THE HERBIVORE HYPOTHESIS FOR BLUEGRASS WOODLAND

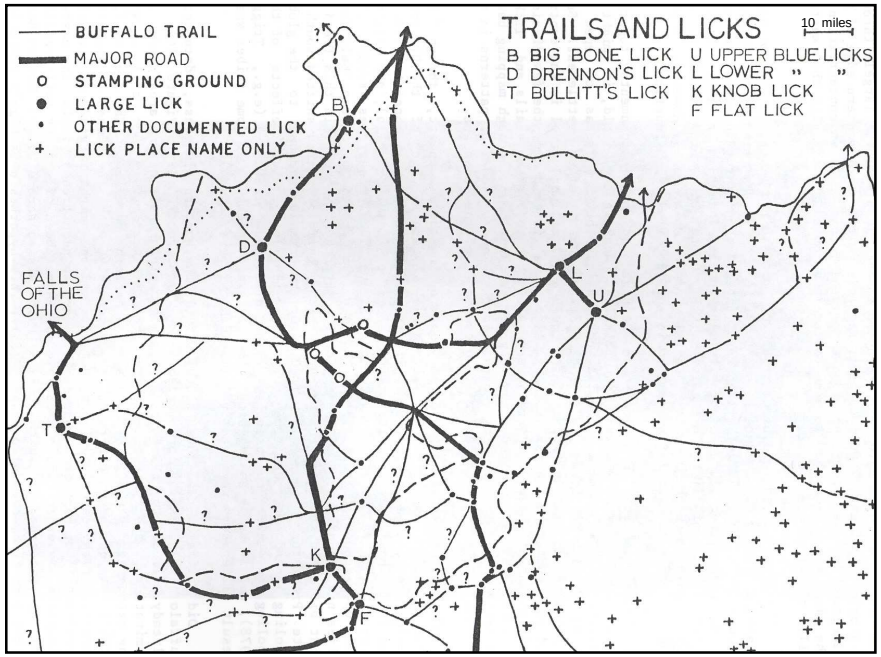
Cover: American Mastodon, a species of spruce woodlands and cool temperate lowlands that fed a lot on woody plants (including bark and fruit), rather than mostly grass as in the mammoths. Once common in the Bluegrass region, it survived on Earth until 4000-5000 years ago. [From painting by Charles R. Knight at the Field Museum (Chicago), via Wikipedia.]

The Herbivore Hypothesis for Bluegrass Woodland.

Notes by Julian Campbell, Feb 2012: htttp://bluegrasswoodland.com.

The Hypothesis. Before human civilization, patterns of herbivory in space and time, especially by larger animals, were a major factor maintaining the diversity of woodland on eutrophic soils in temperate regions. If so, the modern decline in naturally-behaving larger animals has often allowed browsing-sensitive plants to increase in situations where they would have been more controlled in the past. Such plants would include some aliens that have now prospered in more populated regions, where even deer and livestock are restricted. In contrast to fire, the original impact of herbivory was concentrated on mineral-rich soils with productive vegetation. Moreover, regular browsing as well as rapid decomposition would have reduced fuel-loads in woodland on such soils.

There is diverse circumstantial evidence for this concept. At the species level, several native plants are associated with the disturbances of cattle and deer, or with old human paths and mowed areas. These include the endangered species, running buffalo clover. At the habitat level, dynamic patterns in species composition are often correlated with apparent effects of larger herbivores, though historical details are usually obscure. In his book on grazing in forests, Vera (2000) delved deeply into such details for central Europe, suggesting a general theory that can also be applied to Bluegrass Woodland (see p. 6). At larger scales, there is a lot more work to do. For example, using a new tool—the analysis of dung-fungal spores in ancient sediments, Gill et al. (2012, Quat. Sci. Rev. 34:66-80) have shown in midwestern regions that post-glacial collapse of megafauna was followed by anomalous woodland that included much of the relatively palatable ash and elm. Subsequently, there was an abrupt increase in charcoal, and within a millenium or so it appears that frequent burning by humans led to woods with more oak and hickory. Red cedar is one of the most unpalatable trees, but the 'cedar glades' of east-central states could have been refuges for larger migrating herbivores during cold periods (with forage in nearby cane).



Map of old trails and licks in northern Kentucky at the time of settlement (1750-1800), reconstructed from historical accounts and place names. The northern boundary is the Ohio River; dashed line is the geological boundary of Bluegrass region; dotted is the S glacial limit.

Running buffalo clover usually occurs along trails in thin woods.

Potential Tests. This concept can be probed with varied methods.
A. Comparison of plots with different histories of herbivore effects.
B. Experimental use of herbivores on selected plots in woodland.
C. Planting plots with different composition, then experimenting.
D. Studying the selection of plants by herbivores and their responses.
For D, there is already a long history of 'browse-preference' or 'palatability' studies, but there has still been little synthesis and application of such studies into general dynamic models of woodland. Deeper tests will come as we use results from A-D to refine models such as Vera's. For example, we could measure the extent to which large herbivores concentrate their effects in more palatable, nutritious vegetation typical of forest-gaps, and we could measure the extent to which such concentration causes less palatable—or more thorny—vegetation to develop. However, complete tests of such models with diverse free-ranging animals will be difficult in most eastern states.

Yet in the Bluegrass region, there is much potential for an aggregated series of tests at Griffith Woods (on US 62 in S Harrison Co.).
A. The whole farm has a wide range of disturbance-history, with woodlots fenced off from cattle for different periods and suggesting associated differences in vegetation. There is also considerable variation in the effects of deer, which appear to maintain some grassy areas within brushy old fields and even young woods. It would be useful to study such patterns in relation to controlling factors.
B. Simple long-term experiments could be established in existing older woods, younger woods, and old fields, in order to compare effects of browsing, burning, combinations and controls. Several approaches have already been proposed, but we need more careful discussion of technical and statistical issues.
C. Various experimental plantings have been established now for 5-10 years. These include several blocks of cane, which can be compared with warm-season grasses and old fields. In the 'collection field' a diverse set of planted trees and shrubs has already shown spatial pattern in the degree of browsing by deer on blue ash.
D. With expertise of KDFWR, UK Forestry and others, a general review of browsing-studies in east-central states would be a good way to pool talent and 'get on the same page' for developing models.

Remarkable half-acre glade at Griffith Woods, on a well-drained terrace where herbivores have kept out trees and instead promoted bluegrass. Cattle have been absent for at least 40 years (see p. 4).

The author (in his 'woolly' period) offering different trees to bison at the Game Farm (Franklin County) in 1978; they loved sugar maple.

Potential Applications. These can be focused on plant or animal resources. The recovery of rare plants like running buffalo clover should ideally be combined with efforts to restore a more naturalistic habitat. If we discover what browsing regimes by native ungulates—or livestock—can be used to maintain optimal conditions for the clover, significant progress could be claimed. In a broader economic context, optimal browsing regimes might also be developed for maintaining 'orchards' of native nut and fruit trees, as probably existed around regular campsites and villages before Columbus (or even Boone). Also, reduction of invasive aliens can probably be achieved with seasonal use of livestock, or perhaps eventually by rotated bison and elk in enclosures at Griffith Woods. Bush honeysuckle and winter-creeper often appear to be reduced in more intensively browsed woods, and controlled experiments are needed. Original seasonal patterns of browsing may be relevant (see right).

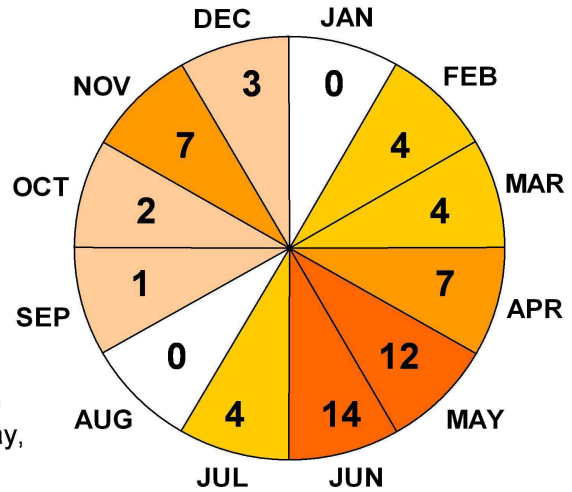
Deeper research into the evolved role of larger herbivores could enhance historical, biological and aesthetic aspects of the hunting experience. If a large enough block of Bluegrass Woodland can be managed, more natural types of 'wildlife opening' might be simulated. Already, a few 'glades' at the Griffith Farm are becoming similar to the remarkable "Grassy Lick" that pioneers of the 1770s found to be covered with bluegrass and "much more frequented by Buffalo than any of the other licks on said creek" (in Montgomery Co. on similar soils to Griffith). To keep the woods thin, maintaining grassy openings and canebrakes, the role of large browsing animals is probably at least as important as fire, if the original ecology is sought. As old William Clinkenbeard recalled in 1842: "Could not burn this country; always too damp. Burn... out in the poor barrens, it did—But never could here, or [it] would [have] been all burnt up, so many hunting fires.—Wet damp soil under the grass, kept it wet."

There would also be much interest in how to use livestock within woodland managed for biodiversity and ecological restoration. Can we find a way—at least in the 'non-profit' world—to balance production of meat with promotion of native plants and simulation of the original disturbance-regime?

Monthly numbers of recorded buffalo sightings in the central Ohio Valley during 1750-86, as reported in all available accounts.

Darker red indicates clustering of records.

The largest herds were reported during Apr-May, with 100-1000+.

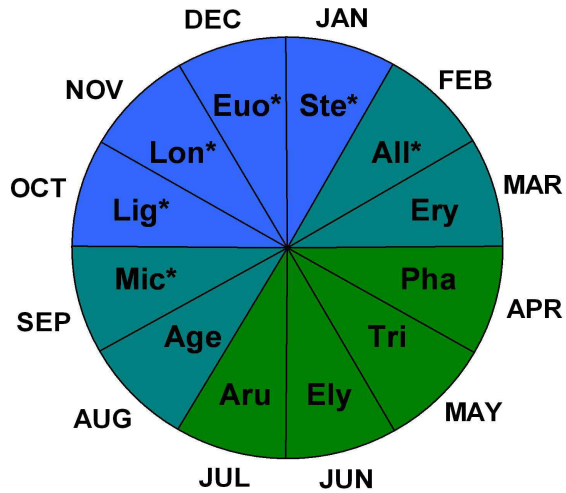


Can some return to the original browsing-regime reduce alien plants? Most of the common aliens during Oct-Dec do provide good forage.

Green: season with most new growth of native forage plants in Bluegrass Woodland.

Blue: season with most exposure of alien plants* relative to native plants.

Cane (Aru) was the only abundant native forage persisting into Oct-Jan.



Abbreviations indicate typical natives and aliens (*) in each month: **Ste**llaria media (chickweed); **All**iaria (garlic-mustard); **Ery**thronium spp. (trout-lilies); **Pha**celia purshii (Miami mist); **Tri**folium spp. (buffalo clovers); **Ely**mus spp. (wild ryes); **Aru**ndinaria (river cane); **Age**ratina (snakeroot); **Mic**rostegium (Japanese grass); **Lig**ustrum spp. (privets); **Lon**icera spp. (honeysuckles); **Euo**nymus spp. (winter-creeper etc.).

Submesic woods at Buckley Hills: no artificial weeding, but intense browsing by deer prevents winter-creeper from covering ground.

Walnut-hackberry woods at the Griffith Farm, with wild rye dominant on the ground. Lack of honeysuckle seems due to deer browsing.

Submesic woods at UK Arboretum: honeysuckle cleared but winter-creeper remains dominant; perfect site for trials with goats or sheep.

Locust-cherry woods adjacent to above site, with much more honeysuckle and much less grass. There seems to be less deer browsing.

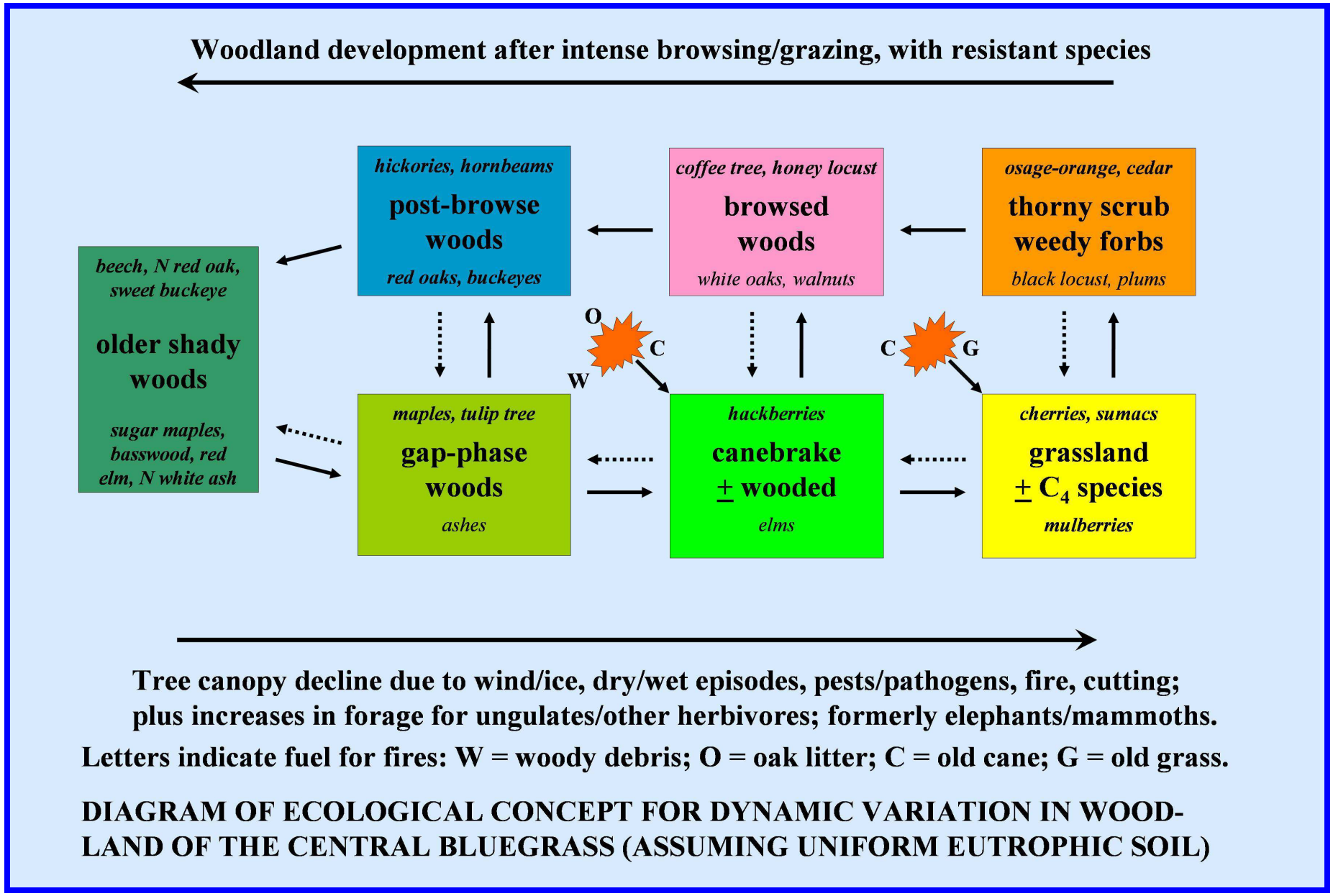


DIAGRAM OF ECOLOGICAL CONCEPT FOR DYNAMIC VARIATION IN WOODLAND OF THE CENTRAL BLUEGRASS (ASSUMING UNIFORM EUTROPHIC SOIL)

Footnote. This model can be extended to much of the eastern U.S.A. based on concepts developed in central Europe. For further discussion, see Vera, F.W.M. 2000. Grazing Ecology and Forest History. CABI Publishing, Wallingford, England. Critics (e.g., Mitchell in J. Ecol. 2005, 93: 168-177) have shown Vera's thesis to be exaggerated in some cases, but generally agree that herbivores often cause shifts in vegetation.