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THE RELATION OF AERATION TO THE GROWTH AND ACTIVITY OF SWAMP PLANTS AND ITS INFLUENCE ON THEIR ECESIS.

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The influence of various soils or substrata on the growth and functional activity of plants is one which has long engaged the attention of investigators. During the past fifty or more years many experiments have been performed in attempts to determine the particular factor or factors in soils that exert the controlling influence on the growth and functional activity of plants. In spite of the repeated experiments there is yet no agreement among investigators as to the operation and relative importance of the various factors. This lack of agreement arises, in part at least, from the fact that the various experimentors take into account only certain phases, for example, the effect of physical or chemical factors to the exclusion of all others. A satisfactory solution, however, must take into account all the factors and their interrelations. Another reason for this lack of agreement seems to be that the effect of the surrounding medium on the functional activity of roots has not been thoroughly considered. The amount of absorption by roots is, in many cases, conditioned by the rate at which absorption proceeds rather than by the area of the absorbing surface, altho in any given set of conditions, the amount absorbed is the product of the rate times the absorbing area.

Any condition which adversely affects the development or activity of roots, if prolonged, prevents the development of the parts above ground. Accordingly, this may be of great importance in determining the growth and productivity of the plant.

The environment of roots is a complex of several factors, all of which are operative to a certain extent in every case, but under given conditions one factor and under different conditions some other factor may exert the predominant influence on the rate of development and the functional activity of the root system. An analysis of the factors concerned is accordingly helpful in determining the probable effect of any single factor. In addition to the direct and indirect mechanical effects of resistance of soils to root penetration the factors determining the growth and activity of roots or underground parts are (1) the amount of water present and its distribution in the soil, (2) the quality and concentration of the soil water, (3) the supply of oxygen and (4) soil temperature. The final form and activity of the root system is the result of the interaction of different variable conditions in which the effect of single factors often cannot be isolated satisfactorily.

The amount of water in a soil varies greatly, since lakes on the one hand and solid rock surface on the other represent the two extremes. Lakes are to be regarded ecologically as soils with a minimum of solid matter and a maximum of water-content. Rock on the other hand represents the opposite condition of a maximum of solid matter and a minimum of water-content. Either open water or exposed rock may be invaded and occupied by plants. The reaction of vegetation on the habitat thru a series of developmental stages, in combination with topographic processes, leads to the establishment of some finally dominant type of vegetation. The character of this finally dominant or climax vegetation is determined by the climate. Within a given area the same climax is reached whether development begins in open water (hydrarch), on a rock surface (xerarch) or on denuded soil. Three climax types are to be recognized in Minnesota (Bergman and Stallard 1916). The series of developmental stages in hydrarch succession may be shown by the following diagram.

Pinus association	Acer-Tilia association	
↑	↑	
Abies-Betula associes	Ulmus-Fraxinus associes	
↑	↑	
Larix-Picea associes →	Salix-Alnus associes	
↑		
Chamaedaphne-Andromeda associes →		Andropogon association
↑		
Carex associes →		
↑		
Scirpus-Zizania associes		
↑		
Castalia-Nymphaea associes		
↑		
Chara-Philotria associes		
↑		
Open water		

The progression of stages to any one of the three climaxes is due primarily to a corresponding decrease in the water-content of the soil. The amount of water contained in a soil, however, has a more or less marked effect on other factors.

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Accordingly a progressive decrease in water-content thru a series of stages involves progressive changes in other factors. On this account the determination of the probable influence of any particular factor or set of factors on the growth and distribution of plants in swamps is very difficult. The problem involves the consideration of a number of variously interrelated factors the general features of which are here presented.

SCOPE OF THE PROBLEM

The problem is a complicated one. A solution of it in order to be at all adequate must take into consideration:

1. The effect of an excess of water on the concentration of solutes. These may be considered under three heads: (1) mineral compounds used by plants and more or less essential to their growth; (2) gases, especially oxygen and carbon dioxide; (3) humus acids or other toxic substances more or less inimical to plant growth.

2. The effect of varying concentration of solutes on the rate of growth of plants. This includes: (1) mineral compounds; (2) gases; humus acids or other toxic substances.

3. The influence of the temperature of the substratum on the growth of plants; (1) the direct influence on the rate of growth and activity; (2) the indirect influence thru the effect of temperature on the solubility of gases in water.

4. The influence of air temperatures, humidity, wind and light on the growth of swamp plants.

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5. The effect of habitats with an excess of water on the structure and behavior of plants.

6. The reaction of vegetation on (1) water-content; (2) the quantity and quality of gases; (3) other solutes.

7. The reaction of vegetation on temperature, humidity, wind and light and the influence of such reaction on the structure and behavior of plants.

8. The effect of the reaction of vegetation on the habitat and its relation to the ecesis and succession of plants.

The work has been in progress about three years, the field work having been done mostly in the summer months in the northern part of the state. The experimental work was carried on during the winters of 1914-1915 and 1915-1916 in the University greenhouse.

AN ANALYSIS OF SWAMPS AS PLANT HABITATS.

The characteristic features of the environment of swamp plants are the excess of water, a continuous and often high rate of transpiration along with a minimum of aeration and low temperatures in the substratum thruout the growing season. The amount of water present in the soil profoundly influences the concentration of solutes, the aeration of the soil and the soil temperature. Chemical analyses of various swamps in Minnesota show that the quantity of minerals in peat soils is very low. The following table may be taken as an example.

Chemical Composition of Minnesota Peat Soils.

Location	Ash per cent	Total N per cent	P_2O_5 per cent	K_2O per cent	CaO per cent
			Musket Peat Soils.		
Kimberly	10.43	2.115	.395	.128	2.53
Skibo	10.53	1.634	.145	.165	2.41
Island	16.41	2.181	.301	.130	1.66
Island	14.86	2.250	.336	.113	2.45
Island	12.22	2.070	.333	.086	.72
Meadowlands	10.97	1.580	.287	.087	.91
Kelliher	34.02	1.601	.274	.124	4.38
Kelliher	14.72	2.060	.329	.166	5.97
Grand Rapids	7.83				.37
Grand Rapids	12.03				.80
Average	14.40	1.930	.300	.125	2.22
			Grass Peat.		
Kimberly	11.24	2.874	.450	.095	1.49
Wallace	14.10	2.274	.217	.082	1.74
Bemidji	10.40	2.860	.290	.079	2.52
Bemidji	6.78	2.820	.270	.105	2.38
Bemidji	9.97	2.790	.273	.139	2.93
Middle River	10.48	2.693	.285	.104	2.80
Middle River	29.07		.349	.094	7.06
Greenbush	15.91	2.901	.369	.103	2.66
Bronson	13.03	2.312	.332	.087	3.23
Lowry	43.83	2.060	.302	.079	2.17
Mendota	23.96	2.530	.378	.120	14.36

Dassel	14.48		.295	.096	1.92
Hector	41.23	1.860	.318	.234	1.03
St. Peter	43.08		.266	.326	3.10
St. Bonificius	17.73	2.755	.323	.071	2.17
Stący	28.27	2.765	.340	.085	2.20
Laporte	52.45	2.295	.557	.076	1.43
Beltrami**	38.07				3.95
Average	26.29	2.569	.331	.114	3.35

*Average of 6 analyses. **Average of 5 analyses

From De Forest Hungerford: Journ. Amer. Peat Soc. Vol. 9:p.74

The following table gives the results of chemical analyses of various kinds of soils from different parts of the state.

Locality	Kind of soil	Total N. Top	Total N. Sub	Potash Top	Potash Sub	P_2O_5 Top	P_2O_5 Sub	Lime Top	Lime Sub
Marshall	Native prairie	.38	.22	.45	.40	.35	.26	.69	.70
Sleepy Eye	Cultivated	.28	.10	.18	.44	.21	.20	.61	.67
Wadena	S'dy loam, cult.	.25	.08	.28	.47	.20	.26	.60	.25
Mille Lacs	Pine Land, s'dy	.07	.	.14		.22		.38	
Wyanette	Sandy, cult.	.15	.05	.08	.08	.10	.13	.21	.22
St. Cloud	Sandy loam	.17	.12	.85	.62	.19	.15	.26	.38

Data from H. Snyder, Minn. Exp. Sta. Bulls. 35 & 70.

The phosphoric acid content of peat soils varies from 0.145 to 0.557 per cent with an average, for ten muskeg soils, of .300 per cent. Peat soils from eighteen grass swamps averaged .331 per cent of phosphoric acid. The average phosphoric acid content of upland soils in Minnesota, according to Snyder ('99:69) is .20 per cent for average of seventy-two surface soils and fifty-two subsoils. The potash content, for ten muskeg peat soils, averages .125 per cent and .114 per cent for eighteen grass peat soils. Snyder ('99:69) states that in surface soils of Minnesota the average amount of potash, based on the analysis of seventy-two samples, is .43 per cent. The analysis of fifty-two subsoils of Minnesota gives an average of .4 per cent of potash. Accordingly, there is a notable deficiency of potash, in Minnesota swamp soils, in comparison with the quantity present in most upland soils. Calcium and nitrogen are usually present in considerable quantities. The amount of lime in peat soils compares favorably with Snyder's (l.c.69) average of 1.29 per cent for surface soils and 1.78 per cent for subsoils of uplands. The chemical composition of peat soils in Minnesota is similar to that found by Dachnowski, in Ohio swamps, and by Transeau ('05:428) in Michigan swamps. Dachnowski ('12: 378,382,387) found that in peat bogs in Ohio the essential mineral constituents were present in inconsiderable quantities, which in the case of phosphoric acid and potash amounted to less than .5 per cent, in most swamps. Calcium and nitrogen were present in relatively high percentage varying from one to nearly four per cent. He states elsewhere, however (l.c.389), that the amount of nitrogen as nitrites and nitrates is very small. Coville ('10:46) has also shown that the nitrogen as nitrates in Kalmia peat varies between .0008 and .0022 per cent with an average of .0015 per cent. Thus, with the exception of available nitrates and potash, the chemical composition of the substratum in swamps compares favorably with that of the average upland soil. Altho the amount of potash present is very small nevertheless, it seems to be sufficient for the maintenance of plant growth.

In an attempt to establish some correlation between the stages of vegetation and the chemical character of peat soils, Dachnowski ('12:387) has given tables showing the amounts of various constituents of peat soils from different developmental stages. The amount of nitrogen and potash does not increase to an appreciable extent. Phosphoric acid shows a slight increase as the mesophytic climax is approached. The ash content also increases from the bog meadow stage to the mesophytic forest. Elsewhere (l.c.379) he states that "these analyses of the ash constituents of peat indicate that the mineral salts are largely of external origin. They are the sediments brought in by stream or carried down by erosion and wind. The material is found mostly as silica in the form of sand and silt, as alumina and silica in the form of clay, and as calcium carbonate in the form of marl." The number of analyses is small and the evidence, therefore, is not wholly dependable. Likewise the available data on the chemical composition of the substratum in the different developmental stages of swamps in Minnesota is insufficient to establish definite correlations between the chemical composition of the peat and the character of the vegetation in the various developmental stages.

Concentration of Swamp Waters.

It might be expected that the concentration of water in

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lakes and swamps would be much less than that of the soil water on account of the great excess of water in lakes and swamps as c compared with that of soils. Livingston ('04:383) has determined the concentration of water from various sources by measuring the amount of lowering of the freezing point. He finds that the water of lakes and rivers lowers the freezing point .005 - .01 C. and that swamp waters lower the freezing point .0025 -.02 C. He concludes that "bog waters do not have an appreciably higher concentration of dissolved substances than do streams and lakes of the same region." Transeau ('05:425) finds "a notable difference between the total mineral content of bog water and that of the soil waters adjoining .... The total mineral content of the ground water varied from 267.7 to 585 parts per million." Three analyses of bog water show "the mineral content to vary from 89.9 to 219 parts per million, the highest figure being that for the sample obtained near the margin of the tamaracks, i.e., nearest the mineral soil." Dachnowski ('12:504) finds in Ohio peat swamps that "the concentration of mineral salts in bog water from various plant associations (associes) ranges from 40 to 160 parts per million" and that "the osmotic pressure of the solutions..... is very nearly alike in the several plant zones and about the same as that of lake or river water." Cameron ('1911) estimates that the soil solution contains about 28 parts per million of K_2O and about 7 of P_2O_5. Thus it appears that the soil solution in swamps is often more dilute than that of rivers and lakes or than the water of adjacent mineral soils. However, in other cases no appreciable difference exists.

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Altho swamp water is a very dilute solution it shows no absolute deficiency of any mineral constituent.

The effect of dilute nutrient solutions on plant growth has been studied by a number of investigators and as a result it has been clearly established that plants may grow readily in very dilute solutions. Cameron ('11:70) states "that if a given ration of mineral nutrients be maintained, relatively small effect is produced on the growing plants by varying the concentration over a wide range." Tottingham (1914) and Stiles (1915) arrive at the same conclusion. Stiles in working with wheat and rye found that the amount of dry matter produced varied but little in concentration of 1, 1/5, 1/10 and 1/20 of a standard solution. Stiles ('15:96) compares the amount of potassium and phosphate in the culture solutions used by him with the amounts found by Cameron in the soil solution. He states that "the weakest solution when first put in the culture jars was of the same strength in regard to potash and phosphate as that of the soil solution." He also says "altho the plants grown in the dilutest solution produced somewhat less dry matter than those in higher strengths, the difference was not great and the plants were perfectly healthy." Brown ('13:10-15) in growing plants of Elodea, found that the dilution of tap water with an equal amount of distilled water produced very little effect on the amount of growth. He also found in comparing the growth of Elodea in tap water with the growth of plants in Knop's solution of 0.5, 1, 2, and 4 times standard strength that the

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plants in Knop's solution made better growth than those in tap water but that there was very little difference in the growth of plants in the different concentrations of Knop's solution. This is in agreement with the results of Cameron, Tottingham and Stiles cited above and supports Cameron's view that the soil solution, altho very dilute, is sufficiently concentrated to support vegetation.

The assumption by some writers that the inability of plants to avsorb a sufficient amount of water from a swamp substratum might be due to high osmotic pressure of swamp waters has resulted in a number of investigations of this property. The osmotic pressure of swamp waters has been found by Livingston ('04:383), Transeau ('05:424) and Dachnowski ('12:372) to be about the same as that of lake and river water of the same region. The evidence does not support this assumption and all three agree that the high osmotic pressure of bog waters is not a factor in explaining the structure and distribution of swamp plants.

Acidity of Swamps.

The acidity of swamp water is another factor which has been assigned as the cause of the inability of certain plants to become established and grow in swamps. Thus Schimper ('03:8) attributes the xeromorphic character of bog plants to a "physiological dryness" brought about by the presence "of humus acids in the soil." Acidity tests have been made of swamp waters in many localities in the northern part of Minnesota. The acidity has

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been found to vary from .001 to .0055 of a normal solution, in most swamps, when titrated with N/10 potassium hydroxide and using phenolphthalein as an indicator. The highest acidity found was .0125 normal but such high degrees are very unusual. There is no constant relation between the degree of acidity and the character of the vegetation of swamps. It often happens that swamps with the very same associes may vary considerably in this respect. In general it may be said that the acidity increases with the progression of stages from the Chara-Philotria associes up to the Larix-Picea associes. Thus, in lakes, in which the Chara-Philotria associes is the first to appear, the water is usually neutral or often alkaline to as much as .001 normal. However, some exceptions are to be found. Dachnowski in Ohio also finds the highest acidity in the Larix-Picea associes. Transeau ('06:37) states that "The acidity of local bog waters varies from .00015 to .00258 normal acid. The lowest values are found in areas covered by bog sedges and swamp plants, and they are approximately the same. The highest occur under the tamaracks."

The increase in acidity is in some way due to the reaction of vegetation and may be due to the formation of humus acids by the slow decomposition of plants under conditions of reduced aeration or to the absorption of minerals from some of their sales thus leaving uncombined acid radicals. Baumann and Gully (1910) correlate the acidity of peat soils with the acidity of Sphagnum and conclude that since peat consists largely of imperfectly decomposed Sphagnum, it is probable that the acidity of peat is the acidity of Sphagnum. They found that peat had a somewhat higher acidity than Sphagnum and that peat was rather more active in decomposing the salts of mineral acids. They attribute the acid reaction to the selective absorption of the cell colloids of disintegrating plant tissue which retains chiefly the basic ions of dissolved salts. They state also that several other mosses have the same property as Sphagnum. These observations are confirmed by Skene ('15:76). Wieler states that these properties are exhibited by tissues of many vascular platns. Czapek (1911) and Wieler (1912) agree with the hypothesis of Baumann and Gully. The deductions of the latter, however, are disputed by other writers among whom are Tacke and Süchting (1911), Rindell (1911), Oden (1912), Ehrenberg and Bahr (1913) and Tacke, Densch and Arndt (1913). The opponents of the colloidal theory attempt to show that the acid reactions of peat soils are due to the presence of more or less soluble humus acids. Whether one or both of these hypotheses are to be accepted as causes of the acidity of peat soils is not apparent and must await further investigation by chemists. Altho it has been clearly established that Sphagnum and other mosses are able to decompose salts, there are swamps in which no Sphagnum or other mosses occur in which the acidity is as high as in a typical Sphagnum swamp. No invariable correspondence is to be noted between the acidity of swamps and their chemical composition or between the acidity and the chemical composition of the soil surrounding the swamp. The acidity of swamps is often the same

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in that part of the state in which the soil consists of the more calcareous drift as in the parts in which the drift is non-calcareous. However, the lime content in swamps within the area of calcareous drift is often, if not generally, higher than in those within the areas of non-calcareous drift.

From the fact that there is no apparent correlation between acidity and the character of vegetation in swamps and that the same species of swamp plants seemingly grow equally well regardless of the degree of acidity, it appears that this can have no important influence on the occurrence of plants in swamps. This same conclusion was reached by Livingston ('05:351). Transeau ('05:427) however, arrives at a different conclusion and says "It would appear, then, that the acidity of the solution is unfavorable for the growth of some plants, and that it is a factor in the selection of species for acid soil conditions." Dachnowski ('12:372) also concludes "that certain species, such as cranberry, blueberry, blackberry, bean and others, favor acid soil conditions while for other plants acidity is not advantageous for growth and hence becomes a factor in the selection of species." In an earlier paper ('11:14) he states that "the stress laid by various authors upon the relation of these two factors (osmotic pressure and acidity) to plant societies in bogs, in so far at least as this region is concerned, will not hold. They are not factors in the selection or distribution of species for bog habitats."

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Toxicity.

Livingston ('05:351) in failing to find any correlation between the osmotic pressure and inhibitory effects of bog waters on plant growth or between acidity and toxicity came to the conclusion that the toxic properties must be due to the presence of certain chemical substances which are present in extremely small quantities. Dachnowski ('12:334) also believes "that there are present in bog water and in bog soils injurious substances which are , at leat in part, the cause of xeromorphy in plants, and of decreased fertility in bog soils. "In spite of the conclusions of Livingston, Dachnowski and others, the assumption of the presence of acids or of very minute amounts of toxic substances does not seem to constitute an adequate explanation. In the first place it is to be observed that the toxic properties of the swamp substratum remain approximately the same thru several developmental stages. Progression in the hydrosere is due primarily to the progressive decrease in the water-content of the substratum. For this reason, it is to be expected that by a variation of the water-relations the stage of development might be either advance or thrown back to some earlier stage. When water is present in excess, aeration is impeded. Conditions of aeration in swamps may be materially altered by the reaction of vegetation, since the character and quantity of vegetation has a marked effect on the amount and kind of gases present under given conditions. The presence or absence of acids or other substances which may exert a toxic influence on plant growth is not disputed. If they are present, however, it is because of lack of oxygen and if proper aeration is provided the alleged toxic substances will disappear.

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Temperatures of the Air and of the Substratum in Various Associes.

Before the consideration of evidence on the effects of aeration however, the temperature, evaporation and light relations of swamp plants as possible factors in their growth and distribution will be discussed.. The amount of water in a soil exerts an influence on soil temperature. On account of the high specific heat of water, any soil having a high or excessive water-content, heats up very slowly, but once heated maintains the temperature for some time. In consequence there is a marked lag in the seasonal rise and fall of temperature in saturated soils or in soils with a great excess of water in comparison with the seasonal rise and fall of temperature of the atmosphere or of soils with a moderate or small amount of water. Numerous readings of the temperature of different substrata have been taken during the three years of field work. Only a few of these are presented in the following table. The readings, however, are representative and will serve to illustrate the differences.

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Date	Cham-Androm air 1.5m	soil 1dm	2dm	Larix-Picea air 1.5m	soil 1dm	2dm	Abies-Petula air 1.5m	soil 1dm	2dm	Pinus or Acer-Tilia 1.5m	1dm	2dm	Prairie Air 1.5m	Soil 1dm	2dm.
June 19*				21.0	9	.05	23	15	13						
" 27*			10	26.5	10.	5.0	33	17	15						
" 23 H				21.5	6.3	5.0	20	14	13						
J'ly 10*	200	16.5	14.5				21	14.5	13.5						
" 18H							29	13	11.8	30	20.4	18.4	32	28	29.1
" 19H	225	14.6	13.5				28.6	13	12.6	28	18.8	17.4	28.4	22.6	22.3
" 22H	320	22.6	18.0				29	15.2	14.1	27.4	17.4	16.8			
" 29B				33	19.8	13.4							26.4	25.	216
Aug.3 H							30	16.2	14.6	31.4	21.2	19.4	35.5	25.	234
" 4 B							21	15.5	15.5						
"8-10 B				18	13.5	12.5	30	14.5	14						
" 20 B							25	16.	13.						
" 27 B				18.5	9	9.5									
" 28 *							20	12.5	12.						

*Meadowlands 1912; H, Hubert 1916; B, Benedict 1915

This table shows that for corresponding associes the temperature of the substratum at any date does not vary greatly altho air tempertures may fluctuate considerably. The swamp shows the greatest divergence between air and soil temperatures, a rapid falling off in temperature at increasing depth and the lowest soil temperature of any habitat. A progressive increase in the temperature of the substratum is to be noted in passing from the Chamaedaphne-Andromeda or Larix-Picea associes to any of the climax associations. This is correlated with the progressive decrease in water-content which takes place in the same direction. Other factors, however, such as the nature of the substratum, the kind and amount of covering as affecting light intensity, evaporation, humidity, etc., must be taken into account before the exact relation can be determined.

In winters of moderate or heavy snowfall the swamps may not freeze or only to a depth of a few inches, but in winters of light snowfall or when a period of severe freezing weather comes before snowfall, it is not unusual for swamps to freeze to a depth of two to four feet. Shallow swamps might thus be frozen to the bottom. When once frozen the substratum does not readily thaw and ice may remain long after the surrounding ground has thawed out completely. In the summer of 1915, between June 15-18, ice was found at a depth of 16-20 inches in swamps north of Gull Lake, near Brainerd. Mr. Harvey Stallard in his work at Meadowlands, during the summer of 1912, found ice at a depth of one foot on the 27th of June. The temperature at depths of two to three decimeters, in swamps during June, varies usually between 4-6 C., while in timbered areas at corresponding depths the soil temperature varies between 11-14C. During July and August the temperature at depths of 2-3 decimeters in swamps rises to 10-14 C., and at corresponding depths in woodland wooded areas to 17-22 C.

Thus it is to be noted that the temperature of swamps even in July and August is several degrees below that of the soil in surrounding wooded areas and a more marked difference exists when compared with grassland or open areas. Dachnowski ('12:297) finds in Ohio swamps that "The persistence of winter cold and ice through the summer months is a point not proved either by observation or by registering recording instruments." Cox ('10:119) in Wisconsin finds that frost remains in the soil of an unflooded

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bog until comparatively late in the season, and there have been instances of frost in the soil in marshes as late as July 4. The observations of the writer are in accordance with the latter. Transeau ('05:420) gives a table of temperatures of the substratum in various associes as compared with upland soils and with air temperatures. The substratum temperatures in the Cassandra and tamarack zone are the lowest and show an increase in progressing to the upland. Low soil temperatures inhibit the growth of plants by retarding absorption and conduction. They also render the substratum unsuitable for the growth of bacteria which under more favorable conditions decompose the complex organic substances of the soil and render them available for the use of other plants. When low temperatures in the substratum are associated with higher air temperatures, evaporation may exceed absorption. In consequence of this, certain plants may be excluded in favor of others with a lower transpiration ratio.

Air temperatures in swamps during the night are usually lower than over upland soils. The difference is less marked on cloudy nights than on clear ones. Consequently frosts are more frequent in swamps than on the neighboring uplands. The reason for this is that the temperature of the substratum is considerably lower than that of soils of the surrounding upland. Consequently there is less radiation as compared with ordinary soils. Cox (1910) finds a lower air temperature over Sphagnum than over bare peat. During the summer of 1914 at Benedict, a Draper recording thermometer was placed in a tamarack swamp

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and another instrument was placed on the upland, having an elevation of not more than ten feet above the level of the swamp. Frost was recorded in the swamp once in July, twice during August and once during the first ten days of September. On the same nights on the upland, the temperature of the air did not fall below 40 F. Similar results are shown by Alway ('16:168). He gives a table of minimum temperatures recorded in a peat swamp at Grand Rapids, during the summer of 1914, as compared with the minimum air temperatures over the adjacent mineral soil. To what extent this is a factor in limiting the growth and distribution of native plants in swamps cannot be stated with certainty. Its effect on the limitation of the use of swamps for agricultural purposes, however, is well known.

Evaporation in Swamps.

The relation of air temperatures to transpiration in swamps and its effect on the growth and distribution of swamp plants is another factor to be considered. The apparent anomaly of plants with xerophytic characters growing in habitats with seemingly unlimited quantities of water has long attracted the attention of botanists. Schimper ('03:8) assumed that the xerophytic character of swamp plants was due to "physiological dryness". It has since been generally accepted that the xerophytic character of swamp plants is due to transpiration in excess of the amount which the plants are able to absorb. However, there has been no agreement as to the cause of the limitation of absorption. There is also no agreement on the effect

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of transpiration as a factor in the limitation of the growth and distribution of swamp plants. The data on the relative evaporation in various plant associes, however, as determined by different investigators are essentially similar. The work of Livingston ('08:10) and Tapp ('09:282) has shown that the evaporating power of the air is to be regarded as the resultant of the interaction of humidity, temperature and wind in so far as they influence water loss from plants. The rate of transpiration has a definite relation to the rate of evaporation, altho Gates ('14:445) found that this relation varied both with species and with individuals.

As a rough measure of the evaporation power of the air in different habitats, at Benedict, in August 1914, two evaporimeters were set, one on top of a bare hill near a tamarack swamp and the other well out in the swamp. At the end of a two week period the evaporimeter in the first station had lost a liter of water, while the one in the swamp had lost less than half that amount. On August 6, 1915 evaporimeters were set in a number of stations in the vicinity of International Falls. The results are presented in the following table.

Station	Amt. lost in cc. 1st Week	2nd Week	Total
In scrubby Chamaedaphne of a cleared, burned and drained Larix-Picea swamp.	268 cc.	127 cc.	295 cc.
Same swamp under single bush of Alnus	165 cc.	78 cc.	243 cc.
Alnus-Salix zone	115 cc.	50 cc.	165 cc.

(continued) Station	Amt. lost in cc. 1st. week.	2nd week.	Total
Populus tremuloides	124 cc.	65 cc.	189 cc.
On exposed rocks of an island in Rainy River	425 cc.	----	------

Evaporation tests were also made at Hubert, in 1916, with the following results. The test was begun July 18th and ended August 14th.

Station	Amount of water lost in cubic cc.								
1. [illegible]	July					August			
	20	23	27	29	31	1	3	9	14
1. Clearing, sparse grass, mostly Danthonia	56	75	60	72	30	80	98	*	87
2. Pinus banksiana associes	35	48	53	59	[illegible]	60	45	121	58
3. In thicket of Betula papyrifera, Ostrya, and Cornus	36	56	38	**	17	34	48	*	56
4. Acer rubum- P. resinosa swamp border	22	27	x		69	14	18	35	26
5. P. resinosa-P. strobus association			x		80	16	30	65	48
6. Prairie on bank sloping toward lake	*	89	72	108		168	98	*	112
7. Partly cleared Pinus association near road				x	100	18	48	95	75
8. Pinus, Quercus, Cornus				x	70		50	61	38

* Not working, reset on same date. ** Reset July 31
x Set July 28.

The weather during nearly the entire period was hot and dry which caused a high rate of evaporation. General cloudiness prevailed on July 25th with rain during the night and forenoon of the 26th. During the last four or five days of the test, also, there was more or less cloudiness with lower temperatures but with little or no rain. On August 11, several evaporimeters were placed in other station and allowed to run 3 days. The locations and results are as follows:

Station	Water loss in cc.
Over Chamaedaphne	65
Under Chamaedaphne	40
Under Carex	25
Under Andromeda	25
Under Ledum - swamp border	25
Picea-Abies-Betula swamp border	28
Under Pinus banksiana	38
Open prairie	72

It is evident from the figures given in the preceding tables that the rate of evaporation at the level of the shrubs in the Chamaedaphne-Andromeda associes is relatively high, even approaching that of grassland. Evaporation is least in the Abies-Picea associes, or in the Alnus-Salix associes, the corresponding stage of the subsere. The results obtained by Dachnowski ('12:302) are similar. He finds greater differences, however, between the central sphagnum-cranberry zone and the University station than the writer does between the Chamaedaphne-Andromeda associes and the prairie station which respectively correspond.

The rate of evaporation is directly correlated with humidity, wind, temperature, kind and amount of vegetative coverings and light. The latter factors operate largely thru their influence on wind and humidity relations. Thus the low rate of evaporation in the Abies-Picea or Alnus-Salix associes is to be attributed to the fact that the taller and denser vegetation greatly reduces the wind velocity and the light. This in some measure affects the humidity and temperature relations. The higher water-content of the substratum as compared with that of the soil in the adjacent upland also influences the humidity, especially near the ground, at the level at which the evaporimeter was placed. The greater evaporating power of the air at higher levels in the same vegetative community has been pointed out by Yapp ('09:275), Dachnowski ('11:145; '12:304), Sherff ('12:421), and Fuller ('12:424).

Numerous readings of temperature, humidity and wind velocity in various associes and in different localities show that the rate of evaporation varies directly with the temperature and wind velocity and inversely with the humidity. Gates ('14:484) reaches the same conclusion. The following experiment at Benedict in 1914 shows these relations. Two soil cans were filled with water. One of them was placed in an open grassy area at a height of approximately 1/2 meter above the soil. The other was placed at the same height under the shade of two isolated jack pines, about 10 meters distant from the first station. After two days the second station was moved to denser shade of of Alnus crispa. The same distance from station 1, and same height from ground were maintained, however. The loss in grams over a period of several days is shown in the following table.

Date	Hour	Loss in grams. Sta. 1	Sta. 2	
Aug. 19	11:00 A.M.			
" 19	7:00 P.M.	12.5	8.7	
" 20	7:45 A.M.	*	*	
" 20	8:00 P.M.	15.7	11.7	
" 21	7:30 A.M.	0.2	0.0	Moved to shade of Alnus
" 21	7:45 P.M.	21.8	8.7	
" 22-25		*	*	
" 26	7:00 P.M.	**	1.9	
" 27	10:00 A.M.	1.0	**	
" 27	7:15 P.M.	9.9	3.7	
" 28	9:30 A.M.	1.2	0.6	
" 28	7:30 P.M.	11.7	6.6	
" 29	9:00 A.M.	*	*	
" 29	7:00 P.M.	13.4	3.5	
" 30	8:30 A.M.	1.0	0.6	
" 30	7:15 P.M.	22.5	3.25	
" 31	7:25 P.M.	15.2	6.65	

*Rain during night, weight increased. ** Not weighed.

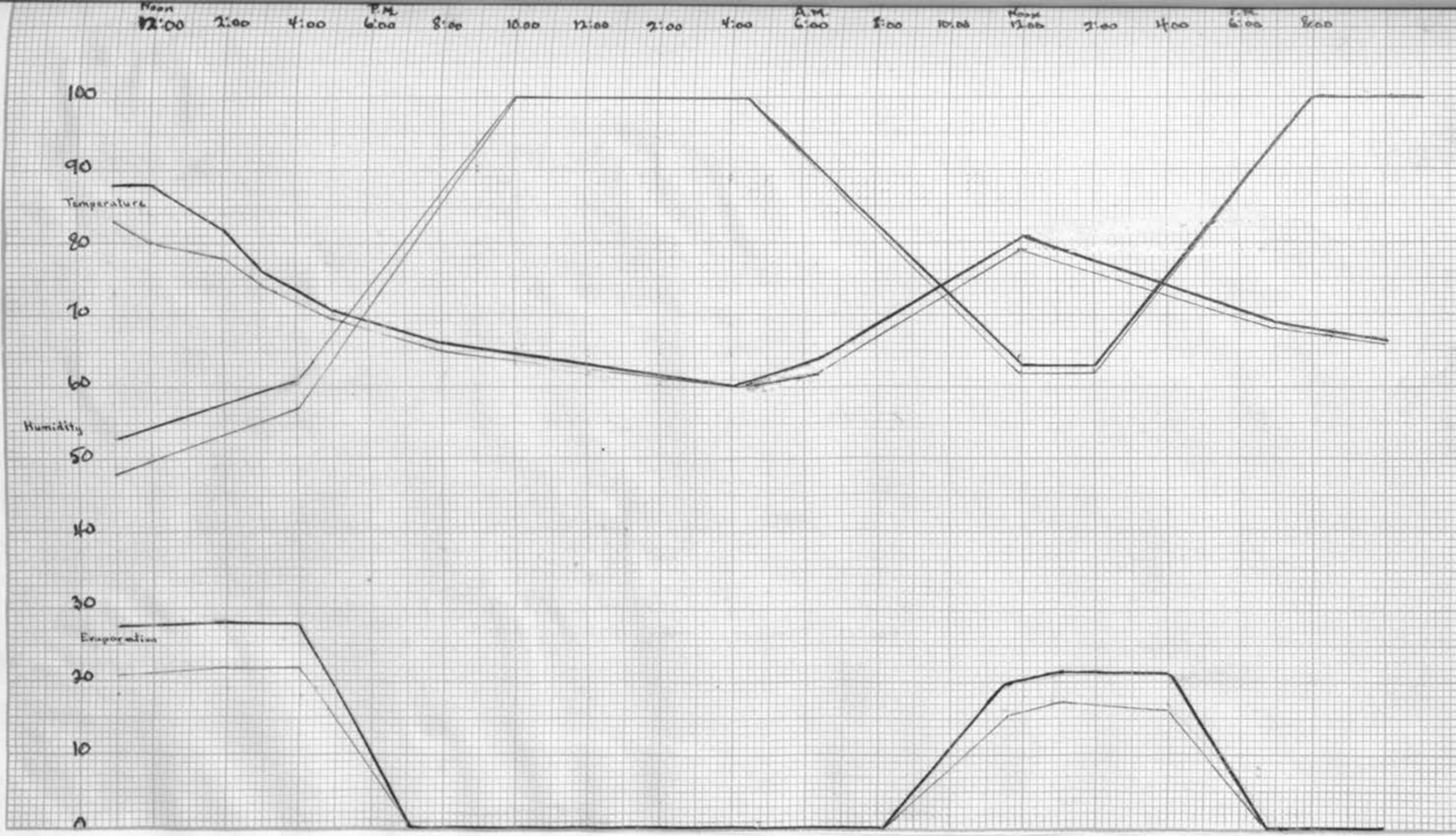

Figure 1. Graphs showing relative evaporation, humidity and temperature of two adjacent stations at Benedict, Minnesota, August 19-20,1914. The water loss in cubic millimeters, temperature in degrees Fahrenheit, and humidity in per cent are shown as ordinates, the time in hours as abscissas. Heavy lines represent station 1, in open grass-covered area; light lines station 2, in shade of two isolated jack pines at a distance o of about ten meters from station 1. Wind velocity, Aug. 19, 11:00 A.M.to 4:15 P. M. 60, 048 ft., Sta. 2. 31, 528 ft.; Aug. 20, 8;00 A.M.±7:30 P.M. Sta. 1. 66,007 ft, Sta. 2. 60, 417 ft. No wind after 4:15 P.M. Aug. 19 or after 7:30 P.M. Aug. 20.

It is to be observed that the evaporation in the second station runs lower than in station 1. The difference is still more marked after the transfer of station 2 to the denser shade of Alnus. It is to be noted also that the evaporation during the day period is much in excess of that for the night period. In some cases the evaporation during the night is very slight or none. In order to determine the correlation between evaporation and other factors, a number of measurements of temperature, humidity and wind velocity were made at the two stations. The results are shown as graphs accompanying.

During the nights of August 19-20 no water loss was observed. On the night of August 20, the humidity reached the point of saturation at 8 P.M. and the humidity was maintained at this point until about 8 A.M. on the following morning. There was no wind during the night on either date.

A similar evaporation test was made at International Falls during August 1915. The test began August 6, and was continued three days. Two soil cans filled with water were placed as follows: the first on a bare, rocky outcrop, the second in the shade of a group of white pines growing near by. The results are given in the following table.

	Water loss in grams. Sta 1.	Sta. 2	Temp. Sta. 1.	Sta. 2	Humidity. Sta. 1	Sta. 2.
Aug. 6 8:45 A.M.						
Aug. 6 8:15 P.M.	19.9					
Aug. 7 7:50 A.M.	1.9	5.4*	23.5	19.	65	78
Aug. 7 7:30 P.M.	22.5	5.0	21.0	19.	68	82
Aug. 8 8:45 A.M.	3.8	0.6	32.0*	25.	47**	56**
Aug. 8 7:30 A.M.	26.5	4.8				

*Total loss from Aug. 6, 8:45 A.M.
**At 12:30 P.M.

The same correlation is evident here also, namely, that greater evaporation occurs under conditions of lower relative humidity and higher temperatures. Wind velocities were not determined but station 2 was somewhat protected from the wind, and evaporation would for that reason also be less than in station 1. As in the experiment at Benedict, in 1914, the evaporation during the night period was much less than during the day period.

The temperature and humidity relations at the surface of the ground and at a height of one meter for several different stations on different days were determined in connection with the evaporimeter experiment at Hubert, in 1916. The results are shown in the following table. The location of the various stations is given in the table on page 16.

Date and Hour.		Relative Humidity						Temperature					
	Sta.	1	2	3	4	5	6	1	2	3	4	5	6
July 29 9:30 A.M.	1 m.	51	54	54	59	59	51	32	30	30	29	29	32
	Sur.	48.5	60	60	73	59	40	34	30	30	28	29	37
July 30 2 P.M.	1 m.	50	82	79			50	37	26	26			36
	Sur.	50	79	79			41	36	26	26			38
Aug. 1 9:00 A.M.	1 m.	66	69	69			61	24	23	23			24.5
	Sur.	64	69	69			64	26	23	23			26
Aug. 1 Noon	1 m.	57	57	63.5				27	27	27			
	Sur.	68	57	64.0				30	27	29			
Aug. 1 7:00 P.M.	1.m.	54	54				54	24	24				24
	Sur.	54	54				54	24	24				24
Aug. 9. 3:00 P.M.	1 m.	47	50	47	47			28	28	28	28		
	Sur.	47.5	53	47	48			29	28	28	28.5		

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From the figures in this table it is evident that the humidity at stations 1 and 6 is lower than at other stations. These stations are cleared areas occupied by grasses, while the other stations are more or less protected by a covering of shrubs or trees. Station 6, which is more exposed than station 1, shows a greater evaporation than Station 1 and has a lower relative humidity and generally a higher temperature. Wind velocities were not determined but Station 6 as the most exposed shows the highest rate of evaporation and has the highest temperature and lowest humidity. Station 1 ranks next to Station 6 with respect to high temperatures, exposure to wind, and low humidity. Station 4, on the swamp border, and much protected by trees and shrubs was the least exposed to wind and shows the lowest rate of evaporation of any of the stations. The humidity at this station was usually slightly higher than at the prairie stations. It has been found from numerous separate determinations that the humidity is usually higher and the temperature lower near the surface of a wet or moist substratum than at a height of 1.5 meters above. The difference is less marked in woods than in swamps and less on cloudy days than on clear. In fact, in woods or on cloudy days the temperature and humidity are often the same at a height of 1.5 meters as at the surface. In prairie, on clear days, the temperature at mid-day is usually higher and the humidity lower at the surface than at higher levels. The velocity of the wind alters these relations more or less in different associes. The velocity of the wind is greater at higher levels than at the surface. This is shown by a measurement at Benedict,

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in 1914. Two anemometers were set out in a clearing, one at 1/2 meter and the other at 3 1/2 meters above the ground. They were allowed to run from noon till 6 P.M. at the end of which time it was found that the first anemometer had measured 117,840 feet and the second 322,715 feet. That is, the velocity of the wind at 3 1/2 meters was found to be nearly three times the velocity at 1/2 meters above the ground. A comparison of the rates of evaporation in various plant associes make it quite evident that wind is the most important factor in promoting evaporation. Yapp ('09:301) came to a similar conclusion.

Light.

The intensity of the light exerts an influence on the rate of transpiration by its effect on the size of the leaf, leaf structure and amount of radiant energy absorbed. It has been observed that for many plants at least, a very definite relation exists between light intensity and the size and structure of leaves. It has been found that leaves of Ledum, Kalmia, Andromeda, Chamaedaphne, species of Salix and of many other swamp plants are larger and thinner on plants growing in shade than on sun plants. They are also less xerophytic in structure than those of sun plants. The differences in structure of leaves of plants of the same species growing in sunlight and in shade has been shown by Stahl ('80:867), Haberlandt (1881), Johow (1884) E.S.Clements (1905), and others. The size of the leaves also effects the amount of radiant energy absorbed. The absorption of radiant energy raises the temperature of the leaf and leads

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to greater water loss. It has been shown that the rate of transpiration bears a definite relation to the evaporating power of the air. Accordingly the determination of the rate of evaporation for any associes of plants would measure the effect of this factor along with that of other variables of which the rate of evaporation is the resultant.

The amount of light may in some cases be a controlling factor, in limiting the growth and distribution of plants. For most plants there is a fairly wide but definite range thru which the light invalue may vary without adversely affecting the growth of the plant. A considerable fluctuation from the optimum in either direction may adversely affect the activity of the plant and if the fluctuation be too great may cause the disappearance of the plant. The bog shrubs Andromeda, Chamaedaphne, Kalmia, Ledum, and Vaccinium are plants which make their best growth in the open. Some of these are not able to withstand a great reduction of light and in consequence soon disappear in competition with taller forms which cut off the light. Andromeda is the first to disappear with light reduction. It has been found in the Larix-Picea associes where the light value varies between 50 and 100 per cent but has not been noted where the light value was reduced to 20 per cent. Ledum and Vaccinium have been found where the light values were as low as 10-5 per cent. Scattered individuals of Ledum and Vaccinium may be found in stations with light values of 2 or even 1 per cent. However, they do not grow successfully in such low light intensities and soon disappear.

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Burns ('11:124) gives .033 as the minimum light requirement of Chamaedaphne in the region of Ann Arbor, Michigan, and decides that "The absence of certain plants from certain zones is due to the decrease in the amount of light." The reduction of light probably operates thru the reduction of the photosynthetic activity.

AERATION.

The study of plant succession in hydroseres of northern Minnesota (Bergman & Stallard 1916) reveals the fact of a progressive decrease in the water-content of the substratum. In the first six stages there is a great excess of water ranging from an absolute deficiency of solids in open water occupied by the Chara-Philotria associes down to 200-1000 per cent water-content in soils on which the Larix-Picea as associes occurs. If present to excess the spaces between soil particles become filled with water and the air is driven out. Aeration must then depend upon the amount of air in solution in the water. It seems evident, therefore, that the progression of stages, to a considerable extent, must also be affected by changes in the conditions of aeration. The aeration of a soil is directly affected by the amount of water present. The amount of water present, however, is the critical factor since only by a change of conditions whereby the excess water is removed can better aeration and its concomitant ameliorations be attained. Accordingly, in determining the effect of various factors on the growth and distribution of swamp plants, it was decided to make the study of conditions of aeration in such habitats the principal feature. In so far

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as possible exact data have been secured as to the oxygen and carbon dioxide content of lake and swamp waters under normal conditions. The influence of other factors, however, has not been neglected. A large amount of data secured in the study of plant succession in northern Minnesota has been used in determining the probable effect of other factors or sets of factors on the growth and distribution of swamp plants.

Experimental Study of Aeration.

In order to determine the degree of aeration under conditions of root submergence and its effects on the growth of plants, experiments with a number of plants have been performed in the greenhouse. The experiment was begun in February 1915. The following were the plants used; wax beans, Phaseolus vulgaris var, balsam, Impatiens ~~noli tangere~~ Balsamine, geranium, Pelargonium sp., umbrella plant, Cyperus alternifolius, crowfoot, Ranunculus sceleratus and golden willow, Salix sp.

The first test was with beans, which were grown in garden loam in four inch pots. After the first leaves were fully developed the pots were submerged, one in swamp water and the second in tap water. After three days the plants began to wilt. The wilting was accompanied by a loss of greenness of the leaves. Oxygen was supplied to the plant in tap water by passing a stream of oxygen slowly thru the water. The oxygen was supplied for a period of four or five hours morning and night.during the remainder of the test. On the following day the leaves were in

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normal condition, as to turgor, and with the exception of the fifth day when they were slightly wilted, remained in good condition up to the end of the test. The plant in swamp water was not supplied with oxygen. Three of the lower leaves of this plant fell off and some others became yellow but no further changes occurred. After a week or ten days roots developed from the hypocotyl at the surface of the water. From this time the plants remained unchanged until the end of a twenty day period when they were thrown away.

At the same time two well-rooted cuttings of golden willow were placed in swamp water and four rooted cuttings in tap water. The roots of two potted plants of Cyperus were submerged in swamp water and tap water respectively. Four potted plants of *Ranunculus sceleratus* were also placed, two each in swamp and tap water respectively. All continued to grow vigorously for three weeks at which time they were discarded. In all these cases the roots grew vigorously at all depths whether in swamp or tap water.

On February 22, two plants of *Pelargonium*, potted in loam soil, were placed with the roots submerged in water. Five days later the leaves began to show signs of wilting. This became more morked and was soon followed by yellowing of the leaves. Eight days after the test was begun it was ended. At this time the loss of green color had become very marked and the leaves began to fall off.

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On the same day, two other plants of Pelargonium, potted in loam, were set up in the following manner. The leafy stems were passed thru the mouth of a wide-mouthed bell jar so that the stems and leaves came out into the air while the roots in the pot of soil were under the bell jar. The mouth around the stems and the bottom of the bell jar were sealed with wax so as to be air-tight. Carbon dioxide was then passed thru to replace the air. This was repeated morning and night for half an hour to an hour, in order to maintain an atmosphere of pure carbon dioxide. A watering device was so arranged that water could be added without admitting air at the same time. On one plant a slight wilting was apparent on the second day following and on the third day following the wilting was very evident. On the second plant wilting did not begin until the fourth day but on the fifth day it had become very pronounced. The leaves on both plants after wilting became yellow and soon dropped off. The yellowing and dying of leaves continued until March 3 when the test was ended. The soil was found to be fairly moist at the end of the test.

A plant of Impatiens, potted in loam, and placed with the roots submerged in water showed wilted leaves two days later. On the third day the plant was so badly wilted that it was removed and allowed to drain. Nearly a week was required for the plant to recover a fully normal condition. Another plant of Impatiens, similarly potted was placed with the stem and leaves projecting into the air while the roots were kept under the bell-jar as described for Pelargonium. The air was then replaced by

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carbon dioxide. On the second day the plant was slightly wilted and on the morning of the third day badly wilted. The plant was removed at noon on the third day. On the following day the plant appeared as if badly frosted. This plant never recovered.

During March four other plants of Pelargonium and four of Impatiens were placed, two plants of each, in cistern water and two each in garden loam. The results were similar to those above indicated for the respective plants in corresponding conditions.

From the above results it appears that Cyperus, Ranunculus, and Salix are able to grow in water without being adversely affected. On the other hand, Phaseolus, Impatiens, and Pelargonium show signs of distress in the wilting, loss of color, and untimate loss of leaves. From the fact that the plants of Impatiens and Pelargonium grown with their roots in a bell-jar, in which the air has been replaced by carbon dioxide, showed the same effects as when grown with their roots submerged in water indicates that the probable cause is the lack of oxygen.

Aeration Experiments during the Winter of 1915-16.

The following autumn the experiment was repeated on a more extensive scale. Six plants each of Ranunculus abortivus and R. sceleratus, potted in soil, were placed in vessels of water so that the roots were submerged. Three plants of each were left in ordinary garden soil as controls. After three months the plants were all in good condition. It was found, however, that the plants with the roots submerged had produced more and larger leaves and considerably more extensive root-systems than those in soil. The roots in all cases, whether submerged or not, were distributed thruout the soil.

Eighteen pots each of corn and golden wax beans were planted October 16. Sets of six pots each for both corn and beans, were or garden soil, peat and sphagnum respectively. After the plants were up the cotyledons of the beans were removed. They were allowed to grow two or three days before the test was begun. On November 3, three pots each of corn and beans, growing in soil, were placed in vessels of water so that the roots were submerged. Three plants of each in soil were left as checks. Similarly three plants of each, growing in peat and sphagnum, had the roots submerged. Other batteries of three of both corn and beans were left in moist peat and moist sphagnum. Swamp water was used for watering except for plants in soil for which tap water was used. The plants were allowed to grow three months. at the end of this time the plants of both corn and beans, growing in soil had made the best development of leaves and roots. Both corn and bean plants in soil had developed extensive root systems. The roots extended thruout the soil, tending to mat at the bottom and were well provided with root hairs. Beans grown in moist peat and sphagnum developed nearly as much foliage as the plants grown in soil. The plants, however, were not quite as tall nor as robust. Root development was normal, the roots extending thruout the peat or sphagnum and tending to mass somewhat at the bottom of the pots. Root development was not

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as extensive as in plants grown in soil but root hairs were present in abundance. Under the same conditions corn plants in peat or sphagnum behaved similarly to the beans.in the development of roots, but the stalks did not reach the height attained by dorn grown in ordinary soil. Bean plants in soil with the roots submerged developed as many leaves as those the roots of which were not submerged. However, the leaves soon dropped off so that at the end of the experiment the plants with roots submerged had only one or two leaves each. Root development after submergence was less extensive.and entirely superficial. The lower parts of the root system died away and new roots developed from the hypocotyl at the surface of the water. Corn plants, in soil, with the roots submerged, showed no retardation in the rate or extent of shoot development as compared with plants in soil with the roots not submerged. The root development, however, was less extensive and was entirely superficial as was observed in beans under similar conditions. Beans and corn when grown in either peat or sphagnum, with the roots submerged, showed a marked inhibition in growth. The stems were nore slender and dwarfed. The leaves were usually less numerous and were reduced in size as compared with plants in soil,peat, or sphagnum, the roots of which had not been submerged. Root development was poor. The roots of corn grew much more extensively than those of beans which seldom reached out to the edge of the pots. Furthermore, they were always less extensive than those of plants in soil with the roots submerged.

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The experiment with corn and beans was repeated twice again during the winter, the plants being distributed in batteries of three each as previously described. In the second experiment the cotyledons of the beans were removed as soon as the hypocotyls had straightened up. The endosperm was removed from corn plants as soon as the first leaf was partly unfolded. The cotyledons of beans and the endosperm of corn were removed to do away with the influence of the stored food on the subsequent growth of the plants. Five days after the roots had been submerged new roots were observed in the process of formation on the hypocotyls of bean plants at the surface of the water. At the end of two months the plants were thrown away. The results were very similar to those of the first experiment.

The third trial with corn and beans was made during the spring, the experiment being set up as in previous trials. Two days after the roots were submerged all the bean plants were slightly wilted. A week after the submergence of the roots the leaves were badly wilted and turning yellow. The leaves soon began to drop off as in previous experiments until only one to three leaves remained on a plant. The final condition of the plants was as described in the other experiments. The early and more or less continued wilting of plants in this experiment is to be attributed to higher temperatures in the greenhouse, brought about by the increased heating power of the sun as its altitude during the day became higher with the advance of spring.

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The experiments just described were varied somewhat by planting corn and beans in quart glass jars partly filled with garden soil. After the plants were well up the roots were submerged. A few days later the leaves of bean plants became wilted, soon turned yellow and finally dropped off. A week or ten days after the submergence new roots developed from the hypocotyl at the surface of the water. By increasing the height of the water-level it was possible to cause the development of new roots at higher levels, in some plants nearly or quite up to the cotyledons. As the height of the water-level was increased the lower roots ceased to grow. These finally died and decayed leaving functional roots only at the surface. In corn, root development occurred regularly at the node at which the cotyledonary sheath is attached but no higher. Roots of corn grew near the surface, as observed in bean, and with an increase in the height of the water-level again grew towards the surface but did not die off below to the extent that the more deeply submerged roots of the bean did.

Experiments with Impatiens.

On November 5th, one plant of Impatiens potted in soil was placed in a vessel of water so that the roots were completely submerged. Several plants of Philotria were placed in the water surrounding the pot in which Impatiens was growing. This was done to determine whether some aquatic plant might not keep the water in a better aerated condition by the evolution of oxygen from photosynthetic activity. Another plant of Impatiens,

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similarly potted, was submerged in the same way, but without Philotria. Three days later the first plant was in good condition while the second was wilted. The wilting of the second plant continued two days more. At the end of that time it was in such bad condition that it was removed. The first plant was still in good condition. This plant was left until December 28, during which time it lost about four or five leaves. Ten days after the submergence of the roots, new roots were coming out along the stem at the surface of the water. These continued to develop and an examination later showed that the roots lower in the jar had died so that the superficial roots only were alive.

The experiment with Impatiens was repeated later, using six plants. All were potted in garden loam. Four of them were placed in water so that the roots were fully submerged. Of these four one was aerated by bubbling air thru the water continuously. Another was aerated by putting some Spirogyra in the water surrounding the pot in which the Impatiens was growing. The other two were not aerated. The fifth plant was grown in a very wet soil. This was done by placing the pot in a shallow basin of water so that only the bottom of the pot was in direct contact with the water and the water was drawn up into the soil by the force of capillarity. The sixth plant was grown in ordinary, moist garden loam as a check. In three days the plants with the roots submerged in non-aerated water were badly wilted and were removed. All other plants were in good condition. In five days the plant in water aerated by bubbling showed a slight yellowing of some of the leaves but no wilting. The plant aerated by Spirogyra was slightly wilted. This was assumed to be due to continued cloudiness on account of which the liberation of oxygen by Spirogyra was reduced to such an extent that the water was insufficiently aerated. On the following day both plants in aerated water were badly wilted, the one in water aerated by Spirogyra being in the worse condition. Ten days after the experiment was begun the plants were still living but each had lost several leaves. The remaining leaves were not wilted. Roots were beginning to develop along the stem at the surface of the water in both plants. The plants grown in soil wet by capillarity and in moist garden loam were in good condition.

The experiment was allowed to run three weeks. All the plants except the two in non-aerated water survived. Those with roots submerged in aerated water lost several leaves in the first week or ten days. After developing roots at the surface of the water, however, they began to grow again and apparently normally. Roots below the surface died and decayed so that only the surface roots were living. Root hairs were developed on some of the roots in aerated water. In the plant in soil wet by capillarity roots also developed at the surface. In this case the upper roots made the greatest growth but all the lower roots were living. In ordinary soil root development was extensive, reaching to all parts of the pot with an abundant development of root hairs.

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Experiments with Pelargonium, Trifolium repens, Ricinus and Coleus.

A similar experiment was carried out with Pelargonium with similar results. On plants with roots submerged and not aerated the leaves began to turn yellow in the course of ten days or two weeks. The leaves dropped off shortly after turning yellow. The loss of leaves, however, was never as great when the water was aerated. Leaves of plants in soil wet by capillarity also turned yellow and dropped off. The behavior of the roots of Pelargonium was similar to that observed in Impatiens. In all cases where the roots were submerged, whether or not the water was aerated, new roots were developed at the surface while the submerged roots died. This was also found to be true of the roots of Pelargonium in soil wet by capillarity, altho with Impatiens the lower roots remained alive. After the development of surface roots the plants again began to frow and produce new leaves. Root development in ordinary moist soil was abundant. Pelargonium was found to be less responsive than Impatiens in that it did not show wilting as clearly nor as quickly. Loss of color was the first sign of distress. Soon after changing color the leaves usually dropped off.

A similar experiment was tried with Trifolium repens. Two plants potted in a loam soil had the roots submerged. A third plant was grown in moderately moist soil. The plants with roots submerged grew more rankly than those in ordinary soil. An

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examination revealed the fact that, in the case of the plants with the roots submerged, the tap root system which was present at the time when the test was begun, had died and that new roots had developed along the stem at the surface of the water. The tap root system of the plant in moist soil had remained alive and had made an extensive growth. The roots branched freely, extended to all parts of the pot and showed an abundant development of root hairs.

Four seedlings of Ricinus, two in loam soil and two in peat with roots submerged, the former in tap water and the latter in swamp water showed similar results. After about ten days the leaves became yellow on all plants with submerged roots and dropped off until only one or two small leaves remained on each plant. The submerged roots on all plants died and new roots developed from the hypocotyl at the surface of the water. By increasing the height of the water-level it was possible to cause the development of new roots nearly up to the cotyledons. Plants grown in ordinary soil developed normally, lost no leaves and showed a normal and extensive development of the root system.

Plants of Coleus blumei, potted in soil, with the roots submerged, showed signs of distress in one or two days. The first evidence was the wilting of leaves. The leaves after remaining in a more or less wilted condition for a few days dropped off until only two or three small leaves, near the top of the stem remained. After ten days or two weeks new roots

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were always found to have developed from the stem at the surface of the water. Plants in soil developed normally.

Experiments with *Vicia faba*.

During the spring of 1916 another experiment was tried as follows. Seeds of *Vicia faba* were planted in batteries of six pots each containing garden loam, peat and spharnum respectively. As soon as the seedlings had broken thru the ground the cotyledons were removed from two plants in each set. From each battery of six, two plants with cotyledons and one with the cotyledons removed were placed in vessels of water so that the roots were fully submerged. The other three pots of each battery of six were kept moist but never wet to saturation. In four or five days all plants the roots of which had been submerged, began to wilt. This condition continued for a week or more in varying degree according to the temperature of the greenhouse. In all cases, however, the plants lived. The plants were permitted to grow ten weeks. At the end of this time it was noted that the plants in soil with the roots not submerged, had gorwn the most, those in sphagnum least, and those in peat were intermediate. In submerged plants less difference was noticeable but the same order seemed to hold here also. Loss of leaves did not occur in any of the plants. Removal of the cotyledons caused a general reduction in the amount of growth. This was least noticeable in plants grown in moist garden loam and quite evident in plants grown in peat or sphagnum. The reduction was most noticeable in plants grown in peat or sphagnum with the roots submerged.

Plants growing in moist loam soil showed the greatest development of roots. However, the form of the root system of plants grown in either peat or sphagnum was similar, and in extent of growth nearly equal to those in soil. The roots of plants in all three media under conditions of submergence were about the same. The lower roots in all cases were dead and decayed, while new roots had developed from the stem at the surface of the ground. The depth of penetration was never more than an inch below the water surface. The longer and more branched roots usually came even nearer the surface. No root hairs were present on submerged roots altho abundantly present on others.

Experiments with Tree Seedlings.

Experiments with *Acer negundo*, *Prunus virginiana*, *Ulmus americana*, *Quercus macrocarpa*, and *Q. ruba*, potted in soil with the roots submerged, all show results similar to those obtained with other plants. Under conditions of submergence, the lower roots die and new roots develop from the stem at the surface of the ground. In ordinary soil the roots develop normally, branch freely and are well provided with root hairs. Two to three year old plants of *Quercus ruba*, *Acer rubrum*, and *Larix laricina* grew whether the roots were submerged in sphagnum, peat or soil, but both *Quercus* and *Acer* made less growth than in moist loam. Roots of *Q. ruba* and of *A. rubrum* submerged in peat or sphagnum were much dwarfed, sparsely branched and apparently had mycorhiza. Other plants of *Q. ruba* and *A. rubrum* grown in soil were

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found to have extensively developed roots, which branched freely and were to all appearances normal and free from mycorhiza. Larix, Betula pumila, and species of Salix grew well during an indefinite period of root submergence altho in both Larix and Betula the roots grew near the surface. Even in such a common swamp plant as Comarum palustre root development is best near the surface but roots lower in the substratum make some growth. Submerged roots of Larix and Betula were very short, little branched, and evidently were better developed. Two to three year old plants of Larix, grown in moist soil, developed extensive and apparently normal root systems. Several plants of Larix, Betula pumila, and Andromeda glaucophylla were planted in the greenhouse garden in the spring of 1916. These were allowed to grow until June 1917. The plants passed the winter without the least winter killing. On examination the roots were found to be well developed, freely branched and with no evidence of mycorhiza.

Mycorhiza.

Transeau ('06:32) has reported the occurence of mycorhiza on the roots of a considerable number of plants growing in swamps in Michigan. In addition to the ericads, most of which have mycorhiza on the roots, a number of other plants growing in undrained sphagnum swamps were found by the writer to have mycorhiza. Among them are the following: Acer rubrum, Betula pumila, Abies balsamea, Larix laricina, Picea mariana, Pinus banksiana, P. strobus, Populus balsamifera, P. tremuloides, Quericus rubra

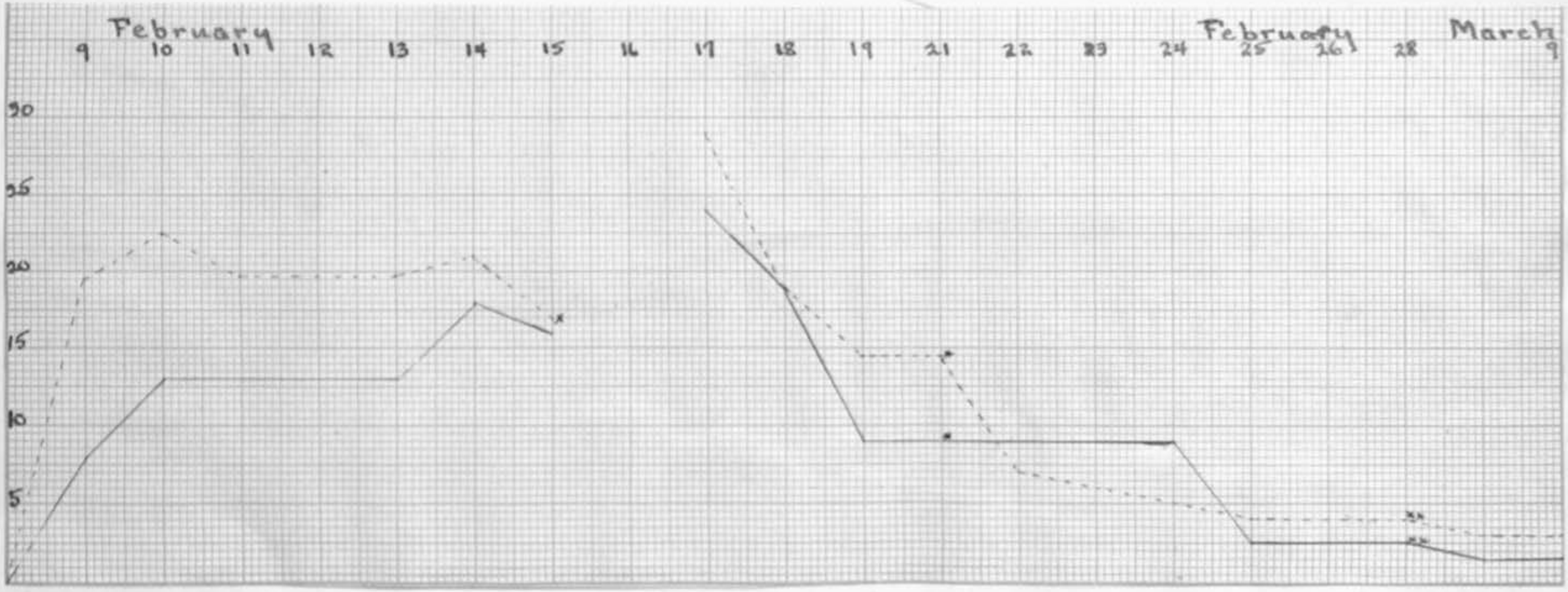

FIGURE 2. Graphs showing comparative rates of transpiration of two plants of Pelargonium, the broken line for the one in moist soil and the solid line for the one in soil submerged. The water loss in cubic centimeters is shown as ordinates, the time in days as abscissas.

x Roots submerged. * Leaves becoming yellow. ** Leaves dropping off.

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and several species of Salix. Transeau ('06:33) has made a study of the conditions which favor or cause the mycorhiza on Larix. He says," It has been found without exception that where the plants were grown under properly aerated soil conditions, normal roots developed in place of the mycorhiza. " The oxygen content of the substratum in swamps, especially when Sphagnum is present has been shown (p.71) to be very low.

Effect of Root Submergence on Transpiration.

The wilting of plants when the roots are submerged indicates that transpiration exceeds absorption. In order to ascertain the effect of root submergence on transpiration, the following experiment was performed. Two plants of Pelargonium, potted in soil, were placed in aluminum pots, the tops of which were covered with sheet rubber to prevent evaporation from the surface of the soil. The plants were weighed each day for a week. The roots were submerged after the last weighing for the week and the daily weighings continued. The results are shown in the accompanying graph. (Fig. 1) On the second day following root submergence it was found that the rate of transpiration had been greatly increased. The rate, however, fell off rapidly and after two more days the rate had fallen to a point lower than that of the same plant when growing in moist soil. Recording instruments showed that the humidity and temperature conditions in the greenhouse had not changed. The reduced rate, then, is not to be explained by lower temperature and higher humidity. After two

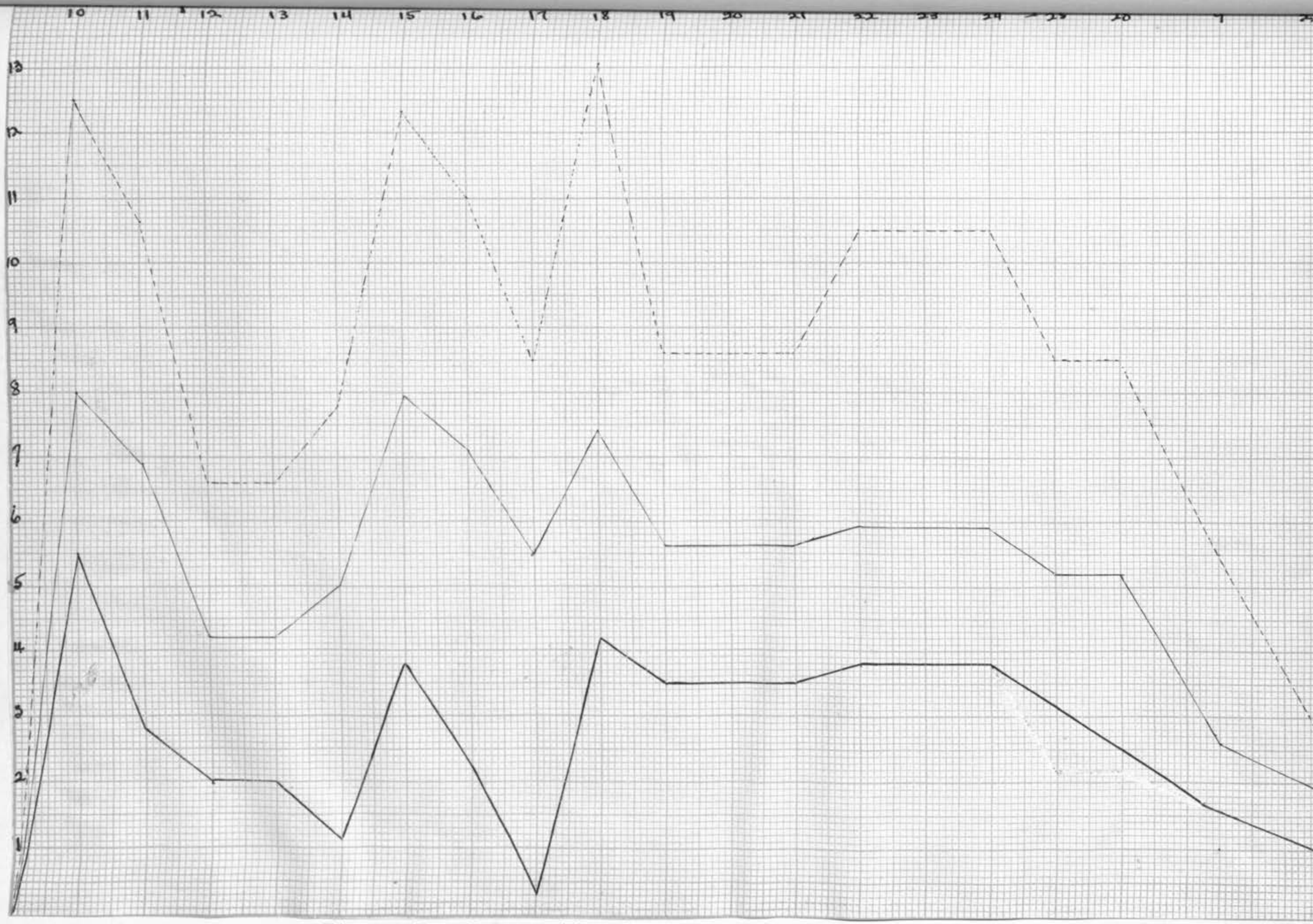

Figure 3. Comparative transpiration of two seedlings of Quercus macrocarpa. The broken line represents a plant in moist soil, the heavy solid line represents a plant in submerged soil. Leaf area of latter 64.27 sq.cm., of former 100 sq. cm. The light solid line represents the rate of transpiration of the plant with the smaller leaf area based on the same leaf area as the plant in moist soil.

days of the reduced rate of transpiration, the leaves began to turn yellow. From this time the average transpiration rate dropped still lower until at the end of ten days after the roots had been submerged the transpiration rate per day averaged 7.3 grams for one plant and 9 grams for the other. This average rate was maintained three days at which time the plants began to shed their leaves. In the nine days following, during which weighings were continued the average daily rate of transpiration was reduced to 2.8 grams for one plant and 1.5 grams for the other. It is to be observed that when the roots of plants had been submerged a decrease in the average daily rate of transpir-soon followed. It is to be noted, further, that this decreased average daily rate of transpiration continued two or more days before the manifestation of any symptoms of distress on the part of the leaves. These facts indicate clearly that transpiration is greater than absorption and that the shedding of leaves is to be regarded as a method of compensating for the reduced ability to absorb by reducing the area of transpiring surface.

On February 8, two seedlings of *Quercus macrocarpa* were potted in garden soil in aluminum pots. The roots of one were submerged while the other was allowed to grow in the moist soil. The pots were covered with rubber tissue to prevent surface evaporation and weighings were begun February 9. The results are shown in the accompanying graph.

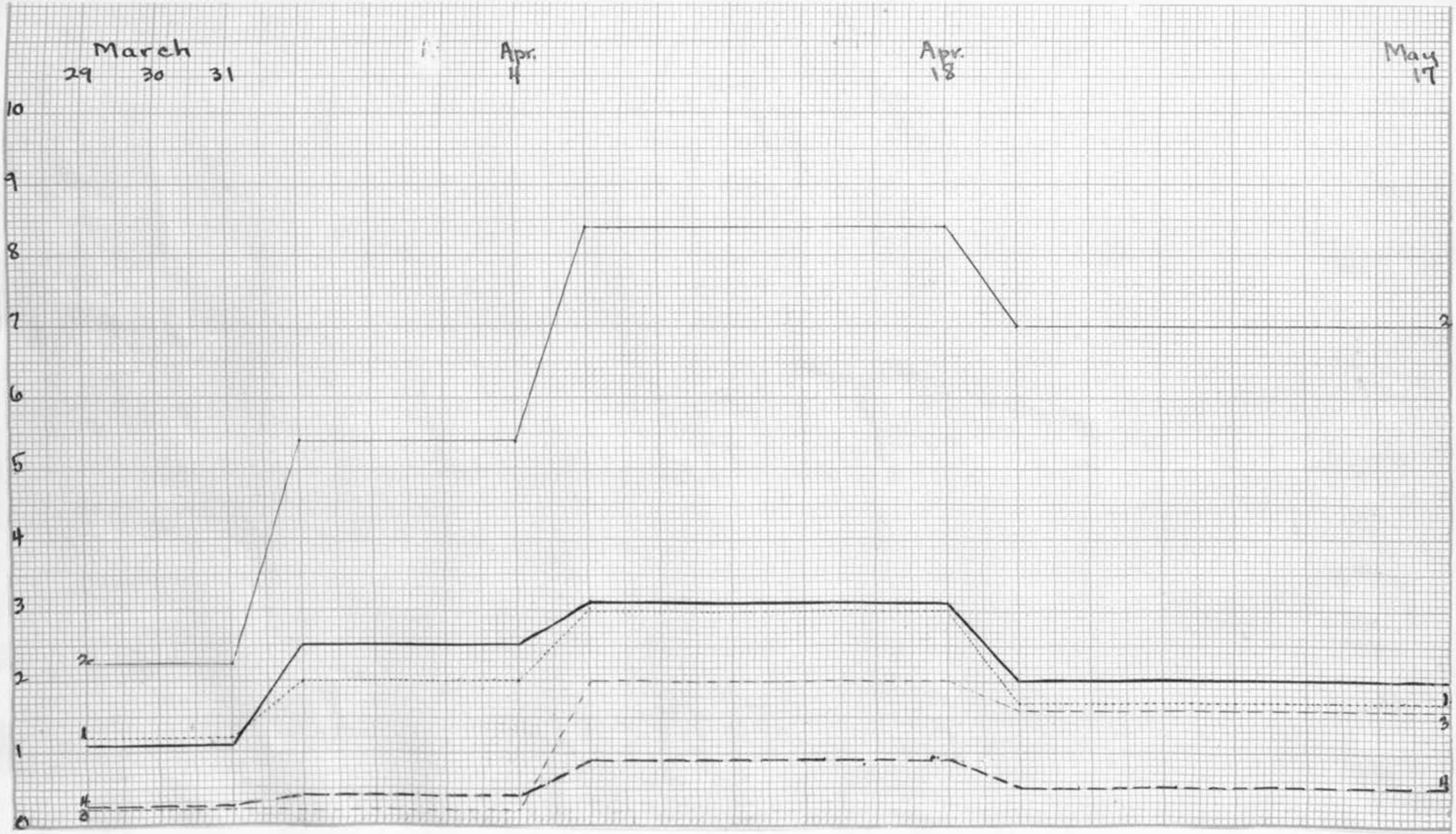

Figure 4. Comparative rates of transpiration of seedlings of Quercus macrocarpa in moist soil and in submerged soil. No.2, in moist soil, leaf area 100 sq. cm. Nos. 1,3 and 4 in submerged soil. Leaf area No. 1. 64.27 sq.cm., No. 3, 48.34 sq.cm. and No. 4, 70.0 sq.cm. The heavy solid line represents the average rate of the three plants in submerged soil based on same leaf area as No. 2, in moist soil.

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The plant with the roots in moist soil had a leaf area of only 64.27 sq.cm. while the other plant had a leaf area of 100 sq. cm. In order to make a comparison of the rates of transpiration the transpiration rate of the former was calculated on the basis of 100 sq. cm. and of the latter on the basis of 64.27 sq. cm. of leaf area and the corresponding curves were platted. It is to be noted, however, that the rate of transpiration for the plant with roots submerged is lower than that of the transpiration rate calculated on either basis. Since the actual rate per unit area of leaf surface probably lies somewhere between the two calculated rates it seems fair to assume that the difference between the calculated rate and the observed rate for the plant with submerged roots is brought about by submergence.

Later two other seedlings of Quercus macrocarpa were added to the first two. The two new plants added had the roots submerged and were potted and covered in the same way that the former ones had been. Weighings were made at intervals during a period of about three weeks beginning March 29. The results are shown in the following graph.

The average daily transpiration is shown for each plant. The plants, however, were of different sizes and with different leaf areas. Number 2, which was grown in moist soil, had a leaf area of 100 sq.cm. The other three plants had the roots submerged. Their leaf areas in square centimeters were as follows: No. 1, 64.27; No. 3, 48.34; No. 4, 70. In order to

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make a comparison the daily transpiration for the three plants was averaged and calculated on a basis of 100 sq.cm. of leaf area and the curve for this calculated rate was drawn. The calculated rate for the average of the three plants was much lower than that of the rate for plant No. 2, the roots of which were not submerged, when calculated on the basis of equivalent leaf areas. Plant No. 1 had the highest rate of transpiration of any plant with submerged roots. Even if the transpiration rate of this plant were calculated on the basis of 100 sq.cm., which is the area of plant No. 2, the rate would be found to be considerably lower than that of No. 2. The second trial with Quercus macrocarpa, thus shows that the rate of transpiration per unit area in submerged plants is much reduced in comparison with the rate of transpiration of plants, the roots of which have not been submerged.

The Effect of Root Submergence on Root-pressure.

The effect of root submergence on root pressure has been tried also. For this purpose Coleus and Fuchsia were used. Usually two plants were set up at a time. The tops were cut off an inch or two above the surface of the ground and a double U-tube filled with water or mercury connected by a rubber tubing tightly wired so as to be air tight. When water was used a longer tube was necessary. One plant was then set in a vessel of water deep enough to cover the surface of the soil to a depth of half an inch to an inch. The other plant was allowed to grow in the moist soil. The column of water or mercury began to rise within an hour or two after the plants were set up. The plants in moist soil usually showed the maximum pressure on the second day. They also maintained this pressure several days before a fall occurred. Those with the roots submerged usually showed a slight rise of pressure at first. Toward evening of the second day or morning of the third, however, the column failed to show any further rise and always remained much below the height reached by the plant the roots of which were not submerged. In many cases the column rose two or three times as high in plants whose roots were not submerged as it did in the others. The experiment was repeated several times with both Coleus and Fuchsia with the same results. It was also varied by aerating the water in which the potted plants were placed. The aeration was accomplished either by bubbling air slowly thru the water from a tank under pressure or by placing Philotria or Spirogyra in the water surrounding the pot. When the surrounding water was aerated the root pressure of the plants with submerged roots was nearly as great and was maintained nearly as well as in the case of plants gorwing in moist garden soil. Since root pressure is due to the activity of roots in absorbing water these experiments show clearly that absorption is hindered greatly, if not wholly prevented in some cases, by a lack of aeration. They show, further, that if aeration be provided, plants may live and function nearly as actively with the roots submerged as they do in ordinary moist soils.

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Effect of Swamp Water with Good Aeration on the Plant Growth.

To determine the effect of aeration on the growth of plants watered with swamp water, six pots of corn and six beans were planted in washed, white quartz sand. The cotyledons of the beans were removed as soon as the first leaves began to expand. The endosperm of the corn plants was also removed as soon as the first leaf began to unroll. All plants were watered with distilled water for three days. Thereafter three plants each of corn and beans were watered with Sach's culture solution and three each with swamp water. In four or five days it became apparent that the plants watered with swamp water were making less rapid growth than those receiving culture solution. This difference was maintained and at the end of the experiment the plants watered with culture solution were somewhat larger, stronger and of darker green color than those which had been watered with swamp water. The root system was equally well developed in all plants. The difference in the growth of plants watered with swamp water and those watered with culture solution was not very great and is probably to be explained by a lack of nitrates or potash or perhaps of both.

Analysis of Air Content of Various Waters.

Many analyses have been made of waters from various sources and under varying conditions. In determining the amount of air dissolved the boiling method was used. This method is described in Dennis' translation of Hempel's "Gas Analysis", and

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and need not be discussed here. In the first analysis a flask containing one litre was used but later this was replaced by a flask containing two liters. Boiling for different lengths of time was tried and it was found that a period of three of five minutes was most satisfactory. After the air was completely boiled out and collected in a receiver, it was passed into a Hempel burette where it was measured. The burette was enclosed by a water jacket and the temperature of the water was kept constant to within 2° C, during the measurement of any sample. The gas was allowed to remain in the burette three to five minutes to allow complete cooling before a reading was taken. The barometric pressure was also noted so that readings could be reduced to uniform temperature and pressure for comparison.

The technical method of analysis was used. Descriptions of this method are to be found in Hempel's "Gas Analysis" and Haldane's "Methods of Gas Analysis", as well as elsewhere. The carbon dioxide was absorbed by a concentrated solution of potassium hydroxide which was contained in a simple Hempel pipette.

After the first measurement of the gas, the sample was passed into the pipette containing the potassium hydroxide solution. The pipette was reconnected with the burette and the gas passed over for measurement. After the second measurement it was passed into a double Hempel Pipette containing a solution of potassium pyrogallate. After shaking for three minutes with this solution it was passed back into the burette for final

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measurement. From the three measurements the amount of carbon dioxide and oxygen was readily determined by subtraction. The residue was regarded as nitrogen altho in some instances small amounts of other gases may be present also. Duplicate analyses were made in nearly every case. The results were found to check within 2/3 cc. which is about the limit of observational error. Lengthening the period of absorption in the potash pipette and in the purogallate pipette gave no additional reduction of volume beyond that determined after a three minute period. Since absorption seemed to be complete at the end of a three minute period, this period was used thruout and the results accepted as correct.

Results of Analyses.

A large number of analyses have been made, however, only a few figures need be given to show the variation of the carbon dioxide and oxygen content of waters from various sources and under various conditions. Distilled water and tap water at 21° C and under atmospheric pressure were found to have the following amounts of dissolved gases. The amounts are expressed as cubic centimeters per liter.

Kind of Water	Carbon Dioxide	Oxygen	Nitrogen
Distilled	1.10	5.5	12.2
"	1.20	5.7	12.4
Tap	1.00	5.4	12.6
"	1.20	5.5	12.6

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Another sample of tap water after standing several days was found to contain carbon dioxide 2.2 cc., oxygen 6.0 cc. The solubility of these gases varies according to the temperature of the water and the atmospheric pressure. According to Winkler ('89:1764), water at 60.1 C. requires 10.14 cc. of oxygen per liter for saturation. Petterson and Sonden ('89:1439) give 10.1 cc. as the amount required for saturation at 0° C. under 760 mm. pressure. The amount required for saturation decreases with the rise of temperature or with a decrease of pressure. According to tables of Roscue and Lunt (1889:569), water under standard pressure requires for saturation at 20°C., 6.28 cc. and at 25°C., 5.76 cc. of oxygen. Carbon dioxide and oxygen, on account of their greater solubility as compared with nitrogen, may be present in amounts greater than is required for saturation. Birge and Juday ('11:51) discuss conditions resulting in the supersaturation of Wisconsin lake water with reference to oxygen. Lake water from Hubert Lake by field analysis was found to contain on an average of five analyses one oxygen 6.8 cc., carbon dioxide 1.2 cc., nitrogen 12.2 cc. The field analyses were made with the burette only, the solutions being introduced directly into the burette. Under the conditions the results are not as accurate as analyses made in the laboratory with pipette. Comparison of the results, however, with carefully checked analyses in the laboratory shows that the errors are not more than two to three times the error of laboratory analyses, and accordingly they may be used in comparing results. Thus it appears that distilled, tap, and lake waters do not vary appreciably in their oxygen, carbon dioxide, or nitrogen content.

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Effect of Philotria on the Gas Content of Water.

The following analyses show the effect of placing *Philotria* in water with good illumination. No. 1 is tap water which had stood several days in the laboratory; No. 2, tap water with *Philotria* over night, analysis made early in forenoon; No. 3, water in which Philotria had grown for two to three weeks, analysis made in afternoon after several hours exposure to good light. Duplicate analyses are given in each case. The results are presented in the following table:

Gas Content of Water with and without Philotria.

Number	Kind of Water	Carbon Dioxide in cc.	Oxygen in cc.	Nitrogen in cc.
1.	Standing tap	2.8	5.4	12.6
1.	" "	2.6	5.6	12.4
2.	Tap over night with *Philotria*	2.8	5.4	12.8
2.	" " "	2.6	5.6	12.6
3.	Tap, Philotria 3 weeks.	0.6	8.2	13.0
3.	" " " "	0.8	7.8	12.8

From this is to be noted that the oxygen and carbon dioxide content are not affected by *Philotria* during the night. During daylight, on the other hand, the carbon dioxide content is decreased and the oxygen content is increased. Accordingly, the value of *Philotria* as a means of aerating water is established by these analysis. Other analyses the figures for which are not presented show that in cloudy weather *Philotria* has little effect on the oxygen content. This accounts for the

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Gas Content of Water with Philotria

Sample Number	Time taken	Carbon Dioxide in cc.	Oxygen in cc.	Nitrogen in cc.
1	10:00 A.M.	1.1	6.2	12.2
2	11:00 A.M.	.8	7.0	12.2
2	11:30 A.M.	.5	7.4	12.4

It is to be noted here also as in the preceding table that the presence of Philotria in good light causes a decrease in the amount of carbon dioxide, and an increase in the amount of oxygen present.

Gas Content of Swamp Water.

During the summer of 1916 at Hubert, a series of analyses of lake and swamp waters was made. The lake water was from Lake Hubert near the shore in water about two feet deep. Other samples were taken in the swamp bordering Mud Lake. Part of the samples were taken in the Carex-Calamogrostis associes and the others in the Larix-Picea associes. All samples were taken in areas in which Sphagnum and other mosses were abundant. A third series of samples was taken from Henderson's bog, north of Lake Hubert. One sample was taken in the Carex associes and the other two below Sphagnum in the Chamaedaphne-Andromeda asspcies. The results are presented in the following table.

Gas Content in Water from Various Associes.

Associes	Sample number	Carbon dioxide in cc./	Oxygen in cc./	Nitrogen in cc.
Hubert Lake	1	1.0	7.6	13.0
" "	2	1.4	7.2	12.6
" "	3	1.2	7.4	
" "	4	1.2	7.6	12.4
" "	5	1.2	7.6	
" "	6	1.0	7.8	12.8
Mud Lake: Carex-Cal.	1	5.8	3.2	16.8
" " " "	2	6.0	3.0	17.2
" " " "	3	6.0	3.0	17.2
" " Larix-Picea	1	8.4	2.8	17.0
Henderson's bog: Carex	1	8.4	4.6	15.4
" " Andromeda	1	9.8	3.9	15.1
" " "	2	10.2	3.8	14.8

It is to be noted from the figures here given that a marked difference exists between the air content of a lake and that of a swamp. Hubert is a spring-fed lake with cold water and a clean gravelly or sandy bottom in most places. The bottom where the samples were taken for analysis was of very coarse gravel or of pebbles. The water proves by analysis to be well supplied with oxygen, and to have more carbon dioxide than tap or distilled water. When a lake becomes converted into a swamp, a very evident decrease of oxygen occurs with a very marked increased in carbon dioxide content. The oxygen content falls off to about half that of lake water or tap water. This undoubtedly is a very important factor in retarding the growth and function of roots of plants which do not have air-conducting systems. Attention is also to be called to the fact that in the experiments in the greenhouse, the plants with the roots submerged in Sphagnum showed the greatest reduction in root development. The low oxygen content of the water in a Sphagnum substratum makes clear the reason for the reduction in growth. The sample from the Carex zone of Henderson's bog was taken just at the edge where Carex was invading the Castalia associes. The oxygen content there is somewhat higher than it is in later stages. The high carbon dioxide content is to be explained by the decomposition of organic matter. Any lake which contains a large amount of vegetation is usually found to be comparatively low in oxygen and high in carbon dioxide content. Birge and Juday (1911) show that similar conditions prevail in Wisconsin lakes with considerable organic matter on the bottom.

The apparently high nitrogen content is due to the fact that considerable quantities of methane are present in swamps, but the quantity was not determined. In making analyses the residue after absorption by potash and pyrogallol was regarded as nitrogen. For this reason the nitrogen content of swamp waters always runs too high.

DISCUSSION OF RESULTS.

Effect of Root Submergence on Development.

The various experiments just described point clearly to the fact that a proper degree of aeration is one of the prime necessities for the development of roots. The roots of plants, when submerged, are retarded in growth except in aquatic or amphibious plants with well developed aerenchyma. In some cases there may be a total suppression of growth. Inhibition of root development may result in a reduction of the size of parts above above ground. In experiments with corn, beans, castor beans, and Vicia faba it has been found that the roots are less developed when submerged than when in ordinary moist soil. The part of the plant above ground in all the species named also under-goes a slight reduction in size as compared with the above-ground parts of plants the roots of which are not submerged. If the submergence is prolonged, the more deeply submerged roots die and new ones develop at or near the surface of the water. It has been found also that if oxygen be supplied, the development of roots under conditions of submergence is not much reduced, if at all, as compared with roots in moist soil. The oxygen may be supplied by bubbling air thru the water from a tank under pressure, by passing a current of oxygen from a generator slowly thru the water, or by placing Philotria or Spirogyra in the water surrounding the pot in which the plants are grown. Aeration by the latter method depends on the liberation of oxygen by photosynthesis. Consequently it accomplishes the result only in good light.

Certain plants such as Ranunculus abortivus, R. sceleratus, Cyperus alternifolius and Sagittaria when grown with roots submerged showed no retardation in root or shoot development. On the contrary a better development of roots and of foliage was to be noted when the roots were submerged than when growing in moist garden soil. The ability of these plants to grow with their roots submerged is to be explained by the presence of aerenchyma in the roots which permits air to be supplied under such conditions. The reduction in root and leaf development of Ranunculus grown in moist soil is probably due to the relatively high water requirement of these plants and to the inability of the roots to absorb readily from ordinary soil the amount of water required. Wacker ('98:82) in experimenting with the growth of aquatic plants in moist soil obtained similar results and drew similar conclusions.

Sachs ('73:410) found that roots of land plants grew more slowly in water than in garden soil. This he explained by assuming that in garden soil all the requirements of the plant were satisfied while in water respiration was hindered. He observed also (l.c.411) that the rate of growth of roots in soil increased up to the sixth day while the rate of those in water showed an evident decrease on the third or fourth day. The writer also has found that the distrubing effects of root submergence first show clearly in about three to five days. A retardation in the growth of roots of land plants in water has been observed by Mer ('79:1277), Schwartz (1883), Wacker (1898), Kraus (1901) and others. Perseke (1877) and Schwartz (1883) found that growing land plants with the roots submerged caused a great reduction in the development of root hairs and that in many instances no root hairs were formed. Snow ('05:33) has shown that air deprived of oxygen stopped the production of root hairs and retarded the growth of roots. Arker (1900) found that by passing air thru water or soil the rate of root growth could be increased. Wacker ('98:85), in growing seedlings of <u>Vicia faba</u> and <u>Helianthus annuus</u> under bell jars in which the atmospheric pressure had been reduced to 1/10 of the usual pressure, found a slight retardation in the root development as compared with plants under full atmospheric pressure. The difference was not great, however, and Wacker could not state with certainty that the retardation was due to the reduction in the amount of oxygen. Kraus (1901) shows that the percentage of germination of seeds and rate of growth of seedlings of land plants in the early stages of development can be greatly increased by supplying oxygen to the water in which the seeds or seedlings are submerged. Most of the results cited above have been confirmed by the work of the writer.

<u>The Amount of Oxygen Required for Growth</u>.

The amount of oxygen necessary for growth is very small according to Wieler ('83:213) but varies in different plants. He found the maximum growth to take place in <u>Vicia faba</u> with 5-6 per cent of oxygen. For <u>Helianthus</u> three percent was the optimum amount, a retardation taking place between .14-6 per cent according to the plant. Deherain and Vesque ('76:340)

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found that when the roots were deprived of oxygen, plants were not able to live. Vöchting ('2:94) found that a reduction of pressure to 3 per cent or below caused the production of hairs on the roots of potato tubers to cease. He also found ('78:132) that water contained sufficient oxygen to support life in willow twigs, but that a supply from the surface was necessary for the production of roots and shoots. Wacker ('98:82) grew seedlings in water without aeration, in water thru which air was passed and in water thru which oxygen was passed. At the end of three days no noticeable difference was to be detected in the rate of growth of the roots under the different treatments. From this Wacker concluded that it was not due to lack of oxygen in water that the growth of roots in water was retarded. However, objection to this conclusion may be made on account of the short period thru which the plants were grown. Experiments by Deherain and Vesque ('76:340) and Sachs ('73:410) show that the effects of the exclusion of exygen are not apparent until three or four days later. The writer's experiments also show that in comparing the growth or behavior of plants with roots submerged the effect of bubbling air or oxygen thru the water is not evident until three to five days usually after the experiment is begun. Accordingly it seems that Wacker terminated his experiment before the effects had an opportunity to make themselves manifest, and that his conclusions are untrustworthy, premature, and therefore unwarranted. Thus, with the exception of Wacker in this one experiment, the results of which seems questionable, the results obtained by all investigators are quite uniform in showing that the growth of roots is prohibited by submergence and that the retardation of growth is directly referable to lack of oxygen. The paucity or absence of hairs on submerged roots, as shown by Snow ('05:34) is also correlated with a lack of oxygen.

In comparing the growth of various plants in soil, peat, and sphagnum, with the roots submerged, it is to be noted that the roots of plants in peat are usually more retarded in growth than those in soil, and that the roots in sphagnum show the greatest retardation in development. A similar relative reduction in the growth of parts above ground is to be observed also. Dachnowski ('12:314) obtained similar results, but more particularly a stunting of roots in cultures of wheat, corn, bean, elm, and other plants in bog waters variously treated. Aeration, he found, remedied the stunting effect of bog water. The writer was at first somewhat at a loss to explain the more marked imhibitory effects of root submergence on plants grown in peat or sphagnum as compared with those grown in soil. Later it was found that seedlings of corn and beans, grown in washed white quartz sand, and watered with Sach's culture solution made only a little better growth than seedlings of corn or beans under the same conditions but supplied with swamp water instead of nutrient solution. Since conditions of aeration in the sand were good, the slight reduction in growth of the plants watered with swamp water suggested itself as being due to a lack of one or more mineral constituents. It was also observed that seedlings of various kinds grown in peat or sphagnum with roots submerged

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showed a much greater reduction in the growth of the entire plant when reserve food in the seed was removed at an early stage in germination than when the reserve food was allowed to remain. On the other hand very little difference was to be observed in the final amount of growth of seedlings in soil with the roots submerged when the reserve food was removed early in germination as compared with the growth of plants which were allowed to use the reserve food. This also seems to indicate a lack of food materials as an explanation in part for the greatly reduced growth of plants in peat or sphagnum with the roots submerged. The principal reason, however, is a lack of oxygen since it has been found that water in which Sphagnum is growing is very deficient in oxygen content as compared with the oxygen content of lake or river water. The same holds good to a lesser extent for peat.

The Retardation of Absorption by a Lack of Oxygen.

It is not only the rate and extent of growth of roots that are affected by a submergence of the root system, but also the absorbing capacity. The latter is of greater importance, and more directly and effectively influences the development of parts above ground. It is conceivable that a root system of very limited extent in direct contact with water, if actively functioning, might be able to supply the needs of the plant even tho great. On the other hand, an extensively developed root system inhibited in functional activity might be of little or no value to the plant. An inhibition of the absorbing capacity of

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roots is indicated in the esperiments performed by the writer by the etiolation and shedding of leaves which soon follows root submergence. This is more clearly shown by the graphs. (pp. 52, 53) which give the comparative rates of transpiration per unit area of plants of Pelargonium and seedlings of Quercus macrocarpa with the roots submerged and other with the roots in moist soil. The significant fact shown by the first graph is that the reduced rate of transpiration precedes by two or more days the etiolation or loss of the leaves. As stated elsewhere (p. 51) the reduction of leaf area by dropping of leaves is to be regarded as a method of compensating for the reduced ability of the roots to absorb. By suitable methods of aeration the absorbing capacity of the roots may be maintained. In this case etiolation and loss of leaves or inhibition in the growth of parts above ground does not occur. Little has been done, apparently, to determine the effect of root submergence on the functional activity of roots. Dachnowski,('12:313), however, shows that the rate of transpiration of plants grown in bog water is increased by aeration as compared with the transpiration rate of other plants, of the same kind grown in unaerated bog water. Very recently Livingston and Free ('17:182) in experimenting with Coleus blumei and Heliotropium peruvianum. show that when oxygen is not supplied to the roots of plants," the first effect of exygen deprivation is an interference with the absorption of water by the roots."

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The oxygen content of the water or other substratum in which the plants are growing is the important factor in determining not only the activity and growth of the roots but of the entire plant. Deherain and Vesque ('76:340) by their experiments established the fact that if the roots were deprived of oxygen the plant itself soon perished. The only explanation offered was the statement that "L'absorption d'oxygen .... c'est un acte respiratoire qu'on ne peut supprimer sans que la plante perisse." Wacker, by similar experiments found that replacing the air of soil by hydrogen caused an enormous retardation of root growth as compared with the growth of roots in soil under ordinary conditions. The writer has duplicated some of the experiments of Deherain and Vesque in excluding oxygen from the soil, with the same results, namely, that the plants soon died. The soil at the end of the experiments seems always to have a normally high water-content and no factor other than the supply of oxygen was altered. Therefore the only reason assignable for the death of the plants was that in the absence of oxygen the roots were not able to absorb water even when present in normally favorable quantity. This conclusion is further supported by the facts that wilting, etiolation, and loss of leaves soon follows after root submergence in unaerated waters. Transpiration also, under these conditions, undergoes a diminution in rate, and as shown previously (p. 51) the diminution in the rate of transpiration precedes etiolation and loss of leaves. The roots themselves soon die unless oxygen is supplied. Aeration by any suitable method maintains a normal or nearly normal

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rate of transpiration, prevents etiolation and loss of leaves and keeps the roots in a live and apparently healthy condition. This indicates that the trouble lies in the disturbance of the normal root functions, that the rate of absorption does not keep pace with that of transpiration and that the inability of roots to absorb is correlated with the oxygen supply. Livingston and Free ('17:182) using different methods, also conclude that the exclusion of oxygen from the roots interferes with the absorption of water.

The Oxygen Content of Various Sub-strata.

The relative amounts of oxygen in different substrata under various conditions, whether such amounts are sufficient for the plant's needs, and the manner of replentishing or maintaining the supply are other points to be considered. Levy and Bossingault ('52:783) and von Fodor ('75:205) found the oxygen content of soils to be somewhat lower than that of atmospheric air. However, since in soils there are abundant spaces between soil particles, thru which air can diffuse, a supply of oxygen is available to the roots at all times. When soil is saturated with water, air is driven out of the spaces between soil particles and the only oxygen then available is that dissolved in the soil water. This amount is much less than that contained in the soil under usual conditions, and accounts for the observations of Wacker (98:109) that seedlings of _Vicia faba_ and _Lupinus albus_ grown in supersaturated soil showed a marked retardation in the growth of roots. He observed, however, that with frequent changing of water the retardation was somewhat less. Wacker's results were confirmed by Arker (1900). Arker found that the rate of growth of roots of Lupinus albus and Helianthus annuus was increased by passing a current of air thru the water. Also that roots of plants in water readily take up oxygen in solution, and that passing a current of air thru water does not increase the oxygen content but merely keeps it up to the usual concentration for a given temperature and pressure. The writer in his experiments has confirmed the results of Arker as to the effect of passing a current of air thru water on the growth of submerged roots. Analyses of samples of water aerated by passing a current of air thru it also confirm Arker's results that the oxygen content is not increased by this procedure. A current of pure oxygen likewise has little effect on the oxygen content. These facts furnish other reasons in addition to those already mentioned (p.) for the failure of Wacker to find differences in the growth of roots, in non-aerated water, water aerated by a current of air and by a current of pure oxygen respectively.

The reason that plants with the roots submerged in non-aerated water, show etiolation, wilting, loss of leaves, and death of roots is that the oxygen content of the water is reduced below the necessary minimum. Oxygen diffuses slowly thru the water so that the supply is not quickly replenished by diffusion. There are few available data on this point, but the investigations of Kraus ('01:13) show that boiled water in vessels sealed to exclude the air prevent completely the germination of seeds. Boiled water exposed to air after eight days

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gave a greatly reduced percentage of germination as compared with the percentage of germination of seeds in unboiled water. The amount of root growth in the former was also much less than in the latter. This indicates that while air was absorbed, at the end of eight days it was still not present in quantity equal to that in the unboiled water. He also shows that submergence at greater depths decreases the percentage of germination of seeds which he explains by the slowness of diffusion of oxygen.

The fact that oxygen diffuses slowly thru water readily accounts for the observation of Wacker (98:109) that Vicia faba and Lupinus albus grown in supersaturated soil showed a greater retardation even than when grown in water as compared with the amount of growth in moist soil. In soils, under usual conditions, air can diffuse thru the spaces between soil particles and thus supply the roots. When the soil is saturated, or has water present in excess, the air is driven out of the interstices of the soil. The only oxygen then available is that in solution in the water. In a supersaturated soil the greater part of a unit volume is occupied by soil particles leaving only a small volume which can be occupied by water containing dissolved oxygen. Water, however, contains a relatively small amount of oxygen. Accordingly, it is evident that much less oxygen is available in a supersaturated soil than in water alone and a much greater difference exists between a supersaturated soil and an ordinary soil. In water, agitation by wind and convection currents tend to replenish the oxygen content of the water. These factors are probably more important than diffusion. A current of air or oxygen passed thru water causes a certain amount of agitation which brings all the water, altho perhaps slowly, in contact with free air. In supersaturated soil, on the other hand, agitation and convection currents are not factors or are of little importance.

The very small amount of oxygen in the substratum of peat or Sphagnum swamps is also to be explained by the difficulty of replenishing the supply by diffusion from the air. In peat or Sphagnum substrata the amount of dry matter in proportion to the water-content of very low. There is sufficient material, however, to prevent surface agitation of the water and to prevent convection currents by which the oxygen content of the water in the substratum could be maintained at or near saturation. But there are other factors which become operative here and which do not affect the aeration of supersaturated soils, or at least only to a slight extent. These factors are the presence of living Sphagnum and of partly decomposed remains of Sphagnum and other plants which absorb the oxygen and prevent its penetration into the deeper lying parts of the substratum. It has been shown (p.) that the oxygen content of water in which Sphagnum is growing is very low. Dachnowski ('12:372) calls attention to the reducing power of peat and shows that it is greatest in the central zone and decreases toward the outside. The nature of the reducing substances is not stated. Whether the oxygen is absorbed by decomposition products in the substratum or is used up by plants growing at the surface is of little importance how-

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ever. The fact remains that the oxygen supply in the substratum in swamps is much lower than that of lakes or rivers of the same region.

A COMPARISON OF EXPERIMENTAL AND FIELD OBSERVATIONS

The Relation of Roots to the Water Level.

Certain peculiarities in the behavior of roots with reference to the water-level are to be noted. It has been found that the roots of land plants if submerged soon cease to absorb. A few days later the roots were found to be dead. New roots invariably developed from the stem at the surface of the water. These roots remained near the surface where they made extensive growth and branched freely. In no case were they found to penetrate more than half an inch to an inch below the water surface. If these surface roots were submerged to some depth by raising the water-level, they in turn died and another set of new roots developed at a higher level. On the other hand, when good aeration was provided, the roots of land plants, when submerged, remained alive, retained their capacity to absorb, and in many cases, even made a fairly extensive growth. The growth, however, was less than for plants of the same kind in moist soil. Roots of plants, with a considerable development of aerenchyma showed no retardation in growth and no cessation of absorbing activity. The only hypothesis that can account for the behavior of roots under the conditions above described is that in soils with excessive water-content the roots adjust themselves primarily to the oxygen supply.

Vöchting (78:132) found that the development of roots on cuttings or Salix in water was very definitely correlated with the oxygen supply. He found that under ordinary conditions new roots developed best at the surface of the water and little or not at all at greater depths. He concluded that water contains sufficient oxygen to maintain the life of Salix cuttings but was not sufficient to bring about production of new roots. The writer's own experiments have shown that roots of land plants cannot live or function under water unless aeration is maintained by passing air or oxygen through the water. Bennett, however, ('04:241) concludes from a series of aeration experiments with seedlings of various kinds that roots are not aerotropic.

A comparison of the relations of roots to the water level in swamps confirms the results obtained experimentally. Yapp ('08:75) finds that the direction of growth of roots is "largely determined by the water content of the soil." In wetter soils he finds that "roots grow much more horizontally", and says that this phenomenon is doubtless correlated with the paucity of oxygen of the more water-logged soils. An examination of the illustrations by Sherff ('12: 415) shows also that the roots of most plants grow above the water level. Those growing under water are of plants with a great development of air-conducting tissue. Although many of the plants the roots of which ordinarily occur above the water level, are able to endure submergence for considerable length of time, they normally develop roots above the water level. When the roots of these plants are submerged, their growth is more or less retarded or even prevented, and new roots are formed at the surface of the water. This has repeatedly

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been observed to happen when roots of Salix, Populus, Betula pumila, Cornus stolonifera, and other shrubs were submerged. This has also been confirmed by the experiments with various plants.

Diversity in Character of Swamp Plants.

It is to be observed that plants growing in swamps may be of hydrophytic, mesophytic, or xerophytic character. These plants grow often in close proximity. The apparent anomaly of hydrophytic and xerophytic plants growing side by side in the same area has brought forth many different explanations by various botanists. Schimper ('03:8) attributed xeromorphy to the presence of free humus acids which cause a "physiological dryness of the substratum." Warming ('09:95) agrees that the presence of free humus acids and other substances is the "weightiest cause" but admits the influence of other factors. Johow (1884), Kihlman (1890), Goebel ('91:11) and Yapp ('09:301) come to the conclusion that low humidity and strong winds in connection with the coldness of the substratum are the important factors. More recently Gates ('16:445) has concluded that winter evaporation is fundamentally responsible for the xerophytic characters of the evergreen ericads and that these characters are advantageous even in summer. Davis ('06:130) regards the bog as a xeropytic habitat, brought about by the drying of surface layers and the ability of peat to hold a large amount of water.which is not available to plants. Crump (1911:'12) also suggests the

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great water retaining power of peat. Burns ('11:119) agrees in part with Davis concluding that the fluctuation of the water table is the important factor but that secondary changes accompanying are to be considered. Früh, Schroeter (1904) and also Transeau (06:38) believe that low soil temperatures and lack of aeration are the important factors.

There has been much controversy also as to the supposedly xerophytic character of certain swamp plants. Many writers regard Scirpus, Equisetum, Juncus, and similar plants as bog xerophytes on account of the absence of leaves and general external appearance. Scirpus, however, has been shown by Sampson and Allen ('09:49) to be a typical hydrophyte in its rate of transpiration. The only plants which are unquestionably bog xerophytes are the ericads. As Groom (10:241) has shown, in the case of Larix decidua, some so-called xerophytic plants transpire more rapidly than some mesophytes. The ratio of transpiration to absorption is the important factor and if plants are xerophytic, it must be due to the imability of the roots to absorb water in sufficient amounts to meet the demands of transpiration. Among the causes assigned for the inability of the roots of bog plants to absorb readily are the following:- coldness of the substratum and shallow root systems, Früh and Schroeter (1904); low temperature and lack of aeration, Transeau ('06:38); presence of humus acids, Schimper, ('03:8); poor aeration, Hesselman, ('11:65), Free, ('11:110); bog toxins, Livingston, ('05:353), Dachnowski, ('12:); root execretions, Livingston, Britton and Reed (1905), and Schreiner and Reed (1907).

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Adjustments and Structural Adaptations of Swamp Plants.

Proximity of location in a swamp does not necessarily mean similarity or identity of conditions either for the roots or for parts above ground. In fact conditions for different layers of vegetation are very different as both Yapp ('09:275) and Sherff ('12: 415) have pointed out. The conditions for root growth above and below the water level are also very different. It is to be noted that the more or less mesophytic plants have their roots in the substratum above the water level. If the water level is raised the roots of these plants may endure submergence for a considerable time. Their activity and growth is usually retarded, however, and if the submergence be prolonged, the submerged roots die and are replaced by new ones formed at or above the water, or else the entire plant succumbs. The roots of hydrophytic plants always grow below the water level. They may grow above the water level for a longer or shorter time but make their best growth under water. These plants have well-developed aerenchyma through which the air may circulate to all parts of the plant. Such plants not only continue to grow with the roots submerged, but grow better than in moist soil as Wacker (1898) has stated. Many plants are able to grow in moist soil, in mud or completely submerged as Askenasy ('70:192) and Glück (1905-06-11) have shown. Schenk (1884), Constantin ('85:171) and others have pointed out that plants which are able to grow on land or in water undergo structural changes, principally in the

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development of large intercellular spaces or air passages through which air may be supplied. These air passages are to be regarded as adaptations to acquatic or amphibious habitats.

Goebel (1886) and Jost (1887) have described adaptations of roots to secure air when growing in swampy places. Both observed that certain plants sent roots to the surface or sent out branches above the surface as "breathing organs". This tendency of the roots to grow up to the surface or to develop upright processes extending above the water surface Jost designated as due to "aerotropism", while Göebel writes of such roots as "negatively geotropic" although he states specifically that they are developed to secure air supply for the roots and that their production is conditioned by the habitat.

The roots of many plants, however, do not undergo a structural change but adapt themselves to the swamp habitat in some other manner. The fact that the roots of many swamp plants grow above the water level has already been discussed in the relation of roots to the water level and need not be repeated. The roots of many of the bog heaths which ordinarily grow above the water level or at least do not extend much below it, may however endure submergence for some-time without apparent injury. The roots of these plants are generally not extensive. During the summer the <u>Sphagnum</u> on which the bog heaths grow, may have but little available water on account of its great ability to retain water. Therefore water in large amounts might be difficult to

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obtain. Gates (14:451) states that in such cases "The xerophytic adaptations . . . . . materially aid by lessening the demand upon root absorption." In winter with continued water loww from the parts above ground and with the present condition of the soil, the xerophytic characters are considered by Gates to be of even greater importance. In the bog heaths then, compensation is made for the lessened ability of roots to absorb by reducing transpiration by means of xerophytic leaf structures. This also probably explains the ability of these plants to endure root submergence.

It has been found by many investigators that nearly all the ericads have mycorhiza on the roots. In general it has been assumed that the presence of mycorhiza on the roots of bog plants is to be considered as an adaptation to bog conditions. Transeau ('06:33) found that "the mycorhizas develop only in poorly aerated substrata" and c.34 says "mycorhiza therefore appears to be an abnormal root condition. Whether the fungus is of advantage to the root under poorly aerated conditions cannot as yet be states." Gates ('14:450) states that "the absence of mycorhiza on Chamaedaphne and these other plants demonstrates that it is not a necessary adaptation to the bog environment." Roots of plants with aerenchymatous tissue even when submerged do not have mycorhiza. The experimental evidence of Transeau, which the writer has been able to confirm both by experiment and field observations, makes it seem very certain that the presence of mycorhiza is induced by lack of aeration. The writer accordingly agrees with Transeau that a mycorhizal condition of the roots is abnormal, and with Gates in that it is not a necessary adaptation to bog conditions. Rather it is to be regarded as a mild form of parasitism which is favored by lowered resistance of the roots under conditions of poor aeration.

Significance of Adaptations of Swamp Plants with Reference to Aeration.

The great diversity of character of swamp plants has, as already stated, called forth many explanations. Some of these lay emphasis on the effect of atmospheric factors while others emphasize the influence of factors of the substratum. In spite of all the differences of opinion as to the cause or causes of the diversity of character of swamp plants, a certain amount of agreement is to be found. There is, in general, either an explicit or implicit assent to the operation of a combination of atmospheric factors which tend to bring about a high rate of transpiration. There is also a fairly general agreement as to the existence in swamps of certain physical factors in the substratum, by the interaction of which absorption of water by the roots is retarded. The disagreement lies in the decision as to which factor is the most important.

It has been pointed out in the preceding papers that aeration of the roots is necessary for continued activity in absorption as well as for growth. Evidence from the experiments of many investigators has been presented in confirmation thereof.

The writer has also presented evidence from his own experiments which indicate the same fact. Livingston and Free (17:182) have shown that absorption of water by the roots is interfered with by depriving the roots of oxygen. The writer using a different method has also shown that absorption is retarded and finally almost completely checked by root submergence. From all the evidence, there can be no question that lack of aeration is a very important factor in reducing the absorbing capacity of submerged roots. It has also been stated previously that the ratio between absorption and transpiration is the critical factor and that if plants are xerophytic it must be due to inability of their roots to absorb water in sufficient amount to meet the demands of transpiration. The position and character of the roots with reference to the water level has been shown to be directly correlated with aeration. If aeration then, is a necessity for the continuation of the process of water absorption by the roots, plants may meet this necessity in several different ways: (1) The plant may undergo structural modifications by the development of an aerating system through which air may be supplied to the roots; (2) The roots may develop above the water level; (3) The aerial parts may be modified in such a manner as to reduce transpiration and thus compensation for reduced absorption by the roots.

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(1) In considering the adjustments and adaptations of plants to the swamp habitat, it was pointed out that hydropytes are provided with extensively developed air-conducting systems. By this means air is supplied to the roots, which are thus able not only to withstand root submergence but to make better growth that in a moderately moist soil. Absorption is not retarded and however great the water loss from aerial parts it is readily replaced by absorption of water by the roots. Water is always available and hence there is no need of structural modifications of the aerial organs to prevent water loss.

(2) In discussing the relations of roots to the water level, it has been pointed out that roots without aerenchyma develop above the water level. This is to be regarded as an adjustment to aeration. In support of this evidence has already been presented. Plants whose roots grow above the water level are usually low growing and consequently more or less protected from excessive water loss. The absorptive capacity of the roots is little or not at all reduced ordinarily since good aeration is provided and other factors are not very adverse. Such plants are usually more or less mesophytic in character. However, in dry years or during dry periods of the summer these plants may be subject to more severe conditions. The upper layers of the substratum become dry or at least do not furnish enough available water for plants on account of the great water-retaining power of peat and Sphagnum. For this reason plants with roots above the water level may show more or less severe wilting on the hotter days. If the drough become too prolonged or too intense some of these plants may perish.

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(3) Plants which are not protected by taller vegetation may be subjected to greater water loss. If, as in the case of ericads, they retain their leaves during the winter, the water loss continues at a time when replacement by absorption is very difficult if not impossible. In such cases as Gates (14:445) has shown the xerophytic structures of the leaves are especially valuable in reducing the rate of transpiration thereby lessening the demand upon root absorption. During the summer the conditions just discussed with reference to other pants with roots above the water level would apply to the ericads also. Here again the xerophytic nature of the leaves compensates for the inability of the roots to secure water readily from the substratum. They are able to endure root submergence for the same reason probably. The amount of water loss tends to be greater than that which the roots are able to absorb. Hence the plants are strongly xerophytic.

Accordingly the presence of hydrophytes, mesophytes, and xerophytes in close proximity in swamps is to be explained by the necessity of the roots of swamp plants to adjust themselves to receive an adequate air supply. This may involve change in the level at which roots grow and thereby affects the amount of water available. Changes in the water level, the temperature of the substratum, and atmospheric factors affecting the rate of transpiration may all exert an influence on the character of the plant. These other factors, however, are incidental to the adjustment of roots with reference to aeration.

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THE RELATION OF AERATION TO ECESIS.

Many plants are able to establish themselves in habitats with excessive water. It has been found by experiments in the greenhouse that seeds of plants adapted to aquatic or amphibious conditions are able to germinate and grow under water. Gluch ('05; '06,'11) found that the seeds of many plants possessed the ability to germinate and grow under water. Other seeds failed to germinate if covered to a depth of half an inch or less. Kraus (1901) has shown that germination of seeds of land plants under water may be brought about by aerating the water. Differences are to be observed, however, in the behavior of various seeds in this respect. Some apparently require less oxygen than others. Salix, Alnus, Betula pumila, Ribes, and many other plants germinate readily on hummocks of sphagnum or on mounds of peat but fail ot germinate if submerged.

Many seedlings are unable to persist if the roots are submerged. Other seedlings are not affected by submergence. Seedlings of many plants such as Salix, Betula pumila, and Rumex britannica are able to encure root submergence for considerable periods but usually send out new root at the surface of the water. Teh behavior of roots of seedlings shows the same relation to aeration that is shown by the roots of older plants. Only those plants having well-developed aerenchyma are able to extablish themselves in habitats with excessive water. If the water level is below the surface slightly many plants are able to invade and become established. The roots of many

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plants, however, remain near the surface. Periods of hot dry weather during the summer which cause the upper layers of the substratum to dry out may then result in the death of seedling with shallow root systems. Thus it is evident that aeration through its effect on the germination of seeds and the development of seedlings is an important factor in ecésis. It determines in a large measure the character of the invaders in swamps.

THE REACTION OF VEGETATION ON VARIOUS FACTORS.

Reaction on Water Content.

The conversion of a lake or open body of water into a swamp is due to the progressive decrease in the amount of water present. In effecting this decrease the reaction of vegetation in the various stages is an important factor. From the time that Chara and Philotria with other members of that associes invade a lake until the regional climax is established the gradual accumulation of organic debris resulting from the death and decay of plant bodies reacts on the habitat to bring about a decrease in the amount of water present. This is accelerated more or less by the deposition of eroded material washed in along the shore. The continuation of these processes finally permits the establishement of members of the Castalia-Nymphaea associes. Thus each associes in turn reacts on the habitat to reduce the depth of water. The reaction of the vegetation of any associes is unfavorable to its own continuance but favorable to the invasion of plants of following associes. This pregression is brought

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about by the continued upbuilding of the substratum which alters conditions of aeration. Along with that a number of other closely correlated changes occur which finally make possible the invasion and establishment of the climax vegetation. On account of the slowness with which the substratum is built up, the Larix-Picea stage may persist for a long time as a sub-climax. Finally, however, it is replaced by later stages leading to the climax.

Reaction of Vegetation on Concentration of Solutes.

The reaction of vegetation on solutes is to be considered with reference to: (1) Mineral compounds used by plants and more or less essential to their growth, (2) gases, especially oxygen and carbon dioxide, and (3) humus acids or other toxic substances more or less inimical to plant growth.

(1) It has been shown elsewhere in this paper that the chemical composition of the water in the substratum is not very different in succeeding stages of development. The actual chemical composition varies somewhat, but the concentration with reference to the total mineral content is not essentially different from that of lake, river, or ground water. The amount of nitrogen as nitrates is very small, the nitrogen being mostly in the form of organic nitrogen. The amount of potash also is much lower than that of the average mineral soil. The amount of phosphoric acid, although usually low, is not much less than that of many mineral soils.

(2) With reference to gases it has been shown on page that the oxygen content of lake water is usually near the saturation point as far as surface water at least is concerned. Birge and Juday (1911) have shown that the oxygen content varies greatly at different times of the year and at different depths. They show also that the water under certain conditions may be supersaturated. Analyses of swamp water at Hubert show that with the progression of stages, and especially with the appearance of Carex and Sphagnum, the oxygen content shows a marked decrease while the carbon dioxide content shows an equally marked increase. The decrease in oxygen content is probably due to the absorption of oxygen by organic compounds in the substratum during the composition. The increase in carbon dioxide is due to its liberation in the decomposition of organic material. Accordingly whereever organic matter is present, the carbon dioxide increases and the oxygen decreases.

(3) With reference to acids it is found that the acidity shows an increase from the Chara-Philotria stage up to the Chamaedaphne-Andromeda or Larix-Picea stages. Between these two there is very little difference in acidity. The increased acidity is to be attributed to the deficiency of oxygen in the substratum. Similarly the presence of toxic substances is to be considered as the result of decomposition of organic matter under conditions of reduced oxygen supply. By providing aeration the acidity and toxicity of the substratum are decreased. However, the relation between toxicity and acidity is not always constant.

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Reaction of Vegetation on Temperature.

It has been shown that the temperature of the substratum decreases in the Chamaedaphne-Andromeda and Larix-Picea associes. The substratum in these associes warms up very slowly in the spring and consequently very low temperatures may prevail even when the temperature of the air and of the neighboring upland soil has reached an average maximum for the season. The low temperatures are due largely to the great evaporation of water from the Sphabnum surface. The sun's heat is expended in the evaporation of water which it prevents from penetrating the substratum.

Air temperatures are more nearly the same in various developmental stages. However, on account of the coolness of the substratum swamps are particularly subject to frosts on clear nights. The temperature at 1.5 m. above the surface in more nearly uniform in the various associes than in the temperature near the surface. Temperature, humidity, and wind velocity affect the rate of evaporation. The evaporation rate over the bog shrubs of the Chamaedaphne Andromeda associes is high and compares with that in grass land. Evaporation is greater at a height of 1.5 m. in swamps than at the surface of the ground.

After the appearance of Larix or Picea or both the light intensity in lower levels is decreased. Larix and Picea usually do not make dense growths and the decrease is less marked in this associes than in later ones.

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THE EFFECT OF REACTION ON ECESIS AND SUCCESSION.

Many writers have attempted to account for the growth and distribution of plants in swamps thru the influence of some single factor such as lack of certain mineral constituents, presence of humus acids, toxic organic substances, and so on. The explanation, however, does not depend upon the influence of any single factor. The factors affecting vegetation are variously interrelated and a change in one factor brings about changes in others. However, a certain ordinal relation in factorial changes may be shown to exist. The chemical composition of the substratum in various associes, the concentration of the soil water with reference to necessary mineral compounds, presence of acids, or other toxic substances has already been discussed at some length.

The chemical analysis of various peat and grass swamp soils shows no absolute deficiency of any important constituent. Available nitrates, potash, and phosphoric acid are present in shall amounts. The soil water is very dilute with reference to these substances. However, the concentration remains about the same thru several associes. Furthermore, evidence of various investigators shows that plants may grow readily in very dilute solutions. Hence, there is no reason to assume that the growth and distribution of vegetation is determined by the chemical composition of the substratum or by too dilute solutions of these substances.

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Lime is present in swamps and in different developmental stages in amounts equal to that in many upland mineral soils. No correlation can be established between lime content and the character of vegetation. No constant correlation can be found between lime content and acidity altho in swamps with relatively high lime content the acidity is usually slight. It is possible that in undrained swamps, on account of lack of aeration, the lime exists as humates and in this condition is not available to plants. With increased aeration the nature of the lime compounds may be changed into more available forms.

The acidity and toxicity of the substratum also remain the same thru several associes. Acidity and toxicity are both high in the Chamaedaphne Andromeda and Larix-Picea associes and decreases in the later stages. No relation between acidity and vegetation or between toxicity and vegetation can be established. It has been proven experimentally that aeration decreases toxicity and acidity. The decrease of acidity and toxicity in later stages is also correlated with increased aeration. Acidity prevents the growth of organisms in the soil which are effective in breaking down organic nitrogenous substances and converting them into nitrates. Acidity and toxicity, however, are only incidental conditions arising from poor aeration. Hence acidity and toxicity are not important factors in the distribution and growth of swamps plants.

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Temperature in the substratum is directly correlated with water content. A high water content prevents the substratum from becoming heater. Low temperatures in the substratum retard bacterial action, chemical action, and diffusion of solutes. They also retard absorption and conduction of water and substances in solution. When associated with atmospheric conditions which cause a rate of transpiration of greater than that of absorption, low soil temperatures may be an important factor. Transeau ('06:28) has shown the importance of a cold substratum in influencing the growth and structure of certain plants. The influence is more marked, he finds, when combined with poor aeration. In swamps which have been drained the temperature of the substratum is more favorable. Since the temperature of the substratum is so intimately correlated with the water content it is to be regarded as a condition incidental thereto with water-content as the controlling factor.

Evaporation is more rapid in the Chamaedaphne-Andromeda associes than in the later ones and is nearly as great as in grass land. The evaporation ever Carex associes is about the same as at the corresponding height over the vegetation of the Chamaedaphne-Andromeda associes. Under Carex, bog heaths or other vegetation the rate of evaporation is considerably reduced and becomes least in the Abies-Picea associes. This is largely due to the reaction of vegetation in affecting temperature, humidity, and wind relations. A covering of vegetation, particularly of the taller shrubs and trees, tends to reduce evaporation by decreasing the amount of wind, decreasing the temperature, and increasing the humidity.

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Evaporation is the resultant of the interaction of wind, temperature, and humidity. Accordingly the rate of evaporation in the various associes is a measure of the reaction of vege- tation on temperature, humidity, and wind as affecting the rate of evaporation. The rate of evaporation is important in affect- ing the growth and distribution of swamp plants only when the rate of evaporation is greater than that of absorption. However the rate at which absorption proceeds is directly affected by aeration. This in turn depends upon the relation of roots to the water-level. Since plants with abundant air-conducting tissues grow readily with the roots submerged, they are always able to secure water. Conditions favoring a high rate of transpiration do not affect them, either as to form of aerial parts or as to the ability of the roots to absorb when submerged. Atmos- pheric factors which promote great evaporation accordingly affect only those plants with the roots above the water level. Such plants must either develop xerophytic leaf structures to com- pensate for reduced absorptive ability or must grow under the protection of taller plants where the rate of evaporation is not so high. Atmospheric factors promoting transpiration are sub- ordinate to the influence of water-content and aeration in con- trolling the distribution and growth of plants in swamps. Ecesis may be prevented by a period of hot weather which re- duces the available amount of water to such an extent that only plants with xerophytic structures are able to withstand it. Even they may be killed by too prolonged or too intense drying weather.

Light apparently does not become an important factor in the ecesis or distribution of plants in swamps until after the development of the Chamaedaphne-Andromeda associes. Up to that stage, not considering stages prior to the Carex associes, plants find a sufficient amount of light to enable them to persist. Dominance in the Chamaedaphne-Andromeda associes is to a considerable extent a matter of competition for light. The light values under shrubs of this associes varies from .005 to .02 in rather dense stands. On account of the reduced light intensity the ground surface under the shrubs is bare of other vegetation. In more open places Larix and Picea are able to invade. They are able to crowd out the bog heaths by overtopping them, thereby reducing the light. Andromeda is the first to disappear and has not been found in places where the light value is below twenty per cent. Ledum and Chamaedaphne often persist in places where the light value is as low as one per cent. However, they finally disappear when the light value is reduced to that extent.

A proper degree of aeration is a necessity in any substratum. The amount of air available to plants is directly affected by the amount of water present. The interrelation of these factors is so intimate that it is advisable to attempt to separate them. It has been shown that roots require oxygen in order to absorb water and that the various structural modifications and the direction taken by roots with reference to the water-level are all adaptations for aeration. Acidity and toxicity are due to lack of aeration and drainage whereby aeration is providedreduces acidity and toxicity. Low temperatures also are correlated with excessive water-content. Low temperatures reduce absorption. They also prevent growth of bacteria. But bacteria cannot live in a substration with an excess of water cause of lack of aeration. Low temperatures disappear with drainage whereby the excess water is removed and aeration is provided. With higher temperature comes increased oxidation which decreases acidity and toxicity and the substratum becomes suitable for bacterial growth. Increased bacterial activity gorwth promotes the formation of nitrates by the decomposition of organic nitrogen. In this way the deficiency of available nitrogen is increased. Other changes in the chemical composition of the substratum are also brought about by increased bacterial activity and chemical processes. A great number of other changes take place which tend to make the habitat better as to physical factors. But chemical and bacteriological properties of the substratum are favorably influenced by better physical conditions. The whole set of factors affecting physical, chemical,and bacteriological properties of the substratum are intimately interrelated. A change in one factor means a change in some other. The amount of water is the controlling factor. But it is the controlling factor only because when present in excess, aeration is prevented,and without`aeration absorption of water and solutes is prevented. Bacterial growth and activity is possible only with reduced water content and consequent better aeration. A progressive decrease in water content thru other various associes involves

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a progressive change in other factors. The progressive decrease in water content is brought about by the accumulation of plant remains thru the various stages of succession. Accordingly the reaction of the vegetation on the habitat in bringing about a progressive decrease in water content is fundamental. It is only thru a decrease in water-content that increased aeration and its concomitant ameliorations can occur. Other changes are dependent on, or incidental to changes in water content and aeration. The influence of other factors may under certain conditions, be of great importance but they are always subordinate to water content and aeration.

ECONOMIC FEATURES OF THE PROBLEM.

The importance of good aeration in the substratum of swamps has been strongly emphasized. Good aeration is necessary in order to secure good root development and normal root activity. With good aeration also, physical conditions with reference to soil temperature are improved. Better aeration and higher temperatures promote bacterial activity, whereby organic notrogen is converted into nitrates. Increased bacterial activity means improved conditions as to chemical properties. Therefore drainage is the first requisity of the utilizations swamps for agricultural purposes.

The chemical composition of swamps with reference to many constituents is not poorer than that of many upland soils. Potash and phosphorus are present in very small quantities, but apparently these quantities are sufficient since many swamps that have been placed under cultivation have produced good yields year after year without the addition of fertilizers. The greatest deficiency is in available nitrates. However, there are vast quantities of organic nitrogen and with drainage which brings about better conditions of aeration and more favorable conditions as to temperature the number of bacteria increases. With an increase of bacteria the organic nitrogen is decomposed and converted into notrates so that with improved physical conditions better chemical condition also results.

However the changes are often slow in taking place and it is often necessary to grow plants which are better adapted to withstand more unfavorable conditions than are many of the crops ordinarily used. For swamps in which the drainage is incomplete, timothy, red top, and blue grass are good since they are able to endure wet soil without much ill effect. Several years culture of mixed grass permits better drainage and subsequent improvements of other onditions to be affected. Later clover may be added with good results. After several years in grasses or mixture of grasses and clover, the ground may be broken and sown to some other crop. A period of years in grass allows the peat to become more disintegrated, removes a great deal of the acidity,and otherwise improves the soil.

The addition of lime or other fertilizers probably would not be necessary if swamps were reclaimed by sowing to grass and allowing this to grow for a period of years before cultivation is begun. Freshly drained and "peeled" bogs require lime and other fertilizer because the change in physical conditions is so recent that opportunity for the reduction of acidity, increase in bacterial flora with its consequent increase in nitrates, and other improvements has not been afforded.

Since, with drainage and its attendent improvement in conditions of aeration, the swamp naturally has a tendency to advance to the climax it is possible to accelerate the progression by seeding to trees. In northern Minnesota the pines, Pinus strobus and P. resinosa are the logical ones to plant since in the natural order of things they would replace other vegetation with the decrease in the water-content of the substratum.

C O N C L U S I O N S

(1) Roots of land plants do not live under prolonged submergence. The roots below the surface die and new ones are formed from the stem at the surface of the water. This occurs whether the plants are grown in loam, peat, or sphagnum.

(2) Land plants grown in peat or sphagnum show an evident reduction in growth of the entire plant when the roots are submerged. This is little or not at all evident in plants grown in loam with submerged roots.

(3) Reduction in growth of plants submerged in sphagnum is greater than under similar conditions in peat. This difference appears to be due for the most part to a greater lack of oxygen in these cases as compated with the oxygen supply available to submerged roots in soil.

(4) When the water is aerated plants are able to endure root submergence as long as aeration is maintained. The roots show some retardation in growth but remain alive.

(5) Ranunculus scelaratus, R. abortivus and Cyperus alternifolius grown in submerged soil show a greater growth of the entire plant than when grown in moist soil. The ability of grow with the roots submerged is undoubtedly due to the presence of aerenchyma. The reduction in growth of plants in moist soil is probably caused by the inability of the roots to absorb water readily under those conditions.

(6) Land plants with submerged roots show more or less pronounced wilting after one to three days. If submergence is prolonged the leaves become yellow and soon drop off.

(7) Land plants with submerged roots do not show these effects or only to a very slight extent in aerated water.

(8) A current of air passed thru water does not produce much effect in increasing the oxygen content. It does, however, keep the oxygen content more nearly at saturation.

(9) Philotria placed in water with good light causes a decrease in carbon dioxide and an increase in oxygen content. The value of Philotria as a means of aerating water has been clearly established.

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(10) Plants in soil from which oxygen is excluded show wilting, etiolation, and loss of leaves. The effects appear in the same order and time as in plants with roots submerged.

(11) The transpiration of plants with submerged roots shows a temporary increase soon followed by a sharp decline in the amount transpired as compared with plants in moist soil.

(12) The reduction in transpiration precedes wilting. It precedes etiolation and loss of leaves by two to four days. This indicates that absorption is reduced below the amount demanded by transpiration.

(13) When aeration is provided the development of plants is essentially as good with swamp water as with a nutrient solution. Plants with swamp water are somewhat smaller. The difference is slightly more evident when the plants are deprived of reserve food than when they are allowed to use it. This indicates that the difference in growth is probably due to an insufficiency of one or more mineral constituents.

(14) Swamp soils compare favorably with upland soils in chemical composition. There is no deficiency of any important mineral constituent. Phosphoric acid, potash, and nitrogen as nitrates are deficient as compared with most mineral soils. The amounts, however, seem to be sufficient to support plant growth.

(15) No correlation can be established at present between the chemical composition of the substratum and the succession

(16) Acidity in swamps varies between .0001 to .0055 normal. No correlation is to be found between acidity and the character of the vegetation. The acidity decreases with improvement of condition of aeration.

(17) If toxic substances are present they are due to insufficient aeration in the substratum and are removed by an increase in the oxygen supply.

(18) The oxygen content of lake water is essentially the same as that of tap or distilled water. The oxygen content of swamp water decreases from the *Carex* associes thru the *Chamaedaphne-Andromeda* and *Larix-Picea* associes.

(19) Carbon dioxide shows a corresponding increase thru the same associes. The increase is due to liberation of carbon dioxide in the decomposition of organic matter.

(20) The adjustment of the roots of swamp plants to the water-level is due to the necessity of securing a sufficient supply of oxygen. This necessity is met by structural modifications or merely by a change in the level of root development.

(21) The presence of hydrophytes, mesophytes, and xerophytes in close proximity in swamps is due to local differences of water-content in the habitat. Local differences in atmospheric factors affecting transpiration also exist. The ratio between the amount of water lost and the amount which the roots are able to absorb determines the character of the plant.

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(22) The rate of evaporation decreases with the progression of stages from the Chamaedaphne-Andromeda associes to the climax. The decrease is due to reduction of wind, slightly lower temperatures, and increased humidity brought about by the reaction of vegetation.

(23) Light becomes an important factor after the appearance of the Larix-Picea associes. Most of the bog heaths require a considerable amount of light. Ledum and Chamaedaphne may persist for some time where the light value is as low as one per cent.

(24) Ecesis is possible for many plants even when submerged. Ecesis can occur only when the oxygen requirements may be satisfied. Atmospheric factors promoting transpiration are effective in controlling the growth and distribution of swamp plants only when the amount of water lost is greater than that absorbed by the roots. When the roots are not able to supply water to equal the demands of transpiration the failure of plants to become established may result.

(25) The reaction of vegetation in building up the substratum is fundamental since it is only thru a decrease in water-content that increased aeration and the consequent ameliorations can occur.

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Figure 1. The effect of root submergence on beans.
No. 1, in soil; No. 2, in submerged soil; No. 3, in peat; No. 4, in sphagnum; No. 5, in submerged sphagnum; No. 6, in submerged peat.

Figure 2. Effects of root submergence on corn.
Nos. 1-2, in peat; Nos. 3-4, in submerged peat; No. 5, in submerged sphagnum.

Figure 3. The effect of various substrata in the growth of corn. No. 1 Soil; No. 2, Peat; No. 3, Submerged Sphagnum; No. 4, Sphagnum.

Figure 4. Effects of root submergence on the growth of corn. No. 1, Soil; No. 2, submerged soil; No. 3, Sphagnum; Nos.4-5 Submerged Sphagnum; Nos. 6-7 Submerged Peat; No. 8 Peat.

Figure 5. A pot of corn showing a formation of surface roots by a plant grown in submerged soil.

Figure 6. Four castor bean seedlings. The middle ones in submerged soil. The one at the right, in submerged peat, and the one at the left, younger seedling in soil. The leaf scars of fallen leaves may be noticed on the three older seedlings.

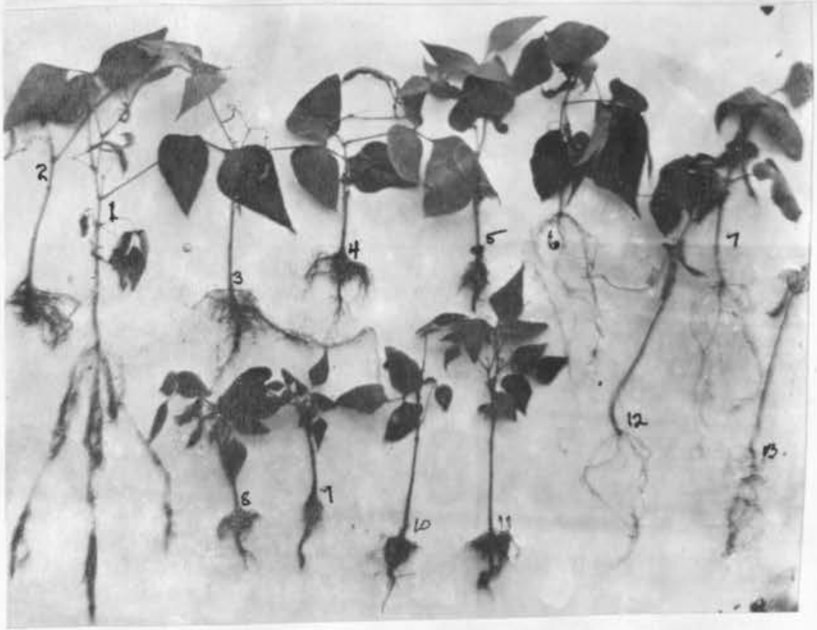

Figure 7. The effect of rDot submergence on the growth of beans. No. 1, in soil; Nos. 2-5, in soil submerged; Nos. 6-7, in sphagnum; Nos. 8-9, in sphagnum submerged; Nos. 10-11, in submerged peat; Nos. 12-13, in peat.

Figure 8. Other plants of the same series asin Fig, 7. Nos. 1-4, same as in Fig. 7; No. 5, in submerged peat; Nos. 6-9, in peat.

Figure 9. Three plants of Ranunculus abortivus, the middle one in submerged soil, the other two in moist soil.

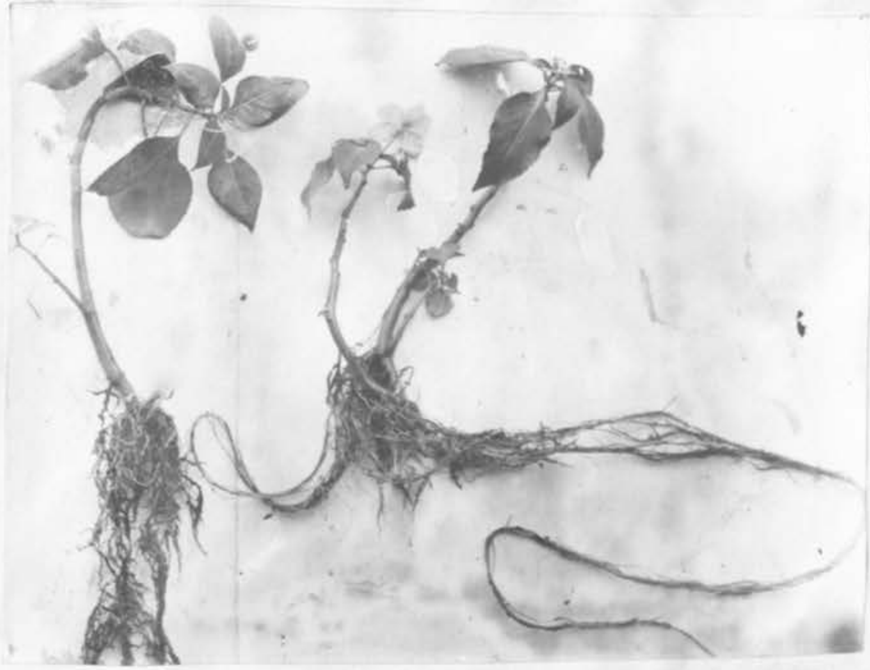

Figure 10. Two plants of Impatiens. The one on the right in moist soil the other in submerged soil aerated by a current of air passed thru the water. Plants in submerged soil and unaerated died after about three days.