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From North to South: A latitudinal look at legume nodulation processes☆

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ABSTRACT

Legumes and some nodulation processes evolved about 55–60 Ma. Since then they have radiated from their origin at either side of the Tethys seaway, to high latitudes in both the northern and southern hemispheres. In many cases this has involved different tribes and genera, and different nodule processes, but with the common feature that almost all legumes in the higher latitudes are potentially nodulated and, with the exception of some herbaceous species of *Chamaecrista*, nodulated caesalpinioid legumes are rare. This is not true of tropical regions where all three sub-families are found, with many of their species lacking the ability to nodulate. Whether or not this is related to the availability of combined nitrogen is a matter of current discussion. This review will consider the range of nodulation phenotypes (infection, morphology, structure) and show how many of these are confined to one or other hemisphere. How this might relate to the different genera and species of endophytic (nitrogen fixing) rhizobia in relation to soil conditions will also be discussed. Better knowledge of the wide variation in nodulation parameters is important for understanding the ecology of different regions and for management purposes. Nodule characters are of great potential use in defining taxonomic groupings in legumes.

1. Introduction

One of the best known features of the Leguminosae is the ability of many of them to associate with soil bacteria, collectively known as rhizobia, which invade and colonise roots (rarely stems), forming specialised organs known as nodules. Within the nodule, the bacteria reduce ("fix") nitrogen to ammonia that is passed over to the host plant for assimilation into organic compounds such as amino acids and nucleotides. Recent intensive studies on the so-called "model" legumes, *Medicago truncatula* Gaertn. and *Lotus japonicus* (Regel) K. Larsen have led to major advances in our understanding of how rhizobia interact with their hosts and induce the formation of nodules (Oldroyd et al., 2011). An unforeseen consequence of this excellent work is that it is often assumed that all legumes are infected via root hairs and form nodules of one of two types, having determinate (*Lotus*) or indeterminate (*Medicago*) growth. A further assumption that has been made is that any swelling on the root of a legume that looks like a nodule, is a nodule. The literature contains numerous false reports of nodulation of this type, mainly on caesalpinioid legumes such as *Eperua* Aubl. and *Mora* Schomb.ex Benth.(Sprent, 2001) but also papilionoids such as *Pickeringia* Nutt. ex Torr. & A. Gray. The latter was reported to nodulate in the major work of Allen and Allen (1981) and because of its tribal placement (Thermopsideae) at the time, the report was not queried. However, when the genus was moved into the *Cladrastris* clade (Cordoso et al., 2012, the other members of which do not nodulate) we checked fresh material and found that the bumps on roots did not contain bacteria and had none of the structures that are associated with root nodules. So what are these features and how do they vary? The following sections give a brief summary – more details can be found in Sprent (2009) and over the next year or two will be entered on the new interactive database ILDON (Interactive Legume Database Of Nodulation: www.ildon.org.)

1.1. Morphological features of nodules

Corby (1988) gave detailed descriptions of the then known morphological types of nodule and grouped them according to legume taxonomy as it was understood at the time. His work is still a major source of information and his observations foreshadowed some later taxonomic changes, for example he noted that *Lotononis* (DC.) Eckl.& Zeyh. section *Listia* had nodules that circled their subtending root (as do *Lupinus* L. nodules), whereas nodules from other species in the genus were indeterminate. Using completely different criteria, *Listia* (E. Mey.) B.-E. Van Wyk. has now been reinstated as a separate genus (Boatwright et al., 2011). There are now no known exceptions to nodule morphology being consistent at the generic level. Fig. 1.1 illustrates the currently recognised range of nodule morphology.

☆ Dedicated to Dr HDL (Tom) Corby, a pioneer of the study of legume nodule morphology in a taxonomic context, who died on the first day of the Johannesburg conference, a few weeks short of his 100th birthday.

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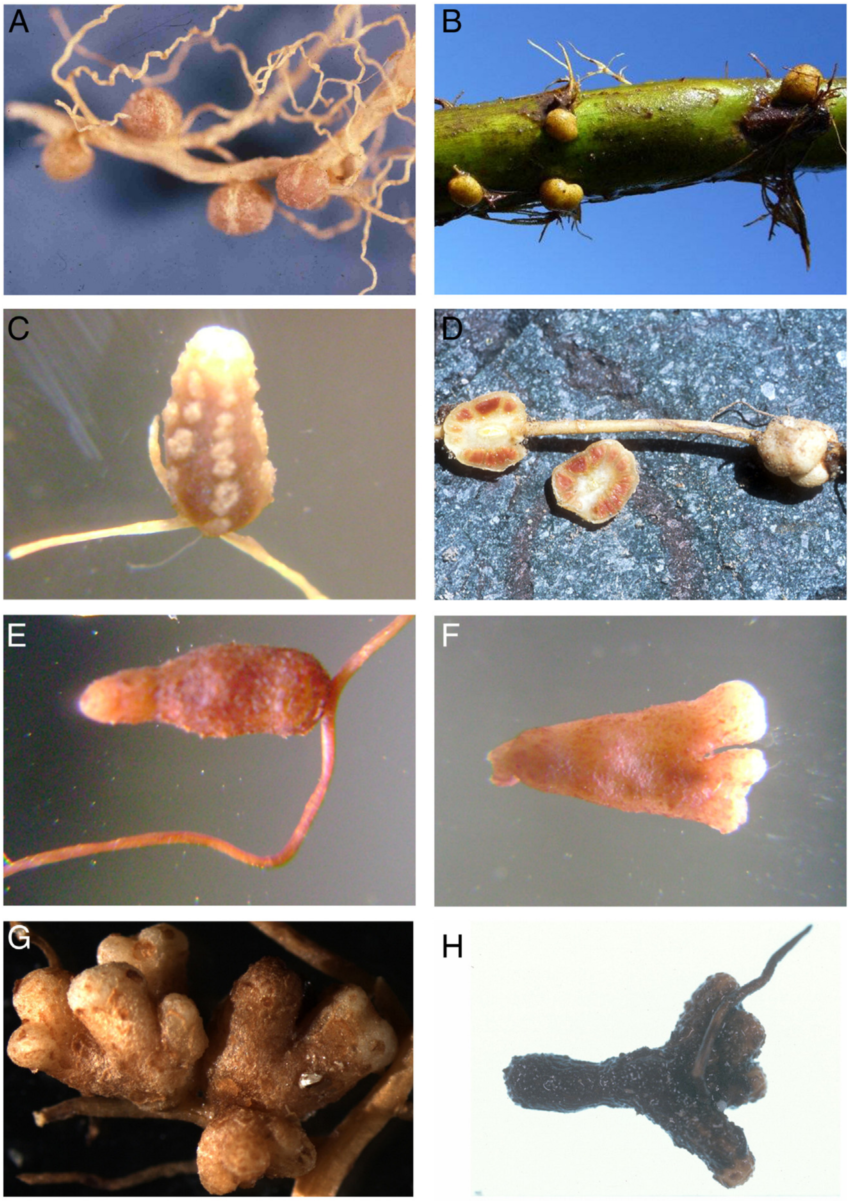

Fig. 1.1. Legume nodule morphology: A, determinate, desmodioid. These nodules are more-or-less spherical and have lenticels, usually as stripes, but occasionally as stars (see C); B, determinate, aeschynomenoid. These nodules are always associated with lateral or adventitious roots and do not have lenticels; C, Indigoferoid, rather like an indeterminate desmodioid nodule, its detailed structure has not yet been examined and has only so far been reported from Indigofereae; D, lupinoid; E, indeterminate unbranched nodules. Common in mimosoids and other groups; F, indeterminate with one or few branches, common in many papilionoids; G, indeterminate with many branches, found in all sub-families and (in some genera such as *Ormosia* and *Crotalaria* branching may be more than shown here. Note that many nodules of types F and G are unbranched when young; H, woody, most nodules that have fixation threads (see 1.3.D), both caesalpinioid and papilionoid, have a woody scleroid outer layer when mature. Reproduced from ILDON, with permission.

1.2. Modes of bacterial infection

There are basically three ways in which rhizobia gain entry into their hosts. The most common and best understood is root hair infection, where bacteria gain entry into (usually) curled root hairs and host cell wall material grows around the developing infection, forming what is known as an infection thread. This grows through the cortex of the root, branching repeatedly. At the same time cell divisions occur in the root cortex and some of the resulting daughter cells become invaded by branches of the infection thread. Bacteria are released from the tips of these infection threads, into host-membrane-bound units called symbiosomes. Within the symbiosomes, the bacteria differentiate into their N_2-fixing form, in which they synthesise the nitrogenase enzyme, and are then known as bacteroids. There are a number of variants on this pattern, leading to the formation of either determinate or indeterminate nodules. Within the former (which have evolved on two separate occasions, see Doyle, 2011) the products exported from N_2 fixation may be either ureides (phaseoloid legumes) or amides (many Loteae), see Sprent (2001).

The second mode of bacterial infection is found in dalbergioid legumes. A defining feature of this clade of legumes (Lavin et al., 2001) is the aeschynomenoid nodule, first described by Corby (1988). However, although Corby carefully drew these nodules with their associated lateral (occasionally adventitious) roots, he did not comment on this. Structural studies on the formation of aeschynomenoid nodules show that infection occurs at the sites of lateral root emergence, rather than by root hair curling, and infection threads are very rarely seen and then not in the infected region (e.g. James et al., 2001). The internal structure of the nodules, although they are determinate, is quite different from those formed following hair

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