U. S. DEPARTMENT OF AGRICULTURE.

DIVISION OF BOTANY.

CONTRIBUTIONS

FROM

THE U. S. NATIONAL HERBARIUM.

Vol. V, No. 5.

ISSUED AUGUST 1, 1900.

THE PLANT COVERING OF OCRACOKE ISLAND; A STUDY IN THE ECOLOGY OF THE NORTH CAROLINA STRAND VEGETATION.

BY

THOMAS H. KEARNEY, JR.

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LETTER OF TRANSMITTAL

U. S. DEPARTMENT OF AGRICULTURE,
DIVISION OF BOTANY,
Washington, D. C., February 28, 1900.

SIR: I have the honor to transmit herewith, for publication as Volume V, No. 5, Contributions from the United States National Herbarium, a manuscript by Mr. T. H. Kearney, jr., assistant botanist, entitled The Plant Covering of Ocracoke Island.

Respectfully,

FREDERICK V. COVILLE,
Botanist.

HON. JAMES WILSON,
Secretary of Agriculture.

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ILLUSTRATIONS.

THE PLANT COVERING OF OCRACOKE ISLAND: A STUDY IN THE ECOLOGY OF THE NORTH CAROLINA STRAND VEGETATION.

By Thomas H. Kearney, Jr.

INTRODUCTION.

In October, 1898, in the course of field work for the United States Department of Agriculture, the writer spent five days upon Ocracoke Island, North Carolina. Owing to its limited size, it was possible, even in that short time, to explore somewhat thoroughly a considerable part of the island. It is to be regretted that visits were not made to the locality earlier in the season, so that the phenological development of the vegetation could be studied. However, as most of the characteristic plants of our southern Atlantic strand are rather late in maturing, it is probable that a better season for a single visit could not have been chosen. It was of course impossible to make any valuable observations upon fecundation and dissemination, important as these subjects are to the study of the geographical distribution of plants. What is said here of Ocracoke will doubtless apply, in a general way, to the other sandy reefs of the North Carolina coast.

The object of this paper is a study of the ecology and geography of the vegetation of the island, the several divisions of the subject being presented in the following order:

(1) Climate; (2) physiography; (3) geology and soils; (4) the plant formations, their composition and physiognomy; (5) ecological forms—adaptations to environment; (6) anatomy; (7) phytogeographical affinities of the flora.

The nomenclature used is mainly that followed in Britton and Brown's Illustrated Flora of the Northern United States and Canada, but, in order that those who are interested in ecological work and are not familiar with this nomenclature may find no difficulty in recognizing the species described, the names used in the later works of Gray and of Chapman are quoted in parentheses. A full list of all plants collected or observed upon the island is appended, and here, again, familiar synonyms are cited in parentheses. A list of the works quoted, with their full titles, is given at the end of the paper.

In the preparation of the anatomical portion of the paper, Mr.

Theodor Holm has rendered valuable assistance, and he has kindly furnished the drawings for figures Nos. 1 to 8, 17, and 18. The other figures were drawn from nature by the author.

CLIMATE.

The following data have been obligingly furnished by the United States Weather Bureau. The observations were made at the Hatteras Station, only a few miles northeast of Ocracoke.

TEMPERATURE.

Readings were taken in the shade.[1] The observations at Hatteras cover a period of about twenty years. The average number of days per annum with a temperature exceeding 6° C. (43° F.) is 365, while at Norfolk, Va., the number is only 295. The sum total of temperatures above 6° C. during the year averages 3,749.4 C. (6,749° F.), which is notably higher than the Norfolk figure of 3,359.4° C. (6,047.0° F.). The normal mean temperature during the six consecutive hottest weeks of summer is 25.9° C. (78.6° F.), as compared with the slightly higher mean of 26.3° C. (79.3° F.) at Norfolk.

The normal annual temperature is 16.3° C. (61.4 F.), as compared with 14.8° C. (58.7° F.) at Cape Henry, Virginia, 15.0° C. (59.0 F.) at Norfolk, Va., and 17.2° C. (63.0° F.) at Wilmington, N. C.

The normal monthly temperatures are as follows:

	Degrees C.	Degrees F.		Degrees C.	Degrees F.
January	7.6	45.7	July	25.5	77.9
February	8.1	46.6	August	25.2	77.4
March	10.0	50.1	September	23.2	73.7
April	14.0	57.2	October	18.0	64.5
May	19.1	66.4	November	13.1	55.6
June	23.3	74.0	December	9.0	48.2

The normal daily range of temperature for the whole year amounts to 6.3° C. (11.3° F.), as compared with 8.2° C. (14.7° F.) at Cape Henry, 8.8° C. (15.8° F.) at Norfolk, and 9.6° C. (17.3° F.) at Wilmington.

The normal daily ranges for each month are as follows:

	Degrees C.	Degrees F.		Degrees C.	Degrees F.
January	7.0	12.7	July	5.5	10.0
February	7.1	12.8	August	5.1	9.2
March	7.2	12.9	September	5.3	9.6
April	6.9	12.5	October	5.7	10.2
May	6.4	11.5	November	6.3	11.3
June	5.7	10.3	December	7.1	12.8

[1] Consequently they do not represent the temperature to which most of the vegetation is actually exposed, being subject to insolation during the hours of sunshine. They are chiefly valuable for purposes of comparison with other climates.

The absolute maximum temperature observed was 38.8° C. (102° F.), as compared with 39.4° C. (103° F.) at Cape Henry, 38.8° C. (102° F.) at Norfolk, and 39.4° C. (103° F.) at Wilmington.

The absolute minimum temperature observed was —13.3° C. (8.0° F.), as compared with — 15.0° C. (5.0° F.) at Cape Henry, — 16.6° C. (2.0° F.) at Norfolk, and — 12.8° C. (9.0° F.) at Wilmington.

The absolute monthly maxima and minima are as follows:

Month.	Maximum.		Minimum.	
	Degrees C.	Degrees F.	Degrees C.	Degrees F.
January	26.1	79	—10.0	14
February	22.8	73	—11.7	11
March	29.4	85	— 3.3	26
April	30.0	86	— 0.6	31
May	33.9	93	6.1	43
June	38.8	102	12.8	55
July	37.2	99	16.1	61
August	36.1	97	16.6	62
September	35.0	95	10.0	50
October	32.2	90	5.5	42
November	26.1	79	— 2.2	28
December	22.8	73	—13.3	8

The average date of the latest killing frost in spring is February 25, as compared with March 19 at Cape Henry, March 26 at Norfolk, and March 15 at Wilmington. The latest recorded was April 5, as compared with April 19 at Cape Henry, April 26 at Norfolk, and April 20 at Wilmington.

The average date of earliest killing frost in autumn is December 13, as compared with November 14 at Norfolk and Cape Henry and November 12 at Wilmington. The earliest killing frost recorded was on November 12, as compared with November 14 at Cape Henry, October 15 at Norfolk, and October 13 at Wilmington.

From the above data the temperature may be characterized as follows: Warm, but not excessive, with a considerable sum total of effective temperatures during the growing season, and usually mild temperatures during the very brief dormant period. The normal temperature is at least 6.5° C. above freezing point during every month of the year. The normal amount of daily variation of temperature is, according to the season, from 5° to 7° C., a relatively very small range. The period between the average dates of the earliest killing frost in autumn and of the latest in spring, which may be taken as very roughly coinciding with the dormant period of most of the vegetation, covers only seventy-four days.

SUNSHINE.

The observations cover a period of nearly thirty years. Normal annual sunshine,[1] stated in percentages of possible sunshine, 54, as compared with 52 at Cape Henry, 51 at Norfolk, and 52 at Wilmington. The monthly percentages are as follows:

Month.	Per cent.	Month.	Per cent.	Month.	Per cent.
January	46	May	59	September	56
February	47	June	55	October	58
March	52	July	55	November	54
April	55	August	52	December	53

Normal annual sunshine, stated in hours, 2,392.2, as compared with 2,314.6 at Cape Henry, 2,270.1 at Norfolk, and 2,312.7 at Wilmington. The normal monthly number of hours of sunshine are:

Month.	Hours.	Month.	Hours.	Month.	Hours.
January	144.7	May	256.2	September	208.3
February	143.7	June	238.9	October	203.0
March	193.4	July	243.1	November	167.4
April	216.0	August	216.9	December	160.6

These records yield the result that the normal annual percentage of sunshine is low compared with that in much of the territory of the United States, especially west of the Mississippi River; but it is not much less than that prevailing in other parts of the Southeastern States, while it exceeds the percentages given for the northern portion of the Atlantic slope.

ATMOSPHERIC HUMIDITY.

This is stated in percentages of possible saturation, which of course varies at different seasons with the temperature, etc. Annual (for a period of seven years), 81.4 as compared with 74 at Cape Henry, and 73 (during nine years) at Norfolk and Wilmington. Monthly, as follows:

Month.	Per cent.	Month.	Per cent.	Month.	Per cent.
January	84	May	82	September	81
February	81	June	83	October	81
March	79	July	83	November	79
April	80	August	82	December	82

The annual percentage thus shown is greater than that recorded for any other station in the United States, excepting those in the

[1] These figures only approximate the real values. They are derived from statistics of cloudiness.

Puget Sound region, and even there the excess over the Hatteras figure is not great. Moreover, this humidity is distributed throughout the months of the year with remarkable uniformity, the variation between any two months amounting to not more than 5 per cent.

PRECIPITATION.

This is stated in centimeters and inches. Annual, 159.4 centimeters (66.41 inches), as compared with 125.6 centimeters (52.34 inches) at Cape Henry, 125.0 centimeters (52.1 inches) at Norfolk, and 130.4 centimeters (54.34 inches) at Wilmington. Monthly, as follows:

Month.	Centimeters.	Inches.	Month.	Centimeters.	Inches.	Month.	Centimeters.	Inches.
January	14.2	5.91	May	11.0	4.60	September	15.4	6.44
February	10.7	4.47	June	10.9	4.57	October	14.8	6.17
March	14.6	6.10	July	15.4	6.43	November	12.4	5.18
April	11.3	4.72	August	15.2	6.35	December	13.1	5.47

The average annual number of rainy days is 123.8, as compared with 125 at Cape Henry, 131.3 at Norfolk, and 128.8 at Wilmington. The average monthly number of rainy days is as follows:

Month.	Days.	Month.	Days.	Month.	Days.
January	15.9	May	10.0	September	13.7
February	10.2	June	9.6	October	7.5
March	11.9	July	10.2	November	6.7
April	8.4	August	10.2	December	9.5

At Hatteras the precipitation consists almost entirely of rain. Rain-bearing storms usually approach from a westerly direction. Winter and spring rains are usually of light intensity and long duration, while those of the summer and fall are more often brief and torrential in character.

The results viewed comparatively are as follows: The normal annual rainfall is remarkably heavy, exceeding that at the nearest station, Wilmington, by 30 centimeters. Only on the coast of Washington and Oregon does the total rainfall within the limits of the United States notably exceed that of Hatteras. The normal variation between the month of least and that of greatest rainfall does not exceed 5 centimeters, so that in ordinary seasons periods of drought do not occur. The heaviest rainfall occurs in the months from July to October. The average number of rainy days is large, about one-third of the days of the year, and is distributed with relatively great uniformity, varying from 6.7 days in the month of least to 15.9 in the month of greatest number of rainy days.

Of dewfall no statistics could be obtained.

WIND.

The average annual maximum velocity of the wind is 21.4 kilometers (13.3 miles) per hour, as compared with 23.2 kilometers at Cape Henry, 15.1 at Norfolk, and 15.4 at Wilmington. The average monthly maximum velocities, stated in kilometers and miles, are as follows:

Month.	Kilometers.	Miles	Month.	Kilometers.	Miles	Month.	Kilometers.	Miles
January	25.0	15.5	May	20.3	12.6	September	17.2	10.7
February	24.5	15.2	June	21.3	13.2	October	18.4	11.4
March	25.2	15.6	July	18.5	11.5	November	19.8	12.3
April	24.2	15.0	August	19.7	12.2	December	24.0	14.9

In regard to direction, the winds of midwinter are usually from the north, while those of midsummer are usually from a little west of south.

As thus shown, the average velocity of the wind is considerable, and the amount of its variation from month to month is remarkably slight. The highest average of course prevails in winter and early spring. In midwinter, when the winds are normally strongest and therefore most affect the perennial, especially the woody vegetation, their prevailing direction is almost due south (from the north), hence, in the case of Ocracoke, from the mainland.

In regard to temperature, rainfall, and atmospheric humidity the climate of Ocracoke and Hatteras is suitable for a vigorous forest growth. But the exposure to strong winds, and the peculiar soil conditions, neutralize these favorable factors and give it a typical strand vegetation, which much resembles that of deserts. In the neighborhood of Norfolk and of Wilmington, where conditions of temperature and of humidity are really somewhat less suitable than at Hatteras to the most luxuriant development of plants, the virgin growth is almost everywhere dense forest, because there the inimical conditions are absent.

PHYSIOGRAPHY.

Ocracoke Island is part of that long chain of narrow sand reefs which fringes the southern Atlantic Coast of the United States, and which forms the eastern barrier to a series of almost land-locked bays and sounds. Ocracoke lies in longitude 76° west and latitude 35° 10′ north, and is therefore somewhat south of the center of the North Carolina coast. It is separated from Hatteras Reef by the 0.8 kilometer (one-half mile) wide strait known as Hatteras Inlet, and from Portsmouth, the next island below, by Ocracoke Inlet, 3 kilometers (nearly 2 miles) wide. Ocracoke itself is about 26 kilometers (16 miles) in length, and extends from that great bulge of the coast line known as Cape Hatteras, in a southwesterly direction. The island's greatest width near its lower end falls short of 3 kilometers; the average width is only 1 kilometer, while in places it is even narrower. Outside rolls the Atlantic, while between island and mainland stretch the waters of Pamlico Sound, here from 30 to 45 kilometers (18 to 27 miles) wide. Pamlico differs from the shallower Albemarle Sound to the north in the important respect that its water is always salt, while Albemarle is normally fresh.

Near the southwestern extremity of the island a broad expanse of tidal flat separates the higher land of the village of Ocracoke from the Atlantic beach. One and one-half kilometers or so toward the northeast this lagoon disappears, and dry land extends from the flat sandy beach and the salt marshes which border the Sound to the dunes which front the ocean. Into these marshes penetrate tiny creeks, whose ramifications cut the lower part of the island in all directions. Almost the whole area is divided between sand strand and tidal marsh. Much of it is only 1 meter or less above normal high tide and subject to overflow when strong easterly gales are blowing, or when stiff breezes from the opposite quarter mass the waters of Pamlico Sound against the western shore of the island. The highest land on Ocracoke is represented by sand dunes often 3, sometimes 8 meters high. These are usually regular in form and fairly well fixed by the vegetation. Those that abut upon the outer beach or rise amid the mud flats are particularly regular and dome-shaped.

GEOLOGY AND SOILS.

Of the geology of Ocracoke and its neighbor Hatteras, we have comparatively little knowledge. Shaler[1] has advanced the theory that these reefs were built up from the detritus which resulted from the glacial excavation of Delaware and Chesapeake bays. Kerr[2] describes Hatteras as a "sort of delta." "The action," he says, "of the tides and ocean currents, the Gulf stream and Arctic current meeting at this point, accumulates upon Hatteras the river silt which reaches the sea by way of the Chesapeake as well as that of the rivers which discharge their burdens through the inlets about this point and southward. * * * Hatteras is not a modern phenomenon It is at least as old as the Cretaceous; the Quaternary as well as the Tertiary of this coast region of North Carolina are laid down upon an eroded surface of Cretaceous rock." From measurements elsewhere made, the probable depth beneath the surface of the Cretaceous formation on Hatteras and Ocracoke would be somewhere between 200 and 300 meters. I am not aware that borings of any considerable depth

[1] Proc. Bost. Soc. Nat. Hist., vol. 14, pp. 110 to 121. 1872.

[2] Bul. Wash. Phil. Soc., vol. 6, pp. 28 to 30. 1884.

have been made upon these islands.[1] Kerr further states that "the reef is increasing in continuity and breadth." But this is not the general opinion, for it is said that there is to-day water of considerable depth where houses stood upon Ocracoke within the memory of living men, and it is stated[2] that "a fine fig orchard and many peach trees, with a fine potato patch and garden," occupied earlier what is now Hatteras Inlet. That the present tendency of this whole coast line is one of subsidence can hardly be disputed.

Beneath the superficial Recent deposits of dune sands and salt-marsh silt which cover the greater part of the island lie the sands and clays of the Columbia formation, which extend to a considerable but unascertained depth. This and the Recent accumulations are the only geological formations of this part of the coastal plain which need be considered in relation to the existing plant covering.

Excepting the areas occupied by creeks and salt marsh, the soil of Ocracoke is a fine white marine sand, almost everywhere devoid of any considerable admixture of humus. Only in the live-oak groves is there enough vegetable matter present to give the sand a gray color. There is doubtless some quantity of calcium carbonate in the soil, owing to the presence of small particles of shells washed up by the waves and scattered by the wind.[3]

As much of the island is subject to occasional inundation and to the deposition of spray by the winds, the soil content of sodium chlorid must be considerably greater at times than in ordinary inland soils.[4] There is no lack of moisture in this sandy substratum. Even in the driest looking beach sand, water usually stands at a depth of only 15 to 30 centimeters (6 to 12 inches) from the surface. The superficial layer of the sand acquires a great amount of heat on sunny days and becomes thoroughly desiccated, in which condition it is subject to being blown about by the wind, its degree of coherency depending upon the character of the vegetation. At night, however, sand gives up its heat rapidly and absorbs much dew, if conditions are favorable.[5]

The soil of the salt marsh, which appears to be usually a thin sheet

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[1] The succession of strata in the North Carolina coastal plain, where exposed in the valleys of the Neuse and Cape Fear rivers, is given as follows, beginning with the oldest:

(1) Potomac gravel, sands, and clays.
(2) Cretaceous sands and clays.
(3) Tertiary (Eocene and Miocene) marls and clays.
(4) Lafayette (yellowish and brownish sands and loams).
(5) Columbia sands, gravels, and clays.

[2] W. L. Welch, Bul. Essex Inst., vol. 17, pp. 37 to 42. 1886.

[3] According to Contejean (Géogr. Bot.), the proportion of calcium carbonate thus supplied to the strand soils is insignificant except near the wave limit, the particles being soon dissolved by the carbon dioxide contained in rain water and then washed down through the readily permeable soil.

[4] Sea water contains from 2.7 to 3.2 per cent of NaCl.

[5] Warming, Lehrbuch, p. 66.

of fine, brown silt overlying a stiff, bluish clay, contains organic matter in considerable quantity and is therefore capable of supporting a denser plant growth than is found upon the sands. It is of course saturated with salt or brackish water.

There is no outcrop of any kind of rock on the island.

THE PLANT FORMATIONS, THEIR COMPOSITION AND PHYSIOGNOMY.

The various assemblages of species and individuals which make up the plant covering of Ocracoke Island may be classified as follows:[1]

I. Sand-strand vegetation.
  1. Treeless (open).
    (*a*) Beach formation: Croton-Physalis association.
    (*b*) Dune formation:[2] Uniola-Yucca association.
  2. Evergreen trees and shrubs.
    (*a*) Tree formation: Quercus virginiana association.
    (*b*) Thicket formation: Ilex vomitoria association.

II. Salt-marsh vegetation.
  1. Creek-marsh (closed) formation.
    (*a*) Spartina stricta association.
    (*b*) Juncus roemerianus association.
  2. Dune-marsh formation: Lippia-Monniera association.
  3. Tidal flat (open) formation: Sesuvium-Tissa association.

III. Pastures and ruderal plants.

IV. Cultivated plants.

It is not to be supposed that the several groups are always or even commonly sharply defined. On the contrary the transition from one to another is almost always gradual, so that portions of the plant covering are difficult to classify. Nevertheless, the formations and associations are distinct features of the landscape, easily recognizable by any observer.

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[1] It has seemed best to use the word "formation" in the same sense as employed by the German and most other plant geographers—i. e., to designate the larger assemblages. For more restricted groups, whether composed of one or many species, the term "association" is to be preferred. The nearly equivalent German word "Verein" is used as a translation of the Danish "Samfund" in one of the most important works on the subject (Warming, Lehrbuch) for the larger assemblages or formations; but, in the want of a better English word it has been thought expedient to employ "association" for the more restricted assemblages, which are peculiar to each biogeographical area. While the formations are purely ecological elements which recur in the strand vegetation of other regions, being for the most part closely dependent upon topographical features, the associations are often quite local; and owe much of their character to the particular groups of species which compose them.

[2] It is not possible to distinguish here several dune formations, such as occur, for example, on the coast of Virginia.

SAND-STRAND VEGETATION.

TREELESS, OPEN FORMATIONS.

BEACH FORMATION.

This formation occurs along Pamlico Sound, occupying the flat or gently sloping sandy beach, especially toward the lower end of the island. The species are almost all herbaceous and usually form an open vegetation, leaving much of the soil uncovered. The most abundant is *Croton maritimus*, which sometimes grows rather closely, excluding other species. By reason of its silvery-gray color, due to a close, stellate, scale-like pubescence, it is one of the most conspicuous plants of the island. It is usually stout and often much-branched. Another noteworthy plant is *Physalis viscosa*, a perennial herb, with slender roots, sometimes 1.5 meters long, creeping near the surface of the sand, and sending up at intervals short leafy shoots. Its color varies from green to gray with the density of its covering of branched hairs. An interesting feature of this formation is the occurrence in places of diminutive thickets only 1 to 3 decimeters high, composed chiefly of *Ilex vomitoria* (*I. cassine* of authors), *Zanthoxylon clava-herculis*, *Juniperus virginiana*, with leaves only of the spreading form, and *Opuntia pes-corvi*, with its long spines. Among other species belonging to the beach formation, there are of annual herbs *Euphorbia polygonifolia*, *Triplasis purpurea*, a canescent form of *Solanum nigrum*, a large-fruited *Xanthium*, and *Salsola kali*, the last being the most abundant; of perennial herbs *Teucrium nashii*, with slender stolons and white-tomentous lower leaf surface, *Chloris petraea*, with decumbent culms, rooting at the nodes, *Panicum neuranthum*, and occasionally *Capriola dactylon* (*Cynodon dactylon* Pers.); of woody plants *Rubus trivialis* and *Smilax bona-nox* occur here and there, with prickly stems trailing over the sand.

DUNE FORMATION.

Open dunes are occupied chiefly by the handsome sea oats, *Uniola paniculata*, the most characteristic strand plant of the Southeastern States. The low, rounded dunes which rise from a bare pebbly shingle on the ocean side of the island, and here and there in the midst of the tidal flats, support no other vegetation. The leafy shoots of this grass are produced in great abundance, but flowering branches are much less numerous.[1] *Muhlenbergia filipes* is abundant on and among the dunes, its delicate purplish panicles, swaying with the lightest breath of air, presenting a most beautiful appearance. It is almost the only cespitose plant of the island, and grows in tufts that are sometimes 3 decimeters in diameter. Rather small

[1] In this respect the Uniola resembles *Ammophila arenaria*, which takes its place farther north.

plants of *Yucca gloriosa*, with fleshy rootstocks often exposed by the shifting of the sands, are frequent on the lesser dunes. The single specimen of *Yucca aloifolia* observed was over 2 meters high, with stem branched several times above the ground. Both species have exceedingly hard and sharp spinous leaf tips. On some of the higher dunes depauperate plants of the shrubby *Myrica carolinensis*, mostly only 3 to 6 decimeters high, associate with the Uniola. Of secondary importance in this association are two perennial grasses, *Panicum amarum minus* and *Spartina patens* (*juncea*); as well as a probably biennial thistle, *Carduus spinosissimus* (*Cnicus horridulus*); and several other herbs, among them the white-sericeous *Oenothera humifusa* and *Croton maritimus*.

EVERGREEN TREE AND SHRUB FORMATIONS.

TREE FORMATION.

Scattered over the island, but preferring the higher dunes which occupy its inner side, are small groves of live oak, *Quercus virginiana* (*Q. virens*), either in pure association or mixed with some other trees. The oaks are usually 6 to 9 meters high and 3 (rarely 7½) decimeters in diameter. Those on the northern edges of the groves have trunks strongly inclined toward the south, and, as a consequence of the denudation of the branches on the windward side, the whole crown of foliage lies to leeward of the axis. One could not desire a better indication of the prevailing direction of strong winds in the region.[1] The branches, gnarled and twisted, are clad with numerous lichens, chiefly *Usnea barbata*, and with occasional small wisps of Spanish moss (*Tillandsia usneoides*), which evidently maintains but a precarious foothold on the trees of this wind-exposed island.

Altogether the aspect of the groves is rather weird and somber. Often associated with the oaks are small trees of *Myrica cerifera*, *Zanthoxylum clava-herculis* and *Ilex vomitoria*, all of about the same maximum size (6 meters high and 2 decimeters in diameter), and occasionally *Juniperus virginiana*, which rarely attains a height of 9 meters and a diameter of 3 decimeters. Lianas are sparingly represented by *Smilax bona-nox*, *Vitis aestivalis*, and *Rhus radicans*, all three species sometimes attaining considerable size and climbing to the tree tops. The last is, however, usually of the creeping form, with the main stem underground. The herbaceous members of this association are, in the smaller groves, chiefly plants characteristic of the open strand, *Chloris*

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[1]All the specimens of live oak seen were apparently of considerable age. Seedlings were few or none, and no acorns were observed. It is probable that instead of increasing, the oak is here holding its ground with difficulty. So highly are the trees valued as wind-breaks by the inhabitants that none are felled, all fuel being brought from the mainland. The rounded shrubby form of this plant, common elsewhere on the coast, was not observed on Ocracoke.

petraea, *Physalis viscosa*, *Diodia teres*, etc., and the difference in soil and light is not sufficiently great to cause any apparent modification in the plants. In larger groves, where the light is more diffused and some humus collects, *Oplismenus setarius*[1] covers the ground with its creeping stems, associated with such normally shade-loving species as *Sanicula* sp., *Asplenium platyneuron* (*A. ebenoides*), *Uniola laxa* (*U. gracilis*), *Panicum laxiflorum* and two mosses, growing on the ground, *Bryum argenteum* and *Rhynchostegium serrulatum*.

THICKET FORMATION.

Thickets of *Ilex vomitoria*, by far the most abundant woody plant of Ocracoke Island, often cover the low dunes, especially near the inner side of the island. The plants are here usually 10 to 20 decimeters high, with short, rigid, thorn-like branches, light-gray bark, thick evergreen leaves and bright scarlet berries. The branches are often shaggy with lichens, notably *Ramalina montagnei*. Occasionally the Ilex gives place to small, dense thickets of *Myrica carolinensis*, sometimes 4½ meters high. This formation corresponds in a measure to the "Maquis" or "Garrigues" of the western Mediterranean region.[2] The herbaceous species that have established themselves among these shrubs are chiefly such as are most abundant on the beach and open dunes. Two thin-leaved, shade-loving herbs are occasional, *Parietaria debilis* with weak, much-branched stems, and *Melothria pendula*, with twining stems.

SALT-MARSH VEGETATION.

CREEK-MARSH FORMATION.

Salt marshes fringe all the small creeks and ditches that intersect the lower part of the island, and sometimes cover broader tracts immediately bordering the sound with a growth that is almost everywhere dense and reed-like. Two rather sharply defined belts are distinguishable along the larger creeks, an outer, covered chiefly with *Spartina stricta*, and an inner, where *Juncus roemerianus* predominates. The latter alone occupies the small creeks and ditches which are farthest from the beach.

SPARTINA STRICTA ASSOCIATION.

The Spartina prefers the edge of open water, where it is in large part submerged at high tide. It has a light, yellow-green color during the growing season, but is brown and discolored much of the year. The stems are usually about 6 decimeters high. *Salicornia herbacea*, often bright red and conspicuous, grows rather abundantly with the

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[1] In southern Mississippi, also, I found this species growing only in the shade of *Quercus virginiana*.

[2] Compare Grisebach, Veg. der Erde, vol. 1, pp. 294, 328, etc.

grass.[1] *Distichlis spicata* (*D. maritima*) usually accompanies this association, but is not of primary importance.

JUNCUS ROEMERIANUS ASSOCIATION.

The Juncus roemerianus association occupies much more ground than that of Spartina, and comprises a much larger number of species. It is best developed on land that is merely wet a great part of the time, and covered with, at most, only a few centimeters of water at high tide. The Juncus is of a dark-green color, and usually reaches a height of about 1 meter, making a dense growth of stiff, sharp-pointed stems and leaves. Among the secondary members of this association certain grass-like plants occur locally in some quantity. Notable are *Chaetochloa imberbis perennis*, with weak, slender culms from short, knotted rootstocks, preferring the borders of the marsh, and *Typha latifolia*, usually standing in water of some depth. *Spartina patens* (*S. juncea*) is occasional, the salt-marsh form being smaller and more slender than that which grows upon the sand strand. *Paspalum distichum* and *Distichlis spicata* are also met with in more open places among the Juncus.

Compositae, with mostly rather succulent leaves, are conspicuous, especially near the margin of this association. *Aster tenuifolius*, a slender rush-like perennial species whose few branches terminate in solitary, rather large heads with showy white rays, is less abundant than the related *Aster subulatus*, a much-branched, often rather stout annual with numerous inconspicuous heads. *Solidago sempervirens* and *Baccharis halimifolia* are most at home on the edge of the Juncus growth. Both are showy plants, the latter with bright white pappus, the former with a golden-yellow panicle. *Borrichia frutescens*, one of the most characteristic plants of the strand, prefers comparatively open spots where the ground is merely wet. It has a stout stem, usually 3 to 6 decimeters high, thick whitish leaves, and yellow sunflower-like heads. *Iva frutescens* is the most abundant composite of the marshes, almost always associating with the Juncus. Two climbing plants, *Galactia volubilis* (*G. pilosa*) and *Vincetoxicum palustre*, a glabrous, narrow-leaved asclepiad, occur near the edges of the marsh, twining around the stems of the rushes and other plants. *Atriplex hastata* is occasional in similar situations. Even *Ilex vomitoria* sometimes strays into the marsh, growing among the Juncus as a low straggling shrub.

Somewhat different is the assemblage of species about the small pools that frequently interrupt the growth of *Juncus roemerianus*.

[1] Likewise in southwestern France, *Spartina stricta* and *Salicornia herbacea* form the outermost association in soil that is submerged at high tide. (Contejean, Géogr. Bot., p. 56.) According to Warming (Lehrbuch, p. 307) *Salicornia herbacea* grows unmixed with other species as the outermost embryophytic vegetation on the eastern shores of the North Sea. *Spartina stricta* does not range so far north in Europe.

Their borders are the favorite habitat of a characteristic malvaceous plant, *Kosteletzkya virginica*, which has rather thin, pubescent leaves and large rose-colored flowers. With it grow a species of Rumex, *Ipomoea sagittata*, *Solidago sempervirens*, *Cladium effusum* (a stout sedge with sharply saw-edged leaves), *Panicum walteri*, and, very conspicuous where it occurs, *Andropogon glomeratus* (*A. macrourus*). In the shallow water of these pools grows *Monniera monniera* (*Herpestis monniera* H. B. K.) in its aquatic, partially submerged form with elongated stems, as well as *Ammannia koehnei*, *Pluchea camphorata*, and a species of Eleocharis.

DUNE-MARSH FORMATION.

A low, rather scanty vegetation covers limited areas of wet sand which fringe the reed marsh, separating it from the dry strand, and also occurs here and there in depressions among the dunes. The most characteristic species are the terrestrial form of *Monniera monniera* with short internodes, and *Lippia nodiflora*, both having repent stems rooting at frequent intervals and leaves usually appressed to the ground. In the case of Lippia, however, the leaves are sometimes nearly vertical in strong sunlight, giving the plant a peculiar appearance. Each of these species sometimes occupies small tracts to the exclusion of other vegetation. They usually grow together, however, and in association with *Hydrocotyle umbellata*, *Centella asiatica*, and *Diodia virginiana*, all small plants with creeping or prostrate stems. Among the dunes Lippia and Herpestis sometimes play a less important part, and an assemblage of species, some of which are not normally halophilous, covers the ground. Of these *Juncus dichotomus*, *J. scirpoides*, *Scirpus americanus* (*S. pungens*), *Triglochin striata*, and *Mikania scandens* are more at home in saline soils, while *Ludwigia microcarpa*, *L. alata*, *Cynoctonum mitreola* (*Mitreola petiolata*), and *Dichromena colorata* (*D. leucocephala*) are character plants of the fresh-water marshes of the region. Such commingling is perhaps to be explained by the fact that these hollows among the dunes derive their moisture largely from the rainfall, while, on the other hand, spray-laden winds contribute a certain amount of salt to the soil.

TIDAL FLAT FORMATION.

This is an open formation, occupying the margins of the shallow lagoon at the lower end of the island, which is under water at flood tide. The soil is a mixture of silt and sand. A sparse growth of *Sesuvium maritimum* (*S. pentandrum*), *Tissa marina* (*Lepigonum salinum*), and *Scirpus americanus* forms a characteristic association. *Paspalum distichum*, with prostrate culms, sometimes 2 meters long, rooting at the nodes, as well as scattered erect tufts of *Fimbristylis spadicea*, were the only other species observed in this formation.

PASTURE AND RUDERAL PLANTS.

A considerable area towards the lower end of Ocracoke, especially in and near the village, is covered with a fine turf composed almost entirely of *Capriola dactylon*, closely grazed by horses, cattle, and sheep. Here and there over these pastures are scattered groups of various weeds, notably *Cassia occidentalis*, *Sporobolus indicus*, and *Solanum carolinense*, as well as a species of *Xanthium*, *Bidens bipinnata*, *Chenopodium anthelminticum*, *Ambrosia artimisiaefolia*, *Verbascum thapsus*, etc., all of which have undoubtedly been imported into the island by the agency of man. Occasionally, strays from the indigenous formations are met with here. Fleshy fungi are sparingly represented.

CULTIVATED PLANTS.

As far as was ascertained, the only plants now cultivated upon the island are fig trees (*Ficus carica*), which are planted about dwellings and freely mature their fruit in this mild climate. Small paper mulberry trees (*Broussonetia papyrifera*) are established in door yards. According to a statement above quoted, peach trees and potatoes were formerly grown. Attempts to cultivate garden vegetables are usually terminated by inroads of the sea during a gale, which leave the soil strongly impregnated with salt.

ECOLOGICAL FORMS AND ADAPTATIONS TO ENVIRONMENT.

In considering the physical environment of plants upon Ocracoke Island, and the various modifications of the vegetative organs whereby they are adapted to their medium, it is evident that many of the latter fall readily into two categories: (1) Adaptations protecting against the mechanical action of the wind[1] and the unstable nature of the soil; and (2) modifications that assist the plant to increase or conserve its supply of water. Sand-strand and salt-marsh species alike require both sorts of modifications, although the latter formation is less exposed to wind and the shifting of its substratum. However, not only the vegetation upon loose sand, but that which covers the muddy bottom of the salt marshes, must accommodate itself to a more or less incoherent and mobile soil. To the first category are to be referred most of the noteworthy life forms of the island, i. e., those in which the epharmonic peculiarities of structure (such as are due to the direct action of the physical environment) extend to the entire organism. To the second belong chiefly modifications of a particular organ, the leaf.

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[1]The exposed position of the island, and its consequent relative poverty in large woody growth, renders herbaceous vegetation here more than usually subject to the action of the wind.

ADAPTATIONS TO THE MECHANICAL ACTION OF THE WIND AND THE INSTABILITY OF THE SOIL.

A notable characteristic of the vegetation is the prevalence of low forms. Tall stems (more than 1 meter high) among herbaceous species which are not grass-like, are almost wanting. Often the stems creep above or below the surface of the ground and root at intervals.

Lippia nodiflora, *Monniera monniera*, *Capriola dactylon*, and *Paspalum distichum* have stems creeping upon the surface. These may be regarded as humble representatives of the Pes-caprae form, which is so characteristic of tropical strands.[1] Species possessing creeping subterranean stems, from which arise subaerial leafy and flowering branches, are *Panicum amarum minus* and *Uniola paniculata*, as well as many of the salt-marsh plants, notably *Juncus roemerianus*, *Typha latifolia*, and *Spartina stricta*, whose strong, creeping rhizomes form a dense sod in the loose mud. In *Uniola paniculata* the rootstock is stout and descends obliquely or almost vertically deep into the sand. *Physalis viscosa* has a long, slender, branching root, which creeps horizontally often a distance of a meter or more near the surface, and originates at intervals erect, leafy and flowering branches. *Teucrium nashii* possesses thickish stolons, which arise in the axils of the scale-like, lowest leaves.

Other species growing on the sands have prostrate stem branches, which do not root after leaving the main axis. These may be long and trailing, as in the woody *Rubus trivialis*, or short and radiating in all directions from the primary axis as in certain annuals, *Diodia teres*, *D. virginiana*, *Mollugo verticillata*, and *Euphorbia polygonifolia*, as well as the biennial *Oenothera humifusa*. This radiant form,[2] as we may term it, is not so abundant and characteristic here as at other points along the Atlantic coast of the United States.

The cespitose form is apparently not well adapted to conditions upon Ocracoke, for it is well developed only in *Muhlenbergia filipes*.

The shrubs and trees of the island show the effect of much exposure to high wind in their short gnarled branches and in the often one-sided position of their crown of foliage, the last peculiarity being especially noticeable in the live oak. Here, however, we have to do rather with the direct mechanical effect of the wind than with a protective modification.

As further adaptations against the coast winds, whose destructiveness to tender vegetation must be greatly increased by the quantity of sand they carry, should be cited the great development of mechanical tissue in the leaves of many species—e. g., *Uniola paniculata*, *Juncus roemerianus*, *Quercus virginiana*—and the strong thickening of the outer cell walls of the epidermis, to which is due the hard pol-

[1] Schimper. Indo-Mal. Strand-flora, p. 78.

[2] Schimper (Strand-flora, p. 81) describes this form as occurring in the East Indian strand vegetation.

ished surface exhibited by the larger grass-like plants and by the evergreen leaves of *Quercus* and *Ilex*. This last peculiarity is, however, doubtless primarily induced by the necessity for protection against loss of water.

ADAPTATIONS FOR PROTECTING THE SUPPLY OF WATER.

Strand plants upon Ocracoke Island, unlike desert plants, are not to any noteworthy extent equipped with special apparatus for collecting or for storing water, if we except the development of water-storage tissue in several of the salt-marsh species. The obvious reason is the absence of a period of drought, there being at all times a relatively high percentage of water in the air and the soil. On the other hand, both maritime and desert vegetations are characterized by certain peculiarities of structure, especially of the leaves, which are usually denominated xerophytic, albeit these are less strikingly developed in strand plants than in those which inhabit deserts. Such common points of resemblance are, as is well known, due to a common necessity for protection against excessive loss of water by transpiration from the leaves, and this despite the abundant supply of water in the environment of strand plants.

In the case of salt-marsh vegetation it is chiefly the presence of a comparatively high percentage of sodium chlorid in the soil water which necessitates a xerophytic structure. Just how this salt reacts upon the life processes of plants and what the precise mode is by which plants protect themselves against its injurious effects are much mooted questions.[1]

[1] Contejean (Géogr. bot., pp. 71, 94) holds that salt is harmful to most plants; that it is not indispensable even to strand plants, and that the latter are confined to an otherwise unfavorable habitat merely by their inability to compete in the struggle for existence with the salt-shunning species of nonsaline soils. That this view is only partially correct is suggested by the known tendency of halophilous (salt-loving) species to take up greater quantities of sodium chlorid, even when grown in nonsaline soils, than do plants which are not halophilous.

Schimper (Strand-flora, pp. 25, 26) attributes to the accumulation of sodium chlorid in the green tissue an injurious effect upon assimilation, particularly upon the production of starch and sugar. More recently (Pflanzengeogr., p. 100) he modifies this view, but still emphasizes the importance of a chemical action of the salt upon metabolism, the synthesis of proteids being the process chiefly affected.

In order to reduce this deleterious action to a minimum, the accumulation of sodium chlorid in the tissues must be as far as possible retarded. This is accomplished, according to Schimper's theory, by diminishing root osmosis and hence the volume of the ascending column of water holding the chlorid in solution, this end being secured by means of certain modifications of leaf structure that reduce the volume of transpired water. Besides this chemical effect, Schimper also admits a direct physical influence which the presence of common salt in the soil exerts upon the process of osmosis. As Sachs (Landw. Versuchsst. vol. 1, p. 223) demonstrated by experiment, the roots of ordinary plants take up with difficulty water which holds in solution sodium chlorid (as well as other salts, notably calcium sulphate), a difficulty that of course increases with the concentration

Factors in the physical environment of sand-strand vegetation which tend to accelerate transpiration from the surface of the plant, and hence contribute to the necessity for xerophytic structure, are:

1. Exposure without shelter to the almost continual and often violent movement of air currents, which keep the plant's atmospheric envelope constantly changing and prevent it from approaching a condition of saturation.

2. Intense light, both direct and reflected from the surface of the sand. Light, which becomes converted into heat in the chlorophyll tissue, increases transpiration [1] in proportion to its intensity. Besides this effect of light, its direct and harmful action, when too intense, upon the chlorophyll is to be guarded against, and this is probably effected by some of the modifications which also serve to reduce transpiration. But in the present state of our knowledge it is impossible to discriminate between the respective modifications which protect the plant against these two effects of light.

3. Great heat during a great part of the year. Much more intense than the atmospheric heat is that which is absorbed by and reflected from the superficial layer of sand.[2]

It is probable, however, that the presence of a high percentage of sodium chlorid in the substratum is at least as effective as any of these causes in bringing about xerophytic structure. This is evident

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of the solution. Whether this is equally true of halophilous species is not established.

L. Diels (Jahrb. Wiss. Bot. vol. 23, p. 316) doubts that osmosis in plants of saline soils is sufficiently reduced to account for the absence of accumulations of salt to an injurious extent in the tissues. He found that salt-marsh plants when transferred to distilled water showed a steady loss of salt from day to day, although the impossibility of an excretion of the sodium chlorid as such could be demonstrated. This author gives a number of analyses of halophilous species which would indicate that in plants of that character the cells are enabled to decompose the accumulated sodium chlorid, the sodium probably uniting with malic acid, while the chlorin possibly combines with water and passes off through the roots as hydrochloric acid. It is known that xerophytic modifications which protect the plant against excessive transpiration at the same time cause an increased evolution of free acids (notably malic acid) in the green tissue, by preventing the ready access of oxygen and otherwise hindering the exchange of gases between the plant and the atmosphere. These researches of Diels, if confirmed for halophilous plants generally, will prove an insuperable objection to Schimper's theory that such plants can prevent an indefinite accumulation of sodium chlorid in their tissues only by reducing root action and hence transpiration. If we accept Diels's conclusions, we should have to refer the xerophytic structure of halophilous plants largely to its efficacy in preventing a free exchange of gases between plant and atmosphere, thus rendering imperfect the combustion of carbohydrates in the plant tissues and occasioning the production of considerable quantities of organic acids, which serve the plant by decomposing the absorbed sodium chlorid.

[1] Wiesner, Untersuch., p. 506.

[2] Volkens (Fl. Ægypt., p. 14) found a difference of from 22° to 24° C. between the temperatures of the surface soil and of the atmosphere in the shade near Cairo, in Egypt, the maximum heat of the sand being 55° C.

when we examine the salt-marsh vegetation. Most of the species of that formation, even those which are wholly or partially submerged at high tide, possess such structure. No plants of the North Carolina strand are more conspicuously xerophytic in structure than *Salicornia herbacea* and *Spartina stricta*. That such structure is closely related to the ability to take up NaCl in considerable quantities is proved by the fact that certain species which do not naturally inhabit saline soils, but which possess strongly developed modifications against excessive transpiration, can absorb that salt in quantities that are fatal to plants not so constituted.[1]

For this reason species belonging respectively to the sand strand and to the salt marsh of Ocracoke Island are not distinguished in the following enumeration of the means by which transpiration is reduced.

1. Reduction of the transpiring surface.

(*a*) Leaves small: *Ilex vomitoria* (smallest-leaved of our species of Ilex), *Galactia volubilis* (unusually narrow-leaved form), *Vincetoxicum palustre*, *Tissa marina* (leaves hemicylindrical), *Monniera monniera*, *Lippia nodiflora* (leaves notably smaller than in nonsaline soils), *Sesuvium maritimum*, etc. Most of the species enumerated have small or narrow leaves as compared with the nearest related inland forms.

(*b*) Leaves scale-like, their functions transferred to the stem, which is succulent; stem succulents: *Opuntia pes-corvi*, *Salicornia herbacea*.

(*c*) Leaves conduplicate or involute, especially in dry, sunny weather, so that only the dorsal surface is exposed: All the grasses, and *Cladium effusum*, *Fimbristylis spadicea*, and other sedges. In the grasses this characteristic is correlated with the position of the stomata, which lie at the bottom of furrows, especially on the unexposed ventral surface, and are further protected from air currents by a network of hairs which line the walls. In *Quercus virginiana* the leaf margins frequently become more or less revolute.

(*d*) Leaves perfectly terete and in structure little differentiated from the stem: *Juncus roemerianus*.

2. Position of the transpiring surface, leaves vertical or nearly so: Many of the grasses and sedges, *Typha*, *Juncus roemerianus*, *Triglochin striata*, young leaves of *Yucca* spp., *Lippia nodiflora* (sometimes), *Vincetoxicum palustre* (leaves reflexed), the Compositae.

3. Development of protective modifications in the epidermis.

(*a*) Thickened cuticle: Many species, notably the larger grass-like plants and woody species with evergreen leaves. A shining upper leaf surface, as in *Ilex vomitoria*, may be of use by reflecting some of the incident light rays, as has been suggested by Wiesner.

(*b*) Waxy covering: *Panicum amarum*, *Uniola paniculata*, *Euphorbia polygonifolia*, etc. This character is but slightly developed in the vegetation of Ocracoke Island.

(*c*) Hairy covering: *Oenothera humifusa* and *Teucrium nashii* (hairs long, simple); *Quercus virginiana* (stellate hairs on the dorsal surface only); *Kosteletzkya virginica* and *Croton maritimus* (hairs stellate, scale-like); *Physalis viscosa* (hairs forked); *Borrichia frutescens* (young leaves very densely covered with short hairs, giving the surface a glistening appearance). Interesting hairs also occur on other species, but not in sufficient numbers to serve as a protective covering (except in the leaf furrows of certain Gramineae).

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[1] Schimper, Pflanzengeogr., p. 99.

4. Succulency.

(*a*) Stem succulents: *Opuntia pes-corvi*, *Salicornia herbacea*.

(*b*) Leaf succulents: *Yucca* spp., *Tissa marina*, *Sesuvium maritimum*, *Euphorbia polygonifolia*, *Vincetoxicum palustre*, *Aster subulatus*, *A. flexuosus*, *Solidago sempervirens*—mostly salt-marsh species. Not only does the increase in thickness of the leaf serve directly as a protection against excessive loss of water, but the thickening tissue consists, in most cases, of colorless, water-storage parenchyma, which is peculiarly tenacious of its water supply.

5. Structure of the chlorenchyma.

Nearly all the species, of both sand strand and salt marsh, are characterized by the development of palisade, a compact chlorophyll tissue with cells more or less elongated at a right angle to the surface and occupying the exposed face or faces—i. e., the ventral face in bifacial leaves, both faces in such as are isolateral. Such tissue is believed to have, among other functions, that of protecting against excessive loss of water the remainder of the leaf (the interior, or the lower face, as the case may be), which is usually occupied by less compact tissue.

6. Aromatic, volatile oil.

An oil of this character is secreted by the species of Myrica. It has been suggested, although the idea needs substantiation, that the possession of such oils affords protection against excessive loss of water by the formation about the plant of an envelope, which is less pervious to heat rays than is ordinary air. At any rate this is a frequent attribute of plants inhabiting very dry regions.[1]

Not to be interpreted as affording protection against excessive transpiration, yet perhaps largely due to the influence of conditions that necessitate such protection, is the development of short, rigid, almost thornlike branches (*Ilex vomitoria*) and of prickles and spines (Smilax, *Rubus trivialis*, Opuntia, Zanthoxylum, leaf apices of the species of Yucca). Probably the depauperate form assumed by some of the woody species when growing on the beach is similarly explicable.[2]

Strong thickening of the under-ground parts for storage of reserve food materials does not occur in many species. The only notable cases detected were *Smilax bona-nox* (rootstocks with tuberous thickenings), *Yucca* spp. (rootstocks large, fleshy), and *Kosteletzkya virginica* (root stout, woody, vertical).

ANATOMY.

In almost all cases the histological structure of the leaf alone is here considered, that being the organ which shows most plainly adaptations to certain factors of the environment, notably those which affect transpiration. The general peculiarities of leaf anatomy in the vegetation of the sand strand and of the salt marsh, respectively, are first enumerated, and the resemblances and differences of plants of the two formation classes are pointed out. Several of the more important species of each category, in all thirty-two, are then

[1] Haberlandt, Pflanzenanat., p. 325. Volkens, Fl. Ægypt., p. 46.

[2] A like depressed habit is characteristic of shrubs growing above the limit of trees in high latitudes and altitudes. It is usually attributed to exposure to strong, dry winds, which is probably the chief factor in its development on the beach of Ocracoke Island.

taken up and described in systematic order. Tables showing what are believed to be the characters that are most important from an ecological point of view have been prepared for the two groups of species. For a number of species the material studied was not obtained upon Ocracoke Island, but from similar situations on the coast of Virginia, and in all such cases the source of the specimens used is mentioned. In some cases comparisons are made with related species, usually from other formations, in order to make clear the differential characters of the strand species.

In a great majority of the sand strand plants the leaf is bifacial, the two species of Yucca being the only exceptions noted. In some species this specialization is imperfect, as in *Oenothera humifusa*. In other cases the differentiation of the two sides of the leaf is complete, as in *Quercus virginiana*. In most cases the leaf is thick as compared with the same organ in related nonmaritime species. Good examples are the evergreen, leathery leaves of *Quercus virginiana* and *Ilex vomitoria*, as well as the leaves of the two grasses, *Uniola paniculata* and *Panicum amarum*. A strongly thickened cuticle is an almost invariable character, and this is conspicuously wrinkled in a few species. The lateral walls of the epidermis cells are undulate in four species, viz, the comparatively thin-leaved *Chloris petraea*, *Teucrium nashii*, and *Physalis viscosa*, and the thick-leaved *Ilex vomitoria*.

Half of the species have stomata on both leaf surfaces, but in every such case they are especially protected—in the grasses by being situated in furrows; in the species of Yucca by being deeply sunken, and in Physalis, Oenothera, and Croton by a covering of hairs. In the woody species they are always on the dorsal or lower surface only, and in *Quercus virginiana* they are further protected by a hairy covering (as also in the herbaceous *Teucrium nashii*).

Hairs form a dense, protective covering on both leaf surfaces of Oenothera, Croton, and Physalis, which species have stomata on both surfaces: only on the dorsal surface in Quercus and Teucrium, agreeing with the position of the stomata on that surface only. In Quercus and Croton the hairs are pluricellular and stellate; in Physalis they are irregularly branched; in Oenothera and Teucrium they are elongated, unbranched, and unicellular. Teucrium also possesses short, glandular, capitate hairs.

The chlorophyll tissue is homogeneous in the monocotyledons of the sand strand, while in the dicotyledons it is more or less differentiated into palisade on the ventral side of the leaf and pneumatic tissue on the dorsal side. The palisade is mostly quite compact, but never of more than 3 and usually of only 1 or 2 layers.

Colorless parenchyma, which probably performs the function of water-storage tissue, occurs in considerable quantity only in the grasses and the species of Yucca.

Stereome occurs subepidermally (especially in the leaf margins) in the Gramineae only. In most of the species of the sand strand, however, it is found as a support to the mestome bundles. These are furthermore reinforced by hypodermal collenchyma or collenchymatic tissue in most of the dicotyledonous species, this tissue probably serving as a protection against loss of water by evaporation from the vessels.

The sand-strand grasses deserve further mention with reference to their leaf structure. It belongs to a type of which *Chloris petraea* exhibits one extreme and *Muhlenbergia filipes* the other—the type exhibited by most grasses of deserts and steppes. The salt marsh *Spartina stricta* exhibits a wholly similar arrangement of tissues.

The margins are more or less conduplicate or involute when the supply of water is small, becoming flat when moisture is plentiful, except in the leaf of *Muhlenbergia filipes*, which is conduplicate, without power to unfold, and appears as if terete. The result of this adaptation is that in dry, sunny weather only the dorsal leaf surface is directly exposed to the air and light. In *Panicum amarum* and *Chloris petraea* the movement is effected by true bulliform cells, while in the other grasses (except, of course, Muhlenbergia) the function is probably performed by certain large but otherwise undifferentiated cells of the epidermis, which may be regarded as undeveloped bulliform cells.

The stomata lie near the bottom of deep longitudinal furrows and usually occur more abundantly on the protected ventral surface of the leaf, but in *Chloris petraea* only on the dorsal surface. The walls of these furrows, in Muhlenbergia, Uniola, and *Spartina patens*, are lined with unicellular, simple, prickle-like hairs, which doubtless hinder the escape of moist air.

Subepidermal groups of stereome occur in the leaves of all the grasses and in the margins of all except the Muhlenbergia. In this great development of strengthening tissue we have in all probability a protection against the mechanical effects of the wind, to which strand grasses are much exposed.

The chlorophyll tissue is in every case radially arranged in single layers around or at each side of each mestome bundle. In most cases the adjacent cells of the parenchyma sheath also contain chlorophyll.

Each mestome bundle is surrounded by a mestome sheath in all the species except *Uniola* and *Muhlenbergia*, and this by a large-celled parenchyma sheath. The parenchyma sheath without the mestome sheath occurs in *Muhlenbergia*.

Among the species of the salt marsh which were examined, the isolateral type of leaf prevails, *Kosteletzkya virginica* and *Lippia nodiflora* being the only exceptions, and in these the leaves are but imperfectly bifacial. In *Juncus roemerianus* the leaf is terete. Thick leaves are also the rule in this formation class, although less strikingly so than in the sand strand, because of the lack of large woody plants; and the thickened leaf is usually of a soft, succulent character rather than leathery. A majority of the species show a conspicuously thickened cuticle, which is strongly wrinkled in 7 out of 15 of them and granular or warty in 3 more.

Corresponding to the isolateral structure of most of the leaves we find stomata on both surfaces in 12 species; on the whole circumference of the terete leaf of *Juncus roemerianus*; confined to the ventral or upper surface only in *Spartina stricta* and *Borrichia frutescens*. In 4 species the guard cells are slightly prominent, in 7 level with the epidermis, in 3 slightly sunken, in 1 (*Spartina stricta*) situated near the bottom of deep furrows. Hairs occur in but 5 species. In Borrichia alone they form a dense covering, nearly every epidermal cell appearing to have developed a pluricellular, thin-walled hair by tangential division. It is evident that we have in this case an admirable protection against excessive transpiration.

Stereome occurs in notable quantity only in the leaves of *Spartina stricta* and *Juncus roemerianus*. In both it is subepidermal as well as about the mestome bundles. *Juncus roemerianus* is especially noteworthy for the strong development of both peripheral and axial stereome groups. Hypodermal collenchyma, or collenchyma-like tissue, occurs opposite the veins in two-thirds of the species examined.

The chlorenchyma is homogeneous in all but 2 species, and in 1 of these, *Lippia nodiflora*, the differentiation is slight. In nearly all the species it consists of compact palisade, interrupted in several cases by ducts or lacunes. In the leaves of most of the species there are only 2 layers on each side of the isolateral leaf, but in *Juncus roemerianus* the bands of well-developed palisade are 5 or 6 layers thick. In several of the Compositae, all decidedly halophilous species, the ends of the palisade layers where they abut upon the midvein converge toward the vein and appear as if radiating from it. This was observed in *Iva frutescens*, *Baccharis halimifolia*, and *Aster tenuifolius*, and may occur in other species. The significance of this arrangement is not known. It is cited by Warming[1] as a halophytic character. *Spartina stricta* agrees in the arrangement of its chlorophyll tissue, as in other respects, with the sand-strand grasses.

Colorless parenchyma, which probably serves for the storage of water, is present in greater or less quantity in 8 species, occupying the greater part of the interior of the leaf in 4, while occurring only about the veins in the others. In Borrichia, which is one of the most xerophytic in structure of all the salt-marsh species, this tissue is best developed. It is also well exemplified in *Tissa marina*.

In the 3 salt-marsh inhabiting monocotyledons examined—*Triglochin striata*, *Spartina stricta*, and *Juncus roemerianus*—each mes-

[1] Halofyt-Studier, p. 250.

tome bundle is provided with a well-marked mestome sheath and, outside that, a parenchyma sheath.

When we compare the species belonging to the two formation classes, sand-strand and salt-marsh, we find that a majority of both have several characters in common, all of which are distinctly xerophytic and are usually interpreted as protecting the leaf against excessive transpiration as well as the effects of too intense light. These are: Thickened leaves, thickened cuticle, and development of the chlorophyll tissue as compact palisade on the most exposed surface or surfaces.

More numerous, however, are the differential characters. The leaves of the sand-strand species are usually bifacial, with stomata only on the dorsal surface or, if on both surfaces, protected by a hairy covering or lying in deep furrows; and the palisade is situated on the more exposed upper or ventral side of the leaf. The salt-marsh species, on the other hand, have mostly isolateral leaves, vertical or nearly vertical in position, with stomata and palisade on both surfaces, and (with one exception) lacking the dense hairy covering. Conformably, the most common grass of the salt marsh, *Spartina stricta*, otherwise so similar in leaf structure to the dune form of *S. patens*, has no hairs lining its stomatal furrows. The cuticle is wrinkled or warty in many more salt-marsh than sand-strand species. Water-storage parenchyma, which is notably developed in the sand-strand vegetation only in the monocotyledons, is present in a majority of the salt-marsh plants of the most diverse relationship.

Corresponding to their growth in usually open formation, and consequently greater exposure to the wind, the sand-strand plants show a much stronger development of stereome than do the salt-marsh species. On the other hand, the latter are better provided with hypodermal collenchyma, or collenchymatic tissue, opposite the veins; but this may be more important as a protection against loss of water than as a mechanical strengthening tissue.

It should be emphasized that not only the peculiarities common to plants of the two formation classes, but likewise most of their respective differential characters, are really of a xerophytic nature.[1] In some cases, however, a different means has been employed by sand-strand species on the one hand and by salt-marsh species on the other to secure the same end—protection against excessive transpiration and the harmful action of too intense light.

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[1] In his most recent paper on the subject, Warming (Halofyt-Studier, p. 235) writes: "It is not possible, from the investigations here described, to draw any clear distinction between characters which are truly xerophytic and such as are truly halophytic, if any really exist." Schimper (Pflanzengeogr., p. 99) also holds that halophytes can not be distinguished as a class from xerophytes, since the principal object of the peculiarities of structure observable in plants growing in saline soil, however moist, is the reduction of transpiration, just as it is in plants surrounded by a physically very dry soil and atmosphere.

SPECIES OF THE SAND STRAND.

Panicum amarum Ell.[1]

Leaf bifacial, strongly involute when dry, midrib not prominent on the dorsal surface and not much so on the ventral surface, shallow furrows (deepest each side of the midrib), with broad and rounded intervening ridges on the ventral surface, corresponding to very slight depressions on the dorsal surface.

Epidermis: Ventral, similar to the dorsal, but with thinner outer cell walls; stomata at each side of the group of 3 thick-walled bulliform cells at the bottom of each furrow; hairs none. Dorsal with very thick, porous outer cell walls, 1 or sometimes 2 short cells alternating with long ones, except in the rows containing stomata; stomata lying in the shallow furrows, with walls of the guard cells much thickened; hairs none.

Subepidermal stereome in large groups above and below the midrib, that above separated from the hadrome by several layers of thickish-walled, colorless parenchyma; smaller groups above and below the other nerves; strongly developed in the margins.

Chlorophyll tissue (palisade) arranged radially in a single layer about each mestome bundle, almost completely encircling the smaller nerves, interrupted above and below the larger ones, each 2 neighboring rows of palisade separated by a single layer of colorless parenchyma; chlorophyll likewise occurring in the cells of the parenchyma sheath which adjoin the palisade.

Mestome bundles surrounded each by a mestome sheath which, in the larger veins, has all, or nearly all, of its cells with walls (especially the inner) strongly thickened; mestome sheath in turn surrounded by a large-celled parenchyma sheath; mestome parenchyma in a single layer of thick-walled cells separating the hadrome from the leptome.

Muhlenbergia filipes M. A. Curtis.[2]

Leaf (fig. 33) conduplicate without power to unfold, appearing as if terete, slightly asymmetrical, margins almost meeting above the midnerve, and hence only the dorsal surface exposed. From the slight opening between the margins to the midrib extends a narrow fissure, with lateral furrows between the larger nerves reaching more than halfway to the dorsal surface of the leaf. The ridges above the mestome bundles between these furrows are broad and rounded at apex, except that of the midnerve, which is narrowed outward (hence conical in cross section). On the dorsal (outer) surface are narrow,

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[1] The typical form of this species was not observed upon Ocracoke Island, but the leaf of var. *minus* Vasey & Scribner, which was collected there, corresponds in every detail to that of the type.

[2] Compare Volkens's figure and description of *Aristida ciliata* (Fl. Aegypt., pp. 49, 150, *t. 16, ff. 4 to 7*).

slit-like furrows between each 2 nerves (hence 2 to every ventral furrow), opening into wider air spaces with stomata at each side of the bottom. Stomata also occur near the bottom of the ventral furrows, but are there less numerous.

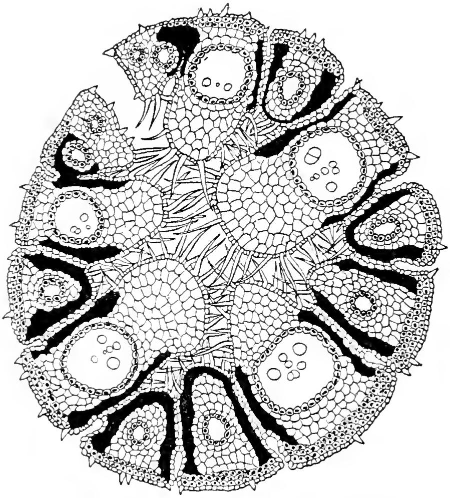

FIG. 33.—*Muhlenbergia filipes*—transverse section of leaf. Scale 75.

Epidermis: Ventral (fig. 34) with cell walls thinner than on the dorsal surface, many of the cells extended into straight or curved, spreading, unicellular hairs which line the main cavity and lateral furrows with a dense cross work, and are larger, thinner-walled, and more slender than those which occur on the dorsal surface; bulliform cells none. Dorsal (fig. 35) with smaller cells, the outer wall and cuticle so greatly thickened as nearly to equal the cell lumen, the areas lying above the subepidermal strands of stereome having single rows of short cells which alternate with several rows of long ones; many of the epidermal cells extended into short, stout, pointed, thick-walled, unicellular, appressed, prickle-like hairs, which line the furrows.

Subepidermal stereome: None on the ventral side of the leaf and in the margin;

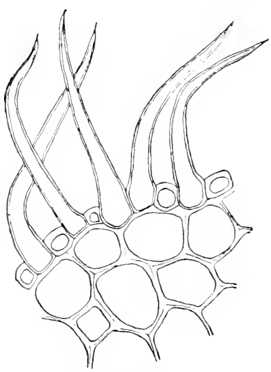

FIG. 34.—*Muhlenbergia filipes*—ventral epidermis of leaf. Transverse section, showing the hairs. Beneath the epidermis are layers of colorless parenchyma. Scale 400.

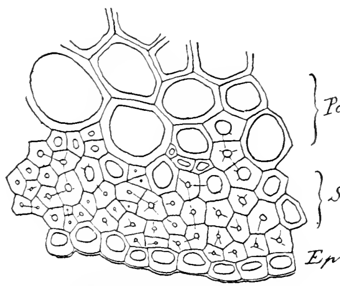

FIG. 35.—*Muhlenbergia filipes*—dorsal part of leaf blade. Transverse section showing the epidermis (Ep.), stereome (St.), and rather thick-walled colorless parenchyma (Pa.), which borders on the mestome bundle. Scale 400.

on the dorsal side in the form of flattened supporting strands[1] beneath the mestome bundles, passing gradually into the often

[1] "Abgeplattete Träger," Schwendener, Mechan. Princ., p. 40.

thick-walled, colorless parenchyma which separates it from the mestome sheath.

Chlorenchyma (fig. 36) consisting of small, branched cells with small intercellular spaces in a single layer radially arranged about each mestome bundle, lying only at the sides of the larger bundles, but extending in horseshoe form around the ventral (hadrome) portion of the smaller ones. Parenchyma sheath of the mestome bundles, where adjoining chlorenchyma, also containing chlorophyll.

Colorless parenchyma (fig. 36) occupying the larger ventral ridges (over the larger mestome bundles), and in 2 or 3 rows of cells between each 2 nerves, extending from the ventral to the dorsal furrows. Also in 1 or 2 rows separating the chlorenchyma from the parenchyma sheath of the smaller bundles.

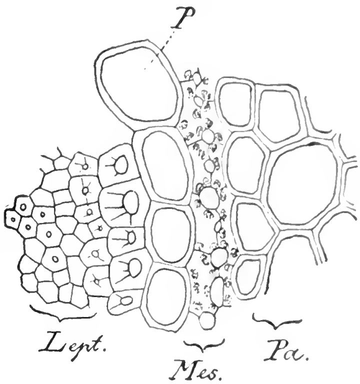

FIG. 36.—*Muhlenbergia filipes*—portion of mestome bundle. Transverse section of blade, showing a part of the leptome (Lept.), the parenchyma sheath (P), the chlorenchyma (Mes.), and the colorless parenchyma (Pa.) between the mestome bundles. Scale 600.

Mestome bundles (fig. 36) with a large-celled parenchyma sheath; mestome sheath none, but mestome parenchyma with cell walls (especially the inner) much thickened, surrounding the larger nerves, simulating a mestome sheath; many of the companion cells in the leptome very thick-walled.[1]

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[1] The two species of Muhlenbergia most nearly allied to *M. filipes* are *M. capillaris* (Michx.) Kunth and *M. trichopodes* (Ell.) Chapm. Chapman regards *M. filipes* as a variety of *M. capillaris*, but the striking histological differences, together with good morphological characters, show that in *M. filipes* we have a perfectly valid species.

A comparison of the leaf anatomy of the three forms gives some very interesting results:

(*a*) *M. capillaris* is a plant of dry sandy or rocky (eugeogenous) soils, but the leaf shows only feebly the strong xerophytic structure of *M. filipes*. Material from Great Falls, Md., was studied. Leaf thinner than in *M. filipes*, conduplicate when dry, but flat when well supplied with water. Ventral face not furrowed, furrows on the dorsal face extending nearly halfway through the leaf, with stomata at bottom.

Epidermis much as in *M. filipes*, but with bulliform cells between each 2 nerves; hairs much fewer than in *filipes*, all short, thick-walled, pointed, and prickle-like, occurring on the ventral face only above the nerves, on the dorsal face lining the stomata-bearing furrows and there thicker-walled, with hardly perceptible lumen.

Subepidermal stereome in flattened supporting strands above and below the mestome bundles, from which they are separated by thickish-walled, colorless parenchyma; and also in the leaf margins.

Chlorenchyma as in *filipes*, but entirely surrounding the smaller bundles, interrupted by colorless parenchyma above and below the larger ones. Also much chlorophyll in the cells of the parenchyma sheath which adjoin the chlorenchyma.

Mestome bundles with no true mestome sheath, but mostly surrounded by a sin-

SPARTINA PATENS (Ait.) Muhl.[1]

Leaf involute when dry, deeply furrowed between the nerves on the ventral face, high, broad, rounded ridges separating the larger

gle row of mestome parenchyma with cell walls thinner than in *filipes* and evenly thickened; mestome parenchyma also in a single layer between hadrome and leptome, and, with a few of the companion cells of the leptome, isolated or in groups of 2 or 3, very thick-walled.

(*b*) *Muhlenbergia trichopodes* is a plant of low, often moist, pine barrens in the Gulf strip of the Austroriparian area. The example here described was collected in Mississippi. It is in several histological characters intermediate between *capillaris* and *filipes*, although morphologically the most distinct of the 3 species.

Leaf conduplicate when dry, nearly flat when supplied with abundant moisture. Ventral surface with only the 2 or 3 nerves nearest each margin prominent and separated by deep furrows, the others, including the midnerve, barely projecting. Dorsal surface with narrow and rather deep furrows between the nerves.

Epidermis: Ventral with single rows of short cells alternating with several rows of long ones; hairs, chiefly in the furrows, shorter, stouter, and thicker-walled than in *filipes;* bulliform cells much as in *capillaris*, rather thick-walled. Dorsal with rather thick-walled cells (less so than in *filipes*), single, quadrangular (from above), short ones alternating with longer ones; hairs short, stout, thick-walled, prickle-like.

Subepidermal stereome rather more strongly developed than in *capillaris* and *filipes*, in flattened supports above and below the mestome bundles (hence at summit of the ventral ridges), strongest on the dorsal side, where it interrupts the parenchyma sheath of the larger nerves; also in the margins.

Chlorenchyma with cells as in *filipes*, radially arranged in single layers about the bundles, entirely encircling the smaller ones, in the larger ones perpendicular to the leaf surface and extending to the stereome at the summits of the ventral ridges (as in *Spartina stricta* and *Uniola paniculata*); parenchyma sheath and the large parenchyma cells above the mestome bundles also containing chlorophyll where they adjoin the smaller-celled chlorenchyma.

Colorless parenchyma (rather thick-walled) filling the interior of the ridges, and in a single row of large cells between each 2 nerves, separating their respective bands of chlorenchyma.

Mestome bundles without a true mestome sheath, but the larger ones surrounded by a layer of mestome parenchyma which is much thicker-walled than in the 2 related species; around the smaller bundles the mestome parenchyma thinner-walled and interrupted by 2 large vessels of the hadrome; mestome parenchyma also in 1 layer between hadrome and leptome, as in the other 2 species.

The important leaf characters of these allied species of Muhlenbergia may be tabulated thus:

[The sign × indicates presence of character.]

Species.	Unrolling when wet.	Always conduplicate.	Deeply furrowed on ventral surface.	Not deeply furrowed.	Midrib greatly projecting on ventral surface.	Midrib only slightly projecting.	Bulliform cells present.	Bulliform cells none.	Subepidermal stereome on both faces and in margins.	Subepidermal stereome only on dorsal face; none in margins.	Much colorless parenchyma above the mestome bundles.	No colorless parenchyma above the mestome bundles.
Capillaris	×	------	------	×	------	×	×	------	×	------	------	×
Trichopodes	×	------	×	------	------	×	×	------	×	------	×	------
Filipes	------	×	×	------	×	------	------	×	------	×	×	------

[1] Compare the figure of *S. versicolor* in Duval-Jouve. Étude Anat., *pl. 16, fig.* [illegible]

furrows, which are 2-cleft at bottom by the low ridges of the smaller nerves.

Epidermis: Ventral with cells much smaller and thinner-walled than on the dorsal surface; stomata on each side of the bottom of the furrows, somewhat prominent; many of the epidermal cells extended into short, rather thin-walled, erect, unicellular papillae with broad, rounded or truncate summits, and, especially at the summit of the ridges, into longer, sharp-pointed, thick-walled, erect, prickle-like hairs; typical bulliform cells none, but at the bottom of each furrow a group of usually 3 large epidermis cells, which are probably functionally homologous. Dorsal with thick, porous walls, which, in the rows containing stomata, are unevenly thickened so as to appear wavy, 1 or more often 2 short cells alternating with the longer ones; cuticle thick; stomata in very shallow furrows; hairs and papillae none.

Subepidermal stereome not as strongly developed as in most of the strand grasses, in small groups on the dorsal side of each nerve; in flattened supporting strands at the summit of each ventral rib and extending some distance down its sides; and in comparatively small strands in the leaf margins.

Chlorophyll chiefly in the parenchyma sheath of the mestome bundles, with a "bridge" of small-celled chlorenchyma connecting each two neighboring sheaths; palisade none.

Colorless parenchyma filling the ventral ribs above the mestome bundles where it interrupts the parenchyma sheath, a few cells also interrupting the parenchyma sheath on the dorsal side.

Mestome bundles surrounded by a mestome sheath whose walls (especially the inner) are much thickened only on the leptome side of the larger nerves; parenchyma sheath (enveloping the mestome sheath) containing chlorophyll, continuous about the smaller nerves, interrupted by colorless parenchyma above and below the larger ones; mestome parenchyma (thick-walled) in a single layer between the leptome and the hadrome of the larger bundles.

SPARTINA STRICTA (Ait.) Roth.[1]

Leaf conduplicate when dry, not furrowed on the dorsal surface, deeply furrowed on the ventral side, the furrows acute, the intervening ridges broad and truncate at summit.

Epidermis: Ventral with cells narrower and not so high as on the dorsal surface, the walls as in *S. patens*, except that the outer wall of each cell is covered with silicified papillae; stomata on each side of the bottom of the furrows; hairs none; typical bulliform cells none, but 1 to 3 epidermal cells at bottom of each ventral furrow somewhat larger than the others and probably functioning as bulli-

[1] Although this species belongs to the salt marsh, it is described here for the sake of convenient comparison with the other Gramineae. Compare Duval Jouve, Histotaxie, *pl. 18, fig. 5.* The Ocracoke plant is nearly of the typical form.

form cells. Dorsal as in *S. patens*, the short cells usually single, here and there rounded, with strongly thickened walls, almost forming papillæ; stomata none; hairs none.

Hypodermal colorless parenchyma in a single layer beneath the dorsal epidermis,[1] interrupted by subepidermal stereome.

Stereome not strongly developed, a small subepidermal group on the dorsal side of each mestome bundle; flattened supporting strands (1 or 2 layers) at the summit of each ventral ridge, not decurrent along its sides; also in the leaf margins.

Chlorenchyma consisting of small palisade cells in a single layer, radially arranged on each side of each mestome bundle and extending immediately beneath the epidermis to the stereome at the summit of each ventral ridge; each 2 neighboring layers of palisade, between each two nerves, either adjoining or separated by a few, large, colorless parenchyma cells; chlorophyll also in most of the cells of the parenchyma sheath.

Mestome bundles with mestome sheath and mestome parenchyma much as in *S. patens*. Parenchyma sheath (around the mestome sheath) of large cells, those adjoining the palisade layer containing chlorophyll, the sheath occasionally interrupted on the dorsal side of the bundle by a few cells of the subepidermal stereome. Large parenchyma cells, in 2 or 3 layers, occupying the thickness of the ventral ridges and appearing to be an extension of the parenchyma sheath; when in 3 layers, the middle one colorless.[2]

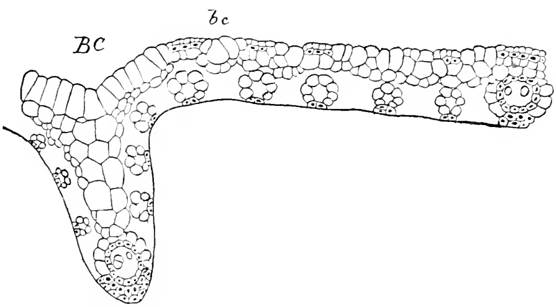

FIG. 37.—*Chloris petraea*—leaf blade. Transverse section, showing the midrib in the keel, covered by layers of colorless tissue and a group of bulliform cells (BC) on the ventral surface; *bc*, a small group of bulliform cells between two mestome bundles. The mestome bundles are indicated by their parenchyma sheaths and by the stereome, which forms small subepidermal groups. The thick walled mestome sheath is drawn only in the two large bundles. Scale 84.

CHLORIS PETRAEA Sw.[3]

Leaf (fig. 37) becoming conduplicate when

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[1] The specimen figured by Duval-Jouve, loc.cit., has 2 or 3 layers.

[2] *Spartina stricta maritima* (Walt.) Scribn., the common form elsewhere along our Atlantic coast, is practically identical in leaf anatomy with *S. stricta* from Ocracoke, except in the following particulars: The epidermis cell walls on the dorsal surface are thinner and less porous and show less of the wavy thickening; the short cells are more often in pairs, and, when single, are more often papilliform; stereome is somewhat more strongly developed, as would be expected from the larger size of the plant and the greater length of the leaves. The material examined was from Lynnhaven Bay, Virginia.

[3] Figured by Duval-Jouve, Histotaxie, p. 355, *pl. 18, f. 1.* For an example of similar leaf structure compare the same author's paper, "Étude histotaxique des Cyperus de France," Mém. de l'Acad. de Montpellier, tome 7, *pl. 22, f. 6.* 1874.

dry, strongly keeled on the dorsal face and slightly impressed ventrally opposite the midvein, with a large mestome bundle at the apex of and 3 smaller ones on each side of the keel. Hairs none.

Epidermis: Ventral, differentiated as bulliform cells in a rather wide band above the keel and in 2 small groups of about 4 cells each, 1 between the first pair of nerves on each side of the keel; elsewhere pluricellular (3 or 4 layers) and occupying more than one-half of the thickness of the leaf, except above the larger nerves, thin-walled (except the outer wall of the outermost layer) and large (except the single outermost layer where it lies above the subepidermal groups of stereome); stomata none. Dorsal epidermis one-layered, with cells all small, the outer wall and cuticle much thickened, radial walls thin, undulate, one row of short cells with strongly silicified walls alternating with several rows of long ones, many of the cells developed into rounded, not silicified, papillae; stomata in the strips of epidermis which lie between the nerves, level with the epidermal surface.

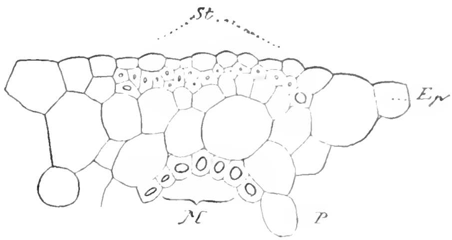

FIG. 38.—*Chloris petraea*—ventral portion of leaf blade. Transverse section, showing epidermis (*Ep*) and subepidermal stereome (*St*); at *M* the mestome sheath of a bundle, bordering on layers of colorless parenchyma. Scale 240.

Subepidermal stereome (fig. 38) in flattened supports above and below the mestome bundles, that on the ventral side in 1 or 2 layers above the larger nerves, reduced to small groups (sometimes only 2 cells) above the smaller ones; on the dorsal side supports stronger, sometimes 3-layered; also in the leaf margins.

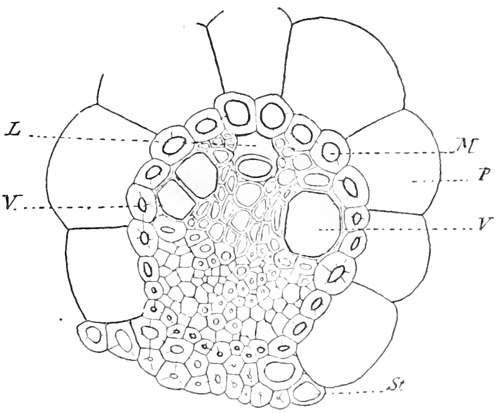

FIG. 39.—*Chloris petraea*—large mestome bundle from leaf blade. St, stereome of lower face of blade, bordering on the mestome sheath (M), which encircles both the leptome and hadrome as a closed sheath of thick-walled, porous cells. Bordering on the mestome sheath is a green parenchyma sheath (P). VV, vessels; L, lacune with an annular vessel. Scale 560.

Chlorenchyma, palisade, arranged radially in a single row of cells on each side of each mestome bundle, with a "bridge" of small-celled chlorenchyma, containing usually a few cells of colorless parenchyma, connecting each 2 neighboring rows; chlorophyll likewise in the parenchyma sheath where it adjoins the palisade.

Mestome bundles each inclosed by a mestome sheath (figs. 38, 39, 40) which has small cells with equally thickened walls; parenchyma sheath with large, thin-walled cells containing chlorophyll where they adjoin the palisade; mestome parenchyma in a single layer separating the hadrome from the leptome of the larger bundles; companion cells of the sieve tubes with much thickened walls.

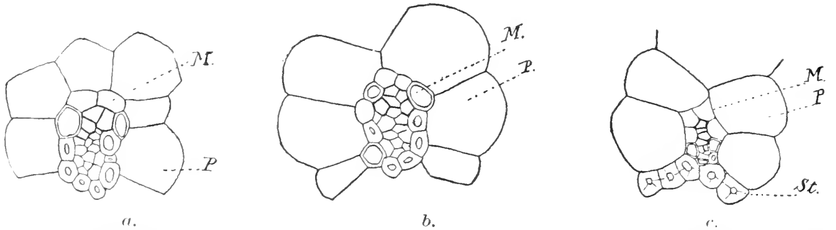

FIG. 40.—*Chloris petraea*—three small mestome bundles from the blade. (Letters as in fig. 39.) In *a* the mestome sheath is thick-walled only on the leptome side; in *b* and *c* the thickening of the mestome sheath is more distinct and begins to show also on the hadrome side. The sheath is closed in all of these small bundles and is a true mestome sheath. Scale 560.

UNIOLA PANICULATA L.[1]

Leaf rather thick and hard, more or less involute when dry, deeply furrowed on the ventral surface, the intervening ridges broad and truncate or but slightly rounded at summit; dorsal surface with very slight corresponding depressions.

Epidermis: Ventral with cells smaller and thinner-walled than on the dorsal surface, the outer walls more arched, many of the cells, especially on the sides of the furrows, extended into short, stout, pointed, unicellular, antrorse, prickle-like hairs with cuticle rough and excessively thickened (lumen almost obliterated except toward the base); stomata near the bottom of the ventral furrows; bulliform cells in very small groups at the bottom of the furrows. Dorsal with conspicuously pitted walls and very thick,[2] strongly wrinkled cuticle, 1 or sometimes 2 or 3 short cells alternating in the same rows with long ones; hairs none; stomata less numerous than on ventral surface.

Stereome strongly developed (more so than in any other of these strand grasses); strong, flattened subepidermal supports at the summits of the ventral ridges, separated from the mestome bundles by thin-walled colorless parenchyma which also contains small, isolated groups of stereome; narrow, mostly 2-layered subepidermal groups on the dorsal side opposite the ventral furrows; strong subepidermal supports on the dorsal side of each mestome bundle; finally, strong marginal groups.

Chlorenchyma: Palisade small-celled, radially disposed on each side of each mestome bundle in single layers, which are perpendicular to

[1] Compare Holm, Bot. Gaz. vol. 16, *pl. 22, ff. 8 to 12*, 1891.

[2] But much less so than in Holm's material from Fort Monroe, Va.

the leaf surface and extend nearly to the summit of the ventral ridges; inside the layer of palisade, and parallel to it, is a single layer of large, thin-walled parenchyma cells containing chlorophyll, which represents an imperfect parenchyma sheath to the mestome bundles.

Colorless parenchyma in several layers which lie below the ventral furrows and separate each two neighboring layers of palisade.

Mestome bundles without a true mestome sheath, but with the leptome surrounded by an unbroken ring of mestome parenchyma having small cells with thick porous walls.

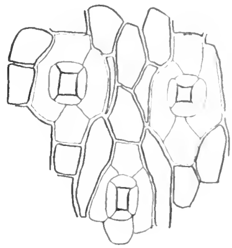

FIG. 41.—*Yucca aloifolia*—leaf surface. Epidermis, showing openings leading to the stomata. Scale 320.

YUCCA ALOIFOLIA L.

Leaf isolateral, thick, especially toward the base, ending in a rigid apical spine.

Epidermis (figs. 41, 42) cells containing chlorophyll, mostly somewhat elongated parallel to the leaf axis, their walls, especially the arched outer ones, greatly thickened and, together with the massive cuticle, exceeding the cell lumen, the radial walls not undulate; cuticle sharply differentiated, beautifully stratified, divided by perpendicular lamellæ corresponding to the radial cell walls; stomata deeply sunken, lying beneath the cuticle at the bottom of urn-shaped passages whose outer orifice is quadrangular with raised, cushion-like borders, the ridges of exit at bottom of the pore very acute; papillæ none (perhaps present in younger leaves).

Interior of the leaf occupied by homogeneous, thin-walled parenchyma, which, toward the apex of the leaf, contains chlorophyll in its entire thickness.

Mestome bundles lying in several rows in the mesophyll, each surrounded by a parenchyma sheath.

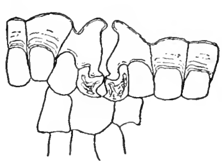

FIG. 42.—*Yucca aloifolia*—a stoma. Cross-section. Scale 320.

Stereome in massive groups on both the leptome and the hadrome side of the bundles, especially strong on the hadrome side. Small bundles of stereome, each with a parenchyma sheath, are scattered among the mestome bundles.

YUCCA GLORIOSA L.

Leaf much like the preceding.

Epidermis with larger (higher) cells; dorsal surface bearing thick, rounded, 1-celled papillæ.

Apical spine with exceedingly thick outer epidermis walls and cuticle, these much higher than the cell lumen, radial and inner walls also much thickened; next a hypodermal layer of thick-walled collenchyma; then 1 or 2 layers of thick-walled collenchymatic tissue; and, finally, a dense mass of stereome, inclosing a small central mestome bundle.

Myrica carolinensis Mill.[1]

Leaf bifacial, thickish, both surfaces sprinkled with resiniferous glands, appearing to the unaided eye as granules of resin.

Epidermis: Ventral, cells small, radial walls not undulate; cuticle thick, smooth; stomata none; long, pointed, unicellular hairs with thick-walled, smooth cuticle scattered along the veins; short-stalked, superficially flat, scale-like, pluricellular glands occupying deep depressions but usually rising above the level of the epidermis, these filled with a mass of bright-yellow resin which breaks down the cell walls and finally itself disorganizes, the stalk of each gland radially surrounded by numerous small foot cells. Dorsal similar, but cuticle less thickened, glands less numerous, and stomata present, lying in all directions, each surrounded by 5 to 7 ordinary epidermis cells, the guard cells slightly prominent.

Chlorenchyma sharply differentiated into one very compact layer of palisade with high, narrow cells, and several layers of open pneumatic tissue with rather large intercellular spaces.

Colorless thin-walled parenchyma in narrow plates interrupting the chlorenchyma above and below the smaller veins.

Hypodermal collenchymatic tissue, thick-walled, in 2 or 3 layers above and below the midvein.

Mestome bundles of midvein reinforced by stereome which adjoins both the hadrome and the leptome, that below the leptome separated from the hypodermal collenchymatic tissue by a little thin-walled parenchyma.

Myrica cerifera L.

Leaf usually somewhat thinner than in *M. carolinensis.*

Epidermis similar, but with fewer hairs along the veins.

Palisade somewhat thicker, in 2 layers of lower cells.

Quercus virginiana L.[2]

Leaf persistent, thick, bifacial, upper surface shining, margins sometimes revolute, veins, especially the midvein, prominent beneath.

Epidermis: Ventral with nonundulate cell walls, the outer, especially, strongly thickened; cuticle thick, smooth; stomata none; hairs none. Dorsal, cell walls as on the ventral surface; stomata with guard cells slightly prominent, lying in all directions, each bordered by several small epidermis cells; hairs (fig. 43) forming a dense covering, stellate, consisting of 8 to 18 acute, thick-walled unicellular arms upon very narrow foot cells, cohering toward their bases so as to form a saucer-shaped scale.

---

[1] Material examined from near Norfolk, Va.

[2] *Q. virens Ait.* Material examined was from near Norfolk, Va. Compare *Quercus ilex* as described and figured by Lalanne, Recherches, p. 3, *pl. 7, ff. 9, 12.*

Hypoderm mostly 2-layered, collenchymatic, continuous on both surfaces (rarely interrupted by palisade), replacing the chlorenchyma and forming thick masses above and especially below the midvein.

Stereome thin-walled, in narrow plates interrupting the chlorenchyma and extending through the leaf opposite most of the smaller veins; in strong masses above and below the midvein.

Chlorenchyma: Palisade compact, mostly in 2 layers, passing gradually into *pneumatic tissue* of which only the lowest layer is comparatively open and short-celled.[1]

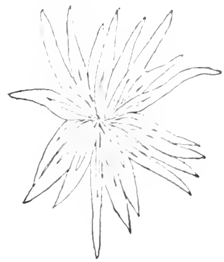

FIG. 43.—*Quercus virginiana*—stellate hair from dorsal leaf surface. Viewed from above. Scale 270.

ZANTHOXYLUM CLAVA-HERCULIS L.[2]

Leaf bifacial, thickish, dark green and shining above.

Epidermis: Ventral, cells large, walls not undulate, the outer strongly thickened, the others thin; cuticle sharply defined, delicately wrinkled; stomata none; hairs none. Dorsal, cells smaller, the outer walls and cuticle thinner; stomata with guard cells slightly prominent, lying in all directions, surrounded by 4 to 6 epidermis cells; hairs none.

Hypodermal collenchyma with strongly thickened walls in 4 or 5 narrow layers above the midvein; collenchymatic tissue in 4 or 5 wide layers beneath the midvein.

Chlorenchyma: Palisade a single compact layer of short cells; pneumatic tissue in 2 or 3 layers, rather open.

Oil reservoirs schizolysigenous,[3] scattered through the mesophyll near the ventral surface, and larger ones at the base of each indentation of the leaf margin, surrounded by 2 or 3 layers of thickish-walled parenchyma with cells strongly compressed parallel to the surface of the cavity.

Mestome bundles surrounded by a thin, interrupted sheath of stereome, which is continuous and (in cross section) crescent-shaped outside the leptome.

---

[1] *Quercus laurifolia* Michx. is a deciduous-leaved species, common along the coast and perhaps occurring upon Ocracoke Island. Leaves from Cape Henry, Va., show the following differences from *Q. virginiana:*

Epidermis: Cuticle thicker; dorsal surface less densely covered with similar stellate hairs, their arms longer, more slender and much thinner-walled.

Collenchymatic hypoderm none except above the midvein. True *collenchyma* (hypodermal) strongly developed beneath the midvein.

Stereome entirely surrounding the midvein, where it is much thicker-walled than in *virginiana*.

Chlorenchyma: Only the uppermost layer typical palisade; pneumatic tissue more compact and with more elongated cells than in *virginiana*.

[2] Material from Virginia and Mississippi.

[3] Compare Solereder, Syst. Anat., p. 201.

CROTON MARITIMUS Walt.

Leaf flat, bifacial, both surfaces densely covered with a gray, scale-like pubescence.

Epidermis: Ventral, cells small, walls not undulate, thin; stomata very numerous, guard cells level with the epidermis, each stoma surrounded by 4 epidermal cells, of which 2 are differentiated as crescent-shaped subsidiary cells parallel with the guard cells; hairs pluricellular, stellate, consisting of a long cylindrical stalk rising above the surface and composed of many small cells partly of subepidermal origin, from the apical cell of which radiate in a nearly horizontal plane numerous unicellular, sharp-pointed arms with thick, smooth cuticle, cohering near their bases so as to form a shallow cup. Dorsal, similar; cuticle thickened and granular underneath the large veins; stomata about equally numerous; hairs (fig. 44) with less numerous and thinner-walled arms.

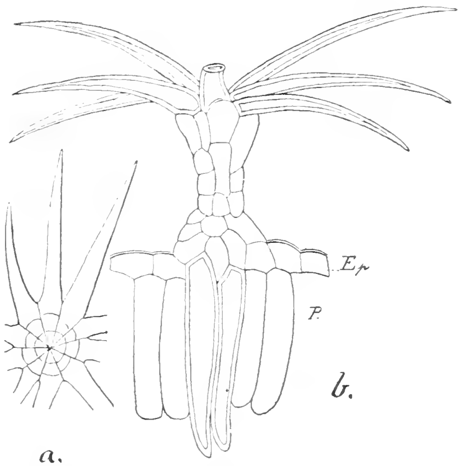

FIG. 44. *Croton maritimus*—hair from dorsal leaf surface. *a*. View from above; *b*. cross section; Ep. epidermis; P. palisade. Scale 240.

Hypoderm, none, except beneath the large veins, where several layers of thin-walled collenchymatic tissue occur.

Stereome, none.

Chlorenchyma: Palisade in one layer, compact, the cells elongated, interrupted only by thick-walled, branching, sclerotic idioblasts; pneumatic tissue of roundish cells.

ILEX VOMITORIA Ait.

Leaf evergreen, thick, shining and dark green above, bifacial.

Epidermis: Ventral, cells rather high (but small in their diameter parallel to the leaf-surface), the outer wall and cuticle much thickened but not nearly so high as the cell lumen, radial walls rather thin, undulate; cuticle smooth; stomata none; erect, short, stout, pointed, often curved, prickle-like unicellular hairs with very thick walls (lumen almost obliterated) and smooth cuticle along the midvein.[1] Dorsal, cells smaller, thicker-walled (outer wall and cuticle exceeding the cell lumen in height), the radial walls nearly straight, porous; cuticle wrinkled; stomata very numerous, guard cells slightly depressed; hairs, none.

[1] This species is, therefore, an exception to the rule that evergreen leaves have no hairs on the upper or ventral surface. (See Lalanne, p. 117.)

Hypodermal collenchymatic tissue in a single narrow layer above the midvein (as in *I. opaca*) and several layers beneath the midvein.

Chlorenchyma: Palisade in two layers; pneumatic tissue rather open (more so than in *I. aquifolium* and *I. opaca*).

Mestome bundle of midvein reinforced by a narrow group of stereome below the leptome, and a thinner-walled group above the hadrome.[1]

OENOTHERA HUMIFUSA Nutt.

Leaf densely silky-pubescent, imperfectly bifacial, midvein slightly impressed above, not prominent beneath.

Epidermis similar on both surfaces, cell walls not undulate, somewhat thickened, especially the outer; cuticle smooth; stomata with guard cells level with the upper surface, slightly prominent beneath, the majority lying parallel to the veins, but many irregular; hairs densely matted, subappressed, long, sharp-pointed, unicellular, with thick, granular cuticle, each radially surrounded by 5 or 6 foot cells.

Hypodermal collenchyma in 2 narrow layers above and 1 wide layer beneath the midvein, separated from the mestome above and below by colorless (water-storage?) parenchyma.

Stereome, none.

Chlorenchyma not sharply differentiated; palisade containing large cells inclosing raphides, which are yet more abundant in the otherwise rather compact pneumatic tissue.

TEUCRIUM NASHII Kearney.[2]

Leaf normally horizontal, bifacial, dark green above, white-tomentous beneath, margins (especially in young leaves) somewhat revolute, veins impressed above, prominent and reticulated beneath.

Epidermis: Ventral, cell walls thin, the lateral not undulate or but very slightly so; cuticle smooth; stomata, none; hairs scattered, mostly 3 or 4 celled, thin-walled, smooth, slender, very sharp-pointed, strongly bent so as to lie nearly parallel to the surface, surrounded radially by 4 to 10 (most frequently 6) foot cells. Dorsal, cell walls more undulate; stomata in the sheltered interstices between the projecting veins, with guard cells slightly prominent, lying in all directions, usually bordered by 2 epidermal cells and at right angles to their dividing wall, but with many exceptions; long-pointed hairs forming a dense covering; also very numerous, spherical, sessile, glandular hairs with roughened cuticle.

Hypodermal collenchymatic tissue in 2 or 3 narrow layers above and

[1] Specimens cultivated at Washington, D. C., differ in having 3 layers of palisade, and no stereome above the hadrome of the midvein.

[2] *Teucrium canadense*, which is never, to my knowledge, a strand plant, differs chiefly in the less dense hairy covering of the dorsal leaf surface and in the distinct granular roughening of the cuticle in the pointed, as well as the glandular hairs.

1 wide layer beneath the midvein, the latter separated from the leptome by several layers of colorless parenchyma.

Stereome, none.

Chlorenchyma: Palisade a single layer of short cells, very compact; pneumatic tissue occupying the rest of the leaf's thickness, also rather compact.

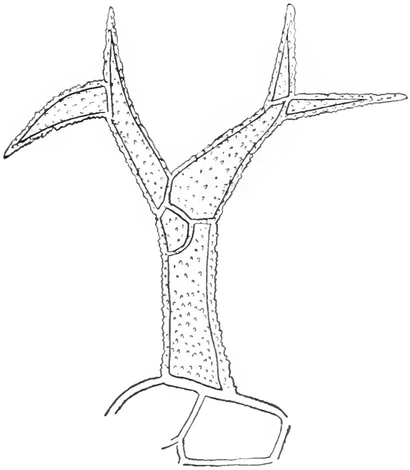

FIG. 45.—*Physalis viscosa*—branched hair from leaf. Scale 240.

PHYSALIS VISCOSA L.

Leaf flat, thin, imperfectly bifacial, gray-canescent or green (depending upon the amount of pubescence).[1]

Epidermis similar on both faces, cell walls not thick, the radial undulate; cuticle above and beneath the veins thick and warty; stomata much more numerous on the dorsal surface; hairs (fig. 45) about equally numerous on both faces, thin-walled with granular cuticle, consisting of a unicellular stalk bearing 3 or 4 (usually 3) conical, acute, unicellular or sometimes bicellular arms, these in turn sometimes once-branched.

Hypodermal collenchymatic tissue above and beneath the veins.

Stereome, none.

Chlorenchyma: Palisade and pneumatic tissue not well differentiated, both compact.

[1] The individuals observed upon Ocracoke Island had greener, less pubescent leaves than at Cape Henry, Va.

Leaf anatomy of sand-strand species.

[The sign × indicates presence of character; ± its imperfect development.]

Species.	Leaf.				Epidermis.				
					Cuticle				
	Bifacial.	Isolateral.	Relatively thick.	Conduplicate or involute when dry.	Thick.	Wrinkled.	Warty or granular.	Radial cell-walls undulate.	Bulliform cells present.
Panicum amarum	×	------	×	×	×	------	------	------	×
Muhlenbergia filipes	×	------	×	×	×	------	------	------	------
Spartina patens	×	------	×	×	×	------	------	------	------
Spartina stricta [1]	×	------	×	×	×	------	×	------	------
Chloris petraea	×	------	------	×	×	------	------	×	×
Uniola paniculata	×	------	×	×	×	×	------	------	×
Yucca aloifolia	------	×	×	------	×	------	------	------	------
Yucca gloriosa	------	×	×	------	×	------	------	------	------
Myrica carolinensis	×	------	------	------	×	------	------	------	------
Myrica cerifera	×	------	------	------	×	------	------	------	------
Quercus virginiana	×	------	×	------	×	------	------	------	------
Zanthoxylum clava-herculis	×	------	×	------	×	×	------	------	------
Croton maritimus	×	------	------	------	------	------	±	------	------
Ilex vomitoria	×	------	×	------	×	×	------	×	------
Oenothera humifusa	×	------	------	------	------	------	------	------	------
Teucrium nashii	×	------	------	------	------	------	------	±	------
Physalis viscosa	×	------	------	------	------	------	×	×	------

Species.	Epidermis.									
	Stomata.									
	Both surfaces.	Ventral surface only.	Dorsal surface only.	Prominent.	Level with surface.	Sunken.	In furrows.	Parallel to leaf axis.	Irregularly disposed.	Subsidiary cells present.
Panicum amarum	×	------	------	------	------	------	×	×	------	------
Muhlenbergia filipes	×	------	------	------	------	------	×	×	------	------
Spartina patens	×	------	------	------	------	------	×	×	------	------
Spartina stricta	------	×	------	------	------	------	×	×	------	------
Chloris petraea	------	------	×	------	×	------	------	×	------	------
Uniola paniculata	×	------	------	------	------	------	×	×	------	------
Yucca aloifolia	×	------	------	------	------	×	------	×	------	------
Yucca gloriosa	×	------	------	------	------	×	------	×	------	------
Myrica carolinensis	------	------	×	×	------	------	------	------	×	------
Myrica cerifera	------	------	×	×	------	------	------	------	×	------
Quercus virginiana	------	------	×	×	------	------	------	------	×	------
Zanthoxylum clava-herculis	------	------	×	×	------	------	------	------	×	------
Croton maritimus	×	------	------	------	×	------	------	------	------	×
Ilex vomitoria	------	------	×	------	------	×	------	------	------	------
Oenothera humifusa	×	------	------	×	×	------	------	×	------	------
Teucrium nashii	------	------	×	×	------	------	------	------	×	------
Physalis viscosa	×	------	------	------	------	------	------	------	------	------

[1] Belongs to the Salt Marsh, but is inserted here for convenience of comparison with other Gramineae.

Leaf anatomy of sand-strand species—Continued.

Species.	Epidermis.										Hypodermal collenchyma or collenchymatic tissue.	
	Hairs.											
	Both surfaces.	Ventral surface only.	Dorsal surface only.	Forming a dense covering.	Unicellular.	Pluricellular.	Simple.	Branching.	Stellate.	Glandular hairs or scales.	Only opposite veins.	Elsewhere.
Panicum amarum												
Muhlenbergia filipes	×				×		×					
Spartina patens		×			×		×					
Spartina stricta												
Chloris petraea												
Uniola paniculata		×			×		×					
Yucca aloifolia												
Yucca gloriosa												
Myrica carolinensis	×				×	×	×			×	×	
Myrica cerifera	×				×	×	×			×	×	
Quercus virginiana			×	×		×			×			×
Zanthoxylum clava-herculis											×	
Croton maritimus	×			×		×			×		×	
Ilex vomitoria		×			×		×				×	
Oenothera humifusa	×			×	×		×				×	
Teucrium nashii	×			×	×		×			×	×	
Physalis viscosa	×			×		×		×			×	

Species.	Stereome.			Chlorenchyma.					Water parenchyma.		Mestome bundles.	
	Subepidermal.	In leaf margins.	Adjoining mestome bundles.	Homogeneous.	Differentiated.	Palisade compact.	Palisade interrupted by water parenchyma.	Chlorenchyma radially arranged about mestome bundles.	Occupying the interior of the leaf.	Chiefly opposite mestome bundles.	With mestome sheath.	With parenchyma sheath.
Panicum amarum	×	×		×		×		×			×	×
Muhlenbergia filipes	×			×				×		×		×
Spartina patens	×	×		×				×		×	×	×
Spartina stricta	×	×		×		×		×		×	×	×
Chloris petraea	×	×		×		×		×			×	×
Uniola paniculata	×	×		×		×		×	×			×
Yucca aloifolia			×	×					×			×
Yucca gloriosa			×	×					×			×
Myrica carolinensis			×		×	×				×		
Myrica cerifera			×		×	×				×		
Quercus virginiana			×		×	×						
Zanthoxylum clava-herculis			×		×	×						
Croton maritimus					×	×						
Ilex vomitoria			×		×	×						
Oenothera humifusa					±					×		
Teucrium nashii					×	×						
Physalis viscosa					±	×						

SALT MARSH SPECIES.

TRIGLOCHIN STRIATA Ruiz & Pav.

Leaf isolateral, thickish.

Epidermis cells with nonundulate walls, the outer strongly thickened; cuticle thick, granular; stomata in rows parallel to the nerves, level with the surface, each bordered by 4 epidermal cells, of which 2 are subsidiary and resemble the guard cells; hairs none.

Stereome none.

Chlorenchyma: Two outer layers compact, continuous on both surfaces, not palisadic except at the leaf margins, where 3 layers of palisade occur; parenchyma of the interior of the leaf containing little chlorophyll, interrupted by lacunes.

Mestome bundles imbedded in the interior parenchyma, each surrounded by a small-celled mestome sheath, whose inner walls are excessively thickened and layered; this surrounded by a sheath of large-celled, colorless parenchyma.

SPARTINA STRICTA (Ait.) Roth.

Treated for comparison among sand-strand grasses, page 289.

JUNCUS ROEMERIANUS Scheele.

Leaf vertical, terete, sharp-pointed, stem-like.

Epidermis cells all small, quadrangular (superficially), regular, without alternation of long and short cells; smaller and thicker-walled over the bands of chlorenchyma than over those of subepidermal stereome, the outer walls much thickened and porous; stomata[1] with guard cells level with the other epidermal cells; hairs none.

Stereome (subepidermal) alternating with the chlorenchyma in strong groups, which in cross section are I-shaped.[2]

Chlorenchyma of typical long, narrow palisade cells, mostly in 5 or 6 layers.

Mestome bundles arranged in several concentric circles, completely surrounded by stereome (which is particularly strong on the two sides parallel to the leaf surface), the whole enveloped by a beautifully regular, large-celled parenchyma sheath. Within the stereome the bundle is encircled by a mestome sheath of small, thick-walled cells. The outer mestome bundles, with the colorless parenchyma between, form a continuous ring, unbroken by lacunes. The inner bundles lie in thin longitudinal plates of parenchyma, which separate large lacunes. Small bundles of stereome, each surrounded by a parenchyma sheath, also occur in the interior of the leaf.

Stem differing but little from the leaf; difference consisting chiefly in the presence of a cortex of some thickness, and in the less elongated chlorenchyma cells.

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[1] Of the type common in Juncaceae, Cyperaceae, and Gramineae.

[2] "I-förmige Träger" of Schwendener.

SESUVIUM MARITIMUM (Walt.) B.S.P.[1]

Leaf isolateral, somewhat succulent.

Epidermis cells with nonundulate, radial walls, the outer somewhat thickened, some of the cells much larger and probably serving for water storage; cuticle smooth; stomata lying in all directions, guard cells level with the epidermis, each stoma bordered by 3 to 6 (usually 4 or 5) undifferentiated epidermis cells; hairs none.

Stereome none.

Chlorenchyma homogeneous and occupying the entire thickness of the leaf, interrupted by large intercellular spaces, which lie beneath the large (water-storage) epidermal cells.

Mestome bundles with a small group of collenchyma on the leptome side.

Stem: Epidermis with cell walls, especially the outer, strongly thickened. Stereome none. Collenchyma in small groups above the leptome of the primary mestome bundles. Cells containing crystal masses in the pith and a few in the cortex.

TISSA MARINA (L.) Britton.[2]

Leaf isolateral, hemicylindric, furrowed, margins sparsely ciliate, especially toward base.

Epidermis with cells somewhat elongated parallel to the leaf axis, the radial walls strongly undulate, the outer walls slightly thickened; stomata always parallel to the leaf axis, guard cells slightly prominent, lying usually between 2 ordinary epidermis cells and at right angles to their dividing wall, but sometimes bordered by 3 cells; hairs (on the margins) glandular (fig. 46), capitate, with a 3 or 4 celled stalk.

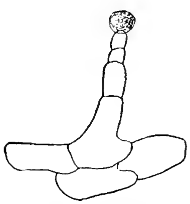

FIG. 46.—*Tissa marina*—glandular hair from leaf margin. Scale 240.

Stereome none.

Chlorenchyma compact, its cells not elongated.

Colorless parenchyma (water tissue) constituting the interior mesophyll.

Mestome bundle of the midvein small, lying deep in the water tissue, with a small group of collenchyma outside the leptome.

Stem: Epidermis with thick outer cell walls and wrinkled cuticle. Outer cortex separated from the inner by an unbroken, 2-layered ring of stereome, with cell walls (especially of the inner layer) comparatively thin.

[1] *Sesuvium pentandrum* Ell.—Compare Warming's description and figure of *S. portulacastrum*, Halofyt Studier. pp. 180, 211.

[2] *Spergularia salina* J. and C. Presl.

Kosteletzkya virginica (L.) A. Gray.

Leaf broad and flat, bifacial, stellate-pubescent on both surfaces.

Epidermis cells with nonundulate, thin walls, except above and below the larger veins, where the cuticle is rather thick and layered; stomata with guard cells slightly prominent, more numerous on the dorsal surface; hairs stellate, consisting of 5 to 8 acute unicellular arms with thick, smooth cuticle, separate nearly or quite to the base, each from a narrow foot cell in the epidermal plane.

Hypodermal collenchyma strongly developed above and below the larger veins.

Chlorenchyma: Palisade 1-layered; pneumatic tissue with numerous small intercellular spaces; mucilage cavities distributed in the chlorenchyma.

Mestome bundles almost completely surrounded by a thin, interrupted sheath of stereome, which is most strongly developed outside the leptome.

Ammania koehnei Britton.

Leaf flat, rather thin, approximately isolateral.

Epidermis: Cells with radial walls strongly undulate; all the walls thin, except above and below the larger veins, where the outer walls are considerably thickened; cuticle smooth; hairs none; stomata chiefly parallel with the veins, but some irregular; guard cells slightly prominent, each stoma bordered by usually 4 undifferentiated epidermal cells.

Collenchyma none.

Stereome none.

Chlorenchyma homogeneous, not palisadic.

Vincetoxicum palustre (Pursh) A. Gray.[1]

Leaves narrow, sharply reflexed and hanging almost vertically, imperfectly isolateral.

Epidermis: Cell walls rather thick, not undulate; cuticle wrinkled, especially above and below the veins; stomata more numerous on the ventral surface, level with the epidermis, each bordered by 4 or (more often) 5 ordinary epidermis cells, generally parallel with the leaf axis on the ventral surface, very irregularly disposed, often at right angles to the axis on the dorsal surface; hairs none.

Hypoderm a single, narrow layer, only above the midrib.

Collenchyma none.

Stereome none.

Chlorenchyma not palisadic, homogeneous through the leaf, but the interior containing less chlorophyll.

Cells containing masses of crystals (calcium oxalate) scattered in the chlorenchyma.

Stem: Epidermis as in the leaf.

---

[1] *Seutera maritima* Decsne.

Hypoderm continuous, 1-layered. Outer cortex with rather thick-walled cells, containing chlorophyll; inner cortex gradually becoming thinner-walled and colorless.

Stereome in a concentric band of isolated groups, lying inside the middle of the cortex.

Lactiferous ducts few, lying just outside the mestome bundles.

Mestome bundles bicollateral, perileptomatic, the leptome most strongly developed on the outer periphery of the hadrome.

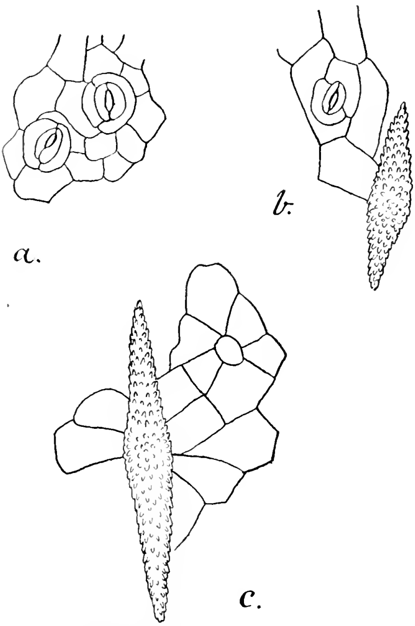

FIG. 47.—*Lippia nodiflora*—stomata and hairs. *a*, Stomata on leaf; *b*, hair and stoma on ventral leaf surface; *c*, hair on dorsal surface. Scale 240.

LIPPIA NODIFLORA Mx.

Leaf[1] imperfectly bifacial, usually horizontal, but sometimes vertical.

Epidermis alike on both surfaces, cell walls thick, not undulate; cuticle wrinkled; stomata (fig. 47) lying in all directions, guard cells almost level with the ventral surface, slightly depressed on the dorsal surface, each stoma bordered by 2 crescent-shaped, chlorophyll-holding, subsidiary cells which are usually at right angles to but often nearly or quite parallel to the guard cells, and of which one is usually considerably larger than the other; hairs abundant on both faces, parallel to the veins, appressed, lying in slight grooves of the epidermis, each attached by its middle (hence 2-armed) to a short cylindrical foot cell, which is bordered by several wedge-shaped (as seen from above) radially arranged epidermis cells, the free cell with a very thick, warty cuticle.

Hypodermal collenchyma (not very typical), in 1 or 2 layers above and 3 or 4 below the principal veins, interrupting the chlorenchyma in full-grown leaves.

Chlorenchyma: Palisade 2-layered, the cells rather short; pneumatic tissue rather compact, not well differentiated from the palisade, but its cells more nearly isodiametric and containing less chlorophyll.

Mestome bundles (of larger veins), with some stereome below the leptome and a small group of collenchyma above the hadrome, which finally becomes continuous with the subepidermal group of collenchyma.

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[1] Compare Warming, Halofyt-Studier, p. 233, and Solereder, Syst. Anat., p. 713.

MONNIERA MONNIERA (L.) BRITTON.[1]

Occurs in 2 forms; one in shallow pools, largely submersed, with long stems, elongated internodes, and larger leaves; the other terrestrial, in wet sand, with short, creeping stems, contracted internodes and smaller leaves.

(*a*) Aquatic form. Structure that of a partially submersed hydrophyte, with thin-walled tissues, much reduced mestome system, no mechanical tissue, etc.

Leaf isolateral.

Epidermis: Cells with undulate lateral walls, the walls thin except the outer, which is somewhat thickened; cuticle delicately wrinkled; stomata more numerous on the dorsal surface, guard cells about level with the epidermis, bordered by 2 to 4 ordinary epidermal cells; hairs none.

Chlorenchyma homogeneous, palisade none.

Mestome bundles immediately bordered by chlorenchyma, not reinforced by stereome or collenchyma.

Stem: Epidermis as in the leaf.

Cortical parenchyma in 1 or 2 continuous layers just beneath the epidermis and around the central cylinder, elsewhere in 1-layered plates, separating the large lacunes.

Mestome cylinder composed of several bundles, inclosing a small quantity of pith.

(*b*) Terrestrial form. The only tangible differences from the aquatic form are: Stomata about equally numerous on both leaf surfaces; mestome bundles somewhat more developed and walls of the vessels more lignified; mesophyll somewhat more compact.

SOLIDAGO SEMPERVIRENS L.[2]

Leaf somewhat fleshy, vertical or nearly so, approximately isolateral.

Epidermis: Cells with nonundulate radial walls, only the outer strongly thickened, except above and below the larger veins; cuticle strongly wrinkled; stomata numerous on both faces with guard cells level with the surface, bordered by usually 4 ordinary epidermal cells; hairs none.

Hypodermal collenchyma in only 1 or 2 narrow layers above and 3 or 4 wide layers below the larger veins.

Chlorenchyma homogeneous, none of it typical palisade, frequently interrupted, especially opposite the mestome bundles, by plates of colorless, thin-walled parenchyma (water tissue), which extend from the ventral to the dorsal epidermis, and ultimately break down into large lacunes close beneath the epidermis.

---

[1] *Herpestis monniera* H. B. K.

[2] The material examined was collected at Virginia Beach, Va.

Ducts (probably resiniferous) numerous, especially near the dorsal surface, apparently always lying in the plates of water tissue, one below the leptome of the midvein.

Mestome bundles of the larger veins with a narrow (in transverse section crescent-shaped) group of comparatively thin-walled stereome above the hadrome.[1]

Aster tenuifolius L.

Leaves narrow, almost vertical, isolateral, thick, with a deep groove on the dorsal surface on each side of the midvein, margins slightly incurved.

Epidermis: Cells comparatively large, walls not undulate, the outer greatly thickened; cuticle wrinkled and with slight furrows corresponding to the radial walls of the epidermal cells; stomata rather few and large, the guard cells slightly sunken, mostly somewhat deflected in direction from that of the leaf axis, bordered by usually 3 ordinary epidermis cells; hairs none.

Hypodermal collenchyma in a few narrow layers above and rather wide layers below the midvein.

Chlorenchyma consisting of palisade with high, narrow cells, in about 2 layers on both faces, strongly converging toward the midvein, especially on the ventral side.

Colorless parenchyma (water-storage tissue) occupying the interior of the leaf in small quantity, and surrounding the midvein, where it replaces the palisade.

Mestome bundles not reinforced by stereome.

Aster subulatus Michx.

Leaves wider and thinner than in the preceding, almost vertical, isolateral, flat, impressed above the midvein, which below is prominent, with a furrow on each side of it.

Epidermis: Cell walls not undulate, thick, the outer very thick, the inner collenchymatic-thickened where hypodermal collenchyma occurs; cuticle wrinkled; stomata, with guard cells lying parallel to the leaf axis, level with the surface; hairs none.

Hypodermal collenchyma above and below the veins (about 4 layers between the leptome of the midvein and the dorsal epidermis) and in the marginal angles.

Chlorenchyma of compact palisade, occupying practically the entire thickness of the leaf except where côllenchyma occurs and about the midvein.

---

[1] The leaves of nonmaritime species of Solidago (e. g., *S. petiolaris*, *S. neglecta*, and *S. erecta*) exhibit some interesting differences from *S. sempervirens*. All three have bifacial leaves with compact palisade and open pneumatic tissue (chlorenchyma least differentiated in *S. petiolaris*). Stomata few (*S. erecta*, *S. neglecta*) or none (*S. petiolaris*) on the ventral surface, guard cells slightly prominent on the dorsal surface. Hairs along the veins, especially on the dorsal face in *S. petiolaris*, 3 or 4 celled sharp-pointed, bent.

Colorless parenchyma (water-storage tissue) above and on each side of the midvein.

Mestome bundles without stereome supports, but with a small irregular group of collenchyma lying outside the hadrome.[1]

BACCHARIS HALIMIFOLIA L.

Leaves thickish, nearly vertical, isolateral.

Epidermis: Cell walls not undulate, thickened, the outer ones greatly so; cuticle warty, especially on the dorsal surface; stomata mostly parallel to the veins, but many somewhat deflected, guard cells slightly prominent, each stoma radially bordered by 4 or 5 small epidermis cells.

Collenchyma (hypodermal) replacing chlorenchyma above and below the larger veins (6 or 7 layers below the leptome of the midvein), containing no ducts.[2]

Chlorenchyma: Palisade occupying the whole thickness of the leaf between the veins, rather open, especially that in the interior of the leaf (but typical pneumatic tissue none), converging toward the midvein on the dorsal side; large, deep air chambers underneath the stomata.

Colorless parenchyma (water tissue) in 2 layers on each side of the midvein (cells circular in cross section), in a single layer entirely surrounding the smaller bundles.

---

[1] Three nonmaritime species of Aster were selected for comparison with the two salt-marsh species: *A. puniceus*, a broad-leaved plant of boggy ground, and *A. dumosus* and *A. ericoides*, narrow-leaved species of dry, sandy soil.

A. ericoides has a practically isolateral leaf, epidermis alike on both faces, with undulate radial and thickened outer walls, finely wrinkled cuticle, guard cells of the stomata level with the ventral surface, slightly prominent on the dorsal surface; chlorenchyma near both surfaces compact and small-celled, more open and larger-celled in the interior of the leaf; hypodermal collenchyma in 2 layers above and below the midvein; water parenchyma none.

A. dumosus has a distinctly bifacial leaf, epidermis much as in *A. ericoides*, but the 2 surfaces more differentiated, the ventral with radial cell walls less undulate and outer walls less thickened than in *A. ericoides*, cells larger and stomata much fewer on the ventral surface, the dorsal with radial walls more strongly undulate, and scattered, slender, pointed, few-celled hairs along the veins; palisade compact, pneumatic tissue open; veins supported by hypodermal collenchymatic tissue.

A. puniceus shows, of course, the greatest amount of difference from the salt-marsh forms. It has a flat, approximately horizontal, bifacial leaf. The ventral surface is rough with thick-walled, prickle-like, 1-celled hairs, mixed with scattered, longer, more slender, and thinner-walled hairs; the stomata lie in all directions in and have their guard cells level with the dorsal surface, but are wanting on the ventral face; the cuticle is smooth; the chlorenchyma is differentiated into a single layer of compact palisade and a few layers of rather open pneumatic tissue; no colorless parenchyma occurs inside the epidermis.

On the whole the salt-marsh Asters show less anatomical divergence from inland forms than does the salt-marsh Solidago. Of the two species, *A. tenuifolius* exhibits a more distinctive halophytic, or rather xerophytic, structure than does *A. subulatus*.

[2] Warming, Halofyt-Studier, p. 195, describes ducts which occur in the collenchyma of the leaf of *Baccharis dioica*.

Mestome bundles with a strong group of stereome only outside the hadrome in young leaves, in older leaves a corresponding group of more numerous and smaller cells outside the leptome also.

IVA FRUTESCENS L.[1]

Leaf thick, usually almost vertical, nearly isolateral.

Epidermis cells small, walls not undulate, thick, especially the outer; cuticle wrinkled, especially above and below the veins; stomata small, about equally numerous on both surfaces, the guard cells sunken, especially on the dorsal surface, lying irregularly in all directions; hairs on both surfaces (fig. 48) appressed, antrorse, thick-walled, 2 or 3 celled, sharp-pointed, the terminal cell abruptly narrowed just above its base, each hair borne upon 5 or 6 radially arranged foot cells which form a cushion that projects above the level of the epidermis; glands, 2 or 3 celled, sessile, nearly spherical, almost filling depressions in the epidermis and rising slightly above its general level.

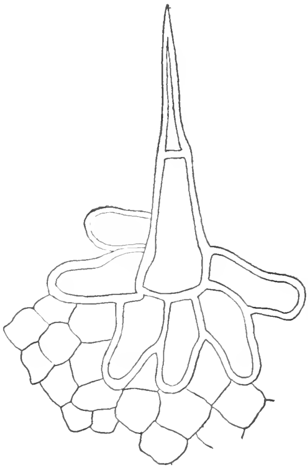

FIG. 48.—*Iva frutescens*—hair from ventral leaf surface. Scale 320.

Hypodermal collenchyma in strong groups above and below the larger veins (about 10 layers above and below the midvein).

Chlorenchyma palisadic, in several layers, the cells small and narrow, those near the midvein converging toward it; palisade frequently interrupted (especially opposite the mestome bundles) by a few rows of thin-walled, colorless parenchyma (water tissue), which ultimately breaks down into lacunes. Large ducts, each surrounded by a sheath of small cells, occur in the water tissue, especially on the ventral side of the leaf.

Mestome bundles with a little thin-walled stereome over the hadrome.[2]

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[1] The material examined was collected near Virginia Beach, Virginia.

[2] *Iva imbricata* Walt. is a common plant of the Atlantic sand strand in the Southeastern States, although not observed upon Ocracoke Island. It presents some interesting differences from the salt-marsh *I. frutescens*. The leaves examined were collected near Cape Henry, Virginia.

The plant is strongly aromatic, the leaf perfectly isolateral, fleshy and smooth.

Epidermis: cells much larger; cuticle not wrinkled; stomata with guard cells level with the ventral surface, somewhat sunken on the dorsal; hairs none.

Collenchyma less strongly developed than in *I. frutescens*.

Chlorenchyma consisting of 2 or 3 layers of palisade on both surfaces.

Colorless parenchyma (water-storage tissue), filling the interior of the leaf and interrupting the palisade above and below all the veins.

Mestome bundles lying in the midst of the water-storage tissue; stereome none.

The most important differences in *I. imbricata* are the strong development of

BORRICHIA FRUTESCENS (L.) DC.

Leaves (fig. 49) fleshy, almost vertical, imperfectly isolateral, the surface glistening, whitish, mealy looking, especially in young leaves.

Epidermis (fig. 49) with small, thin-walled cells, very many of which are extended by tangential division into commonly 2 to 4 celled, thin-walled, pointed, usually bent hairs (fig. 50),[1] the whole forming a very dense covering and giving the leaf its peculiar, glistening aspect; stomata only on the ventral surface, the guard cells slightly sunken.

Collenchyma (hypodermal) in several layers above and below the large mestome bundles (five in the midvein).

Chlorenchyma consisting of very compact palisade, 2-layered on both surfaces; pneumatic tissue none.

Colorless parenchyma (water-storage tissue) (fig. 49) occupying the

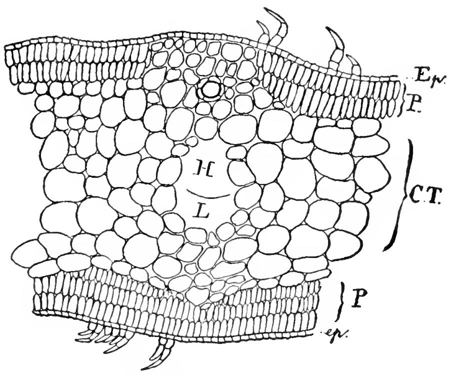

FIG. 49.—*Borrichia frutescens*—leaf section. Transverse section, showing epidermis of ventral surface (Ep); palisade (P); colorless parenchyma (C T); hadrome (H) and leptome (L) of a small mestome bundle; and epidermis of dorsal surface (ep). Scale 320.

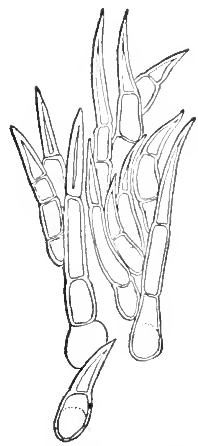

FIG. 50.—*Borrichia frutescens*—leaf-hairs. Scale 240.

interior of the leaf and forming rather more than one-half its thickness, at somewhat regular intervals displacing the palisade on the dorsal side and extending to the epidermis. Ducts (on the ventral side) frequent just beneath these extensions.

Mestome bundles of the veins (fig. 49) lying deep in the water-storage tissue; reinforced on the leptome side by a strong group of very thick-walled stereome, on the hadrome side by a smaller group; leptome and its elements beautifully differentiated, the sieve tubes each with

water-storage tissue in the interior of the leaf and the absence of hairs—just the converse of what one would expect as the differential characters between a dune and a salt-marsh species.

[1] The apical cells are easily broken off, so that in older leaves the covering appears to consist of rounded, usually bicellular papillae.

a companion cell and a band of four or five cribrile parenchyma cells.[1]

Leaf anatomy of salt-marsh species.

[The sign × indicates presence of character; ± its imperfect development.]

Species.	Leaf.				Epidermis.			
					Cuticle.			
	Bifacial.	Isolateral.	Terete.	Relatively thick.	Thick.	Wrinkled.	Warty or granular.	Radial walls undulate.
Triglochin striata		×		×	×		×	
Spartina stricta[1]								
Juncus roemerianus			×		×			
Sesuvium maritimum		×		×	×			
Tissa marina		×		×				×
Kosteletzkya virginica	×							
Ammania koehnei		±						×
Vincetoxicum palustre		±			×	×		
Lippia nodiflora	±				×	×		
Monniera monniera		×				×		×
Iva frutescens		×		×	×	×		
Solidago sempervirens		±		×	×	×		
Aster tenuifolius		×		×	×	×		
Aster subulatus		×			×	×		
Baccharis halimifolia		×		×	×		×	
Borrichia frutescens		±		×				

[1] Characters given under species of the "sand strand," page 289.

[1] *Borrichia arborescens* (compare Warming, Halofyt-Studier, p. 212) is a very similar but larger plant of the tropical American strand. It differs from *B. frutescens* in the following particulars, the characters being taken from material collected in South Florida and Porto Rico:

Hairs much thicker-walled, entirely disappearing in old (more than 1 year old?) leaves; stomata on both surfaces, with guard cells slightly prominent on the ventral face, less numerous and with guard cells slightly sunken on the dorsal face; epidermal cell walls, especially the outer, thick; palisade interrupted both above and below by extensions of the water-storage tissue, which on the ventral side ultimately disorganize and form large lacunes; hypodermal collenchyma occurring where the palisade is interrupted on the ventral side; collenchyma taking the place of stereome as supports of the veins, especially strong on the leptome side.

From Warming's description and figure of *B. arborescens* my specimens showed important differences: (1) The presence of hairs (elsewhere in the same paper Warming mentions their occurrence in this species); (2) stomata with guard cells slightly prominent on the ventral surface (Warming writes "stomata sunken"); (3) collenchyma present and strongly developed; (4) mestome bundles in three planes (one according to Warming), some small ones being situated near the upper and the lower epidermis, while the midvein is central in the water-storage tissue.

Leaf anatomy of salt-marsh species—Continued.

[The sign × indicates presence of character; ± its imperfect development.]

Species.	Epidermis. — Stomata.								
	Both surfaces.	Ventral surface only.	Dorsal surface only.	Prominent.	Level with surface.	Sunken.	Parallel to leaf axis.	Irregularly disposed.	Subsidiary cells present.
Triglochin striata	×	--------	--------	--------	×	--------	×	--------	×
Spartina stricta [1]	--------	--------	--------	--------	--------	--------	--------	--------	--------
Juncus roemerianus	--------	--------	--------	--------	×	--------	×	--------	--------
Sesuvium maritimum	×	--------	--------	--------	×	--------	--------	×	--------
Tissa marina	--------	--------	--------	×	--------	--------	×	--------	--------
Kosteletzkya virginica	×	--------	--------	×	--------	--------	--------	--------	--------
Ammania koehnei	×	--------	--------	×	--------	--------	±	--------	--------
Vincetoxicum palustre	×	--------	--------	--------	×	--------	--------	--------	--------
Lippia nodiflora	×	--------	--------	--------	--------	±	--------	×	×
Monniera monniera	×	--------	--------	--------	×	--------	--------	--------	--------
Iva frutescens	×	--------	--------	--------	--------	×	--------	×	--------
Solidago sempervirens	×	--------	--------	--------	×	--------	--------	--------	--------
Aster tenuifolius	×	--------	--------	--------	--------	×	×	--------	--------
Aster subulatus	×	--------	--------	--------	×	--------	×	--------	--------
Baccharis halimifolia	×	--------	--------	×	--------	--------	±	--------	--------
Borrichia frutescens	--------	×	--------	--------	--------	±	--------	--------	--------

Species.	Epidermis. — Hairs.										Hypodermal collenchyma or collenchymatic tissue.	
	Both surfaces.	Ventral surface only.	Dorsal surface only.	Forming a dense covering.	Unicellular.	Pluricellular.	Simple.	Branching.	Stellate.	Glandular hairs or scales.	Only opposite veins.	Elsewhere.
Triglochin striata	------	------	------	------	------	------	------	------	------	------	------	------
Spartina stricta [1]	------	------	------	------	------	------	------	------	------	------	------	------
Juncus roemerianus	------	------	------	------	------	------	------	------	------	------	------	------
Sesuvium maritimum	------	------	------	------	------	------	------	------	------	------	------	------
Tissa marina	------	------	------	------	------	×	×	------	------	×	------	------
Kosteletzkya virginica	×	------	------	------	------	×	------	------	×	------	×	------
Ammania koehnei	------	------	------	------	------	------	------	------	------	------	------	------
Vincetoxicum palustre	------	------	------	------	------	------	------	------	------	------	------	------
Lippia nodiflora	×	------	------	------	×	------	------	×	------	------		------
Monniera monniera	------	------	------	------	------	------	------	------	------	------	------	------
Iva frutescens	×	------	------	------	------	×	×	------	------		×	------
Solidago sempervirens	------	------	------	------	------	------	------	------	------	------	×	------
Aster tenuifolius	------	------	------	------	------	------	------	------	------	------		------
Aster subulatus	------	------	------	------	------	------	------	------	------	------	------	×
Baccharis halimifolia	------	------	------	------	------	------	------	------	------	------	×	------
Borrichia frutescens	×	------	------	×	------	×	×	------	------	------	×	------

[1] Characters given under species of the "sand strand," page 289.

Leaf anatomy of salt-marsh species—Continued.

[The sign × indicates presence of character; ± its imperfect development.]

Species.	Stereome.			Chlorenchyma.					Water parenchyma.		Mestome bundles.	
	Subepidermal.	In leaf margins.	Adjoining mestome bundles.	Homogeneous.	Differentiated.	Palisade compact.	Palisade interrupted by water parenchyma.	Palisade converging toward midrib.	Filling the interior of the leaf.	Chiefly opposite the mestome bundles.	With mestome sheath.	With parenchyma sheath.
Triglochin striata	------	------	------	×	------	------	------	------	------	------	×	×
Spartina stricta[1]	------	------	------	------	------	------	------	------	------	------	------	------
Juncus roemerianus	×	------	×	×	------	×	------	------	------	------	×	×
Sesuvium maritimum	------	------	------	×	------	------	------	------	------	------	------	------
Tissa marina	------	------	------	×	------	------	------	------	×	------	------	------
Kosteletzkya virginica	------	------	×	------	×	×	------	------	------	------	------	------
Ammania koehnei	------	------	------	×	------	------	------	------	------	------	------	------
Vincetoxicum palustre	------	------	------	×	------	------	------	------	------	------	------	------
Lippia nodiflora	------	------	×	------	±	×	------	------	------	------	------	------
Monniera monniera	------	------	------	×	------	------	------	------	------	------	------	------
Iva frutescens	------	------	×	×	------	------	×	×	------	×	------	------
Solidago sempervirens	------	------	×	×	------	------	×	------	------	×	------	------
Aster tenuifolius	------	------	------	×	------	×	------	×	×	------	------	------
Aster subulatus	------	------	------	×	------	×	------	------	------	×	------	------
Baccharis halimifolia	------	------	×	×	------	------	------	×	------	×	------	------
Borrichia frutescens	------	------	×	×	------	×	×	------	×	------	------	------

[1] Characters given under species of the "sand strand," p. 289.

GEOGRAPHICAL AFFINITIES OF THE FLORA.

According to its geographic position, Ocracoke Island lies well within the Austroriparian area of the Lower Austral life zone in North America.[1] For two reasons, however, this relationship of its flora is somewhat obscured: (1) By the large proportion of strand species, many of which have a very extensive geographic range; and (2) by the absence of many of the most characteristic species of the Austroriparian area, due to the peculiar physical environment.

Of the total number of species of embryophytes (about 135) collected or observed upon Ocracoke Island, between one-fourth and one-third may be designated as maritime, i. e., normally occurring only in the salt marshes or on the sand strand bordering the ocean. These may be segregated into 4 groups, according to geographical range:

1. Species occurring also on the coasts of tropical America.

A prefixed asterisk (*) indicates that the species does not extend north of the mouth of Chesapeake Bay; a prefixed dagger (†) that the northern limit is in North Carolina, probably not far from Ocracoke. *Triglochin striata* and *Monniera monniera* extend north to eastern Maryland.

[1] Merriam, Geogr. Distrib. p. 211; Life Zones p. 45, map.

Triglochin striata R. & P.
**Quercus virginiana* L.[1]
†*Chloris petraea* Sw.
**Uniola paniculata* L.
**Fimbristylis spadicea* Vahl.
†*Yucca aloifolia* L.
**Physalis viscosa* L.
Monniera monniera H. B. K.
**Borrichia frutescens* L.
†*Ipomoea sagittata* Cav.

2. Species mostly or entirely confined to the seacoast of the Austroriparian area: *Zanthoxylum clava-herculis* and, possibly, *Ilex vomitoria* extend northward to Virginia, while the rest attain their northern limit in North Carolina.

Muhlenbergia filipes M. A. Curtis.
Yucca gloriosa L.
Croton maritimus Walt.
Zanthoxylum clava-herculis L.
Ilex vomitoria Ait.
Opuntia pes-corvi Le Conte.
Vincetoxicum palustre (Pursh) A. Gray.

3. Species confined to the Atlantic seacoast of North America and ranging north of the Austroriparian area. The northern limit of each is cited as given in Britton & Brown's Illustrated Flora.

Panicum amarum minus Vasey & Scribn. (Connecticut).
Spartina patens (Ait.) Muhl. (Nova Scotia).
Distichlis spicata (L.) Greene[2] (Maine).
Juncus roemerianus Scheele (New Jersey).
Sesuvium maritimum (Walt.) B. S. P. (New York).
Euphorbia polygonifolia L. (Rhode Island).
Kosteletzkya virginica L. (New York).
Ammania koehnei Britton (New Jersey).
Oenothera humifusa Nutt. (New Jersey).
Limonium carolinianum (Muhl.) Britton (Labrador).
Iva frutescens L. (Massachusetts).
Solidago sempervirens L. (New Brunswick).
Aster tenuifolius L. (Massachusetts).
Aster subulatus Michx. (New Hampshire).
Baccharis halimifolia L. (Massachusetts).

4. Species occurring also on the seacoast of the northern hemisphere in the Old World.

Spartina stricta (Ait.) Roth.
Atriplex hastata L.
Salicornia herbacea L.
Salsola kali L.
Tissa marina (L.) Britton.

Of the nonmaritime species of the island, fifteen are introduced and are chiefly weeds of American origin. The remainder (about two-thirds of the total flora) includes several mainly tropical species, such as *Lippia nodiflora* Michx., *Centella asiatica* (L.) Urban, *Parietaria debilis* Forst., and *Tillandsia usneoides* L., which, while hardly maritime, are found usually near the seacoast in the Austroriparian area. Finally, after excluding all the preceding categories except the second of strand plants, we have a list of species among which the Austroriparian element is sufficiently predominant to leave no question as to the general affinity of the flora.

As previously remarked, however, many of the plants most char-

[1] Normally a strand plant in Virginia and North Carolina.
[2] The typical form.

acteristic of the whole Austroriparian area, and abundant on the mainland, scarcely 30 kilometers distant, are wanting upon Ocracoke Island. Notable among these absentees are the pines (*Pinus palustris*, *P. taeda*), the gums (Nyssa spp.), the bald cypress (*Taxodium distichum*), the deciduous oaks, the cane (*Arundinaria macrosperma*), species of Erianthus, *Carex verrucosa*, *Smilax laurifolia*, and *Berchemia scandens*. Hardly less striking is the nonoccurrence of most of the bright-flowered herbs that abound in the pine forests on the west shore of Pamlico Sound. Such are species of Coreopsis, Helianthus, Lacinaria (Liatris), Eupatorium, Solidago, Rhexia, Gerardia, Hypericum, Sarracenia, Habenaria, and Polygala. The unfavorable environment is doubtless responsible for the absence of many of these plants, conditions upon the island being suitable only to the hardiest species. Scarcity of shade, of humus, and of fresh water accounts in like manner for the poverty of the flora in most of the lower forms, such as fresh-water algae, fungi, hepaticae, mosses, and ferns. The numerous arrangements by which many of the higher plants are protected against excessive loss of water may also serve in some measure for protection against parasitic leaf fungi, and may partly account for the comparative scarcity of the latter.

The general aspect of the plant covering is not attractive. Bright green foliage and flowers of brilliant coloring are too scarce to make much impression, while, except in the salt marshes, the plants are usually so scattered that it is the soil which gives tone to the landscape. Furthermore, the trees and shrubs are mostly characterized by gnarled trunks, many dead branches, and ragged foliage, as a result of exposure to sand-laden winds. Altogether, the picture is one of somber monotony.

LIST OF PLANTS COLLECTED AND OBSERVED.

[The prefixed asterisk denotes that the plant is introduced.]

LICHENES.

Usnea barbata L.
Ramalina montagnei De Not.

MUSCI.

Bryum argenteum L.
Rhynchostegium serrulatum Hedw.

POLYPODIACEAE.

Asplenium platyneuron (L.) Oakes. (*A. ebeneum* Ait.)

PINACEAE.

Juniperus virginiana L.

TYPHACEAE.

Typha latifolia L.

SCHEUCHZERIACEAE.

Triglochin striata Ruiz & Pav.

POACEAE.

Andropogon glomeratus (Walt.) B. S. P. (*A. macrourus* Michx.)
Paspalum ciliatifolium Michx.
Paspalum distichum L.
Paspalum laeve Michx.
Syntherisma fimbriata (Smith) Nash. (*Digitaria fimbriata* Smith.)
Panicum amarum minus Vasey & Scribner.
Panicum lanuginosum Ell. (?)
Panicum laxiflorum Lam.
Panicum neuranthum Griseb.
Panicum walteri Pursh.
Oplismenus setarius (Lam.) Roem. & Schult.
Chaetochloa imberbis perennis (Hall) Scribn. & Merrill. (*C. versicolor* Bicknell.)
Homalocenchrus virginicus (Willd.) Britton. (*Leersia virginica* Willd.)
Muhlenbergia filipes M. A. Curtis.
**Sporobolus indicus* (L.) R. Br.
**Capriola dactylon* (L.) Kuntze. (*Cynodon dactylon* Pers.)
Spartina patens (Ait.) Muhl. (*S. juncea* Ell.)
Spartina stricta (Ait.) Roth.
Chloris petraea Sw.
**Eleusine indica* (L.) Gaertn.
Triplasis purpurea (Walt.) Chapm.
Eragrostis nitida (Ell.) Chapm.
Uniola laxa (L.) B. S. P. (*U. gracilis* Michx.)
Uniola paniculata L.
Distichlis spicata (L.) Greene. (*D. maritima* Raf.)

CYPERACEAE.

Cyperus cylindricus (Ell.) Britton. (*C. torreyi* Britton.)
Cyperus echinatus (Ell.) Wood. (*C. baldwinii* Torr.)
Cyperus nuttallii Eddy.
Cyperus speciosus Vahl.
Eleocharis sp.
Dichromena colorata (L.) A. S. Hitchcock. (*D. leucocephala* Michx.)
Fimbristylis spadicea (L.) Vahl.
Scirpus americanus Pers. (*S. pungens* Vahl.)
Scleria verticillata Muhl.
Cladium effusum Torr.

ARACEAE.

Acorus calamus L.

BROMELIACEAE.

Tillandsia usneoides L.

JUNCACEAE.

Juncus dichotomus Ell.
Juncus roemerianus Scheele.
Juncus scirpoides Lam.

LILIACEAE.

Yucca aloifolia L.
Yucca gloriosa L.

SMILACEAE.

Smilax bona-nox L. (*S. tamnoides* A. Gray.)

MYRICACEAE.

Myrica carolinensis Mill.
Myrica cerifera L.

FAGACEAE.

Quercus virginiana L. (*Q. virens* Ait.)

MORACEAE.

* *Ficus carica* L.
* *Broussonetia papyrifera* (L.) Vent.

URTICACEAE.

Parietaria debilis Forst.

POLYGONACEAE.

Polygonum punctatum Ell.
Rumex sp.

CHENOPODIACEAE.

* *Chenopodium anthelminticum* L.
Atriplex hastata L.
Salicornia herbacea L.
Salsola kali L.

PHYTOLACCACEAE.

Phytolacca decandra L.

AIZOACEAE.

Sesuvium maritimum (Walt.) B. S. P. (*S. pentandrum* Ell.)
Mollugo verticillata L.

ALSINACEAE.

Tissa marina (L.) Britton. (*Spergularia salina* J. & C. Presl.)

ROSACEAE.

Rubus trivialis Michx.

CAESALPINACEAE.

* *Cassia occidentalis* L.

VICIACEAE.

Aeschynomene virginica (L.) B. S. P. (*A. hispida* Willd.)
Meibomia paniculata (L.) Kuntze. (*Desmodium paniculatum* DC.)
Galactia volubilis (L.) Britton. (*G. pilosa* Ell.)

LINACEAE.

Linum medium (Planch.) Britton.

RUTACEAE.

Zanthoxylum clava-herculis L.

EUPHORBIACEAE.

Croton maritimus Walt.
Acalypha gracilens A. Gray.
Euphorbia polygonifolia L.

ANACARDIACEAE.

Rhus radicans L.

ILICACEAE.

Ilex glabra (L.) A. Gray.
Ilex opaca Ait.
Ilex vomitoria Ait. (*I. cassine* Walt.)

VITACEAE.

Vitis aestivalis Michx.

MALVACEAE.

Kosteletzkya virginica (L.) A. Gray.
Hibiscus moscheutos L.
* *Gossypium herbaceum* L.

HYPERICACEAE.

Ascyrum hypericoides L.

CISTACEAE.

Lechea villosa Ell. (*L. major* Michx.)

CACTACEAE.

Opuntia pes-corvi Le Conte.

LYTHRACEAE.

Ammania koehnei Britt.

ONAGRACEAE.

Ludwigia alata Ell.
Ludwigia microcarpa Michx.
Oenothera humifusa Nutt.

APIACEAE.

Sanicula sp.
Hydrocotyle umbellata L.
Centella asiatica (L.) Urban.

PRIMULACEAE.

Samolus floribundus H. B. K.

PLUMBAGINACEAE.

Limonium carolinianum (Walt.) Britton. (*Statice limonium* var. *caroliniannum* A. Gray.)

LOGANIACEAE.

Cynoctonum mitreola (L.) Britton. (*Mitreola petiolata* Torr. & Gr.)
Polypremum procumbens L.

ASCLEPIADACEAE.

Vincetoxicum palustre (Pursh) A. Gray. (*Seutera maritima* Decne.)

CONVOLVULACEAE.

Ipomoea sagittata Cav.

VERBENACEAE.

Lippia nodiflora Michx.
Callicarpa americana L.

NEPETACEAE.

Teucrium nashii Kearney.
Monarda punctata L.

SOLANACEAE.

Physalis viscosa L.
Solanum carolinense L.
* *Solanum nigrum* L.
* *Lycopersicum esculentum* L.
* *Datura tatula* L.

SCROPHULARIACEAE.

* *Verbascum thapsus* L.
Monniera monniera (L.) Britton. (*Herpestis monniera* H. B. K.)
Gerardia maritima Raf.

RUBIACEAE.

Oldenlandia uniflora L. (*O. glomerata* Michx.)
Diodia teres Walt.
Diodia virginiana L.
Galium sp. (probably *G. tinctorium* L. or *G. claytoni* Michx.).

CUCURBITACEAE.

* *Citrullus vulgaris* Schrad.
Melothria pendula L.

CICHORIACEAE.

Hieracium gronovii L.

CARDUACEAE.

Elephantopus nudatus A. Gray.
Mikania scandens (L.) Willd.
Solidago sempervirens L.
Euthamia caroliniana (L.) Greene. (*Solidago tenuifolia* Pursh.)
Aster salicifolius Lam. var.
Aster subulatus Michx.
Aster tenuifolius L.
Erigeron canadensis L.
Baccharis halimifolia L.
Pluchea camphorata (L.) DC.
Pluchea foetida (L.) B. S. P. (*P. bifrons* DC.)
Gnaphalium purpureum L.
Ambrosia artemisiaefolia L.
Iva frutescens L.
Xanthium sp.
Xanthium sp.
Borrichia frutescens L.
* *Bidens bipinnata* L.
Erechtites hieracifolia (L.) Raf.
Carduus spinosissimus Walt. (*Cnicus horridulus* Pursh.)

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