By Daniel H. Janzen

Fruits for Famished Mammoths

Our pawpaws and other native fruits now rot on the ground, but large animals, now extinct, may once have devoured—and dispersed—them

On a fine fall day in Kansas 10,000 years ago, a mammoth on its way to a creek stopped at the edge of a forest to sample newly fallen, slightly sweet honey locust fruits. As the mammoth journeyed across the prairie, the seeds that had been within the honey locust fruits journeyed through the animal's digestive tract. They were eventually deposited far from where the tree had dropped them.

Seed dispersal by large animals like this peripatetic mammoth is likely to have been common for millions of years. Integral to plant biology, it determined the distribution of many plants, by enabling them to colonize new habitats, escape from seed predators and move around within a habitat.

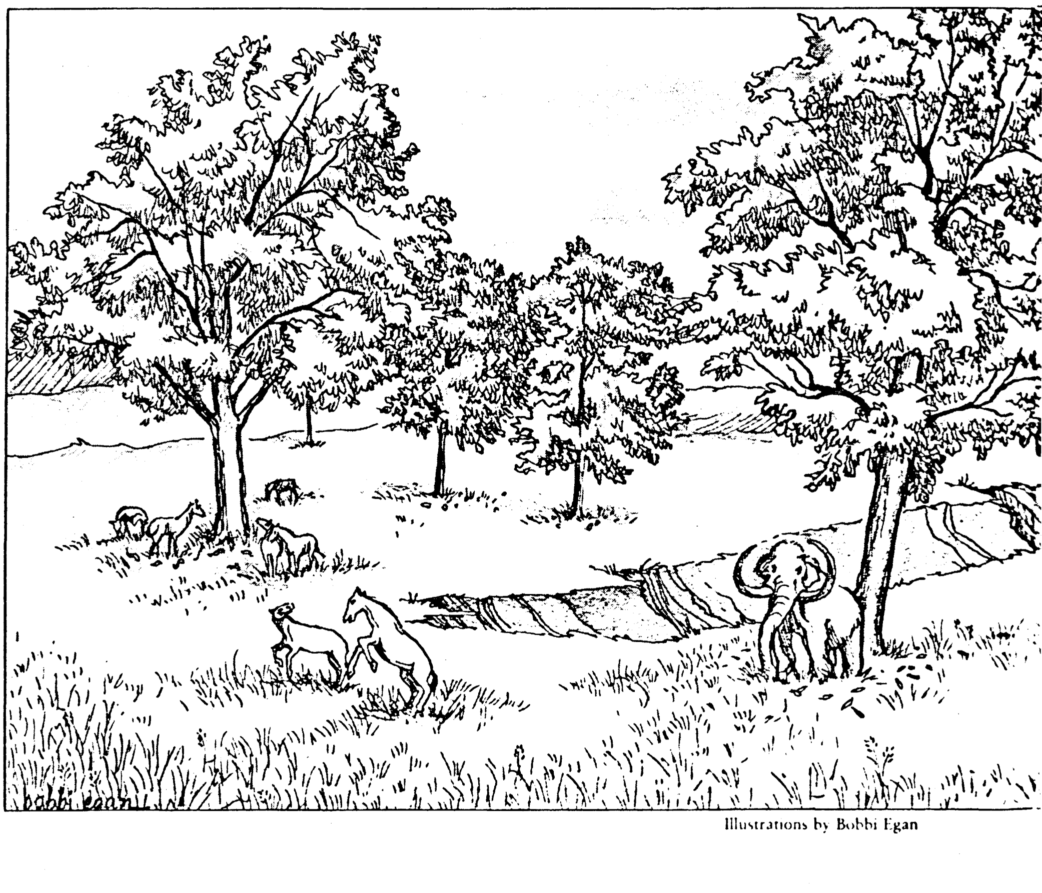
But scientists working in North America, who haven't experienced a landscape filled with big mammals (such as existed on the plains of Africa in living memory), have usually considered insects to be the model for North American herbivores, and birds and small mammals as the primary seed dispersers. In fact, North America up to the Pleistocene was rich in native horses, mammoths, mastodonts, camels, glyptodonts, bison, muskox, pronghorn antelopes, ground sloths, and other large, frugivorous (fruit-eating) and herbivorous (plant-eating) animals.

Big mammals were abundant in the New World for at least ten million years, as we know from extensive fossil evidence; nearly all died out only about 10,000 years ago. I am confident that while they were here they ate our native, large-fruited large perennials: honey locust, persimmon, the Kentucky coffee bean, prickly pear, osage orange, hawthorn, pawpaw, mesquite, yucca and acacia. And they dispersed these species' seeds. In this they would be like the large mammals in today's Old World tropics.

Repast for a mastodont

Let me return to the large honey locust tree in the Kansas of 10,000 years ago. This tree, exactly like its modern counterpart, bears several thousand large, brown, strap-shaped fruits, each filled with rock-hard oval seeds in small cavities in dry, slightly sweet and nutrient-rich pulp.

Each day a few of this tree's fruits fall to the ground and each day the tree



Illustrations by Bobbi Egan

is visited by the members of the local horse herd, three bison that know the tree's exact location, and one camel. An occasional mastodont or mammoth also stops and snuffles around the tree on its way to the water.

Occasionally a squirrel crosses into the crown and takes a fruit, the tallest mammoth reaches up to pick some fruits directly, and mice searching for seeds after dark take a few of the fruits that have fallen. Almost every fruit is eaten within hours of falling.

The large mammals chew the pulpy seed-containing mass a moderate amount, then swallow it. Some of the seeds respond to the warm, moist gut by germinating; these die by being digested or by suffocating in the oxygen-free gut. But others, hard and dormant, pass through the animal in as short a time as one to three days (bison, camel) or as long as two months (horses).

Paradoxically, the seeds are rescued by being eaten. While the fruits hang on the tree, bruchid beetles lay their eggs on them and the larvae mine through the seeds; once the fruits have been eaten by a large mammal, the seeds are safe from attack by these tiny seed predators.

The surviving seeds are defecated over an area of many square miles and in habitats ranging from wet creek beds to the driest prairie hillocks. They fall along game trails where the sod has been broken and in gulleys where they will be washed into high-quality germinating sites such as alluvial fans (small floodplains). If the dung falls in forest, it is mined by mice in search of edible seeds. If it falls near rodent burrow entrances, the seedlings that germinate will not have to compete with other plants but are in danger of being eaten by the rodents.

Although seed predators kill some seeds and animal dispersal agents digest others, most dispersed seeds are in a viable and dormant state, and germinate in years to come as soil processes scarify their coats.

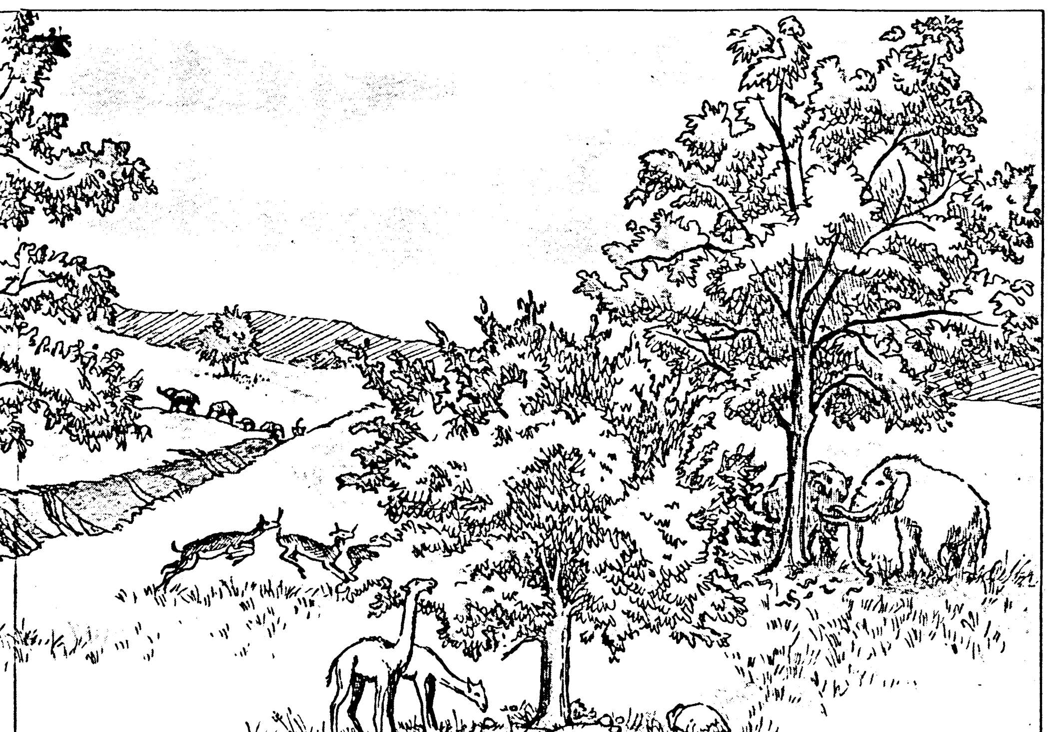
Plant-eating vertebrates make the so-called seed shadow (the overall pattern of dispersed seeds) large, with a farflung, complex pattern of densities.

The Pleistocene honey locust population is widespread and occurs in many habitats, even marginal ones, which requires that a large number of seeds be deposited in order to assure production of an adult plant. The honey locust is even found in habitats avoided by some of the dispersing animals. So successful is the honey locust dispersal system that it is likely that the tree's fruits and seeds have evolved very little, if at all, as they have been passed from one mammal fauna to another over millions of years.

Did dinosaurs love ginkgo plums?

Honey locust seeds were far from alone in their reliance on animal dispersers: Yucca, acacia, osage orange and other Pleistocene contemporaries did the same. Trees bearing fleshy fruits, such as persimmon, pawpaw and prickly pear, may also have been dispersed by small carnivores like raccoons, foxes, opossums and coyotes. (Even some herbs, that is, grasses and broad-leaved herbaceous plants, may have depended on large animals, for example, by having their burr-like seeds hitch a ride on shaggy-haired wanderers.)

In fact, reliance on animal dispersers goes far back in evolutionary history. Scientists have found a fossil dinosaur with its gut full of seeds, and they have also found fossilized dung packed with fruit fragments and seeds from one of the earliest seed plants. If we add this to other evidence that dinosaurs had dietary preferences similar to those of modern vertebrates, we can assume that seed dispersal by



For millions of years, and up to about 10,000 years ago, the North American continent was filled with large, fruit-eating mammals. By eating the fruit and thus dispersing the seeds, these animals ensured a wide distribution for our native fruit trees like (from left) honey locust, persimmon, Kentucky coffee tree and osage orange. This dispersal mechanism has not been generally recognized until recently.

large animals has been going on for at least 60 million years and probably much longer. The ginkgo tree, with its sweet, juicy plums and large soft seeds, is tailor-made for a fruit-eating dinosaur that didn't chew well.

Extinction of the seed-eaters

A dispersal mechanism successful for millions of years ceased to be widely used in North America a mere 10,000 years ago. Then, in the Pleistocene, human hunters came from the northwest, sweeping through North America, including Kansas, and taking almost all of the big game. What they didn't kill was probably taken by the starving animal predators abruptly deprived of their usual prey. The result was that three quarters of all the species and individuals of large mammals were lost.

Now, in the Pleistocene, when honey locust fruits fall, they accumulate beneath the parent tree. The bruchid beetles oviposit on them, and their larvae kill most seeds before cold weather sets in. The mice husk the seeds out of some fruits and consume them on the spot or cache them for later consumption.

The honey locust still has a seed shadow, but it is minute compared to what it was before, and there are many fewer viable seeds. The species doesn't disappear entirely because it is not entirely dependent on animal dispersers for survival, but over the next several thousand years, the honey locust population shrinks, in numbers, in its geographic range and in the kinds of habitats in which it lives.

Because seed dispersal is minimal and seed predation is heavy, the honey locust now grows only in those habitats where a seed has a very high chance of becoming an adult plant. The honey locust has become a rare tree.

The honey locust remains rare for a few thousand years—not enough time for it to undergo the evolutionary changes that could adapt its fruits to a new set of dispersers and its vegetative traits to the restricted habitats in which it finds itself.

While the honey locust enters a period of eclipse, the absence of large mammals may mean that the fleshy fruits—persimmon, prickly pear tunas, pawpaw—receive increased attention from coyotes, foxes, raccoons and opossums. If these small mammals eat many more fleshy fruits, they may provide a somewhat different, but nonetheless quite large, seed shadow of their own.

New animals to exploit

The honey locust remains rare until the arrival of the European hordes sweeping across the North American continent, this time from the east and southwest. The Europeans bring their horses and cows. These animals find in the fallen honey locust fruits the same kinds of dry legume fruits that their ancestors ate in the Old World tropics and subtropics; the horse in particular finds the fruits that its earliest ancestors grew up on.

Field ecologists tend to dismiss introduced horses and cattle as ecological nuisances. But in fact the presence of big mammals allows the honey locust population to grow. It is soon found again over a wide geographic area and in high densities in a wide variety of habitats.

Horses and cattle, however, do not range over as many habitat types as did the entire group of Pleistocene mammals and moreover are restricted in their movements by fencing. Not all honey locust fruits are eaten, because they compete with alfalfa and other cultivated fodders for the attention of livestock. And many of the honey locust habitats have been destroyed by humans. As a result the honey locust is not as widespread as it was before.

At the other end of the scale, the fruits of plants like Kentucky coffee bean and osage orange are only rarely eaten by livestock. These plants, with extremely restricted distributions when the Europeans arrive, remain that way except where they are deliberately planted for fenceposts or garden trees. For these plants to have a wide natural distribution would probably require the reappearance of some other large mammals, such as mastodonts or glyptodonts.

Piecing together a puzzle

Recognition of the influence of big-animal seed dispersers helps to explain many observations that have long puzzled scientists. For example, botanists have long been unable to satisfactorily explain why many New World woody plants are spiny or thorny, even in areas where plant-eating animals are absent. Honey locust, acacia and mesquite in the New World produce a heavy skirt of thorny branches in the lower part of the crown, and nearly thornless branches in the upper part. Many other shrubs or small trees—prickly pear, hawthorn, mesquite, yucca, agave—are also spiny or thorny.

The large mammals we lost in the Pleistocene were not only fruit-eaters and grazers; many of them were browsers. It is not hard to imagine that spininess or thorniness are remnants of the constellation of traits that once protected woody plants from excessive browsing but haven't been needed in the last 10,000 years, a mere moment in evolutionary time.

Today, the forest-grasslands of eastern Africa contain many thorny plants that deter large modern browsers. These, like their counterparts in the New World, produce a heavy skirt of thorny branches below an upper crown of nearly thornless branches. The African acacias, favorite food of giraffes, replace a browsed branch with a new branch having much longer thorns and shorter leaves.

The big-animal connection may also help to explain the secondary compounds (tannins, glycosides, alkaloids, resins, etc.) that plants produce whose presence has long puzzled scientists. We have come to accept the view that plants make a variety of defensive and deterrent chemicals to deter insects that would eat them. As insects evolve to tolerate or circum-

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Famished mammoths
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vent these chemicals the plants evolve new chemicals.

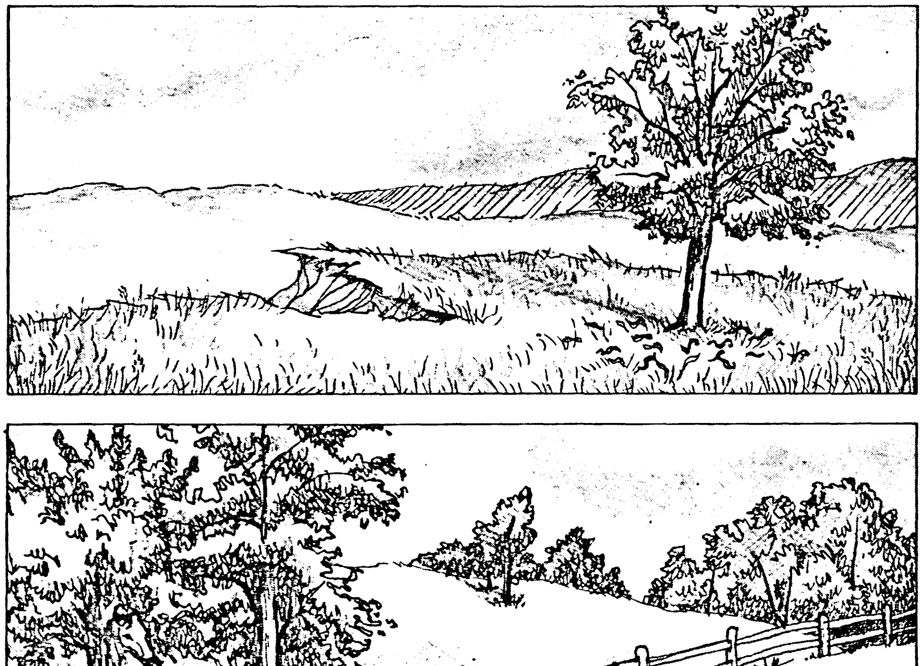
The new view, suggesting that large animal herbivores were significant in New World prehistory ecology, implies that plants' defensive chemicals evolved in response to large animals as well as insects.

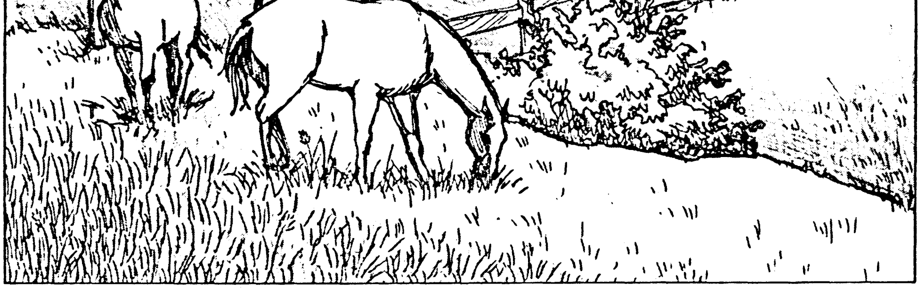
Therefore the scientist trying to understand the chemistry of defense against insect herbivores is really working in a battlefield strewn with weapons designed to work against other animals as well.

A case in point is the problem of trying to understand the chemical defenses of herbs commonly eaten by livestock. Scientists generally view herbivory, whether by large animals or insects, as detrimental to the plant. Unlike insects, however, the large animals are also dispersers of many kinds of herb seeds, through swallowing the seeds. In a certain sense, consumption of a herb, with its seeds, is much like consumption of a fruit with *its* seeds. The entire plant is like a fruit, in the sense that it entices large herbivores.

If we measure the success of a plant by the survival of its offspring, then its ability to be eaten by a large animal may be a very successful adaptation.

If a plant must simultaneously present itself attractively to large mammals and defensively to insects, then the number of chemical options available to it are severely restricted. For example, the pungent oils of the crucifers (mustards) may not only be defenses against herbivorous insects but also attractions to large mammals to consume the foliage and disperse the seeds.





After North American herbivores were hunted to extinction 10,000 years ago, seeds of trees like honey locust were no longer dispersed but rotted on the ground, and the tree population shrank (top). After Europeans introduced livestock, however, seeds were again dispersed; in recent centuries the native tree population has in fact increased (above).

A new look at the New World

Most of all, recognition of the role of big animals helps explain why at present these trees produce many more fruits than current dispersal mechanisms remove; and why introduced livestock accept such tree fruit so readily.

Had North American biology matured in the mammal-rich plains of yesterday's Africa (or in Pleistocene North America), biologists would automatically have taken large mammals into account in their explanations of large plant seed dispersal, thorniness and other physical defenses, and the defensive chemistry of foliage.

This new attention to big-animal dispersers applies to Central America as well as to North America. The Central American fossil record shows that mastodont-like gomphotheres, ground sloths, glyptodonts, horse-like creatures and other large herbivores were common. Many tree species there also have characteristics suggesting that big animals once browsed the plants and dispersed the fruits.

As it now appears, we have only just begun to explore the role of large animals in ancient plant-animal relationships, and have uncovered what is undoubtedly only a small fraction of the details. Portions of modern Africa that have had their large mammals exterminated but still have moderately intact vegetation offer an indication of the stories yet to unfold. ☐

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