

Profile of James R. Ehleringer

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For the past 40 years, ecologist James R. Ehleringer has led students and colleagues to California's Death Valley to collect leaves from Encelia farinosa, a common desert shrub known as brittlebrush. The little shrub launched Ehleringer's career, sending it in multiple directions and leading to major discoveries and unforeseen applications. He has used plant ecology as a window into the effects of climate change, illuminated differences between C3 and C4 photosynthesis, and used stable isotopes to examine ecosystems and unravel forensic mysteries. Ehleringer's dynamic career is rooted at the University of Utah in Salt Lake City and in far-flung collaborations. His Inaugural Article (1) grows out of his doctoral work, synthesizing four decades of brittlebrush observations to describe how climate change is affecting desert plants. Ehleringer, a distinguished professor of biology at the University of Utah, was elected to the National Academy of Sciences in 2016.

Desert Plant Ecology

As stable as Ehleringer's life has been since arriving in Utah in 1977, his childhood was the opposite. The oldest of five siblings, Ehleringer moved with his family every few years. His father was a member of the United States Navy stationed both in the Pacific and the Atlantic, often leaving for a year at a time, while his mother stayed with the children on Navy bases and homes as distant as Honolulu, Hawaii and Nice, France. As Ehleringer moved around, he developed a



James R. Ehleringer. Image credit: Dave Titensor (The University of Utah, Salt Lake City, UT).

love of the ocean and dreamed of studying marine biology, a big leap for a kid with no scientific role models and who would be only the second person in his immediate family to go to college. In the summer of 1966, Ehleringer landed a high school research position at the Scripps Institution of Oceanography in San Diego, studying garibaldi fish with ecologist Thomas Clarke. "It convinced me I wanted to spend my life in science and, in particular, studying oceans," he says.

In 1967, Ehleringer enrolled at San Diego State University with plans to become a marine zoologist. However, a class in plant ecology with ecologist Phillip Miller altered his plans. "Plant ecology was new, it was quantitative, it was an opportunity to be more experimental," he explains. "That was hard to do with oceans at that time."

After the class, Ehleringer changed his major and worked in Miller's laboratory, learning how to use mathematical modeling to study plant primary productivity, which involves calculating energy budgets, leaf temperatures, and transpiration rates. He stayed with Miller for a Master's degree but realized he needed a doctorate. By that time, Ehleringer had married his college sweetheart and together they set out for Stanford University, where Hal Mooney, a physiological ecologist, had agreed to take him on. Mooney and his colleague Olle Björkman had begun a project studying plant ecophysiology in deserts, which became a focus of Ehleringer's doctoral work.

On his first trip to Death Valley, Ehleringer was intrigued by *Encelia farinosa*, a plant with hairy white leaves. "Why white leaves?" he recalls wondering. "Was it related to water loss? It was largely unexplored, so that's what I spent 4 years working on. The crux of my thesis (2) was that the variations in leaf pubescence optimized photosynthesis relative to water loss." That study led Ehleringer on a 40-year journey in desert ecology, as well as research far removed from deserts and plants.

Ehleringer's Inaugural Article (1) harks back to his early interest, examining the four-decade record of *Encelia* leaves he collected to understand how the plants' water use has changed in response to climate change. Carbon isotope ratios measured from the

This is a Profile of a member of the National Academy of Sciences to accompany the member's Inaugural Article on page 18161 in issue 31 of volume 117.

First published August 10, 2020.

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yearly leaf samples act as an annual record, similar to tree rings. The study found that, as the climate changed, *Encelia* plants progressively closed their stomates, increasing intrinsic water-use efficiency. An earlier study (3) suggested that if plants keep their stomates open, the probability of death during a drought increases. The new analysis found that intrinsic water-use efficiency has increased more than 50% over the last four decades.

C₃ vs. C₄ Photosynthesis

Long before Ehleringer collected enough data for his Inaugural Article (1), he chose to settle in Utah over other offers from across the country. "Everyone asked me why I would go to Utah," he recalls. "I said, 'it's a pretty amazing institution... and it's on its way up.' Edna and I decided to stay for 5 years. Despite other subsequent offers, we're still waiting for the 5 years to be up."

The collaborations he fostered at Utah have been one of Ehleringer's career highlights, including a 30year partnership with Utah geologist Thure Cerling. They share a common interest in C_4 photosynthesis, a topic Ehleringer began exploring in graduate school. Back then, he contrasted plants that use C_3 photosynthesis with those that use C_4 photosynthesis and discovered that photosynthetic efficiencies were different (4). Extending that work, Ehleringer examined the consequences on productivity and, by inference, C_3 versus C_4 distributions.

"The physiological observation we made on photosynthetic efficiencies correctly predicted C_3 and C_4 distributions globally, both in time and in space (5)," he says. That finding led Ehleringer, often in collaboration with Cerling, to study how these differences affect animal diets and plants as the climate changes (6). "Mammalian grazers tend to eat C_3 or C_4 plants," he explains. "Very few eat both. So the changes that we predict based on physiology have ramifications for future plant and animal distributions." Indeed, studies show that C_4 plants expanded in a low-CO₂ world and will have trouble remaining competitive under future, high-CO₂ levels, says Ehleringer (7).

Stable Isotopes

Ehleringer's interest in C₃ and C₄ plants in the 1970s led to what many consider his biggest contribution to science: Using stable isotope ratios as a tool to study plant ecology, animal diets, and forensic applications to drugs, explosives, and bacteria. He became interested in stable isotopes after he first read about C₃ and C₄ plants and their carbon isotope ratios. Ehleringer imagined that measuring stable isotope ratios could be a useful research tool, but instrument access for ecological studies was limited. Ehleringer applied to the US National Science Foundation to purchase an instrument that he would make openly available to ecologists around the country. In 1986, he created the Stable Isotope Ratio Facility for Environmental Research, or SIRFER, a nod to Ehleringer's passion for surfing. Today, the facility still supports colleagues from around the country by analyzing their samples or inviting them to conduct measurements.

Ehleringer started by comparing stable isotope ratios in different plants. "We began by asking if the environments of sun versus shade leaf plants resulted in different physiologies that could be detected using carbon isotope measurements," he says. "We also looked at desert plants, asking if small differences in water availability associated with rooting depth and microhabitats influenced stomatal activities of different species. Indeed, there were large differences. That foundational information led us to experiments that could be conducted to ask specific questions."

By looking at carbon isotope ratios researchers can tell how open a plant's stomates are, relative to the photosynthetic need for CO₂. By looking at oxygen isotope ratios, they can determine how humid the climate is, and by looking at both hydrogen and oxygen, they can make inferences about habitat geography. "The isotope ratios all tie back to the same set of biological and physical principles, but it's the fact that the environment varies globally that results in isotope ratio variations," says Ehleringer.

Collaborating with researchers from medicine, zoology, geology, ecology, and atmospheric science, Ehleringer and his team tackled all kinds of puzzles. One of Ehleringer's long-term colleagues is Australian National University biophysicist Graham Farquhar (8, 9). "His strength is theory. Graham has revolutionized studies of photosynthesis and water relations, pulling together concepts to create integrated theories. My strength is physiological and field observations, so it was very exciting early on to help collect data to test his theories," says Ehleringer.

Once the power of measuring stable isotope ratios became established, others started to take notice. In the early 1990s an agent from the US Secret Service called, looking for help locating the source of counterfeit \$100 bills. "We were brought in to determine whether the paper used to make the 'Supernote' counterfeits was stolen US paper or paper from a different part of the world," says Ehleringer, who declined to discuss the findings from this work, citing confidentiality.

In 2003, Ehleringer and Cerling spun off IsoForensics, Inc., a company with forensic applications. The team worked with the US Drug Enforcement Administration, sleuthing cocaine and heroin origins and helping identify the geographic origins of unidentified decedents for law enforcement and the military through bone, tooth, and hair analysis.

"Carbon and nitrogen isotopes in hair record the history of your diet, whereas the oxygen isotopes in your hair record your geographical history," explains Ehleringer. Collecting hair samples to test the notion of a geographical record was a family effort; his wife and her friend drove around the country, collecting discarded hair from barber shops located in small towns, where it was likely that they were sampling locals rather than visitors (10).

Research using stable isotopes to draw conclusions from hair, human, and other, is now commonplace in anthropology, says Ehleringer. In a forthcoming PNAS article (11), Ehleringer and colleagues used hair samples from people living in the Salt Lake City area to examine how socioeconomic status relates to diet. They found that individuals from low socioeconomic regions were more likely to eat a diet heavy in C_4 meat, which primarily comes from cheap, corn-fed beef, poultry, and pork.

Urban Ecosystems

Ehleringer has long used the Salt Lake City metropolitan area as a laboratory. Years ago, he met atmospheric scientist Dave Keeling, a leader in atmospheric CO_2 measurements. Keeling encouraged him to begin CO_2 measurements in both forest ecosystems and urban regions. The result was a long-term, multisite, urban CO_2 network. "At the time nobody would fund long-term urban CO_2 monitoring," he recalls. "So, we bootlegged everything to keep that project going."

The multidecade observations show that whereas urban CO_2 emissions are higher than those of suburban areas, the rate of CO_2 change is lower in urban settings. Over time, suburban CO_2 emissions increase

faster than urban emissions (12). "The most obvious reason for this is that people living in suburbia travel; they don't work where they live so the consequence is higher emissions," says Ehleringer. "If you want to build an urban system with reduced CO_2 emissions, high-density housing, walkable cities, and EV [electric vehicle] transportation are solutions."

Today, Ehleringer is reducing the breadth of his research. With two projects remaining, one on tree rings and climate and the other aimed at summarizing his lifetime of work on *Encelia*, there is more time to pursue his passion for teaching. While he has always favored active learning, the sudden emergence of the coronavirus disease 2019 (COVID-19) pandemic has created new opportunities to make online teaching as engaging as in-class experiences. "My goal is to always make learning exciting and interesting," he says. "Given that many students today have abbreviated attention spans, online lectures become story-telling vignettes melded together to cover a topic. I'm trying to teach this old dog new tricks."

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