

Long-term success of stump sprouts in high-graded baldcypress–water tupelo swamps in the Mississippi delta

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Received 18 March 2006; received in revised form 30 May 2006; accepted 4 June 2006

Abstract

Regeneration of baldcypress (*Taxodium distichum* (L.) Rich.) and water tupelo (*Nyssa aquatica* L.) in swamps of the deltaic plain of the Mississippi River are of major importance for ecosystem sustainability and forest management in the context of regional hydrological changes. Water tupelo often forms prolific sprouts from cut stumps, and baldcypress is one of few conifers to produce stump sprouts capable of becoming full-grown trees. Previous studies have addressed early survival of baldcypress stump sprouts, but have not addressed the likelihood of sprouts becoming an important component of mature stands. We surveyed stands in southeastern Louisiana that were partially logged 10–41 years ago to determine if stump sprouts are an important mechanism of regeneration. At each site we inventoried stumps and measured stump height and diameter, presence and number of sprouts, sprout height, and water depth. We determined age and diameter growth rate for the largest sprout from each stump from increment cores. The majority of stumps did not have surviving sprouts. Baldcypress sprout survival was about the same (median 10%) as previously found for stumps up to 7 years old, so it appears that, although mortality is high soon after sprouting, it is low after age 10. Water tupelo sprouting was rare at our sites but it was not clear whether this may have been because trees were not cut at our sample locations. Baldcypress stump sprouts were more likely to survive on shorter, smaller-diameter stumps, and baldcypress sprout growth was greatest on drier sites with less competition from overstory trees. Surviving baldcypress stump sprouts had high growth rates, but were not regularly spatially distributed within stands and many had advancing decay from stumps into sprouts.

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Keywords: Forested wetlands; Swamp forests; Regeneration

1. Introduction

Forested wetlands are one of the most extensive ecosystems in the southern United States, and are controlled by complex biophysical processes that maintain productive ecosystems while providing important services (Brinson et al., 1981; Brinson and Rheinhardt, 1998). Palustrine swamps dominated by cypress (*Taxodium* spp.) and tupelo (*Nyssa* spp.) occupy the lowest, most hydric topographic position in these forest

ecosystems. Baldcypress (*T. distichum* (L.) Rich.) and water tupelo (*N. aquatica* L.) dominate riverine and deltaic floodplains of the Mississippi River, whereas riverine and depressional wetlands in the lower Gulf and Atlantic coastal plains also include pondcypress (*T. ascendens* Brongn.) and swamp tupelo (*N. biflora* Walt.).

Of the current 1.2–2 million ha of cypress–tupelo wetlands in the United States, approximately 345,000 ha of baldcypress–water tupelo swamps occur in the deltaic plain of the Mississippi River in coastal Louisiana (Conner and Toliver, 1990; Conner and Buford, 1998; Chambers et al., 2005). Pre-settlement baldcypress–water tupelo swamps in the delta, which may have covered more than 1,000,000 ha, were mostly clearcut between

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about 1890 and 1930 and subsequently either converted to agriculture or other land uses or naturally regenerated to second-growth, even-aged stands (Conner and Toliver, 1990). Extensive construction of levees, canals, and other water control structures since the initial logging of these swamps has combined with eustatic sea-level rise and deltaic land subsidence to create widespread and pervasive hydrological changes in these forests (Salinas et al., 1986; Conner and Day, 1988; Pezeshki et al., 1990). The most widespread change is increased flooding depth and duration. For example, flood durations in the Maurepas swamp of the Pontchartrain Basin have doubled since the 1950s (Thomson et al., 2002). The lack of regeneration and survival of the extensive coastal forested wetlands in Louisiana is similar to that of coastal marshes, which have lost about 25% of their area in the 20th century due to factors such as isolation of coastal wetlands from the river and extensive disruption of hydrology (Day et al., 2000). Reintroduction of river water, with the attendant increases in sediment and nutrient deposition, is a primary mechanism for coastal wetland restoration (Day et al., 2005).

Second-growth baldcypress–water tupelo forests are now commercially attractive for harvesting and forest management, but increased flooding is preventing some stands from regenerating naturally by seed (DeBell and Auld, 1971; Conner et al., 1981, 1986; Conner and Toliver, 1990; Wilhite and Toliver, 1990; Chambers et al., 2005) because baldcypress and water tupelo seeds do not germinate under water and seedlings cannot survive prolonged inundation (Demaree, 1932; Shunk, 1939; Souther and Shaffer, 2000). However, baldcypress and pondcypress are some of the few conifers that coppice, and cut stumps can produce sprouts capable of becoming full-grown trees (Wilhite and Toliver, 1990). Stump sprouts are also common on cut stumps of water tupelo and swamp tupelo (Johnson, 1990; McGee and Outcalt, 1990). Thus, understanding viability of coppice regeneration is important in developing sustainable management systems for these ecosystems.

Most investigators have observed prolific stump sprouting initially after cutting baldcypress, followed by poor survival after a few years. Conner et al. (1986) reported that 80% of baldcypress stumps sprouted after logging, but only 21% retained live sprouts 4 years after harvest. Conner (1988), summarizing a number of studies in Louisiana, reported 0–23% of baldcypress stumps with surviving sprouts after 4–7 years. Similarly, Ewel (1996) reported 17% survival of pondcypress stump sprouts 2–4 years after harvests in Florida swamps. Sprouting has been reported to be less prolific from stumps of older (>60 years) trees, or from stumps of trees cut in the spring or summer (Mattoon, 1915; Williston et al., 1980). Sprouting is usually greater on small-diameter stumps (Ewel, 1996; Randall et al., 2005), perhaps regardless of age (Mattoon, 1915).

Stump sprouting by water tupelo has been found to be variously successful. Prolific stump sprouting of water tupelo stumps resulting in vigorous trees for up to 30 years or longer has occurred in swamps of South Carolina (Hook et al., 1967), North Carolina (Brinson, 1977), and Alabama (Aust et al., 1997, 2006; Gardiner et al., 2000). However, Kennedy (1982) observed substantial stump rotting and sprout mortality that led to

regeneration failure of water tupelo in a Louisiana swamp. Stump height, felling method, and harvesting intensity can also influence the vigor of sprouts regardless of species (Hook and DeBell, 1970; Kennedy, 1982; Ewel, 1996; Gardiner et al., 2000).

Unfortunately, previous research has not addressed the long-term growth and survival of sprouts beyond the first few years after logging, and the long-term viability of coppice regeneration beyond the short time scale and limited spatial extent of previous research is unknown. Although there have been several cases of successful stand regeneration by coppice, the factors affecting survival and growth are not well understood. Understanding the reliability of stump sprouting for developing management and restoration plans therefore requires a broad-scale assessment of long-term sprout success. This knowledge is of particular importance in evaluating potential management of baldcypress–water tupelo swamps in the context of modified hydrological conditions of coastal Louisiana.

The goal of this research was to evaluate if stump sprouts reliably become established and develop sufficiently to maintain stand productivity in baldcypress–water tupelo swamps. Therefore, we conducted a regeneration survey across the region of sites harvested 10 or more years earlier. The specific objectives were to (1) determine whether baldcypress and water tupelo stump sprout mortality rates are high beyond the first few years after harvest, (2) determine factors responsible for survival and growth of stump sprouts, and (3) assess whether surviving sprouts are sufficiently numerous and vigorous to form viable new stands.

2. Methods

Field experience suggested that rot in baldcypress stumps older than 50 years would be too great to allow assessment of stump sprouting rates. Thus, we selected sites in coastal Louisiana that were dominated by baldcypress and water tupelo and harvested nominally 10–50 years prior to the survey. We communicated with land owners, foresters, and researchers to find sites meeting these criteria, and visited 18 sites to measure stump sprout and seedling regeneration. Information about site history, silvicultural goals, and logging methods was incomplete for most sites. Harvesting of most sites did not follow a particular regeneration method, but was mainly diameter-limit cutting of baldcypress with less cutting of other species. As a result, stumps were usually larger in diameter than were the remaining overstory trees in most stands. Diameter-limit cutting is normally considered high-grading in these stands because it favors inferior trees and species such as green ash (*Fraxinus pennsylvanica* Marsh.), pumpkin ash (*F. profunda* Bush), and swamp red maple (*Acer rubrum* var. *drummondii* (Hook. & Arn. ex Nutt.) Sarg.) that are more shade tolerant but less desirable on these sites.

2.1. Field sites

We measured stump sprouting on 18 sites between 29°35'N and 30°42'N latitude and between 89°30'W and 91°47'W longitude (Fig. 1). There was a substantial variety of conditions

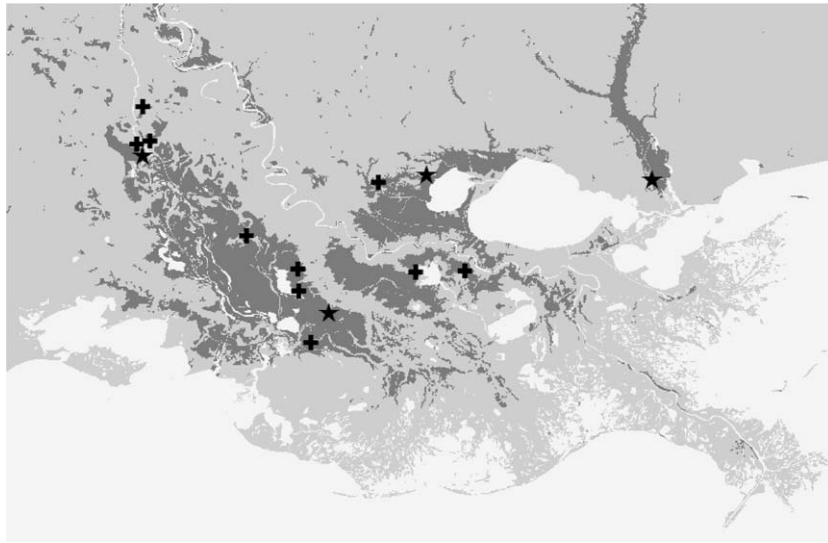


Fig. 1. Site locations in for baldcypress–water tupelo stump sprouting survey in Louisiana. Crosses represent one site and stars represent two sites. Dark gray shading indicates areas of baldcypress–water tupelo swamps.

at the sampled sites. Hydrological regimes ranged from permanently flooded backswamps to seasonal, riverine flooding. Most sites were in backswamp areas flooded mainly by rain water and disconnected from river flooding by artificial levees, but some were near river fronts. Soils in backswamps were Aquents with thin organic accumulations on the surface of semifluid clayey or silty sediments, and soils in sites nearer river fronts were Aquepts formed in silt and smectitic clay. Understory vegetation ranged from none (bare ground) to thick,

submerged and emergent aquatic vegetation more characteristic of treeless marshes (Table 1).

2.2. Data collection

Sampling at each site was done using a series of transects, 12 m wide and 30 m long, placed irregularly to encompass stumps from the previous harvest. We placed at least five transects per site, and added as many additional transects as

Table 1
Characteristics of surveyed stands in south Louisiana swamps

Site	Harvest ^a	Age ^b	Tree basal area ^c (m ² ha ⁻¹)	Trees ^c (ha ⁻¹)	Relative basal area ^d (%)		Baldcypress seedlings (ha ⁻¹) ^e	Aquatic vegetation
					Baldcypress	Tupelo		
1	I	20	54.3	331	91	9	953 (1075)	Moderate
2	P	20	68.9	511	94	4	267 (173)	Heavy
3	P	19	50.2	459	68	31	8 (20)	Light
4	P	18	74.3	573	88	10	6 (12)	Heavy
5	P	24	93.7	1067	98	3	33 (60)	None
6	C	11	47.8	578	75	24	0 (0)	Heavy
7	P	11	48.0	729	62	37	0 (0)	Heavy
8	P	10	26.5	553	57	9	4 (10)	Moderate
9	P	10	52.8	531	67	4	0 (0)	None
10	P	24	43.9	457	59	37	22 (32)	Light
11	P	17	63.0	852	79	2	0 (0)	None
12	P	9	29.2	514	66	0	0 (0)	None
13	P	8	57.8	420	78	0	226 (153)	None
14	P	11	80.8	694	87	0	61 (50)	None
15	P	8	66.0	531	83	1	35 (79)	None
16 ^f	C	18	97.5	872	7	93	146 (42)	None
17 ^f	I	22	50.9	674	16	85	100 (61)	None
18	P	41	58.7	766	56	24	0 (0)	None

^a I = improvement cut; silvicultural thinning. P = partial cut; diameter-limit cut. C = clearcut of all commercially valuable trees.

^b Years between harvest and sampling in 2004.

^c Includes all currently standing trees and baldcypress cut stumps.

^d Relative basal area of standing trees.

^e Values in parentheses are standard deviations.

^f Sites dominated by water tupelo; too few baldcypress stumps for analysis.

necessary to sample 30 stumps per site. In each transect, we measured diameter of all trees and tall shrubs (woody vegetation >1 cm dbh) and counted seedlings of baldcypress and water tupelo less than 1.37 m tall. We classified trees >1.37 m tall but <10 cm dbh as saplings. Measurements at each stump were stump height, diameter of the stump at the cut, depth of water adjacent to the stump at the time of the survey, number of live sprouts, diameter and height of the largest sprout, and distance from the stump to the nearest canopy tree.

We collected radial cores from several baldcypress with an increment borer to determine ages and past growth of trees and stump sprouts in each stand. We cored the dominant sprout from most stumps, at least two overstory trees, and up to three overstory trees if present. Total sample size was 52 sprouts, 60 overstory trees, and 33 understory trees. We cored all sprouts near their base within what we assumed to be the first year's growth. We cored trees at 1–3 m above the ground, avoiding buttressing flutes, and estimated tree ages by adding 3 years to the adjusted ages in these cores (based on seedling growth rates reported by Mattoon (1915) and Keeland and Conner (1999)). We dried, mounted, and sanded cores to aid in visual identification of annual growth rings. After identifying false rings (Young et al., 1993) and eliminating them from analyses, we used a measuring stage designed for tree core analysis under 10–100 power magnification to measure ring widths to ± 0.1 mm. The standard dendrochronological method of crossdating (Douglass, 1941), which ensures correct identification of the year of ring formation by comparing ring sequences from multiple trees in the same stand, was not possible because sample sizes were not large enough at each site. Instead, we compared measured ring width chronosequences to cross-dated chronologies from nearby baldcypress stands (Amos et al., 2005), and corrected growth rate estimates by adjusting dates in uncrossdated ring sequences to match marker rings of notably good and poor growth.

2.3. Statistical analyses

To compare growth rates of stump sprouts and trees of varying ages, we converted growth rates to mean annual increments (MAI), defined as the total growth in height or basal area divided by the age of the tree at the time of measurement. In analyzing cores, it is possible to calculate basal area MAI for each previous year of growth by assuming a circular cross-section.

To analyze environmental effects on stump sprout survival and growth, we used nonmetric multidimensional scaling (NMS) ordination (Kruskal and Wish, 1978). Ordination, or the arranging of items along multiple axes (i.e., in multidimensional space) is often used to summarize complex relationships and extract dominant patterns from data, and is particularly useful in cases when variables are intercorrelated. Because nonparametric ordination does not assume a relationship between calculated distances and the similarity measure (Hair et al., 1998), NMS is suited for analysis of non-normal data or data on arbitrary or discontinuous scales. In contrast, many other ordination methods (e.g., principal component analysis (PCA) or canonical correspondence analysis (CCA)) take into account only the

portion of a configuration that fits the limited perspective specified by the underlying model (McCune et al., 2002).

We used PC-Ord version 4.36 software (McCune and Mefford, 1999) to perform NMS ordinations of variables describing the environment of stump sprouts and to analyze correlations of resulting ordination axes with variables describing stump sprout survival and growth. We used Sørensen (Bray–Curtis) city-block distance to measure multidimensional distances between observations. Ordinations were based on a random starting point with six initial axes and up to 40 runs of 400 iterations each to minimize stress (Kruskal, 1964), and 50 Monte-Carlo ordination runs with randomized data to estimate statistical significance of axes. We used varimax rotation (Mather, 1976) to rotate the ordination to maximize correlation of the first axis with external dependent variables (one rotation of the ordination per dependent variable).

Ordinations and dependent variables were at the transect level. Environmental variables were average water depth near stumps at the time of the survey, mean distance from stumps to the nearest overstory tree, stump quadratic mean diameter, number of individuals of all trees and of individual tree species, basal area of all trees and of individual tree species, and tree species richness. We did not include individual-species variables for rare species (e.g., basal area of a rare species) because many of them occurred in only a few transects, but did include rare species in all-species variables (e.g., transect basal area). Common species that were represented by individual variables in the ordination were baldcypress, water tupelo, ash species (lumped green ash, pumpkin ash, and Carolina ash (*F. caroliniana* P. Mill.) because of difficulty differentiating specimens), swamp red maple, and sugarberry (*Celtis laevigata* Willd.). The single visit to each site did not allow measurement of hydrological regime other than a single observation of flooding depth. Therefore, we assumed hydrological regime followed the pattern of increased tree species richness with decreased growing-season flooding (Conner et al., 1981; Visser and Sasser, 1995).

The dependent variables we compared to the ordinations were (1) percent stumps with sprouts, (2) number of sprouts per stump, (3) sprout mean annual basal area increment, and (4) sprout mean annual height increment. In interpreting correlations of variables with axes, we selected $R^2 = 0.4$ or $|\tau| = 0.4$ as the minimum correlation likely to indicate a meaningful relationship. Although some authors recommend choosing thresholds for interpretation lower (e.g., Hair et al., 1998; Tabachnick and Fidell, 2001), we chose a more conservative threshold to reduce the number of variables and increase interpretability.

3. Results

Across sites, relative basal area (BA) of standing baldcypress ranged from 6.7 to 97.5%, and water tupelo ranged from 0 to 93.2% (Table 1). Baldcypress and water tupelo together represented 66–100% of stand BA and exceeded 75% on 15 of the 18 sites. Other common woody species included green ash, pumpkin ash, Carolina ash, swamp red maple, buttonbush

Table 2
Baldcypress stump sprouting for the surveyed stands in south Louisiana swamps

Site	Baldcypress stumps				Mean annual growth increment	
	Total	With sprouts		Sprouts per stump ^a	Diameter (cm yr ⁻¹)	Height (m yr ⁻¹)
		No.	%			
1	29	2	6.9	1.0	0.46	0.16
2	30	5	16.7	2.8	0.58	0.50
3	31	6	19.4	2.7	0.67	0.46
4	35	6	17.1	2.7	0.92	0.53
5	64	3	4.7	3.7	0.17	0.15
6	33	24	72.7	5.7	0.99	0.75
7	22	14	63.6	4.1	0.99	0.82
8	25	0	0.0	0.0		
9	36	1	2.8	1.0	0.71	0.50
10	32	2	6.2	4.5	0.39	0.33
11	30	3	10.0	2.0	0.81	0.60
12	30	3	10.0	2.7	0.40	0.37
13	31	4	12.9	3.0	0.70	0.56
14	36	0	0.0	0.0		
15	30	0	0.0	0.0		
18	30	0	0.0	0.0		
All combined	524	73	13.9	4.0	0.81	0.62

^a For stumps with any living sprouts.

(*Cephalanthus occidentalis* L.), swamp privet (*Forestiera acuminata* (Michx.) Poir.), Virginia-willow (*Itea virginica* L.), and waxmyrtle (*Morella cerifera* (L.) Small). A few sites were in mixed baldcypress–water tupelo–bottomland hardwood forests, where common overstory species also included sugarberry, water hickory (*Carya aquatica* (Michx. F.) Nutt.), water locust (*Gleditsia aquatica* Marsh.), water-elm (*Planera aquatica* J.F. Gmel.), black willow (*Salix nigra* Marsh.), and Chinese tallow (*Triadica sebifera* (L.) Small).

Stumps of water tupelo were characteristically too degraded for assessment of stump sprouting potential; the few non-sprouting stumps remaining were barely recognizable and impossible to measure. Additionally, we found live water tupelo sprouts at only two, adjacent sites (16 and 17). Because site history was largely unknown, it was not always clear whether the absence of water tupelo stumps was because (1) it was absent from the stand at the time of logging, (2) it was not cut during logging, or (3) sprout mortality was 100% and stump decomposition was rapid.

In contrast to water tupelo, baldcypress stumps were intact, easily recognizable, and amenable to analysis for long-term stump sprout survival and growth. The proportion of baldcypress stumps having live sprouts ranged from 0 to 72% by site (median 10%; Table 2). However, only 2 of the 18 sites had live sprouts on more than 20% of stumps. On four sites, no stumps had live sprouts. All surviving stump sprouts originated from the cambium at or near the cut face of the stump. The bivariate relationship between time since harvest and sprout survival was weak ($R^2 = 0.06$). The spatial distribution of surviving stump sprouts was uneven, so that some sites had surviving stump sprouts on only one or two sampling transects.

The average diameter of the largest live baldcypress sprout per stump across all sites was 10 cm, and the average height was 6.8 m. Normalized for sprout age, site-average diameter

mean annual increment (MAI) ranged from 0.17 to 0.99 cm yr⁻¹, and site-average height MAI ranged from 0.15 to 0.82 m yr⁻¹. Site-average stump sprout MAI was moderately positively correlated to the proportional survival at that site ($R^2 = 0.56$ for height and 0.49 for diameter) (Fig. 2), although removing the two sites with highest survival and growth (6 and 7, which were immediately adjacent to each other) degrades the relationship ($R^2 = 0.26$ for height and 0.25 for diameter).

Time series of annual growth increment calculated using tree rings show that basal area (BA) growth of baldcypress sprouts greatly exceeded that of trees from the study sites at similar ages (Fig. 3). Mean BA of sprouts at age 10 was equal to mean BA of trees currently in the overstory at age 28, and was greater than BA of current understory trees is likely to reach until at least 80 years at current growth rates. However, it is important

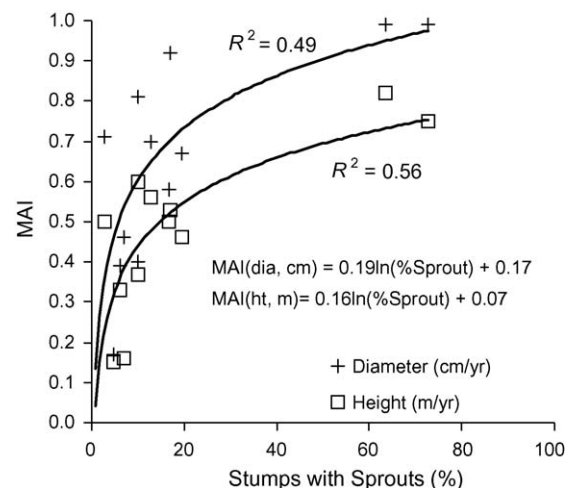


Fig. 2. Relationship of baldcypress stump sprout mean annual growth increment (MAI) to stump sprout occurrence in south Louisiana swamps.

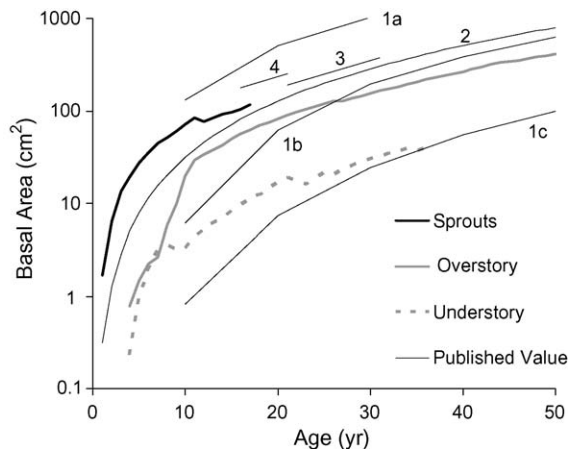


Fig. 3. Study-wide mean basal area growth curves of baldcypress stump sprouts (thick black line), overstory trees (solid gray line) and understory trees (dashed gray line) determined from tree ring analyses in south Louisiana swamps. Thin black lines are growth curves from other research for comparison: (1) natural regeneration (Mattoon, 1915): (1a) maximum, (1b) average, and (1c) minimum; (2) general (Johnson and Shropshire, 1983); (3) plantation (Krinar and Johnson, 1976, 1987); (4) plantation (R.F. Keim, unpublished data).

to remember that the largest trees were likely removed from the sites in diameter-limit cuts, so historical tree growth of trees in the current overstory is likely less than growth of trees in dominant canopy positions.

The baldcypress sprout growth rates were faster than expected for naturally regenerated stands (Fig. 3). In comparison, trees in the overstory at the time of our data collection had grown at about average expected rates and trees in the understory were growing quite slowly. Surviving stump sprouts were growing at rates equivalent to plantation-grown trees.

Most baldcypress stumps were at least 40 cm diameter (50 ± 14 cm) and nearly 1 m high (89 ± 26 cm). Within this narrow range of sizes, there were no strong relationships between characteristics of stumps and their sprouting. Bivariate correlation analysis did not reveal strong relationships between stump sprout survival or size and water depth or other site factors.

The condition of the live sprouts was highly variable (Fig. 4). However most sprouts were present on stumps with poor callus tissue formation and many stumps had advanced decay. In many instances, decay was observed in the base of the sprouts themselves. The hollow nature of some sprouts, the narrow band of living tissue on stumps near sprouts, and the position of sprout–stump interface (usually about 1 m above the ground) suggested that some sprouts would not likely survive to be mature trees. In a few cases, almost the entire stump had callused over and, despite minor decay, the sprouts appeared likely to survive to become mature trees.

The number of baldcypress seedlings at each site ranged from 0 to 953 ha^{-1} (Table 1). Seedlings at permanently flooded sites 1–4 and 10 were rooted in unconsolidated, floating organic

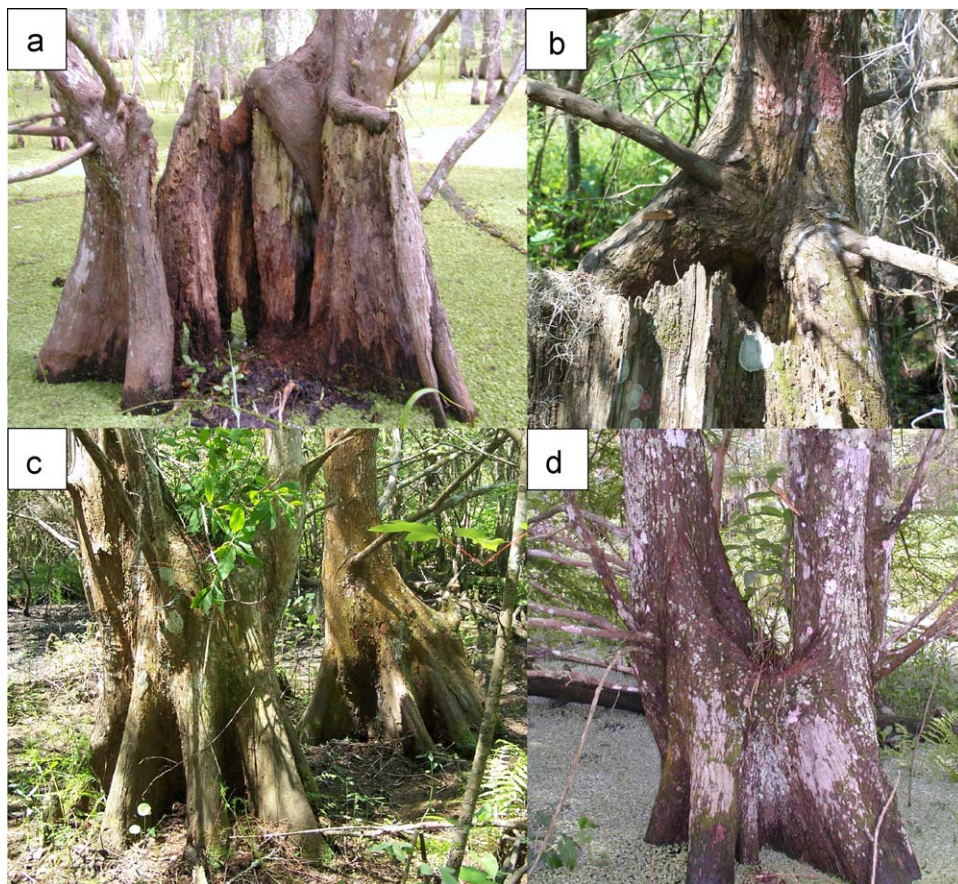


Fig. 4. Baldcypress stump sprouts in Louisiana swamps. (a) Sprouts with low vigor and advanced decay in stump, age 19. (b) Vigorous sprout on decaying stump, age 18. (c) Vigorous sprouts with complete cambium healing over stump, age 18. (d) Multi-sprout stump with decaying stump center, age 19.

Table 3
Correlations of variables with first two axes of ordination of Louisiana swamp ecological data by nonmetric multidimensional scaling

Variable	Correlation measure	
	<i>R</i>	τ
First axis ($R^2 = 0.37$)		
Basal area of baldcypress trees	−0.78	−0.58
Species richness	0.78	0.68
Number of saplings all species	0.76	0.61
Basal area of all saplings	0.73	0.55
Number of baldcypress trees	−0.70	−0.53
Number of swamp red maple saplings	0.69	0.55
Basal area of swamp red maple saplings	0.65	0.53
Basal area of all tree species	−0.64	−0.46
Basal area of sugarberry saplings	0.55	0.66
Number of sugarberry saplings	0.49	0.60
Number of water tupelo saplings	0.46	0.40
Basal area of ash saplings	0.45	0.41
Second axis ($R^2 = 0.57$)		
Stump quadratic mean diameter	0.83	0.49
Number of saplings	0.76	0.61
Basal area of saplings	0.73	0.54
Number of ash saplings	0.65	0.51
Basal area of ash saplings	0.59	0.50
Number of baldcypress trees	−0.51	−0.47
Basal area of all tree species	−0.42	−0.40

Only variables with $R^2 > 0.4$ or $|\tau| > 0.4$ are shown.

substrates, and we judged them likely to be ephemeral and unlikely to survive. Seedlings at sites 13–17 were rooted in mineral substrates at sites with riverine flooding and may survive. We observed water tupelo seedlings only at sites 16 (44 ha^{−1}) and 17 (119 ha^{−1}). Overall, seedling regeneration was not sufficient for regeneration of any of the sites to baldcypress or water tupelo.

3.1. Factors associated with sprout success

The first two axes of the NMS ordination represented 93% of the variation in the matrix of independent variables, although Monte-Carlo simulations indicated at least six dimensions would be statistically significant at $\alpha = 0.05$. Variables most correlated to the first axis were baldcypress overstory (−), species richness (+), and sapling density (+) (Table 3). Variables most correlated to the second axis, which was 78% orthogonal to the first axis, were stump size (+) and sapling density (+) (Table 3). We interpret the first axis as an ecological gradient from relatively dry, dense, species-rich (+) sites to wetter, more-open sites dominated by baldcypress (−). Water depth at the time of the survey was negatively correlated with this axis ($R = -0.45$; $\tau = -0.29$), but below the threshold we selected for interpretation. We interpret the second axis as a gradient in cutting intensity, from sites with large stumps and a strong tree regeneration (+) to sites with high standing tree density (−).

The first axis accounted for 42% of variation ($\tau = 0.26$) in percent baldcypress stumps with sprouts after varimax rotation to maximize correlation. The most important variables related to this rotated axis were stump height and diameter (−) (Table 4). Water depth at the time of survey was negatively

Table 4
Correlations of variables with first axis of ordination of Louisiana swamp ecological data by nonmetric multidimensional scaling, rotated to maximize correlation with dependent variables

Dependent variable	Independent variable	Correlation measure	
		<i>R</i>	τ
Baldcypress	Stump height	−0.84	−0.70
stumps with sprouts (%)	Stump quadratic mean diameter	−0.81	−0.60
Baldcypress	Stump height	−0.80	−0.65
sprouts per stump	Stump quadratic mean diameter	−0.62	−0.47
	Water depth	−0.57	−0.41
	Number of water tupelo saplings	0.47	0.38
	Number of water tupelo trees	0.46	0.32
	Basal area of water tupelo saplings	0.40	0.34
	Species richness	0.30	0.33
Baldcypress	Number of saplings	0.87	0.84
sprout height MAI ^a	Basal area of all saplings	0.84	0.75
	Species richness	0.79	0.65
	Basal area of baldcypress trees	−0.75	−0.56
	Number of baldcypress trees	−0.73	−0.58
	Basal area of all trees	−0.65	−0.46
	Number of swamp red maple saplings	0.65	0.58
	Basal area of swamp red maple saplings	0.63	0.56
	Basal area of sugarberry saplings	0.61	0.67
	Number of sugarberry saplings	0.59	0.66
	Basal area of ash saplings	0.57	0.57
	Number of ash saplings	0.55	0.57

Only variables with $R^2 > 0.4$ or $|\tau| > 0.4$ are shown.

^a MAI = mean annual growth increment.

correlated with this axis ($R = -0.48$; $\tau = -0.39$), but just below the threshold we selected for interpretation. Species richness, a proxy for hydrological regime, was unrelated to this axis ($R < 0.01$; $\tau = 0.16$).

The first axis accounted for 47% of variation ($\tau = 0.43$) in number of surviving sprouts per baldcypress stump after varimax rotation to that variable. The variables most related to this rotated axis were stump size (−), water depth (−), density of water tupelo trees (+) and saplings (+), and species richness (+) (Table 4). The first axis accounted for 36% of variation ($\tau = 0.43$) in baldcypress sprout mean annual increment of height growth after varimax rotation to that variable. The most important variables related to this rotated axis were sapling density (+), species richness (+), basal area of overstory trees (−), and density of overstory ash (+) and swamp red maple (+) (Table 4).

4. Discussion

The proportion of baldcypress stumps with surviving sprouts did not decrease with time since cutting for the range of ages in

our data (10–41 years). The study-wide mean of 13.9% sprout survival is comparable to the range of 0–23% survival across several sites in Louisiana at ages 4–7 reported by Conner (1988). Thus, it appears the mortality rate of baldcypress sprouts after age 7 is low.

The lack of water tupelo stump sprouts or seedlings is difficult to interpret. Water tupelo is less tolerant of shade than is baldcypress, so it would not be expected to reproduce well in the partially logged stands that comprised our study sites. Nonetheless, it is surprising that we saw almost no evidence of successful water tupelo regeneration except in a pair of adjacent sites. The logging practices at sites we visited are not favoring water tupelo, in contrast to what has been reported elsewhere (Brinson et al., 1980; Aust et al., 2006). It is possible that harvest methods (e.g., height of stump, felling method, or skidding method) may be the cause of poor sprouting, although we do not know what methods were used to log our study sites. It is likely that the same unidentified factors that resulted in poor sprout survival previously observed in Louisiana by Kennedy (1982) were also responsible for lack of sprout and seedling survival in this study. For example, differences in hydrological or biogeochemical processes between the delta and the coastal plain may explain why survival is less in Louisiana than elsewhere. It is possible that water tupelo regeneration in Louisiana is being particularly affected by the forest tent caterpillar (*Malacosoma disstria* Hubner). There have been severe and repeated defoliations by this insect in Louisiana, where outbreaks of up to 250,000 ha have occurred since 1948 (Souther-Effler, 2004). Although trees do not usually die as a result of defoliation, their growth is retarded (Abrahamson and Harper, 1973; Goyer et al., 1990). Lower-canopy trees are often most subject to herbivory because caterpillars drop from higher trees, and regeneration may be reduced as a result.

The first axis in the ordination of environmental variables affecting baldcypress stump sprouting reflected a hydrological gradient, which is the most ecologically important gradient in wetland forests. However, water depth at the time of survey was not itself strongly correlated with this gradient, likely because it was a single sample point that did not fully represent site hydrological regime. The success of baldcypress stump sprouting was related to this axis in some ways but unrelated in other ways. Height growth of surviving sprouts was related to variables that were very similar to the unrotated first axis in the environmental variables (Tables 3 and 4), in that growth was best on the higher sites with greatest species richness and regeneration of all species. In contrast, long-term survival of baldcypress sprouts was more related to characteristics of the stumps themselves than to apparent hydrological gradient (Table 4).

Stump size and the position of baldcypress sprouts on stumps have been previously shown to affect survival (e.g., Mattoon, 1915; Forder, 1995; Ewel, 1996; Randall et al., 2005). Forder (1995) found that sprouts on stump tops had the highest growth of any position of origin. Our results support previous findings that sprouting is usually greater on small-diameter stumps. Although some research has found that sprouting is greatest when stumps are tall enough to keep young sprouts

above floodwaters, the results of our study showed that stump height was the most negatively correlated variable with sprout survival. More research is required to understand how stump height and hydrological conditions interact to control long-term sprout success.

Growth of baldcypress sprouts was best on the higher-elevation, drier sites when overstory competition was low (Table 4). This is evidence that, although baldcypress has a competitive advantage to dominate frequently flooded sites, its biological optimum growth occurs when flooding is less severe. Randall et al. (2005) found early pondcypress sprout survival was decreased by competition from overstory vegetation but increased in wetter sites (maximum inundation 50% of the year in drought years). Together, these results indicate that long-term success of baldcypress stump sprouting may be best on transitional sites where flooding is not severe but is sufficient to reduce competition.

Our data were insufficient for robust quantification of spatial variability of baldcypress stump sprouting. However, sampling at two (adjacent) sites (6 and 7) was in a small portion of a large logged area, within which more research had been conducted. Sprouting was ubiquitous in baldcypress in the first 2 years after logging at this site (Forder, 1995). A subsequent extensive survey of the site at age 9 found 25.9% sprout survival for baldcypress and 7.8% sprout survival for water tupelo overall (G.P. Shaffer and W.H. Conner, unpublished data), compared to 69.1% sprout survival for baldcypress and no surviving water tupelo sprouts in the smaller area sampled by our survey at age 11. Within our transects, survival ranged from 0 ($n = 4$ stumps) to 87.5% ($n = 7$). More research is needed to understand why successful stump sprouting is so spatially variable.

Low and spatially discontinuous sprout survival indicates stump sprouts cannot be relied upon to establish a new stand of either baldcypress or water tupelo after disturbance or logging. However, this conclusion has two important limitations. First, the diameter-limit cutting that dominated our sites is not ideally suited to produce either coppice or seedling regeneration because some overstory competition remained. Second, the trees cut were primarily sawtimber-sized baldcypress trees of relatively large diameter. Stump height and diameter were the variables most negatively associated with sprout survival (Table 4), which suggests that sprout density might have been higher at the surveyed sites if logging had removed more than just the largest baldcypress trees. The results of this study and experience in other cypress–tupelo wetlands (Aust et al., 2006) support the conclusion that long-term success of coppice is better on drier sites with smaller trees and more intense cutting. These conditions are also most favorable for regeneration from seed, so that stump sprouting appears to be of least utility in regenerating the wettest, most difficult sites. Stump sprouts can be important sources of seed in some swamps (Ewel, 1998; Randall et al., 2005), but extended flooding in the growing season may prevent this mechanism of regeneration as well.

The high growth rates of baldcypress sprouts up to about age 20 suggests that surviving stump sprouts are capable of growing into overstory trees. Even in the context of competition from remaining trees after partial harvest, the surviving sprouts were

growing in diameter at rates approaching the maximum recorded in the literature through age 10 (Fig. 3). After age 10, growth appears to be decreasing, though more data is needed to determine whether long-term growth will continue to approximate that of plantations or that of natural stands.

It is not clear whether decay originating in the stumps will allow sprout-origin baldcypress trees to remain windfirm indefinitely. We saw no broken sprouts, but most sprouts in our study were not in a dominant or open growing location that would expose them to high winds. Conner et al. (1986) speculated that the stump-top position of most baldcypress sprouts would prevent their development into sound trees, and field experience in Louisiana suggests that much of the early mortality in sprouts is by structural failure at the contact with the stump (although Randall et al. (2005) found early mortality in Florida pondcypress was from herbivory). Our inference of low mortality after about age 7 suggests that breakage is not a major problem in pole-size trees, but advancing decay in stumps will decrease quality of wood in the lower stem and may erode structural support. Nonetheless, some sprout-origin trees have doubtless become dominant canopy trees. During the field surveys we found several trees at least 50 years old that appeared to have originated as stump sprouts, and found about 15% of baldcypress logs from overstory trees more than 100 years old had multiple piths at the base at one logging site in Lafourche Parish, Louisiana.

The poor coppice regeneration and lack of seedlings across the sites suggests that, in the absence of disturbance, successional processes will cause a change in species composition away from domination by baldcypress and water tupelo on many of the surveyed stands. If a site is not excessively flooded during the growing season, it will likely become dominated by shade tolerant hardwood species (Conner and Day, 1976). For example, red maple and ash appear poised to dominate the overstory of the drier survey sites, but with poor quality trees. Aquatic vegetation will likely dominate the permanently flooded sites after the eventual mortality of the overstory, and these forests will become floating marshes or open water.

These results have direct implications for management. First, stump sprouting in baldcypress and water tupelo is occasionally capable of producing large trees quickly. However, it is not a reliable means of regenerating stands after logging, especially after partial cutting on wetter sites with large trees. Unless advancing decay from rot at the stump degrades wood quality, forest management plans should encourage sprout-origin trees if possible. Second, preferential harvesting of baldcypress or water tupelo without specific provisions for regeneration will likely accelerate species conversion. Diameter-limit cutting, which was the dominant harvest type on sites we visited, is therefore high-grading and poor stand management. The preferred approach may be group selection or clearcutting, possibly with preparatory shelterwood cuts to establish advance regeneration (Wilhite and Toliver, 1990; Meadows and Stanturf, 1997). However, frequent flooding on many of the sites may prevent any natural regeneration, regardless of silvicultural treatment.

5. Conclusions

Baldcypress sprout survival for stands logged 10–41 years ago was about the same as previously found for stumps up to 7 years old, so it appears sprout mortality is low after age 10. The proportion of stumps with surviving baldcypress sprouts was low, so that coppice cannot guarantee successful regeneration of disturbed or logged stands. Water tupelo sprouting was rare at our sites but it was not clear whether this may have been because trees were not cut at our sample locations. Baldcypress stump sprouts were more likely to survive on shorter, smaller-diameter stumps, and baldcypress sprout growth was greatest on drier sites with less competition from overstory trees. Surviving baldcypress stump sprouts were vigorous and likely to compete well for growing space in the canopy, but they were not regularly spatially distributed within stands and advancing decay from stumps into sprouts may degrade integrity of the tree bole.

Acknowledgements

We thank the Louisiana Governor's Office of Coastal Activities for funding and supporting this work through the auspices of the Science Working Group on Coastal Wetland Forest Conservation and Use. Other members of the group included Stephen P. Faulkner, Sammy L. King, Kenneth W. McLeod, Craig A. Miller, and J. Andrew Nyman. Field and laboratory assistance for the project was by Blake Amos, Erika Stelzer, and David Wall. Three anonymous reviewers contributed comments that substantially improved this paper. This is manuscript 06-40-0092 of the Louisiana Agriculture Experiment Station and Technical Contribution No. 5158 of the Clemson University Experiment Station.

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