MULTI-YEAR SALUTARY EFFECTS OF WINDSTORM AND FIRE ON RIVER CANE

Paul R. Gagnon[1, 2*], Heather A. Passmore[2], and William J. Platt[3]

[1] Murray State University, Watershed Studies Institute,
561 Emma Drive, Murray, Kentucky 42071, USA

[2] Murray State University, Department of Biological Sciences,
2112 Biology Building, Murray, Kentucky 42071, USA

[3] Louisiana State University, Department of Biological Sciences,
202 Life Sciences Building, Baton Rouge, Louisiana 70803, USA

*Corresponding author: Tel.: 001-270-809-6174; e-mail: pgagnon@murraystate.edu

ABSTRACT

Canebrakes are monodominant stands of cane (*Arundinaria gigantea* [Walter] Muhl .), a bamboo native to and once prominent in the southeastern USA. Canebrakes were important wildlife habitat within the bottomland hardwood forest ecosystem. They have been reduced in areal coverage by an estimated 98 % since European settlement due to land conversion and the drastic alteration of disturbance regimes in their floodplain habitat. Ongoing canebrake restoration efforts are hampered by incomplete understanding of the role of natural disturbance in cane ecology. We used a large tornado blowdown and multiple prescribed fires to quantify the response of cane to the sequential disturbances of windstorm and fire in the Tensas Watershed of northeastern Louisiana using number and condition of bamboo stems (culms) as response variables. We hypothesized that culms would be more abundant in burned than in unburned stands and that culm populations in burned stands would be younger than in unburned stands. In this study, conducted four years post fire, effects of both windstorm and burning were additive and beneficial. Results indicate that periodic aboveground disturbance has three salutary effects on cane ramet demography: 1) clonal growth following disturbances more than compensates for any culms killed; 2) the cohort of new culms is younger than the culms they replace; and 3) disturbance appears to inoculate some cane stands for several years against local die-offs. Fire is a valuable tool for canebrake management. By periodically resetting cane stands, fires and other disturbances may have played a key role in canebrake formation and persistence over time.

INTRODUCTION

Forested riparian wetlands are of outsized ecological importance. These highly productive and species-rich forests conserve soil, filter surface flow of water, produce valuable timber, sequester carbon, and provide critical food and habitat for both terrestrial and aquatic wildlife species of high conservation value (Brinson 1990, Brinson and Verhoeven 1999). Bottomland hardwood trees constitute the forested riparian wetlands of the southeastern USA. These forests have some of the richest tree diversity of any forests in North America (Kellison *et al.* 1998). This ecosystem originally covered perhaps 40 to 50 million hectares, but its coverage has been reduced by an estimated 60 %, and much more in areas like the lower Mississippi alluvial valley (The Nature Conservancy 1992, Noss *et al.* 1995, Stanturf *et al.* 2001). Throughout the entire range, bottomland hardwood forests have been subjected to radical changes in hydrology, disturbance regime, and land use since European settlement (Platt and Brantley 1997, Stanturf *et al.* 2001, King *et al.* 2005).

Historically, disturbances in bottomland hardwood forests were varied and numerous and played important roles in the ecology of the ecosystem. Flooding was the most frequent and regular disturbance; within the habitat, flood duration was the biggest determinant of which species occurred on given sites (Kellison *et al.* 1998, Wilson *et al.* 2007). Hurricanes, tornados, ice storms, and other canopy-opening events were common throughout southeastern bottomlands and could drastically increase light availability near the forest floor (Brinson and Verhoeven 1999, Gagnon *et al.* 2007). Droughts that occurred periodically as a function of ENSO cycles (Beckage *et al.* 2003) could reduce or extinguish annual flooding events and dry up normally submerged watercourses (Lentz 1931). Despite recent efforts, the picture of fire in bottomland hardwood forests remains unclear (Gagnon 2009*a*).

Historically, fires sometimes accompanied major droughts and may have been most prevalent in large canopy gaps filled with thick regenerating vegetation (Lentz 1931, Kaufert 1933). Although many areas within bottomland hardwood forests may not have burned often, in certain locations fires likely returned every 5 yr to 15 yr and structured the vegetation in important ways (Gagnon 2009*a*).

Historically, canebrakes were expansive, monodominant, and disturbance dependent stands of a native North American bamboo (*Arundinaria gigantea* [Walter] Muhl). Canebrakes were very common when early explorers first described these floodplain forests (Platt and Brantley 1997 and references therein). Canebrakes were and still are valued as wildlife habitat (Roosevelt 1908, Platt *et al.* 2001, Benson and Bednarz 2009) but have been reduced in areal coverage by an estimated 98 % over their range because of land conversion and the drastic alteration of hydrologic regimes in their riverine habitat (Noss *et al.* 1995). Fire likely played a role in the formation and maintenance of canebrakes (Hughes 1957, Gagnon and Platt 2008, Gagnon 2009*a*). Numerous canebrake restoration efforts are ongoing, but these are often hampered by incomplete knowledge of historic disturbance regimes, including fire, in southeastern riparian habitat. Works by Hughes (1957, 1966) and others (Gagnon and Platt 2008, Zaczek *et al.* 2010) suggest that cane stands need to be "reset" by fire or some other disturbance, lest they senesce or succumb to woody competitors.

We used a large tornado blowdown and 15 separate prescribed fires over two consecutive days to measure the response of cane to the sequential disturbances of tornado and fire. Our study took place in the Tensas Watershed of northeastern Louisiana, seven years after the tornado blowdown, and four years after the prescribed fires. We had previously demonstrated that, in the short term (1 yr later), fire was beneficial to cane stands growing in the open tornado blowdown but not under forest

canopy (Gagnon and Platt 2008). For this study, we returned three years later to determine longer-term effects of fire on cane and to reexamine the tornado × fire interaction. We compared burned and unburned stands of cane growing under forest canopy and in the tornado blowdown; number and condition of bamboo stems (culms) served as response variables. We hypothesized that: 1) culms would be more abundant in burned than in unburned stands; 2) the tornado × fire interaction would be diminished; 3) burned cane stands would comprise younger culms than unburned stands; and 4) rates of culm damage would be lower in burned stands.

METHODS

Focal Organism and Study Site

River cane, or giant cane, is a true woody bamboo (subfamily Bambusoideae, tribe Bambuseae; Judziewicz *et al.* 1999). It is a "running bamboo," with rhizomes that commonly grow several meters between culms (aboveground stems). Culms are typically 2 m to 5 m tall but can be taller on fertile, mesic sites in river floodplains and along stream courses. New culms typically sprout in early to midsummer, attain full size within weeks, and persist 5 yr to 10 yr. During the first year, one to two branches sprout from most culm nodes. Every subsequent spring, new branches sprout from the nodes of the previous year's branches; as such, the number of branchings approximates culm age (Gagnon *et al.* 2007).

Our study site was the Buckhorn Wildlife Management Area (WMA). The 4556 ha site of diverse bottomland hardwoods is located in Tensas Parish of northeastern Louisiana, USA (32° 01' N, 91° 22' W) in the lower Mississippi alluvial valley. The holding is managed by the Louisiana Department of Wildlife and Fisheries and was previously owned by the Fisher Lumber Company. The site includes closed canopy second-growth forest and numerous small gaps caused by a combination of timber operations and multiple small windstorms. On 8 November 2000, a large and powerful (EF-2) tornado passed over the Buckhorn WMA, causing a blowdown gap ~1 km wide and >5 km long in which the forest overstory and virtually all cane culms were destroyed (Gagnon *et al.* 2007). In previous work, we determined that cane culms were initially smaller, less often damaged, and denser in the large blowdown gap compared to under forest canopy (Gagnon *et al.* 2007). We also found an interaction effect of fire × tornado because, by the year after fires, burned cane stands in the blowdown gap regenerated to higher densities than comparable unburned stands, while those burned under forest canopy had lower densities than comparable unburned stands (Gagnon and Platt 2008).

Experimental Design and Data Collection

We used a split-plot design to elucidate tornado and fire effects on large and small stands of cane. Our first fixed effect was stand type, for which we differentiated among stands that occurred in the large tornado blowdown versus those under intact forest canopy, and also by their area (small, discrete stands versus large, continuous stands). The result was three stand types: small forest stands, blowdown stands (all of which were initially small), and large forest stands. At first census, the small forest stands and blowdown stands ranged in area from 11.1 m² to 6985 m², with a median of 133.2 m²; these were separated by tens to hundreds of meters, by roads or watercourses or both. The areas of large, continuous stands was indeterminable by definition as they covered large areas with diffuse borders. We previously demonstrated that cane stands grow outward at similar rates of radial expansion whether or not under forest canopy (Gagnon *et al.* 2007); being larger in area, we surmised that large forest stands had expanded longer and were therefore demographically older.

After an extensive search of the study site, we established 10 census plots, each in a separate stand within each of the three stand types (n = 30 plots). These included every available stand in the blowdown and a random sample of small and large forest stands. We considered culms growing in these different plots to be discrete populations of ramets. With few exceptions, each plot comprised four 1 m^2 subplots located within individual stands of cane (n = 118 subplots; one plot comprised five subplots, while two subplots in one plot and one in another were subsequently destroyed during fire-line construction). In small forest and blowdown stands, one subplot was located in the stand interior, and three more at stand edges 120° around the interior subplot; subsequent analysis indicated no difference between edge vs. interior subplots, so we analyzed these together. Large forest stands lacked clear edges, so plots there were located 5 m apart, generally in a straight line.

Our second fixed effect was fire. We burned 5 of the 10 stands that contained plots in each of the three stand types (n = 15 burned, 15 unburned). Our research site had not been burned in recent history. To ensure that both burned and unburned plots included both fast and slow growing populations, we grouped the 10 plots in each stand type into five pairs matched by similarity in their growth rates (the two with the highest growth rates within that stand type, then the next two, etc.) during the first year of the study. We randomly burned one of each pair in the spring, when bottomlands would have most likely burned (Kaufert 1933). Using a brush cutter, we had previously cut down each burned stand to approximately 30 cm high and left the cut culms to dry on the ground for two weeks. This slash-and-burn technique was necessary because cane stands naturally would have burned only during severe weather that (by definition) would have precluded prescribed burning. On the day of the fires, we cut fire lines around each stand with a bulldozer. We lit the 15 stands by cir-

cling each with a drip torch so that fires burned toward the center. We executed all 15 individual fires during two consecutive days on 21 and 22 April 2004. The majority of plots burned completely to ash with only the burned hulls of some culms remaining; three to four plots burned less completely during a period of very high humidity and some light precipitation on the first afternoon. We observed a handful of small- to medium-sized trees in cane stands that died following burning, as did various branches of larger overstory trees.

We quantified the number and health of cane culms (ramets) growing in every 1 m^2 subplot. Beginning in late winter 2003, and repeated annually through 2008, we tallied every living culm in the subplots. Here we analyze data from the last annual census only, using data from the first census as covariates. We noted branching number of every culm (see illustration, page 2, in Gagnon 2009*b*). We also noted whether and how culms were damaged or dead above particular nodes.

Analyses

We used analysis of covariance to test main effects of stand type, fire, and their interactions on populations of cane culms. Culm density (culms m^{-2}) was our response variable. Stand type (small forest, blowdown, and large forest) and fire treatment (burned and unburned) were the two fixed effects in our 3 × 2 split-plot design. Culm density at census 1 served as a covariate to account for any initial differences; note that there were no differences among any treatment groups at the time of the first census in 2003. Within stand type and fire treatment, plots paired by initial growth rate of their ramet populations acted as a split. We used *a priori* orthogonal contrasts to examine first the tornado effect (blowdown stands versus small and large forest stands), and then any difference between small and large forest stands (as per Gagnon and Platt 2008). We performed the analyses using the MIXED procedure in

SAS version 9.2 (SAS Institute, Cary, North Carolina, USA) and Kenward-Rogers approximations to address lack of balance (Littell *et al.* 2006).

We compared distributions of culm age in the different treatments by constructing histograms of culms by stage. Stage was a function of culm age as indicated by the number of times a given culm had branched (Gagnon *et al.* 2007). We categorized culms approximately 1 through 5 years old (with 1 to 5 branchings) as stages 1, 2, 3, 4, and 5, respectively (as per Gagnon 2009*b*). Culms with >5 branchings were increasingly difficult to differentiate, so we categorized those with ≥6 branchings as stage 6 (a sink), which included culms 6 or more years old. For targeted pairwise comparisons, we tested statistical significance among stand types and fire treatments with χ^2 tests using the chisq.test function in R version 2.13.1 (The R Foundation for Statistical Computing: http//www.R-project.org). For distributions containing few individual culms in particular classes, we computed *P*-values by Monte Carlo simulation using the simulate.p.value option and 10 000 replicates (Hope 1968).

We explored rates at which populations of culms in subplots went extinct in the different stand types and fire treatments. The question of subplot extinction was not one we anticipated at study outset; rather, it was something we observed over time during our six-year study.

We first attempted to examine the question using the same experimental framework as our other analyses but lacked requisite statistical power for mixed-model logistic regression (i.e., our models failed to converge). Instead, we summarized simple rates of extinction of culm populations at the subplot- and plot-level (Table 1).

We compared proportion of damaged culms at the end of the study across stand types and fire treatment using generalized linear mixed models (logistic regression). The number of damaged culms in 2008 divided by the total number of culms in each subplot in 2008 was our response variable. Stand type and fire treatment acted as two fixed effects in the 3 × 2 split-plot design. Within stand type and fire treatment, plots paired by growth rate of their ramet populations during the first year acted as a split. We performed the analyses with the GLIMMIX procedure in SAS version 9.2 using a binomial distribution and logit link and Kenward-Rogers approximations for lack of balance (Littell *et al.* 2006).

RESULTS

Both windstorm and fire increased density of cane culms four years post fire compared to forest-grown and unburned plots, respectively. Culm density differed among the three stand types ($F_{2,24} = 16.08$, $P < 0.001$), and culms grew more densely in the tornado blowdown

Table 1. Number of plots and subplots of river cane in Tensas Parish, Louisiana, USA, immediately after fires in 2004, and then extinct at the end of the study four years post fire, in 2008. Percent extinct in bold.

Stand type	Fire treatment	Plots	Plots extinct at end	Plots with extinct subs	%	Subplots	Subplots extinct at end	%
Small forest	Burned	5	0	1	**20**	21	1	**<5**
Small forest	Unburned	5	1	3	**60**	20	8	**40**
Blowdown	Burned	5	0	0	**0**	19	0	**0**
Blowdown	Unburned	5	0	0	**0**	18	0	**0**
Large forest	Burned	5	1	5	**100**	20	11	**55**
Large forest	Unburned	5	1	5	**100**	20	13	**65**

than under forest canopy (small and large forest stands; according to orthogonal contrasts, $F_{1,24} = 28.64$, $P < 0.001$). The observed greater density in small vs. large forest stands was not significant ($F_{1,23} = 3.57$, $P = 0.072$). Four years after fire, burned large forest stands contained twice as many culms on average as their unburned counterparts ($F_{1,24} = 7.33$, $P = 0.012$). The end result was that burned blowdown stands had the densest culm populations, approximately four times as many culms m^{-2} as unburned small forest stands, and eight times as many as unburned large forest stands (Figure 1). Culm density in our final annual census was related to initial culm density ($F_{1,110} = 38.17$, $P < 0.001$). There was no interaction between the main effects of fire and stand type ($F_{2,24} = 0.98$, $P = 0.391$).
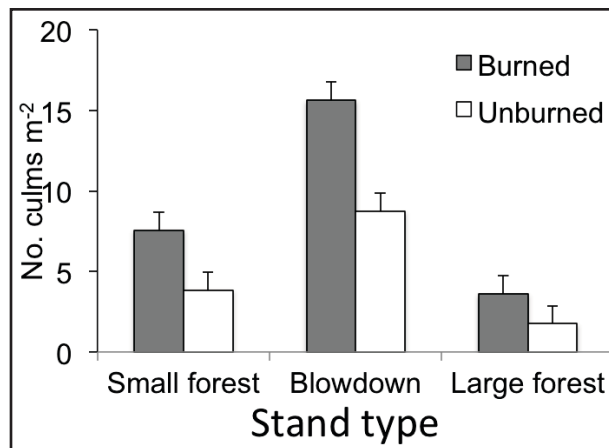

Figure 1. Mean culm density (±1 SE) of river cane growing in burned and unburned small forest, blowdown, and large forest stands in Tensas Parish, Louisiana, USA, in 2008, four years post fire and seven years post tornado.

Demographic age of cane culm populations varied by both stand type and fire treatment. Unburned blowdown stands were younger than unburned forest stands in that they contained proportionally fewer individuals in the oldest stage ($\chi^2_6 = 51.43$, $P < 0.001$; Figure 2). In each of the three stand types, burned stands were demographically younger than unburned

stands; they had proportionally fewer culms in the oldest stages and more in the middle stages than comparable unburned stands (for small forest stands, $\chi^2_6 = 152.45$, $P < 0.001$; for blowdown stands, $\chi^2_6 = 310.30$, $P < 0.001$; for large forest stands, $\chi^2_6 = \infty$, $P < 0.001$). Burned small and large forest stands were younger than burned blowdown stands, with proportionally more culms in the three youngest stages (for small forest vs. blowdown $\chi^2_6 = 61.70$, $P < 0.001$; for large forest vs. blowdown $\chi^2_6 = 80.08$, $P < 0.001$).

We observed lower rates of extinction in blowdown stands and burned small forest stands than among other stand types, but we were unable to test these results statistically. Zero blowdown populations went extinct, including all plots and subplots in both burned and unburned stands (Table 1). Among small forest stands, extinctions were very rare among burned populations (zero plots and <5 % of subplots), but common among unburned populations (20 % of plots and 40 % of all subplots). More than half of all subplots among large forest stands went extinct, whether burned or unburned (20 % of plots in both burned and unburned stands went extinct, including 65 % of burned subplots and 55 % of unburned subplots).

Rates of culm damage were elevated in small and large forest stands compared to blowdown stands, while burning did not affect damage rates. Culm damage rates were highest in small forest stands (41.2 %) and almost as high in large forest stands (32.2 %), but much lower in blowdown stands (14.4 %; Figure 3A). This difference in damage rates among stand types was significant ($F_{2,19} = 5.72$, $P = 0.011$). Damage rates in burned stands did not differ from those in unburned stands despite the fact that burned stands comprised younger populations of culms (Figure 3B; $F_{2,20} = 0.05$, $P = 0.826$). There was no stand type × fire interaction with regard to culm damage ($F_{2,19} = 0.52$, $P = 0.604$).
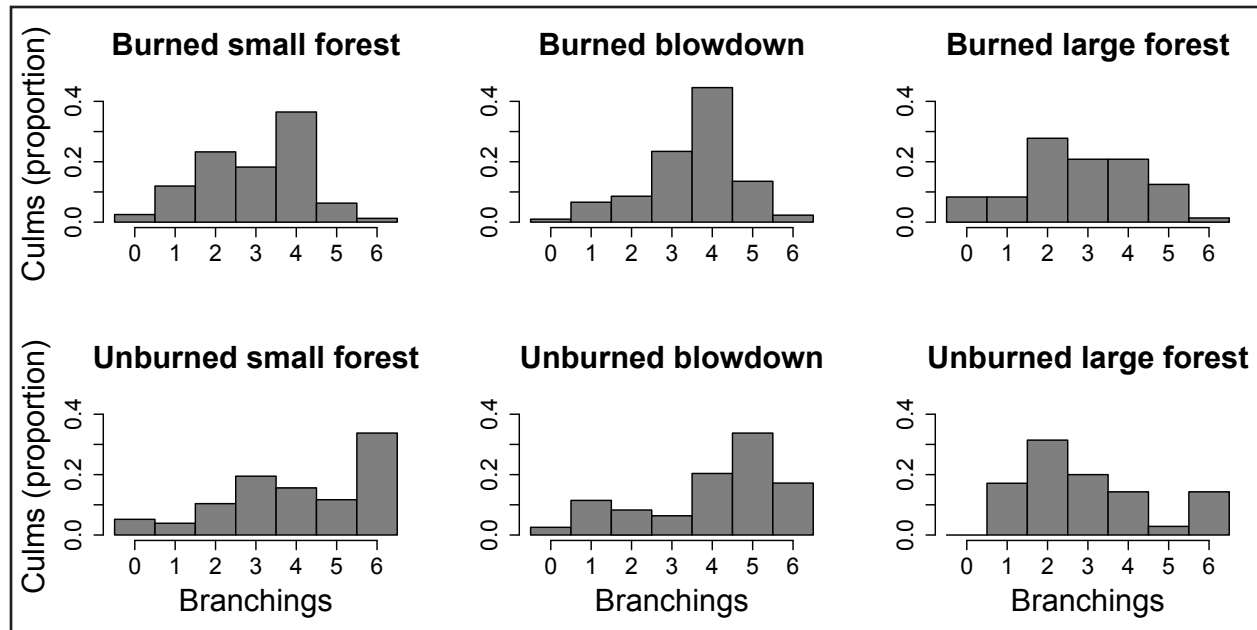
Figure 2. Culm stage distributions of river cane growing in burned and unburned small forest, blowdown, and large forest stands in Tensas Parish, Louisiana, USA, in 2008, four years post fire and seven years post tornado. Stage distributions show the proportion of culms in 0 to 6 branching categories.
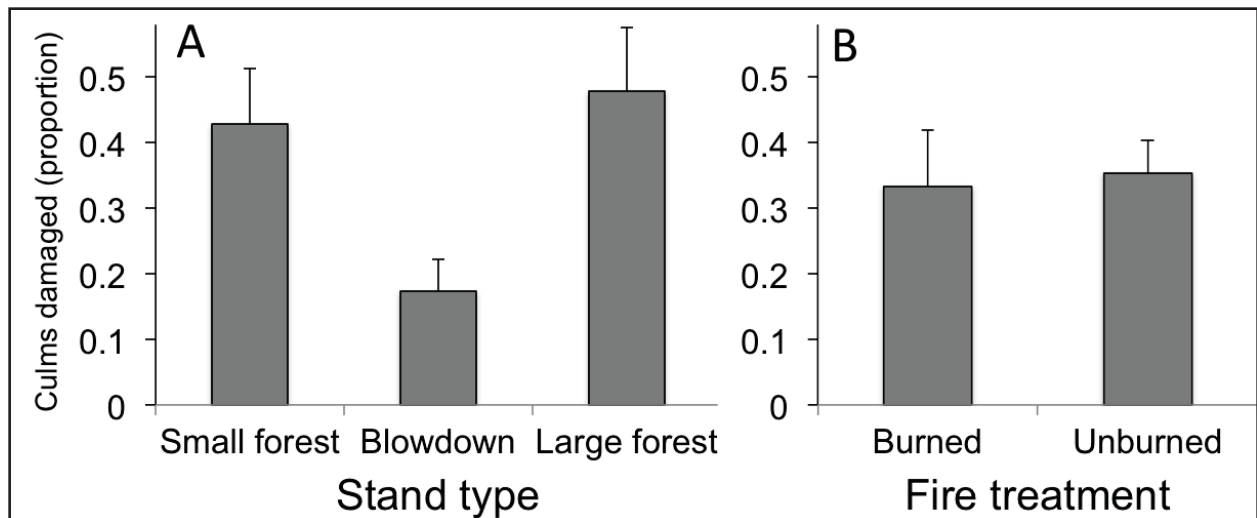

Figure 3. Mean culm damage (proportion, ±1 SE) in river cane growing in burned and unburned small forest, blowdown, and large forest stands in Tensas Parish, Louisiana, USA, in 2008, four years post fire and seven years post tornado.

DISCUSSION

Effects of Fire and Windstorm on River Cane

Seven years post tornado and four years post fire, the effect of each disturbance on cane growth was unequivocally positive. Each effectively doubled culm density compared to comparable plots not subjected to that disturbance, and cane stands subjected to both tornado and fire were many times denser than those subjected to neither. Windstorms and

fires each have the potential to affect cane in both direct and indirect ways. Directly, they destroy cane culms while leaving rhizome networks intact. Indirectly, each can kill and damage trees and thereby increase light levels for cane. At our study site, the effect of the tornado on light levels was very pronounced (Gagnon *et al.* 2007) and much greater than anything caused by burning. To some degree, our results necessarily reflect combined effects of both culm removal and increased light, but this is especially true of results from the large tornado-generated blowdown.

We have previously proposed that destruction of aboveground culms triggers new clonal growth in *Arundinaria*. Our prior study conducted one year post fire indicated a positive short-term effect of burning cane in the blowdown, but a negative effect for cane under forest canopy (Gagnon and Platt 2008). In this longer-term study, the effects of windstorm and fire were additive rather than offsetting, and fire effects were positive on all stand types. This new study reveals that, although the effect is delayed, cane growing in the shade of forest canopy eventually benefits from burning as much as open-grown cane does. The cohort of new culms produced following either windstorm or fire more than compensates demographically for any culms lost during the given disturbance; compensatory growth took longer in shade-grown cane. Such compensatory growth emphasizes the role of periodic disturbance in the formation of the hyperdense, expansive, and monodominant canebrakes that were once common in riparian floodplains of the southeastern USA (Hughes 1966, Platt and Brantley 1997, Judziewicz *et al.* 1999).

Culm populations in burned stands were significantly younger than those in unburned stands. We have previously demonstrated a similar demographic effect—younger culm populations—in cane stands subjected to windstorm effects (Gagnon *et al.* 2007). Although there is no set age at which individual cane culms senesce, we have observed that younger culms are more vigorous in that they survive longer on average than older culms. Our results are consistent with observations by Hughes (1966), who reported that stands of cane in North Carolina naturally senesced beginning around seven years following an aboveground disturbance like fire; he reported that fires "reset" stands and rejuvenated them such that they again grew vigorously for several more years. Given Hughes' observation and the interval since the tornado in this study, we might expect unburned cane in the tornado blowdown gap to begin experiencing demographic collapse shortly after the termination of this study, whereas comparable burned cane should remain demographically vigorous for three to five more years because of the timing of our burning.

Our results suggest that periodic disturbance can inoculate cane stands against both subsequent stressors and eventual senescence. We observed that, in certain subplots, populations of cane culms all died, reflecting patchy senescence in some cases and complete stand die-offs in others. Such events were particularly pronounced in 2004, a drought year, among large forest stands and unburned small forest stands; however, subplots went extinct during later years as well. We suspect that the greater areal extent of large forest stands reflects older rhizome systems with poorer clonal integration than those of small stands. We have demonstrated previously that cane stands spread outward at similar rates regardless of stand type (Gagnon *et al.* 2007), so large stands may have been expanding longer (with older rhizome systems) than small stands. We speculate that compensatory growth triggered by the removal of culms rejuvenated the still-integrated rhizome systems of small stands, and thereby rendered them more resistant to subsequent drought and other stressors. The fact that large stands appeared to be more susceptible to die-offs regardless of whether they burned suggests that cane stands that go too long without disturbance may be susceptible to demographic

collapse. Hughes (1966) described similar die-offs but was unable to attribute the phenomenon to any specific cause, although he suggested disease as the culprit. Cane restoration efforts should anticipate similar local die-offs after multiple years without disturbance. Given these observations, we propose that burning still-vigorous cane stands reduces their likelihood of subsequent local extinction, especially in a shaded environment.

The younger culm populations in burned stands were no less frequently damaged by the end of the study than the older populations in unburned stands. In our experience, branches and debris falling from above frequently damage cane culms, as do herbivores like swamp rabbits (*Sylvilagus aquaticus*) on the ground. We have observed that the longer culms persist, especially under forest canopy, the more likely they are to be damaged. As expected, damage rates were higher for stands growing under forest canopy than for those growing in the open blowdown. We had expected that the younger culm populations in burned stands would have been less frequently damaged than the older culm populations that composed unburned stands, but we found no difference in rates of culm damage as a function of fire treatment. Burning under forest canopy killed branches and occasionally whole trees, and these eventually fell onto the new cohort of cane culms; we hypothesize that burning caused increased branch-falls that equalized damage rates of culm populations in burned and unburned stands.

Implications for Canebrake Management and Understanding of Bottomland Hardwood Forests

These findings have implications both for management of canebrakes and for our understanding of the evolutionary role of disturbances like fires in bottomland hardwood forests. We have demonstrated that periodic disturbances benefit river cane in three important ways: 1) destruction of aboveground culms spurs clonal growth that more than compensates for culms lost in disturbances; 2) the cohort of new culms is younger than culm populations in undisturbed cane stands and is therefore likely to live longer (Gagnon *et al.* 2007); and 3) periodic disturbances appear to inoculate still-vigorous cane stands from subsequent local extinction events, perhaps by invigorating rhizome systems as well as aboveground culms. Hughes (1966) proposed that, when dense, vigorous cane was a management objective, stands should be burned every five to ten years, with seven years being optimal. Based on our observations, we surmise that a somewhat more frequent fire interval (perhaps every three to eight years) for open-grown cane may maximize culm density and help insure against stand-level die-offs. This interval may be a year too frequent for forest-grown cane, but waiting too long between disturbances may risk die-offs. Cane stands most likely burned naturally during periodic droughts (Gagnon 2009*a*). The question of best fire interval for the establishment and maintenance of canebrakes merits additional empirical testing.

That cane thrives with periodic burning (Hughes 1966) underscores the prominent role of disturbance in bottomland hardwood forests over ecological time. It is difficult to overstate the degree to which modern bottomland hardwood forests have been altered since European settlers began logging them, ditching and levying them, plowing them, suppressing fire on the landscape, controlling beaver populations, and myriad other changes (Platt and Brantley 1997, Stanturf *et al.* 2001, King *et al.* 2005, Wilson *et al.* 2007). Unlike modern, closed-canopy, second-growth forests, southern bottomlands historically would have included many old-growth forests in which both small and large gaps would have served as openings for canebrake formation (Wilson *et al.* 2007). Anecdotal accounts and published research descriptions indicate that fires occurred periodi-

cally, if locally, in bottomland hardwood forests, particularly in large gaps during drought years (Lentz 1931, Kaufert 1933, Gagnon 2009*a*). Such forest gaps may have been critical for regeneration of bottomland oaks as well as for canebrakes (Oliver *et al.* 2005, Holladay *et al.* 2006, Collins and Battaglia 2008). Certainly Native Americans would have played some role in reducing fire return intervals locally throughout southern bottomlands (Platt and Brantley 1997). Even without their efforts, periodic disturbances were undoubtedly a natural and influential component of this habitat in ways that may now be difficult to fully fathom when looking at closed-canopy, second-growth bottomland hardwood forests growing alongside tamed, channelized river systems in a fire-excluded landscape.

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