A brief history of *Frankia* and actinorhizal plants meetings

1. Introduction

Meetings of various scopes exist that address various needs of the scientific community. There are meetings of large microbiological societies such as the ASM that occur every year with thousands of participants and several sessions in parallel. These constitute a unique opportunity to get overviews of recent developments in several subfields, in concepts and in technological improvements. At the other end of the spectrum are small meetings such as the '*Frankia* and actinorhizal plants meetings'. These gather people who almost all know each other and have interacted with one another in the past because they work on biological objects with major unusual peculiarities. Such is the case of the '*Frankia* and actinorhizal plants' meetings that have taken place for the last 35 years.

2. Main events

Since the first description of swellings on the roots of alder and Russian olive and the supposed presence of a bacterium (Brunchorst 1886), there have been hundreds of attempts at isolation of the bacterium causing them. If the bacterium causing nodules in Legumes have been described at about the same time as *Frankia*, the fast-growing *Rhizobium* was cultivated much more rapidly (Beijerinck 1888). A very exhaustive review (Baker and Torrey 1979) has been done of published isolation attempts of *Frankia* with the proposed identification of the microbes recovered that highlighted the tremendous variety of microorganisms recovered, ranging from fungi to bacteria, including mycoplasma, proteobacteria and actinobacteria.

Many of these isolates were tested for their ability to fulfill Koch's postulates and for an in vitro morphology comparable to that seen inside the nodules. In retrospect, only the claims made by Pommer (1956, 1959) are valid but the strain was not disseminated and subsequently lost. All other isolates either did not have the expected morphology or else took months to cause nodules on their host plant roots, raising the possibility that contaminations may have occurred. These unfounded claims created a need for standards to decide when to call an isolation a success and an isolate a *Frankia*. When Torrey and his co-workers (Callaham *et al.* 1978) obtained an infective isolate from sweet fern (*Comptonia peregrina*) that had the expected morphological features, they felt the need to interact with their colleagues, convince them of the validity of their claim and create a dynamic cycle of interactions. Another factor was the growing recognition that actinorhizals played an ecological role commensurate with that played by Legumes. That was the backdrop for the organization of the first *Frankia* meeting that took place in Harvard Forest, MA, in April 1978, organized by JG Torrey and JD Tjepkema. The proceedings of the meeting were published as a special issue of the *Botanical Gazette* (Torrey and Tjepkema 1979). This meeting grouped about 35 scientists from the US and Canada. Many papers published in that special issue detailed the course of nodulation (Benson and Eveleigh 1979), the extended host range of the isolate relative to that obtained with crushed nodule (Lalonde 1979), or modifications of the tedious isolation procedure that was thought at the time to be critical (Baker *et al.* 1979), as well as argued the case for commercial or ecological applications of actinorhizal plants in forestry (Gordon and Dawson 1979; Klemmedson 1979).

The second meeting took place the following year in 1979 in Corvallis, OR organized by JC Gordon, CT Wheeler and DA Perry and reflected the need felt to monitor rapid progress done after the first meeting (Gordon *et al.* 1979). It reunited 62 attendees, all from the US except 7 from Canada and 1 from Sweden. The meeting was dedicated to Dr G Bond, FRS (1906–1988, professor of botany, University of Glasgow,

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UK), who had been a pioneer on physiology of actinorhizal plants and who had retired in 1976. Many strains were reported from a variety of hosts, ultrastructure of nodules from several actinorhizal plants was described and a new actinorhizal plant was announced, the herbaceous *Datisca* from California and Pakistan (Winship and Chaudhary 1979). Several papers emphasized applications of actinorhizals such as large scale production of inoculant (Lalonde and Calvert 1979) or industrial uses of red alder (Resch 1980). Published in Nature shortly afterward was the demonstration that contrary to *Rhizobium*, *Frankia* could develop vesicles and fix nitrogen in vitro (Tjepkema *et al.* 1980).

The third meeting took place in Madison, WI in 1982 organized by JG Torrey, JD Tjepkema and their local host J Ensign and the proceedings were published in the *Canadian Journal of Botany* (Torrey and Tjepkema 1983). Sixty scientists exchanged on various subjects such as *Frankia* plasmids with an eye on genetic transformation, ecology of host plants for industrial applications or isolation of DNA for future species delineation and biotechnological work. Host genera from which *Frankia* isolates had been cultured and shown to fulfill Koch's postulates (and form nitrogenase) included *Alnus, Casuarina, Comptonia, Elaeagnus, Hippophae and Myrica* and synthetic medium were compared (Tisa *et al.* 1983). Also a strain from *Casuarina* was shown to be able to infect its original host plant (Diem *et al.* 1983) after the previous mind-boggling isolation of an 'atypical' strain that grew well but was not infective on *Casuarina* (Gauthier *et al.* 1981) but shown to be infective on another host plant, *Hippophae*.

The fourth meeting took place in Wageningen in The Netherlands in 1983 organized by ADL Akkermans, D Baker, K Huss-Danell and JD Tjepkema and the proceedings were published in *Plant & Soil* in 1984 (Akkermans *et al.* 1984). The meeting was dedicated to Dr A Quispel (1960–1983, professor of experimental botany, University of Leiden, The Netherlands) who had been a pioneer on attempts to isolate *Frankia,* on the occasion of his retirement. A large part of the proceedings was devoted to create groups among the increasing number of strains (Lechevalier 1984) with the development of physiology-based tools (Horriere 1984; Lechevalier and Ruan 1984). The diversity of strains was analysed regarding efficiency (Sellstedt and Huss-Danell 1984). Questions on the physiology of the interaction also surfaced with the demonstration of the synthesis of auxin by *Frankia* (Wheeler *et al.* 1984).

The fifth meeting took place in Quebec City in Canada in August 1984, it was organized by M Lalonde, C Camiré and JO Dawson and the proceedings were published in *Plant* & *Soil* in 1985 (Dawson *et al.* 1985). The event reunited 86 participants, including 25 from Canada, 4 from China, 1 from Finland, 8 from France, 1 from the Netherlands and 3 from Spain. Reported work concerned grouping of strains based on DNA (An *et al.* 1985; Simonet *et al.* 1985) and attempts to increase the scale of inoculated seedlings (Périnet *et al.* 1985; Stowers and Smith 1985) with an aim to commercial or large-scale applications.

The sixth meeting took place in Umeå in Sweden in August 1986 organized by K Huss-Danell, A-S Hahlin, A Sellstedt, KR Sundström and P-A Vikman, and the proceedings were published in *Physiologia Plantarum* in 1987 (Huss-Danell and Wheeler 1987). The event reunited 55 participants from 13 countries. Reported work concerned groupings of strains based on various approaches such as host specificity (Baker 1987), or total proteins (Gardes and Lalonde 1987), developments in physiology such as hydrogen production (Sellstedt and Winship 1987) or discussion on sporulation of *Frankia* in vitro and in nodules (Torrey 1987). There was also a very much discussed presentation on protoplast fusion between *Streptomyces* and *Frankia,* that was published elsewhere (Prakash and Cummings 1988), which raised the possibility of genetic work but this result unfortunately could not be reproduced and the putative fusant strains obtained were never transmitted to other laboratories for independant testing.

The seventh meeting took place in Storrs, CT, in August 1988 organized by DR Benson and LJ Winship (Benson and Winship 1989), and the proceedings were published in *Plant* & *Soil* in 1989. The event reunited about 100 participants. Reported work concerned ultrastructure, with among other findings that multiple lipid monolayers served to resist oxygen penetration into the nitrogenase-rich *Frankia* vesicle interior, lipids that were later shown to be hopanoids (Berry *et al.* 1993). Molecular ecology was expanding with the use of synthetic oligonucleotide probes that were developed to identify *Frankia* strains (Hahn *et al.* 1989). There were also applied forestry work such as alder-walnut interplanting assays (Paschke *et al.* 1989) or a study on the influence of mycorhizae on symbiotic performance of alder (Chatarpaul *et al.* 1989).

The eighth meeting took place in Lyon, France in September 1991 organized by P Normand, MP Fernandez, P Simonet and AM Domenach, and the proceedings were published in *Acta Oecologica* in 1992 (Normand *et al.* 1992). The event reunited about 80 participants from 18 countries and was the occasion to honor 4 famous retirees, Yvon Dommergues (ORSTOM, France), Mary P Lechevalier and Hubert P Lechevalier (Waksman Institute, Rutgers University, NJ) and John G Torrey (Harvard University, MA). Reported work concerned the demonstration that *Frankia* could thrive in non-host rhizospheres (Paschke and Dawson 1992), attempts at electroporation (Cournoyer and Normand 1992), and applied work to select salt-tolerant *Casuarina* provenances (Girgis *et al.* 1992).

The ninth meeting took place in Waikato, New Zealand in September 1993 organized by W Silvester and S Harris and the proceedings were published in *Soil Biology and Biochemistry* in 1994 (Silvester and Harris 1994) with a tribute to the recently deceased John G. Torrey (Baker and Berry 1994). The meeting saw various works such as the immunolocalization of nitrogenase and hydrogenase to vesicles (Sellstedt and Mattsson 1994), siderophore synthesis (Aronson and Boyer 1994) or more applied ones such as the use of alder to revegetate polluted mine spoils (Lumini *et al.* 1994).

The tenth meeting took place in Davis, CA in August 1995 organized by AM Berry and DD Myrold and the proceedings were published in *Physiologia Plantarum* in 1997 (Berry and Myrold 1997). The meeting saw various work such as most prominently the characterization of several host plant nodulin genes (Gherbi *et al.* 1997; Guan *et al.* 1997; Pawlowski 1997) after the previous publication of the upregulated *Alnus* protease (Goetting-Minesky and Mullin 1994; Ribeiro *et al.* 1995), the beginning of phylogenetic work on actinorhizal plants (Swensen and Mullin 1997) and on the root hair deforming factor synthesized by *Frankia* (Van Ghelue *et al.* 1997) and compounds synthesized by the plant that modified the physiology of *Frankia* (Benoit and Berry 1997). There was also a rising perception of the similarities between the actinorhizal and the legume symbioses, with an emphasis on the need to use a common language, for instance replacing 'atypical' by Nod$^-$ or 'encapsulation' by infection thread (Akkermans and Hirsch 1997).

The eleventh meeting took place in Urbana, Il in August 1997 organized by JO Dawson and the proceedings were published in the *Canadian Journal of Botany* in 1999 (Dawson 1999). There were 45 attendees from 12 countries. The meeting saw several work on molecular ecology (Clawson *et al.* 1999; Jeong and Myrold 1999; Lumini and Bosco 1999; Ritchie and Myrold 1999), as well as ultrastructural work detailing the *Datisca-Coriaria* nodule type and arguing for the existence of infection threads (Berg 1999a, b; Berg *et al.* 1999) and classical *Frankia* physiology such as a study of the antibiotic resistance pattern of strains (Tisa *et al.* 1999).

The twelfth meeting took place in Carry-le-Rouet, France in June 2001 organized by P Normand, N Alloisio, AM Domenach, I Navarro and MP Fernandez, with the proceedings published in *Plant* & *Soil* in 2003 with JO Dawson and K Pawlowski as co-editors (Normand 2003). There were 80 attendees from 14 countries. The meeting saw work on a new antibiotic from *Frankia*, frankiamide (Haansuu *et al.* 2001), synthesis *in vitro* of the auxin PAA by *Frankia* (Hammad *et al.* 2003), germination of *Frankia* spores (Krumholz *et al.* 2003) as well as the use of ∂^{15}N to monitor nitrogen fluxes in Glacier Bay (Kohls *et al.* 1994) and evolutionary significance of host and *Frankia* DNA sequences (Varghese et al 2003).

The thirteenth meeting took place in Durham, NH, in June 2005 organized by LS Tisa, with the proceedings published in the *Symbiosis* journal in 2005 (Tisa 2005). The meeting saw the first presentation of the genomes that had been initiated at the Genoscope and at the JGI the year before and would only be published two years later (Normand *et al.* 2007). There was also a presentation of work on the physiology and genes coding hemoglobins of *Frankia* (Niemann *et al.* 2005; Schwintzer and Tjepkema 2005).

The fourteenth meeting took place in Umeå, Sweden, in July 2006 organized by A Sellstedt, which proceedings were published in *Physiologia Plantarum* in 2007 with P Normand and JO Dawson as co-editors (Sellstedt *et al.* 2007). Among the works reported, there was a demonstration that a defense-related chitinase-encoding gene (cgchi3) was specifically activated in nodules as compared with uninoculated control roots (Fortunato *et al.* 2007), that coping with reactive oxygen species was critical (Tavares *et al.* 2007) and a first proteomic approach on *Frankia* (Alloisio *et al.* 2007). There was a workshop organized to get to work on the web site housing the three *Frankia* genomes (*https://www.genoscope.cns.fr/agc/microscope/home/index.php*) available at the time, which would eventually result in many in the field exploiting the genomes data in various ways.

The fifteenth meeting took place in Bariloche, Argentina in October 2008 organized by LG Wall, L Gabbarini, L Imanishi, E Chaia, M Solans and G Vobis, which proceedings were published in *Symbiosis* in 2010 with LG Wall, E Chaia and JO Dawson as co-editors (Wall *et al.* 2010). There were 34 attendees from 9 countries. The special *Symbiosis* issue was dedicated to the memory of YR Dommergues, from the overseas French Research Institute (ORSTOM, then IRD) who had been a major contributor to actinorhizal biology, and in particular an indefatigable promoter of *Casuarina* fundamental research and applied uses such as a 500km × 500m filao plantation in Sénégal to supply firewood and stabilize the seafront sand dune. Among the works reported, there was a functional proteomics of *Frankia* from field nodules (Mastronunzio and Benson 2010), the exploration of diversity of *Frankia* and non-*Frankia* actinobacteria in nodules (Ghodhbane-Gtari *et al.* 2010), work on genetic transformation of host plants (Svistoonoff *et al.* 2010) that permitted to show the presence of a Sym kinase governing symbiosis establishment in a manner similar to what happens in Legumes (Gherbi *et al.* 2008), and an evaluation of the contribution of actinorhizal plants to increased soil N fertility (Chaia and Myrold 2010).

The sixteenth meeting took place in Porto, Portugal, in September 2010, organized by A Ribeiro, C Santos, F Tavares and P Santos. The proceedings were published in two separate journals, *Archives of Microbiology* for the microbial papers (Santos and Tavares 2012) and in *Functional Plant Biology* for the plant papers (Ribeiro *et al.* 2011). There were 30 attendees from 9 countries. Among the reported works were transcriptomics EST studies that yielded a global view of host plants response to *Frankia* (Berry *et al.* 2011; Hocher *et al.* 2011), exploration of actinorhizal fruits for their medicinal properties (Goyal *et al.* 2011), taxonomic resolution of *Myrica* sp. (Yanthan *et al.* 2011) and an exploration of the reaction of actinorhizal plants to global change (Tobita *et al.* 2011). On the bacterial side, there was a discussion of the controversial presence of nitrogenase in other actinobacteria (Gtari *et al.* 2012), or the development of a high-throughput system to study the physiology of *Frankia* (Furnholm *et al.* 2012).

The seventeenth meeting, initially due to take place in Tunisia had to be relocated due to the turbulences this country and its neighbors undergo in the wake of the 'Arab Spring'. Dr Arvind K Misra was kind enough to substitute and set up the meeting in April 2013 in Shillong, India, for which his colleagues are all grateful.

3. Conclusion

The visibility of research on *Frankia* and actinorhizal plants, and hence the funding we get depends on several factors, prominent among which are these meetings and publications in high profile journals. A Web of Science search retrieved with keyword 'Frankia' 1 paper in Nature,1 paper in Science and 5 in PNAS-USA, while keyword 'Rhizobium' retrieved 91 papers in Nature, 35 in Science, and 234 in PNAS-USA. This difference is in large part due to the absence of a genetic system in *Frankia*, to the fact so many of our strains have not been given a species name but not only. As a community, we must try again and again, using the new '–omics' approaches but also more classic approaches such as highly resolutive spectrometry and of course the actinorhizal host plants transformation methodology that has been so fruitful so far. And most importantly, we must keep interacting together using one of the tools at our disposal, the *Frankia* and actinorhizal plants meetings.

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