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# John Matthew McDowell: A Visionary Leader in Molecular Oomycete-Plant Interactions and a Wonderful Mentor and Friend to Many

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#### TRIBUTE

## John Matthew McDowell: A Visionary Leader in Molecular Oomycete-Plant Interactions and a Wonderful Mentor and Friend to Many

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John M. McDowell (Fig. 1), a leader in the field of molecular plant-microbe interactions, friend and colleague of many scientists in the molecular plant-microbe community, and a dedicated member of the International Society of Molecular Plant-Microbe Interactions, passed away in December 2024. John was known to many, not just because of his own seminal scientific discoveries but because of his ability to synthesize the progress made in the field of molecular plant-microbe interactions and, in particular, the interplay between oomycete pathogens and the plant immune system, which led to many outstanding reviews. His ability to zoom out from minute details to the big picture also made him an effective mentor, teacher, editor-in-chief of the journal Molecular Plant-Microbe Interactions, and National Science Foundation program director, as well as a great colleague, who was always ready to ask the illuminating questions that would help you in deciding where to direct future efforts or provide sensitive hypotheses to test next. And in whatever he did, in whatever situation he was, he was always supportive and encouraging, lifting people up, making them feel good about themselves, and getting everybody even more excited about the research they were doing. He was the most even-keeled, kind-hearted person, an example to all of how to be better—not just as a scientist but as a human.

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### John's Life

John M. McDowell was born and raised in Tennessee. His scientific journey began at Alcoa High School, where his science teacher and tennis coach, Jim Cobb, sparked a lifelong passion for both disciplines. In the mid-1980s, John discovered rock climbing, and after graduating from the University of Tennessee with a B.A. in cell and molecular biology, he took a gap year to chase big walls out West with friends. During that adventure-filled year he met—and eventually married—Cathy. The newlyweds moved first to Chapel Hill, NC, then to Blacksburg, where John joined Virginia Tech as an assistant professor. He remained committed to his outdoor roots, balancing an academic career with weekend climbing trips, mountain-biking outings, and, most rewarding of all, raising two sons, Jonah and Ethan.

#### John's Science

#### Evolution and genetics of actin in plants

In the fall of 1988, John joined Rich Meagher's lab at the University of Georgia to work on his Ph.D. John arrived as the focus in the Meagher lab, which had pioneered gene cloning and gene characterization in plants, was transitioning away from early models, such as petunia and soybean, to an exciting new experimental system, *Arabidopsis thaliana*. John's work contributed directly to those early days of *Arabidopsis* molecular genetics, taking research on genes encoding the cytoskeletal protein, actin, to an entirely new level, from both a genetic and an evolutionary point of view. His two first-author papers (McDowell

et al. 1996a, b) and a slew of co-authored manuscripts (An et al. 1996a, b; Fletcher et al. 1994; Huang et al. 1996a, b, 1997; McKinney et al. 1995) remain among the most highly cited publications from the Meagher group, giving rise to intriguing new areas of research, including on actin-associated proteins, that continue to this day.

## Plant immunity in the model system *Arabidopsis* thaliana-Hyaloperonospora arabidopsidis

After finishing his very successful doctoral dissertation in Rich Meagher's lab, John joined the then nascent field of molecular plant-microbe interactions. John arrived in Jeff Dangl's lab at the University of North Carolina at Chapel Hill in the summer of 1995, just a month after Jeff and Sarah Grant opened their new labs there, following 9 years at the Max-Planck in Cologne, Germany. Jeff Dangl had begun a collaboration with Eric Holub, who, along with Ian Crute, had genetically characterized Arabidopsis host genotype-specific resistance to downy mildew disease caused by a naturally occurring oomycete pathogen, then called Peronospora parasitica (later reclassified as Hyaloperonospora arabidopsidis, Hpa). Postdoc Murali Dhandaydham had begun genetic characterization of the RPP8 resistance locus in the Arabidopsis accession La-er (Landsberg erecta). John joined this enterprise, quickly learning the relevant techniques and writing a successful NIH postdoctoral fellowship (and after that, a successful USDA-NIFA fellowship). John contributed to several projects using this pathosystem, but his main project was to isolate and study the RPP8 disease resistance locus.

John and Murali quickly mapped *RPP8* to the bottom arm of chromosome 5. The La-*er* accession was specifically resistant to the *Hpa* isolate Emco5 that defined this resistance gene, and the Col-0 accession was susceptible. John also began to isolate loss of *RPP8*-mediated resistance mutants from an EMS mutagenized seed population. These could represent *rpp8* alleles or mutations in other genes required for *RPP8* function.

Positional cloning in the late 1990s was hard work. There were no genome sequences, and one needed to generate new polymorphic DNA markers at each step. John and Murali were successful, but they had help. Yeast artificial clones hybridizing to their most closely linked genetic marker and cosmid clones from both the Col-0 and La-er genomes for construction of physical



Fig. 1. John M. McDowell.

contigs across *RPP8* were community resources that hastened John's success. Steve Goff, then at Novartis, sequenced the cosmid clones from both accessions that covered the locus. Others had isolated TIR-NB-LRR genes encoding resistance to *Hpa*, so John was surprised when their candidate genes were CC-NB-LRR genes, the first defined as recognizing an oomycete. This result suggested that members of either NLR superfamily, TNL or CNL, could direct recognition of any type of pathogen.

John and Murali sequenced the six La-er-derived rpp8 alleles from their mutant screen. These results (and genomic complementation with the RPP8 gene) proved that they had cloned the correct gene. There was a second highly related RPP8 paralog just downstream from the true RPP8 gene (the one with the six mutant alleles). It did not confer resistance to the Emco5 isolate when transferred into the susceptible Col-0 accession. Most interestingly, the duplicated RPP8 ortholog pair in La-er had undergone an unequal recombination to generate the single-copy Col-0 allele. Furthermore, and consistent with emerging data on the NLR genes cloned to that juncture, there was clear evidence of positive selection acting on the LRR domain of RPP8.

John wrote the great majority of the paper describing the above results, which was accepted at *The Plant Cell* with minor revisions (McDowell et al. 1998). John was an exceptional writer: clear, concise and thorough. Rereading this paper now provides an excellent glimpse into the pre-genome sequence gene isolation world in *Arabidopsis* biology, a textbook lesson in how to do genetics, and insight into the early days of plant NLR biology, which was only 4 years old when this paper was published.

The RPP8-Ler allele stood out at the time of its cloning, as it was found to act largely independently from the defense hormone salicylic acid and other canonical signaling components known to regulate plant immunity. Collaborative work of the labs of Jeff Dangl, Jim Beynon, and Eric Holub, led by John, showed this to apply to a second Arabidopsis disease resistance gene as well, the Col-0 allele of RPP7, which mediates strong resistance against the *Hpa* isolate Hiks1 (McDowell et al. 2000). To identify downstream signaling components required for such unconventional R genes, John spearheaded comprehensive mutant screens for enhanced downy mildew (edm) mutants, a fruitful collaborative project of the Dangl and Holub labs. Screening all Col-0-based mutant resources available at the time for loss of RPP7-mediated resistance, numerous rpp7 alleles, along with three second-site mutants (edm1, edm2, and edm3), were identified and genetically characterized. The edm1 mutant turned out to be an allele of the co-chaperone and SCF complex interactor gene Sgt1b (Tör et al. 2002), and edm2 and edm3 seemed to define completely novel and unknown defense components.

When John left for his position at Virginia Tech, he generously passed on these mutants to Thomas Eulgem, a new postdoc in the Dangl lab, and continued to participate in the further characterization and mapping of the *EDM2* and *EDM3* loci. Later on, Thomas Eulgem used these genes as a foundation for his own lab at UC Riverside. John stayed involved and contributed to a total of four collaborative papers on the cloning of *EDM2* and *EDM3* and their roles in *RPP7*-mediated immunity (Eulgem et al. 2004, 2007; Lai et al. 2019, 2020). Although *EDM1/Sgt1b*, *EDM2*, and *EDM3* were not found to encode downstream defense signaling components as initially anticipated, their products play roles in the regulation of *RPP7* expression and protein stability, highlighting the importance of homeostatic control of this immune recentor.

As a junior faculty member of Virginia Tech, John continued to work on *RPP7*. Collaboratively with Eric Holub's group, he succeeded with map-based cloning of *RPP7*, a locus embedded in a highly repetitive and difficult-to-sequence region of the Col-0 genome carrying several similar CNL genes. Sadly, this challenging and important study, which uncovered At 1g58602 as

the *RPP7* locus and showed it to be part of a complex CNL gene cluster with numerous transposon insertions, was never published (J. McDowell, A. Cuzik, X.-J. Wang, M. Tör, J. Dangl, and E. Holub, *unpublished data*). Additional important work from the time of his postdoc to assistant professor transition involved the discovery of a developmentally regulated *R* gene in *Arabidopsis* (McDowell et al. 2005) and the first-ever study on transcriptional regulation of an *NLR* gene (Mohr et al. 2010).

John eventually turned his focus to oomycete effectors (see next section). However, his seminal research contributions and thorough reflection on molecular pathogen recognition in plants, preserved in his research articles and several excellent reviews, have a long-lasting impact and have shaped the field of plant NLR biology (Beers and McDowell 2001; Dangl and McDowell 2006; McDowell and Dangl 2000; McDowell and Simon 2008; McDowell and Woffenden 2003).

#### Oomycete genomics and effectoromics

After making the described significant contributions in understanding how plants defend themselves from microbial threats, John expanded his research interests to the opposite side of the plant-microbe interaction. How do pathogens subvert these complex defense mechanisms and co-opt their host that promoted a pathogen's success? In the early 2000s, only a handful of oomycete effectors had been identified, exclusively owing to their avirulence activity, including *Hpa ATR13*, *Hpa ATR1*<sup>NdWs</sup>, *Phytophthora sojae Avr1B*, and *Phytophthora infestans Avr3b*, but this would quickly change in the coming years.

A large and international collaboration co-led by John resulted in an annotated *Hpa* genome, revealing a large collection of putative effector genes that were identified by their cleavable N-terminal signal peptide and a downstream conserved RxLR motif. In comparison with the *P. sojae* genome, *Hpa* harbored a reduced effector collection with little overlap to its oomycete cousin (Baxter et al. 2010).

In 2005, John and his lab began research on these oomycete effectors using Hpa and P. sojae as models to test a hypothesis that divergent oomycetes maintained core effectors. Using a draft genome of *Hpa*, a handful of homologous effectors were cloned by two of his graduate students, Ryan Anderson and Devdutta Deb, in the mid-2000s. These sequence-related effectors suppressed classic markers of plant defenses. Interestingly, these effectors functioned in non-host plant species, suggesting a potential common, conserved host target. In some cases, these conserved effectors triggered a hypersensitive response in nonhost plants (Anderson et al. 2012; Deb et al. 2018), and others, such as HaRxL10, co-opted plant hormone signaling to suppress immunity (Anderson et al. 2019). These findings were important and underpinned John's later efforts and collaborations in studying methods for developing durable resistance in crops using conserved effectors as molecular probes to map resistance genes.

Beyond John's own research, John was a constant in the oomycete community and a perennial participant at the annual Oomycete Molecular Genetics Network meetings. His willingness to collaborate and love for doing so led to many fruitful partnerships that facilitated our understating of plant-microbe interactions, including the W and Y motifs found in many oomycete effectors (Dou et al. 2008) and the involvement of the exocyst complex and circadian clock in plant immunity (Stegmann et al. 2012; Zhang et al. 2013). The *Hpa* genome was not the last genome to which John made contributions. In 2019, John and his graduate student John Herlihy collaborated with David Haak's lab to use long-read sequencing to create a draft assembly of the *Phytophthora capsici* genome (Cui et al. 2019).

There has been enormous progress in understanding how these unique organisms manipulate their hosts. In the two decades pre-

ceding the initial oomycete genomes, John was always excited to absorb and build upon the latest in oomycete effector biology and genomics.

#### The role of nutrients in plant-microbe interactions

In addition to John's research focusing on understanding the role of pathogen effectors during plant-oomycete interactions, he became interested in the physiology of the two organisms during this tug of war. The sequencing of the Hpa genome showed that it lacks essential genes to assimilate nitrogen and sulfate, suggesting that the pathogen needs to acquire these nutrients in an organic form. The lifestyle of *Hpa* implies that it extracts them from the host, most likely at the interface between the cells, which corresponds to the so-called haustorium. Similar to what was thought for other biotrophic pathogens, John hypothesized that *Hpa* is dependent on plant genes to deliver the nitrogen- and sulfur-containing nutrients, likely amino acids and sugars, to the haustorium for pathogen uptake. He imagined that these genes, likely conserved in plants, would be excellent targets for crop improvement. As he wrote in several grant proposals, knocking out these genes would effectively "cut the supply lines of the pathogen" for nutrients, which would be a very difficult form of resistance for the pathogen to overcome. Indeed, pathogen effectors would have to evolve to modify the expression and possible localization of new transporters to reestablish the flow of nutrients from an engineered plant. This would likely take a large number of generations for the pathogen to achieve, therefore providing crops with a longer-lasting resistance to this type of pathogen.

This approach was funded by the National Science Foundation (NSF), Virginia Tech, and a Virginia-North Carolina collaborative grant and involved the laboratories of John, Guillaume Pilot at Virginia Tech, and Terri Long at North Carolina State University. The team worked to identify the transporters for iron, amino acid, and sulfur-containing compounds that are necessary for the pathogen to grow on Arabidopsis. To investigate gene expression at the plant-pathogen interface, RNA from plant cells containing haustorium would need to be isolated from their non-haustoriated counterparts. These cell sets are ephemeral and have no predetermination, creating quite a challenge when it comes to sample collection. To achieve this aim, John and Guillaume Pilot elected to adapt Translating Ribosome Affinity Purification (TRAP) to currently translating ribosomes in haustoriated cells. Over the course of 5 years, John and Guillaume Pilot worked with their graduate student Kasia Dinkeloo to build constructs, create transgenic Arabidopsis, and eventually collect a robust RNA sequencing data set of gene expression data from haustoriated cells (Dinkeloo et al. 2022). This aspect of the project combined synthetic biology, biochemistry, and plant pathology as yet another example of John's willingness to collaborate across disciplines to solve tricky problems. Then PhD students Unnati Sonawala, Wei Wang, and John Herlihy and current PhD student Iliana Castillo-Machuca used RNA sequencing, genetics, and physiological analyses to uncover the pathways involved in oomycete nutrition. The research prompted the notion that disturbances in nutrient homeostasis are immune signals (Herlihy et al. 2020; Sonawala et al. 2018).

#### RNA interference (RNAi)-based tools

When John heard of his colleague Sherif Sherif's research using dsRNA as a biofungicide against *Botrytis cinerea*, he was impressed by the potential of utilizing bacterial minicells for dsRNA production and encapsulation. Following some brainstorming sessions, John, Sherif Sherif, and Mahmut Tör from the University of Worcester, United Kingdom, pursued a grant application to the NSF's EDGE program, focusing on RNAibased tools for unlocking the functional genomics of obligate

oomycete plant pathogens. The proposal built on John and Mahmut Tör's deep expertise in this field, and Sherif Sherif's lab contributed the necessary dsRNA formulations for their target genes.

John and Mahmut Tör's collaboration spanned many years, marked by a shared commitment to understanding plant immunity and pathogen biology at the molecular level. Mahmut Tör's research had already established critical insights into resistance mechanisms against *Hyaloperonospora* species, and his expertise in RNAi and genome editing complemented John's deep knowledge of oomycete effectors and host-pathogen interactions. Together, they explored ways to develop RNA-based tools for functional genomics, focusing on novel approaches to study and control downy mildew diseases. Their joint efforts resulted in multiple publications that have shaped the field, as well as a transatlantic collaboration that continues to bear fruit (Bilir et al. 2022; Telli et al. 2020, 2024).

Despite everything he was going through (medical reports, doctor appointments, and so on), John remained genuinely excited about this project, as if his own struggles were secondary to the science. Over the past 2 years, Mahmut Tör's lab has led major aspects of the project, building on his longstanding work in oomycete genomics and RNAi-based disease control strategies. Their collaborative research has now reached the stage at which the first draft of a manuscript detailing their findings is ready, and John is acknowledged as a co-author—a testament to his lasting impact on the field of molecular plant-microbe interactions (Göl et al. 2025).

As pointed out earlier, John was not only an accomplished scientist but also an exceptional writer. He had an ability to articulate complex scientific ideas with clarity and precision, making even the most intricate molecular interactions understandable. Because his writing was not just about presenting results but about telling a scientific story, weaving together hypotheses, data, and interpretations in a way that made the research feel alive, he continued to write highly cited reviews (Tör et al. 2023; Wang et al. 2022; Wilson and McDowell 2022).

## John's Scientific Leadership and Professional Service

One of John's greatest strengths that made him a leader beyond his own field of expertise was his ability to see biological systems as interconnected rather than as isolated parts. He had a remarkable way of linking concepts across disciplines, helping his colleagues recognize patterns and relationships that might otherwise go unnoticed. His thought-provoking approach to science constantly challenged his students, collaborators, and scientists whose work he reviewed to ask deeper questions and reconsider conventional thinking. Importantly, he never used the word "weakness" when reviewing proposals. He wrote about the strengths, and then he wrote about "opportunities to improve." There were no weaknesses in John's eyes when it came to how a person did their science, only opportunities to improve.

One of many leadership roles that John held was that as editorin-chief for *Molecular Plant-Microbe Interactions* (MPMI), from 2016 until 2018. John took over MPMI at a time when the journal was declining in the number of submissions. John loved the journal and developed a range of strategies that would result in improving the journal's competitiveness and left a lasting legacy on this flagship molecular journal. Two MPMI Focus Issues were published under his guidance, improving MPMI's impact: "Activation, Regulation, and Evolution of MTI and ETI" and "Effector-triggered Susceptibility." John also developed the format for a groundbreaking white paper: "Foundational and

Translational Research Opportunities to Improve Plant Health," which was downloaded more than 3,200 times in less than 12 months. Moreover, John initiated the "Distinguished Review Article Series"; these articles serve as foundations for topical Focus Issues and will have long-term relevance and impact. John led an editorial board consisting of 19 senior editors and 34 associate editors, who reviewed more than 1,034 papers and counting. Under his leadership, MPMI was solidly ranked as the top molecular and genomic plant pathology journal in the field, with an impact factor around 4. At the end of his tenure as editor-in-chief, he left us with a journal that was thriving again.

Another key leadership role that John held was managing the NSF's Plant Biotic Interactions as a rotating program director. John knew every principal investigator and was a selfless advocate and supporter of all Plant Biotic Interactions proposals. He wanted to grow the program and its impact. During the year preceding John's rotation at the NSF, Nicole Donofrio held that position, working closely with Michael Mishkind, Ann Lichens-Park, and others. She rotated during the Covid pandemic, starting in September of 2020, and quickly fell into a rhythm with Michael, moving smoothly through the Zoom-verse. She recalls the moment she learned that John was to succeed her, breathing a large sigh of relief, knowing that there could not be a better steward of the program. It was almost as though the program was designed for him, and vice versa. His pioneering background in molecular plant pathology and his work as editor-in-chief of MPMI gave him a unique vision of the field, from minutiae to the view from 30,000 feet, and an uncanny ability to see what was on the horizon. John knew the Plant Biotic Interactions community inside and out, and when Nicole came back to NSF to help as a science expert, she had the pleasure of overlapping with him for a short time. When he left NSF, she took over some of John's duties to close out a panel. She hunkered down and prepared to pull double duty, but as soon as she opened his folder, she immediately found that within about 3 days of the panel ending, he had completed just about every chore and checked off every box, a process that usually takes weeks. He must not have slept for 3 days! But, as noted throughout this article, this was how John was. Whatever task was before him was the most important task, and it was no different at NSF.

#### John as a Mentor and Teacher

Terri Long recalls that already as a postdoctoral researcher, John was an extraordinary mentor: "When I walked into Jeff Dangl's lab as a second-year undergrad at UNC-CH and began to work with John, I had no idea how it would change the trajectory of my career and life. I didn't know anything about *Arabidopsis*, much less *RPP8*. All I knew was that I loved the lab environment, and that I wanted to live up to John's expectations." His keen interest in plant biotic stress response was infectious and profoundly inspiring. He introduced his mentees to a model of scientific rigor—one that balanced intellectual intensity with a dynamic and fulfilling life beyond the laboratory. His sharp wit fostered a lively and engaging work environment, and his formidable intellect kept his mentees on their toes.

John instilled a genuine sense of confidence in those he mentored. He challenged them to think critically and analytically about their research, entrusting them with the responsibility to pursue excellence. Dedicated and focused, John set high expectations, and his mentees felt compelled to rise to the occasion. Even when young researchers experienced inevitable setbacks, John's patience allowed them to persevere with grace. Those who entered his lab left with the grit to face challenges in the varied fields they pursued.

His mentorship, however, extended far beyond the confines of his laboratory. On the door of John's lab in Latham Hall, he posted the words, "I seek to understand." This was a call not just for those entering but also for those walking out of the lab to carry a curious and critical eye with them. John knew that science existed outside of the laboratory and classroom, so he exposed his students to the regulation and funding of science, and he opened debates about how society perceives science. In his translational plant sciences course, he exposed his students to how their work fits into a wider world.

John remained a steadfast supporter of his mentees throughout their careers, readily offering counsel, providing invaluable feedback on job applications, facilitating networking opportunities, and even initiating new collaborations with former students. His presence at any conference was not just a chance for professional engagement but an opportunity to reconnect, exchange insights, and, inevitably, share laughter. His influence—both within the plant science community and on the next generation of researchers—is immeasurable.

For example, Unnati Sonawala got to know John during her lab rotations in the Translational Plant Science program at Virginia Tech. He would go on to become her PhD supervisor and deeply influence her research approach, but his impact extended beyond her doctoral studies. Even after graduation, he remained a mentor she consistently turned to for guidance and wisdom. With John, she says that she learned that research was serious business, but never the only pillar of life. He wanted his students to excel at science while encouraging them to balance it with other personal goals. John's approach to research was always collaborative and never combative. Despite his almost encyclopedic knowledge of plant pathology, he remained one of the humblest scientists she ever met. He was extraordinarily kind and generous with both his knowledge and time, whether providing research advice or teaching classes. On Unnati Sonawala's last day in Blacksburg, she stopped by John's office. He wanted to leave her with words Jeff Dangl had told him when he left Jeff's lab: "The one who gives, gets," he said. Unnati concludes, "John truly embodied those words! While I am immeasurably richer for having worked with and learned from him, his absence will continue to leave me bereft for a long time.'

One could write an entire article about John's teaching, but we will just point out here that the same depth and clarity that characterized John's writing came through in his teaching. He would sit down on a desk in front of the students in class, look around the room, make eye contact, and then calmly, but at the same time intensely, start explaining the intricacies of molecular plant-microbe interactions. His words flowed, and it seems it took no effort on his part, but every word was well chosen, no jargon remained unexplained, no concept was brushed over, and every yet-unanswered question in the field was posed, making his students excited about the field, curious about the unknown, and longing to answer the open questions in their own research.

#### John as a Colleague

John's contributions to science and to those who had the privilege of working with him will endure. He was not just a brilliant scientist—he was a mentor, a leader, and a visionary thinker who inspired us to see beyond the immediate details of an experiment and into the broader landscape of biology. This may be his last published work, but his influence will remain in every question we continue to ask and every discovery we make.

Shahid Mukhtar shares that what set John apart was his remarkable combination of scientific brilliance and kindness. He was always approachable, generously sharing his expertise and time, whether it was for a casual conversation or providing thoughtful feedback on a research project. His passion for plant-

pathogen interactions was contagious, and his intellectual curiosity was truly inspiring. Shahid Mukhtar first met John in 2007 at Jeff Dangl's Christmas party, and from that moment, he was struck by his warmth, intellect, and dedication to the field. When Shahid Mukhtar began his faculty position in 2010, he stayed in touch with John, often crossing paths at conferences where their shared interest in molecular plant-microbe interactions only strengthened their bond. John had a unique ability to bring people together to tackle complex scientific challenges. His collaborative spirit fostered innovation and created a strong sense of community among his colleagues. Shahid Mukhtar points out how John's legacy of kindness, generosity, and groundbreaking research will continue to inspire future generations of scientists, and his caring nature will remain in the hearts of all who were fortunate enough to work with him. A phrase that always reminds him of John is his fond use of the word "terrific." Every time he hears it, he cannot help but picture John's smile. John, we will "terrifically" miss you.

Jeff Chang points out how John helped build easygoing and fun but hardworking cultures. John's success in building communities and cultures can be pinned to several strong phenotypes. John's positivity was the most dominating trait. He was able to find happiness in everything he did, and his joy was infectious, lifting and brightening our days. John also never acted like he was in a position of power. He acted like he was in a position to help. He leveled the playing field. He removed barriers. He gave powerful advice and was trustworthy, being THE friend to turn to for help with difficult situations. Lastly, John often bore the burden so others did not have to. Colleagues have even expressed guilt in waiting it out until John volunteered. John's character strengths mixed in paradoxical ways that made him such a unique and special person. John had a strong gravity that attracted people. His smile, his violent head nods, and loud exclamations of "Right on!" punctuated with joyous laughter drew us to him. We wanted to be with John. Yet, John avoided intentionally drawing attention to himself. He could be quiet and introspective, content avoiding the limelight, deflecting the conversation away from him, and drawing others to fill the space.

We dearly miss our friend and colleague. Many of us are inspired to remember John by channeling and applying features of John as best we can. As a community, we need to collectively pitch in to match what he accomplished by himself. We will always ask ourselves, "How would John handle this situation?" and try to lift people up, be it by following a seminar speaker attentively from start to finish, providing comfort by nodding along, or exclaiming "Riiiiiight" with a vigorous head nod and infectious laughter when agreeing with colleagues enjoying each other's company.

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