

Monday, October 4, 2004
SESSION III, SECTION C

Comparative Ecology of Warm-Season (C₄) versus Cool-Season (C₃) Grass Species in Kentucky, with Special Reference to Bluegrass Woodlands

Julian Campbell¹

¹ The Nature Conservancy, 642 West Main Street, Lexington, KY 40508.
Corresponding author: Campbell, 859-259-9655, jcampbell@tnc.org.

Abstract

The distributions of C₄ and C₃ grasses are compared in Kentucky. There is a strong association of C₄ grasses with late summer growth in open, nonforested habitats of Kentucky, including sites maintained by fire. Some 86% of C₃ grasses typically flower between mid-April and late July, whereas 96% of C₄ grasses typically flower between late July and mid-October. Only open habitats that experience much seasonal drying have major concentrations of C₄ grasses: (a) xeric pine/cedar-oak woodlands and associated rocky glades; (b) xeric-tending oak woodlands and associated grasslands, especially on gentle uplands; (c) hydric-tending oak woodlands and associated grasslands, especially on high terraces. A minor concentration also occurs on “shrubby/graminoid streambanks” that experience flooding and other seasonal changes in water level sufficient to maintain a distinct zonation of vegetation between forested banks and the low water levels. Subhydric or hydric sites that experience less seasonal drying appear to have virtually no typical C₄ grasses, but there are a few locally dominant C₃ grasses within these habitats. The few C₄ grasses that occur in deeper shade are all perennials in the genus *Muhlenbergia*.

There is no significant overall trend in numbers of C₄ versus C₃ species along the gradient from acid soils with low fertility to base-rich soils with high fertility. However, locally dominant perennial grasses, especially the few taller species reaching 2 m or more, are mostly C₄ species on low to average soil fertility (e.g., *Andropogon gerardii*), and mostly species C₃ on higher soil fertility (e.g., *Arundinaria gigantea*). Since eutrophic soils support rapid plant growth in general, there is a strong tendency for forest to predominate over the landscape, with rapid recovery from disturbances. Because of this, there may have been relatively little opportunity for selection of grasses that can dominate on sunny, eutrophic soils, especially in phosphatic sections of the Bluegrass region. Moreover, woodlands on eutrophic soils can allow dense grassy ground vegetation with C₃ species to develop in the partial shade, especially in spring before trees are fully leafed out.

This hypothesis is developed further with reference to the literature on the balance of C₄ versus C₃ species. It is suggested that frequent spring fires might maintain openings with C₄ species but at the expense of some native features in Bluegrass Woodlands. In contrast, seasonally intense foraging of ungulates on the nutritious “herbage” is indicated by some historical accounts, and several characteristic native species are associated with moderate ungulate effects in the vegetation. Ungulates may have helped maintain the high proportion of C₃ species due to enhanced nutrient cycling and perhaps overgrazing of incipient C₄ grassland patches along intensely used corridors.

Introduction

Plants with the C₄ photosynthetic system use energy (via ATP) to increase CO₂ concentration for enzymatic fixation into carbohydrate (Sage 1999). This process involves shuttling CO₂ on 3- to 4-carbon acids from mesophyll to bundle sheath cells, where carbohydrate is produced, stored, and exported from the leaf. It appears to have evolved independently within several lineages of grasses and other plants during the Tertiary era, after about 30 million years ago, probably in response to lower atmospheric CO₂ levels and higher O₂ levels—the latter causing wasteful photorespiration of carbon initially fixed in phosphoglyceric acid. In warm sunny habitats, such plants are able to maintain higher rates of photosynthesis and growth than those with the ancestral C₃ system, which are limited by low CO₂ levels and photorespiration. Another physiological advantage in certain situations can be higher water-use efficiency, since stomata can remain closed on warm days with CO₂ levels accumulated and photosynthesis continuing. Also, higher nitrogen-use efficiency has been estimated, along with lower N concentrations in foliar tissue, which may be allowed by higher rates of CO₂ fixation per unit of photosynthetic enzyme. Moreover, some C₄ species are able to allocate more energy to roots and increase N uptake from infertile soils (Long 1999).

The ecological distribution and apparent adaptation of C₄ species has been widely studied and discussed, but there continue to be uncertainties in the relative importance of various factors that control the balance of C₄ and C₃ species in vegetation (Sage and Munson 1999). The strong association of C₄ species with grasslands and savannas in warmer climates, and their virtual absence in colder climates, is extensively documented. Within temperate climates, there is a more equal balance overall but much variation in time and place. Such variation may have significant consequences for ecosystems, including patterns of herbivory and fire regimes.

This study is a provisional comparison of C₄ and C₃ grass species in Kentucky, prompted partly by the observation that relatively few native C₄ species are common on the eutrophic soils of the Bluegrass region. A database on Kentucky's grasses is being developed, assigning ecological characteristics to each species. Associations between characteristics provide initial hypotheses that can be tested with more detailed analysis of vegetation patterns and experimental studies.

Methods

Some 112 native grasses are included in this study. Rare species (with S1, S2, or S3 rank in the state heritage program) are excluded. Also, alien species are excluded from the analysis, although noted in some comparisons. Taxonomy is based on the author's interpretation of recent literature, together with an attempt to maintain consistency in rather broad generic concepts and rather narrow species concepts. Appendix 1 lists these species, together with values for ecological characteristics. The following sources, definitions, and criteria were used to assign values.

C3/C4 photosynthesis: This is based on data in Kellogg and Campbell (1987), Kellogg (1999), Sage et al. (1999), and associated literature.

Native status: This is based on interpretation of Fernald (1950), Gleason and Cronquist (1991), and other regional floras. The following classes were included in the analysis: N = clearly native; Ns = native to North America south of Kentucky but perhaps only adventive in the state; Nw = native west of Kentucky but possibly only adventive in the state; Nn = reportedly native north of

Kentucky and possibly within the state. Excluded aliens are classed as follows: A = native to East Asia; E = native to Europe; En = native to Europe and reportedly northern North America but probably not Kentucky. Note that native status remains tentative for a few species that are provisionally accepted here, including *Phalaris arundinacea* (see Merigliano and Lesica 1998) and *Poa pratensis* plants that key to *P. angustifolia* (see Fernald 1950).

Flowering month: This is based on general knowledge and interpretation of regional floras. Typical dates are for anthesis and fertilization, not extended to seed maturation. These dates are approximate, with most species ranging over one to two months.

Hydrological habitats: These vegetation classes are based on a general model of habitat gradients in the state (e.g., Campbell 1987), as diagramed in Appendix 2. In most cases there is much intergradation. Most grass species occur in a range of classes; the most typical class is listed first for each species in Appendix 1. Brief outlines of these classes are as follows.

I: Shrubby/graminoid streambanks; heterogeneous shorelines of various substrates that often become exposed and droughty in the summer; locally dominated by *Salix* spp., *Cornus obliqua*, *Justicia americana*, locally grasses (e.g., *Chasmanthium latifolium*, *Andropogon gerardii*) or sedges; and locally annuals on exposed areas. This is a somewhat anomalous class within the gradient model, deserving an independent axis for expression.

II: Shrubby/graminoid swamp/marsh/bog; stagnant wetlands too wet for most trees; locally dominated by shrubby species, *Alnus serrulata*, *Cephalanthus occidentalis*, *Salix* spp., *Cornus stricta*, *Forestiera acuminata*; and locally *Polygonum hydropiperoides*, *Leersia oryzoides*, *Scirpus* spp., *Carex* spp.

III: Streamside forest, much influenced by frequent flooding; fairly continuous forest, or rapidly recovering from disturbance; typically with *Acer negundo*, *A. saccharinum*, *Betula nigra*, *Platanus occidentalis*, *Populus deltoides*, *Salix nigra*.

IV: Deep swamps, lakes, ponds; sometimes drying up at margins into broad zones of marshy vegetation; not developed in most of Kentucky except for artificial impoundments; southern natural areas dominated by *Taxodium distichum*, *Nyssa aquatica*, *Gledistia aquatica*, and *Salix nigra*; margins often typified by species of class II or by clonally spreading dominants like *Decodon verticillatus* (rare), *Zizaniopsis miliacea* (rare), *Typha* spp., and *Phragmites australis*.

V: Mesic forest, on well-drained terraces or cool slopes; fairly continuous forest, rapidly recovering from disturbance; typically dominated by *Acer saccharum*, *Fagus grandifolia*, or locally *Tsuga canadensis*; locally *Aesculus* spp., *Carya cordiformis*, *Fraxinus americana*, *Liriodendron tulipifera*, *Quercus rubra*, *Tilia* spp., *Ulmus rubra*, etc.

VI: Subhydric forest, with seasonal flooding or saturation; fairly continuous forest, rapidly recovering from disturbance, or with openings along streams and seeps; typically with *Acer rubrum* var. *trilobum*, *Fraxinus pennsylvanica*, *Liquidambar styraciflua*, *Nyssa sylvatica*, *Ulmus americana*; locally *Quercus michauxii*, *Q. pagoda*, etc.

VII: Submesic forest, typically on gentle topography with dry and damp seasons; fairly continuous before settlement or somewhat open due to fires and locally intense ungulate use; much now converted to farmland; heterogeneous and often transitional to other classes; typical trees vary but include *Acer rubrum*, *Aesculus glabra*, *Celtis occidentalis*, *Diospyros virginiana*, *Gleditsia triacanthos*, *Gymnocladus dioicus*, *Fraxinus* spp., *Juglans* spp., *Liriodendron tulipifera*, *Nyssa sylvatica*, *Prunus serotina*, *Sassafras albidum*, *Ulmus* spp.; various *Carya* spp. and *Quercus* spp.

VIII: Seral thickets, especially with clonal shrubby species; combined here with Class VII but potentially widespread, persistent and distinct under certain disturbance regimes; typical species include *Arundinaria gigantea*, *Asimina triloba*, *Cornus* spp., *Prunus* spp., *Rhus* spp., *Rubus* spp., *Symphoricarpos orbiculatus*, *Viburnum* spp.

IX: Hydric-tending oak woods and grassland, on poorly drained but seasonally drying flats, typically on high terraces or upland swales, potentially flooded by backwaters but without rapid flow; much exposed to fires, ungulates, and recent drainage for farmland; typical trees include *Quercus* spp. and *Carya* spp. but with frequent transitions to Class VI; openings include *Juncus* spp., *Carex* spp., *Rhynchospora* spp., *Scirpus* spp., *Cyperus* spp., *Eleocharis* spp. and many grasses (see Appendix 1).

X: Xeric-tending oak woods and grassland, typically on gentle topography that often dries in summer, above floodplains but sometimes wet where poorly drained; much exposed to frequent fires, intense ungulate use, and recent conversion to farmland; typical trees include *Quercus* spp. (especially *Q. stellata*, *Q. falcata*, *Q. marilandica* on poorer soils; *Q. macrocarpa*, *Q. imbricaria* on richer soils), locally *Pinus* spp., *Juniperus virginiana* or others, depending on disturbance regime; native grassland or open grassy woodland widespread in some regions before settlement.

XI: Subxeric forest, typically on slopes; fairly continuous forest, generally recovering from disturbance but with openings on rocky ground; less exposed than Class X to frequent fires, ungulates, and conversion to farmland; typical trees include *Quercus* spp. (especially *Q. alba*, *Q. velutina*, *Q. montana*, *Q. coccinea*, *Q. muhlenbergii*, *Q. shumardii*), *Carya* spp., *Fraxinus* spp., *Castanea dentata* (before blight).

XII: Xeric pine/cedar-oak woods and glades; on thin rocky soils where droughts maintain open conditions and slow succession to oaks or other forest trees; exposed to fires but fuels often thin and interrupted by outcrops; ungulate use varied (from little along clifftops to intense at mineral licks); much less converted to farmland; typical species include *Juniperus virginiana*, *Pinus virginiana*, scattered other trees, and many distinctive shrubs, herbs, and grasses on more rocky ground.

Sun/shade gradient: Typical position on this gradient is based on general knowledge, including much vegetation survey and discussion among plant ecologists; 1 = clearly most abundant in full sun; 2 = abundant in full sun but also common in thin woods with partial canopy; 3 = most common in the partial shade of thin woods or at edges; 4 = somewhat shade tolerant, growing best in somewhat sunny conditions but clearly persisting into shady forest at lower vigor; 5 = clearly shade-tolerant, and tending to be outcompeted in more sunny conditions.

Soil pH/fertility gradient: Typical position is assigned from general knowledge and interpretation of regional floras; the soil gradient in Kentucky's forests has been revealed by ordination studies (e.g., Campbell 1987), but much more detailed work is needed, especially to examine associations of N and P levels with soil pH; it is generally accepted that soils with pH 6-7 have high natural levels of N and P, especially in the Bluegrass region, but raw data have not been mapped. In addition to direct experience with vegetation and soil data, some initial distributional guidelines are as follows:

- A. Association with low fertility is indicated by concentration on relatively acid shales and sandstones in the Knobs and Appalachian regions, coupled with virtual absence in the Bluegrass region or other calcareous regions.
- B. Transition, mixed, or uncertain assignment between A and B.
- C. Association with average fertility is indicated by widely scattered distribution over the state, including parts of the Bluegrass region as well as the Knobs and Appalachian hills.
- D. Transition, mixed, or uncertain assignment; widespread species that are common on farmland or alluvial soils with high fertility are generally assigned here.
- E. Association with high fertility is indicated by higher frequency in the Bluegrass region or other calcareous regions, and typically lower frequency in the Knobs and Appalachian hills (except in rich valleys and other unusual sites).

Tables were developed to compare the distribution of C_4 and C_3 species among these ecological classes. Tests of independence were used to estimate probabilities that differences could have arisen by random assortment of the species, using the Pearson chi-square statistic with Model I (Sokal and Rohlf 1969, 16.4). It has been argued that an individual species is not an independent observation, when searching for statistical associations among characters because a character may have only evolved once in a phylogenetic group of species (Freckleton et al. 2002). Alternatively, it can be argued that each species should be weighted according to its abundance. This provisional study is concerned only with overall patterns among species; further analysis will have to involve deeper examination of phylogenetic associations and distribution of abundance, together with appropriate statistics that examine phylogenetic correlation. However, for some provisional consideration, the tables include the number of genera provided in parentheses after each species total. Chi-square tests are run with these numbers of genera, in addition to the usually higher numbers of species, but this is still an arbitrary level of analysis.

Results

Flowering month: Table 1 shows the distribution of C_4 and C_3 species in relation to typical flowering month. There is a highly significant difference ($P < 0.0005$), with 55 of the 64 C_3 species typically flowering from mid-April to late July, and 46 of the 48 C_4 species typically flowering from late July to mid-October. Within C_3 species, inspection of the data indicates that early flowering species tend to occur mostly in somewhat wooded habitats on well-drained soils, while later species tend to occur in sunny, dry, or wet habitats. Within C_4 species, there is no suggested association with habitat.

Hydrological habitats: Table 2 compares the distribution of C_4 and C_3 species with respect to typical habitat, as defined from a hydrological perspective. These habitat classes are arranged to form a simple two-gradient model, from relatively mesic conditions to the center left (in mesic

forest and streamside forest), xeric to upper right, and hydric to lower right. Note that the typical habitat assignments of many species are provisional, pending more quantitative analysis of vegetation data, and most species range over several classes. Nevertheless, there is a highly significant difference in distribution between C₄ and C₃ species among the 10 classes where they typically occur ($P = 0.002$). The percentage of C₄ species is consistently higher, at 61 to 64% within the three major habitat classes that have extensive grassland or grassy open woodland: (a) xeric pine/cedar-oak woodland/glades; (b) xeric-tending oak woodland/grassland; and (c) hydric-tending oak woodland/grassland.

The latter, “hydric-tending” class is defined to include sites that frequently dry out in summer. On wetter ground, in transitions to the “deep swamp” class, C₄ species are virtually absent, except on unstable or seasonally exposed shorelines. Instead, a few C₃ species are locally dominant, although these are rare (*Zizaniopsis milacea*) or generally considered alien (*Phragmites australis*), except perhaps *Phalaris arundinacea* and *Leersia* spp. in various terrestrial transitions. This trend is enhanced through consideration of the sedge family, Cyperaceae (Kellogg 1999), which contains C₄ taxa typical of hydric-tending woodland/grassland and marshy transitions to swamps (most *Cyperus* spp., all *Rhynchospora*, *Eleocharis*, *Kyllingia*, *Fimbristylis*, *Bulbostylis*). The C₃ taxa in this family are more widespread, extending either into forests or into deeper swamps, marshes, and seeps with more permanent water supply (*Carex*, *Scleria*, *Scirpus*, *Dulichium*, *Eriophorum*). Moreover, other graminoid taxa of more permanently flooded habitats are also C₃—in Sparganiaceae (*Typha*, *Sparganium*).

In other habitat classes, with one minor anomalous exception, the percentage of typical C₄ species is much lower, with 0% in subhydric or hydric habitats, and 17 to 33% in typically forested mesic, submesic, or subxeric habitats. The exception is the “shrubby/graminoid streambank” class. This is rather heterogeneous, on various substrates, but it is united by the tendency for floods and other seasonal changes in water level to maintain a zonation from forest, through shrubs, graminoids, and herbs, to truly aquatic habitat in the stream (see “Methods”). There are only a few grass species strongly concentrated in this habitat within Kentucky, but most (5 of 6) are C₄ (*Eragrostis hypnoides*, *E. frankii*, *Paspalum fluitans*, *Panicum virgatum*, *Cenchrus longispinus*); others will be added when rare species are considered (e.g., *Sporobolus cryptandrus* and *Triplasis purpurea* along the Mississippi River sandbars). In addition to specialists, more widespread or weedy grasses are often present (e.g., C₄ *Andropogon gerardii* in full sun on rocky banks and C₃ *Chasmanthium latifolium* at upper edges).

Sun/shade gradient: Table 3 shows that the percentage of C₄ species is much higher (76%) among those typical of full sun conditions, with high significance given the model of random assortment ($P < 0.0005$). There is virtually no trend with increasing shade concentration (divisions 2-5 in Table 3), where the percentage of C₄ species averages ca. 10 to 20%. The few C₄ species in more shady conditions are largely restricted to the “closed/non-drying” habitats. Moreover, in partial or deeper shade (divisions 3-4; none at 5), the only genus represented is *Muhlenbergia*.

Soil pH/fertility gradient: Table 4 shows that there is no overall trend in the proportion of C₄ to C₃ species along this gradient of increasing base-status and presumed overall fertility. There may be a somewhat higher percentage at intermediate positions (with ca. 49% at both “average/C” and “slightly above-average/D” fertility), but this will deserve proper analysis only when more data are included in the analysis, with addition of rarer species, real vegetation data, and a broader

regional context. For example, there are several rare but locally abundant C₄ species in Kentucky that are typical of higher pH (especially western species such as *Bouteloua curtipendula* and *Muhlenbergia cuspidata*) and lower pH (especially southern species such as *Gymnopogon ambiguus* and *Panicum longifolium*). But there are also several locally abundant C₃ species with northern geographic ranges at these extremes (e.g., *Schizachne purpurascens* at higher pH, *Deschampsia flexuosa* at lower pH).

As a first step toward deeper analysis, Table 5 selects only species that are fairly widespread, locally abundant perennials in native vegetation on relatively undisturbed ground, without much soil exposure, frequent flooding, or trampling. This selection is based on general knowledge of the vegetation in Kentucky and can be supported by many individual observations, but a comprehensive synthesis of vegetation data will be needed eventually. Although the simple statistical test employed here does not show clear significance, there does appear to be a trend that will deserve deeper analysis. Within the C₃ group, there are increases in the number of species from five typical on lower fertility soils (coded A/B), to seven on average soils (C), to 17 on higher fertility soils (D/E). Moreover, the only really tall species, commonly reaching 2 m or more, are *Arundinaria gigantea* and *Phalaris arundinacea*, both typical of above-average fertility (D). Within the C₄ group, there is an increase from two species typical of lower fertility, to 10 on average, but then a decrease to six on higher fertility. Moreover, taller species (reaching at least 2 m), are mostly on lower fertility (*Saccharum* spp.) or average fertility (*Tripsacum dactyloides*, *Andropogon gerardii*, *Sorghastrum nutans*), with only one (*Panicum virgatum*) on higher fertility. The latter species is relatively uncommon in Kentucky, being largely restricted to rocky riverbanks, but it has been successfully planted in many old fields.

Finally, Table 6 lists widespread, locally abundant alien grasses, either perennial or annual, in relation to this soil gradient. There are increases in numbers of both C₄ and C₃ species on higher soil fertility. Moreover, there are two additional tall perennial C₄ species that can exceed 2 m: *Miscanthus sinensis* on average soils and *Sorghum halepense* (plus the annual *S. bicolor*) on above-average fertility. The only alien C₃ species that reach such stature already have native races on above-average soils in North America: *Phalaris arundinacea* and *Phragmites australis*. Clearly, the invasive C₄ species from the Old World are able to colonize farmland, urban land, and other disturbed sites in Kentucky. It appears that some of these species are adapted to rapid growth in full sun on relatively fertile upland soils, a niche that is occupied by relatively few native C₄ species.

Discussion

The strong association of C₄ grasses with late summer growth in open, nonforested habitats of Kentucky, including sites maintained by fire, accords with many other studies of C₄ versus C₃ distribution (Sage and Monson 1999). In Kentucky, 86% of C₃ grasses flower between mid-April and late July, when average daily maximum temperatures are ca. 15 to 20°C; in contrast, 96% of C₄ grasses flower between mid-July and mid-October, when average daily maximum temperatures are ca. 20° to 30°C.

Further detail is provided here, indicating that only open habitats that experience much seasonal drying have the association with C₄ grasses. The three major habitats with these species are: (a) xeric pine/cedar-oak woodlands and associated rocky glades; (b) xeric-tending oak woodlands and associated grasslands, especially on gentle uplands; (c) hydric-tending oak woodlands and associated grasslands, especially on high terraces. The latter can experience significant drought stress in summer but are often wet in winter. A fourth minor habitat class

dominated by C₄ species is defined as “shrubby/graminoid streambanks” that experience flooding and other seasonal changes in water level sufficient to maintain a distinct zonation of vegetation between forested banks and the low water levels. Similar patterns have been observed in other regions of the world (Sage et al. 1999). Further study of shoreline vegetation along different kinds of water-body is needed to examine the fine spatial scale at which C₄ grasses can concentrate within such zonations.

Subhydric or hydric sites that experience less seasonal drying appear to have virtually no typical C₄ grasses, but there are a few locally abundant C₃ grasses within these habitats. A parallel trend exists within the sedge family (Cyperaceae). The dominance of C₃ species on more permanently hydric sites, even in full sun, is a global trend (Sage and Monson 1999).

The few native C₄ grasses that occur in deeper shade are all perennials in the genus *Muhlenbergia*. However, the weedy invasive Asian C₄ annual, *Microstegium vimineum*, has now spread widely into Kentucky’s forests, especially along streambanks, trails, grazed areas, and other sites with disturbed soil (sometimes including woods burned in the spring before germination).

There is no significant overall trend in C₄ versus C₃ species along the gradient from acid soils with low fertility to base-rich soils with high fertility. However, locally dominant perennial grasses, especially the few taller species that reach 2 m or more, are mostly C₄ species on low to average soil fertility (e.g., *Andropogon gerardii*), and mostly species C₃ on higher soil fertility (e.g., *Arundinaria gigantea*). In contrast, alien grasses of both C₃ and C₄ groups increase in numbers on higher fertility.

High N levels have been shown experimentally to increase the ratio of C₃ to C₄ grasses in cooler regions (e.g., Tilman 1988, Wedin and Tilman 1993, 1996), in accord with the approximately doubled N requirement for photosynthesis that is typically estimated in C₃ species (Long 1999). For physiological reasons, this effect is probably stronger when temperatures and light levels are lower. However, enhancement of N level in warmer climates or later in the growing season may allow “aggressive eutrophiles” in the C₄ group to increase, including invasive aliens such as *Digitaria* spp. that appear adapted to anthropogenic ecosystems with higher fertility (Kretschmer and Pitman 1995, Sage et al. 1999).

A Developing Hypothesis

Since eutrophic soils support rapid plant growth in general, there is a strong tendency for forest to predominate, with rapid recovery from disturbances. Because of this, there may have been relatively little opportunity for selection of tall, potentially dominant C₄ grasses on sunny, eutrophic sites in eastern North America. Moreover, within the predominantly deciduous woods on eutrophic soils, there is more potential for dense grassy ground vegetation with C₃ species to develop, especially in spring when nutrient and light levels are highest. Global trends would support this hypothesis (Archibold 1995, Sage et al. 1999).

The dense, diverse aspect of ground vegetation in eutrophic woods is a generally observed trend in Kentucky, especially when comparing the rich limestone soils of the Bluegrass region with the relatively acid, infertile soils of the surrounding Knobs region. *Elymus* spp. are particularly common in the partial shade of eutrophic woods, including the recently described, early flowering *E. macgregorii* J. Camp. & R. Brooks (Campbell 2000). The local dominance of *Arundinaria gigantea* (cane) in more open woods before settlement on eutrophic uplands in Kentucky may be interpreted as a response to anthropogenic fires, or perhaps intense ungulate effects.

There are many historical indications that herbivores, probably promoted by high productivity and mineral nutrition, played at least a partial role in maintaining features of Bluegrass Woodlands before settlement. Also, several characteristic species of Bluegrass Woodlands have chemical or mechanical defenses that suggest coevolution with large ungulates (Campbell 1984). Bison, cattle, horses, elk, and sometimes deer are known to relish cane forage in certain seasons, but the extensive rhizome system of cane allows rapid regrowth after disturbance. It is likely that canebrakes were frequented by such animals for food and shelter during the winter (Campbell 1984, Platt et al. 2001; and continuing review of historical literature). Passenger pigeons are also reputed to have been associated with canebrakes. Nutrient cycling through such animals could have enhanced regrowth of C₃ species into the summer when the ungulates probably ranged into other habitats, including C₄ grasslands. If small areas of C₄ grassland developed within the Bluegrass Woodlands, it is possible that the intense use of the region by ungulates would have kept such grasslands overgrazed, unless fires were frequent enough to promote regrowth. At least in the summer, there is growing evidence in Kentucky that C₄ grasses are typically preferred by ungulates, due in part to healthier C:N ratios (e.g., ongoing research by the University of Kentucky's forage programs). Such patterns would accord with results of Knapp and Medina (1999) at Konza Prairie and the global review of Heckathorn et al. (1999).

The role of fire in Bluegrass Woodlands is more speculative. Initial research could focus usefully on fuel behavior and its relationship to nutrient cycling. Much potential C₃ fuel may experience relatively rapid consumption, compaction, or decomposition, in contrast to the relatively flammable, upright fuel of dominant C₄ grasses (Sage et al. 1999). Probably due to this factor and the greening-up of ground vegetation through the winter and spring, the woods are generally difficult to burn, especially in the spring. Old fields can easily burn in dry periods, but it is unclear what disturbance regime could have allowed similar habitats to develop before settlement. It is possible that large animal trails, followed by Native American burning and local clearing for campsites and villages, could have caused such openings. But early accounts at the time of settlement indicate that full openings were much less extensive than the typically noted "forests" "thin woods" with "dense herbage of wild-rye, clover & peavine" and "canebreaks" (Campbell 1984, 1988, 1989). It is possible that there were relatively intense fires at longer intervals, perhaps during low points in the ca. 11-year or ca. 22-year periodicities of precipitation (Elam 1973; see also the Kentucky Climate Center Web site for recent data), or after the occasionally intense ice-storms that create abundant woody litter (as experienced in this region during February 2003, 1994, 1951), or after die-back of cane plants following flowering (Campbell 1985).

Within the central Bluegrass region, there is no evidence that C₄ grasslands occurred before settlement, except along rocky banks of major rivers and on the thin shaley soils of the Blue Licks area. However, in transitional areas outside this region, there are extensive remnants of C₄ grassland on dolomitic material, acid shales, old sandy river terraces, glacial deposits, and other soils with lower fertility (Campbell 1984). The only abundant native C₄ grass in old fields of the central Bluegrass region is *Tridens flavus*; minor species include *Andropogon virginicus* (on "worn-out" soils with lower calcium and other nutrients), *Paspalum pubiflorum* (in sunny grazed/mowed sites), and *Muhlenbergia schreberi* (in shady grazed/mowed sites). It is of course possible to plant and maintain the taller C₄ grasses on these soils; *Panicum virgatum* is especially amenable to this. But without mowing, if there are intermixed competitive, root-suckering native woody plants such as *Robinia pseudoacacia*, *Campsis radicans*, *Prunus americana*, *Cornus*

drummondii, and *Arundinaria gigantea*, even frequent burning may be insufficient to prevent the decline of C₄ grasses to a minor proportion. Frequent fires, especially in the spring, may favor C₄ grasses by keeping N levels low (Knapp and Medina 1999), as well as reducing woody vegetation. But such treatment will probably not provide the best overall balance of native species in the vegetation, which includes diverse sedges, wild ryes, winter annuals, and running buffalo clover that grow mostly in the spring (Campbell et al. 1988). Such predictions can be now be tested at the Griffith Farm and other sites for research on native vegetation in the region.

Acknowledgments

This paper is dedicated to the memory of Willem Meijer, who knew the global trends in his bones, provoked us for the better, and rediscovered mesophytic beauties in woodland remnants of the Lexington area. Also, I thank Bill Cohen for still being there 25 years later to answer questions about photosynthesis. And I am particularly grateful to Jeff Hohman, Joe Settles, and others at East Kentucky Power Cooperative for financial support of this work.

Literature Cited

- Archibold, O.W. 1995. Ecology of World Vegetation. Chapman and Hall, London.
- Campbell, J.J.N. 1984. The Land of Cane and Clover. Report from the Herbarium. University of Kentucky, Lexington, Ky.
- Campbell, J.J.N. 1985. Bamboo flowering patterns: A global view with special reference to East Asia. *Journal of the American Bamboo Society* 6:17-35.
- Campbell, J.J.N. 1987. Gradients of tree species composition in the Central Hardwood Region. Pages 325-346 in R.L. Hay, F.W. Woods and H. DeSelm (eds). Proceedings of the 6th Central Hardwood Forest Conference. Southern Forest Experiment Station, USDA Forest Service.
- Campbell, J.J.N., M. Evans, M.E. Medley, and N.L. Taylor. 1988. Buffalo clovers in Kentucky (*Trifolium stoloniferum* and *T. reflexum*): historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome number. *Rhodora* 90:399-418.
- Campbell, J.J.N. 1989. Historical evidence of forest composition in the Bluegrass region of Kentucky. Pages 231-246 in G. Rink and C.A. Budelsky (eds). Proceeding of the 7th Central Hardwood Conference. North Central Forest Experiment Station, USDA Forest Service.
- Campbell, J.J.N. 2000. Notes on North American *Elymus* species (Poaceae) with paired spikelets: I. *E. macgregorii* sp. nov. and *E. glaucus* ssp. *mackenzii* comb. nov. *Journal of the Kentucky Academy of Science* 61:88-98.
- Elam, A.B. 1973. Meteorological drought in Kentucky, 1929-71. University of Kentucky College of Agriculture Experiment Station Progress Report 209.
- Fernald, M.L. 1950. Gray's Manual of Botany. 8th edition (corrected printing in 1970). D. Van Nostrand Company, New York, N.Y.
- Freckleton, R.P., P.H. Harvey and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160:712-726.
- Gleason, H.A., and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and adjacent Canada. 2nd edition. New York Botanical Garden, Bronx, N.Y.
- Heckathorn, S.A., and S.J. McNaughton and J.S. Coleman. 1999. C₄ plants and herbivory. Pages 285-312 in Sage and Monson (eds), *ibid.*

- Kellogg, E. 1999. Phylogenetic aspects of the evolution of C₄ photosynthesis. Pages 411-444 in Sage and Monson (eds), *ibid*.
- Kellogg, E., and C.S. Campbell. 1987. Phylogenetic analyses of the Gramineae. Pages 217-224 in T.R. Soderstrom, K.W. Hilu, C.S. Campbell and M.E. Barkworth (eds). *Grass Systematics and Evolution*. Smithsonian Press, Washington, D.C.
- Knapp, A.K., and E. Medino. 1999. Success of C₄ photosynthesis in the field. Pages 251-283 in Sage and Monson (eds), *ibid*.
- Kretschmer, A.E., and W.D. Pitman. 1995. Tropical and subtropical forages. Pages 283-304 in R.F. Barnes, D.A. Miller and C.J. Nelson (eds). *Forages*. Vol. I. Iowa University Press, Ames, Iowa.
- Long, S.P. 1999. Environmental responses. Pages 215-249 in Sage and Monson (eds), *ibid*.
- Merigliano, M.F., and P. Lesica. 1998. The native status of reed canarygrass (*Phalaris arundinacea* L.) in the Inland Northwest, USA. *Natural Areas Journal* 18:223-230.
- Platt, S.G., C.G. Brantley and T.R. Rainwater. 2001. Canebrake fauna: wildlife diversity in a critically endangered ecosystem. *Journal of the Elisha Mitchell Scientific Society* 117:1-19.
- Sage, R.F. 1999. Why C₄ photosynthesis? Pages 3-16 in Sage and Monson (eds), *ibid*.
- Sage, R.F., and R.K. Monson. 1999. C₄ Plant Biology. Academic Press, San Diego.
- Sage, R.W., M.R. Li, and R.K. Monson. 1999. The taxonomic distribution of C₄ photosynthesis. Pages 551-584 in Sage and Monson (eds), *ibid*.
- Sokal, R.R., and F.J. Rohlf. 1969. *Biometry*. W.H. Freeman and Company, San Francisco, Calif.
- Tilman, D.A. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, N.J.
- Wedin, D.A., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs* 63:199-229.
- Wedin, D.A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274:1720-1723.

Table 1. Comparison of typical flowering months for C₄ versus C₃ grass species.

	Typical Flowering Months						Total Species
	Apr-May 4-5	May-Jun 5,5-6	Jun-Jul 6,6-7,5-8	Jul-Aug 7,6-8; 7-8	Aug-Sep 8,8-9	Sep-Oct 9,9-10	
C4 species	0	0	1(1)	18(9) 1(1); 17(9)	23(10)	6(2)	48
C3 species	4(3)	15(10)	25(11)	19(11) 11(3); 8(7)	1(1)	0	64
Total species	4	15	26	37	24	6	112
C4 percent	0%	0%	4%	49% 8%; 68%	96%	100%	43%

Notes: In Jul-Aug, a tentative subdivision is presented below the number for the whole month. Numbers in parentheses are genera represented in each class. There is a highly significant difference between the distribution of C₄ and C₃ species among the six seasonal divisions; chi-square = 66.4, d.f. = 5, P < 0.0005. The difference between numbers of genera, in parentheses, remains highly significant; chi-square = 29.2, d.f. = 5, P < 0.0005.

Table 2. Comparison of typical hydrological habitat classes for C₄ versus C₃ grass species.

[Cliffs]	XI: Subseric forest	XII: Xeric pine/cedar-oak woodlands and glades
[no typical grasses]	C ₄ = 2(1); C ₃ = 8(6) 20%	C ₄ = 8(5); C ₃ = 5(2) 62%
V: Mesic forest	VII: Submesic forest, VIII: Thickets, edges, old fields	X: Xeric-tending oak woods and grassland
C ₄ = 1(1); C ₃ = 2(2) 33%	C ₄ = 4(4); C ₃ = 20(10) 17%	C ₄ = 17(10); C ₃ = 11(8) 61%
III: Streamside forest	VI: Subhydric forest; and shrubby seeps	IX: Hydric-tending oak woods and grassland
C ₄ = 2(2); C ₃ = 6(5) 25%	C ₄ = 0; C ₃ = 4(4) 0%	C ₄ = 9(8); C ₃ = 5(3) 64%
I: Shrubby/graminoid streambanks	II: Shrubby/graminoid swamp/marsh/bog	[IV: Deep swamps] [<i>Phragmites</i> , <i>Zizaniopsis</i> , etc.]
C ₄ = 5(5); C ₃ = 1(1) 84%	C ₄ = 0; C ₃ = 2(2) 0%	[rare/alien species only] 0%?

Notes: Note that most species range widely, but the most typical habitat class is assigned here. "C₄ =" and "C₃ =" show numbers of modal species in each class; numbers in parentheses are genera represented. The bottom line in each class is the percentage of C₄ species. There is a highly significant difference between C₄ and C₃ species among the 10 habitat classes where they typically occur (excluding Cliffs and Deep Swamps); chi-square = 26.6, d.f. = 9, P = 0.002. The difference between numbers of genera remains significant; chi-square = 19.7, d.f. = 9, P = 0.02.

Table 3. Comparison of typical sun-shade distribution for C₄ versus C₃ grass species.

C ₄ /C ₃ Group	Habitat Classes	Typical Position along Sun-Shade Gradient					Total Species
		Full Shade (code 5)	Transition (code 4)	Thin Shade (code 3)	Transition (code 2)	Full Sun (code 1)	
C₄ species	open drying	0	0	0	3(3)	36(13)	39
	closed/non-drying	0	3(1)	2(1)	2(2)	2(2)	9
C₃ species	open drying	0	0	0	10(7)	12(7)	22
	closed/non-drying	4(4)	10(6)	13(12)	15(7)	0	42
C₄ percent		0%	23%	13%	17%	76%	43%

Notes: Within groups, species are separated further according to "open drying" habitats (classes I, IX, X, and XII in Table 2) versus "closed/non-drying" habitats (all other classes in Table 2). Numbers in parentheses are the genera represented in each case. There is a highly significant difference between C₄ and C₃ species among the five sun-shade divisions; chi-square = 41.2, d.f. = 4, P < 0.0005. The difference between numbers of genera remains highly significant; chi-square = 19.3, d.f. = 4, P = 0.001.

Table 4. Comparison of typical soil gradient positions of C₄ versus C₃ grass species.

C4/C3 Group	Habitat Classes	Typical Position along Soil Gradient					Total Species
		Infertile pH 4-5 (code A)	Transition or Varied (code B)	Average pH 5-6 (code C)	Transition or Varied (code D)	Fertile pH 6-7 (code E)	
C4 species	open drying	1(1)	2(2)	14(8)	22(11)	0	39
	closed/non-drying	0	2(2)	3(3)	1(1)	3(1)	9
C3 species	open drying	2(2)	7(3)	5(4)	6(6)	2(2)	22
	closed/non-drying	0	8(6)	13(7)	18(12)	3(3)	42
C4 percent		33%	21%	49%	49%	38%	43%

Notes: Within each group, species are separated further according to “open/drying” habitats (classes I, IX, X, and XII in Table 2) versus “closed/non-drying” habitats (all other classes in Table 2). Numbers in parentheses are genera represented in each category. The difference in distribution between C₄ and C₃ species is not significant, given the model of random assortment; chi-square = 5.1, d.f. = 4, P = 0.28.

Table 5. Locally abundant perennial grasses of relatively undisturbed native vegetation; in full sun (1/2), partial sun (3), or shade (4/5); taller species (often > 2 m) in bold.

	Low Fertility (A/B)	Average Fertility (C)	High Fertility (D/E)
C4 species	<i>Saccharum giganteum</i> (1)	Sorghastrum nutans (1)	<i>Panicum virgatum</i> (1)
	<i>Saccharum alopecurioides</i> (2)	<i>Andropogon gerardii</i> (1)	<i>Setaria parviflora</i> (1)
		<i>Tripsacum dactyloides</i> (1)	<i>Andropogon gyrans</i> (1)
		<i>Panicum anceps</i> (1)	<i>Sporobolus compositus</i> (1)
		<i>Panicum rigidulum</i> (1)	<i>Tridens flavus</i> (2)
		<i>Aristida purpurascens</i> (1)	<i>Muhlenbergia sobolifera</i> (4)
		<i>Andropogon virginicus</i> (1)	
		<i>Andropogon glomeratus</i> (1)	
		<i>Andropogon ternarius</i> (1)	
		<i>Andropogon scoparius</i> (2)	
C3 species	<i>Poa alsodes</i> (2)	<i>Panicum scoparium</i> (2)	<i>Phalaris arundinacea</i> (1)
	<i>Danthonia sericea</i> (2)	<i>Panicum microcarpon</i> (2)	<i>Arundinaria gigantea</i> (3)
	<i>Danthonia compressa</i> (2)	<i>Danthonia spicata</i> (2)	<i>Leersia oryzoides</i> (2)
	<i>Chasmanthium laxum</i> (2)	<i>Elymus riparius</i> (2)	<i>Leersia lenticularis</i> (2)
	<i>Piptochaetium avenaceum</i> (3)	<i>Cinna arundinacea</i> (3)	? <i>Poa angustifolia</i> (2)
		<i>Panicum boscii</i> (5)	<i>Elymus glaberriflorus</i> (2)
		<i>Brachyelytrum erectum</i> (5)	<i>Elymus v. var. intermedius</i> (2)
			<i>Elymus virginicus</i> (3)
			<i>Chasmanthium latifolium</i> (3)
			<i>Glyceria striata</i> (3)
			<i>Elymus macgregorii</i> (4)
			<i>Elymus villosus</i> (4)
			<i>Elymus hystrix</i> (4)
		<i>Festuca subverticillata</i> (4)	
		<i>Muhlenbergia frondosa</i> (4)	
		<i>Poa sylvestris</i> (4)	
		<i>Diarrhena americana</i> (5)	

Notes: This provisional table is based on general knowledge of Kentucky vegetation; it will need further support from vegetation data. Although C₃ species are about twice as frequent as C₄ species in the high fertility class while about equal in average and low fertility classes, this difference is only marginally significant, given the model of random assortment; chi-square = 4.76, d.f. = 2, P = 0.09.

Table 6. Abundant alien C₄ and C₃ grasses listed in relation to typical soil fertility.

Locally abundant alien species; in full sun (1/2), partial sun (3), or shade (4/5); taller species (often > 2 m) in bold.			
Low Fertility (A/B)	Average Fertility (C)	High Fertility (D/E)	
C4 species	<i>Miscanthus sinensis</i> (1) <i>Arthraxon hispidus</i> (2) <i>Microstegium vimineum</i> (4)	<i>Sorghum spp.</i> (1) <i>Cynodon dactylon</i> (1) <i>Eragrostis spp.</i> (1) <i>Digitaria spp.</i> (1) <i>Setaria spp.</i> (1) <i>Echinochloa crus-galli</i> (1)	
C3 species	<i>Holcus lanatus</i> (1) <i>Anthoxanthum odoratum</i> (1)	<i>Phragmites australis</i> (1) ?<i>Phalaris arundinacea</i> (1) <i>Bromus spp.</i> (1) <i>Festuca arundinacea</i> (1) <i>Phleum pratense</i> (1) <i>Dactylis glomerata</i> (2) <i>Poa spp.</i> (2)	

Notes: This provisional table is based on general knowledge of Kentucky vegetation; it will need further support from vegetation data.

Appendix 1. Printout from database on Kentucky grasses. (See “Methods” on page 97 for explanation of these codes.)

Scientific Name	C3/C4	Native Status	Vegetation Class	Acid/Basic Soils	Sun/Shade	Flw Month
<i>Agrostis gigantea</i> Roth	C3	E	X; IX; VII; VI	D	1	6-7
<i>Agrostis hyemalis</i> (Walt.) B.S.P.	C3	N	X; XII	C	1	4-5
<i>Agrostis perennans</i> (Walt.) Tuckerman	C3	N	VII; XII; V	CB	3	7-8
<i>Alopecurus carolinianus</i> Walt.	C3	N	X; VII	D	1	5-6
<i>Anthoxanthum odoratum</i> L.	C3	E	X	C	1	6-7
<i>Arrhenatherum elatius</i> (L.) Beauv. ex J.& K. Presl	C3	E	VII; X	D	1	6-7
<i>Arundinaria gigantea</i> (Walt.) Muhl.	C3	N	VII; VI; III; V	D	3	5
<i>Brachyelytrum erectum</i> (Schreb. ex Spreng.) Beauv.	C3	N	V; XI; VII	C	5	6-7
<i>Bromus inermis</i> Leyss.	C3	E	X	E	1	6-7
<i>Bromus japonicus</i> Thunb. ex Murr.	C3	A	X	D	1	6-7
<i>Bromus pubescens</i> Muhl. ex Willd.	C3	N	VII; XI; V	D	4	6-7
<i>Bromus racemosus</i> L.	C3	E	X	D	1	6-7
<i>Bromus secalinus</i> L.	C3	E	X; XII	E	1	6-7
<i>Bromus sterilis</i> L.	C3	E	X; XII	E	1	6-7
<i>Bromus tectorum</i> L.	C3	E	X; XII	E	1	6-7
<i>Calamagrostis coarctata</i> (Torr.) Eat.	C3	N	VI; IX	B	2	7-8
<i>Chasmanthium latifolium</i> (Michx.) Yates	C3	N	VII; III; I	D	3	7-8
<i>Chasmanthium laxum</i> (L.) Yates	C3	N	IX; VI	B	2	7-8

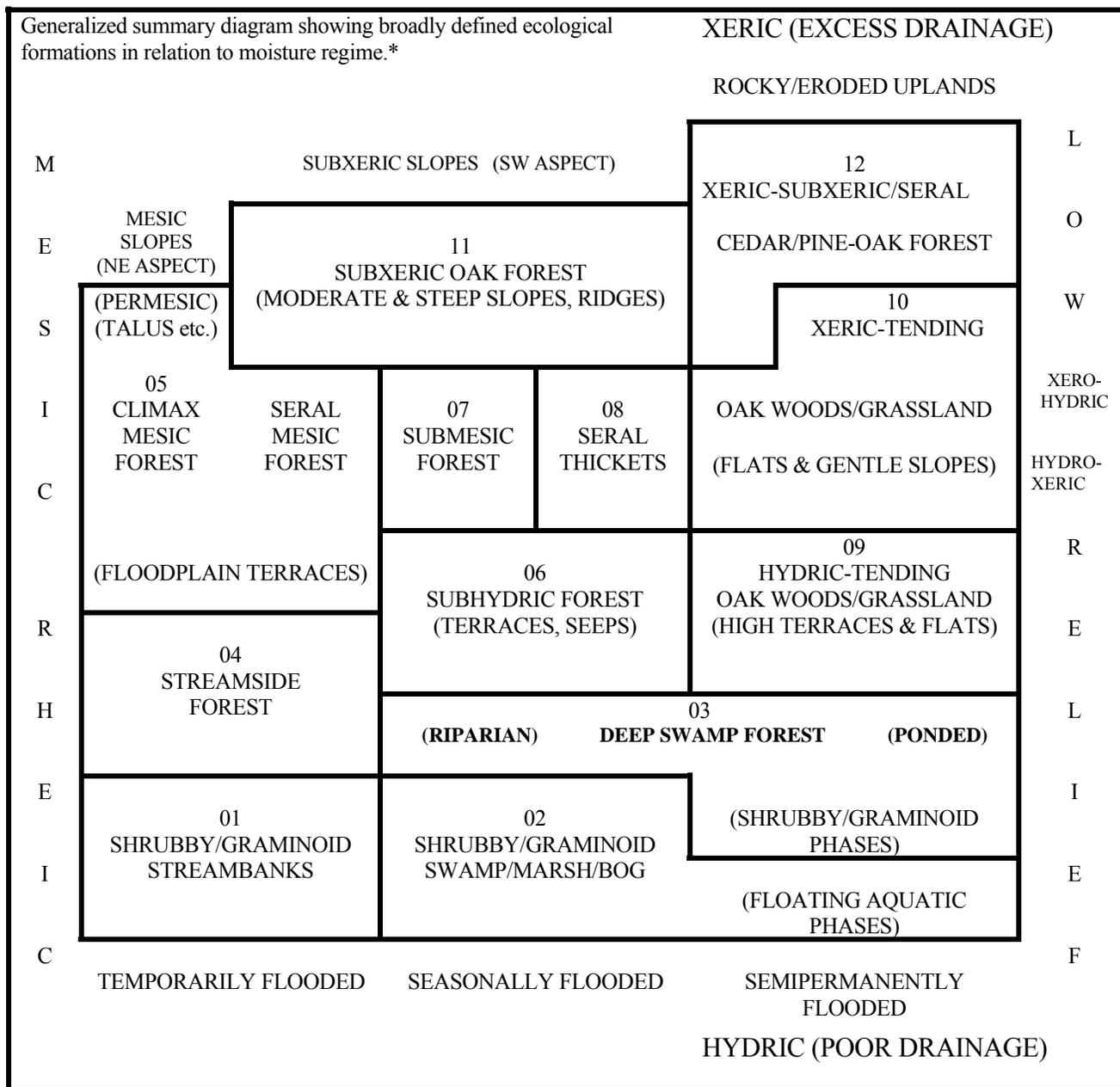
Scientific Name	C3/C4	Native Status	Vegetation Class	Acid/Basic Soils	Sun/Shade	Flw Month
<i>Cinna arundinacea</i> L.	C3	N	III; VI	C	3	7-8
<i>Dactylis glomerata</i> L.	C3	E	VII; X	D	2	6-7
<i>Danthonia compressa</i> Austin ex Peck	C3	N	VII; X; V	B	2	6-7
<i>Danthonia sericea</i> Nutt.	C3	N	XII; X	A	2	5-6
<i>Danthonia spicata</i> (L.) Beauv. ex Roemer & J.A. Schultes	C3	N	VII; XI; XII	C	3	5-6
<i>Diarrhena americana</i> Beauv.	C3	N	XI; V	E	5	7-8
<i>Elymus glabriflorus</i> (Vasey) Scribn. & Ball	C3	N	VII; X	D	2	6-7
<i>Elymus hystrix</i> L.	C3	N	XI; VII; V	D	4	6
<i>Elymus macgregorii</i> J. Camp. & R. Brooks	C3	N	VII; III; X	E	4	5-6
<i>Elymus repens</i> (L.) Gould	C3	E	VII; IV; X	E	1	7
<i>Elymus riparius</i> Wieg.	C3	N	III; I; VII	C	2	7
<i>Elymus villosus</i> Muhl. ex Willd.	C3	N	VII; XI; V	D	4	6
<i>Elymus virginicus</i> L. var. <i>intermedius</i> (Vasey) Bush	C3	N	III; X*	D	2	7-8
<i>Elymus virginicus</i> L. var. <i>virginicus</i>	C3	N	VII; VI; X	D	3	6-7
<i>Festuca arundinacea</i> Schreb.	C3	E	X; VII	D	1	6-7
<i>Festuca octoflora</i> Walt.	C3	N	X; XII	C	1	5-6
<i>Festuca paradoxa</i> Desv.	C3	Nw	X	D	2	6-7
<i>Festuca pratensis</i> Huds.	C3	E	X; VII; VI	D	1	6-7
<i>Festuca rubra</i> L.	C3	En	X; VII; XI	D	2	6-7
<i>Festuca subverticillata</i> (Pers.) Alexeev	C3	N	V; VII; III	D	4	6-7
<i>Glyceria septentrionalis</i> A.S. Hitchc.	C3	N	II; IV; IX	D	2	6
<i>Glyceria striata</i> (Lam.) A.S. Hitchc.	C3	N	III; IV	D	3	6-7
<i>Holcus lanatus</i> L.	C3	E	VII; VI; X	C	1	5-6
<i>Hordeum jubatum</i> L.	C3	S	X; IX	D	1	7-8
<i>Hordeum pusillum</i> Nutt.	C3	Nw	X; XII; IX	E	1	5-6
<i>Leersia lenticularis</i> Michx.	C3	N	VI; IV; IX	D	2	8
<i>Leersia oryzoides</i> (L.) Sw.	C3	N	II; I; IV	D	2	7-8
<i>Leersia virginica</i> Willd.	C3	N	III; VII; VI	D	3	7
<i>Lolium multiflorum</i> Lam.	C3	E	VII; X	D	2	6-7
<i>Melica mutica</i> Walt.	C3	N	XI; VII; X	D	4	5
<i>Panicum acuminatum</i> Sw. var. <i>fasciculatum</i> (Torr.) Lelong	C3	N	VII; X; XII	C	2	6-8
<i>Panicum ashei</i> Pearson ex Ashe	C3	N	XI	B	3	5-8
<i>Panicum boscii</i> Poir.	C3	N	XI; VII; V	C	5	5-8
<i>Panicum clandestinum</i> L.	C3	N	VII; VI; X; III	D	2	5-8

Scientific Name	C3/C4	Native Status	Vegetation Class	Acid/Basic Soils	Sun/Shade	Flw Month
<i>Panicum columbianum</i> Scribn.	C3	N	XII; X	B	2	6-8
<i>Panicum commutatum</i> J.A. Schultes	C3	N	VII; XI; V	C	3	5-8
<i>Panicum depauperatum</i> Muhl.	C3	N	XII; X	B	1	6-8
<i>Panicum dichotomum</i> L.	C3	N	XI; VII; V	C	4	6-8
<i>Panicum jooirii</i> Vasey	C3	N	VI; III C		4	5-8
<i>Panicum laxiflorum</i> Lam.	C3	N	VII; X	C	2	5-8
<i>Panicum lindheimeri</i> Nash	C3	N	IX; X; VI; VII	C	2	6-8
<i>Panicum linearifolium</i> Scribn. ex Nash	C3	N	XII; X	D	1	5-8
<i>Panicum microcarpon</i> Muhl. ex Ell., non Muhl.	C3	N	IX; VI	B	2	5-8
<i>Panicum oligosanthos</i> J.A. Schultes	C3	N	XII; X	E	1	6-8
<i>Panicum polyanthes</i> J.A. Schultes	C3	N	VI; IX; III	B	2	6-9
<i>Panicum ravenelii</i> Scribn. & Merr.	C3	N	X; VII	B	2	5-8
<i>Panicum scoparium</i> Lam.	C3	N	IX; VI; X	B	1	6-8
<i>Panicum sphaerocarpon</i> Ell.	C3	N	VII; X; XII; XI	B	2	6-8
<i>Panicum villosissimum</i> Nash	C3	N	X; XII	A	1	5-8
<i>Panicum yadkinense</i> Ashe	C3	N	I; VI*	C	2	5-8
<i>Phalaris arundinacea</i> L.	C3	Nn	IX; VI; II	D	1	6-7
<i>Phalaris caroliniana</i> Walt.	C3	N	X; VII	C	1	5-6
<i>Pheum pratense</i> L.	C3	E	X; VII	D	1	7
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	C3	En	II; IX	D	1	8
<i>Piptochaetium avenaceum</i> (L.) Parodi	C3	N	VII; X; XI; XII	B	3	4-5
<i>Poa alsodes</i> Gray	C3	N	VII; V; III	B	2	5
<i>Poa annua</i> L.	C3	E	VII; X	D	1	4-7
<i>Poa autumnalis</i> Muhl. ex Ell.	C3	N	VII; V; XI	C	4	4-5
<i>Poa cf. angustifolia</i> L.	C3	Nn	X; VII	D	2	5-6
<i>Poa chapmaniana</i> Scribn.	C3	N	X; VII	B	1	5-6
<i>Poa compressa</i> L.	C3	E	VII; X; XI; XII	D	2	5-6
<i>Poa cuspidata</i> Nutt.	C3	N	XI; V	C	5	4-5
<i>Poa pratensis</i> L.	C3	En	VII; X; III	D	2	5-6
<i>Poa sylvestris</i> Gray	C3	N	VII; V; III	D	4	5
<i>Poa trivialis</i> L.	C3	Nn	III; VI; VII	E	2	6-7
<i>Sphenopholis intermedia</i> (Rydb.) Rydb.	C3	N	VII; VI; III; V	D	3	6-7
<i>Sphenopholis nitida</i> (Biehler) Scribn.	C3	N	XI; VII; V	B	3	5-6
<i>Sphenopholis obtusata</i> (Michx.) Scribn.	C3	Nw	X; VII	D	2	5-6

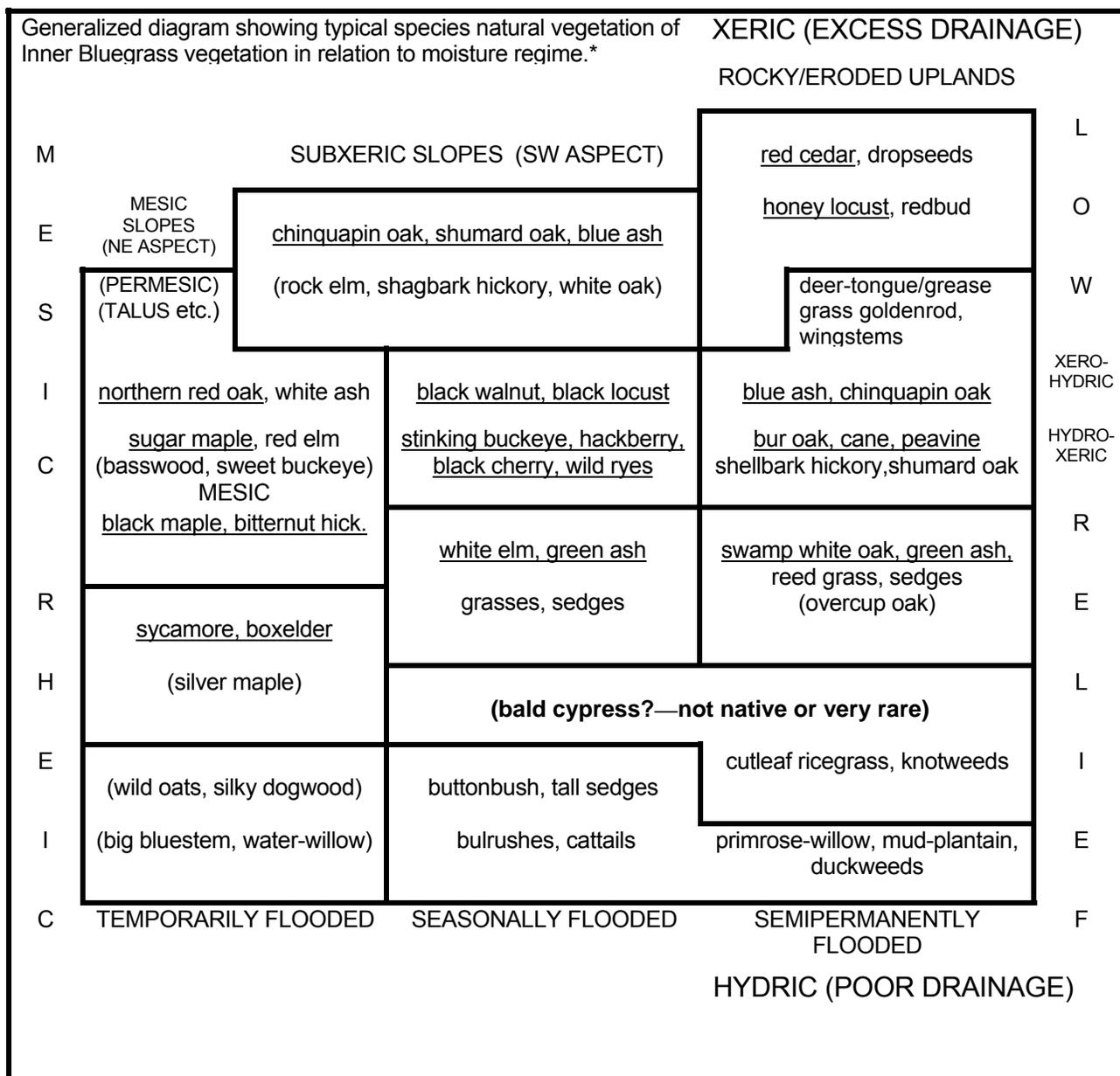
Scientific Name	C3/C4	Native Status	Vegetation Class	Acid/Basic Soils	Sun/Shade	Flw Month
<i>Andropogon gerardii</i> Vitman	C4	N	X; XII; I*	C	1	7-8
<i>Andropogon glomeratus</i> (Walt.) B.S.P.	C4	N	IX; XI	C	1	9
<i>Andropogon gyrans</i> Ashe	C4	N	X; XII	D	1	9-10
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Steud.) Hack.	C4	W	X	D	1	8-9
<i>Andropogon scoparius</i> Michx.	C4	N	XII; X	C	2	9
<i>Andropogon ternarius</i> Michx.	C4	N	X; XII	CB	1	8-9
<i>Andropogon virginicus</i> L.	C4	N	X; IX	C	1	9-10
<i>Aristida dichotoma</i> Michx.	C4	N	XII; X	B	1	8-9
<i>Aristida longispica</i> Poir.	C4	N	XII; X	D	1	8-9
<i>Aristida oligantha</i> Michx.	C4	N	X	C	1	8-9
<i>Aristida purpurascens</i> Poir.	C4	N	XII; X	C	1	8-9
<i>Aristida ramosissima</i> Engelm. ex Gray	C4	N	XII; X	C	1	7-8
<i>Arthraxon hispidus</i> (Thunb.) Makino	C4	A	VI; IX; III	C	2	9-10
<i>Brachiaria platyphylla</i> (Munro ex Wright) Nash	C4	Ns	III	D	2	8-9
<i>Cenchrus longispinus</i> (Hack.) Fern.	C4	N	I; X*	C	1	7-8
<i>Cynodon dactylon</i> (L.) Pers.	C4	S	X; VII	D	1	7-8
<i>Digitaria ischaemum</i> (Schreb.) Schreb. ex Muhl.	C4	E	X; IX	D	1	7-8
<i>Digitaria sanguinalis</i> (L.) Scop.	C4	E	X; VII	D	1	7-8
<i>Echinochloa crus-galli</i> (L.) Beauv.	C4	E	IX; X; IV; VII	D	1	6-8
<i>Echinochloa muricata</i> (Beauv.) Fern.	C4	N	IX; II*	D	1	7-8
<i>Eleusine indica</i> (L.) Gaertn.	C4	E	VII; X	E	1	7-8
<i>Eragrostis cilianensis</i> (All.) Vign. ex Janchen	C4	E	X; VII	D	1	7-8
<i>Eragrostis frankii</i> C.A. Mey. ex Steud.	C4	N	I; VII; X*	D	1	8
<i>Eragrostis hypnoides</i> (Lam.) B.S.P.	C4	N	I; II*	D	1	8-9
<i>Eragrostis minor</i> Host	C4	E	X; XII	D	1	7-8
<i>Eragrostis pectinacea</i> (Michx.) Nees ex Steud.	C4	E	X; VII; I	D	1	7-8
<i>Eragrostis spectabilis</i> (Pursh) Steud.	C4	N	X	C	1	7-8
<i>Leptochloa brachiata</i> Steudl.	C4	Ns	X; IX; VI	D	1	7-8
<i>Leptochloa fascicularis</i> Lam.	C4	Ns	IX; X	D	1	7-8
<i>Microstegium vimineum</i> (Trin.) A. Camus	C4	A	III; VII; IX; V	C	4	9-10
<i>Miscanthus sinensis</i> Anderss.	C4	A	VII; X	C	1	9
<i>Muhlenbergia frondosa</i> (Poir.) Fern.	C4	N	III; I; VI	E	3	8-9
<i>Muhlenbergia schreberi</i> J.F. Gmel.	C4	N	VII; X; III	E	3	8-9
<i>Muhlenbergia sobolifera</i> (Muhl. ex Willd.) Trin.	C4	N	XI; XII; V	E	4	8-9
<i>Muhlenbergia sylvatica</i> Torr. ex Gray	C4	N	V; III; VII	C	4	8-9

Scientific Name	C3/C4	Native Status	Vegetation Class	Acid/Basic Soils	Sun/Shade	Flw Month
<i>Muhlenbergia tenuifolia</i> (Kunth) Trin.	C4	N	XI; V	B	4	8
<i>Panicum anceps</i> Michx.	C4	N	X; VII	C	1	7-8
<i>Panicum capillare</i> L.	C4	N	X; VII	D	1	7-8
<i>Panicum dichotomiflorum</i> Michx.	C4	N	X; IX; VI; I	D	1	7-8
<i>Panicum flexile</i> (Gattinger) Scribn.	C4	N	XII; X	D	1	7-8
<i>Panicum gattingeri</i> Nash	C4	N	X; XII; VII	D	1	8-9
<i>Panicum philadelphicum</i> Bernh. ex Trin.	C4	N	VII; X	C	1	7-8
<i>Panicum rigidulum</i> Bosc ex Nees	C4	N	IX; II*	C	2	7-8
<i>Panicum verrucosum</i> Muhl.	C4	N	IX; VI	A	1	8-9
<i>Panicum virgatum</i> L.	C4	N	I; IX*	D	1	7-8
<i>Paspalum dilatatum</i> Poir.	C4	S	VI; IX; X	D	1	7-8
<i>Paspalum floridanum</i> Michx.	C4	Ns	IX; VI; I*	D	1	8
<i>Paspalum fluitans</i> (Ell.) Kunth	C4	N	I; II*	D	1	8-9
<i>Paspalum laeve</i> Michx.	C4	N	VII; X	C	1	7-8
<i>Paspalum pubiflorum</i> Rupr. ex Fourn. var. <i>glabrum</i> Vasey	C4	N	IX; X; VI; VII	D	1	7
<i>Paspalum setaceum</i> Michx. var. <i>muehlenbergii</i> (Nash) Banks	C4	N	X; VII	D	1	7-8
<i>Saccharum alopecuroidum</i> (L.) Nutt.	C4	N	VII; X	B	2	9
<i>Saccharum giganteum</i> (Walt.) Pers.	C4	N	IX; VI; X	B	1	9
<i>Setaria faberi</i> Herrm.	C4	A	X; VII	D	1	7-8
<i>Setaria parviflora</i> (Poir.) Kerguelen	C4	Ns	X; VII; IX; VI	D	1	7-8
<i>Setaria pumila</i> (Poir.) Roemer & J.A. Schultes	C4	E	X; VII; XII	D	1	6-8
<i>Setaria viridis</i> (L.) Beauv.	C4	E	X; VII; XII	D	1	6-8
<i>Sorghastrum nutans</i> (L.) Nash	C4	N	X; VII	C	1	8-9
<i>Sorghum bicolor</i> (L.) Moench	C4	E	X; VII	D	1	7-8
<i>Sorghum halepense</i> (L.) Pers.	C4	E	X; VII; VI	D	1	7-8
<i>Sporobolus clandestinus</i> (Biehler) A.S. Hitchc.	C4	N	XII; X; XI	D	1	8-9
<i>Sporobolus compositus</i> (Poir.) Merr.	C4	N	X; XII; VII	D	1	8-9
<i>Sporobolus neglectus</i> Nash	C4	N	X; VII	D	1	8-9
<i>Sporobolus vaginiflorus</i> (Torr. ex Gray) Wood	C4	N	XII; X	D	1	8-9
<i>Tridens flavus</i> (L.) A.S. Hitchc.	C4	N	X; VII; XII	D	2	8-9
<i>Tripsacum dactyloides</i> (L.) L.	C4	N	IX; X; I*	C	1	6-7

Appendix 2. Explanatory Diagrams for the Model of Habitat Gradients



* See text for more description of these 12 basic classes, as indicated by the number at top center within each box.



* Underlined species are locally dominant trees in more natural vegetation; others are a selection of typical associates (generally in more open or successional habitats); species in parentheses are generally uncommon in the region but typical of special habitats.