

## Tony Bleecker

Anthony (Tony) B. Bleecker died at the age of 54 on January 30, 2005, after a brave fight against cancer. He was a professor of botany and genetics and a former chair of the Botany Department at the University of Wisconsin–Madison. Born and raised in suburban Detroit, Tony began his college education at Oakland University in Michigan, transferring from there to the University of South Florida, where he earned his bachelor's and master's degrees in botany, with a thesis in natural products chemistry.

In 1982, Tony moved to the Plant Research Laboratory (PRL) at Michigan State University and decided to pursue his PhD studies in the laboratory of Hans Kende. It was there that Tony started to make seminal discoveries on how plants synthesize and sense ethylene. He raised monoclonal antibodies against the ethylene-biosynthetic enzyme ACC synthase and was the first to identify this enzyme on gels and to purify it (1). To elucidate ethylene signaling, Tony designed the seedling screen for ethylene response mutants of *Arabidopsis* and identified and described the *ETR1* gene (2), which as he and coworkers later showed, encodes an ethylene receptor (3, 4). In these early days of his research career, Tony already exhibited the traits that enabled him to probe ever deeper into the question of ethylene action: a capacity to define the important problems that needed



resolving and to choose incisive and critical methods to do so. He was also exemplary in demonstrating how generosity and cooperation can drive progress in research from which the whole field profits. He offered his ACC-synthase antibodies to all workers in ethylene research and collaborated with five research groups at the PRL and one at the University of Michigan, which resulted in publications with six faculty members other than his thesis adviser. Tony received his PhD in 1987 and applied to Elliot Meyerowitz's laboratory at Caltech with a plan to clone the *ETR1* gene, using the methods being developed there for chromosome walking.

Tony moved to Caltech in February 1988 and, working in partnership with Caren Chang, set out to clone the *ETR1* gene, first at Caltech and later in continued collaboration with Caren and others at Caltech after he had left

for the University of Wisconsin (3). Tony's expertise in ethylene physiology and genetics and Caren's artistry in molecular genetics and cloning yielded results of major significance. First, the *ETR1* protein was shown to be a likely ethylene receptor with a hydrophobic domain that contained, presumably, the ethylene binding site and another domain related to bacterial two-component receptor histidine kinases that could function in ethylene signaling. Second, such a two-component receptor, up to then thought to occur only in prokaryotes, was now identified in a eukaryote, a finding confirmed within weeks by the molecular cloning of a two-component receptor in yeast by Varshavsky's group at Caltech. Tony and Caren, along with other members of the Bleecker and Meyerowitz labs, made another discovery as they chromosome-walked to the *ETR1* gene. They cloned a gene that encodes a leucine-rich repeat transmembrane receptor kinase (*TMK1*), the first recognized and published member of this now well-studied and very large family of plant receptors (5).

Tony assumed an assistant professorship in the Department of Botany at the University of Wisconsin–Madison in 1989. He focused his research program mainly on answering the major outstanding questions about how *ETR1* transduced ethylene signals and on determining the biological function of the *TMK1* receptor

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kinase. In a landmark paper, Tony and Eric Schaller showed that ETR1, expressed in yeast, had the capacity to bind ethylene and that the *etr1* mutation abolished this binding (4). They concluded that ETR1 acts as an ethylene receptor in Arabidopsis. Although numerous investigators had attempted to identify plant hormone receptors, it was Tony and his coworkers who were the first to succeed in this task. In a series of elegant biochemical studies, Tony's group demonstrated that dimers of the membrane-spanning domains of ETR1, held together by disulfide bonds, bound ethylene in their membrane-spanning domain, and they resolved the question of how any protein could bind a structurally featureless gas, such as ethylene, as tightly as ETR1 does. They demonstrated that cysteine residues held a copper (II) atom in the ethylene binding site. Transition metal ions interact with the pi electrons of olefins, and this appears to be the mechanism for ethylene binding by ETR1. Good

progress was also made toward understanding the biological roles of TMK1 and its homologs. By knocking out combinations of four members of the *TMK1* clade, Tony's group demonstrated that these receptor kinases are needed for cell expansion, auxin responses, and cell division in emerging leaves. A beautiful set of molecular, genetic, and kinematic studies that lay out a fundamental role for these receptors in plant development is being assembled by Tony's students and colleagues. The hardest task will be to present these important results with the insight and clarity for which Tony will always be remembered. At MSU, Caltech, and the University of Wisconsin, Tony fearlessly followed the research trail, making major discoveries and productively and joyously interacting with his colleagues.

Besides being an outstanding researcher, Tony was greatly appreciated for his dedication and excellence in teaching and in mentoring graduate students and postdocs, some of whom have moved on to

promising careers of their own. Tony is survived by his wife, Sara Patterson, also a faculty member at the University of Wisconsin, and by three daughters, a son, and two grandchildren.

**Hans Kende**

Michigan State University

**Elliot Meyerowitz**

California Institute of Technology

**Edgar Spalding**

University of Wisconsin

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