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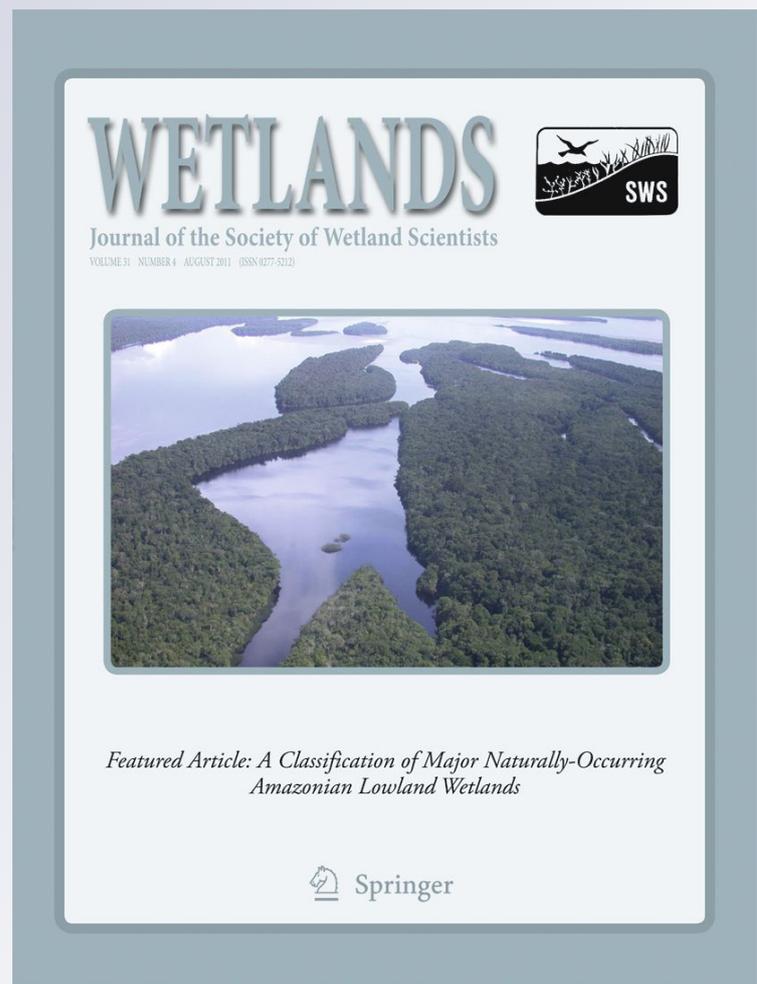
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# Fire Reinforces Structure of Pondcypress (*Taxodium distichum* var. *imbricarium*) Domes in a Wetland Landscape

Adam C. Watts · Leda N. Kobziar · James R. Snyder

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**Abstract** Fire periodically affects wetland forests, particularly in landscapes with extensive fire-prone uplands. Rare occurrence and difficulty of access have limited efforts to understand impacts of wildfires in wetlands. Following a 2009 wildfire, we measured tree mortality and structural changes in wetland forest patches. Centers of these circular landscape features experienced lower fire severity, although no continuous patch-size or edge effect was evident. Initial survival of the dominant tree, pondcypress (*Taxodium distichum* var. *imbricarium*), was high (>99%), but within one year of the fire approximately 23% of trees died. Delayed mortality was correlated with fire severity, but unrelated to other hypothesized factors such as patch size or edge distance. Tree diameter and soil elevation were important predictors of mortality, with smaller trees and those in areas with lower elevation more likely to die following severe fire. Depressional cypress forests typically exhibit increasing tree size towards their interiors, and differential mortality patterns were related to edge distance. These patterns result in the exaggeration of a dome-shaped profile. Our observations quantify roles of fire and hydrology in determining cypress

mortality in these swamps, and imply the existence of feedbacks that maintain the characteristic shape of cypress domes.

**Keywords** Delayed mortality · Edge effect · Fire severity · Logistic regression · Patch size · Wetland forest

## Introduction

Isolated wetland communities often are situated in landscape mosaics among uplands that experience relatively frequent fire events. Such landscape mosaics of widely divergent fire frequencies occur worldwide in regions where lightning strikes provide ignition sources. Due to seasonal variations in hydrology or occasional droughts, fires occurring in the upland components of these landscapes can occasionally enter wetland ecosystems. While the fire ecology of the upland component of these landscapes (e.g., cerrado in Amazonian South America; prairies and pine savannas in North America) tends to be well studied, the effects of fire in their embedded wetlands tends to be less understood due to fire's infrequency and the difficulty of accessing and assessing fire effects in normally inundated areas.

In wetlands, fuel loading and moisture-dependent availability can result in either of two general types of fires. Surface fires move through litter, grasses and short-stature shrubs, and may occur even when soil and large-fuel moisture contents are high. Ground fires, which consume not only the latter fuels but also organic-derived soils such as peat, can occur when organic soils are sufficiently dry to support combustion. Effects from fires in wetland ecosystems include nutrient mineralization from combustion (Smith et al. 2001), changes to soil properties as a result of

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heating (DeBano et al. 1998), and overstory tree mortality. Ground fires, which may smolder for weeks or months, also may consume large amounts of accumulated soil organic matter (e.g., Page et al. 2002). These events may cause local hydrologic changes, such as longer hydroperiods, due to combustion losses and decreases in soil elevation.

One regionally widespread example of wetlands embedded within a frequently burned upland community is found in the southeastern U.S. Coastal Plain, where fire-adapted longleaf pine (*Pinus palustris* [Mill.] savannas or slash pine (*P. elliottii* [Engelm.] forests occur in close proximity to forested wetlands dominated by pondcypress (*Taxodium distichum* var. *imbricarium* [Nutt.]), baldcypress (*T. distichum* [(L.) Rich.] var. *distichum*), or hardwood angiosperms. In addition to occasional lightning strikes, the relatively frequent presence of fire in neighboring upland communities [e.g., fire-return intervals of ca. 2–10 y in pine flatwoods (Abrahamson and Hartnett 1990) or pine rocklands (Snyder et al. 1990)], presents regular ignition sources to cypress wetlands. While these communities burn less frequently than their upland neighbors, fire may be second only to hydrology in its long-term influence on species composition and structure (Duever 1984). Yet despite their proximity to fire-prone communities and the generally recognized importance of periodic fire in cypress swamps, few studies have quantified the impacts of fire in these wetlands.

Periodically inundated cypress forests accumulate organic matter in a histic epipedon ranging in depth from only a few centimeters at their edges to meters near the centers of large, long-hydroperiod swamps. The latter communities are thought to experience fires every 100 years or more (Snyder 1991) because of consistently long hydroperiods. In contrast, smaller depressional cypress wetlands—called “domes” because taller trees toward the centers cause them

to appear dome-shaped from a distance (Fig. 1)—experience far greater seasonal and interannual variability in hydroperiod. This variability, and frequent sources of ignition from surrounding fire-adapted communities, cause cypress domes to experience natural fires more frequently than larger cypress forests such as elongated strands or long-hydroperiod sloughs (Wade et al. 1980). Regular and prolonged inundation, and surface fires at approximately decadal intervals (with soil-consuming ground fires occurring perhaps once or twice per century), are proposed mechanisms for the nearly complete dominance of cypress over potential hardwood competitors in domes (e.g., Gunderson 1977; Ewel and Mitsch 1978; Duever et al. 1984; Hamilton 1984; Ewel 1995; Casey and Ewel 2006), due to the high resistance to and resilience following fire injury in cypress (Beaven and Oosting 1939; Hare 1965), and intolerance of many potential competitors to long hydroperiods.

Cypress domes may remain dry for up to 3–6 months per year (Ewel 1995), allowing sufficient desiccation of large fuels and organic soils to support smoldering combustion. Cypress trees may respond to fire differently depending on their size, as well as due to landscape factors such as dome size and edge effect that may influence local temperature or humidity (Leopold 1933; Forman and Godron 1986; Matlack 1993), with consequences for the structure and size of cypress domes. Beyond the persistence or intrinsic importance of these features, the consequences of fire may impact the quality of ecosystem services they provide (e.g., carbon storage in organic soils, hydrologic storage, and controlled water release to underlying shallow aquifers), and their value for wildlife species. Furthermore, improving our knowledge of the persistent effects of fires on cypress swamps is important in helping to determine whether management efforts to prevent ground fires because of the



**Fig. 1** This circular cypress swamp approximately 2 ha in area displays the dome-shaped profile that lends these common landscape features their name. Pondcypress trees (*Taxodium distichum* var. *imbricarium*) in dome centers may reach heights of 20 m or more in soils a

few meters deep; those toward the edge are far shorter due to thin soils and the influence of fire. Light-colored areas at periphery of dome are periphyton and marl; the surrounding forest is pine rockland with canopy of South Florida slash pine (*Pinus elliottii* var. *densa*)

persistent and hazardous smoke they produce are ecologically justified (See et al. 2007).

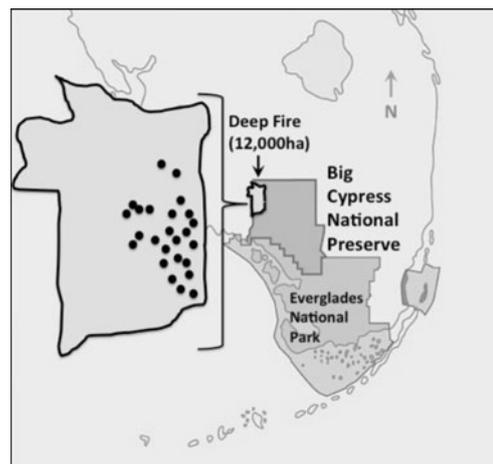
Following a 2009 drought-season wildfire that affected a characteristic landscape mosaic of cypress swamps among pine uplands, we assessed the effects of landscape, ecological, and edaphic factors on cypress tree survival and the resulting changes to forest structure. Our objectives were to explore the effects of cypress dome characteristics on fire severity and their consequences for cypress mortality; to create a predictive model for future post-fire mortality estimation; and to explore potential feedbacks among fire, hydrology, and cypress dome structure. Because cypress domes occur as patches on the landscape, we predicted patch-size effects on severity; i.e., that measures of severity (fuel consumed, trees charred or killed) would be lower in the centers of domes than at the edges, that severities would be lower for larger domes, and that the magnitude of difference in severity would be greater for larger domes than for smaller domes. We also predicted an edge effect on mortality within domes: decreasing mortality with increasing distance from edges toward dome centers. We hypothesized that modeling of mortality would reveal the mechanisms of this predicted differential mortality to be related to increasing tree size and soil depth, and decreasing soil elevation, found at dome centers compared to their edges.

## Methods

### Study Area

Big Cypress National Preserve occupies 300,000 ha of pine uplands, mesic hardwood forests (called hammocks), prairies, and open or pondcypress-dominated forested wetlands in southern Florida (Fig. 2). The latter occur as elongated and irregularly shaped forests called sloughs or strands with long hydroperiods, or as circular or teardrop-shaped patches (called domes) in shallow depressions in the underlying limestone. Regular spacing among adjacent domes (Fig. 3) allows surrounding upland communities, frequently pine-lands, to become potential sources of ignition under conditions when fuels in these frequently inundated areas are available.

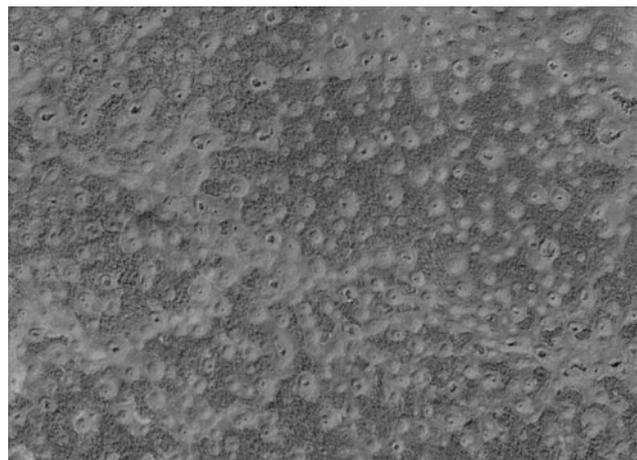
Ignited by lightning on 22 April and contained on 11 May 2009, the Deep Fire burned over 12,000 ha in the northwestern area of the Preserve under severe drought conditions. The area of the burn is characterized by low elevation and low topographic relief typical of southern Florida karstic geomorphology. Major vegetation communities comprise a mosaic of uplands and wetlands: south Florida slash pine (*Pinus elliottii* var. *densa* [Little and Dorman]) forests, prairies dominated by muhly grass (*Muhlenbergia capillaris* [Lam.]) or sawgrass (*Cladium jamaicense* [Crantz]), and infrequently flooded



**Fig. 2** Big Cypress National Preserve, some 300,000 ha in area, is continuous with Everglades National Park in southern Florida. The Preserve was the site of the 12,000 ha Deep Fire in 2009; approximate locations of cypress domes in which sampling took place ( $n=25$ ; inset) are shown here

hammocks of dense hardwoods and palm (*Sabal palmetto* [Walter]) alternate with open-water marshes, cypress domes, and strands. Extreme drought conditions at the time of the fire allowed the fire to burn through nearly all wetlands in the region, and in many areas the organic soil was sufficiently desiccated to ignite. Although a lack of pre-fire soil data prevented an examination of the amount of soil combustion that occurred during the resulting ground fires, evidence of combustion extending 10–20 cm below the presumed level of pre-fire soil surfaces was observed in many locations.

Weather data collected by a local Remote Automated Weather Station (RAWS) located approximately 15 km from the study location indicated that during the five days when the study region burned (24–28 April), maximum daily



**Fig. 3** Rounded or circular cypress domes (gray areas, some with darker-colored marshes at their centers) occur regularly among fire-prone pine forests in this representative satellite image of a 1200-ha portion of Big Cypress National Preserve

temperatures ranged from 29.4 to 35.6°C. Winds from the east or east-northeast reached maximum speeds of 32–38 km/h, and average relative humidity values during daylight hours ranged from 40–61%. Onsite observations by firefighting crews indicated relative humidity readings at or below 40% during afternoon hours of each day and relatively light winds (mean daytime speeds of 8 km/h), conditions favorable for the development of smoldering combustion in desiccated organic soils.

#### Data Collection

From approximately 90 roughly circular cypress domes identified in the Deep Fire perimeter from satellite imagery, we selected a random sample of 25 domes in which to measure fire severity and cypress response to fire. Remote measurements of dome diameter along north–south and east–west axes of each circular dome, using 2.5 m resolution images from SPOT (Satellite Pour l'Observation de la Terre), were used to estimate area of each dome, and subsequently verified by perimeter circumnavigation of a subset of the domes using Wide Area Augmentation System (WAAS) enabled GPS. Sizes of these domes estimated from satellite imagery ranged from 0.2 ha to 3.4 ha, with a mean of 1.2 ha. During June 2009 we tagged each tree  $\geq 2$  m in height or with diameter at breast height (dbh)  $\geq 2$  cm within a randomly oriented strip plot 2 m wide running from the edge to the center of each dome. For each tree ( $n=423$ ) we recorded distance from dome edge in 5-m increments; height, using a laser hypsometer; diameter (at breast height, or above buttress swelling or flutes if present); presence of epicormic or basal sprouting; maximum height of charring on tree boles; and the number, height, and cumulative circumference of scorched areas on cypress boles due to epiphytic bromeliads consumed in the fire. For each tree we also recorded status, i.e., living or apparently killed by fire. Cypress trees we observed within the fire perimeter that had obviously died prior to 2009 but remained standing experienced far greater consumption than those which remained alive; it was on the basis of these observations that we made our determinations of fire-caused mortality.

To estimate fire severity within each cypress dome we assessed changes in five strata of fuels (surface fuels; vegetation <1 m in height; shrubs and trees 1–5 m in height; subcanopy trees; and canopy trees) and calculated index scores of 0 (unburned) to 3.0 (high severity; all fuels completely consumed) based on estimates of canopy scorch, amount and height of char on stems, and change in fuel loads for various fuel classes (i.e., soils, 1-hr fuels, 10-hr fuels, 100-hr fuels, etc.). Our ability to estimate consumption of soils was limited by rainfall and landscape inundation that occurred subsequent to the fire. This ground-based index assessment for fire severity closely follows ground-

truthing methods for large-scale fire severity assessment in the widely used Composite Burn Index (CBI, Key and Benson 2006) method (e.g., Picotte and Robertson 2011). Advantages of this method include the integration of fire effects among soil, groundcover, and mid- and upper-story vegetation; use of CBI methods also allow findings to be meaningful in the context of future assessments of wildfire severity using remote methods. One departure of our methods was to use 10 m  $\times$  10 m plots, smaller than the 30 m  $\times$  30 m plots normally used in the CBI method to correspond to LANDSAT imagery pixels. This difference was necessary to avoid plot overlap in the smallest domes, and to allow us to make comparisons of fire severity at the edges and centers of domes of varying sizes. These plots were located at either end of the mortality-assessment strip plots (i.e., one at the center of each of the 25 cypress domes and one near the edge), to allow us to relate severity assessments with mortality, edaphic, and hydrologic measurements.

In May–June 2010, we revisited the domes to assess delayed mortality among cypress, indicated by a lack of new growth to replace leaves lost by this deciduous species during the intervening winter dry season. During this survey we collected information on soil depth to bedrock at three locations around the base of each tree using a steel probe; high water levels at the time of sampling also enabled the estimate of mean local soil elevation using water depth measurements adjacent to each tree benchmarked to elevation and hydrographic data from a nearby Everglades Depth Estimation Network (EDEN, Telis 2006) monitoring station.

#### Data Analyses

We compared severity measurements at dome-edge and dome-center locations using Wilcoxon's signed-rank test for equality of means (Dalgaard 2002), and among domes of different sizes using Wilcoxon's test and ANOVA, to determine whether dome size or location within dome with respect to edge (i.e., distance from edge) affected the severity of this drought fire in cypress domes and the degree to which severity affected tree survival. These comparisons were performed separately for overall severity values, as well as for understory strata scores (i.e., the average of scores for substrates and vegetation less than 1 m in height) and overstory strata scores (i.e., average of those for tall shrubs and intermediate and canopy trees). Regression analyses were performed to determine whether dome radius, tree height or diameter, or tree density predicted either severity values for dome centers or the difference between severity values at dome edges compared to centers; models were compared using Aikake's corrected information criterion (AIC-c). The influence of environmental (fire severity scores, dome size, distance from edge, soil depth, soil elevation, tree density within plots) and tree (height, diameter

at breast height) characteristics, on probability of survival were analyzed using logistic regression, which is commonly employed to assess tree mortality drivers (Kobziar et al. 2006). Logistic regression equations take the form

$$P_m = (1 + e^{-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)})^{-1}$$

with  $P_m$  the probability of mortality;  $X_1, X_2, \dots, X_n$  independent predictor variables; and  $\beta_1, \beta_2, \dots, \beta_n$  are coefficients estimated from mortality data. This equation is used to generate maximum-likelihood estimators for logit-transformed mortality data (Sokol and Rohlf 1995). Analyses were performed using the software package R (R Development Core Team 2005); models were compared using Aikake's information criterion (AIC; Crawley 2007) and Receiver Operating Characteristic (ROC) values (Hanley and McNeil 1982). While AIC is widely accepted as an indicator of the goodness of model fit, ROC curve analysis assesses the ability of a model to correctly predict the outcome as opposed to generating false positive (Type I error) and is frequently used in evaluating fire-mortality models (Saveland and Neuenschwander 1990; Kobziar et al. 2006; Sah et al. 2010). ROC values of 0.5 indicate that a model's predictions are no better than a chance-occurrence prediction, while perfect predictive ability of a model results in a value of 1.0. Hosmer and Lemeshow (2000) argue that values 0.70 or higher indicate good model discrimination. In addition to regression analyses to detect the influence of ecological or edaphic factors on tree mortality, we also examined influence of dome size and edge effect on tree survival and community structure using Wilcoxon's signed-rank test. For the former, we performed linear regressions on changes in average size of living (or surviving) trees against dome size; we also performed Wilcoxon's signed-

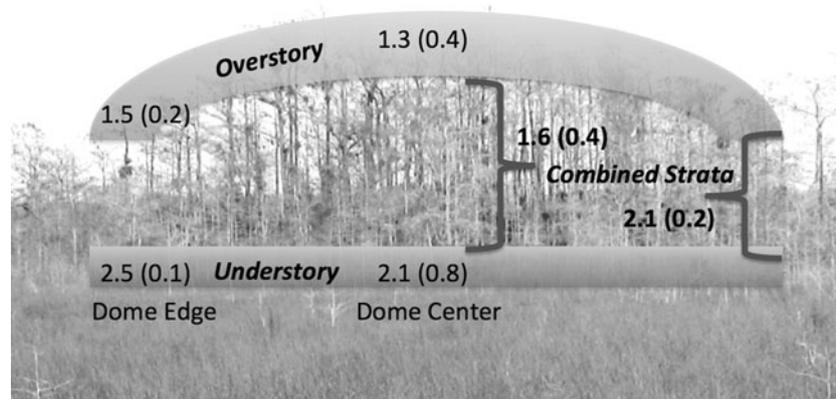
rank tests on tree sizes and post-fire size changes for three size stratifications (<0.5 ha, 0.6–1.0 ha, >1.1 ha) of cypress domes. To assess post-fire changes to pondcypress community structure in domes, we compared the sizes (heights and diameters) of cypress trees presumed to be alive prior to the fire with trees surviving one year beyond the fire.

## Results

### Fire Severity and Initial Effects on Pondcypress

The 423 pondcypress trees we tagged were 2.0 to 19.0 m in height (mean 8.9 m); diameters ranged from 1.5 cm dbh to 81.0 cm dbh (mean 16.9 cm). All trees had at least one additional charred area on the bole resulting from burned bromeliads. Two of the trees surveyed during the initial 2 months following the fire did not display new growth, indicating a 0.5% initial post-fire mortality rate.

Mean values for severity assessments among the 50 plots in which we conducted severity assessments ranged from 0 (nearly unaffected) to 3.0 (high severity; i.e., substantial consumption of fuels, considerable loss of branches, and charring of tree trunks to heights of several meters). Most plots displayed moderate or moderate-high fire severity among understory strata (>40% consumption of light and medium fuels, >50% mortality among understory herbaceous and woody plants) and low-moderate to moderate severity among overstory fuel strata (i.e., cypress trees; <50% incidence of torching, <50% canopy mortality; char heights <4 m on canopy trees). Severity values measured at dome edges were significantly higher than those in dome centers, for both the understory strata ( $P < 0.05$ ) and all strata combined (i.e., overall severity score;  $P < 0.01$ ; Fig. 4).



**Fig. 4** Fire severity was significantly lower at cypress dome centers compared to dome edges, whether measured for overstory vegetation (e.g., canopy and subcanopy trees;  $P < 0.05$ ), understory (e.g., shrubs and groundcover;  $P < 0.05$ ), or all strata combined ( $P < 0.01$ ). Fire

severity was measured using a modified Composite Burn Index method (CBI, Key and Benson 2006), which returns values from 0 (unburned) to 3.0 (highly altered). Mean values (with variances in parentheses) are shown for the 25 domes measured in the study

There was no significant correlation between dome size and the severity scores we recorded at dome edges or centers, neither in overall measures nor among individual fuel classes. Also, the edge-to-center difference between severity values was not correlated with dome size. Comparisons using AIC-c scores of models incorporating combinations of dome size, tree height, tree diameter, and tree density indicated that addition of these additional variables did not improve upon the simple linear regression model using dome size alone.

#### Delayed Mortality

Follow-up census in 2010 revealed that an additional 98 of 417 trees censused (23.5%, excluding three trees which could not be re-identified due to missing tags) had died. Among the 25 domes, this delayed mortality ranged from 0 to 66.7%. There were no correlations or predictive relationships between dome size, tree density, or overall severity scores for domes and the percent tree mortality in a given dome one year following the Deep Fire. However, a difference was noted in the mean severity scores for overstory strata in dome centers between surviving trees and those that died in 2009–2010 (1.3 vs 1.5,  $P < 0.05$ ). Logistic regression analyses indicated that tree size and soil surface elevation at the location of a particular tree were the strongest predictors of mortality. Including tree diameter in regression models, rather than tree height, achieved better model performance measured by both AIC scores and ROC values (Table 1, Fig. 5).

#### Structural Changes

Compared with trees that resprouted immediately following the Deep Fire, those which succumbed during 2009–2010 were shorter (mean height 7.7 vs 9.3 m,  $P < 0.01$ ) and smaller in diameter (mean DBH 12.1 vs 18.6 cm,  $P < 0.001$ ). Additionally, some 10% of surviving trees experienced topkill, i.e., regrowth only occurred via epicormic or basal sprouting. Topkill was negatively correlated with tree size, occurring predominantly in trees shorter than 3 m and rarely in trees exceeding 4 m. As a result of the effective decrease in height

due to topkill, mean height of surviving trees were significantly shorter ( $P < 0.001$ ) than mean heights of trees prior to the fire. Neither regressions on dome size nor Wilcoxon's rank tests performed on three size-class groups of domes (<0.5 ha, 0.6–1.0 ha, >1.1 ha) indicated any effect of dome size on the changes observed in pre-fire versus post-fire mean height.

Trees which we estimated to have been alive just prior to the Deep Fire were larger in the centers of domes than at their edges; this trend also was observed among trees surviving the fire. Linear regressions were performed on tree heights from dome edges to centers, using both pre-fire heights and those of live trees one year following the fire. One year after the fire, regression coefficients for edge distance were nearly twice those for pre-fire heights (Table 2). Differential mortality according to size, and heterogeneous size distribution of trees within the dome, produced differences in fire effects on structure depending on the position within the dome. Mean heights of surviving trees were lower compared to pre-fire heights near dome edges, while those closer to the centers of most cypress domes increased (Fig. 6).

## Discussion

#### Dome Size, Severity, and Pondcypress Mortality

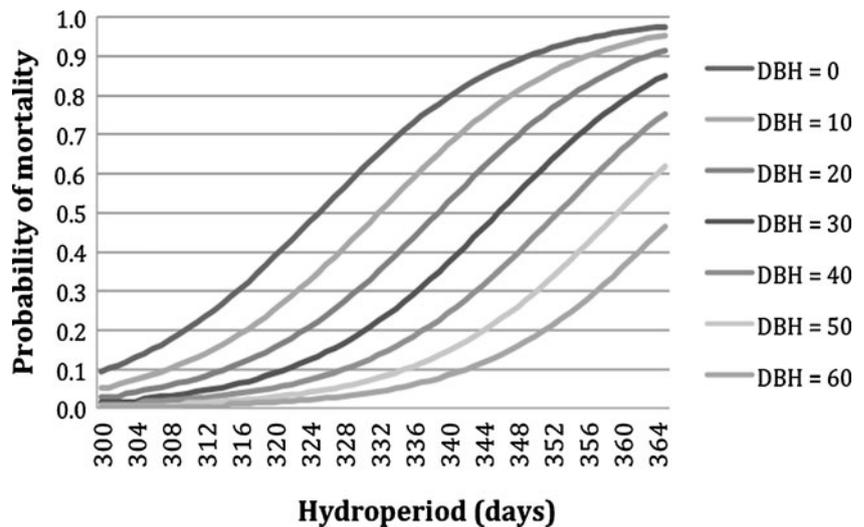
Contrary to our expectations, there did not appear to be a noticeable attenuation of fire severity in larger cypress domes compared to smaller domes. A lack of dome-size effect on cypress mortality reinforces this conclusion. Although data on background mortality are not available (i.e., proportion of trees tagged that might have been dead prior to the fire), the occurrence of only two dead cypress trees among the initial 423 stems tagged immediately following the fire suggests that this rate is low. Our findings lead to the question of whether cypress domes in this region are too small for any size-related effects on fire severity to emerge. Another possibility is that in the case of long or persistent drought events, differences in microclimate between small cypress domes and large ones are not sufficiently great to result in differential fire severity. However, important differences were evidenced in association

**Table 1** Logistic regression models predicting fire-caused pondcypress mortality. Elevation values were calculated for each tree measured based on water depth measurements benchmarked to USGS hydrographic data during landscape inundation

Model	$\beta_0$	$\beta_1$	$X_1$	$\beta_2$	$X_2$	AIC	ROC
Height + Soil Elevation	14.5115	-0.1240	Height	-0.0575	Soil Elevation	421.36	0.701
DBH + Soil Elevation	13.8210	-0.0629	DBH	-0.0552	Soil Elevation	408.14	0.732

$\beta_0$  is intercept;  $\beta_n$  are coefficients;  $X_n$  are model parameters; Soil elevation was calculated at the base of each tree measured; DBH = tree diameter at breast height; AIC = Akaike's information criterion; ROC = receiver operating curve. All regression coefficients differ significantly from zero at  $p \leq 0.0001$

**Fig. 5** Predictions of best-performing logistic regression model incorporating tree diameter at breast height (DBH in cm) and local hydroperiod to describe probability of delayed-mortality response to drought-season fire in pondcypress



with location within the domes. Severity was higher at dome edges than in the centers of domes, suggesting that location within the dome corresponded to differences in fuel availability, microclimate, and perhaps tree resistance.

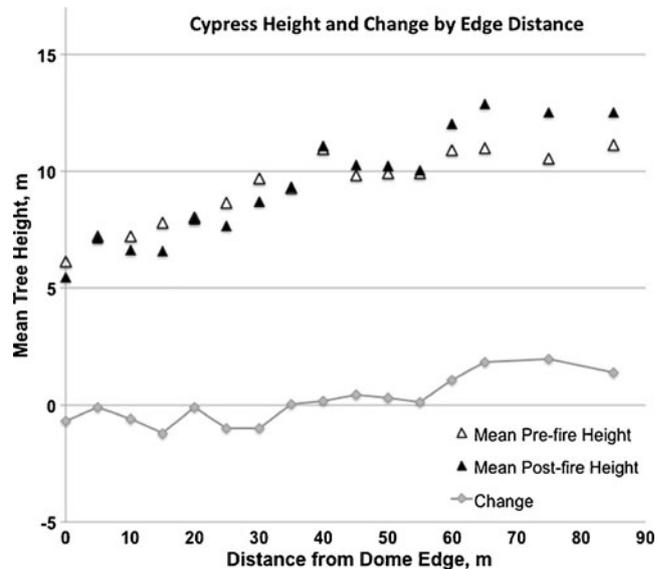
While dome size appears not to make a difference in terms of fire effects in these isolated forested wetlands, tree size does matter: taller trees, or those with larger diameters, displayed greater survival in the Deep Fire regardless of their location in the dome or the depth of soil in which they occurred. While neither soil depth nor edge distance was correlated with severity or mortality, trees were larger in areas with deeper soil and toward the centers of domes. The tendency of larger trees to better survive fire is unsurprising because of the tendency of larger trees to possess thicker bark, shown to be protective against mortality from fire in several tree species (e.g., Ryan and Reinhardt 1988; Hengst and Dawson 1994). This result also may be due to the greater distance between the canopies of larger trees and the surface fire, limiting canopy scorch or foliage consumption during the burn.

**Table 2** Regression models describing tree size and location, pre- and post-fire

Model	$\beta_0$	$\beta_1$	$X_1$	$p (\leq)$
DBH_PreFire $\propto$ DFE	15.1314	0.0538	DFE	0.05
DBH_PostFire $\propto$ DFE	14.8900	0.1045	DFE	0.001
Height_PreFire $\propto$ DFE	7.6737	0.0351	DFE	0.001
Height_PostFire $\propto$ DFE	6.6975	0.0626	DFE	0.001

$\beta_0$  is intercept;  $\beta_1$  is coefficient;  $X_1$  is model parameter; DBH\_PreFire = diameter of surviving trees measured immediately following the Deep Fire (99.5% of all trees in study plots); DBH\_PostFire = diameter of surviving trees one year following fire; Height\_PreFire = height of surviving trees immediately following fire (99.5% of all trees in study plots); Height\_PostFire = height of surviving trees one year following fire. DFE = distance of tree from edge of cypress dome, measured in 5-m increments toward dome center

Local soil elevation appeared to play about as great a role in determining cypress survival as did tree size. Trees occurring in areas with slightly lower soil elevations (as little as a few cm) were more likely to die in the year following the Deep Fire. While soil elevations tend to be lower (and thus hydroperiods longer) as one proceeds toward dome centers (MacPherson 1974), sufficient microtopographic variation appears to exist in these sites to allow variables associated with soil elevation to predict mortality while edge distance does not. One possible mechanism behind this observation may relate to cypress rooting in organic soil. Total soil depth increases from dome edges towards centers, as does the thickness of the uppermost organic layer. While quite thin at edges, peat deposits may be a meter thick close to the



**Fig. 6** Mean heights of trees among all cypress domes in relation to dome edge, prior to fire and one year following fire. The mean decrease in live tree heights toward dome edges and increase in tree heights nearer dome centers indicates that a severe fire has exaggerated the characteristic structure of the domes in the study area

center of a cypress dome; because anoxic conditions limit rooting depth of cypress, a large proportion of cypress roots will be found in the organic soil layer near the centers of domes that at their edges. Fires that occur under drought conditions and result in soil combustion (such as the Deep Fire) will cause damage to a greater proportion of roots in these deep organic soils than nearer the edge, where cypress rooted in sandy marl soils underlying the thinner organic layer will be better protected from combustion and heating. Longer hydroperiods found at lower elevations, usually no threat to mature cypress trees, may represent an additional stress to trees whose roots have been damaged by fire. Increases in hydrologic stress from flooding among root-damaged trees may be greater towards dome centers due to their increased hydroperiods and greater likelihood of experiencing damage from soil combustion. Allocation of stored energy reserves to the production of new leaves shortly following the fire may have prevented damaged trees from repairing damaged roots, perhaps contributing to the delayed mortality response seen here.

Why a substantial number of trees were able to recover foliage lost to the fire, only to succumb during the subsequent period of senescence (corresponding to the dry season, which in 2009–2010 was unusually wet), is unclear. The considerable proportion of tree mortality that occurred only after a season's growth following the fire may be due to the interaction of a number of factors. Explanations that invoke cambial or root damage do not seem to account for the months-long period during which these trees held foliage and appeared to be recovering; also, no noteworthy instances of insect damage or disease to these trees were recorded in the initial post-fire survey, during the 2010 census, or through observations of unburned domes in the area. It may be that the initial post-fire foliage flush represented a stress response, and, after consuming crucial carbohydrate reserves during the dry season, trees succumbed to their fire-induced injuries in the cambium, fine root systems, or both. Delayed mortality following fire has been observed in pines (Thies et al. 2008) and in related baldcypress (*Taxodium distichum* var. *distichum*) following hurricanes (Keeland and Gorham 2009), with similar mechanisms proposed to account for tree death up to several years following disturbance. Trees in this study that died in the year following the Deep Fire were associated with higher overstory severity values in the centers of domes in which they occurred, indicating that a combination of bole damage and stress from canopy scorch at least partly explain the delayed mortality.

Two additional factors are likely to predict fire-caused mortality of pond cypress. First, the consumption of duff (decomposing litter), and associated fine roots, has been shown to be a determinant of mortality among longleaf pine (*Pinus palustris*) in fire-suppressed forests (Varner et al.

2007, 2009); consumption of duff and upper-horizon sapric material is probably also a predictor of mortality (along with organic soil consumption) in desiccated cypress domes. However, our inability to accurately estimate soil and duff consumption due to a lack of pre-fire estimates of soil elevation or duff thickness, precluded use of this parameter in our analysis. Crown scorch and consumption, typically useful in predictions of fire-caused mortality among Western US conifers (Ryan and Amman 1994) as well as those in the southeastern US (e.g., Varner et al. 2007), could not be accurately assessed in this study because the flush of cypress regrowth began to obscure crown scorch and consumption soon after the fire.

#### Fire Maintenance of Dome Structure via Topkill

One of the most compelling results of this study concerns the role of fire in reinforcing dome structure within the wetland landscape. The 10% of trees whose stems were killed, and which resprouted from basal or epicormic shoots, represent a commonly observed morphological characteristic of pondcypress known locally as “hatrack cypress” or “bonsai cypress.” This topkill resulted in changes to the mean heights of surviving trees. We observed a significant relationship between pre-fire tree size and edge distance, with larger trees occurring further toward the centers of cypress domes. This finding is not new and has been discussed elsewhere (e.g., Mitsch and Ewel 1979; Ewel and Wickenheiser 1988), as have the proposed mechanisms underlying it such as longer hydroperiods, deeper soils, and increased nutrient availability (Coultas and Duever 1984).

Fire has been invoked as a factor in shaping cypress dome development as well (Kurz and Wagner 1953; Taylor and Rochefort 1981; Duever et al. 1984), based on the observation that small trees are more susceptible to mortality and topkill than large trees. However, this relationship has never been documented adequately. In this study, we observed a stronger relationship between tree size and edge distance following the fire than existed prior to the Deep Fire. These effects are illustrated in the mean heights of trees found at 5-m increments along our plots, proceeding from dome edges to their centers. The scatterplots of both values recall the characteristic profile that lends the cypress dome its local name, but the changes caused by fire to live tree heights changes according to distance. Towards the edges of domes, the trees are more susceptible to topkill, and the mean heights of live trees are reduced one year following fire. At distances that correspond to the centers of medium- to large-sized domes, tree sizes are larger after the fire. Perhaps owing to deeper and more damage-resistant root systems or thicker bark among the tallest dome-center trees, smaller trees are more likely to be eliminated far from the edges of domes. This phenomenon results in an increase in

the mean heights of surviving trees at distances of about 60–100 m from dome edges. Thus, while hydrology and nutrients may initiate the structural differences among trees in these isolated forested wetlands, our observations quantify for the first time the important role of fire in reinforcing the vegetation structure of these landscape features.

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