Kenneth V. Thimann

1904–1997

BIOGRAPHICAL *Memoirs*

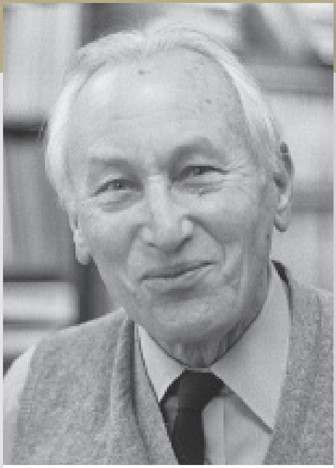
A Biographical Memoir by
Mary Helen Goldsmith

NATIONAL ACADEMY OF SCIENCES

KENNETH VIVIAN **THIMANN**

August 5, 1904-January 15, 1997

Elected to the NAS, 1948



Photography by the Public Information Office, UC Berkely

By Mary Helen Goldsmith

English-born Kenneth Thimann was a major authority on plant growth and development during the 20th century. Early in his career he identified, within auxin, the first known plant hormone, the structure of indole-3-acetic acid (IAA). This achievement initiated what became a long and productive career for Thimann pioneering the biochemistry, physiological roles, and developmental effects of natural and synthetic compounds affecting plant growth. He also developed an interest in the effects of light on the growth of plants, involving processes other than photosynthesis. His ground-breaking book *The Life of Bacteria*, departing from the traditional medical and applied bacteriology textbooks, was among the first to focus on metabolic characteristics in classifying microorganisms and in understanding their ecology.

Studying chemistry and biochemistry at Imperial College, University of London, he earned a B.Sc. and a Ph.D. (1928). He then taught chemistry at King's College for Women in London before taking a position at CalTech in 1930. In 1935 he joined the Harvard University Biology Department, where he remained for the next 30 years. In 1965 he moved to the new University of Santa Cruz, in the California University System, where he served until his retirement in 1989.

Kenneth Vivian Thimann was the third of four sons of Muriel Harding and Israel Phoebus Thimann. He was born on August 5, 1904, in the market town of Ashford, Kent, in southeast England. His father, a Congregational minister, had emigrated in his youth from L'viv, then known as Lemberg. He was Jewish and converted after arriving in England in the late 19th century. His English mother was a teacher and founded the Ashford School for girls, now coed. When Kenneth was eight, his father died and the family moved to a suburb in southeast London. He attributed his early interest in science to his eldest brother, Ralph, who was an apprentice analyst determining the safety of food sold in local markets. Kenneth's questions stimulated Ralph to bring home an introductory text, which led to early brotherly discussions of chemistry. Ralph was killed during World War I when Kenneth was twelve.

From 1915 to 1921 Kenneth attended Caterham School in Surrey, a residential school for sons of ministers. He credited his strong start to personal attention along with emphasis on writing and math as well as excellent instruction in the upper-level science courses. Biology was not part of the curriculum, but chemistry and biochemistry were. He wanted to go to Cambridge, but as this was beyond the family's means, he attended the Imperial College of Science and Technology, University of London, earning a B.Sc. with first class honors in chemistry in 1924 and a Ph.D. in biochemistry and plant physiology in 1928. His thesis, with S. B. Schryver, dealt with the contributions of amino acids to the electrophoretic mobility of proteins. He spent the next two years as a Beit Memorial Research Fellow, learning microchemical techniques in Graz, Austria, and served as a demonstrator in bacteriology at King's College, London.

In 1930 Kenneth married Ann Mary Bateman. He accepted a temporary appointment as instructor in bacteriology and biochemistry at the California Institute of Technology and, with his bride, departed for California. Although he intended to work on copper complexes of amino acids with Henry Borsook, a leading researcher in protein synthesis, new opportunities at CalTech quickly arose. Thomas H. Morgan, soon to be a Nobel Laureate in Physiology and Medicine, was assembling an international group of young scientists in biology. Also, Kenneth and Ann shared a house with Hermann Dolk, a plant scientist from Utrecht, the Netherlands. Dolk was continuing his work on the role of a growth substance in the gravitropism (the effect of gravity on plant growth) of oat seedlings. Intrigued, Kenneth joined Dolk in purifying and determining the chemical structure of the active compound.

In 1880 Charles and Francis Darwin had observed that the tips of grass seedlings were more sensitive to light than the growing region below. They postulated that in phototropism an "influence" travels from the tip where light is detected to the growing region below. Attempts to extract the postulated growth substance failed until in 1928 when Frits Went, then a graduate student at Utrecht, reported capturing the long-sought "Wuchstoff"—growth substance—moving from tips of oat seedlings into moist gelatin blocks. When these blocks were subsequently placed on one side of decapitated oat seedlings (*Avena sativa*), curvature varied linearly with the concentration of the active substance up to a maximum. Went's experiments attracted international attention by suggesting that plants, like animals, have hormones controlling growth as well as responses to stimuli.

Fifty years later, at the event commemorating publication of Went's thesis, Kenneth commented "… Went's discoveries were of exceptional importance. Basically, "he [… brought] the plant growth hormone down from a biological concept to an experimental reality."

Kenneth sought richer sources than coleoptiles (the protective sheath around the emerging tip of a new grass or cereal growth) from which to purify enough growth substance to determine its structure. Felix Kogl, a professor of chemistry in Utrecht, coined the name auxin (from a Greek word meaning increase) for the growth substances that his group had isolated from microorganisms and human urine. Meanwhile, James Bonner, then a graduate student at CalTech, observed that large amounts of growth substance accumulated in the medium when the fungus *Rhizopus suinus* was grown in aerated liquid medium. Kenneth purified and crystalized the active substance from the culture medium. By comparing its physical and chemical properties and characteristic color reactions with various reagents and with an authentic sample of indole-3-acetic acid (IAA), he and Joseph B. Koepfli deduced the purified substance was IAA.

Kogl's group also detected IAA in human urine but insisted on calling it heteroauxin, believing that auxins a and b, previously unknown cyclopentene compounds they had earlier discovered, were the native auxins of plants. Unlike auxins *a* and *b*, IAA contained nitrogen, was stable in alkali, inactivated by acid, and failed to form lactones. Kenneth detected slight growth activity in a sample of auxin *a* from Utrecht. Although, as discussed later, the question of whether IAA is the native auxin produced by the plant remained controversial for many years, he never wavered in his conclusion that it is.

During Kenneth's CalTech years it quickly became apparent that auxin mediated more than cell elongation and tropisms in plant development. Robin Snow at Cambridge showed that IAA stimulates cell division and cambial growth. This was an exciting finding because until this point the role of auxin in growth was thought to be limited to cell elongation.

Following Dolk's tragic death in an automobile accident, Kenneth collaborated with Frits Went, then recently arrived from Indonesia, and Johannes van Overbeek, from Utrecht. They found both natural and synthetic auxin stimulated the rooting of cuttings, and they identified IAA in root extracts. Kenneth showed that auxin, at low concentration, initiated root formation, but at higher concentration inhibited subsequent elongation.

Kenneth observed that growth of pea stems in response to increasing exogenous concentrations of auxin passes through an optimum. Concentrations 10 to 100 times greater than endogenous values inhibited growth. Furthermore, root elongation was inhibited at a hundred-fold lower concentration than that of buds, and sensitivity of buds was lower than for stems. These differences lie behind apical dominance, a phenomenon that determines the shape of plants and had long fascinated botanists.

James Bonner and Folke Skoog became Kenneth's first graduate students, and Kenneth and Skoog began investigating apical dominance. It was well known that the apex of a growing shoot of a dicotyledonous plant inhibits growth of lateral (axillary) buds below, preventing them from growing. Aware of reports that developing leaf buds produced a growth stimulator, they surmised that auxin coming from the growing apical bud might inhibit axillary buds. They found that replacing the apical bud with auxin did indeed inhibit the buds below; moreover, on delaying replacement, lateral buds escaped from inhibition and developed branches.

Testing diffusates from buds, Kenneth and Skoog showed that terminal buds of young broad beans produced auxin during growth, while inhibited axillary buds of the plant did not. Also, younger leaves produced more auxin than older ones. Another striking finding was that within a few hours after removing the apical bud, lateral buds started producing their own auxin and began growing.

The five years in Pasadena were formative and productive for Kenneth. His discovery that a small molecule, indoleacetic acid, had diverse effects on both growth and development of plants opened fascinating questions. Moreover, he and Ann had started a family, which in time grew to three daughters, Vivianne, Karen, and Linda. He had arrived at CalTech a protein chemist but departed a plant physiologist, with questions that engaged him for a lifetime.

In 1935, he joined the faculty of Harvard University as a lecturer in biology, becoming an assistant professor the following year. His rise to prominence in the young discipline of plant physiology was swift. Among his first new studies, he and his doctoral student Beatrice Sweeney demonstrated that low concentrations of IAA increased protoplasmic streaming. In 1936, only four years after his initial paper on auxin, the American Society of Plant Physiologists recognized "his contributions to our knowledge of the chemistry and physiological significance of the growth hormones of plants" with its highest honor, the Stephen Hales Prize.

Kenneth became a United States citizen in 1941. During World War II he served as a consultant in the Office of Scientific Research and Development, and Director of both the Anti-Submarine Warfare and Air Operations Research Group for the U. S. Navy. Operations Research was a new field developed during WWII in which teams of scientists in diverse fields applied insights and tools from their scientific research to military operations. He continued as a consultant for the Navy until 1955 and was a founding member of the Operations Research Society of America.

Reports of auxin *a* causing growth could never be reconfirmed, while reports of IAA being identified from different plants continued to appear. In 1962, during a sabbatical in Kenneth's lab at Harvard, Malcolm Wilkins questioned the identity of the natural auxin in coleoptiles. Any lingering doubts were finally dispelled in 1972 in Wilkins' lab at the University of Glasgow when Michael Greenwood, using gas chromatography and spectrometry, identified unequivocally the auxin diffused from 15,000 coleoptile tips as IAA.

Kenneth had realized early that the relation between molecular structure and auxin activity might reveal how auxin elicited growth. The indole nitrogen proved essential for auxin transport; replacing it with either carbon (indeneacetic acid) or oxygen (coumarylacetic acid) elicited only localized growth. These other substances were not transported, but they stimulated cell elongation and rooting and inhibited lateral budding. Only IAA was transported from the apical end. Kenneth concluded that the structural requirements for polar transport were more stringent than for auxin's stimulation of growth. The relationship between structure and auxin action became a recurrent interest for him. He and graduate student William Porter later suggested that IAA activity required a partial positive charge on the indole ring's nitrogen.

Knowledge of the structure of IAA quickly led to synthesis and testing of structurally related compounds for auxin-stimulated growth. Kenneth, Koepfli, and Went specified that the structural requirements for auxin activity included (a) a ring system with at least one double bond, (b) a carboxyl group or a group easily converted to an acid, and (c) a specific spatial relation between the ring and the carboxyl group.

All plants require IAA for growth, but it is important to understand whether, in addition to cell elongation, synthetic analogs also evoke other known responses to IAA. These include initiating lateral roots and roots on cuttings, inhibiting lateral buds, eliciting cambial division, differentiation of vascular tissues, stimulating fruit development, and delaying abscission of leaves and fruit.

Kenneth was interested in the reception of both phototropic and gravitropic stimuli. His lab made careful measurements of the energy requirements for both tip curvature and a less-sensitive curvature involving most of the length of oat coleoptiles. In the lab, George Curry's action spectrum for phototropic curvature of etiolated oat seedlings and Hans Gruen's for sporangiophores of the fungus *Phycomyces* were the best spectral data at the time. Both spectra had characteristics of carotenoids, with a major peak at 445 nanometers (nm) and secondary peaks at 425 and 472 nm. A broad, low peak at 370 nm in the near UV suggested a *cis*-configuration as in vision. Wavelengths longer than 500 nm were ineffective. These spectral data have survived the test of time, but the receptor molecules turned out to be flavoproteins, now called phototropins.

In 1892 German botanist Fritz Noll had suggested that settling of dense starch-containing plastids or statoliths within certain cells triggered the geotropic response of plants on change in orientation from the vertical. More than seven decades later, in 1965, Barbara Gillespie Pickard and Kenneth attempted an elegant test of the statolith hypothesis. Starch became undetectable either histochemically or by electron microscopy in wheat coleoptiles incubated in gibberellic acid and kinetin. Although starch-depleted plastids no longer settled in a gravitational field, depleted coleoptiles still responded gravitropically, albeit only partially and slower, with a time lag of several hours greater than in the controls. Pickard and Kenneth reasonably concluded that the reduced growth rate accounted for the reduced curvature, and they logically suggested that a reevaluation of the classic statolith hypothesis was in order. This experimental result stands alone in Kenneth's corpus of work in not having an obvious explanation, because later work in many other laboratories has pointed to the importance of statoliths in gravitropism.

Skoog's discovery in the early 1950s that kinetin-stimulated cell division and formation of buds on cultured tobacco pith encouraged Kenneth to reexamine apical dominance. His student Margaret Wickson found that IAA completely inhibits growth of the bud on a short section of stem, but kinetin in an equimolar ratio with IAA relieves the inhibition. Another student, Tsvi Sachs, showed that kinetin applied directly to inhibited lateral buds of intact plants releases the buds from inhibition. Gibberellin, another plant hormone, causes faster growth but fails to release inhibited buds. Thus, whether lateral buds are inhibited or released depends on the balance between auxin in the main shoot and the native hormone cytokinin (whose action is mimicked by kinetin) arising locally in the buds. These findings paved the way for successful culture of plant tissues, pollen, embryo rescue, and regeneration of whole plants from a single transformed cell or protoplast.

Kenneth encouraged histochemist Helen Sorokin to make detailed anatomical studies of pea stems. Her work showed that inhibited lateral buds lacked vascular connections. Addition of kinetin resulted in the downward differentiation of vascular strands to the lateral bud, subsequently connecting with vascular tissues developing upward from the main axis. The buds began increasing in diameter, elongating, and producing auxin. Tsvi Sachs's further discovery that vascular strands from lateral buds only connect with auxin-deficient vascular bundles in the main shoot is crucial in understanding how auxin controls apical dominance.

Although considerable evidence suggested that roots supply natural cytokinins to the shoot, Kenneth showed that buds also produce cytokinin in light, removing the inhibitory effect of auxin. Similar experiments on *Coleus blumei* not only showed these antagonistic interactions of cytokinin and auxin on buds, but provided further evidence that light stimulates the synthesis of cytokinin.

Kenneth's student Stanley Burg was the first to show that ethylene produced by fruit was important in ripening. Burg's later report that auxin accumulation at nodes of pea seedlings stimulates ethylene production and inhibits growth led Kenneth and W. Russell to demonstrate that ethylene was nearly as effective as auxin itself in preventing lateral buds from growing. These experiments suggested that ethylene could exert effects on auxin inhibition in apical dominance.

Kenneth followed the international literature assiduously, adopting new techniques in his own and his students' research. Through timely experimentation, he replaced unfounded conclusions with better ones. For example, when reports appeared that caffeic acid "may be as important a natural growth regulator as IAA," he along with Tomaszewski and Porter showed that diphenols spared endogenous IAA from enzymatic oxidation.

Applications to Horticulture and Agriculture

Many economically significant applications followed the discovery of auxins and elucidation of their physiological effects. Kenneth believed in the capacity of science to improve the human condition, and he frequently reviewed progress in this area, but the search for synthetic auxins and commercial applications was mostly taken over by Kodak and Dupont Corporations.

In the 1950s the biosynthetic pathway for auxin was unknown; 1) tryptophan, 2) indoleacetaldhyde, 3) indoleacetonitrile (IAN), and 4) indolepyruvic acid (IPA) were among possible precursors. Kenneth, aware that intercellular bacteria and fungi might produce some of the plant's IAA content, emphasized the use of sterile systems in determining pathways for auxin biosynthesis. Researchers in the lab of noted Welsh organic chemist E. R. H. Jones extracted IAN, a neutral auxin, from cabbages. They reported that it was ten-fold more active in oats than IAA, but totally inactive on peas. Kenneth showed that oats but not peas were capable of enzymatic conversion of IAN to IAA. Bruce Stowe, then a graduate student in his lab, confirmed this finding. Later graduate student Sundararaman Mahadevan extracted the first plant nitrilase from oat and barley leaves. Surveying 21 families, he detected nitrilase only in the Cruciferae, a few species of Poaceae, and Musaceae. Post-doc Ron Poole resolved the mystery of why IAN was more active in some cases by demonstrating that uncharged IAN, at neutral pH, was more permeable than IAA. Interestingly, the IAN biosynthetic pathway has received independent confirmation with mutants of Arabidopsis.

Clearly plants have more than one route to IAA. IPA, first detected by Bruce Stowe in extracts of corn kernels, might be the immediate precursor in species lacking nitrilase. Kenneth doubted that tryptophan was on the path, because its decarboxylation is rare in higher plants. He and Maria Grochowska ruled out tryptophan as precursor in sterile tips of oat coleoptiles, but tryptamine remained a possibility elsewhere.

With graduate student Larry Nooden, Kenneth examined the relationship between cell enlargement and protein synthesis. They showed that when auxin induced growth in segments of various tissues it accelerated incorporation of ^{14}C-leucine into protein. Was this causal or a correlation? Selective inhibition of cell enlargement by inhibitors of protein or nucleic acid synthesis suggested that auxin action might depend on continual synthesis of an essential, growth-limiting or growth-promoting protein. They favored the possibility that auxin induces synthesis of a protein that loosens the cell wall.

Kenneth came to regard a single primary action of auxin as improbable. Auxin's diverse effects—on cytoplasmic streaming, cell division and elongation, root initiation, vascular differentiation, apical dominance, abscission of leaves, ripening of fruits, and in interactions with other hormones—defied an explanation of a unitary receptor and mode of action. In 1977 he concluded in *Hormone Action in the Whole Life of Plants* that we were still a long way from understanding the molecular basis of auxin's mode of action. Further progress awaited new techniques and insights from molecular genetics.

Role as Mentor

Among Kenneth's greatest and longest-lasting contributions was his support and mentorship of his many students. His timely reviews propelled the entire field of plant growth and regulation forward by exposing ideas that were problematic and focusing attention on outstanding problems and new advances. Kenneth always made time to examine experimental results and discuss their quality and interpretation. He could be counted on to gather with his graduate students, post-doctoral fellows, and visiting faculty for lively discussions over tea each afternoon. He and Ann hosted monthly evenings with dinner at their home for his entire lab and their spouses.

As a graduate student I found him a sympathetic and supportive advisor. For me, he suggested a fascinating problem related to his ongoing interest in tropisms and apical dominance. Then he let me figure out how to proceed. Polar transport of auxin was ripe for reexamination with isotopically labelled IAA that his colleague Bruce Stowe was in the midst of synthesizing. I used this IAA to study transport with greater precision.

By 1965 Kenneth had achieved a distinguished international reputation. As Master of East House, he and Ann had enjoyed creating an enriching intellectual, cultural, and social life in a dormitory for women attending Radcliffe College. But he felt ready for new challenges. He shocked friends and colleagues when he retired early from his Higgins Professorship at Harvard to become professor of biology, provost of a college, and Dean of Natural Sciences at UC Santa Cruz (UCSC), a new branch of the University of California.

The campus, set in a redwood forest, overlooked the town and the Pacific Ocean. Clark Kerr, then president of the UC system, and Dean McHenry, Chancellor of UCSC, were planning an institution devoted solely to undergraduates. The idea that undergraduates would reside and take courses in colleges offering distinctive curricula and academic experiences appealed to Kenneth. The university's first college, emphasizing humanities, was opening in 1965, to be followed by another in social sciences.

Despite his liking for the all-undergraduate idea, from the start Kenneth argued persuasively with Clark Kerr and Dean McHenry that he would be unable to attract eminent scientists to Santa Cruz without graduate students. He refused their offer until they agreed to open the graduate school along with the undergraduate colleges. During these negotiations, Crown Zellerbach Corporation offered a generous endowment for a third college, to be called Crown College and destined to be science oriented, with Kenneth as provost.

UCSC faculty were members of departments known as boards of study, as well as fellows of a college. Each college included faculty from various disciplines. The provost of each college, together with the departments, had responsibility for recruiting faculty to teach college courses. In the early years, the provosts and their colleges held more power and resources than disciplinary departments.

As Dean of Natural Sciences, Kenneth had his hands full recruiting talented scientists for the first two colleges as well as for the new science college. Yet he succeeded in shaping the early development of the natural sciences at USCS with key appointments of both promising young scientists and eminent established scientists in mathematics, astronomy, earth sciences, physics, chemistry, and biology. Physicist Michael Nauenberg came in 1966, but not before, because with people of Kenneth's caliber he "felt serious science would have a chance at Santa Cruz".

Kenneth and Ann bought a house on Pasatiempo Drive, where they lived while the provost's house was built. Ann, an artist and skilled weaver, began visiting local artisans and craftsmen along the coast. She and Kenneth searched together for distinctive furnishings for Crown College.

Kenneth took full charge of both the physical and academic planning for Crown College while it was just a hole in the ground. He and Ann suggested that college buildings surround a patio and fountain. He guided the work of a prominent San Francisco architect, Ernest Kump, assuring that besides classrooms, the college include offices and apartments for resident faculty, places for both quiet study and group activities, and a library. The architects learned that the dining hall must also serve for meetings, lectures, concerts, and theater, but the L-shaped hall with a wall of windows facing the setting sun that they planned was not approved.

At Crown, Kenneth strove to create a stimulating intellectual, cultural, and social life for a community of students with a diverse faculty spanning the arts and sciences. Although he consulted Chancellor McHenry frequently, he enjoyed considerable autonomy in appointments. He believed small classes and personal attention encouraged discussion. In the early years of the college, students appreciated conversing with their instructors during meals and college events. Planning a rigorous college curriculum required time, attention, and sometimes contentious faculty meetings.

Complaints by some students who considered plants irrelevant and uninteresting troubled Kenneth. He felt their view, "plants are boring," might change if they understood how much humans depend upon and modify plants. He recruited Jean Langenheim, a paleo-plant ecologist from Harvard, and invited her to join him in teaching a course. Later they wrote a book with this goal. By attending each other's lectures, their approaches evolved in synchrony. Each wrote the first draft of topics in which they were expert. Then each painstakingly reviewed the other's chapters. The result, *Botany: Plant Biology and Its Relation to Human Affairs*, is informative and delightfully readable. Over the years, hundreds of students enjoyed the course.

Kenneth, recalling the Caltech years and the impressive desert wild flowers he has seen on outings to Death Valley, instituted an annual spring field trip. He invited his friend and coauthor of *Phytohormones*, Frits Went, from the Desert Research Laboratory in Nevada, to come and bring his mobile laboratory, outfitted with microscopes and experimental equipment. Students were treated to the sight of these two pioneers in plant growth, flat on the desert floor, examining diverse species of "belly plants." They discussed adaptations for arid environments and dug roots to observe mycorrhizae. Jean Langenheim recalls, "We learned a lot and had fun—times remembered by all."

Plant Senescence

In spite of considerable administrative responsibilities, Kenneth found time for research. With his students, ranging from undergraduates to postdocs, he opened a new line of investigation on senescence of plants. In more than 40 papers he and his students developed the concept of senescence as an active, controlled, developmental process, important in the plant's overall conservation of scarce resources. Senescence recycles carbon skeletons and scarce nutrients, especially nitrogen, phosphorus, potassium, and magnesium.

Senescence in detached, darkened oat leaves begins within hours with synthesis of new proteases. Extensive proteolysis and breakdown of chlorophyll follow. Respiration, fueled by release of amino acids, rises rapidly, reminiscent of the climacteric in fruit ripening. Increase in the endogenous production of ethylene further illustrates the parallel with fruit ripening.

Light and cytokinins retard senescence. Thus, opening stomates by light or cytokinins strongly delays senescence. But closing stomates osmotically, hormonally, or by restoring darkness hastens senescence. In light, the vacuole retains an acid protease that, in dark, leaks into the cytoplasm where it attacks mitochondrial and chloroplast membranes.

Changes in abscisic acid (AbA) level suggest it plays a role in senescence. Research fellow Shimon Gepstein, monitoring AbA level in the leaf by gas chromatography, showed an increase after treatments that close stomata. Cytokinins largely prevent the increase. Conversely, a decrease in AbA precedes stomatal closure. Similar changes in AbA level also occur during the natural senescence syndrome of intact plants.

Resources were limited, but Kenneth was adept at seizing opportunities. At Harvard, he had found the Arnold Arboretum and Harvard Forest valuable adjuncts for teaching and research. At UCSC he shared Chancellor McHenry's interest in creating an arboretum in the ponderosa pine woods and grasslands on the hillside below the campus. Before construction began, Ansel Adams had photographed and designated this site as worthy of preservation. Ray Collet came to Kenneth to ask where a gift of 80 eucalyptus species from a wealthy donor could be planted. Upon learning Collet had degrees in chemistry, a Ph.D. in geography from Berkeley, and experience in weather forecasting, Kenneth recommended his appointment to the faculty of Crown College, where he created courses in meteorology and native flora of the Monterey Bay region. Kenneth also recommended Collet to be the arboretum's founding director, a post Collet held as professor of natural history until his retirement in 1997. Guided by Collet's initial leadership, the arboretum is now world-renowned for the diversity of its collections of plants native to Mediterranean climates—not only California, but South Africa, New Zealand, New Caledonia, Australia, and Chile. Kenneth served as chair of Arboretum and Plantations and was a familiar presence to staff, students, and volunteers. Long after retirement, he served a term as president of the Arboretum Associates.

In 1967, concerned that Chicano students interested in premedical study were frequently unprepared for university work, Kenneth sought foundation support for a summer program at Crown. Courses in English, mathematics, and sciences helped incoming freshmen cope with college level courses in the fall. He firmly believed Chicano communities deserved physicians who spoke Spanish and understood their problems. Although some students succeeded and became doctors, this program could not be sustained.

In the early years, the university had no programs in music and art. Being a talented musician himself, Kenneth wanted students to interact with professional musicians and artists as both teachers and performers. He established the Crown Chamber Players, working with Rosario Mazzeo, who had been for many years the first desk clarinet with the Boston Symphony Orchestra. Retired in Carmel, he was conveniently nearby. Sylvia Jenkins, an internationally known pianist, was also integral to the group. They drew in a choice cadre of superb performers, and offered chamber concerts for many years, open to the campus and the town.

With his administrative duties in Crown and the University, Kenneth recognized from the start that he needed another plant scientist to help with teaching plant courses. He selected Harry Beevers, an eminent plant physiologist and biochemist, who was elected to the National Academy of Sciences shortly after his arrival. Beevers remembers that

> *KVT ...was quite distressed when the college system was drastically modified. In retrospect, and this is greatly to his credit, only a person of his stature could have achieved what he did as provost of Crown College. Under his leadership the college established a reputation for the serious scholarship of its students, and the core of the early faculty continued to enjoy the camaraderie and genuine fellowship that he instilled. While Provost and many years afterwards, KVT was actively involved in teaching at all levels within the Biology Department. His love of plants and flair for exposition inspired many young students. Undergraduates and graduate students worked alongside him in his laboratory, and he was, unfailingly, a patient and encouraging mentor, sharing their enthusiasms with obvious pleasure.*

Kenneth was one of the scientific statesmen of his generation. He served on numerous editorial boards and was the founding and consulting editor of *Vitamins and Hormones* and the founding editor of *Annual Reviews of Plant Physiology*. He was president of the American Institute of Biological Sciences, Botanical Society of America, American Society of Plant Physiology, Society of General Physiologists, and American Society of Naturalists. He was chair of the XI International Botanical Congress and International Plant Growth Substances Congress. He was honored by membership in foreign academies, including the Royal Society, London, Academia Nazionale dei Lincei, the Paris Academie des Sciences, and the Academie di Agriculture, Paris, and in 1982 he received the Balzan Prize.

When Kenneth arrived on campus in 1965, the first permanent building on the campus, Natural Sciences I, was under construction. On his retirement in 1972, the university renamed it Thimann Laboratories. After Kenneth's retirement and Ann's death, he returned East to be with his daughters. Vivianne Nachmias provided him space in her laboratory at the Medical School at the University of Pennsylvania, where he began to study the interaction of auxin and actin in cell elongation. Two papers resulted; his last paper was published in 1994 when he was 90. He resided in Haverford until he died in January of 1997 at age 93.

SELECTED PUBLICATIONS

1935 With J. B. Koepfli. Identity of the growth-promoting and root-forming substances of plants. *Nature* 135: 101-102.

1937 With B. M. Sweeney. Action of auxin upon protoplasmic streaming. *Journal of General Physiology* 21:123-135.

1938 Plant growth substances. *Nature* 142: 443-444.

1947 Use of 2,4-D weed killers on woody weeds in Cuba. *Science* 106: 87.

1949 With J. E. Gunkel. Studies of development in long shoots and short shoots of Ginkgo biloba. *American Journal of Botany* 36: 145-151.

1949 With W. D. Bonner. Experiments on the growth and inhibition of isolated plant parts; the action of several enzyme inhibitors on the growth of the Avena coleoptile and on Pisum internodes. *American Journal of Botany* 36: 214-221.

With Y. H. Edmonson. The biogenesis of the anthocyanins; general nutritional conditions. *Archives of Biochemistry* 22:33-53.

1950 With Y. H. Edmonson. The biogenesis of the anthocyanins; evidence for the mediation of copper in anthocyanin synthesis. *Archives of Biochemistry* 25: 79-90.

1951 With Y. H. Edmonson and B. S. Radner. The biogenesis of the anthocyanins. III The role of sugars in anthocyanin formation. *Archives of Biochemistry and Biophysics* 34:305-323.

1953 With B. B. Stowe. Indolepyruvic acid in maize. *Nature* 172: 764.

Hydrolysis of indoleacetonitrile in plants. *Archives of Biochemistry and Biophysics* 44: 242-243.

1954 The physiology of growth in plant tissues. *American Scientist* 42: 589-606.

With B. B. Stowe. The paper chromatography of indole compounds and some indole-containing auxins of plant tissues. *Archives of Biochemistry and Biophysics* 51: 499-516.

1955 With E. W. Samuel. The permeability of potato tissue to water. *Proc. Nat. Acad. Sci. U.S.A* 41:1029-1033.

1956 With J. R. Hay. The fate of 2,4-dichlorophenoxyacetic acid in bean seedlings. II. Translocation. *Plant Physiology* 31:446-451.

1957 With E. Eichenberger. Terminal oxidases and growth in plant tissues. IV. On the terminal oxidases of etiolated pea internodes. *Archives of Biochemistry and Biophysics* 67: 466-478

1958 With B. S. Radner. The biogenesis of anthocyanin. VI. The role of riboflavine. *Archives of Biochemistry and Biophysics* 74: 209-223.

1959 With H. Ikuma. Photosensitive site in lettuce seeds. *Science* 130: 568-569.

With B. B. Stowe. Beneficiation of soils contaminated by strontium-90. *Science* 129: 866.

1960 With H. P. Sorokin. Plastids of the Avena coleoptile. *Nature* 187: 1038-1039.

1961 With S. P. Burg. The conversion of 14C-glucose to ethylene by apple tissue. *Archives of Biochemistry and Biophysics* 95: 450-457.

1963 With H. Ikuma. Action of kinetin on photosensitive germination of lettuce seed as compared with that of gibberellic acid. *Plant and Cell Physiology* 4: 113-128.

With B. G. Pickard. Immediate cause of phototropic curvature in the maize seedling. *Science* 140: 384.

1964 With H. P. Sorokin. The histological basis for inhibition of axillary buds in Pisum sativum and the effects of auxins and kinetin on xylem development. *Protoplasma* 59: 326-350.

With T. Sachs. Release of lateral buds from apical dominance. *Nature* 201: 939-940.

1965 With W. L. Porter. Molecular requirements for auxin action I. Halogenated indoles and indoleacetic acid. *Phytochemistry* 4: 229-243.

With L. D. Noodén. Inhibition of protein synthesis and of auxin-induced growth by chloramphenicol. *Plant Physiology* 40: 193-201.

1966 With T. P. O'Brien. Intracellular fibers in oat coleoptile cells and their possible significance in cytoplasmic streaming. *Proc. Nat. Acad. Sci. U. S. A* 56: 888-894.

With L. D. Noodén. Action of inhibitors of RNA and protein synthesis on cell enlargement. *Plant Physiology* 41: 157-64.

With B. G. Pickard. Geotropic response of wheat coleoptiles in absence of amyloplast starch. *The Journal of General Physiology* 49:1065-1086.

1967 With T. P. O'Brien. Observations on the fine structure of the oat coleoptile II. The parenchyma cells of the apex. *Protoplasma* 63: 417-442.

Tropisms in plants. *Embryologia* 10: 89-113.

1968 Biosatellite II experiments: preliminary results. *Proc. Nat. Acad. Sci. U. S. A* 60: 347-361.

1971 With M. Sands. Santa Cruz: Another dimension. *Science* 172: 8.

1975 With H. T. Choe. The metabolism of oat leaves during senescence: III. The senescence of isolated chloroplasts. *Plant Physiology* 55: 828-834.

1977 With H. T. Choe. The retention of photosynthetic activity by senescing chloroplasts of oat leaves. *Planta* 135: 101-7.

1979 With S. Satler. Relation between senescence and stomatal opening: Senescence in darkness. *Proc. Nat. Acad. Sci. U. S. A* 76: 2770-2773.

1980 The senescence of leaves. In *Senescence in Plants*, K.V. Thimann, ed., Boca Raton, CRC Press, 86-115.

1985 The interaction of hormonal and environmental factors in leaf senescence. *Biologia Plantarum* 27: 83-91.

1988 With G. Giridhar. The interaction of senescence and wounding in oat leaves. II. Chlorophyll breakdown caused by wounding in light. *Plant Science* 54: 133-139.

1992 With K. Reese and V. T. Nachmias. Actin and the elongation of plant cells. *Protoplasma* 171:151-166.

1994 With R. Nipradilol. Actin and the elongation of plant cells II. The roles of divalent ions. *Protoplasma* 183:5