

Variation in Buttressing Form and Stem Volume Ratio of Baldcypress Trees

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ABSTRACT

The volume and form of 92 baldcypress (*Taxodium distichum*) tree buttresses and stems were quantified at three locations in the Cache River Watershed of southern Illinois at the northern edge of the species' natural range, and at a plantation in central Illinois. The percentages of total stem volume contained in buttresses, calculated using frustums for buttresses and stems above buttresses, were 19, 27 and 27 in natural cypress stands of southern Illinois with maximum tree ages from 100 to 1,000 years, but only 10 in a 60-y-old planting in central Illinois. No significant difference was found between the buttressing support ratios of the largest trees and smaller trees at a site ($P = .1587$). A stepwise multiple regression analysis of site factors yielded a best-fit equation with mixed categorical and continuous variables. Soil type (site), maximum tree age at a site and crown diameter had the highest significance values ($P < 0.01$). Buttress forms were quantified as [height / (diameter of buttressing at soil level – diameter above buttressing)]. Subjective classification of buttresses into three forms described by Mattoon (1915) could be matched by three distinct ranges in calculated buttress form values. Distribution of buttress-form classes also varied by site. Buttress volume was greater on sites with frequent flooding and minimal on sites having trees that were infrequently flooded or not exposed to flooding at all. The height and forms of buttressing were a function of flooding depths. Low, wide, table-top buttressing topped with buttress frustums occurred on ancient trees in broad alluvial floodplains that had probably experienced shallow floods over the centuries-long course of their development. Tall buttress frustums occurred on sites with frequent, deep floods or reservoir level fluctuations. Results constitute novel quantifications of buttress development using frustums to calculate form values. Results illustrate the capacity of baldcypress to allocate carbohydrate to buttressing in response to flooding frequency and depth of flooding during the time span of baldcypress growth and development.

Keywords: buttress, Cache River, flooding, *Taxodium distichum*

INTRODUCTION

The swollen bases, or buttresses, of tree species are evocative of lowland forests in the wet tropics (Kaufman 1988), but similar basal swelling is common in swamp and floodplain forests in temperate areas. Baldcypress, *Taxodium distichum* (L.) Rich., displays buttressing in wetlands across its range in the Southeastern United States and this species is often the dominant tree in both deep-water swamps and bottomland forests, occurring across a range of poorly drained to well-drained areas (Mattoon 1915).

The Cache River watershed of southern Illinois USA is unique in that it meets at the convergence of four major physiographic regions, one of only six locations in the United States where four or more regions overlap according to the Illinois Department of Natural Resources (IDNR 1997). The regions include southwestern portions of the Shawnee Hills, northern portions of the Mississippi Embayment, southeastern portions of the Salem Plateau, and southern portions of the Till Plains (Wetlands International, 1994). This area contains the last sizable remnants of the once exten-

sive baldcypress and tupelo swamps of the "coastal plain" region of southern Illinois. The watershed is just north of the junction of the Ohio and Mississippi Rivers, which greatly affects the flooding and drainage of the Cache River.

Remnants of biologically rich wetlands are found within the Cache River basin. The primary reason for the shrinking acreage of wetlands in Illinois has been the drainage conversion of wetlands into agricultural lands, which has become the dominant form of land use. Only about 4% of the Cache River watershed remains as native wetland, although efforts are being made to increase this percentage through restoration (Watcher 2006). The least-disturbed remaining wetlands in the area are considered the highest quality aquatic and terrestrial natural communities remaining in Illinois. Wetlands within this area are so important to migratory waterfowl and shorebirds that in 1996 the Ramsar Convention collectively designated them a Wetland of International Importance, only the 19th wetland in the United States to receive the distinction (Wetlands International 1994).

The function of buttresses has been exten-

sively studied in tropical settings (Hennwood 1973; Richter 1984; Kaufman 1988; Lewis 1988; Warren et al. 1988; Young and Pekocha 1994; Crook et al. 1997; Woodcock et al. 2000). Past studies provide evidence that trees allocate volume faster to areas that are subjected to stresses (Ennos 1993, Mattheck and Kubler 1995). Ethylene produced in basal stem tissue of trees results from stress, such as mechanical and flooding stresses, and has been correlated with buttress development (Messina & Conner, 1998). The precise environmental and genetic mechanisms that cause differential buttress development in baldcypress remain to be detailed. Buttressing is thought to be a mechanical adaptation that apparently prevents tipping and uprooting of trees by wind and gravity, especially in shallow or unstable substrates (Mattheck 1991).

The anchorage efficiency of tap roots falls as trees get bigger, and so larger trees would be afforded additional support by having increased buttressing (Ennos 1993). Baldcypress has lateral roots with deep roots developed below cypress "knees" along with buttress development (Mattoon 1915). This

root form makes baldcypress an extremely stable tree under conditions of soft anchorage and lateral mechanical stress of wind or floodwaters.

Larger buttresses lend more support to the tree, and their extent may be an adaptation to the soil types and environment in which they grow. Soil type has been related to buttressing in Malaysia where buttressing has been found to be more common and more massive on loams and clayey soils than on sandy spodosols (Richard 1936). Ecological aspects of buttressing in temperate zones have not been extensively studied.

Variation in buttress form in baldcypress has been observed and qualitatively differentiated (Mattoon 1915; Kurz and Demaree 1934). The differences have been attributed to hydrologic aspects of the trees' environment. Kurz and Demaree (1934) believed curvature in buttressing was a function of the duration of time the trunk was exposed to various combinations of water and air. Mattoon offers no reason for varying form, but associates each form with a wetland type. Kurz and Demaree (1934), and Mattoon (1915), similarly describe three forms of buttressing. Mattoon describes a buttress form with a low, very broad base in shallow swamps associated with alluvial systems. He also describes a high, full basal form in active or fresh water subject to deep inundations, as well as a low, small basal swell typical of broad overflow regions of rivers and of large inland swamps that are subject to periodic, shallow inundation. The images provided by Mattoon (1915) and Kurz and Demaree (1934) closely resemble forms of baldcypress observed in this study.

In order to quantify buttressing and associated stem volume, the height and diameters of conical basal buttresses and connected tree boles can be transformed into frustums for calculating volumes and the volumes can be converted to ratios for each tree. In geometry a frustum is the part of a conical or other solid left after cutting off a top portion with a plane parallel to the base. Using a frustum geometric approximation allows for rapid, practical estimation of stem and buttress volume without the extensive measurement and mathematical effort that would be necessary to obtain the volume of individual buttresses. This latter method would require a large number of approximations of curvatures of the

irregularly-shaped buttress and stem forms or spatial mapping of the actual surface of each buttress above and below water. This degree of accuracy would require technology beyond the needs of comparative ecological studies. We expect that frustums will distinguish buttress and above-buttress tree volumes sufficiently to differentiate ratios associated with site and tree variables.

Quantitatively distinguishing buttress form by calculating values for them and relating these values to site properties could provide empirical evidence for or against the air/water relationship hypothesis presented by Kurz and Demaree (1934) as well as the mechanical support hypotheses.

The main goals of this study were to: 1) Quantify buttress form and volume 2) analyze variation in the ratio of buttress volume to total-stem volume in baldcypress and 3) assess the site and tree variables associated with variation in percentage of tree stem biomass allocated to buttressing and buttress form across sites with different hydrological regimes.

METHODS

Study Sites

This study was conducted in the Cache River Watershed in southern Illinois and in an upland plantation in Urbana, Illinois during the spring of 2010. The Cache River Watershed is south of the limit of glacial drift in Illinois, and has varying elevation and topography. Elevations in this region range from 85 meters above sea level at the junction of the Ohio and Mississippi Rivers to 271 meters above sea level in the northern part of the watershed. Trees were sampled at three different sites in the Cache River Natural Area.

One study site is within the Mermet Lake State Conservation area in Massac County, Illinois (37° 15' 44" N, 88° 51' 2" W) and is on the historic floodplain of the Ohio River within the Mississippi River embayment. Mermet Lake is a baldcypress swamp, which has been dammed for management as a waterfowl hunting area of 1,064 hectares with 279 hectares of permanent water. Baldcypress trees line the edges of the lake in relatively shallow water (0-12 cm depth to soil). Other typical plant species present included sugarberry, *Celtis laevigata* Willd., buttonbush, *Cephalanthus occiden-*

talus L., common cattail, *Typha latifolia* L., Gray's sedge, *Carex grayii* J. Carey, broad-leaf arrowhead, *Sagittaria latifolia* Willd., and giant duckweed, *Spirodela polyrrhiza* (L.) Schleid. Forest basal area at our study site was 28 m² per ha. The soil at the study site is Ginant silt loam, which is classified as poorly drained, with rare flooding (Soil Survey Staff 2010). However, water level fluctuation associated with waterfowl management is extreme. The baldcypress trees in the study area were estimated to be no more than 100 years old, as the area was extensively cut and used for agriculture up until the 1930s (Nelson et al. 2008).

Heron Pond is a 30-hectare baldcypress-tupelo swamp in Johnson County, Illinois (37° 22' 1.2" N, 88° 57' 0" W) and is adjacent to the Cache River, on the historic floodplain of the Ohio River. It is upstream of the Post Creek Cutoff, which was constructed between 1912 and 1915 to divide the river into the Upper and Lower Cache and drain it into both the Ohio and the Mississippi Rivers. Therefore it is considered a hydrologically undisturbed site (Middleton 2000). Baldcypress are canopy dominants at this site, with some codominant water tupelo. Beaver dams account for standing water at this site and the water level fluctuates in accord with precipitation, reaching lows permitting cypress regeneration during drought periods. Two species of small floating plants, *S. polyrrhiza* and Mexican azolla (*Azolla microphylla* Kaulf.) cover the water surface in summer. Drummond's maple, (*Acer rubrum* var. *drummondii* (Hook. & Arn. ex Nutt.) Sarg.), swamp privet, *Forestiera acuminata* (Michx.) Poir., and button bush, are present near the edges of the swamp. Forest basal area at this site is 30 m² per ha. The soil at Heron Pond is Piopolis silty clay, which is classified as poorly drained with frequent flooding (Soil Survey Staff 2010). Trees in Heron Pond are estimated to be 300 years old (Personal Communication, Mark Guetersloh, Natural Heritage Biologist, Illinois Department of Natural Resources).

The Big Cypress Access Area is a floodplain forest in Pulaski County, Illinois (37° 17' 32"N, 88° 58' 30" W). It is on the Lower Cache River within Buttonland Swamp. The study site is approximately 26 hectares in area and does not have standing water, although there is evidence of ponding after

rainfall and minor flooding. Aerial photos show that the surrounding areas were cleared for agriculture in the 1950s. Before this modification, water overflowed the banks of the Cache River onto a wide floodplain for 6-8 months of the year (Cache River Drainage Commissioners of Illinois 1905 as cited in Middleton 2000). The area is dominated by baldcypress and water tupelo, with button bush, sugarberry, overcup oak (*Quercus lyrata* Walter), cherry bark oak (*Quercus pagoda* Raf.), green ash (*Fraxinus pennsylvanica* Marshall), and swamp privet. Forest basal area at this site is 32 m² per ha. The soil of the Big Cypress Access Area is Karnak silty clay, which is classified as very poorly drained with frequent flooding (Soil Survey Staff 2010). However, after the Post Creek Cutoff construction, the Cache River no longer followed its former route in the Buttonland Swamp and Big Cypress Access Area. Coupled with channelization and dredging in the 1960s, the Post-Creek Cutoff caused this area to be dry for extended periods of the year, even though water still drained into the site from Big Creek and Cypress Creek (Middleton 2000). Some of the trees at this site are over one thousand years old (IDNR 2010).

A baldcypress plantation at the University in Champaign County (40° 4' 36" N, 88° 12' 46" W) was a fourth study area. This site is approximately 0.24 hectares in area and is unflooded. Forest basal area at this site is 37 m² per ha. The soil in the plantations is Drummer silty clay loam, which is a poorly drained with no flooding (Soil Survey Staff 2010). The age of trees within the plantation is 60 years, based on planting records from the Department of Natural Resources and Environmental Sciences, University of Illinois (Data available from authors).

Sampling

Individual baldcypress trees were sampled as they were encountered on either side of a transect fitted to the maximum length dimension within each sampling area. To make a distinct record for each tree, a Garmin E-Trex Vista H (Olathe, Kansas) GPS unit was used to record the coordinates (data available from authors). Tree heights were measured with a Laser Range-finder/Hypsometer (Insight 100 LH Opti-logic Corporation, Tullahoma, TN). Cir-

cumference measurements were taken just above the buttress, which is defined as the point at which the buttress no longer angled towards the trunk, as well as at soil level. The height of the buttressing, defined as the distance from the soil level to the height just above the buttress swell, was measured and recorded for use in volume estimation. The diameter at mid stem of each tree was measured with Mantax Precision callipers with attached laser beams (Haglof, Sweden) and the height to this point was again measured with the Rangefinder/Hypsometer. Two perpendicular transects of crown diameter were taken with a tape measure and then averaged. At each tree, the forest basal area was measured with a 10-factor wedge prism. The water depth above soil level at time of sampling was measured at 2 or 3 points around each tree at random coordinates, and then averaged for each tree. Soil information was gathered for each site from the National Resource Conservation Service's Web Soil Survey.

Volume Estimation

Roth (1898) determined that the weights of wood taken from all parts of the baldcypress tree are very similar indicating that volume is directly proportioned to mass and would not be confounded by varying specific gravities between buttresses and stems. Thus volume estimation can be used as a surrogate for buttress and stem mass and as a viable measure of buttressing. The circumference measurements above buttressing and at soil level, and their ratios, as

well as the height of buttresses, were used to create a buttress volume estimate. Buttressing volume was simplified into frustums, $\pi h/12(d^2 + db + b^2)$, where h is the height, d is the diameter at the top of a buttress and b is the diameter of buttressing at the soil level. The tree's stem volume, based on stem height above buttressing and diameter at mid-stem, were projected as frustums, according to Varnell (1998). For trees with table-top buttressing (Form a, Figure 1), the volume estimations were adjusted by incorporating an additional measurement (table-top volume in addition to buttressing above the table-top buttress) to assess volume for this particular buttress form. The total volume of both frustum complexes was then calculated, and the percentage of the total buttress volume with respect to total above-soil tree volume was defined as the buttressing support ratio. This ratio approximated biomass allocation to supportive buttressing tissue in trees. Volume ratio measurements were then used for statistical analysis.

Buttress Form Measurements

Another measure of buttressing, the change in diameters with increasing height of buttressing was used to relate our measurements to previously observed buttress forms. In order to illustrate buttress forms presented by Mattoon (1915), the buttress images were copied in Sketchup version 7 (Google Inc, 2009) to produce a guide to forms similar to those encountered in the field. Measurements of tree buttresses

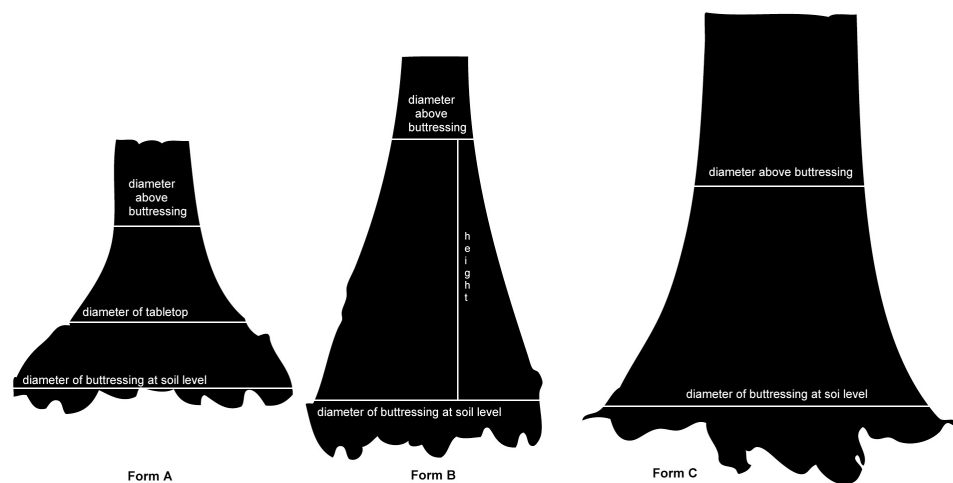


Figure 1. Parameters used to determine baldcypress buttress volume according to Mattoon's (1915) classification of buttress forms.

matching these form classes were taken as indicated on the drawings of the diameter of buttressing at soil level, the diameter just above the buttress flare, and the height difference between the two (Figure 1).

Ratios of change in buttressing [height / (diameter of buttressing at soil level – diameter just above buttressing)] were calculated and then associated with each form and a range of form ratios was determined in order to classify the tree buttresses encountered in the field.

Statistical Analysis

Analysis of variance of mean buttress support ratios, defined as the percent of each tree’s buttress in relation to the estimated aboveground volume of the whole tree, was performed to allocate contribution to variation among selected tree and site variables and estimate the most important selected factors that contribute to overall variation. Employing R version 2.9 software’s base package (CRAN, 2010), variable selection for the multiple regression model was computed using a stepwise approach. The procedure involved a forward selection of variables with a test for backward elimination. A P-value of 0.1 was chosen for both entry and removal from the model. A formal score test for non-constant variance suggested that the constant variance assumption was violated. Based on the Q-Q plot, the normality assumption of the errors appeared invalid. The Box-Cox power transformation method, which maximizes the likelihood of the data, suggested a logarithmic transformation of the dependent variable (the buttress support ratio). After the transformation, the constant variance and normality assumptions were justified. The relationship of baldcypress buttress volume to aboveground tree volume and average crown diameter, water depth at tree base at sampling time, estimated maximum age of dominant trees, presence of regeneration at the site and soil type (representing soil flooding frequency class) was described by the equation $\ln(V) = -1.37 + 0.05 \cdot C + 1.99 \cdot W + 1.92 \cdot A + 2.2 \cdot R + 3.10 \cdot STNA + 1.62 \cdot STA$, where V is the percent volume allocated to buttressing, C is the average crown diameter, W is the water depth, A is the estimated maximum tree age, R is the presence of regeneration (indicating water level fluctuation and dis-

tinct cohorts of trees), STNA is nonalluvial soil type and STA are alluvial soil types. Factors selected were intended to identify variables most-strongly related to variation in buttress support ratios. Additional analysis was performed using Microsoft Excel version 11.5. A two-sample t-test assuming equal variances was used to test for differences between buttressing support ratios between the oldest trees and the remaining sampled trees at each site. Average buttress support ratios were calculated for each site to illustrate the overall role of site in buttressing support ratios.

RESULTS

The model equation explained 57% of the variation in the support ratio ($R^2=0.57$, $P < 0.0001$). Soil type (site) and maximum tree age were the most significant variables in the model ($P < .001$) followed by average crown diameter ($P < 0.01$) and water depth ($P < 0.05$). The root mean square deviation is 0.532. Analysis of the standardized residuals showed no gross departures from the underlying assumptions of regression.

Distinct ranges of height/(diameter at ground level – diameter above buttressing) ratios of buttress were found to conform to the three subjective form classes (Table 1). The range was based mainly on height of buttressing, as it was found to be the most influential form factor.

Table 1. Range of height/(diameter at ground level – diameter above buttressing) ratios was used to quantitatively classify buttressing forms for this study according to the forms described by Mattoon (1915). (Figure 1).

Buttress Form	Comparable range of ratios in field
A - Broad Ledge	0.2-0.5
B - High	0.85-2.0
C - Low to intermediate	0.51-0.84

Mean buttress support ratio varied according to site (Table 2) when related to current flooding regimes. The average support ratio of buttressing on baldcypress plantation sites without flooding was 9.59, for shallow flooding and occasional ponding of a broad alluvial floodplain it was 27 and for impounded water bodies with nearly-continual inundation and water level fluctuations ratios were 19 and 27 ($P < 0.0001$, Table 2).

Trees at each site were classified into one of three forms (Tables 1, 3) based on corresponding ranges of height/(diameter at ground level – diameter above buttressing) ratios of buttresses. The percentage and number of sampled cypress trees in each form category at each site are represented in Table 3.

Table 2. Average buttressing support ratio* of baldcypress (*T. distichum*) according to site features.

Site	Estimated maximum tree age (y)	n	Soil type (long term flooding patterns)	Current flooding regime	Mean buttress support ratio
Illini Plantations	60	20	Drummer silty clay loam (None, but poorly drained soil)	None	10
Mermet Lake	100	22	Ginant silt loam (Infrequent severe flooding by major river systems of the Ohio and Mississippi)	Dam - Nearly continuous flooding. Annual and seasonal variation in water level managed for wildlife.	27
Heron Pond	300	35	Piopolis silty clay (Frequent flooding of Cache alluvial plain)	Beaver dams -Nearly continuous flooding. Annual and seasonal variation in pond water level in undisturbed portion of Cache River floodplain.	19
Big Cypress Access Point	1000	9**	Karnak silty clay (Frequent shallow flooding of broad Cache alluvial plain)	Channel of Cache River deeply cut due to drainage. Flooding and ponding have decreased since drainage.	27

*Buttressing support ratios were calculated as percentage volume of each tree. Differences between averages were significant ($P < .001$).

**Four of 13 trees sampled were excluded from this analysis because they were suppressed.

Table 3. Percentage of above-ground volume contained in buttresses according to their form at study sites. The letters A, B, and C represent forms illustrated in Fig. 1.

Site	% form A, buttress with broad ledge	% form B, high buttress	% form C, low buttress
Heron Pond	0	97 (n=34)	3 (n=1)
Big Cypress	15 (n=2)	23 (n=3)	62 (n=9)
Mermet Lake	0	86 (n=19)	14 (n=3)
Plantations	0	20 (n=4)	80 (n=16)

DISCUSSION

Buttress Form Quantification

Value ranges for height/(diameter at ground level – diameter above buttressing) ratios of buttresses in this study (Table 1) can be used to quantify observations of Mattoon (1915). Where more fluctuations between exposure to water followed by air occur, the more the buttress swells. Indeed, Kurz and Demaree (1934) suggest that without sequences of aeration and flooding, maximum swelling will not occur.

In “Southern Cypress”, the low, very broad base form A (Figure 1) tended to occur in shallow, non-alluvial wet swamps. Form B is classified as having high basal swell extending up the base of the stem in active or fresh water subject to deep inundations. Mattoon described form C as having small basal swell “typical of broad overflow regions of the Lower Mississippi River and large inland swamps”. The three sites in this study in the Cache River Watershed are classified as the overflow region of the Upper Mississippi River, and these sites all have alluvial parent material. Yet Mattoon’s hydrologic associations correspond to specific inundation patterns in the Cache River Watershed.

The only site having trees of Form A with extensive, low, flat ledges was the Big Cypress Access Area, a forested site with scattered, shallow pools of water on the margin of a broad Cache River floodplain. Because the trees at this site include some of the oldest trees in the region, it is probable that the forms found here represent the predominant hydrologic regimes over the past 1000 years prior to drainage of the Cache River watershed. According to Kurz and Demaree (1934) this form suggests there were repeated cycles during which the lower tree stem was exposed to shallow flood waters

followed by exposure to air when the floodwaters receded during buttress formation.

Form B, high buttresses, was dominant at Heron Pond and Mermet Lake, both sites of prolonged variable inundation. Thus, Mattoon’s description of high basal swell with deep inundations was consistent with our findings. Kurz and Demaree (1934) also discuss form B. They suggest (Figure 1, Form B) that a cypress tree’s diameter of buttressing at the soil level was subject to alternating inundation and aeration conditions with nearly twice the amount of time of buttress flooding compared with the stem above buttressing. The conditions of relatively deep standing water with periodic flooding at Heron Pond and Mermet Lake are consistent with these observations.

Form C, low buttresses, was most common in the unflooded plantation site in Central Illinois. Though Mattoon (1915) made no classification for basal swell in dry plantation sites, it is apparent that form C was characteristic of the driest baldcypress stands observed. Kurz and Demaree (1934) suggest that this form has resulted from the least amount of inundation in natural stands.

The other tree form most commonly found at Big Cypress Access Area was form C (Table 3, Fig. 1) having low to intermediate buttresses. This suggests a drier environment influenced the younger trees that were in this form class which would have attained much of their growth after regional drainage in the Cache basin occurred in the mid 20th Century. After this period of drainage efforts, stream channel cutting by the Cache occurred here and at other locations in the Cache watershed. This likely decreased flooding amount and frequency in the 20th century could explain the occurrence of all three form types at the Big Cypress Access Area.

T. distichum appears to have adapted to varying levels of inundation through differential carbohydrate allocation for support as influenced by ecological factors.

Buttress Support Ratios

Results are consistent with the hypothesis that buttress support ratio is associated with different elements of force, including gravity. Soil type, together with maximum

age and crown diameter, components of overall tree volume and mass, were important variables identified using stepwise regression. As a tree ages, the stem grows in height and girth, the crown expands and the buttressing of trees increases.

Depth of water at time of measurement corresponded with nearly-permanent flooding of a site. Only two sites, Mermet Lake with a buttress support ratio of 27 and Heron Pond with a support ratio of 19, were nearly-permanently flooded sites having water around the trees most of the time. The significance of this variable may be that long term inundation of a site along with varying water levels influenced the buttress support ratio as well as the form of buttresses (Tables 2, 3)

Mean allocation of phytomass to buttressing (Table 2) is lower in the dry plantation site and among the cohort of nine younger trees in form C at the Big Cypress Access Area (Table 2, last column). These younger trees are presumed to have developed since drainage and channelization of the Cache basin occurred in the mid 20th Century. Buttress forms associated with the least flooding are also found at these sites (Table 3). This is consistent with the idea that the trees do not produce the largest supporting buttresses absent the influence of flooding (depth and frequency) and probably stress associated with the instability of wet soils.

The Mermet Lake study site was subject to extreme linear winds during a 2003 storm. Most of the angiospermous swamp trees that occurred in this wetland were uprooted. Many were found at the time of the study to be leaning against erect, unmoved baldcypress trees. The baldcypress trees resisted both the storm wind forces and additional forces associated with the weight of the uprooted trees.

The increase in crown diameter of an individual tree tended to be correlated with an increase in the buttressing support ratio, suggesting the importance of gravitational forces in determining the relative size of buttressing. Similarly, buttressing extent and stem size were correlated in a study by Lewis (1988), suggesting that greater mass increases buttressing to support the stem. The similarity of the basal areas for the natural areas in southern Illinois (28, 30

and 32 m² per ha), suggest that differences in tree crown development due to competition were not a likely factor influencing the buttressing support ratios on these sites. The highest basal area of 37 m² per ha was at the plantation site in central Illinois, which had lower individual dbh values, higher tree density and higher stocking value. This condition results in narrower crowns due to competition. Also, younger, crowded trees develop less mass per tree. This is consistent with the plantation's low mean buttress support ratio of 10, which is likely due in part to lower mass values for trees which were tall with thin stems and narrow crowns due to light competition.

Maximum age was significant in the model. The maximum ages used were estimates and largely linked to study sites. The trees at the Mermet Lake conservation area, were short relative to trees at other study sites including the younger trees in the unflooded plantations of central Illinois. Although cypress trees are able to tolerate long periods of flooding and their ecological niche is wetlands, this species actually grows better on mesic sites having growth conditions that are generally better for plants. Trees at the plantation site had greater mean height than the trees at the Mermet Lake site (15.8 m and 8.9 m respectively), despite the fact that they were 20 years younger. This is likely due to the fact that height growth is not affected by density as much as it is by site quality. The rich mollisol of the central Illinois plantation site is more productive than the nearly-permanently flooded alluvial soil of Mermet Lake. Tree buttressing of form B, high buttresses, is dominant at Mermet Lake, which has nearly-permanent flooding and fluctuations in the water level. The mean height value for 13 trees sampled at the Big Cypress location was 26 m in a stand that had cohorts of tall ancient trees estimated to be 1,000 years old as well as cohorts developed within recent centuries. Heights at this location ranged from 58.4 m to 18 m.

The past hydrology of the Big Cypress Access Area, which has both ancient trees and cohorts of younger trees, is uncertain, though it has probably not recently had the fluctuations in water level typical of the Cache River prior to mid-20th-century drainage activities. Overflows of the Cache River in this broad, lowland area

were probably more frequent before drainage accelerated channel erosion, evidenced by downcutting, and lowering of the level of the river. The size (age) of regeneration cohorts suggests that baldcypress seedling establishment, requiring exposed soil substrates, occurred both before and after drainage of the Cache River. Thus past hydrological regimes apparently favored baldcypress regeneration where water levels reached zero at Big Cypress Areas and influenced buttressing form.

At the Big Cypress Access 15% (n=2) of the trees were ancient, perhaps as old as 1,000y, with the "tabletop" buttress form A (Table 3) and with buttress support ratios as high as 50%. Big Cypress had a great range in buttress support ratios and forms in the multiple cohorts of smaller, younger trees in form classes B and C, which had lower buttress support ratios (Table 2). This suggests the probable importance of age in concert with hydrological factors in determining the maximum values of buttress support ratios in old-growth forests, but greater influence of site hydrology on buttressing form and support ratio in younger stands.

Regeneration of baldcypress depends upon fluctuation of water levels so that soil is exposed to enable cypress establishment from seed. Long periods of inundation also reduce competition from plants that are not as flood tolerant as baldcypress. A recent study in Louisiana by the Coastal Wetland Forest Conservation and Use Science Working Group, found that seasonal fluctuations in water level are essential for baldcypress seedling survival (SWG 2005). These findings are consistent with previous studies and observations (Mattoon 1915; Cain 1935; Mitsch et. al 1979). A cohort of young cypress trees at Heron Pond can be dated to drought-induced low water levels of 2004. During this season, the soil was exposed creating conditions suitable for baldcypress seedling establishment. Thus, cypress regeneration is probably a function of variable flood pulses and pulse intervals, which influence stand structure as well as buttress form and buttress support ratio. The historical flood pulse pattern in riverine baldcypress swamps of the northern portion of the southeastern United States is typically high in the winter and low in the summer (Voigt and Mohlenbrock 1964).

Novel, quantitative measures of buttress form and ratio, hence relative stability of baldcypress trees in dynamic environments, resulted from this study. Baldcypress trees apparently are adapted to respond to environmental variables, especially dynamic flooding regimes, by increasing the proportion of stem resources allocated to supportive buttresses. Simple ratios of height/ (diameter at ground level – diameter above buttressing) yielded distinct, quantitative ranges corresponding with each buttress morphology type described in early references.

ACKNOWLEDGEMENTS

This work was supported in part through an internship to Christina Walsh provided by the National Great Rivers Research & Education Center (NGRREC). This is a publication #56. Whitney Hill and Timothy Ward, Interns at the University of Illinois Dixon Springs Agriculture Center funded by the Illinois Agricultural Experiment Station, helped with data collection. Gregory Bopp, University of Illinois Department of Statistics, helped with statistical analysis. Thanks to Anna McClane for image creation and formatting.

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