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INTERVIEW

The people behind the papers – Priyanka Govindaraju and Enrico Scarpella

The veins are the vascular networks of plant leaves, functioning as channels for transport of signals and nutrients. A new paper in Development investigates how the spatial regulation of auxin transport contributes to vein patterning in *Arabidopsis*. We caught up with first author Priyanka Govindaraju and her supervisor Enrico Scarpella, Associate Professor at the Department of Biological Sciences, University of Alberta in Edmonton, Canada, to find out more about the work.

Priyanka (L) and Enrico (R)

Enrico, can you give us your scientific biography and the questions your lab is trying to answer?

ES: I graduated in Biological Sciences at the University of Milan, but I spent my fifth undergraduate year at Leiden University as an exchange student. That's when I met Annemarie Meijer and Harry Hoge, who would later become my PhD supervisors. Every day I am grateful for the life-changing opportunity they gave me and for how patient they had been – before I could start my PhD with them, I had to go back to Italy, finish my last year of undergraduate studies (university degrees took longer then) and complete a year of civil service (in lieu of the mandatory military service to which I objected).

Early in my PhD – I think it was toward the end of the first year – I fell in love with vascular tissues, especially the mesmerizing networks of veins in the leaves. So after my PhD in Mathematical and Natural Sciences from Leiden University, I moved to Toronto, where Thomas Berleth had generously given me the opportunity to do a postdoc with him.

A little more than a year into my postdoc, Thomas selflessly passed on to me an ad for a position in the Department of Biological Sciences at the University of Alberta. I interviewed there toward the end of my second year of postdoc. Though early in my postdoc, the search committee and the department took a chance on me and offered me an Assistant Professor position, which I took on a year later. I have been an Associate Professor there since 2010, and I have just now applied for Full Professor. The questions my lab tries to address are the same that have been haunting me since my graduate days: how do veins form and how are they assembled into networks?

And Priyanka – how did you come to work in Enrico's lab and what drives your research today?

PG: During my undergrad, I came to be interested in plant developmental biology. I was looking for labs in which to continue my training as graduate student, and therefore I was doing a lot of background research about the prospective research groups. One of my undergrad supervisors had suggested that I have a look at the leaf vein development research done in the Scarpella lab, and I was very much interested and encouraged by the lab's research. I also thought it would provide me with the platform to learn techniques such as imaging and molecular biology, and I was very curious and motived to know how veins form: I wanted to solve a small portion of the huge puzzle. I was happy when I saw that there were vacancies in the lab and contacted Enrico showing my interest in the research. The experience that I have gained from Enrico and the lab will certainly help me with my career.

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How has your research been affected by the COVID-19 pandemic?

ES: Well, my lab – like all the labs at our university that do not work on COVID-19 – was shut down on March 15, and, until the end of May, we only had permission to maintain essential plant collections – basically, to water plants. Since the beginning of June, we have received permission to resume research part-time – only a maximum of two people can be in the lab at any given time. We currently do not know when we will be able to resume full-time research, but given time my research will recover. Right now, I am more concerned about that of my trainees and how I can minimize the impact this delay in research will have on their career.

Before your paper, how were auxin and its transporter PIN1 thought to regulate vein development?

PG & ES: We thought that, in the epidermis of the leaf, PIN1 would transport auxin toward discrete points. From these 'convergence points' of auxin transport in the leaf epidermis, PIN1 would transport auxin into the inner tissues of the leaf, where PIN1-mediated auxin transport would select the cell paths that would later become veins.

Can you give us the key results of the paper in a paragraph?

PG & ES: Contrary to our expectations, we found that reintroducing PIN1 in the epidermis of leaves that lack PIN1 failed to rescue the mutant vein pattern. Furthermore, removing PIN1 from the epidermis of normal leaves, or of leaves that lack PIN1's most

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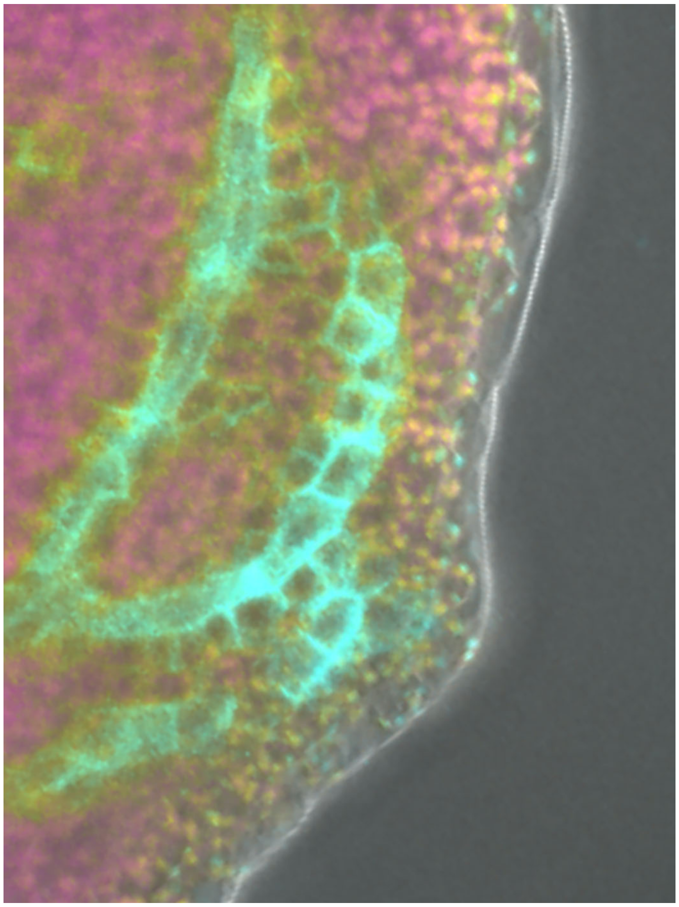

PIN1::cPIN1:GFP expression in a *pin1* mutant.

closely related proteins, had no effect on vein patterning. By contrast, reintroducing PIN1 in the inner tissues of leaves that lack PIN1, or PIN1 and its most closely related proteins, rescued the mutant vein patterns. Finally, eliminating PIN1 from the inner tissues of normal leaves led to abnormal vein patterns.

How do you think vascular PIN1 works to promote vein patterning?

PG & ES: We think that the concept at the core of the Canalization Hypothesis formulated by Tsvi Sachs more than 50 years ago still offers the best starting point to understand how PIN1 in the inner tissues of the leaf may promote vein patterning. The Canalization Hypothesis proposes a positive feedback between the auxin that flows through a segment of a cell's plasma membrane and the capacity of that cell to transport auxin in that same direction. The pre-existing vasculature – at first, the midveins of the cotyledons (i.e. the embryonic leaves) for the first two post-embryonic leaves we analysed in our paper – would act as an auxin sink that orients toward itself auxin transport, mediated by PIN1 and related proteins, in the inner tissues of the developing leaves. Because of the postulated positive feedback of auxin transport on itself, broad domains of auxin transport in the inner tissues of the developing leaf would be gradually refined into narrow paths of auxin transport – the canals the hypothesis refers to. And these narrow paths of auxin transport would define the positions where veins would later form.

How fortunate that we never run out of research questions and opportunities!

But, as usual, the devil is in the details because we still don't know, for example, how auxin finds, as efficiently as it seems to be doing, a sink located cells away. Nor do we know how a cell senses the auxin that flows through it or how some auxin transport paths end up connecting two sinks to each other. How fortunate that we never run out of research questions and opportunities!

Do you think the epidermis plays any role at all in the process?

PG & ES: Yes, we do, and indeed our results do not rule out a role for the leaf epidermis, or for epidermal auxin, in vein patterning.

When doing the research, did you have any particular result or eureka moment that has stuck with you?

PG I found that PIN1 expression in the epidermis was not sufficient to rescue the vein pattern defects of *pin1* mutants but was sufficient to rescue their inflorescence defects; conversely, PIN1 expression in the inner tissues was sufficient to rescue the vein pattern defects, but not the inflorescence defects. This is the moment that stuck with me: when I found that there is a mechanistic difference in leaf vein patterning and inflorescence morphogenesis.

And what about the flipside: any moments of frustration or despair?

PG: I would not exactly term it as despair, but when I had started the research work, based on previous reports, I was using PIN1 expression in the epidermis as a control. And indeed, PIN1 expression in the epidermis did rescue the inflorescence defects of *pin1* mutants. But when I found that the same PIN1 expression in the epidermis did not rescue the vein pattern of *pin1* mutants, I suddenly felt that something was wrong as it was not going in the way I predicted it would go.

I understand you've since left the Scarpella lab – what are you up to now?

PG: There is a lot of uncertainty due to COVID-19. There were certain exams that I was planning to take and now they have been delayed indefinitely. Right now, I am planning to work as a research fellow and look for labs where I could potentially do a PhD in the near future.

Where will this work take your lab?

ES: We are currently testing hypotheses of the possible role of the leaf epidermis in vein patterning.

Finally, let's move outside the lab – what do you like to do in your spare time in Alberta?

PG: When I was new to Alberta, in my spare time I preferred to explore the city and walk around the river valley, which was very close to the university. I constantly made a lot of plans, before I finally made it to beautiful lakes and the National Parks in Alberta. Apart from traveling, I enjoy reading books and do gardening during summer.

ES: I love spending time with my wife and my daughter – I particularly enjoy talking, walking and playing with them. I love the ocean, but there isn't one in Alberta, so I make do with the swimming pool – though, for obvious reasons, I have not been able to see the ocean or its surrogate in a while. And I love listening to and playing music – especially with my daughter – reading, thinking and writing.

Reference

Govindaraju, P., Verna, C., Zhu, T. and Scarpella, E. (2020). Vein patterning by tissue-specific auxin transport. *Development* **147**, dev187666. doi:10.1242/dev.187666