SYMBIOSIS IN A DECIDUOUS FOREST. I

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(WITH THREE FIGURES)

Introduction

In a previous paper[1] symbiosis is defined as the living together of dissimilar organisms, and the phenomena of symbiosis are classified as follows:

I. Disjunctive symbiosis
  1. Social
  2. Nutritive
    a. Antagonistic
    b. Reciprocal

II. Conjunctive symbiosis
  1. Social
  2. Nutritive
    a. Antagonistic
    b. Reciprocal

The writer has felt for some time that there is urgent need of work along the lines of these various types of symbiosis. Considerable work has been done on the relations of plants to their physical environment, but the work done on their relation to the biotic environment has not been in proportion to the importance of this phase of ecology.

Some five years ago the University of Illinois obtained possession of a sixty acre tract of forest. This land is located about five miles northeast of the University in Champaign County, Illinois, and is a remnant of a former much more extensive forest. It is known as the "University woods." Many of the primitive trees are still standing in this tract, although some cutting has been done in the past, and the forest was frequently pastured before it was acquired by the University. It may be said, therefore, to be only semi-primitive. It has been stated that there is very little if any natural forest vegetation in the state of Illinois at the present time, but the use of the word natural in such a statement is ill chosen and makes the statement inexact. It is true that there is very little if any such vegetation that has not been modified to a greater or less extent by man. Vegetation that has been influenced by man, however, is

[1] McDOUGALL, W. B., The classification of symbiotic phenomena. Plant World 21:250–256. 1918.

not necessarily "unnatural." The plants in any forest in Illinois at the present time have life problems that are just as real, just as complex, and just as interesting from an ecological point of view as were the problems of plants in the primitive forests. We should make every effort, of course, to preserve as much of the primitive vegetation as possible, but no ecologist whose location is remote from primitive vegetation need feel that there is nothing he can do, for wherever plants grow there is ecological work to be done even though the land may all be under cultivation.

The work, a part of which is recorded in the present paper, was undertaken for the purpose of making a thorough study of symbiosis in all its phases in the University woods. The present paper

RAINFALL (IN INCHES) AT URBANA; AVERAGE FOR SIXTY YEARS

Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	TOTAL
2.16	2.42	2.92	3.47	4.04	4.11	3.89	3.04	3.60	2.21	2.49	2.24	36.89

TEMPERATURES AT URBANA; AVERAGE FOR FORTY YEARS

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Aver.
Maximum.....	57	60	72	83	89	94	98	96	93	84	72	58	80
Minimum.....	− 5	− 4	12	26	36	46	52	51	39	27	14	2	25
Mean.....	26.6	29.2	39.8	53.0	62.9	71.9	76.4	74.4	67.2	55.3	41.5	30.4	52.4

deals primarily with social disjunctive symbiosis, and it is the hope of the writer to follow it with others treating of the other types of symbiosis.

University woods

PHYSICAL ENVIRONMENT

CLIMATE.—Table I gives a summary of weather conditions at Urbana, Illinois, during 1919. The data for this table were kindly furnished and the table compiled by the Division of Soil Physics of the Agriculture Experiment Station of the University of Illinois. There were slightly more clear days in 1919 than usual, but on the whole the table is typical of the climate of this region. The following tabulations of average monthly and annual rainfall at Urbana for a period of sixty years, and of average maximum, mini-

mum, and mean monthly temperatures for a period of forty years, were compiled from data given by MOSIER.[2] It will be noted that the rainfall is adequate and is well distributed throughout the year. The average data of the last killing frost in spring is April 26, and that of the first killing frost in autumn is October 16, giving an average growing season of 173 days.

SOIL.—The soil of the forest is yellow-gray silt loam, an upland timber soil.[3] There are no streams within the forest, but the region is drained by a tributary of the Salt Fork of the Vermillion

TABLE I

WEATHER CONDITIONS AT URBANA DURING 1919

1919	Temperature			Rainfall in inches	Mean relative humidity	Wind		No. of clear days	No. of partly cloudy days	No. of cloudy days
	Maximum	Minimum	Mean			Average velocity	Direction			
January...	55	− 8	31.2	0.21	76.4	7.5	SW	16	6	9
February..	56	11	31.5	1.92	77.0	8.4	NW	10	3	15
March....	67	9	42.0	4.12	75.5	11.9	S	13	6	12
April.....	76	24	53.2	0.75	76.1	9.1	SW	7	6	17
May	92	38	60.8	3.29	78.6	7.4	NE	8	7	16
June.....	91	52	75.5	6.90	79.9	5.8	SE	10	13	7
July.....	96	56	81.3	2.66	59.3	6.1	SW	23	8	0
August....	94	50	73.9	3.85	63.4	6.4	SW	19	9	3
September.	92	42	70.5	2.47	68.1	6.5	SW	19	5	6
October...	88	33	58.4	5.59	79.8	7.0	SW	11	1	19
November.	63	16	39.1	3.37	78.3	8.9	SW	12	5	13
December.	51	− 4	23.9	0.12	77.6	7.4	SW	9	3	19
Total ...	.....	.....	.....	35.25	.....	.....	.....	157	72	136
Average.	76.8	26.6	53.4	2.94	74.2	7.7	SW	13.1	6.0	11.3

River. This ditch flows in an easterly direction some forty rods south of the present boundary of the forest. The forest itself is only gently rolling, but several acres in the middle eastern portion are several feet lower than the highest parts of the woods, and in the lowest part there is often standing water for a few weeks in spring.

As will be shown later, the vegetation in the lower part of the woods is quite different from that in the higher parts, and this difference seems to be almost entirely due to the difference in the

[2] MOSIER, J. G., Climate of Illinois. Univ. Ill. Agric. Exp. Sta. Bull. 208. 1918.

[3] HOPKINS, C. G., MOSIER, J. G., VAN ALSTINE, E., and GARRETT, F. W., Champaign County soils. Univ. Ill. Agric. Exp. Sta. Rep. 18. 1918.

amount of soil water. A number of measurements of soil temperature were made in both the higher and lower parts of the forest at depths of three inches and twelve inches, but temperatures taken in different parts of the forest on the same day and at the same depth were found to be almost exactly the same. Tests were made also for soil acidity in different parts of the forest, using the indicator method described by WHERRY.[4] The results of these tests showed that the soil of the forest is neutral throughout. Although no chemical analyses have been made, there is no reason for thinking that the mineral constituents of the soil are not practically the same throughout the forest.

THE PLANT COMMUNITY

METHODS.—Before the more special types of symbiosis can be studied adequately in any plant community, it is necessary to have a thorough understanding of the structure of the community and of the disjunctive social symbiosis, that is, of the gross interrelations of the component parts of the vegetation. In order to obtain this information, the entire forest was first staked out into one hundred foot quadrats. The only reason for choosing the one hundred foot quadrat instead of a unit of the metric system was that one hundred foot steel surveyor's tapes are readily obtained and are convenient to use. No attempt was made to have the quadrats exactly one hundred feet square. The tapes were fastened to the stakes by means of straps, and these were of such a length that on level land and with the tapes drawn tight the stakes would be about one hundred two feet apart. In the woods, however, with the tapes running among shrubs, between trees, over fallen logs, etc., and with the tape never very tightly drawn, the quadrats were approximately one hundred feet square. It was found that by making fractional quadrats across each end of the woods and part way along one side, to where there is a jog in the boundary line, there were then 216 full size quadrats (fig. 1).

Having subdivided the forest into quadrats, two methods were used for locating and mapping the components of the vegetation. The first method was used only for the trees and shrubs. Two

[4] WHERRY, E. T., Soil acidity and a field method for its measurement. Ecology 1:160–173. 1920.

FIG. 1.—Quadrat map of University woods showing distribution of the two dominant trees: o = *Acer saccharum*, — = *Ulmus americana*.

rows of quadrats were surveyed at the same time. A hundred foot tape was stretched between the first two quadrats of the first two rows. Then while walking through these quadrats in the directions indicated in fig. 2, counts were made of all species of trees and shrubs present. The frequency of the occurrence of each species of shrub was indicated by the numerals 1, 2, 3, and 4; no. 1 indicating only one to three specimens in the quadrat, no. 4 indicating great abundance, and nos. 2 and 3 representing intermediate degrees of frequency. In the case of trees the actual

FIG. 2.—Two one-hundred-foot quadrats illustrating method used in making counts of trees and shrubs in University woods: heavy line between quadrats indicates position of steel tape; arrows show direction taken by surveyor in making counts.

number of individuals of each species was noted. After counts in these two quadrats had been completed, the tape was taken up and stretched between the next two quadrats and counts made there in a similar way, the procedure being repeated until the entire forest had been surveyed. Having secured these data, a distribution map was made for each species (fig. 1). No attempt was made to locate the individuals within the quadrat, but only to place them in the quadrats in which they occur. Each individual is shown on the maps, therefore, within one hundred feet or less of its actual position in the forest.

For the herbaceous vegetation a somewhat different method was used. Only one row of quadrats was surveyed at a time and no

tape was used. Instead, a pocket compass was employed for keeping on a line running through the middle of the row of quadrats, and each quadrat was surveyed by walking through it in the manner indicated in fig. 3. The middle of each quadrat after the first was found by pacing thirty-three paces from the middle of the preceding quadrat with the compass as a guide to the direction. The place was then marked by sticking into the ground a stick about four feet long which was sharpened to a point at the lower end and whittled off at the upper end so as to give a whitish surface which could be seen for some distance. This stick was carried from quadrat to quadrat as the work progressed. The various species of herbaceous plants present in each quadrat were recorded as nos. 1, 2, 3, or 4; no. 1 signifying rare, no. 2 frequent, no. 3 common, and no. 4 abundant. A map was then made for each species, showing its distribution and relative frequency of occurrence throughout the forest. In surveying for herbaceous plants, only those plants that were in bloom or were otherwise easily recognized were listed; and in order to make the lists complete the survey was repeated once each month during the growing season.

FIG. 3.—A one-hundred-foot quadrat illustrating method used in estimating frequency of herbaceous plant species in University woods: broken line with arrows indicates direction taken in locating center of quadrat; solid line with arrows shows directions taken in making survey.

RESULTS.—By this method a fairly complete list of the plants growing in the woods was obtained, together with the relative numbers of individuals and the locations of each species. No attempt has been made so far to include the bryophytes and the microfungi and algae in the survey, although it is hoped that this may be done later. The bryophytes are nowhere abundant, and

probably are of relatively little importance from the viewpoint of symbiosis or other ecological relations. This is obviously even more true of the algae in such a habitat as this. The microfungi, however, will have to be considered in some detail later in a discussion of their symbiotic relations with other plants. Aside from these three groups, the lists of species are believed to be fairly complete, except that there are probably a few late fall-blooming plants, mostly composites, that have been missed owing to the fact that the last survey of the season was interfered with by duties in connection with the opening of the University and the beginning of classwork for the year.

The lists of species which have been compiled include 31 trees, 12 shrubs, 6 lianas, 134 herbs, 5 ferns, and 83 higher fungi. These figures show that while there is by no means a paucity of species, yet for a sixty acre deciduous forest the flora cannot be said to be an especially rich one. It is not unlikely that the years preceding the acquirement of this property by the University, when it was frequently pastured and the public was allowed to dig up plants by the roots and carry them away at will, had their effect in reducing the number of species.

Acer saccharum and *Ulmus americana* are the dominant trees. These two are present in nearly equal numbers, the count showing 1987 maple and 2073 elm individuals. No other species are nearly so abundant as these two. The nearest competitor is *Fraxinus americana* with 537 individuals, then follow *F. quadrangulata* with 336, *Tilia americana* with 321, and *Carpinus caroliniana* with 303 representatives. All other species are represented by less than 300 individuals. These data show at once that the forest is typically hydrarch mesophytic and relatively mature, *Acer saccharum* being the most typical climax species of the region. While these species are all found more or less throughout the forest, the maple is much more dominant in the southern half and the elm in the northern half. In fact three-fourths of the hard maple and two-thirds of *Fraxinus quadrangulata* are in the southern half of the woods, while three-fifths of the elm, three-fifths of *F. americana*, and two-thirds of the blue beech (*Carpinus*) are in the northern half. It is the higher parts of the woods that are dominated by the maple,

while the lower parts are dominated by elm. In the area between quadrats 59 and 96 and vicinity (fig. 1), which is the lowest part of the woods, there are almost no trees except elms. I shall frequently refer to that part of the woods that is dominated by maple as the maple consociation, and that dominated by elm as the elm consociation.

The great majority of the shrubs are of two species, *Asimina triloba* and *Benzoin melissaefolium*. Both of these are very abundant, and are distributed throughout the forest except in the highest and lowest parts. No other shrubs are abundant except the species of *Crataegus*, which occur mostly along the border.

The subdominants of the herbaceous layer vary with the season as well as with the location within the forest. In the prevernal season *Claytonia virginica*, *Isopyrum biternatum*, and *Collinsia verna* often form extensive and conspicuous societies in the maple consociation. The two species of *Dicentra*, *D. cucullaria* and *D. canadense*, occur together as subdominants in a rather extensive prevernal society. *Phlox divaricata* and *Geranium maculatum* form less extensive but not less well marked societies. *Asarum canadense* is everywhere abundant, but because of its growth habit is not conspicuous. *Viola sororia* is abundant, but is scattered too much to be considered a subdominant. In the elm consociation *Floerkia proserpinacoides* forms an extensive and extremely dense society. Like the elm this plant is present throughout the forest, but is always thickest where the elms are dominant.

During the vernal season *Hydrophyllum appendiculatum* forms an extensive society in the maple consociation. Later *H. canadense* is a subdominant over less extensive but more closely occupied areas. *Cystopteris fragilis* is abundant over considerable areas, and locally is present in such numbers as to become a subdominant. *Podophyllum* is also common, but as usual forms local colonies rather than extensive societies. All of these societies extend into the elm consociation, but there is no subdominant that is characteristic of the elm consociation during this season.

The aestival season is characterized by the subdominance of *Laportea canadensis* over great areas. Like the dominant shrubs *Asimina* and *Benzoin*, the wood nettle is abundant throughout

the woods except in the highest and lowest parts. At the same time *Impatiens biflora* is subdominant in the lower parts of the elm consociation, while *I. palida* is only a little less prominent, and keeps largely to the somewhat higher parts of the same consociation.

During the serotinal season several composites are conspicuous, but perhaps the most characteristic plant is *Campanula americana*, which occurs nearly everywhere in the woods, but usually not abundantly enough to become subdominant. Finally, during the autumnal season species of *Aster* and *Eupatorium urticaefolium* are the principal subdominants.

Social disjunctive symbiosis

This is the type of symbiosis in which the organisms concerned are not in actual contact, at least not all of the time, and in which there is no direct food relation. It includes, therefore, all of the ordinary interrelations of dominant, subdominant, and secondary species in a plant community. These interrelations in deciduous forests have been studied and described by numerous authors. It will suffice here, therefore, merely to mention the salient features of the subject, and to point out their relative importance in the community under consideration. The dominant plants of a community, which in a forest are trees, are those which largely control the environment and so determine what other species may grow in the community. They have very important symbiotic relations, therefore, with all other members of the community through their direct or indirect control of light, space relations, water supply, and to a certain extent available food materials. From this point of view it is of interest to compare a plant community with a human community. In a human community man is the dominant species. As the dominant species he controls the environment to such an extent as to determine what other species may live in the community. Some of the other species usually found in a human community are the horse, dog, cat, mouse, fly, etc. Some of these are not present because man wants them to be, but because man is present and is controlling the environment in such a way as to make it possible for the other species to live in the community. These facts are just as true of the plant community. The presence of

some of the species is distinctly advantageous to the dominant plants, while that of others is just as distinctly disadvantageous, as for example the parasitic fungi, but they are all present because the dominant plants have made it possible by their control of the environment. In the human community we find a well marked division of labor among the individuals of the dominant species; some are engaged in supplying food, others in supplying clothes or fuel, others in administering the law, etc. In the plant community we find a somewhat comparable division of labor among the various species of the community, but not among the individuals of the dominant species. The function in the community of all members of the same species is the same, but some species have the function of manufacturing food, some for supplying a ground cover to check evaporation from the soil, some to act as scavengers in getting rid of dead bodies, etc. Another important difference between the human community and the plant community should be kept in mind. In the human community there are ordinarily more or less definitely organized activities carried on for the good of the community as a whole. On the other hand, in the plant community there is no altruism. It is a case of every plant for itself. The activities of certain species do result advantageously for the community as a whole, but this is due to chance circumstances, and the activities of course would be carried on just as vigorously if they were resulting in harm to the community. This fundamental difference between the two communities, however, is the natural result of the presence of consciousness in the human species and the lack of it in plants, and as soon as we leave that fact out of consideration the two types of communities become strikingly similar.

The individuals of any species, whether a dominant or a secondary species in a plant community such as the one we are considering, all make similar demands upon the environment. For this reason their relations seldom result in any benefits, but on the other hand there is constant competition between them for space, food, and often for other environmental factors such as light or shade. This is often just as true of individuals of different species which make such similar demands upon the environment as to merit being called ecological equivalents. Species which are ecologically

very different, on the other hand, often are incidentally very serviceable to one another. The trees, for example, furnish the shade necessary for some of the herbaceous plants and fungi, while the herbaceous plants furnish a living soil cover which prevents undue loss of the soil water which is needed in great quantities by the trees. The trees, likewise, as well as the shrubs, especially those near the border of the woods, serve as a windbrake which protects many smaller plants from the dangers of too high transpiration rates.

Of very great importance from the viewpoint of social disjunctive symbiosis is the phenomenon of leaf fall. The primary reason for leaf fall, of course, is the reduction of the transpiration surface during the season when absorption is difficult or impossible, and the primary cause is desiccation, but the effect of this habit on other members of the community is perhaps as important as its significance to the deciduous plants themselves. The fallen leaves form an efficient cover throughout the winter season, thus greatly reducing evaporation from herbaceous perennial plants as well as from the surface of the soil. The place of the fallen stems of herbaceous perennials in social disjunctive symbiosis is similar to that of the fallen leaves, as, likewise, is that of the dead bodies of annual plants.

Closely connected with leaf fall are the activities that are concerned with the decay of the fallen leaves. These are due mostly to bacteria and fungi. The bacteria and fungi are regular members of the community, and are living in social disjunctive symbiosis with the higher plants. They are able to live in the community only as a result of the presence of the higher plants, and they render a distinct service to the community by preventing the accumulation of dead bodies.

Although the phenomena just cited all result in benefit to certain members of the community, it must be understood that symbiosis does not necessarily imply any benefit to the symbionts, mutual or otherwise. In antagonistic symbiosis there is often more harm than benefit for at least some of the symbionts, while in social symbiosis there may be a mere tolerance of presence with neither harm nor benefit resulting to any appreciable extent. Thus many of the species in a community such as the one under

consideration are able to live together largely because the main parts of their absorbing systems are placed at different levels in the soil.[5] For example, *Circaea lutetiana* has its rhizomes only about one inch beneath the surface of the soil; the rhizomes of *Asarum canadense*, *Sanguinaria canadensis*, and *Thalictrum dioicum* are about two inches deep; those of *Podophyllum peltatum* and *Sanicula gregaria* average about two and one-half inches deep; the bulbs of *Allium canadense* are placed about three inches, and the corms of *Arisaema triphyllum* about five inches below the surface of the soil. The rhizomes of *Polygonatum commutatum* are produced about three inches down, and are later pulled down by root contractions to a depth of five or six inches. Along with these, of course, are the trees and shrubs which have absorbing organs at all depths to a distance of several feet. Still another factor which tends to make it possible for large numbers of species to live together in a forest community is the fact that different species carry on their more important activities at different times of the year, and so do not interfere with each other as much as they otherwise would. It is this that makes it possible to distinguish prevernal, vernal, aestival, serotinal, and autumnal seasons, each characterized by the prominence of different groups of species.

It is not necessary, however, to carry the discussion further along this line. It is recognized that there is nothing new in the preceding discussion except the point of view. In other words, the kinds of interrelations here pointed out are well known to most botanists, and for that reason it was considered unnecessary to go into much detail; but these interrelations have not usually been considered as cases of symbiosis. The reason for dwelling upon them here, therefore, has been to emphasize the fact that they are instances of the living together of dissimilar organisms, and so properly belong in a discussion of symbiosis. This proper point of view is preparation for further discussion of the other types of symbiosis, some of which are not so well known.

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[5] Sherff, E. E., Vegetation of Skokie Marsh. Ill. Sta. Lab. Nat. Hist. Bull. 9: 575–614. 1913.