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Response of a native bamboo [*Arundinaria gigantea* (Walt.) Muhl.] in a wind-disturbed forest

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Abstract

Numerous bamboos are known to form extensive single-species stands, including species in the United States. Formerly prominent in the southeastern US, canebrakes are dense stands of the bamboos collectively called “cane” [*Arundinaria* (Michx.)]. Canebrakes are now a critically endangered component of the bottomland hardwood forest ecosystem. Cane still occurs in its historic range, primarily in small remnant patches. A poor understanding of the ecological processes that generated large canebrakes limits their restoration and management.

We hypothesize that cane’s spreading clonal structure enables these bamboos to persist beneath a forest canopy and then respond rapidly to large-scale wind disturbances. We quantified patterns of clonal growth in one cane species, “giant cane” [*Arundinaria gigantea* (Walt.) Muhl.], in a very large tornado-generated canopy gap and in surrounding bottomland hardwood forest in Louisiana. We tested these four hypotheses over a 12-month study period in the large canopy gap: (1) production of new culms should be greater, (2) clonal expansion should be greater, (3) culm damage rate should be reduced, and (4) culm size should be reduced compared to giant cane stands under forest canopy.

We found that new culm production in tornado-blowdown plots was twice that in forest plots. Accordingly, culms were younger on average in the tornado blowdown than under forest. Rate of clonal expansion was similar between the two environments, suggesting clonal spread was not disturbance-dependent. With fewer branch-fall impacts, culms in the tornado blowdown were less often damaged. Culms were smaller in tornado-blowdown plots than in forest plots.

Giant cane’s clonal plasticity should enable it to persist in old-growth bottomland forests by responding to local light conditions. Genets should increase culm production in small gaps and senesce as gaps fill in. Giant cane stands could thereby shift location over time. Wind disturbance that opens forest canopy should trigger redevelopment of denser stands that could merge with other expanding stands into expansive canebrakes. Giant cane’s clonal ecology may be a useful model for understanding spreading bamboos and other forest-growing clonal perennials.

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Keywords: Bamboo; Canebrakes; Clonal ecology; Bottomland hardwood forests; Tornadoes; Wind disturbance

1. Introduction

Dense, monodominant stands of the bamboos collectively called “cane” [*Arundinaria* (Michx.)] were once a prominent feature of bottomlands of the southeastern United States. Many early accounts of these *canebrakes* described them as covering “thousands of acres” and “often extending for miles” (Platt and Brantley, 1997 and references therein). Canebrakes were refuge for many game species, neotropical migratory birds and

cane-obligate butterfly species (Roosevelt, 1908; Remsen, 1986, Platt et al., 2001; Moorman et al., 2002). Following European settlement, canebrakes declined by an estimated 98%, becoming a critically endangered component of southeastern bottomland forest ecosystems (Noss et al., 1995). Alteration of disturbance regimes (e.g., fire and flooding), overgrazing and systematic plowing of cane lands contributed to canebrake decline (Platt and Brantley, 1997).

The ecological processes that generate large canebrakes remain a mystery that limits canebrake restoration and management. After recent taxonomic revision, the term “cane” includes three North American species in the genus *Arundinaria*, of which two are known to have formed canebrakes (Triplett et al., 2006). Cane bamboos still occur throughout

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their historic range, primarily as diffuse stands under forest canopy, and as small-scattered patches in canopy gaps and along forest edges (Marsh, 1977). Early accounts suggest expansive canebrakes develop primarily in large canopy gaps or under sparse forest overstory (Platt and Brantley, 1997). Land office survey notes made in the Lower Mississippi Alluvial Valley indicate that large “windfalls” and other forest openings with sparse trees are historically common (Tingle et al., 2001). Windstorms (e.g., tornadoes, hurricanes), ice-storms, fires, river flooding and beaver dams are all likely causes of forest gaps in southeastern bottomlands. Cane dynamics remain unexplored in the low- and high-light environments of forest understory and large canopy gaps. Do large-scale disturbances promote the transformation of small, diffuse cane stands into expansive canebrakes?

We hypothesize that the spreading clonal structure of canebrake bamboos enable them to persist beneath forest canopy and then respond rapidly to large-scale wind disturbance. Cane bamboos are among many New and Old World bamboos that form large, monodominant stands (Judziewicz et al., 1999; Keeley and Bond, 1999). Bamboos are giant grasses, and cane has indeterminate rhizome growth that produces both new rhizomes and culms (Judziewicz et al., 1999). Cane’s rhizome network spreads outward from the site of germination, so genets tend to increase in area as they grow. Individual cane rhizomes can grow more than 6 m in a single season (Marsh, 1977). In the forest understory between wind disturbances, cane genets might survive as diffuse networks of rhizomes and culms. These rhizomes and bases of culms are likely to survive windstorms, just as they often do fires (Hughes, 1957). Where a disturbance generates high light levels, accelerated rhizome and culm production from this underground network could produce a dense canebrake.

We explored responses of cane to wind disturbance. We quantified patterns of clonal growth in one species, giant cane [*Arundinaria gigantea* (Walt.) Muhl.], in two environments within a Louisiana bottomland forest—a large wind-generated canopy gap and surrounding forest understory. We developed four hypotheses based on field observations, anecdotal accounts and work by Hughes (1957, 1966). We proposed that in stands of giant cane within a large canopy blowdown gap (1) production of new culms should be greater, (2) clonal expansion should be greater, (3) culm damage rate should be reduced, and (4) culm size should be reduced compared with similar stands beneath forest canopy. The results enabled us to characterize responses of cane to large-scale disturbances that open southeastern bottomland forest canopies, with implications for other bamboos that form large monodominant stands, and for other spreading clonal forest plants.

2. Methods

Giant cane still occurs in the bottomland hardwood forests of the Tensas watershed in northeastern Louisiana. Geologically and ecologically part of the Lower Mississippi Alluvial Valley (LMAV), the Tensas watershed includes some of the most diverse and productive forest ecosystems in the US (Heggen-

et al., 1999). Virtually the entire Tensas watershed was once forest, with frequent canebrake inclusions (Roosevelt, 1908; Burdick et al., 1989; Tingle et al., 2001). The 20% that remains forested has been subject to selective forestry for many decades (Burdick et al., 1989; Heggen et al., 1999). Although diminished, giant cane is still abundant in the Tensas watershed, typically along edges of forests and under forest canopy. Small remnant canebrakes are still present in some locations.

We conducted our study in the Buckhorn Wildlife Management Area (WMA) within the Tensas watershed. The Buckhorn WMA (3640 ha; Tensas Parish) contains soils and plant species characteristic of the LMAV (Kellison et al., 1998). The topography is a series of ridges and swales common in the Tensas watershed (Heggen et al., 1999). Buckhorn soils are slightly acid clays and silty clays that are moderately well drained on ridges and poorly drained in swales (Wyckoff, 1997). Diverse southern bottomland hardwood forest covers much of the area, with such species as willow oak (*Quercus phellos* L.), overcup oak (*Q. lyrata* Walt.), sweetgum (*Liquidambar styraciflua* L.), bitter and sweet pecan [*Carya aquatica* (Michx.) Nutt. and *C. illinoensis* (Wangenh.) K. Koch] among others (Wyckoff, 1997). Prominent understory components include dwarf palmetto [*Sabal minor* (Jacq.) Pers.], American beautyberry (*Callicarpa americana* L.), briars (*Rubus* spp. L.) and giant cane, which grows virtually anywhere save low sites subject to prolonged growing-season inundation.

The Buckhorn WMA is a mosaic of closed-canopy forest and numerous small and large gaps of various ages, all surrounded by agriculture fields. During the 1920s and 1930s, the tract was owned and logged by the Fisher Lumber Company (T. Tuma, pers. comm.). The forest regenerated naturally to its present canopy height of 20–40 m, with many trees >75 cm DBH, in large part a result of high site productivity. Since purchasing the area in 1995, the Louisiana Department of Wildlife and Fisheries has implemented single-tree and group selection silviculture, resulting in numerous small canopy gaps. Multiple severe storms have caused other canopy gaps of various sizes and ages (T. Tuma, pers. comm.).

On November 8, 2000, a large tornado conservatively estimated as F2 traveled 25 miles across northeastern Louisiana and crossed the Buckhorn WMA (National Weather Service, 2000). This tornado caused major canopy damage within a broad swath running southwest to northeast across the entire WMA. Nearly complete canopy destruction occurred within an area approximately 1 km wide and for the 4 km length of the WMA. Most trees were snapped off; the rest were blown over. Approximately 0.5 km on either side of this central area experienced substantial, though not complete, canopy damage. Numerous stands of giant cane were present and survived the disturbance.

Beginning 18 months after the tornado, we studied giant cane in the blowdown and surrounding forest. We confirmed the cane present was *A. gigantea* [voucher: Gagnon PRG-2006-01 (LSU)]. We considered the blowdown as a “treatment” and the surrounding forest as a “reference” for measuring changes after wind disturbance. In spring 2002, we located eight cane stands as study plots within the large tornado blowdown and

eight more under adjacent forest canopy 0.1–2.5 km away from the blowdown. In selecting cane stands for study, we excluded any whose growth was limited on more than one side by physical barriers, including swales and other low-lying areas subject to frequent or prolonged growing season inundation. Each plot comprised four 1 m² subplots within a separate and discrete stand of giant cane ranging in size from 11 to 1355 m² (mean = 324 m²). We extensively searched the blowdown area for discrete cane stands and used all eight located that matched our criteria. We also randomly selected eight discrete cane stands under forest canopy from among those meeting the selection criterion. Discrete cane stands in the blowdown area were smaller than those under forest canopy, perhaps as a result of the tornado disturbance. Our study plots reflect this size difference (Table 1). We randomly located one subplot within a stand's interior and the other three at stand edges 0°N, 120°SE, and 240°SW from that interior plot. We marked each of the four 1 m² subplots with a circular galvanized steel hoop anchored to the ground.

We used canopy photos to quantify light levels in forest and blowdown plots. We took the photos 1.5 m above every subplot in late summer 2002 using a Coolpix 4500 digital camera with F8 fisheye lens (Nikon, USA). We estimated percent total transmitted light from these photos using Gap Light Analyzer 2.0 (Frazer et al., 1999). The canopy above forest-grown plots had a mean total transmitted light of 16.1%, which reflected the silviculture practiced on the Buckhorn WMA. In contrast, blowdown plots had a mean total transmitted light of 88.3%, as expected for a very large canopy gap (Table 1). We compared least square means of percent transmitted light in plots within the two treatments using a heterogeneous-variance model and logit-transformed data in Proc Mixed in SAS (SAS Inst., 1999). Differences were significant ($P < 0.01$).

We measured all cane culms in every subplot in February/March of 2003 and 2004. During the second census, we

recorded how many new culms were produced in the intervening 12 months. Culms reach full height and diameter in a matter of weeks after sprouting from the rhizomes and then live for 5 or more years before senescing (Hughes, 1957). To approximate culm age, we measured how many times each culm had branched. Culms produce leaves from straight, slender branches that originate at culm nodes. We observed that these nodes typically produce first- and sometimes second-order branches in the culm's 1st year, although occasionally, late-season culms did not branch until their second growing season. Each subsequent spring after their 1st year, culms produce new branches from the previous year's branches (Hughes, 1957, 1966). The order of culm branchings therefore reflects culm age because culm branches grow in this modular way at regular intervals. To approximate culm age in years, we grouped culms into stages based on the number of times they had branched. Stage 0–2 approximates 1st year culms; subsequent stages are each 1 year older on average. We noted whether culms were damaged and how that damage was sustained. By our definition, damaged culms were broken or bent but still alive and green. Some other culms showed no obvious outward damage but were partially dying (these were green from the ground up to some particular node, then dead above that). We observed that in many cases these dying culms were also suffering the effects of branch-fall impacts. We also measured culm height and basal diameter.

To estimate rate of clonal spread, we delineated the perimeter of every plot during censuses 1 and 2. We used a GPS 500 differential receiver (Leica, Switzerland) with Coast Guard beacon receiver and sub-meter accuracy. We used ArcGIS 9.0 (ESRI, Redlands, CA, USA) to calculate the area of the different cane plots in both censuses. We calculated radial expansion as the difference in the radii of circles formed by plot areas in censuses 1 and 2. We chose radial expansion as our primary measure of clonal spread because discrete stands in the

Table 1
Plot-specific metrics

Plot (clone) number	Treatment	Mean culms/m, 2002	Mean culms/m, 2003	%Total transmitted light	Area, 2002 (m ²)	Area, 2003 (m ²)	Radial expansion
1	Blowdown	16.00	26.00	95.88	23.36	89.30	2.60
2	Blowdown	5.50	6.50	93.38	14.64	39.19	1.37
3	Blowdown	9.25	12.25	84.27	13.44	30.57	1.05
4 ^a	Blowdown	7.00	7.75	81.42	Mowed	38.05	Not avail
5	Blowdown	5.75	7.75	73.09	106.49	137.78	0.80
6	Blowdown	5.75	11.50	66.46	159.82	206.18	0.97
7	Blowdown	7.00	11.00	94.95	12.60	14.12	0.12
8	Blowdown	8.50	14.75	88.32	11.11	67.98	2.77
9	Forest	13.00	14.25	22.30	1208.98	Not avail	Not avail
10	Blowdown	6.75	8.00	94.38	69.80	153.93	2.29
11 ^a	Flowering	9.50	9.75	n/a	427.45	Dead	Not avail
12	Forest	6.00	6.75	18.45	6985.81	8016.32	3.36
13	Forest	14.80	11.60	17.82	1358.35	1419.98	0.47
14	Forest	9.75	11.50	17.51	858.49	1354.54	4.23
15	Forest	5.25	5.75	13.26	Not avail	Not avail	Not avail
16	Forest	5.25	5.75	12.62	321.17	287.70	–0.54
17	Forest	6.75	8.50	13.29	371.93	512.00	1.89
18	Forest	4.50	7.25	17.19	901.89	1092.91	1.71

^a Excluded from analyses.

blowdown area were smaller than those under forest canopy, and radial expansion was unbiased by cane stand area (see Section 3). In addition, radial expansion gave a meaningful linear rate of spread easily visualized by land managers in the field.

We performed one-way and nested ANOVAs on these data to test for differences between forest- and blowdown-grown cane culms. Our experimental design included fixed treatment effects and random plot effects, with plots as experimental units and subplots as sample units. We used the Mixed procedure in SAS (SAS Inst., 1999) when analyzing normally distributed response variables like radial expansion and culm size. We used the Glimmix procedure in SAS (SAS Inst., 2005) with binomial distribution and logit transformation for the response variable “damaged and dying culms,” which was in the form of rate data. We used the Glimmix procedure with Poisson distribution and log transformation for the response variable “new culm production,” which was in the form of count data. We fitted heterogeneous-variance models where necessary. We ran linear regressions of the following variables: culm basal diameter on culm height, light level on culm height, initial plot area on total change in plot area and initial plot area on radial expansion. We used Pearson’s Chi-square to check homogeneity of proportions for the categorical culm-age dataset.

3. Results

New culm production rates in tornado-blowdown plots were twice those in forest plots over the 12-month study period. On average, plots in the blowdown produced one new culm for every 2.5 culms present, compared to one new culm per 5 culms present in forest plots. Fig. 1 illustrates the difference calculated as the number of new culms in 2004 divided by number of pre-existing culms in 2003. This difference supported our first hypothesis and was significant ($P < 0.04$).

Culms were younger on average in the tornado blowdown than in the forest. At the time of the 1st census (winter 2003), culms in the blowdown were in disproportionately earlier stage classes than culms in forest plots. Stage classification approximates culm age. There were twice as many culms in the youngest stage (stage 0–2) growing in blowdown plots compared to forest plots (Fig. 2). This difference in stage distributions also supported our first hypothesis and was statistically significant (Pearson $\chi^2 = 78.16$, $P < 0.01$).

Fig. 1. Mean rate of new culm production in forest and blowdown. Means are back-transformed least square means. Error bars are back-transformed 95% confidence intervals.

Fig. 2. Stage distributions of giant cane culms in forest and blowdown. Stage is determined as the number of branchings present at culm nodes; stage approximates culm age in years. Counts are based on 220 culms in blowdown plots and 222 in forest plots.

Fig. 3. Total increase in plot area as a function of initial plot area.

Rate of clonal spread measured as radial expansion was not different between tornado-blowdown and forest plots. We were able to calculate reliable shapes and areas for eight blowdown and six forest plots in both years. As indicated in Fig. 3, large cane stands increased more in total area than did small ones—change in cane stand area was tightly correlated with stand area at first census ($r^2 = 0.84$). Radial expansion and area of cane stands at first census were relatively uncorrelated ($r^2 = 0.14$; see Fig. 4). Radial expansion ranged from -0.54 to 4.68 m (Table 1). Mean radial expansion of forest plots was 1.85 m plus or minus 1.20 m with 95% confidence. Mean radial expansion of blowdown plots was 1.50 m plus or minus 1.04 m with 95% confidence. There was no statistical difference in rate of radial expansion between treatments ($P = 0.64$), suggesting that giant cane rhizomes spread outward regardless of light regime. This result failed to support our second hypothesis. We observed that a cane stand might expand several meters in one direction and not at all in another. Such variation in clonal

Fig. 4. Radial expansion of plots as a function of initial plot area.

Fig. 5. Mean proportion of giant cane culms damaged or dying in blowdown and forest plots. Proportions are back-transformed least square means. Error bars are back-transformed 95% confidence intervals.

expansion could have produced the highly irregular shapes of cane stands in our study.

Giant cane growing in the tornado blowdown was less often damaged or dying than giant cane growing in the forest. Branches falling from the canopy were the most frequent cause of damage to culms in forest plots. Animals browsing also caused occasional culm damage [typically white-tailed deer [*Odocoileus virginianus* (Zimm.)] and swamp rabbits [*Sylvilagus aquaticus* (Bachman)]}. Fig. 5 illustrates that <10% of the culms in the blowdown were damaged or dying, whereas almost a third of forest-grown culms were damaged or dying. These differences supported our third hypothesis and were significant ($P < 0.01$).

Culm damage rates were stage related. Older culms were more likely to have been damaged or dying than younger culms (Fig. 6), presumably as a function of their greater age. We examined the first three culm stages from our 2003 census. In support of our third hypothesis, in all three stages culms in tornado-blowdown plots were less likely to be damaged or dying than culms in forest plots (Fig. 6). Both stage and treatment (forest versus blowdown) had significant differences ($P < 0.01$ in both cases). We excluded the fourth stage (5+) from the figure because there were only three surviving culms of this stage in the blowdown. Since all three of these older culms would have survived the tornado, their damage status was directly confounded by the storm itself.

Giant cane culms were smaller in tornado-blowdown plots than in forest plots. When we measured them in our late winter censuses, all culms were already full size because culms cease

Fig. 6. Proportion of all culms in given branching classes damaged or dying in the blowdown and forest in 2003. Proportions are back-transformed least square means. Error bars are back-transformed 95% confidence intervals.

Fig. 7. Mean culm size of *Arundinaria gigantea* in the blowdown and in surrounding forest. Means are least square means. Error bars indicate 95% confidence intervals.

growing only weeks after sprouting (Hughes, 1957). Culm height in blowdown plots was less than half that in forest plots (Fig. 7). Similarly, mean basal diameter of culms in blowdown plots was approximately half that in forest plots. Both results supported our fourth hypothesis and were significant ($P < 0.01$). Regression analysis on these two metrics of culm size indicate that height and diameter were tightly linked ($r^2 = 0.84$). Culm height was inversely correlated with transmitted light levels ($r^2 = 0.54$), meaning culms grew taller in shade than in sun.

4. Discussion

Giant cane's quick response to disturbance and likely ability to persist between disturbances are functions of its clonal plasticity. In this study, culm production in the large tornado blowdown gap greatly exceeds culm production under forest canopy, signaling rapidly increasing culm density in open-grown giant cane. We expect culm production to vary with light levels, being greater in gaps and beneath sparse canopy than in shade. Our results indicate that giant cane is capable of continual, albeit irregular clonal spread, both in the open and under forest canopy. Hughes (1957, 1966) observed that without periodic disturbances, individual cane stands eventually decline. This implies that cane stands in forests might well shift location over time as canopy gaps open and close. Giant cane genets might thereby persist for many years beneath overstory trees in old-growth bottomland forests.

Wind disturbance should trigger redevelopment of denser stands. Greatly increased light levels should spark new culm production, while culm damage rates decrease. As they expand, these denser stands are likely to grow together with other stands. Following a windstorm that opens the forest canopy, we thus propose that giant cane stands that survive the disturbance-free interval might rapidly attain a dense, canebrake-like structure via clonal growth. Historically, large blowdown gaps are common in the Lower Mississippi Alluvial Valley (Tingle et al., 2001). In Tensas Parish, Louisiana (1560 km²) where this study is set, the National Climatic Data Center records 18 tornadoes in the 20 years between 1981 and 2001 (NCDC, 2006). Large canopy-dominant trees in bottomland hardwood forests may be more susceptible to wind damage than smaller trees (Glitzenstein and Harcombe, 1988). If so, we would expect more and larger canopy gaps, and thus canebrakes, in old-growth than in second-growth bottomland forests.

While increased light levels spur culm production, these new open-grown culms should be smaller than those under forest canopy. In this study, culm height and diameter are inversely related to light level. Hughes (1957) notes a similar trend in cane from the Atlantic coastal plain of North Carolina. In his experimental plots, mean culm size increases each subsequent year after fire. Given the inverse correlation we find between culm height and light level, we hypothesize that new culms grow taller each year following disturbance because of increasing shade cast by previous years' growth.

Our study results suggest the relationship between canebrakes and forest trees are disturbance-driven. Historically, the landscape mosaic of forests and canebrakes would have changed with local small- and large-scale disturbances. Perhaps canebrakes on fertile bottomland soils grow so rapidly that resulting dense stands suppress young trees, and thus extend site occupancy by giant cane for years. Regardless, in the absence of subsequent disturbance, we expect trees to eventually overtop and suppress cane, over time reducing a canebrake to scattered cane stands growing beneath forest canopy.

Giant cane occurrence and spread in bottomland forests is likely limited by environmental barriers. In riverine forests, we have observed that flooded swales and other sites subject to long-term inundation act as natural barriers to rhizomatous spread of giant cane (Marsh, 1977). Similarly, new sources of prolonged flooding (e.g., river meanders, beaver dams) should kill extant giant cane rhizome networks. Compacted soil, as might occur in floodplains under roads and well-used skid-trails, could inhibit cane clonal spread (Hughes, 1957). Overgrazing is also a potential barrier. Cane is rich fodder for cattle and is susceptible to overgrazing (Hughes, 1957). For cane growing in shade at low density, grazing pressure and the trampling that often accompany it could have particularly antagonistic effects. The forest understory beneath dense canopies of regenerating second-growth forests may have reduced local variation in light levels and lower overall transmitted light. Given enough shade for enough time, we expect culm density to decrease slowly and approach zero. Ultimately, cane's shifting cycle of expansion and decline may be limited by its flowering. Like many woody bamboos, cane usually dies after flowering (Hughes, 1951; Judziewicz et al., 1999). We expect that reduced culm density caused by grazing and/or dense shade should reduce successful pollination and seed production.

5. Conclusion

Giant cane's clonal ecology may be a useful model for understanding spreading bamboos and other forest-growing clonal perennials. Our results suggest that giant cane's rhizome network enables genets to persist under forest canopy by accelerating culm production where light levels increase in small gaps, and senescing as gaps fill in. Large-scale wind disturbance that opens forest canopy will trigger new culm production. These open-grown culms will be smaller, but grow more densely than under forest canopy. Where present in large disturbance-generated gaps, cane stands could grow together to form extensive canebrakes.

Managers attempting canebrake restoration should consider canopy manipulation if the preferred restoration site is densely forested. Today's younger, managed second-growth forests may be more wind-resistant than old-growth forests. If so, fewer and smaller canopy gaps would offer fewer opportunities for canebrakes to form. Depending on management objectives, smaller gaps created by uneven-aged forestry may be sufficient to increase cane as an understory component.

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