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THE KNEES OF THE *TAXODIUM DISTICHUM*.

BY ROBERT H. LAMBORN.

IN a "Preliminary Notice of Some of the Results of the United States Geological Survey Examination of Swamp Land," by Prof. N. S. Shaler, of Cambridge, Mass. (*Science*, March 8, '89), it is stated as the result of observations begun in 1874, while engaged on the Kentucky State Survey, and continued and recorded in various publications by the author, official and otherwise, extending up to date, that the occurrence of knees on the *Taxodium distichum* is explained "through a need of an aëration of the sap which is denied the roots that are under water." He also ascribed the enlarged base of the tree to the same need of aëration of the sap, and discards as disproven the hypothesis that such enlarged or buttressed base is useful to the tree as securing greater resistance to storms.

In the Memoir (by the same author) of the Museum of Comparative Anatomy (Harvard College, 1887), the theory of aëration is still more distinctly enunciated. "The failure of knees to develop when they grow on high ground; the development of the knees when the roots are in permanent water; the rise of the knees above permanent water level, and to a height varying with that level, and, finally, the destruction of the trees whenever the level of permanent water rises above the tops of the knees,—these facts incontestably show that there is some necessary connection between them and the function of the roots, when the latter are permanently submerged." "It seems likely, therefore, that some process connected with the exposure of the sap to the air takes place in these protuberances." Following these official publications, a communication was presented to the Academy of Natural Sciences, of Philadelphia (pp. 67 to 69, Proceedings, April, 1889), by Prof. Wilson, of the University of Penna., in which the result of certain observations made by him in Florida in 1885-6 are given. He records a careful series of experiments made by dig-

ging up young trees, by cultivating the plant from the seed, and by observing exposed root systems. He finds that "if the tree requires, from inundation or other causes, more aerating surface than can be readily or rapidly produced by young and growing roots, then either the whole upper surface of the root in question may become more active and rapid in its growth, or the places of growth may be limited to certain definite points"—so knees are produced. He continues: "I do not propose at this time to discuss the function of these knees, further than to say that their *location* and *occurrence* indicate beyond a doubt that they are for purposes of aerating the plant."

In the monthly publication of the Pennsylvania Forestry Association (*Forest Leaves*, December, 1889), in a careful article on the Taxodium, Prof. Wilson, referring to Prof. Shaler's work, again adverts to the knees, and says: "From recent experiments made by the writer at the department of Biology, it has been demonstrated that the knees are organs produced by the roots for the purpose of taking in a greater supply of oxygen than could otherwise be had from the surrounding water.

This theory which finds in the knees and swollen boles of the cypress the sole function of conveying something advantageous from the atmosphere to the sap of the tree during periods of submergence, seems to have been entertained as early as 1847, when Dr. Dickinson and Andrew Brown read before the Association of American Geologists, in Boston, a study of "The Cypress timber of Mississippi and Louisiana." In this interesting illustrated article of eight pages in *Silliman's Journal* for January, 1848, they say, "The cone-shaped, leafless protuberances, sometimes ten feet high, growing from the interlacing roots in a dense forest, resemble in all but their color the crowded stalagmites in some enormous cavern. By means of these protuberances the roots, though totally submerged, have a communication with the atmosphere. We suggest," they say, "that this function is fulfilled by the knees." When this communication is cut off by the annual overflow rising above the tops of the knees, the swollen base carries the similar structure of the roots up the bole of the tree to an elevation sufficient to reach the atmospheric air.

Until recently this aerating theory seems to have met with no opposition, and it bid fair to become the generally accepted explanation for these strange vegetable growths, which travelers in our Southern states so often observe and mention.

A paper in *Garden and Forest*, the result of careful studies in Florida, which we now reproduce, will be found interesting because it explains the same phenomena upon an entirely different assumption. It is as follows:

From time to time, during and since my first visit to our southern tier of states in 1876, I have examined, sketched and photographed the roots of the Deciduous Cypress—the *Taxodium distichum* of Richard. I was attracted to the tree because of the singular beauty of its forms and foliage, and by the unusual boldness with which it raises its great, gray, smooth column, sometimes over a hundred feet perpendicularly, above and upon what an engineer would pronounce a most dangerous foundation—loose submerged sand, the saturated morass or the soft alluvium of low river margins.¹ But notwithstanding this seeming insecurity, I have never found a healthy cypress that had fallen before the fierce hurricanes that sweep through the southern forestlands.²

The surprising and characteristic temerity of the tree is accompanied by another striking peculiarity—it almost invariably, in soft soils, throws upward from the upper surface of its roots conspicuous protuberances that are known as “Cypress knees.”

These seemingly abnormal growths have attracted much attention, and for more than half a century have furnished an enigma to the so-

¹ It is a pleasure to follow Bartram in his enthusiastic burst of admiration for this tree as he writes of it in east Florida 116 years ago: “This Cypress is in the first order of North American trees. Its majestic stature is surprising. On approaching it we are struck with a kind of awe at beholding the stateliness of its trunk, lifting its cumbrous top toward the skies and casting a wide shade on the ground as a dark intervening cloud, which from time to time excludes the rays of the sun. The delicacy of its color and the texture of its leaves exceed everything in vegetation. . . . Prodigious buttresses branch from the trunk on every side, each of which terminates underground in a very large, strong, serpentine root, which strikes off and branches every way just under the surface of the earth, and from these roots grow woody cones, called Cypress knees, four, five and six feet high, and from six to eighteen inches and two feet in diameter at the base.

² Elliot (“Bot. of S. C. and Ga.,” 1824, p. 643) says: “This Cypress resists the violence of our autumnal gales better than any other of our forest trees.” By my friend, Dr. J. S. Newberry, whose extended geological labors have led him to examine many widely separated Cypress-bearing regions in the Mississippi Valley and elsewhere, I am assured that he remembers no instance of the overthrow by the wind of a living *T. distichum*.

lution of which scientific travelers have addressed themselves. Michaux made a careful study of the Cypresses, and in his "*Sylva*," published in 1819, says: "The roots are charged with protuberances eighteen to twenty-four inches high.³ These protuberances are always hollow, and smooth on the surface, and are covered with a reddish bark, like the roots, which they resemble in softness of wood. They exhibit no sign of vegetation, and I have never succeeded in obtaining shoots by wounding the surface and covering it with earth. They are peculiar to the Cypress, and begin to appear when it is twenty to twenty-five feet high." Michaux adds, with the frankness natural to a scientific mind, "No cause can be assigned for their existence." Hoopes says in his "*Book of Evergreens*" (1868): "No apparent function for which the knees are adapted has been ascertained." And Veitch, who seems to have studied the protuberances in England, gives in his "*Manual*" (1881, p. 216) a picture of a tree growing at Ilesworth, surrounded by scores of knees, and says: "They are peculiar to this Cypress, and no cause has been assigned for their existence." That the question continued in this unilluminated condition until recently was shown in 1882, when I had the privilege of visiting, in company with the highest botanical authorities,—Dr. Gray, Thomas Meehan, John H. Redfield, John Ball, Professor Carruthers and others,—the classic collection of trees planted by William Bartram on the borders of the Schuylkill. There we examined a fine Cypress and the knees it had produced. Dr. Gray then told me that the use to the tree of the knees was unknown. I remarked that they might be a means of raising a point on the root above surrounding water to the end that a leaf-bearing shoot could readily sprout therefrom. To this suggestion he made the same statement made by Michaux and above recorded. Unaware that the subject had been so thoroughly investigated, I have since that period examined hundreds of living "knees" in southern swamps, and found upon them no trace of bud, leaf or sprout, except where some seed may have lodged in a decayed or depressed portion of the surface and there taken root.

In 1887 I had the good fortune to find a number of Cypress trees under such unusual conditions that their aforesaid subterranean anatomy could be studied without obstruction, and I reached a conclusion respecting the use to the tree of the protuberances which I have retained in my note-book, awaiting an opportunity to make some further illus-

³I have ridden among them in central Florida, in temporarily dry upland basins, where they arose to my breast as I sat upon the saddle, and were not less than seven feet in height above the root.

trative sketches before placing it before botanists. Some recent publications on the subject by widely and favorably known authors have, however, ascribed to the Cypress-knees the sole function of aërating the sap of the parent tree, and this idea bids fair to become embedded in botanical literature. Therefore this communication comes to you earlier than I had purposed sending it.

Stretches of the shore of Lake Monroe, in central Florida, are closely set with large Cypress-trees. They grow in various kinds of bottom, —clay, mud and sand. Those of which I shall here speak stood in sand so loose that when the level of the water was lowered the waves readily washed it away and carried it into the depths of the lake. Some four vertical feet of the root-system were thus finely exposed. After several days spent in examining a score or more large trees that had been thus denuded I became convinced that the most important function of the Cypress knee is to stiffen and strengthen the root, in order that a great tree may anchor itself safely in a yielding material.

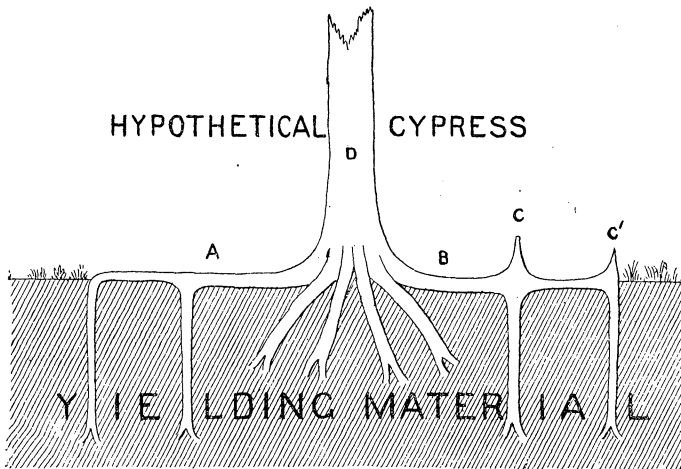
The word "anchor" is indeed an apt one here, for the living root, curved to its work and firmly grasping the sandy bottom, suggests vividly the best bower-anchor that a man-of-war may throw into similar loose sands, when threatened by the very atmospheric forces that the *Taxodium* has been fitting itself to resist since Tertiary times.⁴

Truly a most admirable and economical arrangement to stiffen and strengthen the connection between the shank of the anchor and its fluke is this knee, and usually in the living anchor the fluke branches or broadens as it descends, so that its effectiveness is greatly increased, like the sailor's anchor of many flukes, or the "mushroom anchor" that he may have learned to depend upon where the bottom is softest.

The accompanying picture (see page 20) is from a photograph that I made in 1887 of the lower portion of a tree that rises some seventy feet above the shore line of Lake Monroe. The original surface of the sand was near the level of the higher roots. The picture shows the manner in which this peculiar species throws out horizontal roots from its conical (usually hollow) buttressed base. At different distances from this conical base these horizontal roots project strong branches more or less perpendicularly into the earth. When such perpendicular "flukes" branch from the main horizontal "shank," it will be seen,

⁴ My friend Thomas Meehan informs me [December 17th, 1889] that he has "observed a case where the interior hollow makes an annual layer of bark equally with the exterior," and he is of the opinion that "it is by the decay of the outer layer of this inside course of bark after several years that the knob becomes hollow." If this habit is general it is an admirable means of forming and of preserving undecayed, at the smallest cost to the tree, a living elastic strengthener at the forking of the roots.

there is formed a large knob, which is the "knee" under discussion. This knee, when fully developed, is generally hollow, comparatively soft, gnarled, and very difficult to rupture, so that it has the quality of a spring that becomes more rigid as it is extended or compressed out of its normal shape. When in a hurricane the great tree rocks back and forth on its base, and with its immense leverage pulls upon this odd-shaped wooden anchor, instead of straightening out in the soft material, as an ordinary root might, thus allowing the tree to lean over and add its weight to the destructive force of the storm, it grips the sand as the bower-anchor would do, and resists every motion. The elasticity at the point of junction allows one after another of the perpendicular flukes attached to the same shank to come into effective action, so that



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before being drawn from the sand or ruptured the combined flukes present an enormous resistance.

The above drawing I have made for the purpose of simplifying the discussion. It shows a hypothetical Cypress with two roots of the same length and diameter—one with knees, the other without them. The superior strength of the stiffened root would seem sufficiently evident; but, with the view of obtaining the judgment of a mind thoroughly trained in questions of this nature, I submitted the drawing to my friend, Charles Macdonald, late Director of the American Society of Civil Engineers, whose eye has been accustomed to estimating the value of strains in structures by an active experience of twenty-five

years, and who has just finished the largest drawbridge in America, at New London. Mr. Macdonald agreed with me that the root B, which is trussed with the knees C and C', would very largely exceed in capacity for holding the tree firmly in yielding material the root A, which is similar but destitute of knees. This greatly increased security against destruction by storms is, I think, a sufficient advantage to account for the existence and maintenance of an organ that draws so slightly upon the vitality of the plant.

It is proper to record here another observation that may explain the existence of the elevated, narrow point which the knee sometimes develops, and which rises higher than the curved growth that would be necessary to secure the maximum resistance to compression and extension. The home of the Cypress is in broad, level river-margins subject to periodic overflow, where hundreds of square miles become covered with a shallow bed of slowly moving water, or in basin-like depressions, sometimes of vast extent, where from time to time water rises above the level of the horizontal roots. Then these stake-like protuberances, rising into and through the current formed by the drainage or by the winds, catch and hold around the roots of the parent trees many thousand pounds of "plant food" in the form of reeds and grass, or small twigs among which dead leaves become entangled. The tree that exclusively possesses this source of nutrition is at an advantage over all others in the neighborhood, and the higher these attenuated "drift-catchers" rise in the stream, the more drift will they arrest, for the highest stratum of water is richest in float. The theory that some distinguished writers have suggested that the knee is a factor in the aëration of the sap, and that the tree's death is prevented by such aëration taking place in the upper portion of the knee during periods of high water, would seem to need careful experimental confirmation. Where nature forms an organ whose purpose is to preserve the life of the individual, she takes special care to adapt such organ to the function it is depended upon to perform. In this case the rough, dry bark of the knee offers a most imperfect means of access for the oxygen or other gases of the atmosphere to the interior vessels of the plant, and instead of presenting broad surfaces of permeable membrane, formed for transmitting elastic fluids, at its upper extremity the protuberance becomes more narrow and presents less surface as it rises, so that when during periods of high water the life of the tree is most jeopardized, the life-saving organ attains its minimum capacity. In the presence of this manifest want of adaptation it also seems important for the acceptance of the aërating theory that some one should experimentally

show that the aërating organ of the Cypress really aërates to an extent sufficient to make it of material advantage to the plant.⁵

It was long ago observed that no knees are developed when the tree grows in upland upon a firm bottom, in which ordinary simple roots can obtain in the ordinary way the hold necessary to resist overturning forces, and where there is no stratum of water to transport food. So conservative is nature, that she reverts to an original or adopts a simpler form of root even in a single generation if the need for the more complicated arrangement ceases to exist.

Finally, I may perhaps be permitted to add an observation regarding the roots of other trees that trench upon the same soils affected by the Cypress and often take advantage of the anchors it sets so boldly in treacherous bottoms. These trees project their cable-like, flexible roots in every direction horizontally, interlacing continually until a fabric is woven on the surface of the soft earth like the tangled web of a gigantic basket. Out of this close wicker-work, firmly attached to it, and dependent for their support upon its integrity, rise the tree trunks. Thus slowly, and by a community of growth and action, a structure is formed that supplies for each tree a means of resisting the storms. Such communities of trees, provided with ordinary roots, advance against and overcome enemies where singly they would perish in the conflict. The cyclone, the loose sand, the morass—these are the enemies they contend with, as it were, in unbroken phalanx, shoulder to shoulder, their shields locked, their spears bristling against the foe; but the graceful plumed Cypress, the knight-errant of the sylvan host, bearing with him his trusty anchor—the emblem of Hope—goes forth alone and defiant, afar from his fellows, scorning the methods of his vassals, and planting himself boldly amid a waste of waters, where no other tree dare venture, stands, age after age, erect, isolated, but ever ready to do battle with the elements. Twenty centuries of driving rain and snow and fierce hurricane beat upon his towering form, and yet he stands there, the stern, gray and solitary sentinel of the morass, clinging to the quaking earth with the grasp of Hercules, to whom men were building temples when his wardenship began.

⁵ The "Chemical Theory" of the Cypress knee seems to be but a revival of the elaborate hypothesis of Dickinson and Brown, published in their memoir on *T. distichum* in the *American Journal of Science and Arts*, in January, 1848. These industrious observers discard the "Mechanical Theory" entirely, and consider both the spongy knees, and, strangely enough, even the spreading base of the tree, as organs of communication with the air, forgetful that the successful and most celebrated lighthouse in the world—the Eddystone—was avowedly modeled after a similar spreading tree-base for the purpose of withstanding the storm shocks of the English Channel. By means of a curious drawing they show how the swollen portions of the base rise "to the top of the highest water level, which must, in some instances, attain an elevation of at least twenty-five feet;" thus continuing the functions and the structure of the knees, "up the body of the tree to the atmosphere."