A round forty-five million years ago, the Arctic was ice free, scarcely the expanse of lichen-encrusted rock and glaciers that we see there today. Fossil records reveal that an extensive forest flourished throughout the early Cenozoic, when the canopy was predominated by *Metasequoia* and other deciduous conifers. The single remaining species of this genus, *M. glyptostroboides*, is known as the dawn redwood and is now restricted to a small population in south-central China, around forty-two hundred miles (sixty-eight hundred kilometers) south of this historic distribution. When botanists first learned about the living population more than seventy years ago, no one could have imagined that those plants would provide crucial clues for understanding more than one hundred million years of historic climate change—not to mention changes to come. Yet the rare discovery of fossils containing exquisitely preserved organic tissues and biomolecules, coupled with new molecular research techniques, has revealed just that.

Traditional paleobotanical studies are comparative—drawing links between the anatomy of fossils and their living relatives—while molecular analyses of isotopes and biomolecules (such as lipids, carbohydrates, and lignin) are usually reserved for modern samples of freshly harvested material. Recent innovations with laboratory instruments, however, have made it possible for researchers, including ourselves, to extract valuable molecular information from so-called rocks. With *Metasequoia*, which boasts a long fossil record, the implications of this research are especially pronounced given that we can test hypotheses at the molecular level across an enormous timescale.

**The Green Arctic**

Scientists (and museumgoers) usually encounter two types of plant fossils: either imprints or compressions. Imprints are analogous to animal tracks, occurring when plant tissue remains pressed into sediments and subsequently decomposes, while compressions occur when the tissue becomes sandwiched between flattened layers of sedimentary rocks. In the late 1990s, however, Ben LePage and Chris Williams, then working at the University of Pennsylvania, showed us three-dimensionally preserved *Metasequoia* fossils that they had collected from the Canadian islands of Ellesmere and Axel Heiberg, on the northwestern side of Greenland. We could hardly believe that the fossils were from Cenozoic strata that was around fifty millions years old. The dark-brown leaves, stems, and cones resembled a pile that someone had raked in their backyard—loose but delicate, soft but brittle, individually separated but tightly packed.

When *Metasequoia* lived in the warm and humid Arctic, the plants shed their leaves in autumn, before the four months of total darkness. The litter was buried for tens of millions of years, including beneath the weight of a continental ice cap. Ironically, the tundra surface in the high Arctic has been increasingly exposed due to recent global warming, revealing some of the best fossil material to study ancient climate change. The unrivaled quality of these mummified *Metasequoia* fossils extends beyond what was visible to the naked eye. Using molecular technologies, we detected biomolecules—plentifully! Although cellulose and other polysaccharides are abundant in living plant tissues, they are rarely found in ordinary fossils. Preserved for around fifty million years, these *Metasequoia* fossils possess the oldest biomolecules of this kind ever recovered. Moreover, our molecular evidence suggests that these molecules actually provide both the physical enforcement and chemical stability for maintaining the three-dimensional structures of these exceptional fossils.

The Arctic plays a crucial role in the dynamics of Earth climate. Not only does it actively influence climate on a global scale, but the Arctic passively receives climate change feedback as well. Interestingly, *Metasequoia* has been a witness...
Fossilized *Metasequoia* trunks from the late Paleocene and early Eocene have been discovered on Ellesmere Island, Canada, along with three-dimensionally preserved leafy fossils, from which the authors have extracted biomolecules and isotope signals. The leafy branchlet in the upper right corner measures 0.83 inches (2.1 centimeters) long.
and faithful recorder of such changes. At Axel Heiberg and Ellesmere Islands, with latitudes higher than 80° north, large amounts of fossilized Metasequoia trunks—up to twenty-six feet (eight meters) long and ten feet (three meters) in diameter at breast height—indicate the large size of these forests, which were nurtured by a warm and humid high-latitudeclimald.

Williams and colleagues demonstrated that the productivity of these dense Metasequoia forests was comparable with modern-day temperate rainforests, like the rich landscape of the Olympic Peninsula in Washington State. Yet the Metasequoia landscape was primarily populated with deciduous plants, not evergreens—evidence of adaptations for four months of complete darkness at the northern latitudes. Animal fossils are rarely found with these Metasequoia remains, but fossils found in similar-aged strata at Ellesmere Island include rhinoceros- and hippo-like mammals, along with giant tortoises and alligators—all indicative of a humid swampy environment, consistent with the reconstruction by plant fossils. Clearly, the ice-free Arctic during the early Cenozoic was a completely different world compared with the barren landscape today.

**Living Climate Legacies**

To understand the climate that supported such impressive forests in the Arctic, however, our ability to study a living Metasequoia species is essential. The first climate-related experiment involving the living species, *M. glyptostroboides*, was launched inadvertently. When trees were discovered in western Hubei Province, China, in 1944, two American scientists immediately recognized the importance of this plant: Ralph Chaney from the University of California, Berkeley, and Elmer Merrill, the director of the Arnold Arboretum. Through separate collaborations with Chinese colleagues—notably Wan-Chun Cheng and Hsen-Hsu Hu—both Chaney and Merrill arranged for the collection of dawn redwood seeds from China and distributed them to botanical gardens around the United States and Europe. Despite their arguments about who should get the credit for making these seeds available for cultivation, the resulting widespread dispersal to gardens in dramatically different climatic zones (essentially all corners of the contiguous United States) set up a natural experiment that we have dubbed the Chaney-Merrill Experiment.

The remnant population of Metasequoia in China represents a relatively homogenous genotype, so we can obtain information about how the seedlings survived in disparate gardens, and eliminate some confusion about nature versus nurture. Physiological studies based upon samples from these trees revealed that *M. glyptostroboides* can endure a wide range of climate conditions. We have obtained leaf samples from forty trees across this range, and these are stored in our Laboratory for Terrestrial Environments at Bryant University, tightly packed in yellow envelopes and frozen. These leaf tissues have helped us generate systematic molecular and biochemical data, which we compared with climate data from the past seventy years from the locations where the trees have been growing. We found that biomolecular compositions within the leaves changed relative to latitude, average temperatures, and average annual precipitation. These correlations established a necessary baseline for interpreting biomolecules and biochemicals that we would later obtain from Metasequoia fossils.

Another recent experiment on Metasequoia glyptostroboides provided additional context. Richard Jagels and his colleagues and students at the University of Maine designed a greenhouse experiment to examine how the genus would have performed within its historic distribution inside the Arctic Circle. The climate in this northern region was temperate during the early Cenozoic, yet the unique light regime would have remained consistent: up to four months of complete darkness and four months of twenty-four-hour sunshine. To test the physiological adaptation of *M. glyptostroboides*—as a living stand-in for the Cenozoic species, *M. occidentalis*—to this light regime, the team partitioned a large greenhouse on their campus into two different compartments: one with normal light, corresponding to the middle latitude of Maine (45° north), and the other with continuous light, mimicking the same low angle and low intensity of Arctic light conditions during summer months.
Metasequoia glyptostroboides is the only extant member of a genus that once flourished at warm Arctic latitudes during the early Cenozoic. Clockwise from top left: Seed cones hang on winter branches (notice that the deciduous leaves have already fallen), small pollen cones emerge in the spring, and trees at the Arnold Arboretum showcase an affinity for moist habitats.
Seedlings of *Metasequoia glyptostroboides* were grown along with those of two other deciduous conifers: bald cypress (*Taxodium distichum*) and tamarack (*Larix laricina*), whose fossil relatives were also common in warm Arctic floras during the early Cenozoic. These plants were grown for two consecutive years under the two different light regimes with otherwise identical conditions, including temperature, relative humidity, carbon dioxide level, and greenhouse irrigation. This research revealed that, in addition to deciduous leaves, which would drop during the prolonged darkness of Arctic winters, *Metasequoia* possesses physiological characteristics, such as high photosynthesis capacity and improved water-use efficiency, that help it take advantage of the weak but continuous Arctic summer light. This helps explain how this genus outcompeted other plants in the warm Arctic.

At the end of the two-year Jagels Experiment, we corresponded with the researchers and obtained leaf tissue from *Metasequoia* seedlings grown in these greenhouse conditions. We wanted to learn how the ratios of carbon and hydrogen isotopes—slight variations of these elements built into plant tissues through photosynthesis—changed under different light treatments. These isotopes have been commonly used to understand ancient patterns for temperature, precipitation, and carbon dioxide level, and indeed, we discovered noticeable differences between seedlings grown under these alternate light regimes. Even more importantly, our work, published in 2009, established precise empirical relationships between isotope values of plant lipids and environmental water, allowing us to infer ancient moisture levels in this Arctic habitat.

**New Technologies for Old Molecules**

Experiments based on fresh *Metasequoia glyptostroboides* samples have enhanced the ability of researchers to interpret data from *M. occi-
Metasequoia fossils, including biomolecules stored within the seasonal growth rings of the large trunks on Ellesmere and Axel Heiberg Islands. Hope Jahren—a geochemist at the University of Oslo, now well-known for her science memoir, Lab Girl—conducted analyses on seasonal variation of isotopes within these rings. Jahren and her colleague Leonel Sternberg observed high-resolution patterns in these isotopes, allowing them to reconstruct the impact of subtle climate variations on the growth habit of Metasequoia in the warm Arctic. They estimated a mean annual temperature for this high-latitude region to be around 55°F (13°C) during the Eocene—about double the present-day measurements. Relative humidity estimates were equally high: around 67 percent during the growing season and close to 100 percent towards the end of the growing season.

This climate information has direct implications for understanding global precipitation patterns during the early Cenozoic. At present, Arctic ice reflects back large amounts of solar radiation, keeping the global temperature low and simultaneously creating a steep temperature gradient across different latitudes. This equator-to-pole temperature difference significantly impacts the general circulation of heat—and moisture—through the atmosphere and ocean. Given what we know about Arctic temperatures, relative humidities, and carbon dioxide levels during the early Cenozoic, we know that this gradient of temperatures between latitudes would have been less pronounced, significantly impacting precipitation patterns. We used the relationship between environmental water and isotopes in fossilized Metasequoia leaves (established with the Jagels Experiment) to propose a model for early Cenozoic moisture patterns in the Arctic.

To our surprise, the relatively low hydrogen isotope values we measured were not compatible with the conventional understanding that the reduced temperature gradient from the equator to the Arctic should result in less precipitation during the long-distance transport of moisture within the atmosphere, depositing water with heavier hydrogen within the Arctic. Although there is no modern analogue for these high-latitude forests, dense forests at lower latitudes, such as the temperate rainforests, offer clues that could explain these low isotope measurements. Due to moisture generated through extensive evapotranspiration of the vegetation, a portion of the heavy precipitation above these dense forests is composed of locally recycled moisture with lighter hydrogen. The greenhouse simulation in the Jagels Experiment supported this interpretation, demonstrating that photosynthesis under four-months of continuous light enhanced water evapotranspiration. These observations suggest that Metasequoia forests had a dynamic impact on moisture patterns in the ancient Arctic and may, in that sense, have even played an important role in maintaining the air circulation at the ice-free Arctic.

**Climate Predictions**

Strikingly, it took millions of years for the Arctic to transform from a humid Metasequoia-dominated forest into the landscape we recognize today, but the inverse warming trend now appears to be happening at a much faster rate. Over the last thirty years, Arctic warmth has accelerated along with rising carbon dioxide levels in the atmosphere. Arctic sea ice is melting, and glaciers are retreating at an unprecedented pace. In 2017, sea ice reached the lowest extent since the earliest time of satellite measurement in the 1960s. Recent global circulation modeling suggests that if the warming trend continues, by as early as the 2030s, the Arctic Ocean will change from perennially ice-covered to seasonally ice-free, further decreasing the temperature gradient between the equator and the poles. The weakened moisture delivery towards the poles will likely alter storm trajectories and increase temperature and precipitation anomalies, affecting the life of plants and animals, humans included, at the global scale.

In addition to informing what we know about ancient climate, Metasequoia has also contributed to future climate models. The scientific community has long accepted that atmospheric carbon dioxide has been one of the primary drivers for global temperature changes, but the rate at which temperature increases in response to changes of this greenhouse gas—a metric known
as climate sensitivity—has been the subject of significant and ongoing research. Paleoclimatologists do not have the luxury of directly measuring ancient carbon dioxide levels; instead, they rely on indirect estimates, known as proxies, to make an inference. One of the most reliable proxies for reconstructing atmospheric carbon dioxide levels for geological eras that predate the oldest ice-core records is stomatal frequency. Stomata are small openings on the surface of leaves, and are the means through which terrestrial plants control the balance between absorbing carbon dioxide and losing water into the air. Species-specific relationships between stomatal frequency and atmospheric carbon dioxide (under high carbon dioxide levels, plants produce fewer stomata) thus allow scientists to predict one from the other.

The ideal plant to study this phenomenon should have a continuous, abundant, and widespread fossil record, along with living representatives to provide detailed comparative analyses and calculation. The genus Metasequoia fits the bill perfectly. The only challenge is that, as a deciduous conifer, Metasequoia has a very thin and fragile cuticle—the waxy layer covering its leaves—making it difficult to calculate stomatal frequency from fossils. Recent studies using improved experimental treatments and bioimaging techniques of Metasequoia fossils were successful, however, and surprisingly, work by Daniel Maxbauer and colleagues, based upon Metasequoia fossils from the Axel Heiberg Island and published in 2014, found that carbon dioxide levels during the middle Eocene (about thirty-seven to forty-seven million years ago).
Metasequoia’s Legacy Continues

As we look toward future research involving Metasequoia, we can’t help but marvel over the unintended consequences of scientific discoveries. When Japanese paleobotanist Shigeru Miki made the seemingly routine description of a new fossil species belonging to an extinct genus in 1941, he had no idea that its living equivalent was growing a few thousand miles away and waiting to be discovered. When Chinese botanist Zhan Wang encountered a splendid dawn redwood tree in Hubei Province (then part of Sichuan) for the first time, he could not have predicted that this rare conifer would produce important clues for understanding the vexing problem of climate change.

From the Chaney-Merrill Experiment to the Jagels Experiment, from the discovery of exceptional fossils in the Arctic to the applications of molecular isotope technology, science, as illustrated with Metasequoia, is a continuous endeavor in which new technologies facilitate new questions and, ultimately, new breakthroughs. Whether inconspicuously planted along a roadside in Sydney, Australia, or proudly planted on the Bryant University campus. These trees were planted in 2006 during the Second International Metasequoia Conference held at Bryant and Yale.

The authors examine Metasequoia glyptostroboides on the Bryant University campus. These trees were planted in 2006 during the Second International Metasequoia Conference held at Bryant and Yale.
showcased on our campus at Bryant University in Rhode Island, the dawn redwood has thrived through cultivation around the globe. In terms of sheer numbers, *Metasequoia* seems to have survived from the brink of extinction, yet its native population remains isolated with low levels of genetic diversity. While the natural population’s long-term survival remains uncertain under the changing climate, what is certain is that, along with the advancement of technology, both living and fossil *Metasequoia* will continue to offer us invaluable information about its past secrets and the future of our global climate.

**Acknowledgement**

With limited pages here, we can only highlight the many exciting scientific inquiries about *Metasequoia* contributed over the past two decades. This is the duration since Hong Yang’s first *Arnoldia* article on *Metasequoia* fossils and molecules, which was published in a 1998 special issue celebrating the genus. Readers can obtain further reading from the references and especially the proceedings of the three International *Metasequoia* Conferences. We would like to thank Jonathan Damery for discussing the structure and editing the manuscript, Chris Williams and Jonathan Fonseca for providing photograph images, and Yuyang Zhuge for illustrating the Eocene Arctic *Metasequoia* forest and its surrounding environment based on the scientific data we provided.

**References**


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