James H. Tumlinson III

1938-2022

BIOGRAPHICAL *Memoirs*

A Biographical Memoir by
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NATIONAL ACADEMY OF SCIENCES

JAMES HOMER **TUMLINSON III**

February 28, 1938–February 9, 2022

Elected to the NAS, 1997

James Homer Tumlinson III was a pioneer in the field of chemical ecology. His early research focused on identifying the pheromones used by insects for attraction and mating and led to the development of effective lures for the sustainable management of a variety of agricultural pests. Jim subsequently turned his attention to examining how parasitoids locate their insect hosts in complex ecosystems, and his team discovered that the attractive chemicals were released not by the insect hosts but rather by the plants on which they were feeding. This foundational discovery opened the door to a new field of research, developing new tools and approaches to elucidate the remarkably intricate chemical communication systems that have evolved in the dance among plants, herbivores, and natural enemies.

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By Christina M. Grozinger

Jim loved a mystery and built sophisticated research studies on simple questions of why an insect or plant was observed to behave in a certain way. When tackling new lines of inquiry and developing new techniques or study systems, Jim was undaunted by setbacks and challenges—instead these served as fodder for his dry sense of humor. Throughout his career, he thrived on collaborations and diverse perspectives, and he was always eager to build teams of researchers that spanned multiple disciplines to tackle whichever natural history question or insect management challenge had caught his attention. His legacy will continue through the creative and dynamic programs of the scientists he mentored and the generations of researchers he inspired through his work. As his longtime collaborator Joe Lewis stated in his 2022 eulogy,[1] Jim was a "gentleman scholar with a big heart, who went through life touching people, warming hearts, and changing lives."

Early Life, Education, and Family Life

Jim's fascination with the natural world and his commitment to making agricultural practices more ecologically sustainable were undoubtedly gifts bestowed by his childhood spent wandering the farms and fields of northeastern Mississippi. Jim was born to Marie and James Homer Tumlinson Jr. on February 28, 1938. Together with his younger sister and two brothers, Jim grew up on the family's cattle and cotton farm, which spanned 1,300 acres. He spent his days exploring the landscape with his brown and white pony, Trigger; his love of horses and horseback riding continued throughout his life (indeed, in his early seventies he completed a 50-mile endurance ride on his horse, Brass). Jim recalled that pesticides were used liberally and often to control corn and cattle pests during his childhood, which helped motivate his future interests in developing more sustainable approaches to agriculture. Indeed, as Jim's daughter Katherine "Kat" Tumlinson noted, "It's not difficult to imagine this young boy growing up and devoting his professional life to identifying the way these wild things—these plants and trees and insects—commune and communicate with one another. The magic of those long days outdoors formed the foundation for his fantastical and fascinating scientific work."[2]

Figure 1: In 2008, Jim completed an endurance ride at age 70. (Photo courtesy of Sue Tumlinson.)

Figure 2: In 1961, Jim returned to VMI to formally receive the Marine Corps Commandant's Trophy for placing first in the Platoon Leaders' Class. Trophy presented by General Shell, a marine and superintendent of VMI. (Photo courtesy of Sue Tumlinson.)

In school, Jim was drawn to the experimental methodology and precision of chemistry. As he wryly noted in his autobiographical essay, "Although I enjoyed biology, it was a more descriptive science in those days, and we were taught to observe and draw what we observed. This was a disaster for me. I couldn't draw a leaf."[3] Being inspired by the presidency of Dwight D. Eisenhower to consider a military career, he enrolled at the Virginia Military Institute (VMI) in 1956 as a chemistry major. Jim earned his bachelor's degree in chemistry from VMI in 1960 and graduated first in his battalion in the

U.S. Marine Corps Platoon Leaders Class program. After completing Officer Candidate School, where he again placed first in his class, Jim joined the United States Marine Corps as a second lieutenant. In that role, he experienced, in October 1962, a six-week deployment of his ship to Cuba during the Cuban Missile Crisis.

Ten days after he returned from Cuba, Jim married Sue Skelton, whom he had met in the fall of 1959 on a blind date. Together they raised two daughters, Anne and Kat. Jim adored his family, saying that marrying Sue was the best thing he ever did. Sue was very supportive of Jim's research; indeed, she remembered that Jim would joke that he appreciated that Sue was never suspicious when he would tell her that he did not come home at night because he was working in the lab during his graduate studies.[4] Although Sue would accompany him on many international trips to conferences or to visit colleagues, Jim largely kept his work and personal lives separate, to the point where his daughters were not aware of his many awards, accomplishments, or international recognition. His daughter Anne remembered, however, "Our father instilled in us the values he brought to his work: curiosity, commitment, courage to fail."[5]

Despite his intense focus on his research, Jim also nurtured a life outside of the lab through activities like sailing and gardening. He always made time to visit his parents on the farm and took many camping trips with his brothers in Colorado. As his career progressed, he shifted even more purposefully from long hours in the lab to his true passion, horseback riding. He spent hundreds of hours alone on his horses, enjoying the outdoors and preparing them for endurance races. One can imagine for a mind as active and dynamic as Jim's, this focused engagement provided much needed balance and joy.

Graduate Studies and Early Research

Jim's love of nature fueled both his fascination with decoding the intricate communication systems among species and his desire to protect the natural world. Jim cited the publication of Rachel Carson's *Silent Spring* in 1962 as an inspiration for his graduate studies, which began in 1964 at Mississippi State University (MSU), after he left his service in the Marines.[6] This time period coincided with the emergence of chemical ecology as a research field, in which the chemical signals underlying plant and animal communication systems were elucidated and used for improving control and management of these populations.

When Jim entered the graduate program at MSU, the U.S. Department of Agriculture's Agricultural Research Service (USDA-ARS) had just completed a new, state-of-the-art, analytical chemistry lab to study and eradicate the boll weevil at this campus. The boll weevil, *Anthonomus grandis*, had emerged as a key pest of U.S. cotton fields in the 1920s, with approximately one-third of all pesticide use in the nation directed at managing this pest.[7] Because of its enormous agricultural and economic damage, the U.S. federal government committed to eradicating it in 1958. Jim was offered the opportunity to work in this group, under the guidance and mentorship of James P. "Jim" Minyard, whom Jim described as a brilliant chemist and a wonderful mentor. Since boll weevils exclusively fed on cotton plants, Jim's first research efforts aimed at identifying the chemicals in cotton that attracted the weevils. He initially used standard natural-product chemistry techniques, which involved extracting chemicals from the plant using harsh processes (steam distillation). This strategy failed to capture the biologically relevant chemicals, which were most likely highly volatile compounds released from living plants.

In 1966, researchers published a paper demonstrating that male boll weevils released a pheromone that could attract females from more than thirty feet away.[8] Using a behavioral assay developed by Richard "Dick" Hardee, an entomologist in the boll weevil lab, Jim began to test different extracts. He found that feces of male boll weevils were attractive and proceeded to steam distill 54 kilograms of feces that he collected from the millions of weevils that the lab was rearing. Jim identified four terpenoids that together could attract female weevils.[9,10,11] The blend was named Grandlure and was used to bait pheromone traps. Deployment of these traps and a new insecticide control strategy targeting late fall populations, termed "reproduction-diapause control," were successful in fully eradicating the boll weevil.[12]

Jim completed his master's degree in 1966 and his Ph.D. in 1969 and then joined Milt Silverstein's research group as a postdoctoral fellow at the New York State College of Forestry (now the State University of New York College of Environmental Science and Forestry), with a goal to identify the trail pheromone of the Texas leafcutter ant (*Atta texana*).[13] Although it was well understood that ants produced pheromone trails to help their nestmates locate food sources or nest sites,[14] the chemical identification of these pheromones eluded scientists because the quantities of chemicals that trigger these behaviors are minute, and the available chemical analysis techniques were not sufficiently sensitive.[15] By using newly developed instrumentation that linked gas chromatography (which separates chemicals in a mixture) with mass spectrometry (to identify the individual, separated chemicals), and extracting 3.7 kilograms of dried ants, Jim was able to identify methyl 4-methylpyrrole-2-carboxylate as the *A. texana* trail pheromone.[16,17] Jim's research paved the way for the identification of trail pheromones from a wide variety of ant species, providing insights into the proximate and ultimate mechanisms underlying these behaviors,[18] and new tools for managing ant populations.[19,20]

USDA-ARS Career

After one year as a postdoctoral fellow, Jim was offered and accepted the research leader position for the Insect Chemical Group for the USDA-ARS' Insect Attractants, Behavior and Basic Biology Laboratory in Gainesville, Florida. Jim built an outstanding team of scientists, who spanned organic chemistry, analytical chemistry, and insect physiology and behavior, and together they were enormously successful, identifying pheromones and developing lures for more than twenty insect species. These included the sex pheromones of major agricultural pests, such as western corn rootworm and fall armyworm.[21,22] Jim was a focused, dedicated, rigorous, and endlessly curious scientist, and he instilled these qualities in his research team. Former graduate student Ted Turlings remembers Jim telling his team, "When you see something you cannot explain, that is what you go after."[23]

Among these studies, Jim's research on the challenges and insights gained from identifying the sex pheromone of the Japanese beetle (*Popillia japonica*) stand out. Japanese beetles are native to Japan and were introduced to the United States in 1916.[24] They can feed on more than 300 host plant species, and their soil-dwelling larvae cause significant damage to plant roots; thus, they are significant pests for agricultural, ornamental, and turfgrass industries. Initial control efforts for Japanese beetles involved heavy pesticide applications, as highlighted in Carson's *Silent Spring*.

Jim worked with Michael G. (Mick) Klein from the USDA Japanese Beetle Laboratory in Wooster, Ohio, to identify the Japanese beetles' sex pheromone. The biology of the beetle made these studies particularly challenging. The beetles could not be reared or maintained in a laboratory and were responsive to the pheromone components for only six weeks in the summer. Thus, Jim would send Mick samples by overnight mail to test, and Mick would conduct tests on golf courses that were plagued by Japanese beetle larvae. After two summers, they had identified the chemicals that seemed to be serving as female-produced sex-pheromone components. Robert Doolittle, the synthetic chemist in Jim's team, synthesized the key compound, but testing in the third year was unsuccessful—male beetles were not attracted to the synthesized lure. Further evaluation revealed that the compound could exist as two enantiomers, and both were included in the original synthesized test material. When the team tested each enantiomer separately, they found that (R,Z)-5-(1-decenyl) dihydro-2(3H)-furanone [(*R*)-japonilure] was attractive to male beetles, but even small amounts of *(S)*-japonilure attenuated this attraction.[25] Subsequent research studies from Walter Leal revealed that the Osaka beetle (*Anomala osakana*) uses the *S* enantiomer as its female-produced sex pheromone, and the *R* enantiomer serves as the behavioral antagonist.[26] Thus, the use of these two enantiomers allows the males of these two species to find their female conspecifics, even if they are in the same location. This is one of the many examples in Jim's research career in which seeming setbacks led to remarkable insights into the extraordinary sophistication of chemical communication systems. Indeed, in 2007, Jim gave a talk at the Entomological Society of America meeting titled, "The best discoveries result from mistakes and serendipity."[27]

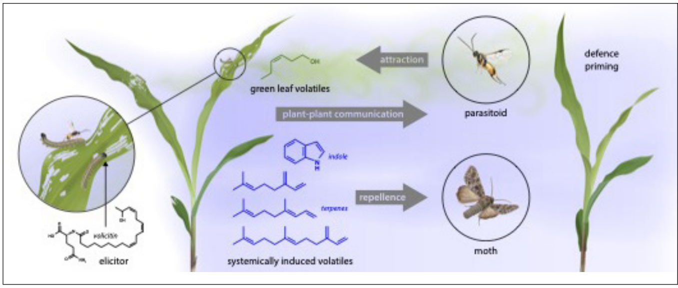

Figure 3: Chemical communication systems among plants, herbivores, and natural enemies. Elicitors in the saliva of caterpillars will trigger production of plant volatiles. Different types of plant volatiles will attract parasitoids that lay eggs on the caterpillars, repel lepidopteran females from laying their eggs on plants, and prime nearby plants to activate their defenses. Plants release different volatiles depending on the species of herbivore that is feeding on them, which triggers attraction of herbivore-specific parasitoids. (Graphic courtesy of Thomas Degen.)

Biological control, in which a natural enemy (parasitoid or predator) of a target pest species is released in an effort to control the pest, was first successfully used in 1888.[28] But the mechanisms by which these biological control agents find their hosts in complex environments were obscure. In an effort to understand these processes, Jim began working with a former MSU graduate school colleague, W. Joseph "Joe" Lewis, who was based in the USDA-ARS Laboratory in Tifton, Georgia, in the late 1980s. Jim continued exploring these questions, in collaboration with Joe and others, for the next forty years.

Although Jim and Joe initially assumed that the parasitoids were finding their hosts by tracking chemicals directly emitted from the hosts, their studies instead revealed that parasitoids were indirectly locating hosts by detecting chemicals released by insect-damaged plants. Thus, the host insect feeding on the plant stimulates the plant to release chemicals that attract the parasitoid, thus ridding the plant of its pest. This revealed a remarkable mutualism between plants and parasitoids and opened an entirely new field of study in chemical ecology and biological control. It was often referred to as a plant's "cry for help." Moreover, their studies demonstrated that in addition to attraction to plant-released volatiles, parasitoids could learn the odors of their host and thus gain even greater precision in identifying hosts in the field.[29] This field provided tremendous opportunities for the next generation of chemical ecologists, and many of the researchers who worked with Jim and Joe on these projects have become recognized leaders in the field of chemical ecology.

Jim's student Ted Turlings' discovery that oral secretions from caterpillars feeding on plants stimulated production of chemicals that attracted parasitoids led to a cascade of studies. This first study focused on beet armyworms (*Spodoptera exigua*), their parasitic wasps (*Cotesia marginiventris*), and corn plants (*Zea mays*).[30] USDA team member Hans T. Alborn identified the compound volicitin from beet armyworm oral secretions that triggered volatile release in corn plants.[31] Subsequently, Alborn found that fatty acid-amino acid conjugates (FACs) served as elicitors in grasshoppers,[32] and Eric A. Schmelz showed that fall armyworms (*Spodoptera frugiperda*) have a peptide, inceptin, in their oral secretions that stimulates volatile release in cowpeas.[33] Interestingly, inceptin is derived from digested fragments of plants that the caterpillar previously consumed. Cameron Lait demonstrated that tobacco hornworm (*Manduca sexta*) biosynthesized FAC elicitors in multiple digestive tissues, including the salivary glands, crop, and midgut.[34] Thus, plants have evolved to use a diversity of types of chemicals to detect feeding by pest insects.

These studies led to an important question: if the plants can detect these elicitors and use them to defend themselves against herbivores, why do the herbivores continue to produce them? Is there some benefit to the herbivore to produce these? To answer these questions, Jim collaborated with Naoki Mori from Kyoto University. Studies led by Naoko Yoshinaga demonstrated that FACs, being derived from amino acids, may serve an important role in nutrition acquisition, assimilation, and storage.[35] Moreover, FACs are found in multiple phylogenetically distinct insect taxa, spanning lepidopteran caterpillars, *Drosophila*, and crickets.[36] Thus, this may represent a core physiological pathway in insect herbivores that the plants are now exploiting to detect feeding.

Jim's team also explored the origins of the volatiles that the plants released. These volatiles include stored chemicals that are readily available for rapid release, whereas others are newly synthesized.[37] The plant response was found to be systemic,[38] and thus feeding on one leaf could trigger volatile release more broadly.[39] The release of volatiles had a circadian rhythm, with more volatiles released during the day when the stomata are open.[40,41] Moreover, some plant species, including tobacco plants (*Nicotiana tabacum*), release different volatiles during night and day, with the nighttime volatiles potentially serving to repel egg-laying female moths.[42] These studies were again highly collaborative, and included projects led by Paul W. Paré, Ursula S. R. Röse, Irmgard Seidl-Adams, Consuelo M. de Moraes, and Mark C. Mescher.

There was also considerable variation and specificity in the types of volatiles plants released, indicating that the plant-herbivore-parasitoid systems were finely tuned and exquisitely evolved. John H. Loughrin found that naturalized cotton cultivars released significantly more volatiles upon insect feeding than commercial cultivars, and thus this phenotype could be a vehicle for evolutionary or artificial selection.[43] Studies by Consuelo M. de Moraes demonstrated that three different plant species (tobacco, cotton, and maize) produce different volatile blends depending on the pest caterpillar species, such as tobacco budworm (*Heliothis virescens*) and corn earworm (*Helicoverpa zea*). *Cardiochiles nigriceps*, a parasitoid of *H. virescens*, uses these differences to identify plants infested with its host.[44] Similarly, Naoko Yoshinaga demonstrated that FACs produced by *Manduca sexta* triggered volatile emission in eggplant and tobacco, which are host plants for *M. sexta*, but not in its nonhosts, such as corn.[45]

Figure 4: Tumlinson lab group hike at Black Moshannon State Park in Pennsylvania in October 2018. Bipana Paudel Timilsena (graduate student), Tristan Confer (graduate student), Arash Maleki (graduate student), Jim Tumlinson, Irmgard Seidl-Adams (research professor) and Pingping Liu (visiting scholar from China).

Jim's research also demonstrated that plants could communicate with each other and began exploring the underlying processes. Juergen Engelberth demonstrated that damaged corn plants release green leafy volatiles (GLVs), which prime adjacent plants to upregulate their antiherbivore chemical responses, such that they produce greater amounts of a signaling hormone, jasmonic acid, and also release higher amounts of volatiles as soon as caterpillars start feeding on the plants.[46] Subsequent studies from Engelberth and Irmgard Seidl-Adams demonstrated that exposure to GLVs increased expression of genes in the jasmonic acid biosynthesis pathway.[47] Studies from Jim's three most recent graduate students, Bipana Paudel Timilsena, Anne C. Jones, and Tristan Confer, focused on elucidating how GLVs are produced and function. Confer explored the molecular and biosynthetic pathways in plants that generate GLVs and how they evolved.[48] Timilsena expanded this system to *Nicotiana benthamiana,* demonstrating that primed plants emit volatile blends specific to the herbivore species feeding on them, not the volatile signals with which they were primed.[49] Jones demonstrated that caterpillars can produce effectors in their saliva that can reduce biosynthesis of GLVs, thereby reducing cross-plant signaling and defense priming.[50] Moreover, several of these effectors are found across lepidopteran species but not in a phylogenetically determined patterns, suggesting convergent evolution.[51]

Jim conducted a series of studies seeking to identify the chemical attractants of the woodwasp (*Sirex noctilio*). This wasp is native to Europe, Asia, and Africa and was found in the northeastern United States for the first time in 2004.[52] The females lay their eggs under the bark of pine trees and prefer stressed trees. Katalin Böröczky, a research scientist in Jim's group, identified the female-produced sex pheromone that functions as a contact pheromone and stimulates copulation attempts in males.[53] The team also identified male-produced volatiles that could attract males and females in behavioral assays.[54] With assistance from technician Nate McCartney, the team also developed a system (via injection with an herbicide) for trapping volatiles from stressed and unstressed pine trees.[55] Despite these successes, the team was not able to develop an effective lure for field trapping of the woodwasp.

Jim's research career demonstrated the great power of leveraging chemical ecology to support crop productivity and control insect pests. Indeed, the building where he served for more than thirty years as research leader for the USDA-ARS Insect Attractants, Behavior and Basic Biology Laboratory in Gainesville, Florida, was constructed in response to the call to action outlined in Carson's *Silent Spring*. In 2015 Jim was awarded the USDA Secretary's Award for Personal and Professional Excellence "for pioneering research on insect pheromones that provided the basis for control of major insect pests, including the boll weevil, thereby reducing environmental contamination by pesticides."

Honey Bee Health in Africa and Beyond

Although Jim would tell me that he was not a "bee person," he had a tremendous impact on honey bee (*Apis mellifera*) research. Jim had a long collaboration with researchers at the International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi, Kenya. Together with Baldwyn Torto (ICIPE) and Peter Teal (USDA-ARS), Jim demonstrated that the small hive beetle (*Aethina tumida*), a pest of honey bees in Africa and introduced to the United States in 1996, is attracted to the alarm pheromone produced by honey bees.[56] Moreover, the beetle carries a yeast on its body, and the yeast grows readily on the stored pollen in the honey bee colony. As the yeast ferments the pollen, isopentyl acetate, the main component of alarm pheromone, is produced. Thus, the inoculation of the colony's food stores with the yeast may attract more beetles, allowing the beetles to overwhelm the colony's defenses. Traps baited with yeast-inoculated pollen can be used for attracting the small hive beetle.[57]

Figure 5: Family photo in 2018. Mehul Patel (spouse of K. Tumlinson), Katherine Tumlinson, Jim Tumlinson, Sue Tumlinson, Erik Johnson (spouse of A. Tumlinson), Anne Tumlinson, Grace Stohr (grandchild), James Stohr (grandchild). (Photo courtesy of Anne Tumlinson.)

Jim sought to expand the collaborations between ICIPE and Penn State and in 2009 brought Maryann and Jim Frazier to Nairobi. While Maryann and Elluid Muli were inspecting colonies, they found *Varroa destructor* mites.[58] *Varroa* is a major parasite of honey bees in North America and Europe, and this was the first identification of *Varroa* in East Africa. Jim served as the leader for our team of researchers in our subsequent studies, funded by the National Science Foundation's Basic Research to Enable Agricultural Development Program, to evaluate the health of honey bee colonies in Kenya and the potential impacts from *Varroa* and other stressors.[59] This project stimulated new research on bee health in Africa and laid the groundwork for collaborations that have continued for over a decade. When we decided to create a center related to bee health at Penn State, Jim provided invaluable assistance and guidance. I still remember the twinkle in his eye when he told me, "You should call it the Center for Pollinator Research. It's CPR for the bees!" We adopted the name, and now the CPR is known worldwide, but few people realize the name was inspired by the process of cardiopulmonary resuscitation.

Commitment to Collaboration

Jim's daughter Kat remembers him telling her, "Find someone who can do something you can't do and work together. And don't worry about who gets the credit."[60] In 2008, Jim, Joe Lewis, and John Pickett were awarded the Wolf Prize in Agriculture from Israel's Wolf Foundation in honor of the fact that their research and efforts were "a major force in reorienting the thinking of agricultural scientists and educators toward a more ecologically sound approach to pest management." Upon learning of the award, Jim said,

> *The research recognized by this award was conducted over at least three decades by numerous really excellent students and research associates, and in collaboration with Joe Lewis, a co-recipient of this prize, and other colleagues.... It has been an interdisciplinary team effort. No one person or laboratory alone could have accomplished this.*[61]

This work involved forty-one visiting scientists from seventeen different countries. Thus, there could be many opportunities for misunderstandings, conflict, and competition. But as Joe Lewis noted,

> *financial, human and other resources were freely shared and we functioned as a single interactive team across the two laboratories, without the need for defined boundaries or formal understanding beyond basic mutual respect.... Never in a single instance did I see him try to promote his own self-interest at the expense of others."*[62]

Jim brought this commitment with him to Penn State, when he accepted the Ralph O. Mumma Endowed Chair in the Department of Entomology in 2003. Jim was the second director of the Center for Chemical Ecology at Penn State and served in this role for fifteen years. Under his guidance, the center hosted the 2008 annual meeting for the International Society for Chemical Ecology and the International Short Course on Chemical Ecology and formed the multistate USDA project on chemical ecology.

In his eulogy for Jim, Joe Lewis paraphrased Eleanor Roosevelt, saying: "Many people walk in and out of our lives, but a special few dwell there for a season and leave footprints in our hearts so profound and sweet that we are forever changed." Jim's footprints have led us to new frontiers in chemical ecology and sustainable agriculture, created paths that span multiple disciplines, launched a generation of scientists, and continue to inspire us all.

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Additional insights into Jim's personal and professional life can be found in his autobiographical essay, "Complex and Beautiful: Unraveling the Intricate Communication Systems Among Plants and Insects" in the January 2023 *Annual Review of Entomology* 68:1-12.

REFERENCES

1. Lewis, W. J. Eulogy for James Tumlinson. February 18, 2022, at Robinson Funeral Home, West Point, Mississippi.

2. Tumlinson, K. Eulogy for James Tumlinson. February 18, 2022, at Robinson Funeral Home, West Point, Mississippi.

3. Tumlinson, J. H. 2023. Complex and beautiful: Unraveling the intricate communication systems among plants and insects. *Annu. Rev. Entomol.* 68:1-12. All other quotes from Tumlinson about his life come from this essay.

4. Tumlinson, S., personal communication, telephone call, July 25, 2022.

5. Tumlinson, A., personal communication, email, October 24, 2022.

6. Carson, R. 1962. *Silent Spring.* New York: Houghton Mifflin Company.

7. Reisig, D. 2017. The boll weevil war, or how farmers and scientists saved cotton in the South. *North Carolina State University News,* May 17; https://news.ncsu.edu/2017/05/boll-weevil-war-2017.

8. Cross, W. H., and H. C. Mitchell. 1966. Mating behavior of the female boll weevil. *J. Econ. Entomol.* 59:1503–1507.

9. Tumlinson, J. H., et al. 1968. Boll weevil sex attractant: Isolation studies. *J. Econ. Entomol.* 61:470–474.

10. Tumlinson, J. H., et al. 1969. Sex pheromones produced by male boll weevil: Isolation, identification, and synthesis. *Science* 166:1010–1012.

11. Gueldner, R.C., et al. 1971. Identification and synthesis of the four compounds comprising the boll weevil sex attractant. *J. Org. Chem.* 36:2616–2621.

12. Reisig, D. 2017. See Reference 7.

13. Tumlinson, J. H., et al. 1971. Identification of the trail pheromone of a leaf-cutting ant, *Atta texana. Nature* 234:348–349.

14. Bonnet, C. 1779. Observation LXIII. Sur un procédé des Fourmis. *Oeuvres d'Histoire Naturelle et de Philosophie,* Vol. 1, pp. 535–536. Neuchâtel, France: Imprimerie de Samuel Fauche.

15. Morgan, E. D. 2009. Trail pheromones of ants. *Physiol. Entomol.* 34:1–17.

16. Tumlinson, J. H., et al. 1971. See Reference 13.

17. Tumlinson, J. H., et al. 1972. A volatile trail pheromone of the leaf-cutting ant, *Atta texana. J. Insect Physiol.* 18:809–814.

18. Czaczkes, T. J., C. Grüter, and F. L. W. Ratnieks. 2015. Trail pheromones: An integrative view of their role in social insect colony organization. *Annu. Rev. Entomol.* 60:581–599.

19. Westermann, F. L., V. A. Bell, D. M. Suckling, and P. J. Lester. 2016. Synthetic pheromones as a management technique—Dispensers reduce *Linepithema humile* activity in a commercial vineyard. *Pest. Manage. Sci.* 72:719–724.

20. Sunamura, E., et al. 2011. Combined use of a synthetic trail pheromone and insecticidal bait provides effective control of an invasive ant. *Pest Manage. Sci.* 67:1230–1236.

21. Guss, P. L., J. H. Tumlinson, P. E. Sonnet, and A. T. Proveaux. 1982. Identification of a female-produced sex pheromone of the western corn rootworm. *J. Chem. Ecol.* 8:545–556.

22. Tumlinson, J. H., et al. 1986. Sex pheromone of fall armyworm, *Spodoptera frugiperda* (J. E. Smith). *J. Chem. Ecol.* 12:1909–1926.

23. Turlings, T., personal communication, November 1, 2022, seminar at Pennsylvania State University, State College, Pennsylvania.

24. Althoff, E. R., and K. B. Rice. 2022. Japanese beetle (Coleoptera: Scarabaeidae) invasion of North America: History, ecology, and management. *J. Integr. Pest Manag.*13:2.

25. Tumlinson, J. H., et al. 1977. Identification of the female Japanese beetle sex pheromone: Inhibition of male response by an enantiomer. *Science* 197:789–792.

26. Leal, W. S. 1996. Chemical communication in scarab beetles: Reciprocal behavioral agonist-antagonist activities of chiral pheromones. *Proc. Natl. Acad. Sci. U.S.A.* 93:12112–12115.

27. Tumlinson, J. H. 2007. The best discoveries result from mistakes and serendipity. Lecture at Symposium: Entomological Connections to Science, Innovation, and Influence: Impacts and Professional Development. Entomological Society of American Annual Meeting, December 9–12, 2007, Town and Country Convention Center, San Diego, California.

28. Heimpel, G. E., and M. J. W. Cock. 2018. Shifting paradigms in the history of classical biological control. *BioControl* 63:27–37. 29. Lewis, W. J., and J. H. Tumlinson. 1988. Host detection by chemically mediated associative learning in a parasitic wasp. *Nature* 331:257–259.

30. Turlings, T. C., J. H. Tumlinson, and W. J. Lewis. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250:1251–1253.

31. Alborn, H. T., et al. 1997. An elicitor of plant volatiles from beet armyworm oral secretion. *Science* 276:945–949.

32. Alborn, H. T., et al. 2007. Disulfooxy fatty acids from the American bird grasshopper *Schistocerca americana*, elicitors of plant volatiles. *Proc. Natl. Acad. Sci. U.S.A.* 104:12976–12981.

33. Schmelz, E. A., et al. 2006. Fragments of ATP synthase mediate plant perception of insect attack. *Proc. Natl. Acad. Sci. U.S.A.* 103:8894–8899.

34. Tumlinson, J. H., and C. G. Lait. 2005. Biosynthesis of fatty acid amide elicitors of plant volatiles by insect herbivores. *Arch. Insect Biochem.* 58:54–68.

35. Yoshinaga, N., et al. 2008. Active role of fatty acid amino acid conjugates in nitrogen metabolism in *Spodoptera litura* larvae. *Proc. Natl. Acad. Sci. U.S.A.* 105:18058–18063.

36. Yoshinaga, N., et al. 2014a. Plant volatile eliciting FACs in lepidopteran caterpillars, fruit flies, and crickets: A convergent evolution or phylogenetic inheritance? *Front. Physiol.* 5:121.

37. Paré, P. W., and J. H. Tumlinson. 1997. De novo biosynthesis of volatiles induced by insect herbivory in cotton plants. *Plant Physiol.* 114:1161–1167.

38. Turlings, T. C., and J. H. Tumlinson. 1992. Systemic release of chemical signals by herbivore-injured corn. *Proc. Natl. Acad. Sci. U.S.A.* 89:8399–8402.

39. Röse, U. S. R., A. Manukian, R. R. Heath, and J. H. Tumlinson. 1996. Volatile semiochemicals released from undamaged cotton leaves (a systemic response of living plants to caterpillar damage). *Plant Physiol.* 111:487–495.

40. Loughrin, J. H., et al. 1994. Diurnal cycle of emission of induced volatile terpenoids by herbivore-injured cotton plant. *Proc. Natl. Acad. Sci. U.S.A.* 91:11836–11840.

41. Seidl-Adams, I., et al. 2015. Emission of herbivore elicitor-induced sesquiterpenes is regulated by stomatal aperture in maize (*Zea mays*) seedlings. *Plant Cell Environ.* 38:23–34.

42. De Moraes, C. M., M. C. Mescher, and J. H. Tumlinson. 2001. Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410:577–580.

43. Loughrin, J. H., A. Manukian, R. R. Heath, and J. H. Tumlinson. 1995. Volatiles emitted by different cotton varieties damaged by feeding beet armyworm larvae. *J. Chem. Ecol.* 21:1217–1227.

44. De Moraes, C. M., et al. 1998. Herbivore-infested plants selectively attract parasitoids. *Nature* 393:570–573.

45. Yoshinaga, N., et al. 2014b. N-(18-hydroxylinolenoyl)-L-glutamine: A newly discovered analog of volicitin in *Manduca sexta* and its elicitor activity in plants. *J. Chem. Ecol.* 40:484–490.

46. Engelberth, J., H. T. Alborn, E. A. Schmelz, and J. H. Tumlinson. 2004. Airborne signals prime plants against insect herbivore attack. *Proc. Natl. Acad. Sci. U.S.A.* 101:1781–1785.

47. Engelberth, J., I. Seidl-Adams, J. C. Schultz, and J. H. Tumlinson. 2007. Insect elicitors and exposure to green leafy volatiles differentially upregulate major octadecanoids and transcripts of 12-oxo phytodienoic acid reductases in *Zea mays. Mol. Plant-Microb. Interact.* 20:707–716.

48. Confer, T. 2022. An investigation of the metabolic fate and possible evolutionary origin of green leaf volatiles. Ph.D. dissertation, Pennsylvania State University.

49. Timilsena, B. P., I. Seidl-Adams, and J. H. Tumlinson. 2020. Herbivore-specific plant volatiles prime neighboring plants for nonspecific defense responses. *Plant Cell Environ.* 43:787–800.

50. Jones, A. C., et al. 2019. Herbivorous caterpillars can utilize three mechanisms to alter green leaf volatile emission. *Environ. Entomol.* 48:419–425.

51. Jones, A. C., T. M. Confer, J. Engelberth, and J. H. Tumlinson. 2022. Herbivorous caterpillars and the green leaf volatile (GLV) quandary. *J. Chem. Ecol.* 48:337–345.

52. Ayres, M. P., R. Pena, J. A. Lombardo, and M. J. Lombardero. 2014. Host use patterns by the European woodwasp, *Sirex noctilio,* in its native and invaded range. *PLoS One* 9:e90321.

53. Böröczky, K., et al. 2009. Monoalkenes as contact sex pheromone components of the woodwasp *Sirex noctilio. J. Chem. Ecol.* 3:1202–1211.

54. Cooperband, M. F., et al. 2012. Male-produced pheromone in the European woodwasp, *Sirex noctilio*. *J. Chem. Ecol.* 38:52–62.

55. Böröczky, K., et al. 2012. Volatile profile differences and the associated *Sirex noctilio* activity in two host tree species in the northeastern United States. *J. Chem. Ecol.* 38:213–221.

56. Torto, B., et al. 2007. Multitrophic interaction facilitates parasite–host relationship between an invasive beetle and the honey bee. *Proc. Natl. Acad. Sci. U.S.A.* 104:8374–8378.

57. Torto, B., A. T. Fombong, R. T. Arbogast, and P. E. A. Teal. 2010. Monitoring *Aethina tumida* (Coleoptera: Nitidulidae) with baited bottom board traps: Occurrence and seasonal abundance in honey bee colonies in Kenya. *Environ. Entomol.* 39:1731–1736.

58. Frazier, M., et al. 2010. A scientific note on *Varroa destructor* found in East Africa; threat or opportunity? *Apidologie* 41:463–465.

59. Muli, E., et al. 2014. Evaluation of the distribution and impacts of parasites, pathogens, and pesticides on honey bee *(Apis mellifera)* populations in East Africa. *PLoS One* 9:e94459.

60. Tumlinson, K. Eulogy for James Tumlinson. February 18, 2022.

61. Gill, C. 2022. Colleagues mourn internationally renowned chemical ecologist James Tumlinson. *Penn State News*, February 16; https://www.psu.edu/news/agricultural-sciences/story/colleagues-mourn-internationally-renowned-chemical-ecologist-james.

62. Lewis, W. J. Eulogy for James Tumlinson. February 18, 2022.

SELECTED BIBLIOGRAPHY

1968 With D. D. Hardee, J. P. Minyard, A. C. Thompson, R. T. Gast, and P. A. Hedin. Boll weevil sex attractant: Isolation studies. *J. Econ. Entomol.* 61:470–474.

1969 With D. D. Hardee, R. C. Gueldner, A. C. Thompson, P. A. Hedin, and J. P. Minyard. Sex pheromones produced by male boll weevil: Isolation, identification, and synthesis. *Science* 166:1010–1012.

1971 With R. C. Gueldner, D. D. Hardee, A. C. Thompson, P. A. Hedin, and J. P. Minyard. Identification and synthesis of the four compounds comprising the boll weevil sex attractant. *J. Org. Chem.* 36:2616–2621.

With R. M. Silverstein, J. C. Moser, R. G. Brownlee, and J. M. Ruth. Identification of the trail pheromone of a leaf-cutting ant, *Atta texana. Nature* 234:348–349.

1977 With M. G. Klein, R. E. Doolittle, T. L. Ladd, and A. T. Proveaux. Identification of the female Japanese beetle sex pheromone: Inhibition of male response by an enantiomer. *Science* 197:789–792.

1986 With E. R. Mitchell, P. E. A. Teal, R. R. Heath, and L. J. Mengelkoch. Sex pheromone of fall armyworm, *Spodoptera frugiperda* (J. E. Smith). *J. Chem. Ecol.* 12:1909–1926.

1990 With T. C. Turlings and W. J. Lewis. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250:1251–1253.

1992 With T. C. Turlings. Systemic release of chemical signals by herbivore-injured corn. *Proc. Natl. Acad. Sci. U.S.A.* 89:8399–8402.

1994 With J. H. Loughrin, A. R. A. Manukian, R. R. Heath, and T. C. Turlings. Diurnal cycle of emission of induced volatile terpenoids by herbivore-injured cotton plant. *Proc. Natl. Acad. Sci. U.S.A.* 91:11836–11840.

1996 With U. S. R. Röse, A. Manukian, and R. R. Heath. Volatile semiochemicals released from undamaged cotton leaves (a systemic response of living plants to caterpillar damage). *Plant Physiol.* 111:487–495.

1997 With H. T. Alborn, T. C. Turlings, T. H. Jones, G. Stenhagen, and J. H. Loughrin. An elicitor of plant volatiles from beet armyworm oral Secretion. *Science* 276:945-949.

With P. W. Paré. De novo biosynthesis of volatiles induced by insect herbivory in cotton plants. *Plant Physiol.* 114:1161–1167.

1998 With W. J. Lewis. Host detection by chemically mediated associate learning in a parasitic wasp. *Nature* 331:257-259.

With C. M. De Moraes, W. J. Lewis, P. W. Pare, and H. T. Alborn. Herbivore-infested plants selectively attract parasitoids. *Nature* 393:570–573.

2001 With C. M. De Moraes, and M. C. Mescher. Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410:577–580.

2004 With J. Engelberth, H. T. Alborn, and E. A. Schmelz. Airborne signals prime plants against insect herbivore attack. *Proc. Natl. Acad. Sci. U.S.A.* 101:1781–1785.

2005 With C. G. Lait. Biosynthesis of fatty acid amide elicitors of plant volatiles by insect herbivores. *Arch. Insect Biochem.* 58:54–68.

2007 With H. T. Alborn, et al. Disulfooxy fatty acids from the American bird grasshopper *Schistocerca americana*, elicitors of plant volatiles. *Proc. Natl. Acad. Sci. U.S.A.* 104:12976–12981.

With B. Torto, D. G. Boucias, R. T. Arbogast, and P. E. A. Teal. Multitrophic interaction facilitates parasite–host relationship between an invasive beetle and the honey bee. *Proc. Natl. Acad. Sci. U.S.A.* 104:8374–8378.

2008 With N. Yoshinaga, et al. Active role of fatty acid amino acid conjugates in nitrogen metabolism in *Spodoptera litura* larvae. *Proc. Natl. Acad. Sci. U.S.A.* 105:18058–18063.

2009 With K. Böröczky, et al. Monoalkenes as contact sex pheromone components of the woodwasp *Sirex noctilio. J. Chem. Ecol.* 3:1202–1211.

2015 With I. Seidl-Adams, et al. Emission of herbivore elicitor-induced sesquiterpenes is regulated by stomatal aperture in maize (*Zea mays*) seedlings. *Plant Cell Environ.* 38:23–34.

2019 With A. C. Jones, et al. Herbivorous caterpillars can utilize three mechanisms to alter green leaf volatile emission. *Environ. Entomol.* 48:419–425.

2020 With B. P. Timilsena, and I. Seidl-Adams. Herbivore-specific plant volatiles prime neighboring plants for nonspecific defense responses. *Plant Cell & Environ.* 43:787–800.