MPF's Schwartz Prairie in St. Clair County, an example of a complex prairie ecosystem millions of years in the making.

By Doug Ladd

Tallgrass prairies are the most fertile and diverse expression of America's grassland heritage, providing endless opportunities for inspiration and learning. Appreciation and understanding of these fascinating natural systems are enhanced by taking a multidimensional approach, considering them not only in the present, but also considering their origins and history. Just as a rich stew brewing on the stove is the product of a diverse set of ingredients and processes that are not evident by merely peering into the pot, today's prairies are the result of a complex web of diverse interrelated factors extending back millions of years.

To achieve a full understanding of the why, where, and how of tallgrass prairies, we must consider two phases: Deep Time and post-glacial history. Eons before tallgrass prairies existed, millions of years of planetary history and the relentless engine of evolution created the foundations for grasslands and their biota. Then, in the more recent past, the post-glacial origin and spread of tallgrass prairies are intimately linked to seemingly unrelated factors, including the earliest history of humans in the New World.

Although the prairie story starts 125 million years ago, this is only a very recent part of Earth's history. If the 4.5-billion-year history of the planet were compressed into a single year, the formative events shaping our prairies would start around December 20. All the times given here are approximate and provide a general timeline—uncertainties and various interpretations result in differing opinions about exact dates. Additionally, new discoveries are changing our understanding of times and processes.

FOUR BILLION YEARS AGO LIFE ON EARTH BEGINS ▶

Setting the Stage: Peering into Deep Time

Life has been on Earth for some 4 billion years, but from a prairie perspective, things became interesting perhaps as early as 200 million, and certainly by 125 million years ago, with the emergence of the first true flowering plants (angiosperms). By 100 million years ago, flowering plants around the planet were rapidly diversifying into the precursors of our modern flora in all its varied expressions. Closely associated with many of these early plants was an evolving, highly specialized interdependency with insects for pollination, which remains essential to the continued existence of our modern prairies.

In 2015, a stunning discovery in a 100-million-year-old fragment of amber from Myanmar confirmed that grasses are far older than previously thought. The fossil on (illustrated on page 10) clearly shows a well developed grass that is visibly infected by an ergot fungus—a group of highly specialized fungi adapted to specific host plants. This find documents that grasses must have been sufficiently developed well before 100 million years ago to have allowed parasite evolution. Here in North America, grasses have been present for at least 57 million years.

As these early grasses evolved, they also acquired some characteristics that would render them well suited to their eventual role in prairie systems. Early land plants had the tissues responsible for growth and elongation, called meristems, located near their apices. If a shoot or branch tip was damaged or eaten, growth stopped. Some plants, including grasses, developed meristems at or below ground level, allowing plants to regrow and develop after fire, grazing, or (much later) lawn mowing. Many grasses and their relatives went a step further, developing additional specialized growth centers at the leaf bases and nodes of the stems. Called intercalary meristems, these growth points allowed plants to flourish under heavy grazing and browsing, illustrating the intimate evolutionary relationships among plants, animals, the physical environment, and natural processes.

Other families of plants that are important in prairies are also ancient. The first legumes (Fabaceae) appeared 60 million years ago, and the first sunflower relatives (Asteraceae) appeared by 50 million years ago, probably in South America, arriving in North America by 26 million years ago. Similarly, oaks, the most important trees in the prairie biome, appeared in modern form by 30 million years ago. The ancestral roots of the building blocks of modern prairie run deep into the past.

In the Old Days . . .

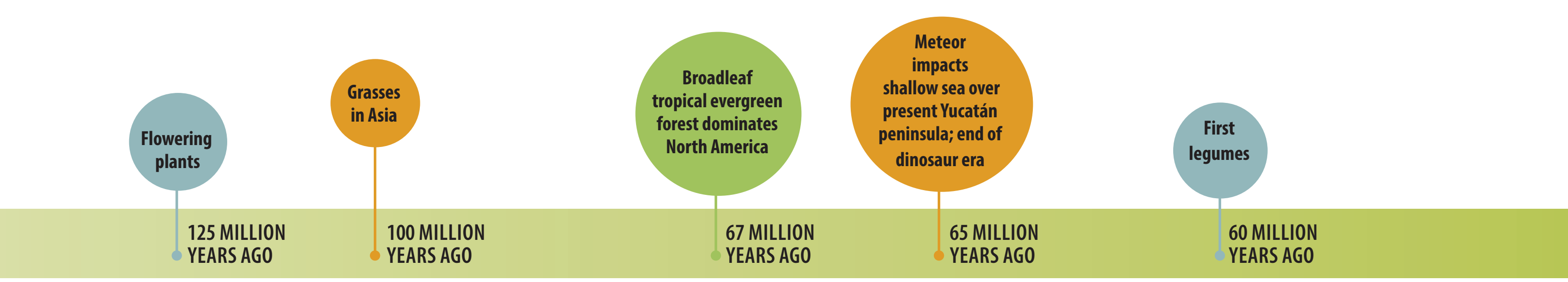
By 67 million years ago, near the end of a long period of stable, warm, humid, tropical climate, a vast swath of broadleaf evergreen tropical forest stretched across most of the North American continent that was above water. Interspersed among these magnolia-like trees were some giant trees—remnants of the extensive tropical coniferous forests that had preceded them. For the previous 40 million years, the Bearpaw Sea divided North America into separate eastern and western portions, covering much of the interior. This sea had been slowly draining for several million years.

When a small chunk of cosmic dust some six miles wide slammed into this shallow sea over the present-day Yucatán Peninsula 65 million years ago, it triggered a chain of catastrophic changes and extinctions, ending the dinosaur era. The age of mammals began, as they rapidly diversified from small, shrew-like creatures to a dazzling array of life forms occupying all of the world's major habitats. The prairies to come were foreshadowed in a period 55 to 40 million years ago, with a sharp rise in global temperatures and increasing dryness, perhaps allowing the first grassy areas to occur in forest openings of drier sites. This was compounded in North America by the rise of the Rocky Mountains, creating a rain shadow eastward even into Missouri as moist clouds from the west were scraped of their water as they crossed the peaks.

Then, 37 million years ago, in the late stages of the breakup of the supercontinent Pangea, the Antarctic and Australian land masses separated. This might not seem related to modern prairies, but it triggered a period of global cooling and increasing dryness resulting in a decline of global forest coverage and the rise of grassland habitats.

These conditions stimulated the evolution of a new type of photosynthesis in some grasses, called C4 photosynthesis. Plants with C4 photosynthesis are more efficient when there is limited carbon dioxide and/or dry conditions. This C4 photosynthesis, the defining trait of warm-season grasses, is a combination of altered plant structure and novel biochemical pathways. Over time, C4 capability evolved separately at least 45 times across many plant families, but grasses remain the champions of C4 expression: some 46% of all grasses are C4, compared with 3% of the world's total flora. The evolution of C4 grasses millions of years ago presaged their eventual flourishing in the seasonally hot, dry environments of central North America's grasslands in stages to come.

These trends continued through the next several million years, so that by around 25 million years ago, although woodlands and forests covered much of North America, grasslands domi-



❶ 100 million-year-old fragment of amber from Myanmar showing well developed grass spikelet infected by an ergot fungus. ❷ 45-million-year-old fossilized flowerhead from the Aster family resembling modern thistles from 45-million-year-old Patagonian rock. ❸ North American fossil of *Quercus prelobata* in the white oak group, 35 million years old, closely resembling modern relatives. ❹ 35-million-year-old fossil of mesquite (*Prosopis linearifolia*), showing well developed modern legume fruits.

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❶ COURTESY OF GEORGE POINAR, JR. ❷ ROM: EOCENE PATAGONIA FOSSILS OF THE DAISY FAMILY BY V.D. BARREDA, L. PALAZZESI, M.C. TELLERÍA, L. KATINAS, J.V. CRISCI, K. BREMER, M.G. PASSALIA, R. CORSOLINI, R. RODRÍGUES BRIZUELA, F. BECHIS; SCIENCE 24 SEP 2010:1621. REPRINTED WITH PERMISSION FROM AAAS. ❸ COURTESY UNIVERSITY OF MICHIGAN MUSEUM OF PALEONTOLOGY UMORF SITE; UMORF.UMMP.LSA.UMICH.EDU, ©2017 BY THE REGENTS OF THE UNIVERSITY OF MICHIGAN. ❹ COURTESY UNIVERSITY OF COLORADO NATURAL HISTORY MUSEUM BOTANY COLLECTION ❺ (PDF) BULLIFORM PHYTOLITH RESEARCH IN WILD AND.... AVAILABLE FROM: HTTPS://WWW.RESEARCHGATE.NET/PUBLICATION/283078545_BULLIFORM_PHYTOLITH_RESEARCH_IN_WILD_AND_DOMESTICATED_RICE_PADDY_SOIL_IN_SOUTH_CHINA?_SG=N02LOUCJWOYIKZYHJOVCUABIYFVNPWDM7PBWLXLEELQ8E07CSSOYYXXXKXJNPONJBIRZ1EX1MW [ACCESSED AUG 20, 2018].

nated much of the central portion of the continent. This spread of grasslands was accompanied by an increasing diversification of both grasses and grazers, including the evolution of mammals with durable, high-crowned, enamel-rich teeth adapted to feeding in these grasslands. This trait, called hypsodonty, is an adaptation to grazing in gritty environments and eating plants with lots of small silica particles in them. These microscopic silica particles, called phytoliths ("plant stones") are thought to be an adaptation to grazing pressures, and are well developed in grasses. The ancient evolutionary dance of influence and counterinfluence between grasses and grazers continued.

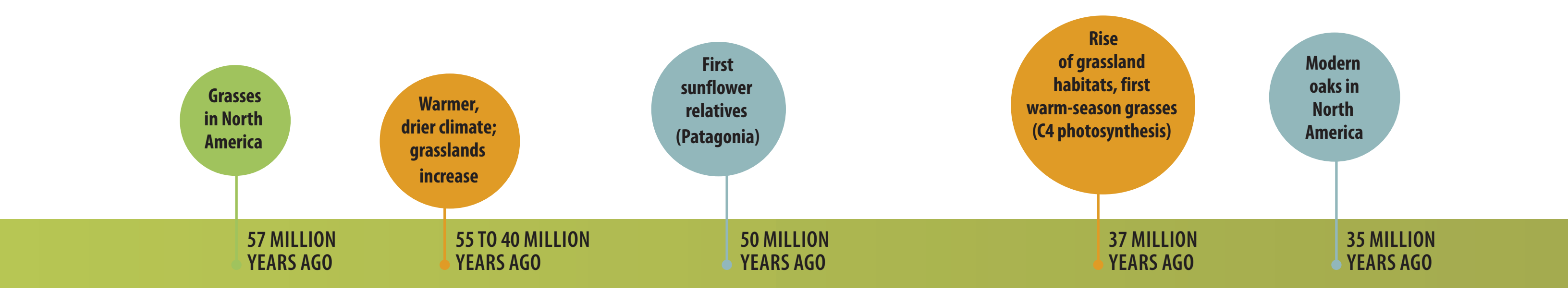
By 8 to 6 million years ago, there was a global expansion of grasslands and grazers marked by an increasing prevalence of C4 grasses. At about this same time, a group of primates arose from a common ancestor with chimpanzees. This genetic lineage was already using stone tools and implements by 3.3 million years ago, and would eventually lead to the modern humans that were to be an essential part of both the development and demise of tallgrass prairies.

In North America, multiple glacial events began impacting the region some 2.5 million years ago. These glacial periods were once thought to comprise four well defined glacial intervals, but we now know there were millions of years of repeated glacial advances and retreats covering various areas. Glacial activity was accompanied by extensive scouring, meltwater impacts, and other processes that transformed the landscape, biological patterns, and soils over much of the continent. This complex of cyclic glacial interactions continues, although impacted by human influences of climate change. Thus, the past few million years in North America can be summarized as more glacial than ice-free. The extensive grasslands in the heartland retreated during much of this period, as cooler, wetter periods favored woodland systems.

The stage was set: through millions of years of interactions, adaptation, and selection, a complex web of interdependencies had evolved among grasses, grazers, and grassland systems including a diverse flora. Although there were many incarnations of grasslands during this period, there had not yet been a tallgrass prairie on the planet—but the parts were assembled and waiting.

Humans Engender the Prairies

The last key ingredient for the genesis of tallgrass prairies arose some 200,000 to



300,000 years ago, when modern humans (*Homo sapiens*) arose in Africa, spreading through much of Europe and Asia by 40,000 years ago. We became a technologically sophisticated, tool-using species that was supremely adaptable and able to rapidly populate new regions and habitats. Still, the Americas remained untouched by humans for thousands of years.

Near the peak of the most recent glacial advance 17,000 years ago, much of the world's water was tied up in glacial ice, lowering sea levels. A broad, icy, wind-swept, barren grassland steppe hundreds of miles wide connected eastern Asia and northwestern North America (now Alaska). This was the most recent appearance of Beringia, a land bridge between the continents. Beringia had appeared and disappeared multiple times through the glacial millennia, creating an intermittent biological highway allowing plants and animals to cross.

During this most recent opening, humans, probably pursuing the grazing and browsing mammals upon which they depended for their survival, crossed from eastern Asia into the Americas. The exact time and sequence of human occupation of the Americas is largely unknown, and there are tantalizing, but controversial, data suggesting earlier occupations from various vectors, but certainly near the time of the last glacial maximum, humans were in North America (15,000 to 18,000 years ago). After entering the New World and finding a land rich with resources, including an astounding and often fearsome abundance and diversity of large mammals, humans rapidly dispersed through much of the Americas. For the past 12,000 to 14,000 years this has included an essentially continuous human presence in what is now Missouri. At the time of their arrival, because of glacial climate influences, Missouri was mantled in pine and spruce forests—likely some combination of jack pine, red pine, white spruce, and black spruce.

The arrival of humans, with their sophisticated, tool-using, cooperative and communicative culture, including hunting and land management practices, transformed the continent's biota. Paleontological evidence shows a rapid decline in large mammal diversity, likely because of an unprecedented level of hunting efficiency of which the fauna had no genetic memory and, in many cases, no time to adapt from an evolutionary standpoint. This is testimony to the level of hunting ability of early human cultures in the New World, since central North America was at the time home to fearsome predators, including short-faced bears, dire wolves, and saber-toothed cats. Additionally, humans brought the capability to deliberately burn vegetation during periods when it was sufficiently dry, a process heretofore reserved for the capricious role of occasional lightning strikes.

Humans also directly shaped the evolutionary creation of one the most iconic symbols of modern prairie: the bison. The first bison, *Bison palaeosinensis*, arose in South Asia, some 2.6 million years ago from a complex genetic amalgam of yaks, zebu, and early bison-like ancestors. By two million years ago, this species gave rise to the steppe bison (*B. priscus*), which again indulged in a proclivity for interbreeding with yaks before crossing an earlier version of Beringia and entering the Americas by 135,000 years ago.

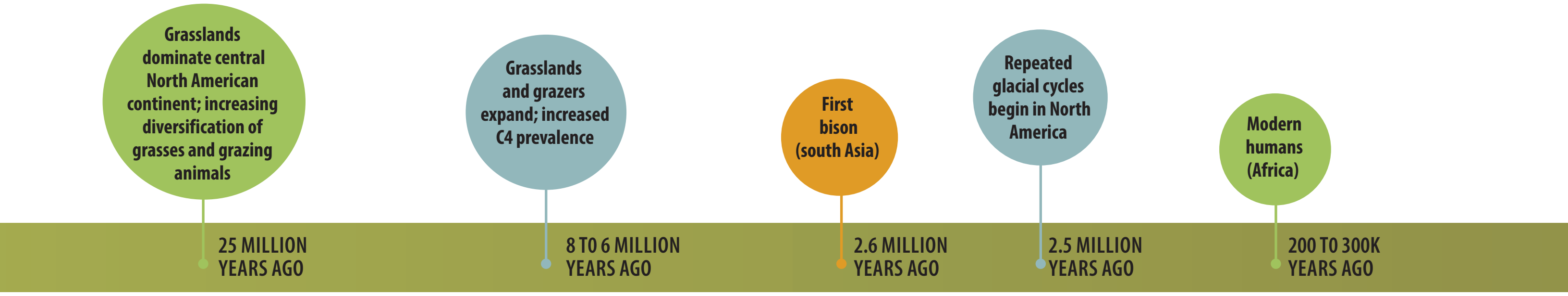
Once in North America, the steppe bison radiated into two additional bison species by 100,000 years ago. All of these now-extinct bison shared common traits, including strong sexual dimorphism, heads held erect, and males with broadly spreading horns. The modern bison (*B. bison*) arose within the past 10,000 years, probably as a direct result of the evolutionary pressures of human hunting. This species, and a short-lived sister species (*B. occidentalis*) that appeared about the same time, had adaptations that were effective tradeoffs only under intense hunting pressures, such as tight herding behavior and social groups, reduced horn size preventing neighbor damage, and heads lowered for constant grazing among the crush of other bison.

As the glaciers retreated and the climate warmed, some combination of fire and a drying climate in the now human-occupied landscape resulted in expanding grasslands through much of central North America. In Missouri, this was marked by a transition from conifers to hardwoods, notably oaks, and an increasing prevalence of grasses.

By 8,000 years ago, the climate entered a dry, warm period that would last for several thousand years, inducing a dramatic increase in C4 grasses and the spread of prairies and prairie-associated woodlands and savannas through most of the Midwest. These grassland systems extended eastward through what is called the "prairie peninsula" into Indiana, Kentucky, Ohio, and beyond. This was likely the first incarnation of contemporary tallgrass prairie, reassembling a diversity of ancient grassland-adapted species into a new natural system annealed since its inception by the influence of the newcomer species—humans.

By 4,000 years ago, the climate entered

Microscopic silica particles (phytoliths) in cells of grass leaves. Scale bar is 10 microns (one one-hundredth of a millimeter).



a wetter phase favoring woodland over much of the tallgrass region, as shown in Missouri by an increase in pine pollen and decrease in grass pollen from sediment cores of that era. However, by then, Native American fire practices overrode weather as a formative factor for natural systems, ensuring the continuing survival of prairies even in forest-supporting climates as people manipulated the landscape with fire and other cultural practices to meet their societal needs.

Thus, humans have been a key ecological influence shaping tallgrass systems since the initial prairies formed in the post-glacial dry period. Human influences extend even deeper to their first occupancy of the New World, such as their role in shaping bison evolution. Well before the Anthropocene, humans were making an indelible mark on the planet's ecosystems. Not only fire, but other ancient, enduring cultural practices such as fuelwood removal, hunting, and harvest of plants for food, medicinal and other uses, had profound influences on the landscape.

George Catlin, *Prairie Bluffs Burning*, 1832, oil on canvas

We Almost Lost It

Just as humans were an essential part of the genesis and perpetuation of tallgrass prairies and associated natural communities, we have also been the key agents of its destruction in the past two centuries. The seeds for this destruction were literally sown far from the prairies, in Sumer, the region of the Middle East near the confluence of the Tigris and Euphrates rivers, some 10,000 years ago. There, someone noticed a desirable plant near a habitation—likely a species of edible or medicinal value. Seeking to favor this plant, Sumerians perhaps used a sharp stick or implement to scratch around the favored plant and reduce competition.

This deliberate, intentional husbandry and growing of food plants arose independently soon after in other areas of the Old World (and perhaps concurrently in southern Mexico), and rapidly developed and improved in its techniques and outcomes. Thus was born agriculture, a practice that transformed human society and is still altering global ecosystems in an ever-increasing intensity. For the first time in the history of the nomadic, hunter-gatherer human species, a few people could produce sufficient food for many, allowing technological specialization, increased and more permanent concentrations of people, with all the benefits that accrue to an inquisitive and communicative species when more stability, resources, and networking opportunities arise.

Soon after the development of agriculture came the first cities, fostering the development of a highly sophisticated, sedentary, agrarian/metropolitan culture that rapidly spread through the Old World. From the first tentative steps of agriculture, profound ecological disruptions were also shaping other species. Early cultivation attempts favored desirable plants, but some non-desirable plants survived these impacts, and, as agriculture developed, some species became adapted to tolerate, or even favor, these impacts. Thus, over thousands of generations, were born agricultural weeds, as well as a host of other plants and animals gradually adapting to the processes and landscape conditions imposed by a human culture of ever-intensifying environmental impacts.

Meanwhile North America remained a separate world, where agriculture was a latecomer of limited extent and impact, as recently as 4,000 years ago confined to

a small pocket of the Mississippi Valley. Nomadic or seasonally nomadic, largely hunter-gatherer lifestyles persisted in much of central North America—humans, prairies, and prairie-associated woodlands existing in a complex interrelationship with regular dormant-season fire, grazing, and hunting patterns at its core.

Because of this, since Eurosettlement of the Americas our native systems and their component plants and animals face a double handicap: not only are they totally unadapted to the type, magnitude, intensity, and frequency of impacts and altered process regimes imposed by the post-Eurosettlement agrarian civilization, but they are also competing with thousands of non-native species that have deliberately or accidentally been introduced to the New World. Through thousands of years of winnowing and selection, these species are supremely adapted to the altered processes and disturbances in the modern environment.

Tallgrass prairies, some of which had been accruing meters-deep, black, carbon-rich, fertile loams since the last glacial period, became an irresistible target for the agricultural needs of a growing population of the new wave of invading humans. This was of course facilitated in 1837, when John Deere invented the steel moldboard plow that allowed exploitation of the stored wealth of tallgrass prairies, in the process creating one of the most productive agricultural regions on Earth, but also scribing the death warrant for the tallgrass landscape, a victim of its own fertile success.

Magnificent prairies once covered more than a third of Missouri, and biologically influenced all the state's natural systems. Today their last remnants lie on the verge of permanent degradation or extinction. Each remaining prairie remnant contains a unique assemblage of species and genetic information—the irreplaceable distilled biological legacy compiling genetic memory of complex events and interrelationships extending back to the dinosaur era.

There is an imperative need, from multiple perspectives, to sustain and restore the remaining examples of our prairie heritage. Partly this is from a standpoint of pure human self-interest, since these are the systems that sustain our soils, deter erosion, temper our floods, cleanse and hydrate our streams, recharge our groundwaters, nourish our pollinators, and provide a plethora of other economic, cultural, and aesthetic benefits. It is also a direct link to our humanity, reflecting how a culture understands and interacts with the environment on which it ultimately depends. This is as true today as it was for the Osage people roaming southern Missouri 500 years ago, although the relationship has been obscured by a technology facilitating deferred accountability. Millions of years in the making, a quick century to destroy, and now a chance to steward the last remnants for the benefit of all.

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Additional readings
(references in **bold** are comprehensive, readable, and highly recommended)

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