

A Review of Native Vegetation Types in the Black Belt of Mississippi and Alabama, with Suggested Relationships to the Catenas of Soil Series

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A review of historical information and scientific literature concerning vegetation of the Black Belt region, in Mississippi and Alabama, is used to generate a hypothetical framework of ecological gradients. Remnants of native grassland are well known, but the original pattern of grassland versus woodland appears to have had a complex relationship with soil and disturbance regime. This paper approaches the problem by first displaying variation among soil series along two sets of catenas: (1) from alluvial lowlands, to chalky slopes, to more acid uplands; and (2) from relatively mesic well-drained soils, usually more sloping and often relatively shallow (above parent material), to more poorly drained soils, including xerohydric vertisols that often erode down to seasonally xeric subsoils. Fifteen types of native vegetation are outlined, with brief descriptions based on diverse sources. These types are overlaid on the diagram of soil catenas, showing the most characteristic vegetation that appears to have existed in different sections. The result provides a useful initial model for the gradient from lowland to upland vegetation (1). However, variation of disturbance regime in space and time has probably limited the consistency of associations between vegetation and the drainage-related gradient (2). Deeper woods are concentrated on more mesic sites, and became increasingly restricted when human influence spread over the landscape. Grasslands may have originally occurred on a wide range of chalky, clayey or sandy soils, from hydric to xeric, but became greatly modified after European settlement.

The Black Belt in Mississippi and Alabama is readily defined in terms of its calcareous geology and chalky soils, together with its largely agricultural modern land uses (USFS, 2007). Several authors have provided useful studies of this region's vegetation: Hilgard (1860), Mohr (1901), Lowe (1911, 1920), Harper (1913a, 1920, 1943), Myers (1948), Rostlund (1957), Jones and Patton (1966), Rankin and Davis (1971), DeSelm and Murdoch (1993), Brown (2003), Barone (2005a), Barone and Hill (2007), Schotz and Barbour (2009), and others. However, details of the original vegetation have remained somewhat obscure, since so much of the land became agricultural early after colonization. Cotton became dominant economically during the 19th Century, but was partly replaced in the 20th Century by soybeans and corn,

especially on lowlands, and by forage and pasture, especially on uplands (Cleland, 1920; Wiygul et al., 2003).

The purpose of this paper is to outline the varied native vegetation types within the Black Belt, based on available historical and scientific literature. Given the apparent importance of soil in controlling patterns of vegetation, an effort is made to express the fundamental 'catenas' in geological and topographic gradients among soil series, as defined by the U.S. Department of Agriculture. Based on the literature, typical original vegetation is then suggested for each section of the gradients in soils. The paper does not present a definitive analysis, but builds a hypothetical scheme of relationships to be tested with more systematically collected data in the future.

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This review was prompted by field work during 2009 at the Pulliam Prairie in Chickasaw County, Mississippi (Campbell and Seymour, 2011b, 2011c). Although initial hypotheses were developed mostly at that site, the context here has been extended to the whole Black Belt region. Moreover, similar soils and vegetation occur in other ‘blacklands’ on the Gulf Coastal Plain, from Texas to Georgia (NatureServe, 2010). Outside the strictly defined Black Belt on Cretaceous cherts, there are some calcareous soils with remnants of native grassland on Paleocene or lower Eocene parent material, from Tennessee (D. Estes, pers. comm.) to Georgia (Echols, 2007; Echols and Zomlefer, 2010). Further south, the Jackson Prairie region of Mississippi and Alabama lies on calcareous clays of upper Eocene age, and has much similarity to the Black Belt (Moran et al., 1997; Barone, 2005b; Barone and Hill, 2007). Although this paper is focused on the Black Belt, it does make some reference to similar vegetation in those other regions (as local ‘associations’ or ‘floristic vicariants’), in order to advance more functional descriptions of broader types that might be applied to blacklands in general (as ‘alliances’ or ‘ecological classes’).

OCCURRENCE OF NATIVE GRASSLAND

Barone and Hill (2007) have recently conducted a broad floristic survey of native grassland remnants in the Black Belt and Jackson Prairie regions. The concentration of several conservative or rare grassland plant species in the Black Belt suggests that grassland has existed here for much of the post-glacial era and before. There is also increasing evidence that several populations of animals found in the region are—or were—disjunct from more extensive populations in the Great Plains. These animals include extant insects (e.g., Brown, 2003; Hill, 2007; Hill and Brown, 2010) and extinct horses (Kaye, 1974).

However, there has been some controversy about the degree of openness, which may have had complex relationships to patterns in soils and in the frequency of burning by native people. If the region is broadly defined to include river valleys with alluvial soils, and intermixed ridges with

more acid soils, it is estimated that about 10–35% of this whole landscape was truly open grassland or savanna with no more than 10 trees per acre (Harper, 1913b; Cleland, 1920; Jones and Patton, 1966; Rankin and Davis, 1971; Barone, 2005a). But these openings were concentrated on about 70–75% of the more calcareous uplands, where soil pH is generally 6.5–8.5. Much other land across the whole region probably had woods with some degree of opening caused by fires or other disturbances, and about 10–40% appears to have been completely closed forest. Before European settlement, adjacent regions generally appear to have had less grassland than the Black Belt, but the woods in some of these regions were probably much influenced by fire as well (Rostlund, 1957; Brewer, 2001; Peacock et al., 2008).

When Europeans first entered the Black Belt in 1540, there were significant concentrations of native people, who provided the first serious resistance to De Soto’s expedition in North America (Clayton et al., 1993). During 1500–1760, the Alabama tribe and others were based in central Alabama, numbering several thousand (Hook, 1997; see also www.ac-tribe.com/ac). The Choctaw were centered in western Alabama and east-central Mississippi, with several villages in the Black Belt, as described in accounts cited by Rostlund (1957). Further north, the Chickasaw tribe was centered in northwestern Alabama, northeastern Mississippi, western Tennessee, and southwestern Kentucky, numbering about 10,000–15,000 (Nairne, 1708; Morgan, 1996; Sultzman, 1999; Johnson, 2000; O’Brien, 2003). In Mississippi, there was a relatively dense concentration of people along the Tombigbee River and its tributaries from near Columbus to Tupelo. Many villages existed in this region, usually on the low bluffs (‘cuestas’) along the western or south-western side of these streams, often adjacent to openings on the chalky slopes and overlooking lowland plains with the most productive fields (B. Lieb, pers. comm. from The Chickasaw Nation; Peacock and Miller 1990). The land of the Chickasaw was even “better provided with these plains than the Choctaw country, the landscape more beautiful, and the soil better” (Anonymous source ca 1755, cited by Rostlund, 1957).

As described by Nairne (1708) and other early authors (see above), these native people used much lowland to grow corn and other crops, including nuts and fruits from various trees and shrubs. Based on Rostlund's (1957) review, it is likely that some of these lower open areas—often described as “fields” or “savannas”—were burned on a rotation. His historical sources also suggest that native people burned adjacent uplands in the region, as well, in order to increase production of game and other wild food. Burning may well have caused grassy openings to spread up from the thinner chalky soils. Bison were hunted in the Black Belt region about the time of European conquest, and may have increased in numbers when native human populations declined (Johnson et al., 1994).

After Spanish invasion, subsequent colonization and removal of the tribes, the Black Belt became increasingly used for intensive farming, with cotton becoming the major exported ‘cash-crop’ (Cleland, 1920; Gibson, 1941). Burning of native vegetation became greatly reduced. Good stable remnants of native grassland—or grassy open woodland—became virtually restricted to a few upland areas with relatively shallow, erodible or otherwise unproductive soils.

GEOLOGY, TOPOGRAPHY AND SOILS

The Black Belt is largely underlain by Upper Cretaceous sediments that are generally known as the Selma Group, of which the Demopolis Chalk is predominant. The Demopolis is composed of “chalk and marly chalk containing fewer impurities than underlying and overlying formations” (Moore, 1985). [Chalk is limestone of calcite, i.e. CaCO_3 deposited by unicellular haplophyte algae; marl is mudstone of clay and much aragonite, i.e. CaCO_3 deposited by molluscs, corals and other animals.] Overlying the Demopolis Chalk are varied sediments of the Cretaceous-Tertiary transition, which are either included in the Selma Group or segregated as the Midway Group. This transition includes the Ripley Formation, which forms the Pontotoc Ridge—a more sandy physiographic strip along the western side of the Black Belt in Mississippi. The Ripley is composed of “gray to greenish-grey fine glauconitic sand, clay and sandy

limestone” (Moore, 1985). [Glauconite is iron silicate plus minor amounts of other minerals.] Underlying the Demopolis Chalk is the Mooreville Chalk of the Selma Group, and below that is the Eutaw Formation, which is a glauconitic sandstone of the Tuscaloosa Group.

The USDA (2010a,b) has provided detailed descriptions of soil series, regional maps and maps for each county. Relationships of soil series to topography and geology are generally summarized with diagrams in the published soil surveys. From a detailed review of this material, it is possible to construct a two-dimensional diagram that displays ‘catenas’ of soils (i.e., sequences along gradients that sort out attributes) among typical series reported from the Black Belt (Fig. 1). This diagram was arrived at through successive approximation, the organizing goal being to place the most similar soil series closest to each other; for an earlier application of the method, see Campbell and Grubbs (1992). Overall similarity was judged subjectively based on parent material, texture, landscape position, slope, depth, drainage, acidity, and color [for overlays of individual attributes, see Supplementary Material appended to this paper].

The vertical dimension in Fig. 1 displays the elevation-related gradient, from alluvial lowlands, to the chalky soils on gentle side slopes, to the overlying clays and sands on broader ridges. The horizontal dimension displays the drainage-related gradient, from well drained slopes with generally shallower soils above parent material (left), to poorly drained flats with generally deeper soils (right). Some of the poorly drained soils have ‘xerohydric’ character, with great fluctuations in water table through the seasons. For example, the Trebloc soil series, on upland flats (at upper right in Fig. 1), is known to experience particularly wide fluctuations (Pettry et al., 1995).

Soil series on chalk are mostly classed as various vertisols (Fig. 1)—with expansive ‘shrink-swell’ clays (Pettry and Switzer, 1993), and ‘self-mulching’ of organic matter into deep A horizons. Similar vertisols (as chromic hapluderts) have been detailed in the Jackson Prairie by Moran et al. (1997). More local soil classes include entisols (especially on recent colluvium or alluvium), inceptisols (especially on deep, damp colluvium or

alluvium), mollisols (often with more stable grass, cane or cedar cover), and alfisols (on more weathered loamy uplands with more woodland history just above the chalk). In contrast, loamy ultisols (with generally less base saturation) predominate above the chalky soils, on more sandy uplands or on high terraces, usually with a history of more woodland than grassland.

Uplands in the Black Belt, as in some other blacklands (e.g., Moran et al., 1997), are prone to severe sheet and gully erosion, even on gentle slopes. Natural erosion is already a widespread feature of chalky soils in the region, while land clearance and farming have caused substantial increases. For example, the valley floor of Saka-tonchee Creek in Chickasaw County, Mississippi, appears to have risen by 10–20 feet within the past century, based on observations at bridges (S. Pulliam, pers. comm.). Similar observations have been made across north-central Mississippi (Grissenger et al., 1982). Adair (1775, p. 358, 413), Harper (1913a), Gibson (1941) and several other early geographers pointed out that erosion often exceeds weathering on uplands in the Black Belt, leaving a thin layer of clayey soil or disintegrating chalk—‘rotten limestone’—above more consolidated parent material. However, erosion appears to be retarded where there are remnants of thicker acid clays on ridges, often associated with post oak and other trees.

Based on available literature, the following vegetation types can be broadly defined, with additional segregates indicated in several cases. These types are ordered here with an informal letter code—(a) to (o)—that is used for cross-reference to an accompanying paper (Campbell and Seymour 2011b). Numbers in parentheses after “NVC” refer to the “CEGL” codes for the most similar vegetation types in the National Vegetation Classification of NatureServe (2010). Botanical nomenclature primarily follows the list of vascular plants in Mississippi that has been developed at the Pullen Herbarium in Oxford) by McCook and Kartesz (2010; based initially on Kartesz, 1999).

Uplands with Acid Soils Overlying Calcareous Sediments. These diverse soils have varied components of clay, silt or sand, occurring on uplands within the Black Belt and in transitions to the Pontotoc Ridge or other adjacent uplands. Subsoils have red, brown, yellow or gray hues.

(a) Oak woods on ridges and knolls (NVC 7246, 2075). Several observers have indicated the historical place of such woods in the landscape. In addition to the locally wet “flatwoods” with much post oak that were extensive just outside the western and southern borders of the Black Belt (Mohr, 1901; Lowe, 1921), there were more fragmented oak woods on uplands scattered within much of the region. For example, in the northern

Figure 1 (next page). Diagram showing generalized catenas of soil series in the Black Belt region, as related to parent material and topography.

See USDA (2010a) for detailed descriptions of each soil series.

Soil orders are color-coded as shown in the lower bar.

Within each box: 1st line = soil group modifier

2nd line = soil group/class (upper case)

3rd line = series name

4th line = typical texture

Some common soils in peripheral sections of the Black Belt are included here, but soils more typical of disjunct blacklands elsewhere in southeastern states are excluded (e.g., soil series Hannon, Okeelala and Toxey). [Supplementary Material with details of trends in edaphic data is appended to this paper.]

TYPICAL PARENT MATERIAL	TYPICAL TOPOGRAPHY										
	MORE HILLY LANDSCAPES IN GENERAL shallow-rocky soil	TRANSITIONAL	INTERMEDIATE LANDSCAPES IN GENERAL moderate-deep soil	TRANSITIONAL	LESS HILLY LANDSCAPES IN GENERAL less well-drained						
Mixed uplands or high terraces: fine sandy loams to silt loams		Typic KANDIUDULT Faceville fine sandy loam	Glossic FRAGIUDULT Prentiss loam	Fluvaquentic PALEUDULT Brewton fine sandy loam	Typic PALEAQUULT Trebloc silt loam						
Sandy uplands or high terraces: sandy loams to fine sandy loams		Typic FRAGIUDULT Ora sandy loam	Typic FRAGIUDULT Savannah fine sandy loam	Fluvaquentic PALEUDULT Stough fine sandy loam	Note: Brewton is close to Stough but with more eluviated clay						
Clayey uplands: acid clay and locally sand or silt above calcareous	Ultic HAPLUDALF Brantley fine sandy loam	Vertic PALEUDALF Boswell fine sandy loam	Vertic PALEUDALF Kipling silt loam	Aquic HAPLUDERT Brooksville silty clay loam	Chromic DYSTRAQUEPT Eutaw silty clay						
Clayey uplands: more influence of acid clay than chalk; not loamy	Note: Boswell and Brantley are mostly mapped on Paleocene/Eocene	Leptic HAPLUDERT Watsonia clay	Chromic DYSTRUDERT Oktibbeha clay	Aquic DYSTRUDERT Vaiden clay	Note: "Houston" included fine sandy loams on Paleocene (Harper 1920)						
Chalky uplands: gentle slopes with influence of overlying clay		Oxyaquic HAPLUDERT Maytag silty clay	Oxyaquic HAPLUDERT Okolona silty clay	Oxyaquic HAPLUDERT Houston clay	Note: "Houston" has often eroded down to Sumter (Gibson 1941)						
Chalky uplands: steeper sideslopes to local alluvial flats with clay	Typic HAPRENDOLL Binnsville silty clay	Rendollic EUTRUDEPT Sumter silty clay	Aquic HAPLUDERT Griffith silty clay	Chromic EPIAQUERT Sucarnochee silty clay							
Chalky uplands: loamy toe-slopes, swales and alluvial transitions	Note: mesic soils on NE-facing bluffs with sugar maple need definition here	Typic UDORTHENT Demopolis silty clay loam	Aquic HAPLUDERT Faunsdale clay loam	Vertic EPIAQUEPT Leeper silty clay loam							
Floodplains: loamy alluvium along perennial streams		Note: some toe-slopes and high terraces may need definition here	Fluvaquentic HAPLUDERT Marietta loam	Aeric FLUVAQUENT Belden silty clay loam	Note: more open marshy wetland soils need definition here						
Floodplains: deep clayey alluv. along streams and backwater sloughs		Typic HAPLUDERT Trinity clay	Fluvaquentic HAPLUDOLL Catalpa silty clay loam	Vertic EPIAQUEPT Tuscumbia silty clay loam	Typic EPIAQUEPT Una silty clay						
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Figure 1 (for caption see previous page).

Black Belt, Nairne (1708, p. 36-39) described traveling “up and down the savannas... among a tuft of oaks on a rising knoll, in the midst of a large grassy plain.” M. McGee (1841, p. 60 in Atkinson, 2004) recalled “Old Fields” ca. 1750-70 in the Tupelo area, from “Old Town” towards “Long Town” and “Post Oak Town”—these fields were “some 13 or 14 miles long by about 4 broad, with here & there a copse of wood to dot the wide & long extended expanse.” In the western transition, Ward (1987) used details of the 1834 survey to map islands of post oak within the prairie, just above sites of human occupation. Hilgard (1860) provided several notes of such oak woods, and Harper (1913a) generally noted “oak groves on broad low knolls of poorer soils.”

There has been little botanical description of these oak woods. In Mississippi, Lowe (1921) noted: “On the lighter and usually higher [yellowish-brown to] reddish soil areas which dot the prairie surface like islands, an entirely different assemblage occurs. The soil is not so rich in plant food as the black soils, lime especially being in much smaller proportions. These areas support a rather dwarfish growth of a few species of trees, chiefly oaks, the commonest being...” [here with modern names] chiefly *Quercus stellata*, *Q. marilandica* and *Q. falcata*; also present, *Q. velutina*, *Q. durandii* Buckl. (= *Q. sinuata* auct.), *Carya tomentosa*, *Diospyros virginiana*, *Pinus echinata*, *Prunus serotina* and *Rosa carolina*. He noted more distinct flora in the red sandy hills that intermix with the Black Belt, on soils typical of the Pontotoc Ridge and plains further west, adding *Liquidambar styraciflua*, *Sassafras albidum*, *Rhus* spp., *Vaccinium arboreum* and *Vitis rotundifolia*.

In Alabama, Bartram’s (1791) early account of the “expansive illuminated plains” south of Montgomery is insightful: “They are invested by high forests, extensive points or promontories, which project into the plains on each side, dividing them into many vast fields opening on either side as we passed along.” Hawkins (1798-99) also described these plains: “They are waving, hill and dale, and appear divided into fields. In the fields the grass is short, no brush; the soil in places is a lead color, yellow underneath, and very stiff [suggesting the dystrudert series, Vaiden, in Fig. 1]. In the wooded parts the growth is generally post oak, and very large, without any underbrush, beautifully set in clumps. Here the soil is dark clay, covered with long grass and weeds, which indicates a rich soil...” [suggesting the more alfic Brooksville or Kipling soil series]. Mohr (1901) and earlier authors (Romans, 1775; Darby, 1818; W. Roberts 1818, quoted in Rostlund, 1957) described oak woods in Alabama similar to Lowe’s (1921), adding other species of *Carya* (*glabra*, *?ovata*), dogwood (*Cornus florida*), ironwood (*?Ostrya*) and, locally, poplar (*Liriodendron*) to the list of typical trees. Mohr also detailed the poorly drained condition in some areas, with distinctive grasses, diverse sedges and allies in *Carex*, *Cyperus*, *Eleocharis* and *Scleria*; the latter appears to have been locally abundant in drier transitions. On drier ground, legumes were relatively common: *Desmodium* spp., *Lespedeza* spp., and “Japanese clover” [*Kummerovia striata*].

Today, post oak is generally dominant in older woods on uplands, and large open-grown post oaks are frequently left around old home sites for shade, or along old surveyed boundaries. Hill et al. (2009)

Figure 2 (next page). Diagram showing suggested associations of gradients in original native vegetation to catenas of soil series in the Black Belt region. Lettered codes in parentheses (a to o) refer to the sequence of notes in text. Color-shading indicates the general degree of openness in the vegetation. Asterisks at the bottom of each cell indicate the general degree of agricultural conversion, based on descriptions of USDA (2010a), overall review of literature and general observation. The densest asterisks indicate land that was most suitable for crops in early agricultural development. Moderately dense asterisks indicate additional land that is now generally used for row crops, especially cotton, corn or soybeans. Less dense asterisks indicate that pasture and hay-production are at least as extensive as row crops. Lack of asterisks indicates that native vegetation is at least as extensive as agricultural land—native vegetation is mostly woody, except for concentrations of prairie remnants on the Binnville and Sumter soil series.

TYPICAL PARENT MATERIAL	TYPICAL TOPOGRAPHY				
	MORE HILLY LANDSCAPES IN GENERAL shallow-rocky soil	TRANSITIONAL	INTERMEDIATE LANDSCAPES IN GENERAL moderate-deep soil	TRANSITIONAL	LESS HILLY LANDSCAPES IN GENERAL less well-drained
Mixed uplands or high terraces: fine sandy loams to silt loams		(a) post oak woods (or deeper woods) *****	(a/b1) post oak or oak-pine woods *****	(a/b2) post oak or blackjack oak woods?	(n2) swampy woods; post and water oak?
Sandy uplands or high terraces: sandy loams to fine sandy loams		(a) post oak woods (or deeper woods) *****	(b1) oak-pine woods *****	(b2) blackjack oak woods? *****	
Clayey uplands: acid clay and locally sand or silt overlying chalk	(a) post oak woods or deeper woods? *****	(a) post oak woods *****	(a/b2) post oak or blackjack oak woods *****	(a/b2) blackjack oak or post oak woods *****	(c2) wetter acid grassland
Clayey uplands: more influence of acid clay than chalk; not loamy		(a) post oak woods *****	(b2) blackjack oak woods or grassy mixes *****	(c1) drier acid grassland *****	
Chalky uplands: gentle slopes with influence of overlying clay		(i/h1) red cedar drier thickets, or grassy mixes *****	(d1) xeric-tending chalk grassland *****	(d2) xero-hydric chalk grassland *****	
Chalky uplands: steeper side-slopes to local alluvial flats with clay	(i/h) red cedar, thickets or grassy mixes?	(f) subxeric chalk grassland *****	(e) transitional cha. grassland, often disturbed *****	(g2) more hydric chalk grassland? *****	
Chalky uplands: loamy toe-slopes, swales and alluvial transitions	(j1) submesic woods below bluffs & on toes	(h2) damper thickets or grassy mixes? *****	(g1) more mesic chalk grassland or varied mixes *****	(k) lowland grassland? (seasonally dry) *****	
Floodplains: loamy alluvium along perennial streams		(j2) more mesic woods on toes and terraces? *****	(j3) submesic woods on terraces *****	(l) canebrakes and varied transitions *****	(k) lowland grassland? (marshy) *****
Floodplains: deep clayey alluv. along streams and backwater sloughs		(m1) more mesic riparian woods *****	(m2) subhydric riparian woods *****	(n1) swampy open woods	(o) marshes and ponds?
Mostly woods	Mostly mixed	Mostly grassland	Asterisks indicate degree of agricultural conversion		

Figure 2 (for caption see previous page).

surveyed a hectare of woods adjacent to the Osborn Prairie in Oktibbeha County, Mississippi. These woods were dominated by post oak and red cedar (*Juniperus virginiana*), plus scattered loblolly pines ca. 30–60 years old. Other trees included oaks (*Quercus: marilandica, durandii, falcata, velutina, alba*), hickories (*Carya: ovata, myristiciformis, tomentosa*), white ash (*Fraxinus americana*) and winged elm (*Ulmus alata*). Ground vegetation contained common shade tolerant species, and none typical of grassland.

(b) More open woods with local blackjack oak (b1) or shortleaf pine (b2), plus associated thickets and glades (NVC 4053, 3952—or 4670 on more calcareous soils). As emphasized by Rostlund (1957)—but perhaps overemphasized—before the 1830s, there are indications of open woods with grassy conditions at many localities in regions with acid soils adjacent to, or intermixed with, the Black Belt grasslands on chalk. Rostlund suggested that frequent fires were involved in maintaining these areas, and that the Black Belt itself was not much more open.

On plains west of the Black Belt in Mississippi, a regional increase in pine began about 2400 years ago, which is attributable to promotion of fires by people (Whitehead and Sheehan, 1985). Based on early surveys, fire-tolerant oaks and pines were generally more abundant in upland woods of north-central Mississippi during the 1830s than they are in woods today, but patterns varied much in space and time (Brewer, 2001; Peacock et al., 2008; Surette et al., 2008). The pyrophile, blackjack oak (*Quercus marilandica*—probably including much “black oak”), was locally dominant then, but it has now greatly declined. Pines—shortleaf (*Pinus echinata*) or loblolly (*P. taeda*)—were locally more frequent than blackjack oak, especially on lower slopes with more sandy soils, where fire regimes may have been somewhat less intense or less frequent. Today, shortleaf pine remains one of the most common trees in mature woods on drier sites of north-central Mississippi, but white oak (*Q. alba*) predominates on more mesic uplands, often with much southern red oak (*Q. falcata*) and hickories. Also, the highly fire-

sensitive sweetgum (*Liquidambar*) has generally increased, spreading from lowlands onto uplands.

For areas within the Black Belt, there are few historical clues to patterns in the degree of openness, but blackjack oak appears to have been locally abundant, at least in Mississippi. A relevant note on the Tupelo area comes from Nutt (1805; p. 43 in Jennings, 1947): “The country around Big Town for many miles affords good farming land. Many prairies, no running water near the town... [But] The country between Big Town & ... 20 mile creek [main branch of Tombigbee to the east]... is poor broken blackjack land. No running water. On the creek is fine cane, the bottom subject to overflow in spring season... the branches of this creek interlock with the head of Tal,la,hat,chee [of Yazoo River to the west, and] is high broken land very little fit for cultivation.” From Pontotoc to Chickasaw County, Hilgard (1860, p. 91 and 100) noted “ridges characterized by an excessively heavy soil, bearing the Black Jack Oak, and popularly termed “beeswax hommocks”...[on] gray calcareous clay which frequently overlies the limestone and calcareous sand” [perhaps matching the hapludert, Houston, in Fig. 1].

Pines were virtually absent within the Black Belt of Mississippi before modern planting programs, which concentrated on loblolly pine. Shortleaf pine was locally frequent only on the more acid soils in adjacent western regions, including the Pontotoc Ridge and Post-oak Flatwoods (Harper, 1913a; Brewer, 2001; Peacock et al., 2008; Surette et al., 2008). But in Alabama, pines—mostly shortleaf—formed ca. 5–9% of witness trees across the whole Black Belt in 1830–50 (Jones and Patton, 1966; Rankin and Davis, 1971). Especially in the relatively hilly sections of eastern Alabama, there is more intermixing of geological and topographic features, and marly soils predominate rather than pure chalk. This mix was reflected in a more intimate combination of shortleaf pine or other pines with hardwoods typical of the Black Belt (Mohr, 1901; Harper, 1913b). Some notable remnants of grassland in Alabama are today surrounded by pine-oak woods (Schuster and McDaniel, 1973; Schotz and Barbour, 2009).

(c) Upland prairies on somewhat acid soils: (c1) xeric-tending or (c2) locally xerohydric (suggesting NVC 2242, 2405 and 5057). Chalk prairies can grade into less calcareous grassland on adjacent uplands. Extensive prairies on relatively acid soils were not well documented in early botanical literature. But, traveling south across Pontotoc County into the Black Belt of Mississippi, Hilgard (1860, p. 79-81) noted: "...on the Connewar, Chiwapa and Tallabinella [Creeks], the regular prairies set in, with their 6 to 10 foot stratum of yellow clay overlying the Rotten Limestone"; see also the quotation from Hawkins under (a) above. Hilgard noted that these "larger bodies of prairie" extended east from the "Orange Sand" at base of the Ripley Formation to cover the broad "dividing plateau" of major streams within the Black Belt, including the "Mayhew Prairie" below Palo Alto. Nearby, there were "greatly inferior" soils on residual uplands, presumably including more sandy ultisols (as in upper rows of Fig. 1). His note of the "12 to 18 inches" of "black prairie soil" above (2) 5-7 (10) feet of "pale yellow clay containing small round ferruginous concretions" suggests dystruderts like the series Oktibbeha and Vaiden (Fig. 1). This general upland prairie was distinct from the "small prairies" or "bald prairie spots" on lower stratigraphy with chalk closer to the surface, especially "on the [eastern] outskirts, in these wooded portions, and on the streams, not in the prairie proper."

More open oak woods and edges on transitional uplands do contain diverse sun-loving species that could have been promoted by fires before De Soto, as well as by xeric or xerohydric conditions at some sites. In Mississippi, Lowe (1921) listed the following sun-loving plants as characteristic of more acid uplands around the Black Belt [converted here to modern names]: *Apocynum cannabinum*, *Ceanothus americanus*, *Gamochaeta purpurea*, *Krigia virginica*, *Oenothera* sp., *Orebexilum* sp., *Opuntia* sp., *Penstemon laevigatus*, *Phlox pilosa*, *Plantago aristata*, *Schrankia microphylla*, *Stylosanthes biflora*, *Tephrosia virginiana*, *Triodanis perfoliata*, and *Verbena* sp. S. Brewer (pers. comm.) is currently investigating the extent to which suppressed populations of sun-loving plants, in general, can be increased with fire in seasonally dry woodlands of north-

central Mississippi. He has found strong responses by several legumes (Fabaceae), *Dichanthelium* spp. (Poaceae), and, especially in thinned woods, *Helianthus* spp. and allies (in Asteraceae). Less common potential increasers with fire in this region include *Aletris aurea*, *Aureolaria pectinata*, *Eryngium yuccifolium*, *Eurybia hemispherica*, *Gentiana villosa*, *Gratiola pilosa*, *Helianthus silphoides*, *Liatris squarrulosa*, *Matelea carolinensis*, *Phlox pilosa*, *Piptochaetium avenaceum*, *Polygala cruciata*, *Pogonia ophioglossoides*, *Sabatia campanulata*, *Silphium integrifolium*, *Trifolium reflexum* and *Xyris jupicai* (Denley et al., 2002).

In Alabama, thin woods on uplands may have often graded into prairies, which sometimes occurred in small patches or on transitional soils from sandy to calcareous. Gosse (1859, p. 82) reported contemporary usage of the term "forest prairie" for the vegetation he found on a "little knoll" within denser woods. Mohr (1901) described much of the general upland vegetation south of the Black Belt as "post oak prairies"—a term also used around the Jackson Prairies by Hilgard (1860) and others (Moran et al., 1997). Open post oak woods are known today across southeastern states, often with seasonal extremes of wetness and dryness that promote extensive graminoid ground vegetation and some shrubby openings (as in NVC 5057 and 2405). Mohr also noted that "sand hills near Montgomery" had openings with several distinctive xerophile or annual grasses (*Aristida*, *Eragrostis*, *Panicum*) and herbs, including *Brickellia eupatorioides*, *Croptilon divaricatum*, *Mirabilis* sp. ("hirsuta"), *Symphyotricum* spp. ("patens" and "undulates"), and *Tragia urticifolia* (see NVC 2242). There were some frequent acidophiles in Harper's (1920) prairie, e.g. *Polygala grandiflora*, and in Schuster and McDaniel's (1973) three-acre glade within pine-oak woods, e.g. *Hypoxis hirsuta* and *Schoenolirion croceum*. In some of the grasslands surveyed by Schotz and Barbour (2009), such as the Cahaba River Prairies, several of the reported common plants are more typical of acid or sandy soils, rather than purely calcareous, e.g., *Agalinis tenuifolia*, *Aristida virgata*, *Desmodium marilandicum*, *Liatris squarrulosa*, *Physalis carpenteri* and *Sporobolus junceus*.

Uplands with Calcareous Soils. In the National Vegetation Classification (NatureServe, 2010), calcareous grassland and associated vegetation on the southeastern Coastal Plain is treated in a few broadly defined alliances that reflect the general gradient in vegetation from xeric, open conditions to more mesic, shady conditions. However, at moderate scales of ca. 1–10 acres [0.4–4 ha], there is usually much intermixing of such vegetation types, as outlined below (d to g), and these types are often partly or completely combined in published descriptions.

(d) Upland prairie on xeric-tending (d1) or locally xerohydric (d2) sites. At dry open extremes on shallow, eroding or disturbed soils, there is mid-sized to short grassland, locally dominated by annuals and usually mixed with patches of bare ground that has relatively little organic matter (Schauwecker, 1996). In poorly drained swales, there can be extremes of both wetness and dryness, with particularly unstable and relatively bare soil surfaces. This type of grassland occurs locally in much of the Black Belt on or near outcrops of chalk (Harper, 1920; Schuster and McDaniel, 1973; Morris et al., 1993; Leidolf and McDaniel, 1998), and similar vegetation has been described in other blacklands (e.g., Echols and Zomlefer, 2010). NatureServe (2010) has defined a variant of such vegetation from the Cook Mountain Prairie of Louisiana (NVC 4021) that could be extended and applied to much of the Black Belt: *Schizachyrium scoparium*-*Panicum flexile*-*Carex microdonta*. But at the Pulliam Prairie (our personal observations) and at some other sites in the northern Black Belt (C. Bryson, pers. comm.), *Carex crawei* largely replaces *C. microdonta*.

Other characteristic graminoids in such vegetation include *Aristida* spp. (*longespica*, *oligantha*, *purpurascens*), *Bouteloua curtipendula*, *Fimbristylis puberula* and *Sporobolus* spp.—*vaginiflorus* (on bare ground), *clandestinus* (in less xeric transitions) or *compositus* (locally on deeper soils). Typical herbs include *Asclepias viridiflora*, *Coreopsis lanceolata*, *Croton monanthogynus*, *Dalea candida*, *Erigeron strigosus*, *Euphorbia corollata*, *Heliotropium tenellum*, *Heterotheca camporum*,

Houstonia nigricans, *Hypericum sphaerocarpon*, *Liatris squarrosa*, *Linum sulcatum*, *Lithospermum canescens*, *Lobelia spicata*, *Mirabilis albida*, *Pentstemon tenuiflorus*, *Solidago nemoralis*, *Symphotrichum patens*, *Silphium laciniatum* and *Verbena simplex*. The number of vascular species in small plots tends to be relatively low: ca. 5–15 per 0.25 m² (Weiher et al., 2004). However, composition varies greatly across larger plots, in relation to local topography, erosional patterns, and broad intergradation with the taller grassland outlined below (types e, f and g).

(e) More disturbed prairie on stressed or eroded sites, often transitional from (d) to (f). Mixing of characteristic species from more xeric sites (type d) and less xeric sites (type f) has probably been enhanced where soils are disturbed by grazing, mowing or plowing. Many remnants today are in various stages of recovery from farming, especially on deeper soils of lower ground that receives or holds more moisture. Several authors have noted that disturbance has led to local abundance of more weedy native species plus more frequent aliens (Mohr, 1901; Harper, 1913; Harper, 1920; Leidolf and McDaniel, 1998; Echols and Zomlefer, 2010; NatureServe, 2010).

Commonly reported grasses based on these sources are *Andropogon* spp.—*virginicus* on drier sites (most/all as var. *decipiens*), or “*glomeratus*” on damper sites (most/all as var. *pumilus* = *A. tenuispatheus*). *A. glomeratus* was used by NatureServe in earlier names for some regional variants. Other locally common native grasses that are relatively tolerant of disturbance include *Panicum anceps*, *Muhlenbergia capillaris*, *Paspalum floridanum* and *Setaria parviflora*. Characteristic herbs include relatively weedy natives, such as *Ambrosia* spp., *Cuphea viscosissima*, *Erigeron* spp., *Prunella vulgaris* var. *lanceolata*, *Sabatia angularis*, and *Symphotrichum pilosum*. Aliens are locally common, including the rather short but rapidly spreading grasses, *Bromus japonicus*, *Digitaria ischaemum*, *Paspalum dilatatum* (formerly planted for forage) and *Sporobolus indicus*, as well as taller species that often extend into less frequently stressed or disturbed sites (see f).

(f) Upland prairie on average sites, generally subxeric. This mid-sized to tall grassland appears to have been the most widespread type in blackland prairies of southeastern states. NatureServe (2010) and others have described regional variants from the Black Belt of Tennessee, Mississippi and Alabama (NVC 4664; see also Schotz and Barbour, 2009), the Grand Prairie of Arkansas (NVC 7769), the Jackson Prairie of Mississippi and Alabama (NVC 4020), the Jackson Prairie west of Louisiana (NVC 4721), and the prairies on lower Eocene clays in Alabama (Harper, 1920) and Georgia (NVC 4247; see also Echols and Zomlefer, 2010). Among the most widespread and locally abundant species are *Schizachyrium scoparium* (except in Georgia), *Sorghastrum nutans*, *Panicum virgatum* and *Ratibida pinnata*. Species that are less generally abundant but still typical of better remnants within the Black Belt, include *Dalea* spp. (*candida*, *purpurea*), *Liatris* spp. (*aspera*, *spicata*, *squarrosa*), and *Silphium* spp. (*integrifolium*, *laciniatum*, *terebinthaceum*).

Historical sources support this general description of the prevailing grassland on uplands (Bartram, 1791; Mohr, 1901; Harper, 1913a; Lowe, 1921). From Harper's transects of the region, he noted: "The comparatively large numbers of herbs, and the occurrence of a few genuine prairie species, such as *Ambrosia bidentata*, *Silphium laciniatum*, *S. terebinthaceum*, *Mesadenia tuberosa* [= *Cacalia* or *Arnoglossum plantagineum*], and *Polytaenia nuttallii* (the last three seen only once, and therefore not listed), are reminders of the prairie conditions that once existed in this region." Some earlier narratives indicate, with colorful language, that wild strawberries (*Fragaria virginiana*) were also locally abundant in the general upland prairie (e.g., De Montigny, 1736, as quoted in Rostlund, 1957; Romans, 1775; Bartram, 1791). That species presumably proliferated after burning, grazing, cropping or other disturbance.

Other typical species can be inferred from Mohr (1901), Lowe (1921), DeSelm and Murdoch (1993), Schauwecker (1996), Leidolf and McDaniel (1998), Schotz and Barbour (2009), and NatureServe (2010), though taxonomy remains uncertain in some cases. Reported species include *Agalinis* spp. (*auriculata*, *oligophylla*, *purpurea*), *Asclepias*

spp. (*tuberosa*, *viridis*, *verticillata*), *Blephilia ciliata*, *Buchnera americana*, *Coreopsis* spp. (*lanceolata*, *grandiflora*), *Desmanthus illinoensis*, *Desmodium* spp. (especially *ciliare*), *Dracopsis amplexicaulis*, *Eupatorium* spp. (*altissimum*, *serotinum*), *Helianthus* spp. (especially *hirsutus*), *Lythrum alatum* (perhaps all as var. *lanceolatum*), *Neptunia lutea*, *Oenothera* spp. (*biennis*, *speciosa*, *triloba*), *Rudbeckia* spp. (*hirta*, *laciniata*, *triloba*), *Sabatia angularis*, *Sisyrinchium albidum*, *Solidago* spp. (especially *nemoralis*), *Spiranthes magnicamporum*, *Sporobolus compositus* (perhaps all as var. *drummondii*), *Symphotrichum* spp. (*dumosum*, *ericoides*, *patens*), and *Verbena* spp. (*angustifolia*, *canadensis*, *?hastata*). The number of species in small plots tends to be relatively high: ca. 10–20 in 0.25 m² (Weiher et al., 2004).

Although there are many small remnants of the original grassland covering ca. 1–10 acre [0.4–4 ha], larger remnants are rare. NatureServe (2010, with reference to NVC 4664) stated: "Nearly all of this association has been destroyed for agricultural uses, or altered by grazing and fire suppression. No high-quality examples are known." The aliens, Bermuda grass (*Cynodon dactylon*), Johnson grass (*Sorghum halepense*), and sweet clovers (especially *Melilotus alba*), became widely abundant in the region ca. 1850–90, after being introduced for pasture and hay (Gosse, 1859; Mohr, 1901; Harper, 1913a). The highly persistent sericea lespedeza (*L. cuneata*) has been widely sown to build soils on dry or eroded during 1950–1990. Also, fescue (*Festuca arundinacea*) has been widely sown for forage in converted grasslands after 1950, though it does not generally invade more intact remnants of drier native grassland. In recent decades, cogon grass (*Imperata cylindrica*) has become another serious alien threat to this grassland and other types, especially in seasonally damp swales.

(g) More mesic (g1) or hydric (g2) prairie. These variants can include more tall grasses, especially (in g1) big bluestem (*Andropogon gerardii*) and locally (in g2) gamagrass (*Tripsacum dactyloides*). Also, there are more tall herbs—notably *Symphotrichum novae-angliae*—and more marginal wetland species—notably *Lythrum alatum* on "seepy inclusions" (within NVC 4664 of NatureServe,

2010). Although *A. gerardii* is now rare to absent in most remnants, it was probably much more common in the original vegetation before agricultural conversions, especially where there was frequent burning that reduced woody thickets on lower slopes (Mohr, 1901; Leidolf and McDaniel, 1998; Hill and Seltzer, 2007; Echols and Zomlefer, 2010). Even without woody encroachment, Johnson grass (*Sorghum halapense*) and other aggressive aliens can preempt habitat for taller native grassland. In more shady transitions to riparian thickets and woods, there are several characteristic cool-season grasses. Mohr (1901) listed *Elymus* [*glabriflorus*, *virginicus*], *Bromus* [*pubescens*] and *Chasmanthium* [*latifolium*, *sessilifolium*] for “sheltered borders” [using suggested modern names instead of his usage]. Sedges and allies (Cyperaceae) are also locally abundant on wetter sites.

Good examples of such vegetation appear to be rare, and almost no sites have been described in detail. In Mississippi, Hill and Seltzer (2007) recently added *Andropogon gerardii* and *Tripsacum dactyloides* to the list for a relatively well known site—the Osborn Prairie of Oktibbeha County. In Alabama, Schotz and Barbour (2009) listed *A. gerardii* as a common species at only one of their ten best sites for Black Belt prairie in the state—Pleasant Ridge in Greene County—and they did not list *Tripsacum* at any site. Species that were originally associated with *A. gerardii* are difficult to discern from the literature, and remnants of their populations may often be suppressed in non-flowering condition by encroaching woods. Based on general knowledge, these species probably included some that are now inconsistently documented or rare in the region, e.g., *Agalinis auriculata*, *Desmodium ochroleucum*, *Echinacea purpurea*, *Prenanthes aspera*, *Silphium integrifolium* (or perhaps *S. glabrum* in more brushy transitions), *Solidago rigida* (especially var. *rigida*), and *Veronicastrum virginicum*.

(h) Upland thickets, often in drier (h1) or damper (h2) transitions to woods. Shrubby transitions to upland or riparian woods often have distinctive species that are not typical of open grassland or deeper woods. More thorny variants were probably associated with larger herbivores before

human interferences (Kaye, 1974). Distinctive examples of such vegetation are still widely scattered but generally restricted to small patches, narrow strips, or truncated woodland edges. There is only one variant that has been fully described by NatureServe (2010) from the blacklands of southeastern states, i.e., in the Cook Mountain Prairie of Louisiana (NVC 3879): *Crataegus spathulata* – *Cornus drummondii* – *Berchemia scandens*. But similar vegetation is documented for the Black Belt of Mississippi and Alabama (Leidolf and McDaniel, 1998; Schotz and Barbour, 2009; NatureServe, 2010, as part of NVC 4664). Thickets in the blacklands of central Georgia can be included for a broader definition, with *Cornus asperifolia* Michx. instead of *C. drummondii*, and with *Celtis tenuifolia* Nutt. instead of *C. laevigata* (Echols and Zomlefer, 2010).

There are several historical indications of shrubby bands along edges of upland oak woods and in riparian zones, plus “isolated boskets” or “scattered clumps” mixed with the prairies, fields or villages. Sources range from diaries of the De Soto expedition in 1540 (Rostlund, 1957; Clayton et al., 1993) to Nairne (1708), Bartram (1791), Jones (1833), Gosse (1859), Hilgard (1860), Mohr (1901), Harper (1913a,b) and Lowe (1921). Nairne (p. 57) noted: “on the Top of these knolls live the Chicasaws, their houses... with their... plum trees about them.” In the abandoned Chickasaw Old Fields, Jones noted “small... cottonwoods, persimmon, bushes, wild plum, briers, and grass.” In Dallas County, Alabama, Gosse did not list cedar anywhere, but reported from the prairies that “Several species of Thorn (*Crataegus*) grow in impenetrable thickets or in single bushes over their surface, and one or two kinds of wild plum, bearing a harsh sour sloe or bullace, are often mixed with them” (p. 75). Notes of “crabapple thickets,” “haws” and “plum” also come from early descriptions of the Jackson Prairie (Moran et al., 1997).

In general, these thickets originally had much Rosaceae, including frequent plums (*Prunus angustifolia*, *P. umbellata*), hawthorns (especially *Crataegus engelmannii*; see also Mohr, 1901), or crabapples (probably *Malus angustifolia*). Other locally common thicket-forming species are indicated by pre-1950 accounts (especially *) or by

more recent general observations (especially #): *Berchemia scandens*#, *Celtis laevigata**, *Cercis canadensis*#, *Cornus (drummondii*#, *florida**)#, *Diospyros virginiana**, *Frangula caroliniana*#, *Gleditsia triacanthos**, *Ilex decidua**, *Juniperus virginiana*#, *Maclura pomifera*#, *Ptelea trifoliata*, *Rhus* spp. (*aromatica*, *copallina*, *glabra*)#, *Sideroxylon (lanuginosum*, *lycioides*)#, *Ulmus alata*# and *Vitis* spp. (including *rotundifolia** on more acid soils). Some species of such vegetation are now rare, at least within the region, notably *Crataegus ashei*, *C. triflora* and *Rhamnus lanceolata* (Schotz and Barbour, 2009).

(i) Red cedar woods. Red cedar (*Juniperus virginiana*) appears to have been uncommon or rare in the Black Belt of Mississippi before De Soto (Peacock and Miller, 1990). In 1832, it made up only ca. 0.3% of the recorded trees across the Black Belt of Sumter County, Alabama (Jones and Patton, 1966). Mohr (1901) noted “cedar hammocks” in Alabama “on the highest swells of the plain where the strata of the rotten limestone are overlaid by lighter loams.” In the Black Belt of Mississippi, Lowe (1913, 1920) reported red cedar only from ledges where limestone comes to the surface or as scattered clumps in low or wet areas. Harper (1913a) noted red cedar only once in Mississippi, though he stated: “It is rather common in the black belt of Alabama.”

Red cedar has now become locally dominant in woods and thickets on calcareous soils at various elevations. Older stands tend to occur on drier bluffs and ridges adjacent to chalk outcrops, sometimes grading into soils of the Ripley Formation at higher levels (e.g., Morris et al., 1993; Leidolf and McDaniel, 1998; Hill et al., 2009). In addition to directly colonizing old fields, red cedar can invade thickets of the species noted in the previous section (h), along with sugarberry (*Celtis laevigata*), ashes (*F. americana*), scattered oaks (especially *Q. muhlenbergii*), and other trees. NatureServe (2010) has outlined a generalized type for the Black Belt (NVC 7747): *Juniperus virginiana* – (*Celtis laevigata*, *Prunus angustifolia*, *Sideroxylon lycioides*). Similar woods have been widely documented in other blacklands, from Louisiana (Bekele et al., 2006; together with species of

Crataegus, *Diospyros* and *Berchemia*) to Georgia (Echols and Zomlefer, 2010; where *Celtis tenuifolia* often occurs instead of *C. laevigata*). Schauwecker (1996, 2001; see also Weiher et al., 2004) has shown that succession to red cedar causes ground cover to decline abruptly in biomass and richness, usually leading to a few relatively common shade-tolerant species. However, more sun-loving species can prosper locally in thinner woods, including the vine, *Berchemia scandens*, the sedge, *Carex cherokeensis*, and the alien legume, *Lespedeza cuneata*, which often persists from plantings in old fields.

The research of Schauwecker (2001), Weiher et al (2004) and Bekele et al. (2006) has indicated that, as well as the increase in shade during succession from grassland to cedar to hardwoods, there is increased organic matter in the soil, increased moisture-holding capacity, decreased pH (from ca. 7.5–8.25 to ca. 6.5–7.5), and shifts in the balance of available minerals (especially from Ca to Fe). Also, Hill and Brown (2010) have documented a distinctive group of ant species associated with red cedar in the Black Belt.

(j) Submesic mixed hardwoods. These varied woods occur on relatively moist but well-drained soils, usually in areas protected from disturbance on steeper bluffs or sheltered hillsides, or along streambanks where they grade into the riparian woods of broader floodplains, as outlined below (type m). Such vegetation is widespread in small patches and riparian strips, especially in peripheral parts of the region, but there have only been a few miscellaneous published notes on composition.

At the western side of the Black Belt in Mississippi, Ward (1987) used the 1834 survey to indicate red elm, hickory, ash, walnut and sassafras in groves of trees on lower slopes, along with post oak and blackjack on drier ground. In a nearby locality, Hilgard (1860, p. 84) noted the following trees on hillsides with Paleocene limestone [using modern names]: *Quercus velutina*, *Q. falcata*, *Carya* sp., *Liriodendron*, *Juglans nigra*, *J. cinerea*, *Tilia* sp., *Magnolia* cf. *pyramidata*, and *Robinia pseudoacacia*; lower in the valley, he noted *Platanus*, *Gleditsia*, *Prunus* and *Cercis*. At the southern side of the Black Belt in central Alabama, Bartram

(1791) noted: “Immediately after leaving the plains we enter the grand high forests. There were stately trees of the *Robinea pseudacacia* [sic], *Telea* [*Tilia*], *Morus*, *Ulmus*, *Juglans exaltata* [?*Carya ovata*], *Juglans nigra*, *Pyrus coronaria*, *Cornus Florida*, *Cercis*, &c.” In Alabama, some of the “cedar hammocks” described by Mohr (1901) were at least transitional to shrubs (*Asimina*, *Ilex*, *Forstiera*, *Zanthoxylum*) and hardwoods: *Fraxinus americana*, *Quercus* spp. (“*laurifolia... texana*”), *Celtis laevigata*, *Ulmus americana* and *Acer floridanum* (Chapm.) Pax [= *A. barbatum* auct.].

More modern descriptions of hardwoods on calcareous soils in or near the Black Belt remain scattered, but somewhat consistent. At the southern side, Harper (1920) listed the commonest trees in “a small wooded valley” adjacent to his prairie: *Quercus* spp. (*muhlenbergii*, [*shumardii* var.] *schneckii*, *stellata*), *Fraxinus americana*, *Ulmus alata*, *Juniperus*, *Juglans*, *Liquidambar*, *Tilia* and *Liriodendron*. At the western side, Morris et al. (1993) listed typical trees of a NE-facing mesic bluff: *Quercus* spp. (*muhlenbergii*, *shumardii*), *Carya* spp. (*carolinae-septentrionalis*, *myristicaeformis*), *Fraxinus* spp. (*americana*, *pennsylvanica*), and *Ulmus* spp. (*americana*, *alata*), plus lesser numbers of some mesic, shade tolerant species, *Acer floridanum*, *Aesculus glabra* Willd., and *Tilia americana* (sensu lato). In Alabama, Schotz and Barbour (2009) noted similar woods on slopes below prairies at several sites, with *Quercus* spp. (*alba*, *muhlenbergii*, *shumardii*), *Carya* spp. (*glabra*, *carolinae-septentrionalis*, *myristiciformis*), *Fraxinus* spp. (*americana*, *pennsylvanica*), *Celtis laevigata*, *Ulmus* spp. (*alata*, *rubra*) and *Pinus taeda*. In the blacklands of central Georgia, the woods are somewhat similar, but more varied from damp to dry soils, i.e., with much more *Q. nigra* in general, locally *Q. pagoda* on terraces, and much transition to *Q. velutina* or *Pinus taeda* on more sandy uplands (Echols and Zomlefer 2010).

There are several, varied types in the National Vegetation Classification that might be partly applied here (NatureServe, 2010), but only a few well-described types have been directly linked with blacklands. These include: (1) *Quercus stellata* – *Q. muhlenbergii* / *Schizachyrium scoparium* – *Sorghastrum nutans* (NVC 4670), which is a

transition to open post oak woodland in the Black Belt; (2) *Quercus durandii* – *Fraxinus americana* – *Q. muhlenbergii* / *Rhus aromatica* – *Cornus drummondii* (NVC 7256), which is a transition to dry thicket described for the Jackson Prairie of Louisiana; and (3) *Quercus muhlenbergii* / *Q. durandii* – *Cercis canadensis* / *Viburnum rufidulum* / *Scleria oligantha*, which is mixed with *Q. velutina* in the blacklands of central Georgia, and grades into *Crataegus*–*Cercis* thickets (Echols and Zomlefer, 2010). More mesic woods with less oak, as noted by Morris et al. (1993), could be included within the broadly defined Upper East Gulf Coastal Plain type: *Acer floridanum* – *Aesculus glabra* – *Carya myristicaeformis* – *Quercus shumardii* – *Q. muhlenbergii* (NVC 4671; see also NVC 7971 of Arkansas).

Lowlands with Alluvial Soils. Distinction of lowlands from uplands is arbitrary in many areas, especially where topographic relief is slight. Calcareous uplands and toe-slopes contain local colluvium and alluvium along swales and gullies that often lead gradually into the more extensive—and locally exogenous—alluvium on terraces along broader valleys. Agriculture tends to be most intense on well-drained soils in these transitions.

(k) Lowland prairie or open woodland. Several historical accounts indicate that extensive grasslands (“prairies” or “savannahs”) occurred locally on relatively well-drained toe-slopes and bottomlands that were occupied and cultivated by native tribes, especially the Chickasaw: Nairne (1708), Atkin (1755, p. 67), Adair (1775, p. 352), Romans (1775, p. 124), Baily (1797, p. 30), Nutt (1805, p. 43), and other sources cited by Barone (2005) and Cook (2010). Atkin’s account of the Chickasaw, with only “350 adult men” remaining, provides special insight: “These Indians live in seven Towns, having each a Palisade Fort with a Ditch, in an open rich Champain Plaine about ten Miles in Circumference, accessible only on one side, being almost surrounded by Swamps in a circular manner, about a mile from any running Creek...” Similar notes came from lowlands along the Alabama River and its tributaries (D. Taitt, 1772, in Rostlund 1957; Bartram, 1791; Hawkins, 1798-99).

It is likely that gamagrass (*Tripsacum dactyloides*) was dominant in some of these areas, along with big bluestem (*Andropogon gerardii*) and other tall grasses, especially on vertisols that start wet in the spring but often dry out and crack during the summer and fall (Myers, 1948). Harper (1913a) found that gamagrass was the most common native grass in the Black Belt region of Mississippi, and it was also frequent on lowlands within adjacent regions to the west, on sandier soils of the Pontotoc Ridge and on stiff clays of the Post-oak Flatwoods.

In early settlement, livestock no doubt concentrated on such land and greatly reduced the palatable taller grasses. On farmed lowlands of the northern Black Belt, Romans (1775) stated: “the earth is very nitrous... this produced a grass of which cattle are so fond as to leave the richest cane brakes for it; and notwithstanding the soil appears barren and burnt up, they thrive to admiration.” In the Jackson Prairie region, A.J. Brown (1894, cited by Moran et al., 1997) contrasted the following two types of grassland: (1) the true “prairie grass” of former “woodland prairie” with post oak, then much converted to cotton on deeper lowland soils [Hilgard’s “black prairies”]; and (2) the “upland grass” of drier “shell prairies” that were much less productive for agriculture and becoming scrubby [Hilgard’s “bald prairies”]. Regarding (1), he stated: “... of which the cattle were very fond and which was a great milk and fat producer. Most of these grasses have become extinct, or so dwarfed by constant grazing and trampling by stock, as not to be observed as an original grass.”

Such vegetation has now become almost all converted to fields for corn, cotton and soybeans, except for the frequent strips of land with gamagrass along rights-of-way and ditches. NatureServe (2010) has outlined a *Panicum virgatum* – *Tripsacum dactyloides* type for the Grand Prairie of Arkansas (NVC 4624), but has not yet listed a *Tripsacum* type for the Black Belt in Mississippi or Alabama. Nevertheless, gamagrass is now widely promoted for native forage and general restoration by the Mississippi Extension Service.

(l) Lowland canebrakes and other thickets. Originally, there were extensive canebrakes dominated by *Arundinaria gigantea* on some lowlands,

with the tallest cane on levees close to larger streams and rivers (Hawkins, 1798-99; Nutt, 1805; W. Roberts in Darby, 1818; 1834 survey summarized in Ward, 1987; Lyell, 1849; Mohr, 1901; other sources of Rostlund, 1957). Mohr even noted: “So conspicuous was this formation in the western part of the plain that it is called emphatically the canebrake region” (see also Cleland, 1920). This vegetation was presumably most widespread on sites that were frequently flooded for short periods, but burned less often than the lowland prairies (type k) or associated fields. Cane was “a delightful range for stock” (Hawkins) and its soil was highly suitable for farming after clearance. It declined rapidly to become a minor species in the settled landscape, here (Harper, 1913a) and elsewhere in its range (Platt and Brantley, 1997).

From these early accounts, it appears that several small or shrubby trees were also locally abundant in thickety transitions between grassland—and cultivated fields—and woodland of various types: including edible grapevines (*Vitis* spp.), plums (*Prunus* spp.), pawpaws (*Asimina triloba*), persimmons (*Diospyros virginiana*) and mulberries (*Morus rubra*). NatureServe (2010) has outlined a generic canebrake type (NVC 3836), plus some bottomland forest types with cane that can be applied or modified for the Black Belt region (especially NVC 8429 and 2099).

(m) Riparian woods. From historical to modern sources, mixed hardwood forests of diverse types have often been noted along banks and terraces of streams and rivers within the Black Belt and other nearby blacklands (D. Taitt, 1772, quoted by Rostlund, 1957; Bartram, 1791; Hawkins, 1798-99; 1834 survey summarized by Ward, 1987; Hilgard, 1860; Mohr, 1901; Harper, 1943; Lowe, 1921; Whitehead and Sheehan, 1985; Morris et al., 1993; Echols and Zomlefer, 2010; NVC 2427, 2431, 7335, 7340, 7353, 7915). Frequent trees have included *Acer* spp., *Aesculus* spp., *Betula nigra*, *Carya* spp., *Celtis laevigata*, *Fraxinus* spp., *Gleditsia triacanthos*, *Juglans nigra*, *Liquidambar styraciflua*, *Morus rubra*, *Nyssa* spp., *Platanus occidentalis*, *Populus* spp., *Prunus serotina*, *Quercus* spp., *Salix nigra*, *Tilia* spp. and *Ulmus* spp. Several shrubs and vines are also common, and there is local

intergradation with canebrakes (type l).

Such woods varied much in width, structure and composition depending on the size of streams, hydrology, soil conditions and management. Groves of nut trees and persimmons on low slopes or terraces were noted by some early observers, and may well have been selected by the inhabitants, based on diaries from De Soto's 1539-43 expedition (Clayton et al., 1993), Bartram (1791), and others cited by Rostlund (1957). Along the larger rivers of central Alabama, where alluvium is often sandier, Mohr (1901) added listed *Fagus*, *Liriodendron* and *Magnolia*, and other early observers noted "poplar" [probably *L. tulipifera*], "laurel" [probably *M. grandiflora*], "cypress", "bay" and "white cork" (Rostlund, 1957).

(n) Wooded swamps, sloughs and ponds. Such vegetation is widely scattered across the region, but there are few extensive remnants in a relatively natural condition (Mohr, 1901; Harper, 1913b; Whitehead and Sheehan, 1985; Leidolf and McDaniel, 1998). Before agricultural conversions and excessive hunting, beavers—and even people in some areas—probably formed extensive dams on lowlands of the Black Belt (Ward, 1987; Cook, 2010). Nairne (1708, p. 47, 50) noted "multitudes of Beavor dams" among the Chickasaw villages. Black willow may have been a typical tree around more open wetlands within the grassland (e.g., Roman, 1775, p. 15-16).

Some larger sloughs have overcup oak (*Quercus lyrata*—see NVC 2424) or water tupelo (*Nyssa aquatica*—see NVC 2419). However, bald cypress (*Taxodium distichum*) is largely absent, except locally along larger streams and rivers. Paleoecological studies of an oxbow along the Tombigbee River detected bald cypress only after 1800, and "suggest that the modern vegetation of *Nyssa-Taxodium* developed very recently... Increased discharge due to European land clearance may have increased both water level and the length of time that standing water was present in the oxbow sufficiently to permit growth of both cypress and *Orontium*" (Whitehead and Sheehan, 1985).

(o) More open ponds and marshes. These must have existed locally before European settlement,

for example around beaver ponds. They do exist in varied contexts today, but generally in rather small patches that tend to escape attention, description and conservation. For example, the valley of Sakatonchee Creek in Chickasaw County, Mississippi, is locally dominated by marshy vegetation. On more open lowlands managed by native people before 1540, such vegetation may have graded into the wetter grassland indicated above (types k & g).

DISCUSSION

Based on the preceding notes, Fig. 2 presents a hypothetical scheme of associations between vegetation types and soil series. Gradients among vegetation types are overlaid on the catenas of soil series (Fig. 1). It is hypothesized that, during pre-Columbian times, each vegetation type was most extensive on or near its overlaid soil series. However, some modern descendants of original vegetation types cannot be reliably associated with particular soils today, especially on damper or lower ground with more drastic changes in disturbance regime, agricultural development and fragmentation. These more uncertain associations are indicated with question marks.

This framework does provide a useful initial model, but deserves refinement. It will be important to cross-reference such schemes in more detail with descriptions and mappings of vegetation types in the National Vegetation Classification and State Heritage Programs. Moreover, robust classifications should be built on a more detailed analysis of raw data from across the region. Such classification should ultimately be rooted in models of major ecological gradients and dynamic processes, rather than just hierarchical concepts of formations, alliances, associations and the like.

The gradient outlined here from lowland to upland vegetation is readily related to mapped soil series. However, the independent gradient from closed forest to open grassland is clearly influenced by dynamic factors that can reduce consistent associations with soil, even among better remnants of the original vegetation. Such factors have probably changed much during recent centuries. Deeper woods have probably remained best developed on relatively mesic, well-drained sites or on

swampy soils. But red cedar has spread much into former prairies, whilst the original thickets and other transitions between woodland and grassland have probably declined a great deal. Native grassland appears to have originally occurred on a wide range of soils, but became greatly modified after European settlement. Better remnants are now mostly restricted to shallower chalky soils (left-center of Figs. 1 and 2). More disturbed variants of native grassland, grouped under type (e) above, may have been concentrated below actively eroding exposures of chalk before settlement, on local alluvial soils such as Griffith (Fig. 1), but now appear to be widespread on several soil series.

These concepts can be tested. Research on modern or historical vegetation of the region could record soil types in a systematic fashion at study sites. But it will be important for ecologists to add local precision in mapping soils, since existing maps of the USDA are unreliable at scales less than 10–100 acres [4–40 ha]. And, for more general application of soil classification, it will be useful to quantify parameters for better descriptions of ‘catenas’—these are traditional concepts in soil science, but they deserve revival and more regular application across the ecological literature of eastern North America. Intensive, coordinated analyses of spatial variation in both soil and vegetation could allow more definitive correlations between soil and vegetation. Residual variation or ‘noise’ in those relationships could then be separated statistically to examine potential involvement of changes in ‘disturbance regime’—broadly defined, from climatic disruptions to human land uses—and especially changes within recent centuries. In this way more dynamic models of interaction between soil and vegetation might be advanced.

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