

Gretchen Hagen and Tom Guilfoyle

How did you spend your career?

After receiving a BS from Illinois State University in 1968, Tom began graduate school at the University of Illinois (U of I) in the lab of John (Jack) Hanson. Tom was awarded an MS in 1969 before departing for 18 months of service in the Army as a draftee. He returned to Hanson's lab to complete a PhD (1974). His research interests spanned both plant physiology and biochemistry, with a specific interest in the effects of auxin on chromatin-bound RNA polymerase in soybean.

After completing a BS (1970) and MS (1972) from the State University of New York, I (Gretchen) joined a lab at the U of I as a research assistant. The lab was adjacent to the Hanson lab, where Tom and I met.

In 1974, Tom was awarded an NIH postdoctoral fellowship and joined Joe Key's lab at the University of Georgia (UGA), where he continued to study plant RNA polymerases. In 1976, Tom took a faculty position at the University of Minnesota (U of MN). In addition to the ongoing studies of RNA polymerases, two additional projects were initiated in the lab—determining the molecular structure and replication of cauliflower mosaic virus (CaMV) and the molecular analysis of auxin-regulated gene expression.

I began a PhD program at UGA in 1974, studying algal development in *Volvox* in the lab of Gary Kochert. In 1978, after completing my PhD,



I joined the lab of Irwin Rubenstein at the U of MN. The lab was working on molecular genetics of maize, with a focus on molecular aspects of zein storage proteins. In 1980, I was awarded an NIH postdoctoral fellowship to work on RNA polymerases in Tom's lab. During the fellowship period, I also participated in the CaMV project and began expanding the ongoing studies on auxin-regulated gene expression.

In 1986, Tom and I were recruited to the Biochemistry Department at the University of Missouri in Columbia. While we continued the studies on RNA polymerases, a major focus became the characterization of the molecular components involved in auxin-regulated transcription, and this remained the predominant focus in the lab until our retirement in 2016.

What do you consider to be your most important contributions to science?

In the early to mid-1970s, little was known about the transcriptional machinery in plants. In nonplant

systems, it was known that nuclear DNA-dependent RNA polymerases were a crucial component in transcriptional activities. With this knowledge and a curiosity about plant transcription, Tom began to focus his research efforts on the purification and characterization of these enzymes in plants. In a collaboration with Jerry Jendrisak at the U of MN, they were the first to purify plant RNA polymerases I, II, and III to homogeneity and determine their subunit structure and enzymatic activities. Subsequently, Tom's lab was the first to clone and sequence several genes encoding different subunits of plant RNA polymerase II. Antibodies raised against the purified subunits were used to define interactions between them. Comparison of the gene sequences and subunit interactions, with information from nonplant systems, revealed not only similarities but also differences and unique features of plant RNA polymerase II.

Tom's observations of the increase in RNA polymerase activities in response to auxin prompted him to investigate a possible connection between auxin-related growth responses and transcriptional activity. Early observations of a rapid increase in cell elongation in response to auxin application led to the hypothesis that this was an "acid growth" response within the plant. Taking a molecular approach to study rapid growth responses, Tom's lab used *in vivo* labeling and was the first to show that the abundance of a subset of proteins was changed in soybean hypocotyls following auxin treatment. Using in

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vitro translation of mRNA, the lab showed rapid increases in a small population of mRNAs in response to auxin. These seminal observations in the early 1980s led the lab in a decades-long pursuit of the molecular mechanism of auxin action.

I consider my most important contribution to plant science to be my work with Tom and the lab in defining several molecular components involved in auxin signal transduction. We took a methodical approach, isolating cDNAs representing mRNAs that were rapidly increased following auxin treatment, and subsequently cloned and sequenced the genes encoding these mRNAs. We showed that following a brief exposure to auxin (within minutes), the accumulation of these mRNAs resulted from increased transcription on these genes. The rapid nature of these responses suggested that the genes contained auxin-response elements (AuxREs). A detailed analysis of the promoter of the GH3 gene identified a minimal, auxin response *cis* element, leading to the construction of the synthetic auxin response element *DR5* that was used to make the auxin-responsive reporter *DR5:GUS*. This reporter was used widely to study auxin signaling in our lab and in numerous others over the years.

Subsequently, the highly active, synthetic AuxRE was used to isolate transcription factors that specifically bind to the element. A family of auxin response factors (ARFs) was identified and characterized. ARFs were shown to interact with another family of auxin-regulated

proteins called Aux/IAAs. Unlike ARFs, the Aux/IAAs do not bind to the AuxRE, but interact with ARFs through a similar C-terminal dimerization domain. We showed that Aux/IAAs are active repressors of auxin response gene expression, and their stability and activity are modulated by auxin.

Based on our results, we presented a model in 2001 for auxin-regulated gene expression in which Aux/IAA repressors are recruited to promoters of auxin-regulated genes by dimerization with ARFs that are bound to the AuxRE on these genes. Auxin concentration in the cell would influence the stability of the interaction, such that when auxin levels are low, the repressor is stably associated with ARF. When auxin levels are elevated, the repressor is destabilized and degraded. In this latter case, an Aux/IAA repressor that was associated with an AuxRE-bound ARF activator protein would dissociate from the ARF protein, relieving repression and permitting the activation of gene transcription. In the ensuing years, the lab focused on specific structural domains of ARFs and Aux/IAAs. In particular, the lab characterized the mechanism of repression of the Aux/IAA proteins and described in more detail the C-terminal interaction domain found in both Aux/IAAs and ARFs.

What was your motivation for becoming Founding Members of the Legacy Society?

Throughout his career, Tom maintained an affiliation with ASPP/ASPB. He attended annual meetings

and presented his research results in the form of posters and talks, networked with colleagues and senior scientists, and encouraged his students and postdocs to attend and participate at these meetings. He read both *Plant Physiology* and *The Plant Cell* regularly, respected the quality of research being published in these journals, and published many articles in both. He was on the editorial boards of *Plant Physiology* from 1982 to 1995 and *The Plant Cell* from 2003 to 2014. As an editor, he was able to evaluate plant research in diverse fields and to contribute to maintaining the high scientific standards of both journals.

Throughout my career, membership in the Society played an important role. The journals kept me informed of advances in plant science. The annual meetings gave me the opportunity to present my research and learn about unpublished data in my own field. I attribute networking at these meetings, at least in part, to invitations to sit on the Women in Plant Biology Committee and to become the chair of the newly formed Membership Committee. Further, networking may have given me the visibility that resulted in requests to review manuscripts and sit on grant panels—activities that are important for advancing one's career.

Tom and I considered ASPP/ASPB to be a vibrant Society, with robust membership, good journals that showcase high-quality science, and interesting and informative annual meetings. To its credit, the Society has continued to grow over

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ASPB Legacy Society Founding Member

the years, expanding its involvement in, for example, educational programs, outreach, public policy, women's issues, diversity, and efforts to foster early career scientists.

Upon our retirement, we reflected on our involvement with the Society and were grateful for the many opportunities. Further, Tom and I have been honored to be recognized by ASPB; I received the Charles Reid Barnes Life Membership Award in 2009, and in 2014 Tom was presented with the Lawrence Bogorad Award for Excellence in Plant Biology Research.

The recent formation of the Legacy Society is a valuable asset for ASPB. It will ensure that ASPB will continue to be a leader, a strong advocate, and a resource for the plant biology community and

the nation. When we were asked to become Founding Members of the Legacy Society, it seemed a truly appropriate way for Tom and me to give back to the Society that has served us both well.

What important advice would you give to individuals at the start of their career in plant science?

Define one project (or a few projects) that truly interest you. Read the pertinent literature—become an expert in your subject areas. When designing a research plan, focus on asking realistic, interesting, and fundamental questions.

Read the literature, new *and* old.

Become a member of ASPB, and encourage your students and post-docs to become members. Attend

the annual meetings and participate by presenting data. Network with your peers within and outside of your area of expertise, but also interact with senior scientists—your visibility may give you opportunities to advance your career (e.g., collaborations; invitations to give seminars, review manuscripts, sit on grant panels).

Read both *Plant Physiology* and *The Plant Cell*. When appropriate, submit your manuscripts to these journals. They are highly regarded plant journals and have a broad audience of plant biologists.

Academic Family Trees

<https://academictree.org/plantbio/tree.php?pid=808794>

<https://academictree.org/plantbio/tree.php?pid=734613>