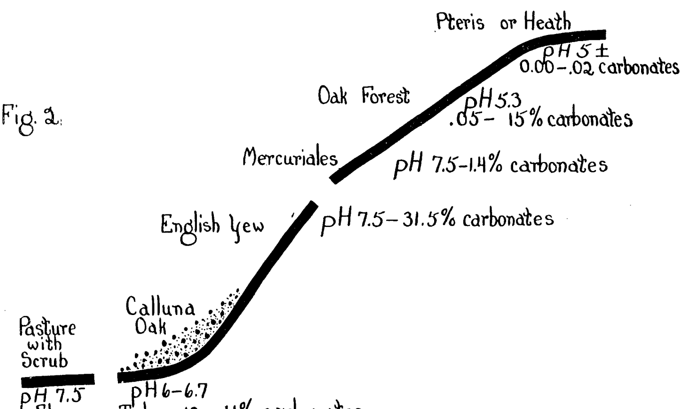
essential factor in the distribution of lichens. These reactions vary for tree species as well as for species of lichens. But at the same time he points out that the cause for various affinities between nitrophilous species and tree species is not the pH of the tree bark, but rather the various ammonium contents of the differently constituted humus which the lichens receive or "catch."

The gist of his work, if the reader interprets him correctly, is that there are nitrophobous and nitrophilous tree lichens. The nitrophobes betake themselves to the top where by necessity they must grow on a more highly acid substratum. The nitrophiles, on the other hand, betake themselves to the bases where their nitrogen requirement is present. After the nitrogen requirement is met the various species group themselves around characteristic pH values.

Some Special pH Correlations

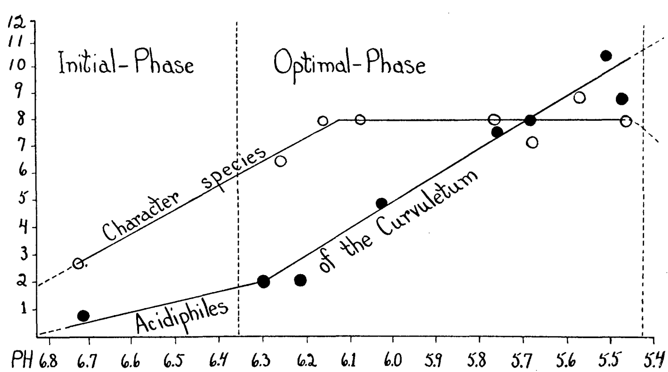
pH, leaching and successions.—From the foregoing survey of the plant kingdom and pH it will be seen that a good inroad has been made into all major divisions. We might now consider in particular a few special cases of broader pH interrelationships, for example, pH to plant succession and leaching. Salisbury (1921) has shown that leaching and removal of carbonates result in accumulation of humus and proportional increase in acidity. He gives examples of oak forests invading hilltops as humus and acidity develop. Humus favors moisture conditions of the soil and therefore germination of forest tree species. In some cases, however, leaching has resulted in soils so acid that germination and growth of tree species become impossible. Many of the typical moors with their heath and *Pteris* vegetation owe their initiation to such leaching and concomitant extreme acidity. On the gentle slopes of hills where leaching sometimes lags will be found such herbs as *Mercuriales perennis* or shrubs like the English yew on alkaline soil. If

Fig. 2.



Schematic Composite after Salisbury '22 to show relation of pH to leaching and succession.

the slope is steep enough, leached soils may be removed and deposited near the bottom as acid talus. In such cases there will also be an acid vegetation at the base of the slope, while over the valley floor alkaline shrubs and grasses usually prevail. In general he sees forests advancing downward from the higher elevations as a result of progressive downward leaching. In extreme cases more acid moors and vegetation in turn chase the once dominating and acid oaks from the top table lands (see Fig. 2). Braun-Blanquet and Jenny (1926) have shown how indifferent associations first inhabit circumneutral soils; how such an association slowly gives way to a more acidic one, and how the latter is finally replaced permanently by the curvuletum, an acidic climax (see Fig. 3). They have also shown how leaching and accumula-



Curve of the character species and direction of succession in the Elynetum(Elynetum[moderately acid] → Curvuletum[very acid])
Fig. 3 from Fig.19 Braun-Blanquet & Jenny '26

tion of humus parallel these successional states. In other words, simultaneously with the development of an acidic climax vegetation there is also a development of an acidic climax, humus soil.

pH and soil profiles.—In Fig. 4 Braun-Blanquet and Jenny present also soil profiles to show four stages of humus soil development in the Alps. A condensed explanation follows. The pioneer stage consists of only a

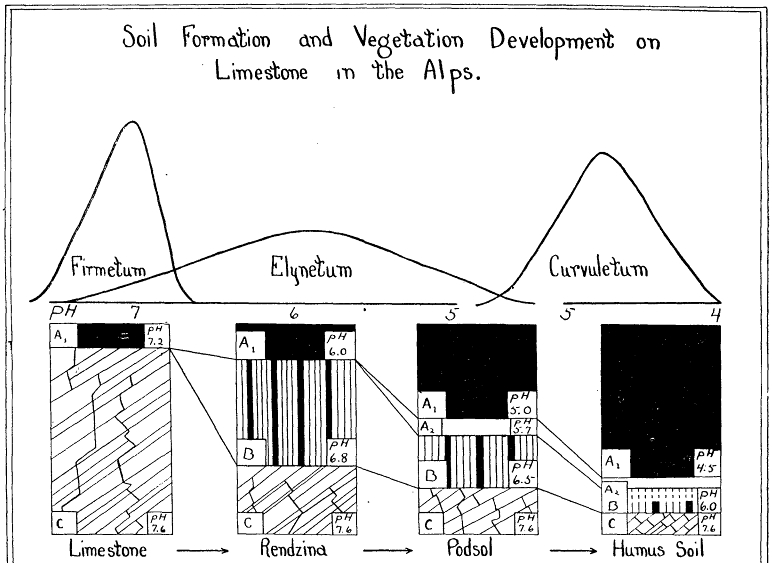


Fig. 4 from Braun-Blanquet & Jenny '26 fig. 15

humus layer (the A-horizon) and an unchanged calcareous mother rock (the C-horizon). At this stage the *Firmetum* (*Carex firma*-association) takes possession. This association consists of alkaline or circumneutral reaction species. As humus accumulates and carbonates are leached out there results a clay or loam horizon (B)—a layer rich in minerals derived from the partially depleted A-horizon. Now the *Elynetum* (*Elyna myosuroides*-association), because of its relative indifference to great pH variability, replaces the *Firmetum*. Luxuriant plant growth increases the humus and acidity of the A-horizon. As a consequence, leaching increases so that the latter horizon becomes completely depleted of its carbonates. Horizon A attains now an acidity of pH 5.0. Next the upper part of the B-horizon becomes leached of bases and bleached in color. This pale layer indicates the beginning of the degeneration of the B-horizon. There are now four horizons: (1) a relatively thick and well-leached and acid humus A_1-horizon; (2) a white or gray leached A_2-horizon differentiated from the upper part of the B-horizon; (3) a diminished B-horizon possessing among others iron and aluminum compounds leached from above, and (4) the mother rock C. Such a soil profile is usually referred to as a "podsol," a term of Russian origin. Ordinarily the podsol is considered the climax soil, but Braun-Blanquet and Jenny consider the podsols as transitory in the higher Alps where they are superseded by the climax humus soils. These humus climax soils are distinguished by a higher acidity, a thicker humus A_1-horizon and the very diminished and indiscernible A_2- and B-horizons. This humus climax soil is inhabited permanently by the *Curvuletum* (*Carex curvula*-association), an acid climax vegetation which has its incipiency during the previous podsol stage at which time the *Elynetum* is replaced.

Negative evidence between pH and succession.—Quite in contrast Miss Geisler (1926), an American worker, saw no relations between pH and plant successions, but found on the contrary that her climax habitats in the vicinity of Cincinnati exhibited a wider range of acidity than the pioneer calcareous soils. The writer (1923), too, has reported that the sandy soils of certain beech-maple-hemlock forests run almost the whole gamut of reactions. On page 20 we read,

> The sandy flood-plain has a very irregular H-ion concentration, varying from 1 to 300 [pH 7.0–4.5]. Alluvial material washed in from the up-stream moraine probably is one of the factors operating toward neutrality. Decaying logs, organic matter, together with a high water table, on the other hand, increase acidity locally.

These are very patchy, unstable and in a measure exceptional conditions. Nevertheless, there it is, the climax forest with its typical climax forest undergrowth.

Plants as pH indicators.—Establishing the frequency with which certain species group themselves around given pH values, Olsen (1921) has been able to predict the acidity by taking the census of the species in a given association (consult Table IV). Here we find that the

Table 4

Meadow locality in Strogaards Vang (Grib Forest)

Species	No. of Fr.	PH classes								
		3.5-3.9	4.0-4.4	4.5-4.9	5.0-5.4	5.5-5.9	6.0-6.4	6.5-6.9	7.0-7.4	7.5-7.9
Festuca rubra	100					—	—	—	—	—
Holcus lanatus	100				—	—	—	—	—	
Anthoxanthum odoratum	100			—	—	—	—			
Geum rivale	100				—	—	—	—		
Plantago lancolata	100					—	—			
Rumex acetosa	60					—	·	—	—	
Galium palustre	40				—	—	—	—	—	
Poa pratensis	20									—
Lathyrus pratensis	20					—	—			
Taraxacum sp.	20									
				1	4	8	8	5	4	2

Determination of pH by Vegetation
Instance 2 p. 61 Olsen '21
Both pH 5.5–5.9 & 6.0–6.4 probable ∴ calc. = pH 6.0
Soil sample = pH 5.8

values pH 5.5–5.9 and pH 6.0–6.4 contain the same number of species. Olsen therefore predicted the intermediate pH 6.0. The soil really tested pH 5.8 so that he came remarkably close.

Kotilainen (1927) makes graphs (Figs. 5 and 6) to express the percentage of times that certain species or associations participate in given reactions. Observing then the typical species of the habitat and applying these graphs he is able to predict reactions. From his graphs it will be seen that the plant association, because of its greater restriction to narrower pH limits, is more accurate than a single species. Since pH indicates a set of conditions he is able to determine the agricultural value of his moors by the vegetation. For example, *Meny-*

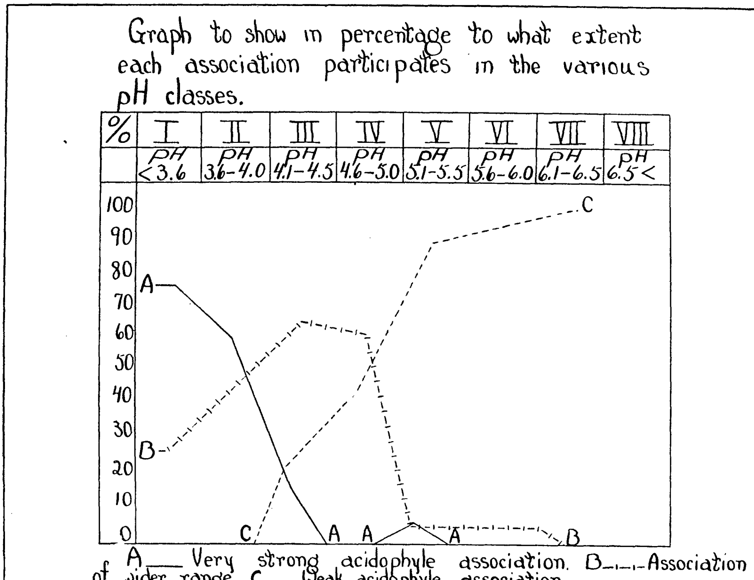


Fig. 5 from Kotilainen '28 Table VII

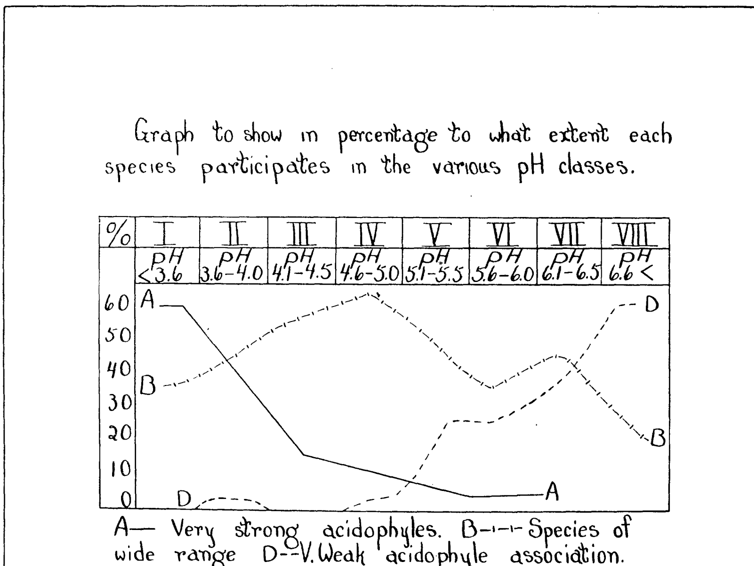
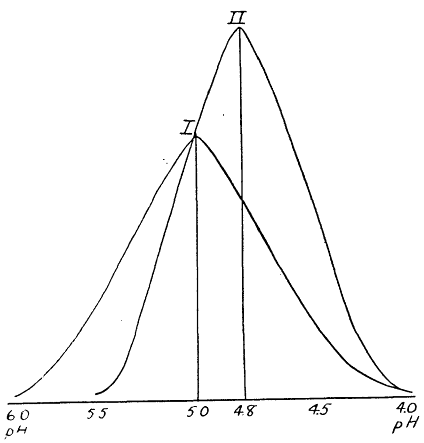


Fig. 6 from Kotilainen '28 Table IV

anthes trifoliata, Phragmites communis, Cypripedium calceolus and *Juniperus communis* indicate good peat for culture, but *Ledum palustre, Calluna vulgaris* and *Empetrum nigrum* indicate great acidity and poor peat for culture.

Frequency curves.—Braun-Blanquet and Jenny (1926) made a frequency study of pH of the *Carex curvula*-association and of *Carex curvula* individually. From the values they derived two typical bell-shaped curves. The dispersion is narrower and the mode higher for the



pH-variation curves of the species Carex curvula (I) and the association Curvuletum (II) (for a 100 individuals each)
Ordinate : frequency
Abscissa · pH

Figure 7 from Figure 5
Braun-Blanquet and Jenny '26 R.S.

association than for the species. These two curves also demonstrate that the association is more reliable as an indicator than the species. Applying Gauss's formula which is familiar to all statisticians and substituting normal distribution values they predict the probability of finding a given species in the habitat of a given pH (consult Table V).

Mono- and bimodal curves.—Salisbury (1925) gives a number of bimodal and monomodal distributional curves. For illustration see Fig. 8 with *Mercuriales perennis* and its bimodal curve. As if to disarm possible critics he points out that the frequency of the soil's pH and plant

Table 5.

Frequency table of the pH values of *Carex curvula* (125 Samples)

pH values (x)	6.0	5.9	5.8	5.7	5.6	5.5	5.4	5.3	5.2	5.1	5.0	4.9	4.8	4.7	4.6	4.5	4.4	4.3	4.2	4.1	4.0
Frequencies observed (y)	0	1	2	1	3	4	8	10	10	13	14	15	11	12	8	7	3	0	2	1	0
Frequencies Calculated (y)	0.2	0.5	1.0	1.9	3.3	5.1	7.4	9.8	12.0	13.5	14.1	13.5	12.0	9.8	7.4	5.1	3.3	1.9	1.0	0.5	0.2
Difference	-0.2	+0.5	+1.0	-0.9	-0.3	-1.1	+0.6	+0.2	-2.0	-0.5	-0.1	+1.5	-1.0	+2.2	+0.6	+1.9	-0.3	-1.9	+1.0	+0.5	-0.2

Application of Gauss' Formula:

$X = pH$

$y =$ Frequency

$h =$ parameter

$e = 2.718$

$\pi = 3.142$

$$y = \frac{h}{\sqrt{\pi}} \cdot e^{-h^2 x^2}$$

$y = 100$ million

∴ *Carex curvula* should occur in a soil of pH 7.0 once in 100 million cases. Braun-Blanquet and Jenny '26 pp. 303–304

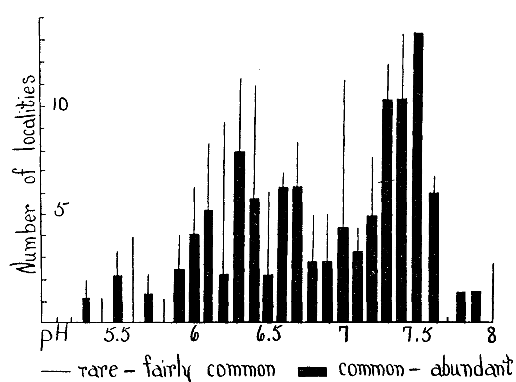


Fig. 8 from fig. 5 Salisbury 1925

MBG

species' pH are not coincident. Moreover, two or more species growing on the same soil may each have its own frequency. For example, *Pteris aquilina* and *Psamma arenaria* have respectively the modes around pH 5.5 and pH 7.1 on the same soil. He also calls attention to monomodal soils with bimodal species. Nevertheless, Pearsall (1926) offers data from English siliceous and calcareous soils intended to fill the depression of Salisbury's *Mercuriales perennis* bimodal curve and thus assume a monomodal form (see Table VI).

TABLE VI

pH VALUES OF SOILS ON WHICH MERCURIALES WAS ABUNDANT

pH	4.5–4.9	5–5.4	5.5–5.9	6–6.4	6.5–6.9	7–7.4	7.5–8
Number of records	1	5	6	9	16	9	2
Per cent. of total number of soils	2.3	16.6	15.8	14.5	36.3	15	6.2

INFLUENCE OF PLANTS ON pH

Unless neutralizing bases are at hand plants themselves acidify the soil by their excretions, remains and selective removal. Such an increase in acidity may be quite an incidental consequence of plant growth and presence. Arrhenius (1926), though, takes a rather teleological point of view, saying that plants themselves change the substratum to a pH most suitable to themselves. Chodat (1924) in the way of opposition states that if anything one plant association may create its own downfall by making the reaction more favorable for successors. This latter point of view is in harmony with the successional studies of Salisbury (1921) and Braun-Blanquet and Jenny (1926). Quite apropos here is the work of Beauverie and Martin-Rosset (1926) who found that raised or heaped up neutral (pH 7.0) *Carex* peat is populated by a flora less specialized for marshes (amphibious and even strictly land plants) which acidify the peat and prepare it for forest species. In Lac des Echets, France, for example, the peat was removed and otherwise modified from 1481 to the nineteenth century so that it is no longer marsh, but on the contrary now developed into forest prairies and even suitable for cultivation. This peat originally around pH 7.0 is now pH 6.0–6.2. The writer (1928) has shown that *Sphagnum* and other mosses, especially *Aulacomnium palustre,* increase the acidity of bogs. The fact that these mosses are responsible for the acidity in which they grow could very well be fortuitous. It is very clear, however, that the acidity thus produced results in the invasion of heaths and a few other species usually associated with acid habitats.

pH AND SPECIES CHARACTERS

Clausen (1922) found that *Viola tricolor* and *Viola arvensis* grow typically on acid and alkaline soils respectively. In circumneutral soils he found both species and various intermediate taxonomic forms (see Table VII).

Table 7.

Reactions of Soil

	basic	faintly acid	neutral	neutral to faintly acid	acid
No. of habitats with: Viola arvensis	7	3	8	5	
No. of habitats with: V. tricolor			1	4	4

Basic soil: small, yellowish white flowers—pure arvensis

Acid ground: large, blue, white, yellow, rose, and purple flowers—pure tricolor

Neutral-Faintly acid: pure arvensis, pure tricolor, and intermediates

From Clausen on Viola spp. 1922.

pH AND CONCOMITANTS

From the cases just gone over it is perfectly clear that pH is a factor operative in plant distribution. At the same time, all authorities mentioned in this paper agree, by word or act, that other factors of the soil and atmosphere must not be minimized or ignored. Obviously, types of soils, light and water relations are paramount. But such a general statement is a platitude. Still, anything more specific approaches speculation, for there is little in the way of precise data concerning factors attending the reaction. The difficulty of measuring these concomitants and reducing them and pH all to a common denominator makes a clear picture of the soil impossible. And yet, as Pearsall (1926) would say, an ignorance of them does not rule them out of consideration. In the following a few circumneutral relationships will be presented.

pH constant but other factors variable.—In working out his frequency tables Olsen (1921) recognized the potency of other factors. He was therefore careful to select a locality where all conditions like soil, water and light were relatively constant. In this way he proved a correlation between hydrogen-ion concentration and plant distribution. One can reverse the choice by selecting localities where the pH shall be constant, but water, light and soil factors shall vary. For an illustration see the following circumneutral habitats: (1) a dry, unstable, foredune with intense light, supporting a pioneer association; (2) a moist, stable, shady dune, dominated by a climax forest and undergrowth, Kurz (1923); (3) a raw peat with pioneer aquatics or subaquatics; (4) an old, well-decomposed peat or muck with forest trees and undergrowth, Kurz (1923 and 1928), and (5) Montfort and Brandup (1927) for a circumneutral salt marsh with its halophytic species. Atkins (1922) and later Kurz (1928) call attention to the fact that acid clays and acid sands may differ remarkably in their species.

Kotilainen on concomitants.—Kotilainen (1927) found good correlation between pH and plant distribution, yet he considers pH as a secondary, and sometimes even an unimportant, factor. Even though a certain vegetation is characterized by certain acidity it must nevertheless be understood, he holds, that acidity—itself an indicator of other edaphic conditions—although an important factor is only one of all factors that influence species. Relation between acidity and vegetation will never be clear until pH is studied as a partial factor of a factorial complex. He admits the influence of pH, but, in contradiction especially to Arrhenius, Olsen and Chodat, thinks its influence is an indirect one. Criticizing in particular Olsen's culture work, he says that by changing acidity with the use of calcium carbonate one changes also other factors besides hydrogen-ion concentration. Olsen has stated that poverty of minerals is not important in his cases, for he found both acid and alkaline soils poor in minerals and the vegetation was totally different in the two impoverished soils. Kotilainen taking the opposite view maintains that species of *Sphagnum* can stand alkaline soil water if it is poor in nutrient salts. He states that water level, electrolyte concentration, calcium-ions, oxygen content of superficial water as well as top form of moors are often more direct factors than acidity, for these often are the very producers of acidity. Kotilainen ties up weak acidophiles with high electrolyte concentration, especially lime. Such acidophiles occur on thin layers of peat near a calcium substratum and on edges of moors. In the species *Carex capillaris, Cypripedium calceolus, Polygonum bistorta, Ranunculus propinquis* and *Epipactis palustris,* he sees a correlation between low acidity and high calcium-ion concentration. Because of their seeming dependence on calcium-ion he thinks that they had better be considered by the older concept of calciphiles. Another example: *Sphagnum papillosum* and *S. compactum* are hygrophiles and acid-loving species. In a wet habitat of pH 5.0–6.0 and a calcium salt content of 1–2 per cent. he finds them excluded. Here the acidity is proper but these species of *Sphagnum* are excluded by the calcium-ion. If hummocks form so that leaching and drying take place locally, more xerophytic acidophiles come in. Here then water content and calcium play the important rôles. Having reference to Olsen's work in particular, page 180, Kotilainen suggests that changing the reaction by adding acids and calcium carbonate might also bring about other changes in the "factorial constellation." He admits the influence of acidity on plants if all factors are constant as Olsen has shown, but he doubts that it is a direct influence of acidity.

Salt and water content as concomitants.—Montfort and Brandrup (1927) have come to very suggestive conclusions regarding the distribution of salt marsh plants. Their work indicates that other factors outweigh the influence of pH. For instance, in Table VIII the pH is

Table 8.

Habitats	pH	Water Content of Soil %	Salt Content of Soil %
1. Meadow without Salt Vegetation on edge of Phragmites-Station	6.8	86	0.1
2. Phragmites-Station without Aster	7.0	75	0.13
3. Aster Vegetation	6.9	80	0.65
4. " "	7.1	55	0.62
5. " "	7.1	35	1.9
6. Triglochin-Vegetation	7.1	50	2.8
7. Without Vegetation	7.1	20	18.0 !

From Montfort and Brandrup '27

relatively constant for all habitats. It will be seen, though, that there is an enormous variation of total salt and water content and that different types of vegetation are tied up with salt and water content of the soil. These workers conclude that *Aster tripolium* is sensitive to a high salt content and *Salicornia* to a high chlorine-ion sulphate-radical ratio. Coupled with such peculiarities of species is the fact that some of these halophytes are most sensitive to fluctuations in salt concentration as seedlings. Montfort and Brandrup make the point then that any one of a whole set of conditions, by no means static, might swing the balance in the matter of successful establishment of salt marsh species. Only a comparison of the springtime germinating conditions with those of the summer gives an adequate understanding of the vegetational zones that correspond with gradations of salt.

Antagonism between hydrogen-ion concentration and salt concentration.—Åslander (1929) explains in a unique way the presence of neutral or alkaline soil weeds like *Chenopodium album, Sonchus oleraceous, S. arvensis, Cirsium arvense, Stellaria media* and others on acid, manured fields of northern Sweden. His experiments show that barley, a neutral soil plant, will grow in nutrient solutions with acidity as high as pH 3.75 provided only that the solution be a concentrated one as to salts. He attributes the good growth of barley in such a highly acid medium to the counteracting influence of the salts, for he found that if this high acidity was maintained in media about the concentration of soil solutions the growth declined and several plants died. On page 125 we read:

> This poor growth can not be interpreted as a result of starvation. In the nearly neutral solution the growth was practically unaffected by dilution up to 1/40. By more frequent changes (or perhaps less sodium content) the 1/80 solution would probably have been found just as suitable as the more concentrated solutions. The result can not be interpreted in more ways than one. *There is a clear antagonism between hydrogen-ion concentration and salt concentration.* No other interpretation seems possible.

Applying the information of these experiments he concludes (page 135) that the highly concentrated soil solution of newly manured fields "is responsible for the invasion of these acid soils by plants which grow ordinarily only in neutral or alkaline soils." He states further (page 136) "that the nature of the soil solution greatly affects the soil reaction at which plants thrive in nature."

pH and nitrogen content.—The importance of nitrogen content as a factor of the soil is quite generally recognized by all ecologists. However, it is difficult to study and state the exact influence of a compound, so fluctuating as to quantity and chemical constituency as nitrogen content of the soil, on plant distribution. The reader is referred to Olsen (1921), Arrhenius (1920), Hesselman (1926), who have made some correlative studies between nitrogen content, pH and plant distribution. Wherry (1926) has fallen back on total nitrogen content to explain certain pH anomalies. On Mount Desert Island, for example, a high nitrogen acidity ratio accounts for the scarcity of jack pine. The reaction pH 4.6 is suitable but the total nitrogen content too high for this pine. By a similar logic Wherry would account for the presence of certain typically acid plants in an alkaline substratum. Reference has already been made to Trümpener's (1926) conclusions about the importance of nitrogen content of the substratum for lichens. Braun-Blanquet and Jenny studied a number of depauperate and normal individuals of *Carex curvula* with reference to both pH and humus (nitrogen). They found that the species' optimum range, pH 4.6–5.6, embraced both normal and depauperate plants. But the percentage of humus ran from 34.7 to 59.0 for the normal individuals and from 12.4 to 24.7 per cent. for the depauperates. Assuming that humus content parallels nitrogen content they conclude that nitrogen is the limiting factor.

pH and salt or ionic ratios.—A number of investigators have offered various types of chemical ratios as possible adjuncts to or even substitutes for hydrogen-ion where the latter in itself seems to fail as a satisfactory explanation. Thus Pearsall (1926) advances his basic ratio hypothesis. According to him the tissues of heaths and other acid plants are rich in fats. This presence of fats suggests a soil with a high proportion of potassium and sodium to calcium and magnesium. The essence of this theory may be quoted from his article:

> We may thus find healthy species growing profusely on soils whose pH values lie between 6.0–7.0. In order to explain cases of this kind the writer suggested in 1922 that soil sourness might be attributed (*a*) to a deficiency in the soil and (*b*) to a high proportion of potassium and sodium to calcium (and magnesium).

In some of Braun-Blanquet and Jenny's soil profiles of the Alps they find that the leached horizon sometimes presents a magnesium oxide/calcium oxide ratio which is greater than unity, because calcium is leached faster than magnesium. Such soils, they state, are said to be poisonous to plants and to restrict their growth. In connection with this paragraph, Wherry's nitrogen/hydrogen-ion and Montfort and Brandrup's chlorine/sulphate ratios should be recalled. The conclusions about electrolyte content and chemical ratios are admittedly preliminary and as yet in part speculative. Nevertheless their very presentation is highly suggestive and will undoubtedly lead to a more general and thorough attack on concomitants.

SUMMARY

All workers agree that reaction is a factor in plant distribution. In cases it is undoubtedly the most important factor—notably in the *Ericaceae, Orchidaceae* and many other species. Many species are restricted to habitats of narrow reaction ranges. In fact, the correlation between distributions of species and pH may be so close that the pH data may be presented in the form of the well-known frequency curves of statisticians. Indeed, by making reverse use of such close correlations certain investigators can predict the pH accurately by means of the vegetation. It has also been shown that certain soils and vegetation develop in orderly succession toward an acidic climax vegetation on an acidic climax humus soil.

In opposition to the foregoing it must also be stated that a great many species have a wide range. And even where there is a closer relationship between species and pH it need not necessarily be laid to the direct influence of reaction unless all other factors are constant. Now in nature it is hard to find marked changes in pH without at the same time encountering drastic changes in physical, chemical and biological differences in soil and atmosphere. It has been shown that habitats of the same pH but differing in other factors show a corresponding difference in vegetation. However, the difficulty involved in measuring these other factors and reducing them to common denominators has caused us to minimize their potency and to assign a false supremacy to pH.

It is probably best to think of reaction relationships as a triangle whose apices are pH, plant species and concomitants. That reaction affects the distribution of plants is admitted. But when we can measure simultaneously all factors and arrange the data in overlapping and crossing frequency curves we shall be more informed on how pH affects the distribution of plants in nature.[2]

LITERATURE CITED

Arrhenius, O. von.

1920. ''Öcologische Studien in den Stockholmer Schären,'' Diss. Stockholm.

1926. ''Kalkfrage, Bodenreaktion und Pflanzenwachstum,'' Leipzig.

Åslander, Alfred.

1929. ''Concentration of the Nutrient Medium *versus* its Hydrogen-ion Concentration as Manifested in Plant Growth,'' *Svensk Botanisk Tidskrift,* 23 (7): 96–140.

Atkins, W. R. G.

1922. ''Some Factors Affecting the Hydrogen-ion Concentration of the Soil and its Relation to Plant Distribution, *Notes,* Bot. School, Trinity College, Dublin, 3: 133–177.

Beauverie, Jean, and Martin-Rosset.

1926. ''Contribution a l'étude de l'influence de la concentration in ions hydrogène sur la flore des terrains marécageux,'' *Bull. Soc. Bot. France,* 72: 1045–1051.

Braun-Blanquet, J., and Hans Jenny.

1926. ''Vegetationsentwicklung und Bodenbildung in der Alpinen Stufe der Zentral Alpen,'' Denkschr. Schweiz. Naturf. Ges., 63: 175–349. 1926.

Chodat, Fernand.

1924. ''La concentration en ions hydrogène du sol et son importance pour la constitution des formations végétales,'' Thèse 748, Universitè de Genève, 1–115.

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Christophersen, Erling.

1925. "Soil Reaction and Plant Distribution in the Sylene National Park, Norway," Conn. Academy of Arts and Sciences, 27: 471–577.

Clausen, J.

1922. "Studies on the Collective Species of *Viola tricolor* L. II," *Botanisk Tidskrift,* 37: 363–416.

Coville, F. V.

1913. "The Agricultural Utilization of Acid Lands by Means of Acid Tolerant Crops," Bull. U. S. Dep't Agric. 6.

Geisler, Sylvia.

1926. "Soil Reactions in Relation to Plant Successions in the Cincinnati Region," *Ecology,* 7 (2): 163–184.

Hesselman, Henrik.

1926. "Studien över Barrskogens Humusstacke, dess Egenskaper och Bervende an Skogsvården" [The Humus Cover of Coniferous Forests], *Meddelanden Fran Statens Skogförsöksanstalt,* 22 (5): 176–506.

Kelley, A. P.

1923. "Soil Acidity, an Ecological Factor," *Soil Sci.,* 16: 41–54.

Kotilainen, Mouno, J.

1927. "Untersuchungen über die Beziehungen zwischen der Pflanzendecke der Moore und der Beschaffenheit, besonders der Reaktion der Torfbodens," Wissenschaftliche Veröffentlichungen des Finnischen Moorkulturvereins, No. 7. Helsinki.

Kurz, Herman.

1923. "Hydrogen-ion Concentration in Relation to Ecological Factors," *Bot. Gaz.,* 76: 1–29.

1928. "Influence of Sphagnum and Other Mosses on Bog Reactions," *Ecology,* 9: 56–69.

Mevius, Walter.

1927. "Naturwissenschaft und Landwirtschaft. Reaktion des Bodens und Pflanzenwachstum," Heft 11. 1–48. Verlag. F. P. Datterer et Cie. Freising-Munchen.

Montfort, Camill, and Wolfgang Brandrup.

1927. I. "Physiologische und pflanzengeographische Seesalzwirkung." II. "ökologische Studien über Keimung und erste Entwicklungen bei Halophyten," *Jahrb. Wiss. Bot.* 66 (5): 902–946.

Olsen, Carsten.

1921. "Studies on the H-concentration of the Soil and its Significance to the Vegetation, especially to the Natural Distributions of Plants," Comptes-rendus du Laboratoire, Carlsberg, 15. No. 1: 1–166.

Pearsall, W. H.

1926. "Soil Sourness and Soil Acidity," *Journ. of Ecol.,* 14: 156–163.

Robinove, Joseph J., and C. D. La Rue.

1928. "The Hydrogen-ion Concentration of the Habitats of the Bryophytes and Pteridophytes of the Douglass Lake Region," Dep't. of Bot, U. of Mich.

Salisbury, E. J.
1921. ''Stratification and Hydrogen-ion Concentration of the Soil in Relation to Leaching and Plant Succession with Special Reference to Woodlands,'' *Journ. Ecol.*, 9: 220–240.
1925. ''The Incidence of Species in Relation to Soil Acidity,'' *Jour. Ecol.*, 13: 149.
Steagall, Mary Minerva.
1926. ''Some Illinois Ozark Ferns in Relation to Soil Acidity,'' *Trans. Ill. Acad. Sci.*, 19: 113–137.
Trümpener, Egon.
1926. Über die Bedeutung der Wasserstoffionenkonzentration für die Verbreitung von Flechten,'' *Beih. Bot. Central Sl.*, Abt. 7, 42 (3): 321–354.
Ulehla, V.
1923. ''Über CO_2- und pH-Regulation des Wassers durch einige Süsswasseralgen,'' *Berichte der deutsch. bot. Gesellschaft*, 41: 20–31.
Wehrle, Emil.
1927. ''Studien über Wasserstoffionenkonzentrationsverhältnisse und Besiedelung an Algenstandorten von Freiburg in Breisgau,'' *Zeitschr. Bot.*, 19: 209–287.
Wherry, E. T.
1916. ''A Chemical Study of the Habitat of the Walking Fern, *Camptosorus rhizophyllus* (L.) Link,'' *Journ. Wash. Acad. Sci.*, 6: 672–679.
1920. ''Soil Acidity—its Nature, Measurement and Relation to Plant Distribution,'' Annual Report Smithsonian Institution, Publication 2622: 247–268.
1926. ''Nitrogen as a Factor in Plant Distribution on Mount Desert Island, Maine,'' *Ecology*, 7 (2): 140–142.