

The anomalous Kentucky coffeetree: megafaunal fruit sinking to extinction?

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Abstract The Kentucky coffeetree (*Gymnocladus dioica*, Fabaceae) is an ecological paradox. A rare tree in nature in eastern and central North America, *G. dioica* produces legumes that are only known to be dispersed by water, but appear similar to fruits consumed and dispersed by elephants and rhinoceros. One would expect the pods to be consumed by livestock, but the pulp and seeds are toxic to cattle and sheep. We examine the puzzle of *G. dioica* dispersal in light of its other reproductive and life history characteristics and find that it probably is a botanical anachronism, in terms of both a set of dispersal agents long extinct and habitats, including what we term megafaunal disclimaxes, which have disappeared. Large seeds, the megafaunal gestalt of the fruit, a dioecious mating system, and shade-intolerance combined with vigorous cloning suggest a widely dispersed pioneer of Miocene through Pleistocene habitats profoundly altered by large-mammal herbivory. As to what ate it, we can only say there were once many candidates. We hypothesize that the plant is an ecological anachronism, sinking to extinction in the wild.

Keywords Botanical anachronism · Megafaunal disclimax · *Gymnocladus dioica* · Megafaunal fruit hypothesis · Seed dispersal syndromes

Introduction

The Kentucky coffeetree [*Gymnocladus dioica* (L.) K. Koch, Fabaceae] is a rare, usually dioecious tree of eastern and midwestern North America. Its range in nature extends from southern Ontario in the north, west to Minnesota, south to Arkansas, and north and east to New York. The species seems to be absent from surveyor's records in pre-settlement Indiana (Lindsey et al. 1965), while even exhaustive censuses of natural habitats in the center of its range barely record *G. dioica* (e.g., Lindsey et al. 1961). Secondary references simply refer to it as "rare" except where planted by people (Deam 1921). Across its entire natural range, the tree is found in floodplains (Barnes et al. 1981), alongside old locations of human habitation (Curtis 1959), and in scattered locations in upland forests (McClain and Jackson 1980). In nature, the species appears to be disappearing.

The only known dispersal agent of *G. dioica* is water, and that is puzzling. The legume of this tree is a large indehiscent pod that contains a sweet pulp and three to seven large seeds. Hundreds of mature pods may hang on pistillate trees from autumn through winter and into spring. Seeds are brown, round, and compressed, measure 2 cm across at the widest point, and are surrounded by a thick, hard seed coat. Physical dormancy can be broken by scarification or soaking in concentrated acid (Baskin and Baskin 1998). The legume does not resemble the fruit of other water-dispersed species: it is not very buoyant, contains a sweet pulp, and is large (15–25 cm long) rather than small and hard; seeds do not germinate underwater and sink even after prolonged immersion (see van der Pijl 1982; Murray 1986). Despite the anomalous characteristics for a water-dispersed species, nothing animate appears to be its primary or secondary dispersal agent in natural and semi-natural habitats anywhere in North America.

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The natural history of *G. dioicus* is inconsistent with a large-seeded K-selected species restricted to floodplains. First, the species grows well in uplands outside of its contemporary floodplain habitats, and it is considered to be drought resistant (Huxley and Griffiths 1992). Both traits are inconsistent with floodplain specialization. The flowers appear to be adapted for generalized insect pollination, but the species is both sparsely scattered and usually dioecious. It is odd that an obligate outcrosser that depends on a generalized insect pollination system should be rare and sparsely scattered, as generalized pollinators are unlikely to fly long distances from one flowering tree to another. On first principles, either a more efficient pollination system that directly delivers pollen to its targets or a greater density of individuals should be expected (we predict that strong pollen limitation in *G. dioicus* may be common in nature where isolated trees cannot cross with conspecifics, although we are not aware of any studies addressing the subject). In addition, *G. dioicus* clones vigorously in early seral upland and floodplain sites (McClain and Jackson 1980) and is shade-intolerant, which in combination are often characteristics of early-successional trees (Grime 1979). Large seed size is usually but not always an attribute of late-successional tree; pioneer exceptions are likely tied to particular disperser guilds (e.g., Cordeiro et al. 2004). The Kentucky coffeetree's contemporary ecology is a study of contradictions.

Anachronism?

Anomalous fruits, an anomalous life history, and a dioecious breeding system with generalist pollinators make it most unlikely that this tree is “born to be rare” as a sparsely distributed tree disseminated by water. Rather, it appears to have the characteristics of a megafaunal fruit. Its large heavily protected seeds, sweet pulp, and an indehiscent pod certainly appear to put it into the “megafaunal fruit” syndrome, thought by Gautier-Hion et al. (1980, 1985) to be adapted for consumption and dispersal by large mammals (also see Alexandre 1978). Typical fruits dispersed exclusively by African elephants tend to be large, with a fibrous pulp, indehiscent, thick-husked, brown or dull-colored, and with seeds mechanically or perhaps chemically defended against digestion (Gautier-Hion et al. 1985; Baskin and Baskin 1998). This syndrome applied beyond West Africa fits with rhinoceros-dispersed *Trewia nudiflora* L. fruits in South Asia (Dinerstein and Wemmer 1988). In the case of *G. dioicus*, there are no known biotic agents (Beal 1898; Werthner et al. 1935), leaving the paradox of a poisonous legume that looks edible, now dispersed by water along river courses, but thriving as rare individuals and clones in upland sites.

An obvious hypothesis put forth by others is that the legume of *G. dioicus* is a botanical anachronism; the species was once dispersed by large mammals that are now extinct (Janzen and Martin 1982; Barlow 2000). Janzen and Martin (1982) elaborate this hypothesis in detail, arguing that many tropical and temperate fruits, large and small, fall into a megafaunal fruit syndrome of species widely and consistently dispersed by American horses, cattle, camels, sloths, titanotheres, and pachyderms that disappeared before or during the Pleistocene (see Webb 1983; Janis et al. 2004). The megafaunal fruit argument is based on the idea that a suite of fruit attributes, including tough indehiscent pods and large seeds like those of *G. dioicus*, indicates adaptation to megafaunal dispersal. The hypothesis is plausible in light of the immense fauna of large animals—rivaling and even exceeding that of East Africa today—that once roamed North America (Kurtén and Anderson 1980; Tiffney 2004). At the same time, the pod contains a thick pulp that is sweet but poisonous to humans and livestock (Tehon et al. 1946; Kingsbury 1964; Evers and Link 1972). Apparent toxicity to contemporary ungulates sets the legume apart from other megafaunal fruits, which are often avidly consumed by domestic livestock that Janzen and Martin (1982) plausibly view as surrogate megafaunal dispersal agents. Cattle and other livestock are not surrogate dispersal agents of this tree.

We agree that *G. dioicus* belongs in the megafaunal syndrome, despite paradoxical attributes of this tree and ambiguities in the syndrome itself (Howe 1985). Although there is a virtual absence of primary literature on the ecology of this rare and apparently vanishing species in nature (i.e., we know of two papers in the last 50 years: Janzen 1976; McClain and Jackson 1980), we find enough evidence in secondary and tangential resources to have confidence that the tree has an interesting story that should be told. Accordingly, we extend the megafaunal syndrome to include corroborating evidence from its life history and mating system, discuss characteristics of *G. dioicus* that could help it survive without its primary dispersers, and puzzle about the toxic anomaly.

The established syndrome

“A dispersal syndrome is a constellation of fruit and seed characteristics which is associated with a general mode of dispersal” (van der Pijl 1982). Dispersal syndromes define trends, but they are of less use in predicting particular dispersal interactions (Howe and Smallwood 1982; Howe 1985; Herrera 2002). In the case of *G. dioicus*, the question is not what eats the fruit, but whether anything ever ate the fruit. It is easier to distinguish between abiotic and biotic dispersal than between different biotic agents. The strong

resemblance to general characteristics of megafaunal fruits and its deviation from usual characteristics of water-dispersed species suggests that this legume is adapted to be consumed. Fruit size is well correlated with disperser size (Jordano 1995), and seeds as large as those of *G. dioicus* are almost always dispersed by large vertebrates (Hughes et al. 1994) or large rodents. In this case, both are either absent or do not eat or hoard the seeds where the tree occurs.

The key characteristics used by Janzen and Martin (1982) to define a megafaunal fruit syndrome include: (1) a large and indehiscent structure; (2) pulp that is rich in sugar, oil, or nitrogen; (3) similarity to Old World fruits currently dispersed by extant megafauna; (4) nuts and seeds that are well protected mechanically to prevent damage by the teeth of megafauna; (5) fruits attract few or no extant native vertebrates; (6) undispersed seed crops that rot on the ground beneath fruiting trees; (7) fruits that are avidly consumed by horses, pigs, and cattle, which act as replacements for the extinct megafauna. The hypothesis is eminently plausible, although Howe (1985) noted that species ascribed to the syndrome would have to experience low seedling mortality near the parent tree to persist and that some fruits listed as examples had known extant dispersal agents. The syndrome has since been quantitatively described by Guimaraes et al. (2008), who distinguish large-seeded species, such as *G. dioicus*, from other compound fruits with many small seeds. In any event, *G. dioicus* fits the Janzen and Martin criteria almost perfectly, except that the legume and seed are toxic to livestock. For this to be a megafaunal fruit, the *extinct* megafauna would have to have included taxa that could consume toxins not metabolized by livestock alive today.

It is not obvious what the active mammalian toxin in *G. dioicus* might be. Early evaluations noted the alkaloid cytosine, which has similar bonding properties as nicotine but which is not as potent for humans (for an ecological interpretation, see Janzen 1976). More recent evaluations have found triterpenoid saponins in an Asian congener that are biologically active enough to be potential anti-human immunodeficiency viral (HIV) agents (Konoshima et al. 1995). *Gymnocladus dioicus* itself has nonprotein amino acids (Oh et al. 1995), which can be extraordinarily potent allelochemical defenses for most herbivores (Rosenthal 1991). However, the collection of nonprotein amino acids found in *G. dioicus* is similar to that found in another North American legume, *Gleditsia tricanthos* L. (Southon et al. 1994), which has legumes that are not poisonous to humans and are readily consumed by livestock (Evans and Bell 1978). Glycosides of terpenoid derivatives isolated from *G. dioicus* are also suspected of being sources of toxicity (Burrows and Tyrl 2001). There is no direct evidence that these are the active compounds that deter contemporary

mammals, much less active toxins or their synergies once overcome by extinct megaherbivores. Given the reality of multiple defenses in many trees and the absence of relevant surrogates in the modern fauna of North America, the roles of allelochemicals will probably remain a mystery without a massive, and unlikely, titration of livestock responses to chemical and structural components of the plant.

Persistence

The loss of megafaunal dispersers can be catastrophic to dependent tree populations, leading to rapid decline and extirpation (Alexandre 1978; Dinerstein and Wemmer 1988; Cochrane 2003). How could *G. dioicus* survive for so long? The persistence of *G. dioicus*—or any species—after 13,000 years without its primary dispersers begs for explanation. We argue that traits which allow for resilience are an important part of a refined megafaunal fruit syndrome. Several characteristics of *G. dioicus* increase the odds that it could persist for millennia without its primary dispersers (Barlow 2000). As an ornamental, the foliage and, more importantly, the seeds of *G. dioicus* are afflicted by very few pathogens (Pirone 1978) and are free from almost all herbivores and seed predators (Werthner et al. 1935; Pan et al. 1995). Moreover, its seeds resist decay for years (DNZ, personal observation) and are protected by an exceedingly hard seed coat. This fits the criterion of “indestructible offspring” (Howe 1985, 1989) required for persistence for millennia without megafaunal dispersers. The absence of seed predators is important because a plant with high seedling mortality near the parent tree would not survive for thousands of years without some agent dispersing its seeds effectively. Species with seeds that are dispersed in clumps, such as in fecal piles of large fruit-eating dispersal agents, should be more likely to develop adaptations for protection against pathogens and seed predators and thus should be more likely to persist without primary dispersers.

In studies on suspected anachronistic fruits in Brazil, Guimaraes et al. (2008) found that many species were able to persist because of the water dispersal of seeds, asexual reproduction, and Native American use. All three of these factors are probably important in the survival of *G. dioicus*. As mentioned earlier, seeds are now water-dispersed despite poor flotation. Additionally, *G. dioicus* is able to multiply asexually through basal sprouts extending from the root system (McClain and Jackson 1980), and stands of *G. dioicus* often occur near abandoned human habitations (often along rivers) where Native Americans and early European pioneers used seeds for game pieces and as a substitute for coffee (Curtis 1959; e.g., stands of trees on ridgetops near 1000-year-old burial mounds at Effigy Mounds National Monument, Iowa; HFH, personal observation).

The tree is not physiologically dependent on floodplains. Indeed, the comprehensive autecology of the tree by McClain and Jackson (1980) suggests that many floodplain sites probably correspond to former Native American settlements. Even floodplain presence may be an agency of something besides water.

What is missing?

Gymnocladus dioicus is hypothesized to have arrived in North America in the Miocene (Tiffney and Manchester 2001), coincident with the explosive adaptive radiation of large mammalian herbivores on the continent (Wing and Tiffney 1987; Janis 1993; Alroy 1999; Tiffney 2004). During the Miocene, 25–5 mybp, mammalian herbivores capable of dispersing *Gymnocladus* could have included North American rhinos, camels, or small- to medium-sized gomphotheres (Webb 1983; Janis et al. 2004). Modern livestock would have been dwarfed in diversity and size by many Miocene mammals, and thus are not necessarily good surrogates for extinct megafaunal dispersal agents.

Could some of the large herbivores have eaten the fruit and its toxins without ordeal, and be the primary dispersal agents? No one knows, but the Miocene had numerous candidates. A particular genus or species might have evolved a capacity to detoxify the active agent. The more likely scenario is that the capacity for feeding on toxic plant compounds increases with body size because the number, diversity, and volume of bacteria and protozoan symbionts that detoxify plant defenses increase with body size (Farlow 1987; Van Soest 1994; Fritz et al. 2002), suggesting that extinct megafauna substantially larger than contemporary sheep (30 kg) or large cattle (250 kg) could have consumed the legume of *G. dioicus* and been responsible for its dispersal. This hypothesis is entirely consistent with Tiffney's (2004) interpretation that megafaunal dispersal is a diffuse process. Elephants (*Loxodonta africana* Blumenbach) readily eat and disperse some fruits that are not eaten by other animals (Gautier-Hion et al. 1985; Dudley 2000), and black rhinoceros in southern Africa often consume the fruits and stems of highly toxic *Euphorbia* species that are avoided by other animals (Heilmann et al. 2006; see Kinghorn 1979). A variety of large non-elephantine mammals may have had similar capacities, followed by mastodont- and mammoth-sized herbivores. Extinct North American ground sloths (*Nothrotheriops shastensis* Hoffstetter), for instance, did not leave fruits like *G. dioicus* in coprolites, and in general seemed to feed on fairly digestible forage, but they did eat some plants (*Ephedra*, *Gueterria*, *Larrea*) that livestock—and just about everything else—now avoid (Hansen 1978; Hofreiter et al. 2000). It is quite possible that the body size and enhanced gut volume of very large

mammals of the pre-Pleistocene and Pleistocene made *G. dioicus* legumes a regular food for megaherbivores that “mesoherbivores” like horses and cattle cannot eat. The toxicity of the legume and seeds may have served as protection from seed predators and ineffective dispersers (Cipolinni and Levey 1997). In keeping with the consensus that interaction of a fruiting plant is usually with a group of functionally equivalent dispersal agents rather than a single species (Janzen 1980; Howe 1984; Herrera 1985; Wing and Tiffney 1987; Tiffney 2004), diffuse dispersal between *G. dioicus* and a set of large mammalian dispersal agents is likely part of what is missing.

In addition to missing dispersal agents, the habitats to which *G. dioicus* is well-suited almost certainly no longer exist in North America. African trees that survive in habitats frequented by elephants are likely to be highly toxic (Sheil and Salim 2004). The same may have been true of now extinct North American habitats once frequented and probably shaped by extinct mastodons, mammoths, less familiar gomphotheres, rhinos, and camels of the Miocene or early and middle Pleistocene. Reconstructions of flora tens of thousands of years ago paint only in a broad brush, but show ample evidence of massive changes in climate and vegetation during the tenure of *G. dioicus* in North America (see Webb 1983). More detailed reconstructions of Pleistocene habitats from much more complete fossil records leave little doubt that contemporary grasslands, savannas, and forests are incomplete reflections of the much more diverse associations of animals and plants that existed even 500,000–10,000 years ago (Guthrie 1984; Davis 1986; Overpeck et al. 1992; Graham et al. 1996; Jackson et al. 2000). As recently as 12,000 years ago, most of Central North America, probably coinciding with most of the range of *G. dioicus*, was covered with forests of compositions with no modern analogs (Overpeck et al. 1992). The contrast between contemporary environments in which *G. dioicus* barely persists in the wild and a much richer diversity of habitats of the recent to distant past leads us to speculate what world the tree might have found suitable.

Megafaunal disclimaxes

We hypothesize that the entire life cycle of *G. dioicus* is a relict of processes and environments driven by large mammals, long gone. Owen-Smith (1987) points out that African megaherbivores, such as elephants and giraffes, are so large that they are invulnerable to significant non-human predation. Unless disease intervenes, they saturate their habitats, causing so much destruction that forest is converted to scrub and grassland. We suggest that these highly disturbed habitats, what we term “megafaunal disclimaxes,” were the cradle for the evolution and proliferation

of species adapted to megafaunal dispersal. One could imagine population cycles of North American megaherbivores, sometimes decimated by disease and at other times released to their destructive potential, that created permanent transitional plant dynamics. With their world in a permanent state of successional flux, even modest dispersal rates of large seeds of a species that grows anywhere in a disturbed habitat, clones freely, is shade-intolerant, resists insects and pathogens, and is distasteful or toxic to most mammals might be a winning megafaunal tree. Such trees might grow in poorly dispersed clumps where dioecy is not a disadvantage, with occasional or even frequent dispersal by very large mammals that could eat a few fruits without ill effects. Such a tree might have been *Gymnocladus dioicus*.

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