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Canebrakes: An Ecological and Historical Perspective

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ABSTRACT

Cane (*Arundinaria gigantea* (Walter) Muhl.) is found throughout the southeastern United States and forms monotypic stands known as canebrakes. Canebrake ecology has been largely ignored by contemporary workers and this paper is intended as a comprehensive review. Reproductive biology is poorly understood and various flowering cycles have been reported. Seed dispersal and seedling development remain largely unknown. Density estimates range as high as 160,000 culms/ha. Historic accounts suggest canebrakes were a dominant feature of the frontier landscape, particularly in alluvial habitats. Canebrakes developed under regimes of moderately intense disturbance, and probably originated when Indian agriculture was greatly curtailed following population declines caused by introduced European diseases. Subsequently, Indian burning practices maintained and expanded canebrakes by eliminating competing woody vegetation. Settlers valued canebrakes for livestock grazing and considered them indicative of fertile soils. Decline was rapid following settlement due to a combination of overgrazing, altered burning regimes, and landclearing. Large canebrakes are no longer extant and are not favored by current regimes of extreme disturbance.

INTRODUCTION

When European explorers and settlers began to penetrate the interior of North America they encountered extensive tracts of cane (*Arundinaria gigantea* (Walter) Muhl.), the only species of native bamboo. These cane communities figure prominently in literature of the time, but were eliminated rapidly following settlement. Few remnants exist for study, and canebrake ecology has been largely ignored by contemporary workers. Available information is fragmentary and sometimes contradictory, and in widely scattered and often unobtainable sources (Marsh 1977). Canebrakes are now regarded as critically endangered ecosystems (Noss et al. 1995). Considerable recent interest has been expressed in cane as wildlife habitat (Meanley 1966, Eddleman et al. 1980, Remsen 1986, Black Bear Conservation Committee 1992) and for restoration projects (Feeback and Luken 1992, Platt and Brantley 1992, 1993). This paper is intended as a comprehensive review of cane in both an ecological and historical context.

TAXONOMY AND DESCRIPTION

Taxonomic variation in cane has been variously interpreted, and as many as three taxa have been recognized (Gilly 1943, McClure 1973, Tucker 1988). Some authors (Young and Haun 1961, Hitchcock 1971, Tucker 1988) consider a small form of cane (*Arundinaria gigantea* ssp. *tecta* (Walter) Muhl.) to be a full species (*Arundinaria tecta* (Walter) Muhl.) distinguished from *A. gigantea* primarily by the presence of longitudinal air canals in the rhizomes (McClure 1963). Others consider the two taxa conspecific (Vines 1960, Voigt and Mohlenbrock 1964, Radford et al. 1968, McClure 1973). McClure (1973) treated these taxa as two subspecies (i.e., *A. gigantea* ssp. *gigantea* (Walter) Muhl. and *A. gigantea* ssp. *tecta* (Walter) McClure), and recognized a third taxon (*A. gigantea* ssp. *macrosperma* (Michx.) McClure) believed to be derived from the introgression of the preceding two subspecies. In most accounts it is not possible to determine which taxon is being referenced. For the purposes of this paper, nomenclature will follow McClure (1973).

Cane is a monopodial bamboo with erect culms bearing evergreen foliage, arising from rhizomes, and growing to a height of nine to ten meters. Segmented leptomorph rhizomes are found within the upper 15 cm of soil, range in diameter from two to 20 mm, and produce culms of an equal or slightly larger diameter at intervals of about 50 cm (McClure 1966). Diageotropic rhizome growth may continue for an indefinite length (Marsh 1977). Culm growth is initiated in early spring and ceases by mid-summer (Hughes 1951), with growth rates up to 38 mm/24 hours during this period (Biswell et al. 1945). Culms then harden and may sprout additional foliage, but will not increase in height or diameter (Farrelly 1984). Longevity of individual culms has been estimated at 5 to 10 years based on observations of tagged plants, and uniform stands may represent single genetic individuals (Hughes 1957, Marsh 1977). The mature culms form dense stands known as canebrakes (occasionally spelled "canebreak" in older literature). Stand longevity is unknown and may be dependent on flowering cycles (Harper 1928, Deam 1929, Marsh 1977).

REPRODUCTION

Prolonged periods of vegetative growth followed by mast seeding (synchronized production of seed at long intervals by a population) and subsequent die-off of culms is a common phenomenon among many temperate bamboo species (Janzen 1976). Reports of mast seeding by Asian bamboos led to assumptions of a similar cycle in cane, but evidence is conflicting and phenology remains poorly understood. Some reports suggest synchronous flowering after periods ranging from three to over 50 years, followed by die-offs of entire stands (Fleming 1779–1780, Elliott 1816–1824, Lamson-Scribner 1896, Deam 1929, Wells 1932). However, others found flowering to be unpredictable (Hughes 1951, Winterringer 1952), or noted an irregular cycle with some plants flowering repeatedly every year, and others flowering only once before dying (Dunbar 1749–1810, Cocks 1908, Brown 1929, West 1934, Marsh 1977). Culm death after flowering results from depletion of nutrient reserves in rhizomes and can be prevented by fertilization (Janzen 1976). Reports of relatively brief intermast cycles are suspect as sufficient energy reserves for mast seeding cannot generally be accumulated in less than 15 years by most bamboo species (Janzen 1976).

Flowering occurs from February to June, and while evidence is fragmentary, may follow a latitudinal gradient with earliest flowering in the Gulf Coastal states (Chapman 1897, Hughes 1951, Marsh 1970). Extreme winter temperatures, drought, and cutting or browsing of culms have all been suggested to stimulate flowering (Brown 1929, Hughes 1951, Winterringer 1952), but attempts to induce flowering experimentally have been limited and largely inconclusive (Marsh 1971). Marsh (1977) suggested flowering is initiated by a combination of internal and external factors (primarily temperature), but Janzen (1976) discounted the role of external cues and speculated flowering is triggered by an internal calendar under genetic control.

Panicles produce four or five seeds per spikelet, and fertile florets become increasingly abundant as area and density of the flowering stand increases (Hughes 1951). Seeds are present about one month after flowering and viability is reportedly low, with only one in 10,000 florets producing viable seeds (Hughes 1951). Seed predators included passenger pigeons (*Ectopistes migratorius*; Lincecum 1874), squirrels (*Sciurus* spp.; Deam 1929), an unidentified moth (Hughes 1951), humans (Swanton 1946, Banks 1953, McWilliams 1953), and possibly bobwhite quail (*Colinus virginianus*; Janzen 1976), wild turkey (*Meleagris gallopavo*; Janzen 1976), and Carolina parakeet (*Conuropsis carolinensis*; Janzen 1976, Daniel McKinley pers. comm.).

Seed dispersal has not been documented; however in most bamboo species the florets bearing mature seeds are released and fall to the ground beneath parent culms (McClure 1966). Hughes (1951) provided the only description of cane seedlings and early development. Mature seeds collected directly from panicles germinated within a week of planting, but dried seeds failed to germinate. A single basal branch with three to six leaves was produced annually. This study was terminated at the conclusion of the third growing season and seedlings remained less than 30 cm high. Substantial rhizome elongation appears necessary before culms undergo significant height growth (Hughes 1951). Descriptions of seedling development into a mature clump are not known for any bamboo species (McClure 1966).

DISTRIBUTION AND HABITAT

Cane is found throughout much of the eastern United States. Range maps showing distribution by county are presented in Marsh (1977) and Farrelly (1984). In a comprehensive review of distribution records, Marsh (1977) reported cane from 22 states (Alabama, Arkansas, Delaware, Florida, Georgia, Illinois, Indiana, Kentucky, Louisiana, Maryland, Mississippi, Missouri, New Jersey, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, and West Virginia). Distributional limits are defined by low winter temperatures in the north and xeric conditions in the west (West 1934). Cane grows under a wide variety of environmental conditions ranging from sea level on the Gulf and Atlantic coastal plains to 670 m in the Appalachian Mountains and on soil types ranging from sandy to highly acidic (Farrelly 1984).

Cane is an important understory component in both deciduous and evergreen forests, and has been reported in pocosins and Carolina bays (Wells 1928, 1932; Wells and Whitford 1976; Sharitz and Gibbons 1982), loblolly and longleaf pine barrens (Claiborne 1906, West 1934, Gemborys and Hodgkins 1971), loblolly-shortleaf pine forests (West 1934), upland hardwood forests (Shull 1921, West 1934, Marsh 1977), oak-hickory forests (Loughridge 1888, West 1934), beech-magnolia forests (Lockett 1874, West 1934), blackgum and white-cedar swamp forests (Penfound 1952), and bottomland hardwood forests (Lockett 1874, West 1934, Voigt and Mohlenbrock 1964). Braun (1950) listed cane as an understory plant in mixed mesophytic, western mesophytic, and southeastern evergreen forest types.

The largest canebrakes occurred in alluvial floodplains. Cane can tolerate inundation, but not prolonged submergence and canebrakes were restricted to the first ridge or natural levee (Imlay 1792, Nuttall 1821, Braun 1950, Delcourt 1976). Along the Mississippi River these ridges were as high as 8 m and extended inland up to 5 km, while on lesser rivers they were proportionally smaller (Hudson 1976). Early accounts of river travel and exploration invariably mention canebrakes along the shoreline, often extending continuously for many miles (Cramer 1818, Bradbury 1819, Evans 1819, Nuttall 1821, Hawkins 1848).

A continuous series of bluffs adjacent to the Mississippi River floodplain and extending from western Kentucky to southeastern Louisiana, were formerly known as the "cane hills" (Shull 1921, Bryant et al. 1993). These hills were covered by mesophytic hardwood forests with a dense undergrowth of cane (Loughridge 1888, Bryant et al. 1993). The loess soils composing these hills allowed bottomland vegetation such as cane, to extend into the uplands (Bryant et al. 1993).

DESCRIPTIONS OF CANEBRAKES

Historic accounts provide descriptions which suggest canebrakes were a dominant feature of the frontier landscape (Table 1). Furthermore, throughout the Southeast, place names attest to the former abundance of cane. Over 100 places in 56 counties, and 60+ streams in Arkansas are named after cane (Marsh 1977), 49 place names refer to cane in South Carolina (U.S. Geological Survey 1987), and cane is frequently used in place names in parts of Kentucky (Campbell 1985). Place names of Indian origin also reflect the past abundance of cane (Nelson 1950, Parkerson 1969).

Canebrakes were frequently described as "extensive" (Long 1819–1820), or "vast tracts" (Nuttall 1821). Cuming (1810), writing of early Kentucky, stated the "whole country was then an entire canebrake." Bartram (in Van Doren 1928) made reference to "vast cane meadows," "an endless wilderness of canes", and "widespread cane swamps." Buttrick (1831) reported canebrakes of "many miles in extent" and Roosevelt (1908) wrote of canebrakes "extending for miles." Shane (1840, in Campbell 1985) described a canebrake covering "thousands of acres." Few actual measurements of canebrakes were recorded, although Bartram (in Van Doren 1928) travelled for "about 20 miles through . . . cane meadows" in Alabama, and "about eight miles in a cane forest" in Louisiana. Rogers (1790, in Campbell 1985) described a canebrake as "15

Table 1. **Selected historic accounts of canebrakes in present day states**

State	Source
Alabama	Taitt 1772, Romans 1775, Imlay 1792, Landreth 1818–1819, McGuire 1834, Hawkins 1848, Lyell 1849, Mohr 1901, Bartram in Van Doren 1928, Harper 1943
Arkansas	Dunbar 1749–1810, Stoddard 1812, Long 1819–1820, Nuttall 1821, Flint 1828, Featherstonaugh 1844, Gregg 1845
Florida	Imlay 1792, Stoddard 1812, Bartram in Van Doren 1928
Georgia	Catesby 1731–1748, Bernhard 1828, Hawkins 1848, Bartram in Van Doren 1928, Plummer 1975
Indiana	Croghan 1750–1765, Flower 1822, Woods 1822, Flint 1828, Harrison and Hickie 1931, Ernst 1958
Illinois	Marquette 1673, Long 1819–1820, Flower 1822
Kentucky	Fleming 1779–1780, Filson 1784 in Jillson 1930, Imlay 1792, Michaux 1793–1796, Michaux 1805, Cuming 1810, Schultz 1810, Cramer 1818, Bradbury 1819, Nuttall 1821, Woods 1822, Munro 1868, Stickney 1872, Audubon 1897, Shull 1921, McHargue 1926, Kenton 1930, McHargue 1941
Louisiana	Iberville 1689–1702, Tonty 1693, D'Artaguiette 1722–1723, Dunbar 1749–1810, Le Page du Pratz 1774, Imlay 1792, Perrin du Lac 1807, Cuming 1810, Stoddard 1812, Darby 1816, Landreth 1818–1819, Long 1819–1820, Wilhelm 1822–1824, Lockett 1874, Davis et al. 1891, Roosevelt 1908, Bartram in Van Doren 1928, McWilliams 1953, Davis 1968
Mississippi	De la Vega 1605, Iberville 1689–1702, Dunbar 1749–1810, Imlay 1792, Cuming 1810, Cramer 1818, Evans 1819, Nuttall 1821, Buttrick 1831, Grant 1885, Claiborne 1906, Rowland 1925, Daniels 1987
Missouri	St. Cosme 1699, Schoolcraft 1821, Steyermark 1963
North Carolina	Lawson 1714b, Brickell 1737, Sondley 1930
Oklahoma	Stoddard 1812, Long 1819–1820, Nuttall 1821
South Carolina	Lawson 1714a, Catesby 1731–1748, Drayton 1802, Logan 1859, Bacot 1923, Bartram in Van Doren 1928
Tennessee	Imlay 1792, Michaux 1793–1796, Cramer 1818, Buttrick 1831, Killebrew 1878, Williams 1928
Texas	Correll and Johnston 1970
Virginia	Lawson 1714b, Penfound 1952, Ewan and Ewan 1970, Simpson 1990

miles long and perhaps half as wide." Nuttall (1821) estimated the width of one canebrake as "about half a league" (1 league = 5 km).

Canebrakes were often described as treeless areas (Imlay 1792, Nuttall 1821, Hawkins 1848, Logan 1859), although other accounts suggest an open woodland or savannah with dense cane growing beneath scattered trees (Drayton 1802, Michaux 1805, Loughridge 1888, McHargue 1926). Greatest culm densities occur where no overstory is present (Hughes 1957), and it is doubtful that canebrakes were present under mature, closed canopy forests (Campbell 1985). Because of rapid decline, information on associated vegetation is particularly fragmentary (Campbell 1985). Pea-vine (*Amphicarpa bracteata*; Imlay 1792, Long 1819–1820, Logan 1859, Stickney 1872) and greenbrier (*Smilax* spp.; Tonty 1693, Dunbar 1749–1810, Nuttall 1821, Wilhelm 1822–1824) are occasionally mentioned growing intertwined among cane.

In the past, culms were frequently reported as 10 to 12 m tall and up to 10 cm in diameter (Iberville 1689–1702, Stoddard 1812, Michaux 1793–1796, Lyell 1849). Dunbar (1749–1810) reported culms the "size of a mans leg or more," Lawson (1714a) stated a single culm segment could "hold above a pint of liquor," and Bartram (in Van Doren 1928) described culms "as thick as a mans arm." The longest culm recorded was 47 ft (ca. 1,410 cm) from the third node to the terminus (Romans 1775). Culms of the size described by early writers apparently no longer exist (Harper 1928). The largest culms Meanley (1972) observed after years of searching were 4.5 to 6.0 m tall and 3.1 cm in diameter. Contemporary size maxima may reflect a past history of disturbance as culm size is dependent on rhizome development, and heavily disturbed or declining patches tend to produce smaller culms (Marsh 1977).

Few estimates of culm density or biomass are available. An average of 49,400 culms/ha was reported in the Ocmulgee River floodplain, Georgia (Meanley 1966), densities in Arkansas ranged from 1,076 to 160,314 culms/ha (Marsh 1977), and mean densities of 5,075 ± 6,498 living culms/ha (range = 0 to 29,000/ha) and 15,192 ± 18,007 dead culms/ha (range = 0 to 84,750/ha) were reported in southern Illinois (Eddleman et al. 1980). However, the latter study was conducted near the northern distributional limit of cane, and most culms were killed annually by low winter temperatures. Cultivated cane in Louisiana yielded 151,408 culms/ha and 40,000 kg dry material/ha (Sineath et al. 1953). In ungrazed North Carolina canebrakes, Shepherd et al. (1951) found 4,356 kg dry material/ha.

FIRE ECOLOGY

Cane is flammable and burns readily during dry years, and in certain seasons and stages of its life cycle (Campbell 1985). Culms are killed by fire, but resprout quickly from rhizomes (Shepherd et al. 1951; Hughes 1957, 1966). The effect of fire on cane depends on the frequency of burning. Fires about once every 10 years will maintain stands (Shepherd et al. 1951, Hughes 1957); more frequent burning favors fire resistant trees and shrubs, and annual burning will eliminate cane (Wells 1928, Garren 1943, Wells and Whitford 1976). Frequent fires followed by resprouting deplete rhizome nutrient reserves, eventually resulting in plant death.

Canebrake fires are extremely hot due to heavy fuel loads and have been described as "explosive" (Hughes 1957). Fires maintain canebrakes by eliminating competing woody vegetation (Shepherd et al. 1951, Hughes 1966). Both winter (Hughes 1957) and spring and summer burns (Stevenson 1991) are reported to improve conditions for cane. Under complete fire exclusion cane stands lose vigor and are gradually replaced by woody vegetation (Hughes 1957, 1966). Cane stands may be particularly vulnerable to fire following flowering when dead culms provide an abundance of fuel (Campbell 1985). The effect of fire on cane seedlings is undocumented, but lacking a well developed rhizome, they are probably killed, and burning at this stage in the life cycle may eliminate canebrakes.

ORIGIN OF CANEBRAKES

Canebrakes develop under regimes of moderately intense biotic disturbance (Campbell 1985). Decline of cane growing under a forest canopy has been noted and some form of disturbance is necessary to maintain canebrakes (Meanley 1966). Marsh (1977) believed canebrakes developed as secondary seres in disturbed areas such as field edges, roadsides or logged sites, Penfound (1952) reported rapid invasion of cane into cut-over sites, and Eddleman et al. (1980) recommended overstory removal and clearcuts as management techniques to improve vigor of declining stands. Hamel (1986) concluded canebrakes develop in response to both natural and human disturbance.

The large canebrakes recorded by European settlers and explorers were probably anthropogenic in origin resulting from abandonment of Indian agricultural fields and Indian burning practices. By about 1000 AD Indians throughout the Southeast had adopted an intensive system of permanent agriculture based on corn (*Zea mays*), a seed crop which rapidly exhausts soil fertility unless renewed by manuring or lengthy fallow periods (Hudson 1976, Delcourt et al. 1993). To avoid soil nutrient depletion, corn was planted in alluvial habitats subject to periodic flooding and deposition of nutrient-rich silts (Doolittle 1992). Likewise, Indian villages were situated in floodplains because of proximity to corn fields and additional food resources available in nearby swamps and lakes (Delcourt et al. 1993).

The adoption of corn agriculture in conjunction with other technologies led to a significant population increase throughout the Southeast (Delcourt et al. 1993). The regional Indian population immediately prior to European contact has been estimated as high as 1,700,000 (Smith 1987, Denevan 1992). Population densities of 60–149 people per 100 km^2 occurred throughout much of the Southeast, and were considerably higher in some coastal plain regions (Driver 1961). Because one to two acres of cropland were required to sustain each person, the large pre-contact population coupled with land clearance for floodplain agriculture resulted in extensive environmental modification along most riverine corridors in the Southeast (Delcourt et al. 1993).

A drastic demographic collapse occurred within 50 years of contact due to introduction of Old World diseases, and Indian populations may have been reduced by 80 to 90% (Dobyns 1983). This population reduction was accompanied by a decline in agriculture followed by substantial regrowth of early and mid-successional vegetation on abandoned Indian fields (Delcourt et al. 1993). By 1750, when Europeans began to penetrate the interior of the continent they failed to realize the "pristine wilderness" they encountered was actually 200 year-old regrowth in a formerly extensively modified environment (Denevan 1992).

Following depopulation, invasion of fallow fields by cane would have occurred rapidly. Intact rhizomes were scattered throughout fields, and cane grew around field margins (Hudson 1976). Canebrakes were also maintained near villages to supply raw material for construction of dwellings, fences and other structures, and a wide array of weapons and personal items. Additionally, cane was an important food resource and shoots were boiled and eaten in spring and early summer (McHargue 1941, Swanton 1946, Banks 1953). Expansion from these existing stands probably occurred quickly as vegetative growth is rapid, particularly in loose, well-drained alluvial soils, where rhizomes can grow up to 6.0 m in a single season (Marsh 1977, Platt and Brantley 1993).

Historic accounts support this model. Iberville (1689–1702), Nuttall (1821), Hawkins (1848), and Bartram (in Van Doren 1928) reported abandoned Indian agricultural fields reclaimed by cane, and Dunbar (1749–1810) encountered "thick canebrakes" covering an abandoned mound complex on the Catahoula River, Louisiana. Froeschauer (1988) attributed current vegetation, including canebrakes, along the Ocmulgee River, Georgia to past agricultural practices of Indians. This floodplain was once densely settled by Indians and Bartram (in Van Doren 1928) noted "ancient Indian fields . . . " extending for 25 to 33 km (15 to 20 miles) along either bank, an area where some of the largest extant canebrakes are found (Meanley 1972).

Despite drastic population reductions, Indians continued to greatly modify their environment with fire. Broadcast fire was widely employed for warfare, agriculture, hunting, and to improve pasturage for game and horses (Pyne 1982). These burning practices created significant areas of grassland in eastern North America (Rostlund 1957, Martin 1973). Indians regularly burned cane (Lawson 1714a, Buttrick 1831, Flagg 1838, Featherstonhaugh 1844), and these practices maintained and expanded canebrakes (Campbell 1985, DeVivo 1991). The suggested Indian burning regime of once every 7 to 10 years (Williams 1989) is consistent with management recommendations of Shepherd et al. (1951) and Hughes (1957). Little is known about the timing of these fires, although burning was reported during the "autumn" when dry conditions favored ignition (Flagg 1838), November and December (Dunbar 1749–1810), and February (Buttrick 1831).

Indians may have purposefully managed cane stands with fire to encourage the expansion of bison (*Bison bison*) herds, a preferred game species (Rostlund 1960, Roe 1970, Campbell 1985). Burning created and maintained habitat, and probably served to concentrate animals, as bison preferentially graze on recently burned grasslands (Vinton et al. 1993). Bison were not present in the Southeast until the mid-1600s and reached their greatest extent by 1700 (Rostlund 1960). The presence of canebrake and other anthropogenic grasslands, coupled with human population declines, played a significant role in this range expansion (Rostlund 1960). Cane is considered the highest yielding native pasture in the Southeast, providing excellent grazing for bovines (Biswell and Foster 1942, Biswell et al. 1945), and historic accounts frequently mention bison in association with cane (Marquette 1673, Tonty 1693, Dunbar 1749-1810, Wesley 1737, Michaux 1805, Stickney 1872).

The roosting habits of passenger pigeons could also have favored establishment of canebrakes, although this remains speculative. In late fall and winter, passenger pigeon flocks, sometimes numbering millions of birds, moved through the south in search of acorns. These flocks formed large temporary roosts and during accumulating beneath roosts killed the overstory (Schorger 1955, Blockstein and Tordoff 1985). Overstory removal and fertilization by decomposing dung may have favored vegetative expansion of cane into these openings.

DECLINE OF CANEBRAKES

The timing and disappearance of the large canebrakes has not been chronicled (Remsen 1986). Canebrakes disappeared faster than any other bottomland plant community (Meanley 1971), and causal factors most often cited include overgrazing by domestic stock, altered burning regimes, and landclearing for agriculture (Hughes 1966, Marsh 1977, DeVivo 1991). Although difficult to traverse and clear, canebrakes were highly regarded as sites for settlement. Early surveyors in Tennessee categorized canebrakes as "first-rate" (DeSelm 1994), and mention of "rich" or "fine canelands" is often made in period accounts (Cuming 1810, Flint 1828, Kenton 1930). Settlement of the southern frontier proceeded in two waves; stockmen subsisting by grazing livestock and hunting, were followed by agricultural settlers who cleared land for crop production (Owsley 1945). While there was some overlap and intermingling between the two groups, herding and sedentary agriculture were not compatible, and as agricultural settlers began to move into an area, stockmen gathered their herds and moved to less settled regions. The practices of both groups devastated canebrakes.

The southern frontier was a major livestock producing region and extensive herds of cattle, sheep, horses, and swine were maintained under an open range system of grazing (Dick 1948, Clark and Guice 1989). Over 12 million cattle were present on southern ranges by 1860, and swine were far more numerous (Williams 1989). These are conservative figures as it was virtually impossible to accurately tally livestock on open ranges, and herdsmen reported low figures to tax assessors (Clark and Guice 1989).

Cane was an important forage, more so because it provided grazing and shelter throughout the winter (Killebrew 1878, Lamson-Scribner 1896). Cane is the highest yielding native pasture in the south and comprised the bulk of cattle diets whenever plentiful (Biswell and Foster 1942, Shepherd and Dillard 1953). Cane foliage contains up to 18% crude protein and is rich in calcium and phosphorous (Shepherd et al. 1951, Smart et al. 1960). Cattle grazing on cane exhibit significant weight gains (0.18 kg/day), produce a 95% annual calf crop (Shepherd et al. 1951), and are reputed to produce superior milk and butter (Imlay 1792, Flint 1828). Horses fed cane were able to work nearly as well as those fed corn (Imlay 1792). For these reasons, canebrakes were highly sought as pastures (Cramer 1818, Evans 1819, Ogden 1823, Mohr 1901).

The large numbers of livestock present on the southern range were not compatible with the continued existence of canebrakes. Cane is particularly sensitive to overgrazing, especially during the growing season, and continuous grazing leads to rapid decline (Shepherd et al. 1951, Hughes 1957). Shepherd et al. (1951) found 80% to 100% of readily accessible cane was defoliated after a single season of grazing, and further grazing led to decreases in foliage production, the number and size of new culms, and eventually death of existing culms.

Numerous references to overgrazing cane are present in historic accounts. Drayton (1802) stated continuous browsing by cattle kept cane closely cropped and eventually destroyed it. Michaux (1793–1796) noted additional damage when cattle broke down culms to graze on foliage that was otherwise out of reach. Cuming (1810) and Audubon (1897) both attributed the demise of canebrakes in Kentucky to overgrazing by domestic stock. According to Long (1819–1820) stockmen "confined themselves to one spot no longer than the range continues to afford a sufficient supple of the articles most necessary for life. When the canes are fed down and destroyed . . . the squatter goes in search of a place where all the original wealth of the forest is yet undiminished." Swine also destroyed canebrakes by uprooting and consuming rhizomes (Michaux 1805), which are rich in carbohydrates (Lindahl et al. 1949).

Altered fire regimes acted in concert with grazing to hasten the destruction of canebrakes. Stockmen applied fire widely on open ranges to encourage growth of new forage and prevent encroachment of woody species (Wells and Whitford 1976, Pyne 1982). Culms which resprout following burning are high in digestible cellulose and consequently heavily grazed (Shepherd et al. 1951, Smart et al. 1960). Range burning was conducted annually and few areas escaped burning at least once every two years (Pyne 1982). This burning regime results in conversion of canebrakes to open savanna (Wells and Whitford 1976), and when combined with heavy grazing, rapidly eliminates cane (Biswell et al. 1945, Shepherd et al. 1951). Conversely, fire suppression in some regions allowed woody vegetation to become established leading to an eventual decline of cane stands (DeVivo 1991).

The agricultural settlers who followed stockmen found the presence of canebrakes indicative of fertile soils suitable for agriculture (Lillard 1947, Dick 1948). Logan (1859) stated "cane growth [was] . . . the standard by which settlers estimated the value of lands. If it grew no higher than five feet . . . the soil was deemed ordinary, but a growth of twenty or thirty feet indicated the highest degree of fertility". Clearing canebrakes before the advent of mechanization was difficult and time consuming. Culms were cut with axes or cane knives, and rhizomes dug out with mattocks and heavy iron plows. Canebrakes were cleared in fall and winter and then burned in late winter or early spring, just before planting. Rhizomes which resprouted were grubbed out by hand (Le Page du Pratz 1774, Imlay 1792). Once rhizomes are eliminated cane will not become reestablished because of dependence on vegetative propagation rather than seed production (Hughes 1951).

Demise was rapid following settlement. As early as 1778 Simon Girty, a white adoptee of the Seneca tribe, cited destruction of canebrakes as a reason to attack Kentucky settlements which had been established only a few years previously (Faragher 1992). Michaux (1805) stated canebrakes disappear ". . . in proportion as new plantations are formed." Cuming (1810) found cane eradicated except in the unsettled regions of Kentucky, and Audubon (1897) writing in the 1830's, stated "activities connected with the progress of civilization . . . reduced the cane . . . [to] comparatively small limits." According to Killebrew (1878) the only canebrakes remaining in Tennessee were restricted to Mississippi River bottomlands and remote river valleys. Shull (1921) concluded that by 1919 canebrakes had been eradicated in most of Kentucky. This pattern of disappearance was repeated throughout the South except in some of the more thinly settled and remote riverbottoms where large canebrakes persisted well into this century (Roosevelt 1908, Meanley 1972). More recently dam construction along the White River and its tributaries in Missouri inundated "vast acreages" of cane (Steyermark 1963). Similar flood control projects have probably had a severe impact on remaining canebrakes throughout the region.

CONCLUSIONS AND SUMMARY

While cane persists as an understory plant throughout most of its historic range, large canebrakes are essentially non-existent today (Meanley 1972, Remsen 1986). Noss et al. (1995) estimated canebrakes have been reduced to less than 2% of their former abundance. The largest extant canebrakes are in the Ocmulgee Basin, south of Macon, Georgia (Meanley 1972), and these are but a remnant of the "vast tracts" and "endless cane forests" reported by early writers. It is unlikely large canebrakes will ever be a significant feature of the modern landscape, for the regime of moderate disturbance which favors canebrakes no longer exists, and cane is not adapted to the extremes of disturbance which occur today (Campbell 1985). Cane restoration is extremely difficult because of slow growth of transplanted rhizomes and competition from weeds and vines (Eddleman et al. 1980, Feeback and Luken 1992, Platt and Brantley 1993). Perhaps a more feasible strategy is to manage and expand existing stands through a combination of overstory removal, periodic burning, and perhaps fertilization.

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