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Current Opinion in
Plant Biology

Tracing the evolutionary path to nitrogen-fixing crops☆

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Nitrogen-fixing symbioses between plants and bacteria are restricted to a few plant lineages. The plant partner benefits from these associations by gaining access to the pool of atmospheric nitrogen. By contrast, other plant species, including all cereals, rely only on the scarce nitrogen present in the soil and what they can glean from associative bacteria. Global cereal yields from conventional agriculture are dependent on the application of massive levels of chemical fertilisers. Engineering nitrogen-fixing symbioses into cereal crops could in part mitigate the economic and ecological impacts caused by the overuse of fertilisers and provide better global parity in crop yields. Comparative phylogenetics and phylogenomics are powerful tools to identify genetic and genomic innovations behind key plant traits. In this review we highlight recent discoveries made using such approaches and we discuss how these approaches could be used to help direct the engineering of nitrogen-fixing symbioses into cereals.

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Current Opinion in Plant Biology 2015, **26**:95–99

This review comes from a themed issue on **Biotic interactions**

Edited by **Uta Paszkowski** and **D Barry Scott**

http://dx.doi.org/10.1016/j.pbi.2015.06.003

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Introduction

Nitrogen is a key element for plants and is a limiting nutrient for plant growth. Although nitrogen is the commonest element in the atmosphere, few plants can access this unreactive pool. Thus, current agricultural practices rely on the application of large quantities of chemical fertilisers that represent reactive forms of nitrogen capable of boosting crop productivity [1]. Legumes, such as soybean and alfalfa, are among a limited number of plants with the capability to utilise atmospheric nitrogen through an association with beneficial nitrogen-fixing bacteria, which are housed within root nodules. One strategy to overcome the use of chemical fertilisers in agriculture would be to engineer such nitrogen-fixing symbioses into non-legume crops [2,3].

Engineering relies on the interconnection between three main processes: discovery of candidate genes and pathways, building constructs and finally testing these constructs for their effects on the desired phenotype. Recent advances in the field of DNA synthesis and the development of high-throughput modular cloning strategies have significantly reduced the economic and time constraints of building large multi-gene constructs [4]. These assembly strategies, reviewed by [4], can be categorised into ligation-dependent methods such as the type IIS restriction endonuclease-based GoldenGate cloning or overlap-dependent methods such as Gibson Assembly [4]. With the costs associated with synthesis predicted to go even lower, it is now possible to envision introducing entire genetic pathways into plants in order to obtain a desired phenotype. In addition, next-generation sequencing methods have facilitated the rapid monitoring of gene-expression changes that might be central to the engineering efforts. As a result of the development of these resources, the main challenges associated with engineering traits into plants have now become the transformation of constructs into these plants and a comprehensive knowledge of the exact traits and pathways to engineer.

Quantitative and comparative phylogenetic and phylogenomic approaches have demonstrated the potential for discovery in analyses focused on the evolution of traits and associated genomic innovations [5••,6••,7]. Previous reviews have highlighted how current knowledge of nitrogen fixation can be utilised to initiate the engineering of nitrogen-fixing crops [2,3] and here we explore how complementary approaches focusing on the evolution of nitrogen fixation may further facilitate this process.

The multiple paths in the evolution of nitrogen fixing symbioses

Nitrogen-fixing symbioses between plants and bacteria evolved at least ten times in land plants (Figure 1). These symbioses can be divided into two main classes: root nodule symbioses (RNS) and plant–cyanobacteria symbioses. While plant–cyanobacteria associations are widely distributed across land plants [8] the root nodule symbiosis is much more restricted, occurring in several, but not all, species belonging to four related orders of flowering

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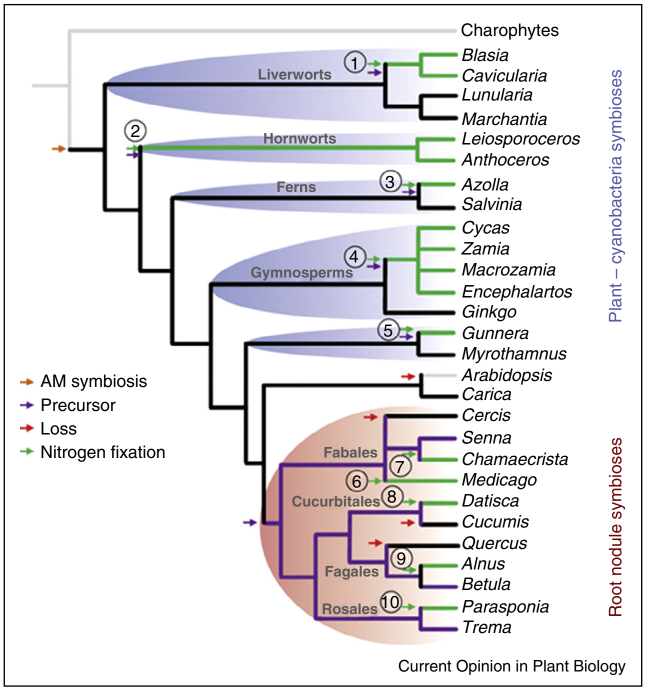
☆ This paper is part of a Virtual Special Issue based on the Current Opinion Conference ‘Agriculture and Climate Change — adapting crops to increased uncertainty’, chaired by David Edwards and Giles Oldroyd in 2015.

Figure 1



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Evolution of nitrogen-fixing symbioses in plants. Nitrogen-fixing symbioses evolved several times in land plants. Proposed origins of nitrogen-fixing symbioses are indicated with green arrows. Green branches indicate nitrogen-fixing clades. Purple branches indicate predisposed clades. Black branches indicate species able to form arbuscular mycorrhizal (AM) symbiosis and grey branches indicate species clades that did not evolve or have lost this association. Red arrows indicate loss of the predisposition to evolve nodulation or to form AM symbiosis (*Arabidopsis*).

plants: the Fabales, Fagales, Cucurbitales and Rosales. This restricted distribution of RNS [9], led to the suggestion of a predisposition event, a prerequisite for evolving nodulation, occurring before the divergence of this large group of plants [9,10].

Both classes of nitrogen-fixing symbioses involved the emergence of innovations in the plant partner from macroscopic traits to biochemical modifications. These innovations appeared independently in the various nitrogen-fixing lineages but a consensus seems to emerge: the host plant consistently releases signals to attract the symbionts, encloses it in a newly developed structure, and provides it with carbon and a proper environment to fix nitrogen (Table 1). Evolution of such complex plant traits has been shown to start with preliminary modifications and progresses through various intermediary stages [11] and an understanding of the modifications and intermediate stages during the evolution of nitrogen-fixing symbioses could facilitate the engineering of nitrogen-fixing crops.

Quantitative and comparative phylogenetic approaches reveal the path of evolution

Recently, several studies have used comparative phylogenetic analyses to determine the evolutionary trajectories to the emergence of complex traits. Ogburn *et al.* used such an approach to find a surprising correlation between the evolution of succulence in plants and the architecture of the leaf venation system and thus proposed that evolution of three-dimensional venation is a predisposition allowing for the ability to reach maximum succulence in leaves [7]. Using a similar approach, Christin *et al.* identified the succession of anatomical modifications required to evolve C4 photosynthesis from a C3 ancestor in grasses [12]. These approaches used available pheno-

Table 1

Independent evolution of nitrogen-fixing symbioses recruited different mechanisms

Event	Partners		Innovations	
	Plants	Symbionts	Attractant	Accommodation
1	*Blasia*	Cyanobacteria	Sugars	Mucilage-filled auricles
2	*Anthoceros*	Cyanobacteria	Sugars	Slime cavities
3	*Azolla*	Cyanobacteria	Sugars	Mucilage-filled leaf cavities
4	*Cycas*	Cyanobacteria	Sugars	Coralloid roots
5	*Gunnera*	Cyanobacteria	Sugars	Shoot glands Intracellular
6	*Medicago/Lotus*	Rhizobia	Flavonoids	Nodules — peripheral vasculature Intracellular
7	*Chamaecrista*	Rhizobia	Flavonoids	Nodules — peripheral vasculature Intracellular
8	*Datisca*	Frankia	Flavonoids	Nodules — central vasculature Intracellular
9	*Alnus*	Frankia	?	Nodules — central vasculature Intracellular
10	*Parasponia*	Rhizobia	?	Nodules — central vasculature Intracellular

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