Cypress Knees: An Enduring Enigma

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> **The cypresses keep their secrets from the prying investigator.**
> **—J. E. Rogers, 1905**

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Baldcypresses in the Wolf River, near Memphis, Tennessee.

The function of cypress knees has long intrigued botanists. In 1819, François André Michaux wrote, "No cause can be assigned for their existence," and in 1882 Asa Gray concurred. Nevertheless, throughout the nineteenth century and continuing to the present, botanists have put forth hypotheses about the function of these peculiar formations, hypotheses that have included aeration of the root system, vegetative reproduction, mechanical support, nutrient accumulation, and carbohydrate storage. The aeration theory has been the most popular and, indeed, is presented without question in some botany texts, but in fact, no explanation has been generally accepted.[1]

The genus *Taxodium* has been present in North America since at least the Upper Cretaceous, approximately seventy million years ago, but very little is known about when knees first developed and why. Knees can be found on both varieties now extant in the United States. Baldcypress *(Taxodium distichum* var. *distichum)* is distributed along the coastal plain from southern Delaware to southern Florida, west to southeastern Texas, and inland along the Mississippi Valley as far north as southern Illinois and Indiana. Pondcypress *(Taxodium distichum* var. *imbricarium)* has a more limited distribution, with its northern limit in southeastern Virginia and its range extending south throughout Florida and west to southeast Louisiana. The two varieties are readily distinguished by their leaf morphology and the orientation of both their leaves and branchlets. While the leaves of baldcypress are needlelike and generally arranged in two rows, those of pondcypress are scalelike and radially distributed around the branchlets. Also, baldcypress branchlets are horizontally oriented, whereas pondcypress branchlets are often ascending. Where they overlap in distribution, however, there is considerable morphological intergradation.[2]

Visitors to the cypress swamps of the southeastern United States are often intrigued by the swollen bases, or buttresses, of cypresses, and by the woody conical structures—the knees—of varying size found around the base of many trees. More than anything else, the knees resemble termite mounds, but are in fact outgrowths of the shallow, horizontal roots of the cypress trees and are not caused by insect activity. Knees are formed on the upper surface of these roots by the vascular cambium, the

ROBERT H. LAMBORN, FROM GARDEN AND FOREST

The denuded roots of a baldcypress, showing the knees and underground structure.

meristematic layer that produces xylem and phloem, the tissues that transport water and nutrients through the plant. The knees are generally solid, but may become hollow over time due to rotting. In cypress plantations, knees are found on trees as young as twelve years old.[3]

Cypress knees vary greatly in size. In 1803, Andrew Ellicot observed knees as high as eight to ten feet; the tallest on record is a knee fourteen feet in height seen on a tree growing along the Suwannee River, which flows through Georgia and Florida.[4] Many researchers have agreed that it is average water depth that determines the height of knees, and one observer, Mattoon, reported that the knees on trees growing in softer soils were larger than those produced by trees growing on firmer land.[5]

In spite of much research and a plethora of hypotheses, exactly what stimulates cypresses to form knees remains, like the knees' function, unknown. In the following, I will review all these hypotheses and the present state of our knowledge about cypress knees.

The Aeration Hypothesis

Knees are most often found on the roots of trees growing in wet soil and in relatively shallow water; they are generally absent from trees growing in deeper water and only occasionally on trees growing on land that is dry year-round. In 1934, Herman Kurz and Delzie Demaree, working in Florida, suggested that knees may be caused by the root system being alternately exposed to water and air. In 1956, L. A. Whitford, a researcher working in North Carolina, came to a similar conclusion: "The formation of cypress knees seems . . . to be a response of the cambium of a root growing in poorly aerated soil or water to chance exposure to the air during the spring or early summer." Another indication that aeration may play a role in knee development emerged from research done in 1991 by Fukuji Yamamoto, who observed that the number of knees per tree declined with increasing water depth. The fact that knees have been reported on trees found on land that is dry year-round, of course, throws into question the need for periodic flooding or drying to stimulate knee formation.[6]

The need for aeration has been a favorite hypothesis for explaining the function, as well as the formation, of knees. Since all plant roots need a source of air to carry out cellular respiration, some researchers have suggested that knees are simply a form of pneumatophore, or breathing root. Pneumatophores are specialized roots that characterize many woody plants growing in poorly aerated soils, such as in swamps or in the intertidal zone; examples include *Avicennia nitida* (black mangrove), *Sonneratia alba* (mangrove apple), and *Bruguiera parviflora* (small-leafed orange mangrove). Pneumatophores grow either entirely above the level of the water, or in such a way as to be exposed only during low tide. They are characterized by the presence of lenticels (porous regions in the bark that allow gas exchange with the atmosphere) and of aerenchyma, the specialized internal tissues that transport gases through many hydrophytic plants.[7]

The first published suggestion that cypress knees may be a form of pneumatophores dates from 1848, when Montroville W. Dickenson and Andrew Brown wrote in the *American Journal of Science and Arts* that by means of knees "the roots although totally submerged, have a connection with the atmosphere." They also suggested that when the knees were inundated, the connection with the atmosphere could be maintained by the swollen base of the tree, sometimes called the "bottle buttress": "Such enlargements never fail to rise to the top of the highest water level . . ." In 1887 Nathaniel Shaler conjectured that "[the] function of the knees is in some way connected with the process of aeration of the sap . . . " with air entering the knees through newly formed bark at their apex. He also observed that trees died when the water rose high enough to inundate the knees. Two years later, in 1889, another researcher was even more categorical: "[the] location and occurrence [of knees] indicate beyond a doubt that they are for purposes of aerating the plant." In their 1934 paper, however, Kurz and Demaree stated just as categorically that it is "difficult to reconcile the aeration hypothesis with the fact that cypresses of the deeper waters are devoid of knees."[8]

Single young baldcypress with buttressed base growing in Chipman Pond, Delaware.

As early as 1890, Robert H. Lamborn, writing in *Garden and Forest,* had suggested that tests be conducted to learn whether or not knees were indeed "aerating" the trees' roots. Nevertheless, in spite of all the theorizing, little was done to test the pneumatophore hypothesis until 1952, when Paul J. Kramer and his colleagues at Duke University used modern physiological techniques to ascertain the amount of oxygen consumed by knees on living cypresses. They enclosed the knees in airtight containers sealed with a mixture of paraffin and beeswax, and used an oxygen analyzer to measure the amount of oxygen consumed over several weeks. The rate of oxygen consumption was actually lower than for other plants, leading the researchers to conclude that "the available evidence indicates that cypress knees play no important role as aerating organs."[9]

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Baldcypress knees appear to march from dry land into the Wolf River, Tennessee.

Anatomical evidence presents another problem for the hypothesis that knees are a form of pneumatophore. Two studies found that knees lacked aerenchyma—the spongy tissues in true pneumatophores that transport air from the knee to the rest of the root system. In addition, lenticels—the regions of the bark that in pneumatophores allow air to be taken up from the atmosphere—are also absent from cypress knees.[10]

The Methane Emission Hypothesis

A less frequently heard theory is one presented by William M. Pulliam in 1992: "Given the possibility that cypress knees provide a conduit to the below-ground environment, it was hypothesized in the present study that knees may also show methane emissions." Methane is not toxic to plants, but neither is it of use to them.

Pulliam measured total methane emissions from trees in swamps bordering the Ogeechee River in Georgia, finding rates that averaged 0.9 milligrams per day." His tests showed that cypress knees accounted for a negligible amount of the methane emissions from the swamp—less than one percent. This methane is commonly referred to as "swamp gas." Furthermore, it is quite possible that even this miniscule amount of methane was being produced by the bacteria that are found on the outside of the knees, rather than being vented from the soil through the knees.[11]

The Vegetative Reproduction Hypothesis

Lamborn, in his 1890 review of what was known about cypress knees at that time, mentioned and then quickly discarded the idea that cypress knees were organs of vegetative reproduction: "I have . . . examined hundreds of living 'knees' in southern swamps, and found upon them no trace of bud, leaf or sprout . . ." No one has since revisited this hypothesis.

The Mechanical Support Hypothesis

Buttresses and stilt roots provide mechanical support for a number of tropical trees. It was again Lamborn, in 1890, who first proposed that knees perform the same function for cypress trees growing in wet soil: "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." Increased support, he believed, allowed cypresses to withstand strong winds such as those produced by hurricanes. Lamborn suggested that knees located on horizontal roots add stiffness and strength to the junction between the horizontal root to which the knees are attached and the vertical roots that branch off directly below the knees. In 1915, Wilbur R. Mattoon, working for the United States Forest Service, concurred with Lamborn, opining that knees were involved in "enlarging and strengthening the basal support" provided by the rest of the root system. He pointed out that deep roots growing down from the base of the knees provided considerable anchorage for the tree. Both Mattoon and Lamborn premised their hypotheses on the assumption that vertically oriented roots and knees always occur at the same location on horizontal roots, as was apparently the case in their observations. However, Clair A. Brown and Glen N. Montz found that cypresses sometimes produce knees at locations other than above downward-growing roots, and, conversely, that some downward-growing roots do not share a junction with knees on the horizontal roots. And, as with the pneumatophore theory, the absence of knees on the roots of trees growing in deeper water casts doubt on this hypothesis, since there is no reason to believe that they too wouldn't need support. The hypothesis could be tested empirically in the same way that researchers have used cables and winches to pull down trees in order to

Looping Roots vs. Knees

Cypress, as well as water tupelo *(Nyssa aquatica)*, red maple *(Acer rubrum)*, and a number of other swamp and mangrove species, also produce looping roots that somewhat resemble knees. In baldcypress, normal knees are often found at their apex. These looping roots are essentially roots that grow up out of and then back into the soil, producing an aboveground loop or fold. In water tupelo, looping roots can reach a height of 22 inches and a width of 26 inches. The function of these structures, beyond that of normal roots, is obscure. Penfound observed that aerenchyma was lacking in the looping roots of water tupelo and questioned the efficacy of these structures as pneumatophores. Knees have even been reported on pond pine *(Pinus serotina)* growing under wet conditions in Georgia. It is unclear if these resemble normal knees or looping roots.[16]

A looping root of red maple (Acer rubrum) *growing in a swamp at Adkins' Mill Pond, Maryland.*

Knees are beginning to form at the apex of the looping roots of a cultivated baldcypress.

compare the stability of buttressed versus non-buttressed tropical trees—such a test could compare trees with knees to trees that have had their knees removed—but no one has yet done so.[12]

The Nutrient Acquisition Hypothesis

Lamborn postulated that another secondary function of cypress knees, along with that of giving mechanical support, was to act as "drift catchers" that accumulate organic nutrients during periods of water movement. A hundred years later, Hans Kummer and his colleagues at Zurich made a similar supposition about looping cypress roots, which they also called knees, after studying baldcypress in a Florida cypress dome. (A cypress dome is a group of cypresses growing in a shallow depression where the largest trees are located in the center and tree height declines toward the periphery.) They found that the number of looping cypress roots present were highly correlated with the number of dead cypress trees in the dome, but not with the number of live trees. In other words, looping root density increased with an increase in the number of dead cypress stumps. They also observed that approximately 98 percent of the youngest looping roots spread over the stumps and penetrated the dead wood. Older looping roots were not generally in direct contact with decaying stumps. Direct evidence of nutrient acquisition was not obtained, however. Kummer and his colleagues suggested that further work was needed to determine if "young root loops extract nutrients from stumps . . . [or] . . . use stumps merely as vertical supports to reach air above the water table.[13]

Baldcypress trees with buttresses at Trussum Pond, Delaware

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The Carbohydrate Storage Hypothesis

Clair A. Brown in 1984 and again with Montz in 1986 postulated that the primary function of cypress knees is as a storage organ. They reported the presence of "granules"—presumably amyloplasts (organelles that store starch)—and confirmed the presence of starch by performing iodine tests on the cut surface of sectioned knees. Even if their hypothesis is accurate, unanswered questions remain about the function of knees. Why do cypresses need an auxiliary storage organ when growing under wet conditions, but not dry? Is it possible that cypress roots in general store starch, and that knees are simply extensions of these storage areas? Unfortunately, no comparison of the storage capacity of roots and knees has been made to test the hypothesis.[14]

After nearly two hundred years of speculation and research, the function or functions of the knees of cypresses remain unclear. Darwin referred to the origin of the flowering plants as an "abominable mystery"; it appears that the function of cypress knees is another.[15] The truth may be that cypress knees evolved in response to past environmental pressures that no longer exist, in which case their function may be lost in the depths of time. Before we accept this conclusion, however, much further research is needed on this fascinating subject.

Endnotes

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