

Actinorhizal plants

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Abstract. Actinorhizal plants are a group of taxonomically diverse angiosperms with remarkable economic and ecological significance. Most actinorhizal plants are able to thrive under extreme adverse environmental conditions as well as to fix atmospheric nitrogen due to their capacity to establish root nodule symbioses with *Frankia* bacteria. This special issue of *Functional Plant Biology* is dedicated to actinorhizal plant research, covering part of the work presented at the 16th International Meeting on *Frankia* and Actinorhizal Plants, held on 5–8 September 2010, in Oporto, Portugal. The papers (4 reviews and 10 original articles) give an overall picture of the status of actinorhizal plant research and the imposed challenges, covering several aspects of the symbiosis, ecology and molecular tools.

Additional keywords: actinorhizal plants, *Frankia*, nodulation, root nodule symbioses.

The importance of actinorhizal plants

Actinorhizal plants are a group of taxonomically diverse angiosperms distributed over 8 plant families and 25 genera, mostly woody shrubs or trees (Table 1). Most actinorhizal plants are capable of high rates of biological nitrogen (N₂) fixation due their capacity to establish root nodule symbioses with N₂-fixing actinomycetes of the genus *Frankia* (Sprent and Parsons 2000). Besides that, the formation of tripartite symbiotic relationships (i.e. root nodules and endo- and ectomycorrhizal fungi) has implications for ecosystem nutrient cycling as well as plant nutrition. As pioneer species in many environments, actinorhizal plants have demonstrated an impressive capacity to tolerate extreme environmental conditions, such as salinity, drought or heavy metals. Hence, several actinorhizal species are of remarkable economic and ecological significance (Schwencke and Carú 2001). Notably, trees in the Casuarinaceae family have a wide range of applications in agroforestry and land reclamation, including the production of biomass, fuel and timber; interplanting with crop trees; as shelter belts in crop fields; prevention of desertification; coastal dunes stabilisation; and restoration of degraded soils (Diem and Dommergues 1990). Another promising actinorhizal species is *Hippophae rhamnoides*, which is now being domesticated because its fruits are very nutritious (rich in vitamin C) and their seed oil is highly unsaturated making it suitable for cosmetics and phytopharmaceuticals (Beveridge *et al.* 1999; Li *et al.* 2007).

The 16th International Meeting on *Frankia* and Actinorhizal Plants

For decades, several groups have been working to evaluate the genetic and ecological potential of actinorhizal plants as well as to understand the mechanisms underlying their capacity to establish N₂-fixing root nodule symbiosis with *Frankia*. Due to the woody nature of actinorhizal plants, which interferes with the isolation of proteins and nucleic acids, and their long generation time, which prevents experimentally feasible genetic analysis, as well as the fact that *Frankia* is slow growing and non-transformable, research on the topic has been hampered for many years and therefore the information available is still limited. Nevertheless, with the availability of new research technologies, considerable advances have been achieved over the last few years.

This special issue of *Functional Plant Biology* is dedicated to actinorhizal plant research, covering part of the work presented at the 16th International Meeting on *Frankia* and Actinorhizal Plants, held on 5–8 September 2010, in Oporto, Portugal (Fig. 1). Such meetings have a biennial periodicity and constitute a unique opportunity for the small actinorhizal research community to meet and discuss the major advances, perspectives and constraints and to strengthen and build up new partnerships. Three main topics were addressed: (i) Systems Biology ('omics'); (ii) Ecology and Biodiversity; and (iii) Physiology and Biochemistry. A total of 35 communications (20 oral presentations and 15 posters)

Table 1. Families and genera of actinorhizal plants

Family	Nodulating genera
Betulaceae	<i>Alnus</i>
Casuarinaceae	<i>Allocasuarina</i> , <i>Casuarina</i> , <i>Ceuthostoma</i> , <i>Gymnostoma</i>
Coriariaceae	<i>Coriaria</i>
Datisceae	<i>Datisca</i>
Elaeagnaceae	<i>Elaeagnus</i> , <i>Hippophaë</i> , <i>Shepherdia</i>
Myricaceae	<i>Comptonia</i> , <i>Myrica</i>
Rhamnaceae	<i>Adolphia</i> , <i>Ceanothus</i> , <i>Colletia</i> , <i>Discaria</i> , <i>Kentrothamnus</i> , <i>Retanilla</i> , <i>Talguenea</i> , <i>Trevoa</i>
Rosaceae	<i>Cercocarpus</i> , <i>Chamaebatia</i> , <i>Cowania</i> , <i>Dryas</i> , <i>Purshia</i>

covering different aspects of actinorhizal research were presented. From the plant side, the following issues were highlighted: (i) major advances in functional genomics of *Alnus glutinosa*, *Casuarina glauca* and *Datisca glomerata* root nodule symbioses; (ii) hairy-root genetic transformation of *Coriaria trinervis* and *Datisca glomerata*; (iii) comparative studies through the heterologous expression of nodulin gene (i.e. genes up-regulated in nodules versus roots) promoters; (iv) ecological potentialities and the main effects of *Alnus*, *Casuarina*, *Ceanothus* and *Coriaria* in natural and limiting environments; (v) biogeography studies in Africa; (vi) nodulation signalling and nodule nitrogen metabolism; and (vii) photosynthetic and antioxidant abilities. Regarding *Frankia*, major breakthroughs in genomics, nodulation factors, transformation tools, phylogeny and metabolism, were discussed. The papers focusing on *Frankia* research are being published in parallel, in a special issue of *Archives of Microbiology*.

In this issue, 14 articles (4 reviews and 10 original papers) are presented. In the first review, Pawlowski *et al.* (2011) give a general overview of actinorhizal plant research, focusing on Nod factor signal transduction, phytohormones and nodule formation, symbiosis versus pathogenesis and general stress, nitrogen assimilation and transcriptome profiling. The induction of host stress-related genes and their putative function during symbiosis is further detailed in the review of Ribeiro *et al.* (2011). Berry *et al.* (2011) summarises the recent advances in actinorhizal nodule nitrogen assimilation with emphasis on *D. glomerata*. The last review (Gtari and Dawson 2011) is quite pioneering as it presents the first comprehensive report on species distribution and current uses in Africa.

The first group of original papers focuses on the initial steps of actinorhizal symbiosis. Gabbarini and Wall (2011a, 2011b) present two papers in which the modulation of diffusible *Frankia* factors by *A. acuminata* and *Discaria trinervis* is exploited. Popovici *et al.* (2011) focus on the adaptation of the secondary metabolism of plants from the *Myricaceae* family according to the compatibility status of *Frankia* strains. Auguy *et al.* (2011) provide the first (though preliminary) insights on the involvement of isoflavonoids as signal molecules during *C. glauca* nodulation. Regarding nodule functioning, Goyal *et al.* (2011) discusses the antioxidant profiling of *Hippophae salicifolia* from the sacred forests of Sikkim, India. A detailed evaluation of the effects of elevated atmospheric CO₂ concentration, soil nutrients and water conditions on photosynthetic and growth responses of *Alnus hirsuta* is provided by Tobita *et al.* (2011). From a more ecological perspective, Taft and Dawson (2011) discuss the influence of *Ceanothus americanus* on the species composition and diversity in tallgrass prairie. Additionally, Reyes *et al.* (2011) presented the results of reproductive ecology studies in *Ochetophila trinervis* from north-west Patagonia in view of



Fig. 1. After the final banquet of the 16th International Meeting on *Frankia* and Actinorhizal Plants, 5–8 September 2010, Oporto, Portugal. Back row (left to right): Katharina Pawlowski, Valérie Hoher, Louis Tisa, Linda Stoxen, Arnab Sen, Mike Anderson, Arvind Misra, Sergio Svistoonoff, Teal Furnholm, Hiroyuki Tobita, Faiza Benabdoun, Roger Ruess, Aude Herrera-Belaroussi, Alison Berry, Philippe Normand and Masatoshi Yamaura; Sitting: Ana Ribeiro, Nicholas Beauchemin, Luis Wall, Michaela Swanson, Ken-ichi Kucho, Didier Bogusz, Jeffrey Dawson and Kentaro Kakoi; Front row: Catarina Santos, Fernando Tavares and Perpétua Tavares.

reclamation of disturbed lands. Finally, the last group of papers (Rashidi *et al.* 2011; Yanthan *et al.* 2011) discuss the suitability of some molecular tools for different purposes. Rashidi *et al.* (2011) present the main constraints of using the *C. glauca metallothionein I* promoter as a tool for the expression of transgenes in hairy roots. Yanthan *et al.* (2011) provide molecular taxonomic tools to discriminate *Myrica* species.

Altogether, as molecular genetic and global analytical tools continue to evolve, and as additional *Frankia* genomes as well as root nodule EST sequences are becoming available, such new options will continue to expand our horizons for the study of actinorhizal symbioses.

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