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PAUL JACKSON KRAMER

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A Biographical Memoir by

JOHN S. BOYER AND AUDREY W. NAYLOR

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BY JOHN S. BOYER AND AUBREY W. NAYLOR

PAUL KRAMER WAS A gifted plant physiologist whose life was characterized by a special ability to conceive undeniable experiments and explain them simply and convincingly. He spent his entire professional career at Duke University, arriving at the new West campus in 1931 while the grass was being planted, "retiring" in 1974, but continuing his experiments with his many friends and devoted colleagues until he died. He was also a student of history and the arts, and his sixty-four years in science formed perspectives that few of us have. He could expound on the development of science in the United States or the history of politics in China, and he had a unique understanding of human nature that gave him uncommon persuasiveness when he developed a large project or administered complex organizations.

As an adviser to students, Paul was a listener and would say "Why don't you try it?" when an experiment was proposed. To the wilder ideas, he would lean back in his chair, fold his hands in back of his head as he looked at the ceiling, and whistle tunelessly. After a moment, he would say he needed to give it further thought and the student knew it was time to move to a different idea. This gentle guidance and intellectual liberalism gave many students the courage to work on diverse projects, and his lab bubbled with interactions between his own students and others from biochemistry, ecology, forestry, and elsewhere.

THE EARLY YEARS

Paul was born in Brookville, Indiana, near the Ohio border where his father farmed his mother's family farm. Paul milked the cows and weeded the garden at an early age, and was delayed in going to school until his younger sister also could go, because travel was so difficult. They rode by horse and buggy for four or five miles to a one-room school house. In 1912 his father, who was a devoted educationist, moved the family to a farm near Oxford, Ohio, where Miami University is located, "in order to educate his children," he often said.

They attended the village school in Oxford and eventually graduated together from high school. As he and his sister grew up, they saw the farm change from mostly hand labor to machine operations, and young Paul became good at mechanical repairs at the same time he learned about plants and animals of many kinds. His father had attended a small college for one year and Paul read often in the family's unusually large library. Family conversations ranged widely, with heavy use of the encyclopedia and dictionary, and the children enjoyed many cultural events on the Miami campus nearby. After completing high school, they entered Miami University but continued to live at home for financial reasons. They missed a lot of social life, but Paul felt the chance for an education far outweighed this disadvantage.

Paul enrolled in an economic botany course almost by accident in his first semester because of a chance conversation and recommendation by the president of the university R. M. Hughes, whom he had met a few days earlier. The economic part of the course appealed to his background and gave him an early introduction to the subject. He finally majored in botany partly because he liked the laboratory work and partly because he was allowed considerable freedom and a small stipend as a teaching assistant. In fact, during his senior year, after the instructor in plant physiology became ill, Paul taught the remainder of the course.

One of Paul's problems in college was that he liked almost everything and was well acquainted with the arts and history. Science won out because plants were already so familiar and his mentor at Miami convinced him he had a promising future in the plant sciences, encouraging him to go to graduate school. The one subject he did not like was mathematics, which plagued him in his later life, although he insisted on doing the family taxes every year. Paul felt that one of the most important lessons from this breadth of interest was the ability to distinguish what was important from what was trivial. His writing and teaching were marked by exceptional clarity, reflecting this ability to think logically, and he often counseled students to identify what instructors regarded as important and focus on it.

In his senior year Paul decided to go to graduate school partly because he could be paid at the same time. Most schools offered $350 per year, but the University of Idaho offered $750, a magnificent sum in 1926. He worked there for a year with Prof. Floyd W. Gail, but decided to return closer to home. Before going he worked for the summer in northern Idaho in the U. S. Department of Agriculture's eradication program for white pine blister rust. In an isolated lab he studied the germination of wild *Ribes*, an alternate host for the disease. This gave him a little income and an enjoyable summer in the woods with other workers, thereby gaining some experience in dealing with people.

Paul's scientific career came increasingly into focus in 1927, when he entered graduate school at Ohio State University, where his adviser was the noted ecologist E. N. Transeau. Osmosis had been understood in the 1870s by J. Willard Gibbs at Yale and Wilhelm Pfeffer in Germany, but they did not explain how water moved to the top of tall trees. Dixon had subsequently shown that water columns could hold together and come under large tensions before breaking, thus providing a mechanism for "pulling" water to the tops of trees through the hollow vessels in the stem. It remained, however, to relate how living cells of the root absorbed water from the soil, because these cells could carry on osmosis and separate water in the root vessels from that in the soil. In 1928 this question was very much alive and Paul read the opinion of B. E. Livingston, supporting the view of Renner in Germany, that osmotic absorption is unimportant in transpiring plants.

As a model Paul chose a petiole from a large leaf and began by comparing the flow of water under tension or pressure with that caused by osmosis. He could fill the central cavity in the petiole with sucrose solutions to simulate the solution in the vessels of a root and he could pressurize the outer surface of the petiole while observing the cut end at atmospheric pressure. He found that much more water was moved across living cells by pressure and suction than by osmosis. He then similarly measured the water movement across roots. In all cases, the amount of water was much greater when suction was applied. If he killed the root systems, the flow increased under suction indicating that tensions could extend through the living tissues, ". . . reducing the role of the living cells of the roots to that of a mere absorbing surface, a role which might in some respects be filled as well by dead as by living cells . . ." (1932). He concluded that the living cells allowed rapid and passive water movement through them under tension in transpiring plants. At night they acted as a membrane, allowing osmosis into the vessels of the nontranspiring plants and creating "root pressure" and root exudation. The living cells mostly prevented air from entering the vessels and by growth extended the absorbing area of the roots.

THE MOVE TO THE SOUTH

Positions were few and pay was low in 1931 when Paul finished his Ph.D. He nevertheless refused an offer in peach research in Georgia for pay he considered too low ($1,600 per year) and held on for a few weeks until the young lady whom he later married noticed that the biology department of Duke University, recently formed from Trinity College, was looking for a plant physiologist. He was pleased to be offered the appointment at a salary of $2,000 per year, and he accepted.

Since Paul was about to be employed, Edith Vance and he married in June 1931; their honeymoon was a trip to North Carolina to inspect the university he had agreed to join. Later in the summer they moved to Durham with all their belongings in the rumble seat of a Model A Ford coupe purchased with money borrowed from a professor at Ohio State.

At Duke he was given a heavy teaching load. As the Depression was deepening, his salary was cut. Graduate students were few. He threw himself into his work and built on the experiments from his dissertation. Edith had graduate training and had taught botany at Vassar for two years. She encouraged him, knowing the purpose behind his dedication, and added her judgment to his thoughts. Soon daughter Jean Jackson was born and, later, son Richard Vance.

Paul recognized that the dead root experiments he had been conducting eliminated all theories of water absorption depending on live roots. He began more experiments of this type and found that intact plants with dead roots transpired copiously although not as much as plants with live roots. This indicated that forces originating above the roots were responsible for much of the water flow from the soil into the plant, which was consistent with the findings of his dissertation that tensions could be transmitted long distances through living root tissues and into the soil. He soon investigated whether temperature affected water movement into roots and could not distinguish between soil and root effects, so he investigated the soil alone using a porous clay surface to simulate a root surface. He observed a marked effect of temperature that he attributed to the viscosity and vapor pressure of the soil water. This paper was the first to measure temperature effects on soil water movement and is a good example of how easily he could isolate complex problems into simpler testable units.

As he worked, Paul became increasingly convinced that transpiration in the shoot was the origin of much of the force for water absorption, and he began to study the relationship between them in detail. He grew plants with an auto-irrigating reservoir to show how much water was absorbed by the roots and he weighed the plants and reservoir to obtain the amount transpired by the shoot. Transpiration always started before absorption, and the reverse occurred at the end of the day. This indicated that shoot dehydration was necessary before water could move. He postulated that the dehydration generated tension in the vessels and moved water into the roots, and the time to dehydrate caused a lag of about 2 h. He termed the effect the "absorption lag." This explained the role of the shoot in moving water into the roots and formed the basis for the present theory of water uptake by plants.

He began to think that the roots might be an important resistance to water uptake and measured the effects of excising the roots. Their removal shortened the absorption lag considerably, and absorption was transiently increased. He concluded in 1938 that ". . . the living cells between epidermis and xylem offer considerable resistance to the passage of water and are probably responsible for a large part of the lag of absorption behind transpiration . . . This resistance is much greater at low temperatures than at high temperatures, probably because the viscosity of both protoplasm and water increases as the temperature decreases."

Next, Paul quantified the water movement by transpiration and by osmosis by measuring transpiration in whole plants, removing the shoot, then determining how much water the roots delivered by forces generated in the roots alone. Initially, after removing the shoot, water was absorbed into the root through the stump and thus was opposite to that in the intact plant. Eventually, a small amount of exudation occurred from the stump. In no case could root exudation account for the water absorbed when the plant was intact and transpiring, and he said (1939), "Most, and possibly under some conditions all, of the water absorbed by transpiring plants is absorbed as a result of forces set in motion by the loss of water in transpiration." Further experiments showed that forces generated by transpiration moved less water when aeration was poor, temperatures were low, and water was deficient around the roots; the cause was resistance by the roots.

Thus was built the idea that water absorption in plants occurs slowly by osmotic means at night when transpiration is negligible and results in "root pressure" in the vascular system often leading to the formation of droplets around the margins of leaves (guttation). During the day water is absorbed by forces originating in the shoot because of the dehydration caused by transpiration, and these forces extend through the living tissues of the root into the soil water. The forces are much larger than can be generated with a vacuum pump and indicate that large tensions can be generated in the vessels and cause correspondingly large flows through the root. These concepts had a great impact on the field of plant physiology. They explained how water movement could be passive but still be affected by root metabolic activity. They also explained why plants could become water deficient in a flooded field. Farmers were amazed when they saw their tobacco leaves wilt after rain that flooded the soil, but Paul had the answer.

THE LABORATORY FLOURISHES

The decade of the 1930s marked Paul as a particularly capable scientist. His lab began to attract students. Paul called one prospective student on the telephone, saying, "I see that you want to be a physiological ecologist. What about becoming an ecological physiologist?" The student was so pleased that he accepted. Eventually more than forty students would receive their Ph.D. degrees from him. He would say, "I am not going to look over your shoulder. You know where I am when you need advice," and he was always willing to listen. He was kind in his suggestions and frequently gave a student a chance if he saw signs of commitment. He thought work could make up for a late start and would sometimes offer a summer fellowship to someone in need or encourage a promising technician to go on to graduate school. He and his students would often read scientific papers containing statements with which they could not agree. Paul would suggest that they write the author and would pen a letter that was polite but firmly in disagreement. Many of his students gained confidence from this display of scientific forthrightness.

Soon after arriving at Duke in 1931, Paul had made the acquaintance of C. F. Korstian, who had come from Yale to develop Duke Forest and establish the School of Forestry. Korstian thought physiology and ecology were essential for training in forestry and provided Paul with some equipment and support for his first two graduate students. A lifelong collaboration began with the forestry school and many original papers were written with students from forestry. With woody plants he found that tree dormancy was regulated in part by photoperiod and thus light was an important signal for the onset of winter. He and his students found that the eventual transformation of pine forests to hardwood forests resulted from the inability of pine seedlings to grow in the low light intensities under deciduous trees, which was one of the first physiological explanations of the succession of plant species in natural communities. Much forest practice is now based on this principle.

Paul was probably the first to measure the uptake of phosphorus by mycorrhizal roots of trees with radioisotopes. With his student H. H. Wiebe, Paul also investigated the absorption of water and radiolabeled phosphate along roots and discovered that much salt uptake occurred some distance behind the root tip where the xylem was well differentiated. He continued to study salt uptake in roots whose anatomy had been changed by becoming dormant or by developing suberized bark. Many of his findings had practical applications, such as the need for mycorrhizal organisms in tree culture, the importance of root temperature for salt and water uptake in plant culture, and the necessity of soil aeration in trees planted in urban settings.

NATIONAL ATTENTION

Paul's simple experiments were clearly described and interpreted with compelling logic, resulting in his publications being quickly recognized. By 1952 he had already published forty papers and one book. In the early 1940s he had become involved with the American Society of Plant Physiologists and served in several offices, including the presidency in 1945. The Botanical Society of America elected him president a few years later. He was appointed director of Duke Gardens, where he oversaw expansion during his twenty-nine years of service that made it a regional and national showplace. During the 1950s he became involved in faculty affairs, because he felt the faculty should have a voice in university governance. After a few years Paul became vice-chairman of the Faculty Council of the university. During this service a difficult power struggle began between the president and the vice-president of the university. Paul was caught in the middle of an unfortunate situation that incurred the dislike of several supporters of one faction or the other, and great diplomatic skills were required. When the National Science Foundation offered him a year as a program director for developmental biology in 1960, he was glad to leave the campus. While at the NSF he was asked to apply for the director's position for the Division of Biology, but he declined because of memories of the administrative problems at Duke. He continued to spend time on panels and committees in Washington and became president of the American Institute of Biological Sciences, an organization he had helped create as a voice for all biologists. Unfortunately, AIBS had overextended its finances based on grants for several years and Paul had the difficult job of sorting this out during his presidency. His persuasiveness with the sponsors and ability to prune the institute's activities brought the organization through.

THE FATEFUL SABBATIC

In the mid-1950s, as the number of graduate students was increasing, Paul decided he needed to get away and took the family on a sabbatic leave at the California Institute of Technology, where he worked in the Phytotron. This experience with controlled environments caused him to think that whole plants could be studied much as an enzyme is studied under controlled conditions in a test tube, and here was a way of bringing biochemistry and whole plants together. He wrote (1973), "Instead of being the master of whole organism biology, molecular biology really is its useful servant, helping to explain at the molecular level why organisms behave as they do," and the controlled environment promised to bridge this complexity.

Paul believed fervently in the concept that genetics and the environment play equal roles in growth and development, and he knew from his farm and research experience that environmental resources frequently control plant performance (1973), "There are specialists on the carbon pathway in photosynthesis, the energy transfer system, and the structure of chloroplasts, but the effectiveness of photosynthesis as a supply of energy for plant growth is limited more often by stomatal behavior, leaf structure, mineral nutrition, or water supply than by processes at the molecular level."

The experiences in Washington and at the NSF gave Paul confidence to apply for funds for a controlled-environment facility that he had so admired at Caltech. He campaigned for one in the eastern United States and in 1965 obtained a large grant from The NSF to build two! One was to be at Duke and the other at North Carolina State University. The two facilities have provided major boosts to plant research on the two campuses, and his own work made extensive use of them. In the Duke facility there were investigations of the coupling between solute and water flow that unified disparate results from other labs that had been unexplained for years. Further work, with his colleague Aubrey Naylor, showed that differences in membrane lipids caused differences in root resistances to water flow, which helped explain why roots had a high resistance to water flow and why killed roots transmitted more water than live roots. There were experiments with how CO_2 affected growth and why water deprivation inhibited photosynthetic CO_2 fixation.

Paul and his students showed that pineapple uses a specialized photosynthetic metabolism found in desert plants and thereby conserves water. Later, after reaching emeritus status, he became interested in nuclear magnetic resonance imaging as a way to follow paths of water movement from soil to roots, and he published with other colleagues the first pictures of water depletion zones around roots in undisturbed soil.

THE BOOKS

Despite all this heavy work, in 1949 he found time to publish a book on water relations of plants that was so well received that he did it again in 1969 and then in 1983. He published books on tree physiology and ecology with his student T. T. Kozlowski in 1960 and 1979 and with Kozlowski and S. G. Pallardy in 1991. These books were immensely popular because of Paul's ability to simplify complexity and concern himself with the main points of the arguments. He took it as a compliment when one reviewer said that he made complex concepts too simple. The books were translated into several languages, sometimes without his knowing it. He is probably as well known for these works as for his distinguished laboratory experiments.

IN CONCLUSION

Paul gave credit to many other scientists for his own contributions. He felt that any discoveries he may have made were initiated by the work of others. Others tended to recognize his accomplishments more than Paul, who sometimes would say that he never made a major discovery. Nevertheless, he was given an award of merit from the Botanical Society of America, an achievement award from the Society of American Foresters, a Barnes Life Membership in the American Society of Plant Physiologists, and a distinguished services award from the American Institute of Biological Sciences. He was elected a fellow of the Australian Academy of Sciences and was invited to membership in the American Academy of Arts and Sciences, the American Philosophical Society, and the National Academy of Sciences (1962). He was given honorary degrees by the University of North Carolina, Miami University, Ohio State University, and l'Université Paris VII. He served on the original board of editors for *Annual Review of Plant Physiology* and several committees of the National Academy of Sciences, including one that brought the American Institute of Biological Sciences into existence.

Paul felt that the best way to know oneself was to lose oneself in some kind of work, and his steady stream of papers and books demonstrates that idea. His last academic effort was a book with John Boyer on the water relations of plants, written when Paul was ninety. He was still hoping to dehydrate a plant in a magnet and see the effects on roots, which had not been done before, when the end came from pneumonia.

MOST OF THE MATERIAL for this memoir came from the "Autobiographical Statement of Paul Kramer" (National Academy of Sciences, Washington, D. C., 1987) and from personal conversations with Paul while John Boyer was his student and while Aubrey Naylor was his faculty colleague for forty-three years.

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