Editorial

A tribute to Sally E. Smith

Prof. Sarah (Sally) E. Smith, a long-standing *New Phytologist* Advisory Board member, and friend to the journal, died in September 2019. Sally will be remembered not only for her outstanding body of work, but for her friendship, mentorship and leadership of the mycorrhizal research community. By way of tribute we invited colleagues of Sally to share their recollections, and we publish this Virtual Issue in her memory.

Sally was born in 1941, and received Bachelor and PhD degrees from Cambridge University, UK, before relocating to Adelaide, Australia in the late 1960s, alongside her husband Andrew (FA) Smith. Upon arrival in Adelaide, Sally undertook a number of positions at the University of Adelaide's Botany Department, followed by research work at the Waite Research Institute. In 1991 she was appointed Senior Lecturer in the Department of Soil Science, and she received a Doctorate of Science from the University of Adelaide that same year. Sally was appointed Professor in 1995.

Sally was elected a Fellow of the Australian Academy of Science in 2001, and, among numerous awards, she received an Australian Centenary Medal for contribution to Australian society and services to biology (2003), the Taylor (2006) and Prescott (2012) medals of the Australian Society of Soil Science, and the International Mycorrhiza Society's Eminent Mycorrhiza Researcher Award (2019). Sally was also Honorary Professor at the Research Centre for Eco-Environmental Sciences (Chinese Academy of Sciences), and an Honorary Research Professor at the Chinese Agricultural University, Beijing.

Sally officially retired in 2006, but remained very active, holding an Adjunct and later Emeritus Chair at the University of Adelaide, contributing to many international meetings, including the 2014, 33rd *New Phytologist* Symposium 'Networks of Power and Influence: Ecology and Evolution of Symbioses between Plants and Mycorrhizal Fungi' (Bender *et al.*, 2014), and continuing to act as an Advisory Board Member at *New Phytologist*, providing much-valued critical insight and advice to our Editors. Her reviews, even when she disagreed, were always supportive and positive; she often provided much detailed advice and her large view of the literature to the authors.

In January 2019, *New Phytologist* published a Profile of Sally (Smith, 2019), which outlines her achievements in more detail, but importantly, it also highlights her many personal qualities. In the profile, Sally outlined the successes and challenges she faced throughout her career, but she also dwells on the many friendships and relationships she developed; her warmth, and generosity, is evident throughout the piece, and also in the personal recollections outlined below (Fig. 1).

In a way, Sally is still here with us. We are still prepared to hear her unforgettable voice at conferences; we still use the precious and irreplaceable textbook '*Mycorrhizal symbiosis*' she wrote with David Read, which will forever remind us of the first steps of our research community and the broad view she had of the symbiosis (Smith & Read, 2008). Sally will be greatly missed, as a scientist, friend, colleague and mentor.

Fig. 1 The photograph of Sally E. Smith featured in her 2019 profile. This photograph was later used in a banner as part of a state-wide celebration of the 125th anniversary of female suffrage in South Australia. Sally was featured as one of 46 eminent women associated with the University of Adelaide.

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Sarah Elizabeth 'Sally' Smith: 'no microphone required', by Roger Koide

At more than one conference, Sally announced to her audience that her voice was naturally of sufficient volume that she didn't need a microphone. It is equally true that the impact of her research and the influence she had on her many colleagues and students are truly impressive without additional amplification.

Sally was my host during a 6-month sabbatical in 1992 at the Waite Research Institute of the University of Adelaide. My wife, three children and I arrived in Adelaide to a furnished home that Sally had arranged for us to rent and her daughter's car for us to use until we could arrange our own transport. She showed us many such kindnesses as I am sure she has for countless others. Later, when she came for a visit to Penn State University, rather than waste time chatting with me, she immediately sought out my students,[1] making herself useful by helping to sort plant samples. I will always remember her as a woman ready, willing and able to help.

Considering her large contributions to the understanding of arbuscular mycorrhizal symbioses, many of you may be surprised to learn that Sally did not have the advantage of a conventional academic career. After earning her PhD on orchid mycorrhiza physiology in 1965 and publishing her first two papers in 1966 and 1967, there were no other publications until 1977. In the intervening years Sally was busy raising two daughters and holding various temporary teaching positions, and there was little opportunity for research. Collaborations were instrumental in restarting Sally's research career; her third, fourth and fifth publications resulted from collaborations with Melvin Daft (Smith & Daft, 1977), Andrew Smith (Smith *et al.*, 1979) and Glyn Bowen (Smith & Bowen, 1979), marking a fateful shift to the study of arbuscular mycorrhizas. As an expert on orchid *and* arbuscular mycorrhizas, it made sense in the early 1980s for Sally's father, Jack Harley, to ask her to co-author the first edition of *Mycorrhizal Symbiosis* (Harley & Smith, 1983). Throughout the 1980s other significant research was initiated (e.g. Smith & Gianinazzi-Pearson, 1988), all before her first permanent academic position in 1991 in the Department of Agricultural Biochemistry at the Waite.

Australia is plagued by some of the most phosphorus (P)-deficient soils on earth (Lambers *et al.*, 2013), and there are three times as many sheep in Australia as there are people. Not surprisingly, much of Sally's research concerned the impact of arbuscular mycorrhzial fungi (AMF) on uptake of P by forage crops such as alfalfa and subterranean clover. In much of Sally's research, there is a clear progression from the description of broad phenomena to the understanding of specific mechanisms that explain those phenomena. For example, Sally and her students quantified with great care the transfer of P from fungus to root (Smith, 1982; Smith & Dickson, 1991) and, subsequently, the anatomical, physiological and genetic mechanisms responsible for those transfers (Gianinazzi-Pearson & Smith, 1991; Smith *et al.*, 1994; Murphy *et al.*, 1997; Ezawa *et al.*, 2001a,b, 2004; Smith & Barker, 2002; Glassop *et al.*, 2007; Rosewarne *et al.*, 2007, Rosewarne *et al.* 1999; Manjarrez *et al.*, 2010).

Sally and her students also described how mycorrhizal fungal colonization is influenced by various aspects of the physical environment, including light (Tester *et al.*, 1986; Son & Smith, 1988), P availability (Smith, 1982), temperature (Baon *et al.*, 1994), fertilizer ions (Chambers *et al.*, 1980), propagule concentration (Walker & Smith, 1984), fallow (Haugen & Smith, 1992) and soil compaction (Nadian *et al.*, 1996). Subsequently, they investigated the genetic, physiological, cellular and anatomical considerations in the establishment of symbiosis (Smith *et al.*, 1992; Bruce *et al.*, 1994; Barker *et al.*, 1998; Rosewarne *et al.*, 2007).

Phosphorus transport would always be of major interest to Sally, but it would always be placed within the context of the entire physiological interdependence between plant and fungus. Indeed, Sally maintained an interest in the carbon economy of the host plant as influenced by the fungus (Silsbury *et al.*, 1983) and in the flow of carbon from host to fungus (Manjarrez *et al.*, 2008).

Although at heart a physiologist, Sally appreciated the ecological context in which all organisms existed. Consequently, she and her students and colleagues studied the significant variation that exists among communities of AMF species in their morphology (Cavagnaro *et al.*, 2001; Dickson *et al.*, 2007), colonization phenotype (Gao *et al.*, 2001), their ability to colonize roots from a distance (Drew *et al.*, 2006), their ability to acquire P from soil (Cavagnaro *et al.*, 2005), their propensity to transfer P to host plants (Smith *et al.*, 2000), and in their capacity to mine soil at a variety of distances from the root (Jansa *et al.*, 2008). They also studied mycorrhizal fungal dispersal mechanisms (Pattinson *et al.*, 1997) and the role played by arbuscular mycorrhizal fungi in soil aggregation (Tisdall *et al.*, 1997), plant competition (Facelli *et al.*, 1999) and plant diversity and community structure (O'Connor *et al.*, 2002; Lambers *et al.*, 2008).

[1]Editor's note: *New Phytologist* Editor Ian Dickie feels fortunate to have been one of these students.

Sally authored or co-authored several choice review articles. My favorite is the review on structural diversity in AM symbiosis (Smith & Smith, 1997). And, of course, the three editions of *Mycorrhizal Symbiosis* (Harley & Smith, 1983; Smith & Read, 1997, 2008) have educated multiple generations of scholars.

Sally's many direct contributions to our field are highly significant. But her greatest impact may be indirect, stemming from the many individuals she influenced for good. Generations of undergraduate and postgraduate students, postdoctoral researchers and local and international colleagues owe much to Sally Smith. *Goodonya*, *Sal*.

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A tribute to Sally Smith, by Iver Jakobsen

With the passing of Sally Smith, the world of science and of mycorrhizal research, in particular, has lost an outstanding and passionate expert, teacher and role model; her impact on our current understanding of mycorrhizal functioning cannot be overstated. This tribute to Sally is based on three decades of research collaboration that developed into a deep friendship.

Back in 1990, I visited Sally in Adelaide together with my family and was struck by Sally's impressive knowledge on mycorrhizas, by her very intense and constructive scientific support and by her great hospitality. Thereby, a foundation was established for several later research collaborations and exchanges of students. Together with her husband and colleague Andrew Smith, Sally came to conduct experimental work in my lab on three occasions to use radioisotopes to enhance our understanding of phosphorus uptake in arbuscular mycorrhizas. The work resulted in the development of a now widely used model system that enables the determination of the fungal contribution to overall plant P uptake. This successful collaboration was largely driven by the enthusiasm and energy that Sally brought to and disseminated in the lab. Everyone, at all levels, enjoyed working with Sally due to her thoughtful and timely approaches. Sally eagerly monitored all possible plant variables during an experiment, and she was likewise the main driving force and active participant during plant harvest as well as data collection and analyses. Her eminent writing skills always ensured that novel findings got published in prominent journals.

Everybody in the lab looked forward to visits by Sally, because she so generously spread her enthusiasm, inspiration and support in a straightforward, yet passionate, empathetic and friendly manner. It was a pleasure to experience her active and constructive contributions at lab meetings and seminars. Furthermore, Sally truly cared about the younger scientists and became an invaluable mentor for students, who were always excited to be invited to visit Sally's lab. In return, we were lucky to also host several of Sally's excellent students on experimental research visits.

In conjunction with her world-recognized contributions to science, Sally had a positive impact on the Danish research environment by her active participation in the evaluation of proposals for a major national granting foundation.

Collaborating with Sally developed into a good friendship. It was always enjoyable and with a lot of cheerful laughter when she and Andrew came to visit. Her sense of humour and lively reports from their daily life and many bird-watching trips contributed to the joy. Sally will be missed in Denmark.

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Sally Smith: more than a mentor – a sponsor and friend

Sally's research output is extraordinary. Here we focus on Sally's work from 2000 and onwards, but it is worth noting that in a comprehensive search for published works we encountered 82 papers pre-2000. The period 2000–2009 was a time when the Smith lab was busy with PhD students, Postdocs and visitors, and the first decade of the 2000s alone saw a further 91 papers co-authored by Sally, many of which saw her as senior author. The quality and impact of Sally's work is highlighted by her repeated inclusion (more than a decade after her official retirement) in *Web of Science*'s Highly Cited Researcher list.

Much of Sally's research focused on understanding how arbuscular mycorrhizal fungi transport phosphorus (P) to the host plant, and on questions of function surrounding this important role. A major influence on this was the ongoing collaboration Sally (and Andrew Smith) had with Prof. Iver Jakobsen's lab (then at the Technical University of Denmark, which is outlined above).

Sally and her collaborators' findings on P uptake spurred further work to discover the underlying cause of 'non-responsive' plants, such as wheat and barley, which included comprehensive studies of fungal biomass, mycorrhizal pathway (MPU) activity and phosphate transporter (PT) gene expression (Li *et al.*, 2008; Grace *et al.*, 2009; Smith *et al.*, 2009). Indeed, Sally's work at the Waite campus of the University of Adelaide (an agricultural research hub) was often geared towards answering fundamental questions, but generally came with a broader agricultural applicability. Her lab's comprehensive work on how crop P-efficiency related to AMF in different varieties of wheat (Zhu *et al.*, 2001a,b,c, 2006; Li *et al.*, 2005, 2006) , rice (Geng *et al.*, 2005; Glassop *et al.*, 2007), buckwheat (Zhu *et al.*, 2002a), and barley (Zhu *et al.*, 2002b, 2003; Li *et al.*, 2003), challenged the tightly held beliefs of many that AMF do not have a role to play in field crops. A key feature of this work is the way in which Sally combined different threads of information (gene expression, whole plant physiology, etc.) to discover underlying processes and mechanisms, and their significance.

Many of Sally's students and Postdocs continued to explore radioisotopes and the MPU, including the use of radioisotopes to discover how AM fungal functional diversity works to explore P patches in soil (Cavagnaro *et al.*, 2005), and to understand how phosphate transporters and their encoding genes interact with the MPU (Glassop *et al.*, 2005). More recently, P radioisotopes have been used in Sally's extended lab group to test the effect of carbon (C) limitation on AMF contribution to plant P (Stonor *et al.*, 2014). This work was undertaken to demonstrate the P contribution to wheat in the field (Smith *et al.*, 2015), and to explore the

interaction between AMF interactions with elevated CO_2 and P availability (Jakobsen *et al.*, 2016).

The identification and characterization of a tomato mutant with a reduced mycorrhizal colonization (*rmc*) phenotype changed how Sally's lab approached questions on the mycorrhizal symbiosis, and how experiments should be conducted. Now, instead of relying on a sterilised growth substrate to act as the 'nonmycorrhizal control' (a sticking point with many reviewers, still), there was scope to grow the mutant and wild-type tomato plants in nonsterile field soil with the indigenous microbial (including AMF) community. Sally's lab rigorously tested the *rmc* mutant, both to ensure its suitability as a nonmycorrhizal control (Gao *et al.*, 2002; Cavagnaro *et al.*, 2004a,b), and to discover the underlying mutation(s) in its genome that caused the defective colonization phenotype. Eventually Sally and collaborators converged on the answer: the CYCLOPS/IPD3 gene, along with four other genes, had been disrupted in the *rmc* genotype (Larkan *et al.*, 2007, 2013) to cause the *rmc* phenotype. The *rmc* genotype also answered questions about whether a colonised 'nurse' plant can facilitate colonization of a nonmycorrhizal plant (Cavagnaro *et al.*, 2004). This continues to be used to this day as a tool to answer diverse questions relating to AMF function (see Watts-Williams & Cavagnaro, 2014, for a recent review).

Another research topic of Sally's group that was aided by the *rmc* tomato mutant was the intricate work of characterizing AM fungal colonization phenotypes (Pen–, Cort– or Myc+) and morphology (i.e. *Arum* vs *Paris*-type colonization). Due to the disruption of the CYCLOPS/IPD3 gene in *rmc*, colonization by different species of AMF was impaired at different steps in the colonization process, from inability to penetrate the epidermal cells in a few species, up to almost 'normal' functional colonization by one species (Gao *et al.*, 2001). Furthermore, it was discovered with *rmc* that colonization of cortical cells was not an absolute requirement for P or C reciprocal transfer between some AMF species and its host plant (Manjarrez *et al.*, 2008, 2010). Sally's group provided detailed insight into the often overlooked *Paris*-type colonization morphology, concluding that AM morphology is not solely under plant control, but also influenced by fungal identity (species) (Cavagnaro *et al.*, 2001), as well as observing how the *Paris*-type colonization develops and provides P to the host plant (Cavagnaro *et al.*, 2003; also van Aarle *et al.*, 2005; Dickson *et al.*, 2007).

Sally produced many papers of the highest possible quality. But more than this, she trained, supported and inspired more people than we can count. For this, we are in her debt.

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