WATER RELATIONS OF POCOSIN OR BOG SHRUBS

MARY G. CAUGHEY

(WITH SIX FIGURES)

Introduction

The pocosins, or broad-leaved evergreen shrub bogs, constitute one of the most distinctive plant communities of the southeastern coastal plain. They occupy flat, poorly-drained areas where the soil is frequently waterlogged for long periods of time, but where surface water seldom stands to a depth of more than a few inches, and then only for comparatively short periods. The water relations of the plants growing in pocosins present an interesting problem to the plant physiologist because structurally the leaves of many of the species resemble those of plants growing in a dry habitat rather than those of plants of wet places. The shrubs have simple, more or less elliptical leaves which are rather thick, leathery, and heavily cutinized. The leaf structure is of a type generally believed to have a low rate of transpiration, but there is never a lack of soil water except during severe summer droughts.

Though the problem of the water relations of bog plants has long been a subject for discussion, all of the earlier workers confined their investigations to northern bogs. Schimper (25) was among the first to notice the discrepancy between leaf structure and habitat. He advanced the theory that bogs are physiologically dry, the absorption of water being hindered by the presence of certain humic acids and soluble salts released during decomposition of the organic matter in the soil. He believed that the structure of the bog sclerophylls materially aided in preventing excessive water loss from plants whose root systems were unable to absorb much water because of the physiological dryness of the habitat. This theory of physiological drought was more or less generally accepted. Most of the earlier workers merely speculated as to the cause of the alleged physiological drought, however, and failed to present much real experimental data on the actual water relations of the plants.

A number of causes of physiological drought have been suggested. Low soil temperature was regarded by Schimper (25), Warming (30), and Transeau (27) as a factor in northern bogs. Davis (13) and Burns (3) ascribed the "xerophytic nature" of bogs to the water-retaining power of the peat and to periodic droughts. Transeau (27), Clements (6), and Bergman (2) regarded the lack of oxygen in bog soils as the controlling, or at least the primary, factor in physiological dryness. The importance of toxic compounds was first suggested by Livingston (17, 18) and has been advocated by Dachnowski (9, 10, 11) and Rigg (23). These so-called toxic compounds are supposedly the result of incomplete decomposition of organic substances in a soil deficient in oxygen.

The hypothesis of physiological drought, originally developed in connection with bogs of cool climates, has been extended to explain the vegetative
type characteristic of southern bogs or pocosins. In the southeastern coastal plain, obviously, low soil temperature could not be a factor in producing physiological drought. Wells (31) stated that the soil toxin theory furnishes the most probable explanation of the supposed physiological dryness of the southern pocosin. According to Wells (32), the low soil oxygen in a bog habitat during periods of flooding interferes with root growth and absorption. He suggested that, although no transpiration data are available for bog shrubs, there could be little doubt that the coriaceous leaves of these plants protect them against excessive water loss, enabling the poorly developed root system, in its poorly-aerated environment, to maintain the proper water balance. Wells and Shunk (33) believe that this low oxygen content is responsible for a complex of soil factors in grass-sedge bogs which prevent other species from entering the area for several years after drainage. Dachnowski-Stokes and Wells (12) suggested that this “lag effect” in grass-sedge bogs and a similar effect which they observed in a pocosin may be attributed to high acidity or possibly to organic toxins.

A few investigators, among them Montfort (21) and Stocker (26), have rejected the theory of physiological drought of the habitat and of low transpiration rates of typical bog plants. Montfort, in experiments on guttation and exudation from cut stems, found that bog water had little effect upon absorption of water by plants and therefore concluded that the bog habitat was not physiologically dry. Stocker’s investigations revealed that, per unit of leaf area, the transpiration rate of evergreen heath plants of northwestern Germany was between that of xerophytes and mesophytes, and the rate of deciduous species was equal to that of mesophytes or hydrophytes. He also calculated the ratio of daily transpiration to the fresh weight of the roots and concluded that bog plants absorbed more water per unit of root surface than did mesophytes.

The water relations of shrubs characteristic of bogs is, therefore, a controversial question, and no data are available for species of southern bogs. In order to clarify our knowledge of the water relations of these plants, a series of experiments was performed to compare the transpiration rates of pocosin species with those of certain mesophytes of the southeastern coastal plain. Since a knowledge of the environmental factors of a habitat is essential to a complete understanding of plant behavior and since no such data were available for a pocosin, a study of the habitat was carried out simultaneously with the transpiration experiments. It was hoped that such a study might furnish information which would aid in explaining the so-called xeromorphic leaf structures of these plants and lead to a better understanding of their water relations. The effect of certain of these environmental factors on the transpiration rates of these species was determined by experiments in the field and in the greenhouse.

Habitat study

A study of the environmental factors of both a pocosin and a nearby upland was made. First, because plants of both habitats were to be used
in the transpiration experiments; second, it was hoped that such a comparative study would lead to a better understanding of the factors in the bog habitat which are directly or indirectly involved in the water relations of these plants. A pocosin located in Beaufort County, North Carolina, about one-fourth mile north of the Craven County line, on U. S. highway no. 17, and an adjoining well-drained upland forest, representing a mesic habitat, were selected as sites for the field investigations. The most common shrubs in the pocosin were: Clethra alnifolia L., Cyrilla racemiflora L., Gordonia lasianthus L. (Ellis), Ilex glabra (L.) A. Gray, Ilex lucida (Ait.) T. and G., Magnolia virginiana L., Myrica cerifera L., Persea pubescens (Pursh) Sarg., and Zenobia cassinifolia (Vent.) Pollard. The dominant species in the upland were Pinus palustris Mill. and Pinus taeda L. Numerous hardwood species and several pocosin shrubs made up the understory.

Since the available soil water and the relative humidity of the atmosphere are probably the most important environmental factors affecting the transpiration of a given plant, the data reported in this paper bear on these factors only.

Continuous records of air and soil temperature, relative humidity, evaporation, and rainfall were obtained from March, 1940 to August, 1941. All the recording instruments were of the standard Friez type. Since the data obtained were too voluminous for complete tabulation, only summaries for weekly periods during the spring and summer of 1941 are reported in this paper. Compared with available records of the United States Weather Bureau for the nearby town of Washington, North Carolina, these data indicate that the period reported is typical of average conditions with respect to temperature and rainfall.

Minimum relative humidity values as recorded in the middle of the day and rainfall in inches are shown in figure 1. It is believed that the minimum relative humidity of the two sites is more important than the average or maximum humidity in respect to plant growth; therefore, only these values are reported. The curves show that minimum relative humidity in the pocosin was usually higher than in the upland, but the greatest variation between the two sites was only 10 per cent.

Average evaporation per week from four standard white bulb atmometers at each station is shown in figure 2. During the entire season evaporation rates were considerably lower in the pocosin than in the upland. A difference was to be expected since the relative humidity of the air in the pocosin was higher than in the upland. Some weeks there was approximately 40 per cent. more evaporation in the upland than in the pocosin. Although no records of wind velocity were obtained, repeated observations indicated that there was considerably more wind in the upland than in the pocosin. This difference in air movement may partially account for the greater variation in evaporation than in relative humidity in the two sites.

There was very little difference between air temperatures in the pocosin and at the upland station, and the same was true of soil temperatures. This
is not surprising since the two habitats were within a few hundred yards of each other. It seems probable that the small differences recorded were of little significance with respect to plant behavior, and they are, therefore, not included in this paper.

The pocosin soil consisted of a layer of organic matter approximately five to seven inches thick, overlying a sandy soil. This humus layer was composed of shrub leaves and sphagnum in various stages of decay interlaced with numerous fine roots and formed a fibrous mat over the underlying sand. The surface of the bog was made very irregular by numerous hummocks which varied from a few inches to 12 or 15 inches in height in the wettest parts. With the exception of sphagnum, the vegetation was largely confined to these hummocks. The floor of the upland was very different from the pocosin since it was practically bare of litter. This was the result of frequent fires and the rapid decomposition of organic matter in the hot humid climate of the region. The surface layer, six or eight inches in depth, was similar to the sandy layer beneath the peat in the pocosin.

The shallow root systems of the pocosin species were largely confined to the fibrous peat mats and, as far as could be ascertained, only a few roots

---

**Fig. 1.** Minimum relative humidity in the pocosin and pine stand and rainfall in inches (1941).
penetrated beneath the peat into the mineral soil. There was a deeper distribution of roots in the mineral soil of the upland, but even in this site, most of the roots were very close to the surface. The soil in both habitats was acid in reaction, but that of the peat was much more acid with a pH value of 3.5.

The level of the water in the pocosin soil varied only a few inches during the spring and summer of 1941, the variations being related to the amount of rainfall. From May 9 to June 6 there was only a half inch of rain, and the water level at the instrument shelter dropped from the surface of the peat in the depression to approximately four inches beneath the surface. Eight inches of rain fell between June 27 and July 11, temporarily raising the water level in all parts of the pocosin. In the wettest part of the pocosin,

![Fig. 2. Average evaporation per week from atmometers in upland and pocosin (1941).](image)

water stood during the spring and summer several inches deep in the depressions between the hummocks. Nowhere in the pocosin was the water level ever more than 6 inches below the surface. Since water could always be squeezed out of it, the peat soil was considered always to contain readily available water for plant growth.

Although these data do not furnish a description of the habitat very different from that which might have been obtained by generalizations from careful observations, the writer believes that they, nevertheless, are of considerable value. They furnish the first exact measurements of some of the environmental factors in a pocosin, and with these specific data it is possible to interpret more accurately the relation between the environment and plant behavior.

**Phytometer studies**

These experiments are presented in four parts. The first concerns a comparison of transpiration rates in the two habitats. The second is a com-
parison of transpiration rates of pocosin species and mesophytic species. The third deals with the effects which flooding the soil has on transpiration rates. The fourth concerns the effects on transpiration which are produced by saturating the soil with carbon dioxide.

**MATERIALS AND METHODS**

The plants studied were *Clethra alnifolia* L., *Gordonia lasianthus* L. (Ellis), *Ilex glabra* (L.) A. Gray, *Liriodendron tulipifera* L. (tulip poplar), *Myrica cerifera* L., *Pinus taeda* L. (loblolly pine), *Quercus alba* L. (white oak), and *Quercus borealis* var. *maxima* (Marsh) Ashe (eastern red oak). All of the pocosin species were potted in sandy soil obtained at the pocosin. The mesophytes were grown in the sandy loam used as potting soil in the greenhouse. The pots were placed in buckets and sealed to make them rain-proof and to prevent loss of water by evaporation from the soil. All plants had been growing out-of-doors in pots for several weeks prior to the periods of investigation. In each experiment at least three individuals of each species were used in the determinations.

The transpiration rates were determined by weighings, and the moisture content of the soil was maintained at its field capacity throughout the experimental period by replacing, after each weighing, the amount of water which had been lost.

The results are expressed as grams of water lost per square decimeter of leaf surface or, on a per-plant basis, as percentage of the expected rates which were determined prior to the test period. The leaf areas were determined by means of the photo-electric method, modified and described by Kramer (15).

**Results**

**COMPARISON OF TRANSPIRATION RATES IN THE TWO HABITATS**

If the pocosin is physiologically dry, there must either be some factor in the plant or in the environment which retards excess loss of water from the plant, and thus enables it to survive under such conditions. This experiment was devised to determine whether or not the atmospheric factors in a pocosin, as compared to those in the upland site, might limit transpiration sufficiently to be of any real protective value to the plant if its roots are in a physiologically dry habitat. The soil was maintained at or near field capacity, and, therefore, the important variable factors in the experiment were the atmospheric differences in the two sites.

Three typical pocosin species, Gordonia, Clethra, Myrica, and one mesophytic species (white oak) were used to compare transpiration rates at the two habitats. Four individuals of each species were arranged at random at each station. The containers were placed on the ground and covered with excelsior to prevent excessive heating of the soil by the sun. The transpiration rates for two-day periods were determined by weighings. The amount of water lost, expressed in grams per square decimeter of leaf surface, is shown graphically in figure 3.
A statistical analysis of the data showed that there was no significant difference between the transpiration rates of plants in the two habitats.

![Graphs showing transpiration of three pocosin shrubs and one mesophytic forest species in the pocosin and upland, also temperature and evaporation rates in the two habitats (1941).](image)

About ten inches of rain fell during the three-week period prior to the beginning of the investigation, raising the water table in the pocosin to an unusually high level. High air temperature and high relative humidity
prevailed during the entire experimental period. If transpiration of pocosin plants is limited to any great extent by the atmospheric factors of the habitat, it certainly should have been evident during this hot, humid period.

**Comparison of transpiration rates of pocosin and mesophytic species**

The thick, leathery leaves of many of the pocosin species have led some investigators to assume that the leaves are well adapted to prevent excessive water loss, but no quantitative data on the transpiration rates of these shrubs have been reported. In this study the transpiration rates of three pocosin species were compared with those of four native forest species.

Three investigations were conducted out-of-doors during August and September, 1940. The experimental plants were the pocosin species Ilex, Myrica and the forest species tulip poplar, loblolly pine, white oak, and eastern red oak.

**Table I**

<table>
<thead>
<tr>
<th>Species</th>
<th>Experiment I; Aug. 1-10, 1940</th>
<th>Experiment II; Aug. 20-23, 1940</th>
<th>Experiment III; Aug. 24-Sept. 3, 1940</th>
<th>July 16-31, 1941</th>
<th>July 12-20, 1942</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ix. glabra</strong></td>
<td>19.22</td>
<td>16.10</td>
<td>16.81</td>
<td>9.17</td>
<td>16.25</td>
<td>17.09</td>
</tr>
<tr>
<td><strong>Myrica cerifera</strong></td>
<td>12.31</td>
<td>10.80</td>
<td>10.36</td>
<td>7.27</td>
<td>15.56</td>
<td>10.69</td>
</tr>
<tr>
<td><strong>Clethra alnifolia</strong></td>
<td>11.45</td>
<td>9.73</td>
<td>9.43</td>
<td>6.03</td>
<td>14.58</td>
<td>12.27</td>
</tr>
<tr>
<td><strong>Quercus alba</strong></td>
<td>11.34</td>
<td>14.21</td>
<td>13.21</td>
<td>9.03</td>
<td>14.58</td>
<td>12.27</td>
</tr>
<tr>
<td><strong>Q. borealis var. maxima</strong></td>
<td>11.20</td>
<td>12.02</td>
<td></td>
<td>12.02</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Liriodendron tulipifera</strong></td>
<td>11.78</td>
<td>4.65</td>
<td></td>
<td>11.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pinus taeda</strong></td>
<td>11.96</td>
<td>23.58</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Gordonia lasianthus</strong></td>
<td>11.96</td>
<td>23.58</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Experiment I was a comparison of the transpiration rates of the pocosin species and white oak during the period from August 1 to August 10. Experiment II was a comparison of the transpiration rates of the three pocosin shrubs and the four forest species during the period from August 20 to August 23. In Experiment III, conducted from August 24 to September 3, different individuals of the four species included in Experiment I were used in the investigation. A summary of these three experiments together with some other transpiration data reported more in detail under Part I and Part III of this section is given in Table I.

An inspection of Table I shows that all of the pocosin species had transpiration rates comparable to those of the broad-leaved forest species. In fact, Ilex and Gordonia had a higher rate of transpiration than any of the forest species; and Myrica and Clethra showed rates very similar to those of white oak, eastern red oak, and tulip poplar. Clethra had the lowest rate of the pocosin species, and loblolly pine had the lowest rate of the forest species. However, the transpiration rate of Clethra was about 60 per cent.
higher than that of pine. These results clearly show that with similar conditions typical pocosin species transpire as readily per unit of leaf surface as the mesophytic species of the region.

**Effects of Flooding the Soil on Transpiration Rates**

It is well known that pocosin plants have root systems which are capable of surviving for comparatively long periods of time in poorly-aerated, waterlogged soil. The question naturally arises as to the effect of submergence on water absorption of these species. Two experiments were performed, one in the summer and the other in the fall of 1942, to determine the effects on transpiration of flooding the soil.

The first experiment, conducted out-of-doors in July, included Gordonia, Clethra, Ilex, and eastern red oak. The roots were constantly submerged from July 12 until July 18, at which time the excess water was drained off. The results are shown as percentages of the expected rate per square decimeter of leaf surface in figure 4. At the end of six days of submergence the rate of transpiration had decreased to less than 10 per cent. of the expected rate in Ilex, to 36 per cent. in Gordonia, 60 per cent. in Clethra, and 55 per cent. in eastern red oak. Foliage injury occurred in Ilex and Gordonia and it was necessary to drain off the free water on July 18. Clethra and red oak showed no visible signs of injury during this period.

A noticeable recurrence of growth was noted in both Ilex and Gordonia after the beginning of the experimental period. Since both the control and the test plants, as far as could be judged, showed approximately the same amount of growth, it was thought that no great error existed in the results obtained. The young growth at the tips of the branches of Ilex and Gordonia showed visible wilting on July 17 and 18. At the same time serious injury of numerous older leaves took place in both species. Because foliage

![Figure 4](https://www.plantphysiol.org)
injury and low transpiration continued even after the excess water had been drained from the soil, it was necessary to terminate this experiment on July 20. It seemed probable that the serious injury occurring in Ilex and Gordonia might have been partially lessened had there not been a recurrence of growth at the time of complete submergence of the roots.

The submergence of the roots came simultaneously with a period when the air temperatures rose to nearly 38° C. and continued at that high level for approximately ten days. It was impossible to keep the temperature of the soil inside the containers below these high air temperatures. It seems unlikely that the temperature of bog water and soil is ever this high since the highest soil temperature recorded during the period of observation was 28° C. Cannon (4) says that roots require more oxygen for growth at high than at low temperatures. Probably poor aeration is much more injurious at high than at low soil temperatures. In this experiment it seems possible that a high oxygen requirement, at a time when the oxygen supply was greatly reduced, was partly responsible for the inability of the roots to supply the tops with sufficient water.

The second experiment was performed in the greenhouse during the fall of 1942. The soil of the test plants was flooded on October 9, and the roots were continually submerged until the termination of the experiment on

---

**Fig. 5.** Showing effects of water saturation of the soil on transpiration during the autumn of 1942. Soil was flooded on October 9.
October 29. The results are given in figure 5 as percentages of the expected rates of transpiration on the basis of the average rate of four individuals of each species.

Although transpiration rates were reduced, there was no evidence of injury to any of the plants during the twenty-day period of submergence of the roots. The greatest reduction in transpiration occurred in Gordonia on October 17, with 35 per cent. of the expected rate; and Ilex came next with a reduction to 55 per cent. of the expected rate on October 28. The results of the two experiments indicate that those plants, which tend to have a relatively high transpiration rate under normal conditions, are more seriously injured and show a greater reduction in transpiration than those plants with a lower rate of transpiration. In table I it is shown that Ilex and Gordonia have relatively high transpiration rates, and in both of the experiments involving submergence of the roots they were more seriously affected than any of the other species.

These results indicate that transpiration of pocosin species is reduced by flooding the soil, even for relatively short periods, but that there is no serious injury except when flooding occurs at the same time as high air temperature and high soil temperature. During the milder autumn days, even after 20 days of submergence, there was no evidence of injury.

Effects of Carbon Dioxide in the Soil on Transpiration

Water absorption, by roots of pocosin plants growing in water-logged soils, is probably affected not only by lack of oxygen in the soil but also by a high concentration of carbon dioxide. Russell and Appleyard (24) have shown that the air dissolved in water-logged soils consists chiefly of carbon dioxide and nitrogen and contains practically no oxygen.

Kossowitch in 1892 was, according to Clements (5), the first to show that carbon dioxide exerted a specific effect on transpiration regardless of the presence of oxygen. More recently Kramer (16) stated that this rapid reduction in water intake by transpiring plants, caused by high concentrations of carbon dioxide, resulted largely from decreased passive absorption caused by physical changes in the protoplasm of the root cells. He said that high concentration of carbon dioxide is probably the most important factor in the reduction of water intake for the first few hours, but lack of oxygen is probably the most significant factor later. Whitney (34) believes that oxygen deficiency is more important than an excess of carbon dioxide in reducing water absorption. Chang and Loomis (5) reported that high carbon dioxide decreased absorption of water and minerals by wheat, maize, and rice.

An investigation to determine the extent to which transpiration of certain pocosin species may be reduced by high concentrations of carbon dioxide was conducted out-of-doors in October, 1941. The species studied were Ilex, Myrica, Clethra, and white oak; three individuals of each species were used as check plants and three individuals as test plants. Prior to the test period
transpiration rates of the six individuals of each species were determined in order to calculate the percentages of the expected rates. The soil was saturated with carbon dioxide from October 6 to October 11. Following the test period determinations were continued for five days in order to ascertain the rate of recovery. The average transpiration rates for the three individuals of both the test and the control plants were used to calculate the percentages of expected rate. The results are plotted in figure 6.

The curves show that transpiration rates were reduced in all species by the end of the first 24 hours of treatment. Ilex and Clethra were the least affected during the five-day period. Transpiration was reduced about 50 per cent. of the expected rate in Clethra, 55 per cent. in Ilex, 60 per cent. in Myrica, and 70 per cent. in white oak. On the fifth day after the treatment was discontinued, Clethra and Ilex had recovered to approximately 80 per cent. of their normal rates, while Myrica had recovered to only about 50 and white oak to 35 per cent. of their normal rates. Two of the three individuals of the white oak receiving the treatment died within a week after the experiment was discontinued, but none of the pocosin species was visibly injured by the severe carbon dioxide treatment.

The period of investigation had clear skies, high temperatures, and high evaporation rates as measured by atmometers and was, therefore, quite

![Figure 6](image-url)

**Fig. 6.** Transpiration rates as affected by saturation of the soil with carbon dioxide (October, 1941).
favorable to high transpiration rates. It is believed that if pocosin species are especially sensitive to the injurious effects of carbon dioxide, visible symptoms would have developed during a period so favorable to high transpiration. Therefore, although these pocosin species show reduction in transpiration when their roots are growing in soil containing appreciable amounts of carbon dioxide or in water-logged soil, they appear to be more tolerant of such conditions than species such as white oak and eastern red oak, which normally grow only in well-aerated soil.

Discussion

The data as shown by the curves in figure 3, reveal that transpiration in the pocosin is not significantly different from that in the upland forest. This might seem surprising since the relative humidity in the pocosin was found to be higher than in the upland. The phytometers in the pocosin probably received more direct sunlight than those in the upland although no direct measurements were made. In the pocosin there were only a few scattered pines, whereas, in the upland, the pines and the few hardwood understory trees furnished considerable shade. Although the shrub cover in the pocosin was dense, and an area had to be cleared to place the phytometers, the experimental plants were not shaded as much as were those in the upland. It appears, then, that the shrubs normally growing in the pocosin would receive more sunlight than similar shrubs growing in the upland. It was impossible to estimate to what extent, if any, this difference in amount of sunlight affected the transpiration rates at the two sites. Since the atmospheric factors are the only known variables in this experiment it seems logical to conclude that the atmospheric factors in the bog are not effective in limiting transpiration. This being true, if the plants are growing in a physiologically dry habitat the plant itself must limit transpiration sufficiently to balance the low water intake.

The data in table I furnish no evidence to support the view that the coriaceous leaf structure of these species is an adaptation enabling the plants to survive physiological or physical drought by virtue of low transpiration rates. The phytometer studies conclusively show that the pocosin species, Clethra, Gordonia, Ilex, and Myrica, growing in fairly well aerated soil with moisture content near the field capacity, have transpiration rates at least as high as those of such mesophytes as white oak, eastern red oak, and tulip poplar. In fact, Gordonia and Ilex consistently had higher rates than those of any of the forest species.

These data, of course, do not prove that the plants are not drought-resisting forms, but they do indicate that their leaf structure does not prevent water loss. Maximov (19) has pointed out that not all drought-resisting plants have low transpiration rates but that actually many have comparatively high rates of transpiration when there is plenty of available soil water. It has been shown by Turrell (28) that some plants having so-called xeromorphic leaves actually possess a high ratio of internal to
external surface that makes them capable of relatively high transpiration rates.

An anatomical study of the leaves of several pocosin species by McMenamin (20) has revealed the relatively large amount of surface exposed to internal air spaces. In Gordonia lasianthus the palisade is made up of two or three moderately compact layers and the spongy layer contains many air spaces. In Ilex glabra, in spite of the compact appearance of the palisade, there is a vast exposure of internal surface as revealed by sections cut parallel to the epidermis. Although the palisade layer is somewhat compact in Clethra alnifolia and Myrica cerifera, both possess comparatively open spongy tissue. Turrell (28) cited several experiments which showed sun leaves and leaves with much palisade to have higher transpiration rates than shade leaves. Turrell (29) also said that experimental plants, in his studies of the correlation between internal surface and transpiration rate, showed a high degree of correlation between the ratio of internal to external surface and the rate of transpiration. Since the amount of surface exposed to internal air spaces is an important plant factor in determining transpiration, it is not surprising to find that the pocosin shrubs used in this study had transpiration rates comparable to those of mesophytic species.

It is reasonable to suppose that transpiration rates obtained with phytometers are representative of the rates of shrubs growing in the pocosin under the same conditions. The root systems of the plants involved in these studies were certainly no more extensive, and probably much less extensive, in proportion to the tops, than similar systems in the peat layer of the pocosin. Under conditions of adequate moisture and in fairly well-aerated soil the roots of the experimental plants apparently were capable of supplying the aerial parts with relatively large amounts of water. The evidence indicates that the alleged xeromorphic leaf structures of the pocosin plants really do not retard transpiration.

Figures 4, 5, and 6 show that the absorption rates of pocosin species are reduced by excessively poor aeration. Injury to the plants is greatest when periods of poor aeration coincide with high air temperatures which favor rapid transpiration rates. However, there are several reasons which seem to indicate that situations comparable to the severe treatments to which the experimental plants were subjected are rarely, if ever, duplicated in the natural habitat. The water level, in the pocosin under investigation, fluctuated considerably during the period of observation. At certain seasons water stood to a depth of several inches in the depressions between the hummocks; but during June, July, and August, the water table was, with few exceptions, several inches below the surface of the peat in the depressions. The water table fell rapidly to a few inches below the surface during these months, even after having been raised considerably by heavy summer rains. Since the root systems of pocosin plants are mostly shallow and most of the shrubs grow on hummocks, the roots are in sphagnum and peat above the normal summer water table. Observations revealed that when extremely
wet periods occur during the growing season, many new roots develop at or near the surface of the peat above the high water level. Similar behavior was also observed in the potted plants, particularly Clethra and Myrica, after their roots had been submerged for several days.

It seems probable that the non-flooded peat layer is well aerated, although no determinations were made of the oxygen or carbon dioxide content of the soil-air. Clements (7) stated that, in Vageler's (1907) studies of the soil-air of various moor communities, the greatest amount of carbon dioxide present was 2.68 per cent. and the least oxygen was 16.68 per cent.; no injurious effects from soil-air with a few per cent. of carbon dioxide was found anywhere in the moor. Wells and Shunk (33) reported that the soil-air in the non-flooded soil of a grass-sedge bog was similar to atmospheric air but that during a flooded period the oxygen content of mid-bog water was only about 0.3 p.p.m. Emerson (14) stated that on account of the fibrous spongy structure of peat, aeration is possible down to the water surface, and he found that roots grow more normally in peat soil than in garden soil with the same water level. According to Coville (8) the necessity of well-aerated soil for the growth of blueberries accounts for their distribution either about the margin of bogs or on hummocks where, as he said, spaces in the sphagnum provide air passages even when it is saturated. Assuming, then, that the peat layer, above the water level, has an oxygen concentration at least comparable to that found in the soil of moor communities or in non-flooded, grass-sedge bogs, it may well be questioned whether inadequate absorption caused by poor aeration ever becomes a serious factor to plants in this pocosin. During weather favorable to high transpiration the water table is generally low enough to permit adequate aeration; and, when the water table is high, atmospheric factors are such as to limit transpiration. During the three summers' observation of this pocosin the water table never dropped more than six inches below the surface of the peat, and even then the peat was always so wet that water could be squeezed from it. One of these summers was a dry season, with a rainfall deficiency of five inches. It appears, therefore, that the shrubs in this pocosin would suffer from a deficiency of soil moisture only during the most severe droughts.

If we accept Montfort's (21) conclusion that absorption of water is not hindered by any toxic properties of the water or soil, and if aeration is not a problem during periods when water loss tends to be high, there seems to be no basis for considering the pocosin a physiologically dry habitat. Stocker's (26) findings that the root systems of bog shrubs are more efficient in absorption per unit of surface than those of mesophytes, and our observation that some bog species have transpiration rates of the same magnitude as mesophytes do not support Wells' (32) theory that the root systems of these plants are not capable of supplying any great amount of water to the tops. The water requirements of these plants apparently are high as indicated by the high transpiration rates and by their natural occurrence in bog habitats. That they have high oxygen requirements, at least during the
actively growing season, has also been demonstrated. The lack of aeration in bog soils apparently is compensated for largely by the shallow root systems and the growth of shrubs on hummocks in the wettest areas of the bog. The ability to survive in water-logged soil, when other plants cannot, may be due to their tolerance of high soil acidity. These shrubs probably are confined largely to the bog habitat more by their high water requirement than by any other factor.

The coriaceous leaf structure, characteristic of many pocosin species, cannot then be explained in terms of water relations. Some evidence points to the possibility that the characteristics of the vegetation of certain habitats are determined partly by mineral deficiencies. According to Mothes (22), the coriaceous structures of bog plants may be attributed to a nitrogen deficiency and not to physiological dryness. Albrecht (1) suggested that lack of calcium in soils is correlated with a highly carbonaceous vegetation. The acid soil of the pocosin might be assumed, then, to favor the development of leaf structures with high carbon content which was described by McMena-min (20) as characteristic of pocosin shrubs.

In conclusion, it seems that we probably need to revise our ideas about bogs and bog plants. Most discussions have been influenced by the somewhat archaic concepts of bogs as "physiologically dry" and of the plants growing in them as "bog xerophytes." It appears that these concepts have outlived their usefulness and could well be discarded. It will be possible to explain the physiology of the plants in our pocosins only after the accumulation of more experimental data, unhampered by traditional views.

Summary

A physiological and ecological study was made of a pocosin located in Beaufort County, North Carolina.

A comparison of the environmental factors of the pocosin and of an adjacent pine stand was made. Soil and air temperatures, as recorded by thermographs, are quite similar in the two habitats. Relative humidity is lower, and evaporation rates are considerably higher in the pine stand than in the pocosin. It is probable that the higher evaporation in the pine stand is caused partly by greater air movement in this site.

Phytometer studies indicate that transpiration rates at the two habitats are similar. The atmospheric factors do not appear to be sufficiently different in the two habitats to affect transpiration.

Soil factors of the pocosin and the pine stand differ more than do atmospheric factors. The accumulation of peat, the higher water table, and the greater acidity in the pocosin make its soil conditions quite different from those of the pine stand. The water level in the pocosin fluctuates considerably during the year. At certain times water stands to a depth of several inches in the depressions between the hummocks, and at other times it falls several inches below the surface of the peat. When the water level is high the roots of the shrubs may be submerged and thus subjected to low soil oxy-

Copyright © 1945 American Society of Plant Biologists. All rights reserved.
CAUGHEY: WATER RELATIONS OF SHRUBS

...en, but when the water level falls the roots are in relatively well-drained, and probably well-aerated peat. Since most of the shrubs grow on hummocks it appears unlikely that the root systems suffer from inadequate aeration for any great length of time.

Phytometer experiments in which the soil was saturated with water or carbon dioxide indicate that transpiration of pocosin species is reduced as much by poor aeration as is transpiration of mesophytic species. The pocosin species, however, seem to be injured less by poor aeration of the soil than do mesophytes.

Observations extending over three years indicate that generally during periods when atmospheric factors favor high transpiration rates the shallow root systems are seldom submerged for more than a few days at a time. The problem of aeration, therefore, seems to be of less importance than has commonly been supposed.

Experiments show that the pocosin species Clethra alnifolia, Gordonia lasianthus, Ilex glabra, and Myrica cerifera have transpiration rates at least comparable to those of mesophytic forest species. The xeromorphic structures of the leaves of the pocosin shrubs apparently are not effective in reducing transpiration.

The pocosin habitat is probably not physiologically dry so far as the pocosin plants are concerned, and these plants are not xerophytes in the sense of having low transpiration rates. No clear explanation for their xeromorphic appearance can be offered.

The writer gratefully acknowledges her indebtedness to Dr. Paul J. Kramer for suggesting the problem and for aid and guidance throughout the investigation and to Dr. Kramer and Dr. H. J. Oosting for their critical review of the manuscript. The assistance of Mr. T. H. Wetmore in the care of the seedlings is greatly appreciated. The work was done at the Department of Botany, Duke University.

EAST CAROLINA TEACHERS COLLEGE
GREENVILLE, NORTH CAROLINA

LITERATURE CITED


