FLOODING EFFECTS ON STAND DEVELOPMENT IN CYPRESS-TUPELO

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Abstract—The effects of inundation on growth of cypress (*Taxodium* spp.) and tupelo (*Nyssa* spp.) trees have been extensively researched, but conclusions are often complicated by attendant effects on stand development. Flooding affects development of cypress-tupelo stands by limiting seedling germination and survival, truncating species richness, and reducing site quality. Persistence of the cypress-tupelo type therefore depends on flood stress sufficient to prevent establishment of other species, and sufficient stability of hydrologic regime to prevent mortality. This research investigated the role of flooding stress in controlling stand development in a pair of natural bald cypress (*T. distichum*)-water tupelo (*N. aquatica*) stands in Louisiana. Both stands have been at high enough density to experience self-thinning during the duration of the measurements, 1980 to 2005. Bald cypress is establishing dominance in both stands because of crown breakage in water tupelo, but flooding stress itself does not appear to be favoring one species over another. The most obvious effect of flood stress on stand development is to slow the rate of growth and self-thinning.

INTRODUCTION

There are presently about 342 000 ha of second-growth, even-aged bald cypress [*Taxodium distichum* (L.) Rich]-water tupelo (*Nyssa aquatica* L.) forests in coastal Louisiana (Chambers and others 2005). Most of these stands originated after clearcut logging from about 1880 to 1930; much of the area regenerated naturally then received little subsequent attention (Conner and Toliver 1990). Commercial timber management in some second-growth stands is attractive because many stands now consist of sawtimber-sized trees (Williston and others 1980). In addition to concerns about the role of forest management in these complex wetlands that have multiple ecosystem services subject to degradation from logging (Aust and others 2006, Shepard 1994), there is also a paucity of information on basic silvical processes such as regeneration, intraspecific competition, self-thinning, and responses to stand manipulations that are needed for development of appropriate management strategies.

Perhaps the most salient property of cypress-tupelo swamps is that they occupy sites with the highest degree of stress from flooding of any forest type in the region. Flooding effects on stand initiation and intraspecific competition have been extensively researched. Flooding delays or prevents germination of most species, and tolerance varies across species (Hosner 1957). Inundation of seedlings similarly reduces species diversity because many species cannot survive more than 2 weeks of inundation (Hosner 1960). Timing of flood events interacts with germination times to stochastically control seedling establishment (Jones and Sharitz 1998; Jones and others 1994, 1997). Flooding stress can also eliminate many species from the stand by causing mortality long after establishment (Broadfoot and Williston 1973, Conner and others 2002, Kozlowski 2002). All these processes reduce competition with *Taxodium* and *Nyssa* by other species less tolerant of flooding (Eggler and Moore 1961, Young and others 1995).

Less is known about the role that flood stress plays in the development of cypress-tupelo stands once they reach the self-thinning stage. Rapid changes in hydrological regime that cause extensive mortality (e.g., Eggler and Moore 1961, Harms and others 1980) are obvious drivers of stand development, but differences in stand development among sites with relatively stable hydrological regimes have been more difficult to explore. For example, although there has been extensive work to understand differences between cypress and tupelo in regeneration (e.g., Effler and Goyer 2006), the role of competition and flood stress on species composition and canopy structure is less certain. Dicke and Toliver (1990) compared 5-year growth rates and mortality in two sites with differing flood regimes and concluded that bald cypress outcompetes water tupelo in a seasonally flooded site, whereas continuous flooding favors neither species.

The archetypal cypress-tupelo stand has experienced sufficient flood stress to eliminate nearly all other overstory species. However, variation in hydrological regime and resulting flood stresses can threaten these stands. *Taxodium* (and to a lesser extent *Nyssa*) are very long-lived individuals that can persist even when the site hydrological regime has changed and is no longer suitable for regeneration (Devall 1998). Many cypress-tupelo swamps in the Delta of the Mississippi River now occupy sites where hydrological regimes are changing rapidly (Conner and Brody 1989). In addition to observed reduction in regeneration (Conner and Toliver 1990, Conner and others 1986), there are also indications that mortality and decreased growth of existing trees are widespread conditions across the region (Chambers and others 2005, Keim and others 2006).

The objective of this work is to identify how flood stress affects stand development in cypress-tupelo. We test the hypotheses that (1) flooding slows development of structure in established cypress-tupelo stands but does not affect the nature of the self-thinning process, and (2) flooding does not give a competitive advantage to either *Nyssa* or *Taxodium*. To make these tests, we use stand density as a measure of competition (Jack and Long 1996, Long 1985). We track development of two stands through stand density space,

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and employ established competition theory to address the hypotheses.

METHODS

Study Sites

The study area is a pair of stands in the Atchafalaya River Basin Floodway in southern Louisiana. The stands are in the same large area of swamp but differ in their hydrological condition. The Pigeon site, which was termed “seasonally flooded” by Dicke and Toliver (1990), is slightly drier than the Mallet site, which was termed “continuously flooded” by Dicke and Toliver (1990). Pigeon is slightly higher elevation and is on the lower elevation portion of the natural levee of Bayou Pigeon. Mallet is on the crest of the natural levee of Bayou Mallet. Thus, Pigeon receives only backwater flooding and experiences an average of 116 unflooded days during the growing season. In contrast, Mallet is directly hydrologically connected to the adjacent bayou and experiences an average of 35 unflooded days during the growing season (Keim and others 2006).

Increment cores and historical cruise data indicate trees at Pigeon were established about 1917 after a clearcut of the primary bald cypress-water tupelo forest, and we assume the origin of the stand at Mallet is similar. The stands were first measured in 1980 and selected for similar stand structure in terms of basal area and species composition (Dicke and Toliver 1988, 1990; Prenger 1985. The sites were selected for use in a thinning study, but data only from unthinned plots were used by Dicke and Toliver (1990) and by us to infer natural stand dynamics in contrasting hydrological regimes.

Data

Twelve 0.05-ha circular plots were originally established at each site. Nine of the plots at Pigeon were thinned and three remained as control, which we used for this study. The control plots were randomly assigned within a grid of plots, interspersed with thinned plots. Trees cut from the thinned plots were felled in place but not removed from the site. There was no thinning at Mallet, but only four of the plots could be located in 2005, so they were the only ones included in this study. Differences between our results and those presented by Dicke and Toliver (1990) are because our analyses were restricted to a subset of the plots they were able to use. All trees >3.8 cm diameter within the plots were permanently marked with aluminum tags and unique identification numbers affixed to nails driven at the point of diameter measurement in 1980, which was 50 cm above the maximum extent of stem buttressing, i.e., normal diameter. Tree diameters in both stands were measured in 1980, 1984, 1986, and 2005 using diameter tape (1980, 1984, 2005), calipers (1986 only), or Wheeler’s Pentaprism Caliper (2005 only).

In 2005, we could not repeat the measurement of diameter at the marked points because the height of buttressing had increased in some trees between 1980 and 2005. Parresol and Hotvedt (1990) recommended standardizing diameter measurement of bald cypress at 3 m (d3) above the ground. Therefore, we measured diameter both at the location of normal diameter in 1980 and at 3 m above the ground in 2005. To compare diameter measurements across time periods, we used a stem profile equation in conjunction with d3 or normal diameter to estimate diameter at breast height (d.b.h.) as if stem buttressing were not present (d.b.h.0). We used a polynomial curve to interpolate between two local stem profile equations (Hotvedt and others 1985, Parresol and others 1987) and extrapolate stem profile from above the buttressing, thereby estimating expected stem form in the absence of buttressing:

$$d_h/D = 0.40(h/H)^3 - 1.51(h/H)^2 + 2.06(h/H) \qquad (1)$$

where

H = total tree height

h = height of diameter measurement as distance from top of the tree

D = reference diameter

d_h = diameter measured at h

To estimate d.b.h. in the absence of buttresses, d.b.h.0, we calculated D from field measurements of d3, h, and H using equation (1), then solved equation (2) for d.b.h. at $h = H - 1.37$ m. We used d.b.h.0 as the basis for all diameter analyses.

Tree heights at Pigeon were measured using a clinometer (1980, 1984, 1986) or Haglöf Vertex hypsometer and Criterion laser height finder (2005). Tree height data for Mallet before 2005 were lost, but Dicke and Toliver (1990) published stand-average data by species.

To estimate volume of each stem in 2005, we used the equation of Hotvedt and others (1985) with coefficients modified for S.I. units:

$$V = 0.0001063(\mathrm{d3})^{1.7876}(H)^{0.9522} \qquad (2)$$

where

V (m^3) = total volume inside bark

d3 (cm) = diameter measured outside bark at 3 m

H = total tree height (m)

To estimate volume of Mallet trees prior to 2005, we applied a regression of volume on normal diameter (dn) parameterized using 2005 measurements ($R^2 = 0.83$):

$$V = 0.0010462(\mathrm{dn})^2 - 0.0089963(\mathrm{dn}) \qquad (3)$$

Equations 2 and 3 were developed locally for bald cypress, but we assumed they held for water tupelo as well.

Analyses: Stand Density

To quantify density and infer competition, we calculated stand density index (SDI) for each stand and each measurement period:

$$\mathrm{SDI} = \sum n_i(d_i/25)^{1.6} \qquad (4)$$

where

n = the number of trees (per ha) of species i

d = quadratic mean diameter (cm) of trees of species i

This form of SDI assumes the contributions of each species to stand density are additive and allows estimation of competition in mixed-species stands (Ducey and Larson 2003, Williams 2003). The SDI has been shown to be mostly independent of site quality (Jack and Long 1996), so it is an appropriate tool for evaluating effects of stress on stand dynamics. The ratio of SDI to the maximum SDI observed for that species (or mixture of species) is a measure of relative density (RD) of that stand. As rules of thumb, crown closure begins near RD = 0.15, full site occupancy near RD = 0.35 and self-thinning begins near RD = 0.55 (Drew and Flewelling 1979).

Woodall and others (2005) applied theoretical relationships between stand density and tree stem mechanical properties proposed by Dean and Baldwin (1996), by applying equation 4 to U.S. Forest Service, Forest Inventory and Analysis data across the United States for multiple forest types. Their result is a broadly applicable expected maximum stand density, $SDI_{99} = 2057.3 - 2098.6(SG_g)$, where SDI_{99} is the 99th percentile of observed densities (s.i. units), and SG_g is the mean of the green specific gravity of wood for each tree in the stand. We applied the Woodall equation to estimate the relative density of the two study stands for each measurement period and compared RD to expected thresholds to infer competition processes in the stands. The maximum stand density for bald cypress ($SG_g = 0.42$) is 1176, for water tupelo ($SG_g = 0.46$) is 1092, so SDI_{99} for a stand of equal proportions bald cypress and water tupelo is 1134.

RESULTS

In 1980 at Pigeon, bald cypress were 81 percent of the trees, 83 percent of the basal area, 85 percent of the volume, and 83 percent of the stand density (table 1). By 2005, bald cypress were 77 percent of the trees, 83 percent of the basal area, 87 percent of the volume, and 82 percent of the stand density.

In 1980 at Mallet, bald cypress were 65 percent of the trees, 75 percent of the basal area, 75 percent of the volume, and 73 percent of the stand density. By 2005, bald cypress were 70 percent of the trees, 83 percent of the basal area, 87 percent of the volume, and 81 percent of the stand density.

There was mortality at Pigeon of 39 percent of the trees present in 1980, 96 percent of which were smaller diameter trees in intermediate or suppressed crown classes in 1980 (fig. 1). Only 11 percent of the mortality was of tupelo (22 percent mortality of the original trees, compared to 43 percent for bald cypress), all of which were intermediate or suppressed. Only 5 percent of trees in dominant and codominant crown classes died, none of which were tupelo.

There was mortality at Mallet of 15 percent of the trees present in 1980. Crown classes were not recorded in 1980, but mortality was mostly of the small trees; the average 1980 diameter of trees that died was 23.2 cm, compared to 27.2 cm for trees that survived. The largest tree in the study—a tupelo 58 cm diameter in 1986—died between 1986 and 2005. Omitting this large tree, the average diameter of trees that died was 21.8 cm. Sixty percent of the mortality was of tupelo (27 percent mortality of the original trees, compared to 9 percent for bald cypress). The average diameter of bald cypress trees that died was 24.0 cm, compared to 22.7 cm for tupelo (20.2 cm omitting the single large tree).

Volume of tupelo decreased in both stands from 1980 to 2005. At Pigeon, volume lost to tupelo mortality (10 m^3/ha) was 9 percent of the total volume lost to mortality, which approximates the 11-percent mortality of tupelo by number of trees. The net gain in stand-level volume of bald cypress was by concentration of growth in large trees, whereas there are few large tupelo trees. Thus, although mortality of tupelo was less than bald cypress, the surviving tupelo are mostly in subordinate crown classes.

Table 1—Characteristics of two baldcypress-water tupelo stands in Louisiana

		Trees		Basal area		Volume		SDI		Average height	
Site	Species	1980	2005	1980	2005	1980	2005	1980	2005	1980	2005
		------ per ha ------		*------ m^2/ha ------*		*------ m^3/ha ------*		*----- s.i. units -----*		*-------- m --------*	
Pigeon	BC	1320	753	44.4	42.1	483	537	976	836	19.4	24.2
(less flood)	WT	300	233	8.8	8.5	86	81	199	183	17.6	17.9
	All	1620	986	53.2	50.6	569	618	1175	1019	19.1	22.7
Mallet	BC	707	480	35.6	38.1	430	423	681	705	21.4	21.9
(more flood)	WT	373	205	11.8	7.9	140	63	247	169	17.6	13.9
	All	1080	685	47.4	46.0	570	486	928	874	19.9	19.5

SDI = stand density index; BC = bald cypress; WT = water tupelo.

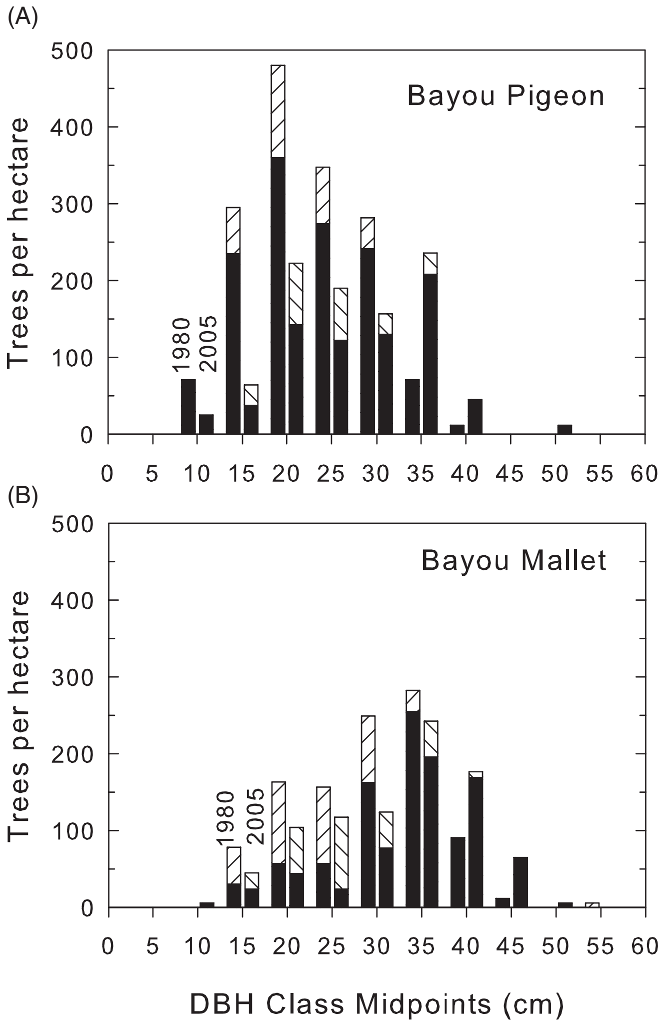

Figure 1—Diameter distributions of two cypress-tupelo stands in Louisiana. (A) Bayou Pigeon and (B) Bayou Mallet. Solid portions of bars are bald cypress and hatched portions of bars are water tupelo.

Volume of both species decreased from 1980 to 2005 at Mallet. Volume lost to tupelo mortality (43 m^3/ha) was 61 percent of the total volume lost to mortality, which approximates the 60-percent mortality of tupelo by number of trees. Excluding the single large tupelo that died, the volume lost to tupelo mortality (27 m^3/ha) was 49 percent of the total; this reflects the fact that bald cypress mortality was of trees that were slightly larger than tupelo mortality.

The average height of bald cypress has been more than tupelo throughout 1980 to 2005 because tupelo trees were more likely to be in intermediate or suppressed canopy positions. Average height of bald cypress was 1 m more at Mallet than at Pigeon in 1980, but by 2005 the bald cypress at Pigeon were 2.3 m taller than those at Mallet. Height of the tallest 15 percent of bald cypress trees, i.e., dominant and strong codominants only, at Pigeon was 24.9 m in 1980 and 30.0 m in 2005. Height of the tallest 15 percent of bald cypress at Mallet in 1980 is unknown, but in 2005 it was 26.1 m.

The differences in tree height between 1980 and 2005 were strongly affected by crown dieback and breakage, especially for tupelo. Sixty-six percent of tupelo trees at Pigeon were shorter in 2005 than in 1980, and 34 percent were more than 3 m shorter. In contrast, 20 percent of bald cypress trees at Pigeon were shorter in 2005 than in 1980, and 6 percent were more than 3 m shorter. Thus, dieback and breakage occurred throughout the study, but large breakage events (loss of 3 m or more) were concentrated in the 1986 to 2005 period. During the first period of the study, from 1980 to 1983, 71 percent of tupelo and 46 percent of cypress trees decreased in height, but only 10 percent of tupelo and <1 percent of cypress decreased in height by more than 3 m. From 1986 to 2005, 69 percent of tupelo and 31 percent of cypress trees decreased in height, and 29 percent of tupelo and 6 percent of cypress decreased in height by more than 3 m. Nearly all (95 percent) tupelo trees decreased in height during at least one measurement period, and most (84 percent) cypress trees did also. However, 40 percent of tupelo trees experienced loss of at least 3 m of height in at least one study period, but only 5 percent of cypress trees experienced such a large loss. By 2005, almost all water tupelo showed evidence of past crown damage; this was true for both Pigeon and Mallet.

Overall, Pigeon had a RD = 1.01 in 1980 and RD = 0.88 in 2005. Mallet had a RD = 0.80 in 1980 and RD = 0.75 in 2005 (fig. 2). Because the threshold density for self-thinning is generally about RD = 0.55, both stands have been dense enough to experience self-thinning for the entire duration of the study. Although Pigeon has been denser than Mallet since at least 1980, the temporal changes in RD between the two stands have been nearly identical.

DISCUSSION

Differences in the heights of dominant trees in the two stands is evidence that Pigeon (less flooding) is a more productive stand than is Mallet (more flooding). In 2005, the dominants at Pigeon were 3.9 m taller than dominants at Mallet. Although data are not available for the height of dominant trees in Mallet in 1980, we can estimate from diameter distributions (fig. 1) and mean heights of the stands at that time (table 1) that dominants there were likely taller than at Pigeon. Based on height growth history and the general negative correlation between flood stress and productivity, the most likely conclusion is that Pigeon is a younger stand and more productive site.

The stand densities at both sites were clearly high enough to cause mortality from self-thinning. The loss of density at both sites has been at approximately on the same trajectory, but at a slower rate at Mallet. Mortality causes episodic losses of density that can only be replaced by continued growth of the residual trees, so stand development typically follows a stochastic sawtooth pathway in density space (Long 1985), and predicting future stand development from recent history

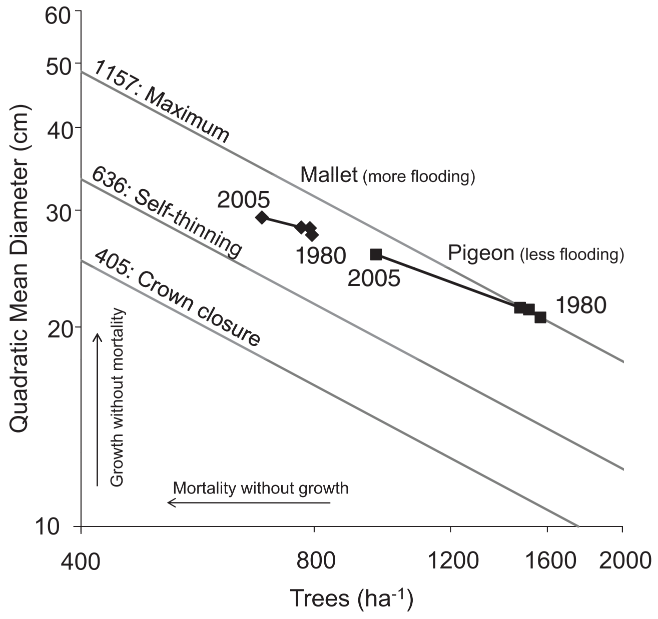

Figure 2—Density diagram for two cypress-tupelo stands in Louisiana. Gray lines indicate important threshold densities for a stand of evenly mixed bald cypress and water tupelo.

is therefore difficult. However, the slower tree growth at Mallet means that remaining trees will be slower to capture resources made available by mortality, and also slower to come into competition with other residual trees.

Although the stands were chosen for similar initial basal area, the trees at Mallet were larger. It is possible this stand is older, had a lower initial stand density, or that it was initially a more productive site than Pigeon. However, stand volume was similar in 1980, so it is also possible that stand structure was simply different. For example, the current canopy trees may have established dominance sooner at Mallet than at Pigeon, so that growth was concentrated on larger trees for a longer period of time compared to Pigeon.

The long-term prospect for tupelo at Pigeon appears to be continued loss of volume, with a few codominant trees remaining in the stand indefinitely. To date, most mortality in this stand has been of intermediate and suppressed trees of both species. If there were to be mortality of larger trees that created openings, it is not clear whether surviving tupelo trees in subordinate canopy positions would be able to occupy the new growing space, in part because of their generally poor condition and broken tops. The situation at Mallet is slightly different but the long-term prospects appear similar. There were originally more tupelo in that stand, and fewer suppressed trees than in Pigeon, but there has been mortality of large tupelo at Mallet. The loss of larger trees, in combination with broken tops and generally poor condition of many surviving trees, has resulted in loss of more than half the volume of tupelo. Whereas in 1986 it appeared that tupelo would continue to be near equal to bald cypress at Mallet (Dicke and Toliver 1990), it now appears that tupelo is losing dominance to bald cypress in much the same way as at Pigeon.

A recent complicating factor in the development of these stands may be disturbance by Hurricane Andrew in 1992. We have no observations of effects on our study stands, but tree damage was ubiquitous throughout the Atchafalaya Basin (Doyle and others 1995). Cypress-tupelo stands were the least damaged stand type in that storm (Doyle and others 1995), as is regionally typical (Loope and Duever 1994), but most tupelo trees in our study stands and in the surrounding area have broken tops and show signs of general decline. There are few signs of significant damage to bald cypress and only isolated breakage in the study stands, so it is possible the hurricane favored dominance by bald cypress. Rates of tupelo mortality were the same, e.g., 4 percent of eventual total mortality per year at Mallet, for the prehurricane 1980 to 1986 period and for the 1986 to 2005 period which included the hurricane; however, major crown breakage in tupelo was concentrated in the 1986 to 2000 period. Hurricanes Danny (1985), Juan (1985), Lili (2002), and Tropical Storm Beryl (1988) also passed near the research stands, but we have no information on damage that may have occurred during these storms. The degree to which tropical cyclones may affect stand development and species composition in general is unknown but likely varies between coastal and inland swamps. If tupelo is more likely to experience crown damage from windstorms, as it appears was the case in this study, tupelo would be at a competitive disadvantage in coastal stands.

CONCLUSIONS

The differences in flood stress between the two cypress-tupelo stands did not apparently fundamentally alter competition within the stands, and both stands are developing approximately according to expectations based on stand-density relationships for other species. However, the slower rate of growth appears to be slowing the rate of development at the site experiencing more flooding stress. We conclude that flooding stress does not fundamentally alter density-dependent stand development in cypress-tupelo. There is also little evidence that flooding stress itself is responsible for the apparent competitive advantage that bald cypress has in the study stands, but that water tupelo is decreasing in importance because of greater susceptibility to crown breakage in tropical storms.

ACKNOWLEDGMENTS

This research was funded in part by the U.S. Department of Agriculture, Cooperative State Research, Education, and Extension Service under project numbers LA-B93735. Williams, Inc. provided access to the research site. Original data were graciously provided by John Toliver. Data collection and analysis were assisted by Jason Zoller, Tahia Devisscher, Chris Allen, Melinda Hughes, Erika Stelzer, Luben Dimov, and Mike Deliberto. This is manuscript 2009-241-2505 of the Louisiana Agricultural Experiment Station.

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