Quercus macrocarpa:

The Consummate Tree of the Nearctic Savanna

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Savanna communities are, by definition, transitional habitats comprising both forest and prairie species. The predominate forest canopy tree species which visually and biologically rules savannas throughout the Tallgrass Prairie Region of midwestern North America is the versatile Bur Oak, *Quercus macrocarpa* Michx.

A unique combination of physiological and morphological characteristics gives this tree, a classic ecological generalist of many climatic and edaphic zones, the ability of a specialist to thrive under savanna conditions where almost no other temperate forest tree can exist. This species is arguably the most important single biotic factor in the molding of a savanna community.

An insight into the capability of the bur oak to adapt to tallgrass savanna conditions is presented, toward a better understanding of suitable techniques for management and restoration of these vanishing natural systems.

Introduction

The deciduous forest of eastern North America is a dynamic, but morphologically stable, ecosystem. The prairie of the upper Midwest is stable, too, as a disclimax maintained by environmental forces. But the transition between them -- the oak savanna -- is war. Woody plants attack from the East, with their ally, shade; herbaceous plants counter-attack from the West, with their own allies of drought, wind, fire, and lightning. And so the battle persisted for millennia, ebbing and flowing with every subtle climate shift and every stochastic local environmental anomaly, from Manitoba to Texas.

Recently, it seems that the herbaceous plants have been losing, due to human interference with natural systems of balance. Restoration scientists understandably are rushing forward to apply their craft in behalf of the vanishing herbaceous understory. But the savanna could still exist without any single plant species, except for one: the bur oak, with a little help from some of its co-generic counterparts, is the sole element that defines our oak savannas, and creates the conditions that make them what they are.

How much thought do most of us give to the management of the oak resource, other than as an increaser to be beaten back? Have we considered the long-term welfare of this strategic element?

Bur Oak Influences

When the first European settlers advanced into the prairie, looking for new lives, they naturally sought the open oak groves, which they called "oak openings" or "scattering timber." The bur oaks trees they found there furnished shade, shelter from wind, building materials, fuel, and forage for livestock. These trees also offered a psychological connection to more familiar forest environments, since bur oaks, and oaks in general, had been dominant components of forests back in the Ohio Valley. Perhaps they even appealed to human genetic memories of the supposed savanna origins of the human species.

But the oaks provided more than wood, shade, and homey comfort. They gave the savanna structure; they were its bones. The inclusion of scattered oaks in the tallgrass prairie created the major source of diversity in areas devoid of streams, potholes, or topographic breaks. The oaks nurtured obscure organisms like bullet galls, and spectacular ones like the giant silkmoths. They furnished roosting and nesting sites, browse, and mast for tree-dwelling birds and mammals. They modified their own micro-environments to the benefit of the grasses like *Chasmanthium* and *Elymus*, and forbs like *Polygonatum* and *Zizia*.

When they died, the oaks became hunting perches for hawks, and dens and forage for woodpeckers. They served as carbon sinks and sources of lignin, and as they fell, they sheltered amphibians, and supported the fungi and other recyclers that expanded and renewed the food chain. Sometimes the bur oaks were joined or replaced on good upland soils by white oak (*Q. alba* L.), on dry or calcareous soils by chinkapin oak (*Q. muehlenbergii* Englem.), on wet soils by swamp white oak (*Q. bicolor* Willd.), and on poor soils by black oak (*Q. vellutina* Lam.) or post oak (*Q. stellata* Wang.) or others. But bur oak was the principal tree in most of the upper Midwest savannas, and the predominant biological and visual force which shaped them.

The Unique Adaptability of Bur Oak

Conventional wisdom sometimes holds that the oak components of our savannas existed mostly as relics of forest, persisting temporarily in the face of the advancing prairie. This certainly could be true in some areas, but the special ability of bur oak to colonize the prairie should not be overlooked. This capability is due to several morphological and physiological tendencies which combine to make bur oak resistant to, and tolerant of, the forces which created and maintained the prairie.

Bur oak acorns are different from those of most other oaks in that they frequently are more than 50% enclosed by the cupules, or caps, that develop from the floral involucre. This can cause them to fall with the caps still attached, and those which happened to lodge "nose down" in the savanna could be held in that position by the unique broad fringe. The oak embryo, thus brought into direct soil contact by its inverted position and protected from light autumnal fires by the thick, woody cap, would germinate that same autumn, sending its radicle deep into the soil during the fall rains. The root would continue to grow, fed by the large cotyledons, until the soil froze. The following spring, the plumule would emerge, while the tap root continued to deepen, racing against the onset of summer drought and the competition of other plants.

The author with a mature specimen of *Quercus macrocarpa*.

Guy and Edie Sternberg

These acorns are sweet, and attractive to wildlife. Jays and woodpeckers would carry them away, occasionally dropping one into a favorable seedbed, potentially starting a new grove. Fox squirrels would venture more than 100m into open territory from their secure oak dens, planting hundreds of acorns and retrieving, perhaps, a few less, thus helping to expand existing groves. Large mammals (chiefly bison) would track from grove to grove, tearing apart the prairie grass in their wallows; bur oak acorns occasionally could have become established in the open, moist seedbeds of abandoned wallows.

The new seedlings which resulted were susceptible to top-kill by fires, like all woody plants. The roots would continue to deepen and thicken, forming "grubs" from which vigorous new sprouts would arise after each fire. But most trees could not develop beyond the root-grub stage as long as annual, or frequent, fires burned through them. However, in a forest-prairie landscape econtone measuring some 2500km from north to south, occasional opportunities obviously existed for a few oak seedlings or sprouts to develop for a decade or two without significant damage from fire. This might occur downwind from a stream, or along a topographic break, or near a bison wallow, or even behind a rock, or an old log, or the carcass of a large animal.

Once this happened, the saplings quickly became among the most fire-resistant of all temperate-zone trees. The thick bark, which had begun to develop as early as the second year, provided the trunks with ample protection from most grass fires, and the crowns became elevated above the flames' reach as the trees grew. Then, as the dense foliage began to spread and shade out the most flammable tall grasses, and as large mammals began to mat down the remaining herbaceous understory in their quest for shade, the local fuel load was reduced and the trees had strengthened their hold.

Bur oak gained great advantage from its variability. Populations, and individuals within populations, are notoriously heterogeneous. There are many introgressive populations with hybrid ancestry involving other species within oak subgenus *Lepidobalanus*; some "bur oak" populations are hybrid swarms, adapted to niches intermediate between those preferred by either parent species. In such situations, each parent confers a specific advantage, and the heterosis which can result from their combination could allow the progeny to achieve a fire-resistant size very quickly.

In wet decades or in sheltered areas, where the fires were patchy, oak reproduction could advance. Then, in dry, fire-prone periods, the trees dug in, and some survived. The long lifespan of bur oak enables individual trees to bridge two or three centuries, waiting for the next climate cycle or local anomaly favorable to recruitment. Those that could escape lightning, wind, and the occasional firestorm that might breach their formidable cortical defense would be ready to reproduce in better times. Old bur oaks frequently are the only presettlement savanna organisms which have survived our human army of occupation. Within their layers of annual growth are contained the chronicles of our invasion and conquest of the West. Some of the oldest of these trees witnessed the passing of the baton from the Native American race to the encroaching Europeans.

They tend not to reveal such information, though, nor even whether or not they are old enough to possess it, to the casual observer. Stem diameter, in the absence of other data, unfortunately is not a reliable indicator of individual tree age. Many really big trees are relatively young, having benefited from ideal growing conditions under passive human land management. Sometimes their juvenile branching patterns and youthful symmetry will suggest their limited age to the experienced eye. But only by including observations of the relative maturity of crown form, the productivity of the site, the known growth rates and ages of fallen neighbors, and some increment core data, can we make more reliable estimates of which trees might be "original" presettlement relics, or perhaps even pre-Columbian.

Large old trees, though, whatever their actual years, provide the matrix around which we can restore or recreate our savanna heritage. Regardless of their chronological ages, they, unlike the herbaceous understory, cannot be wrought from nothing in a year, or a decade.

Management Implications

Since the onset of human immigration from Europe, our oak savanna ecotype has been transformed from a vast aggregate area to a scattering of remnants where the understory has been depleted, the old trees are fading, and brushy invasion is advancing to the detriment of both. The effect of the young woody understory upon the herbaceous plants is direct and obvious; the effect upon the woody overstory can be less direct, but more insidious.

As we attempt to bring back the savanna understory by cutting, herbiciding, and burning surplus woody plants, we must remember that misdirection of these techniques can affect the trees we wish to retain as well. Fire-damaged trees no doubt were common in presettlement savannas, but they were scattered over an expansive landscape. We no longer have the luxury of leaving the health of our remaining individual savanna oaks to chance, especially considering the unnatural fuel loads we create during our brush-killing activities. The understory can be renewed in a decade, but the old oak, with all of its biological and visual character, cannot be renewed in a century. Careless use of herbicides, or a dead limb or brush pile burning too near one of our relic oaks, or a hot ground fire which cannot discriminate at such a small scale between those trees that we wish to retain and those we wish to remove, can cause damage that cannot be reversed in a human lifetime. To allow the oaks to be forced into decline by careless management techniques, planned only to implement the removal of surplus woody growth, will not serve well the restoration objective we follow.

There is a significant difference between prairie restoration and savanna restoration. Savanna managers should not neglect to explain this difference, in detail, to anyone who wishes to work on a savanna restoration project. The great monarch oaks are not really savanna bones, or other static, lifeless structures, but living system components existing on a longer time-line. These are dominant organisms that have persevered for so long, and without which the savannas would not exist. They need protection from overfiring or careless management, and they need periodic opportunities for controlled recruitment. In our zeal to restore the native herbaceous understory, let's not turn our savannas into bur oak graveyards.

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