16 Nitrogen fixation in arid environments

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Introduction: the pathways of nitrogen fixation

Plants have two main natural sources of combined nitrogen, nitrate and ammonium ions. In addition, many have access to urea, from either animals or fertilizer. Although it can be absorbed and metabolised by plants, in many soils urea is hydrolysed by the enzyme urease to ammonia and carbon dioxide. Urease is one of a number of enzymes found in a more or less free state in soil, following secretion by, or death of the organisms which produced them (Nannipieri *et al.* 1982, Nor 1982). Nitrate, ammonium and urea form essential parts of the familiar nitrogen cycle, as does the reduction of nitrogen gas (N_2, now often called dinitrogen) to ammonia. This latter process is carried out by an enzyme complex called nitrogenase which occurs only in certain prokaryotic organisms ('primitive' organisms lacking many of the components of cells of more advanced organisms (eukaryotes), i.e. plants, animals and fungi). Many of these nitrogen fixing prokaryotes associate more or less closely with eukaryotic organisms. The biology of the various systems has been described in recent books by Sprent (1979) and Postgate (1982). We shall be considering some examples of significance to arid zones in the next section.

The main stages from the reduction of nitrogen gas to the incorporation of reduced nitrogen into protein are summarised in Fig. 16.1, p. 216 (note that in cells, ammonia is protonated to ammonium which is the form which predominates in cell physiological reactions). For comparison, nitrate reduction and urea hydrolysis are also included. Ammonium assimilation can be seen to offer the simplest route. Additional comparisons amongst these sources of nitrogen will be made in later sections. Further details may be obtained from Postgate (1982) and Sprent (1984a).

CONDITIONS UNDER WHICH NITROGEN FIXATION MAY LIMIT PLANT GROWTH

The nitrogenase reaction is generally considered to be more costly in terms of photosynthate used than the assimilation of ammonium or nitrate (see Sprent *et al.* 1983). When internal physiological considerations, such as pH regulation, are taken

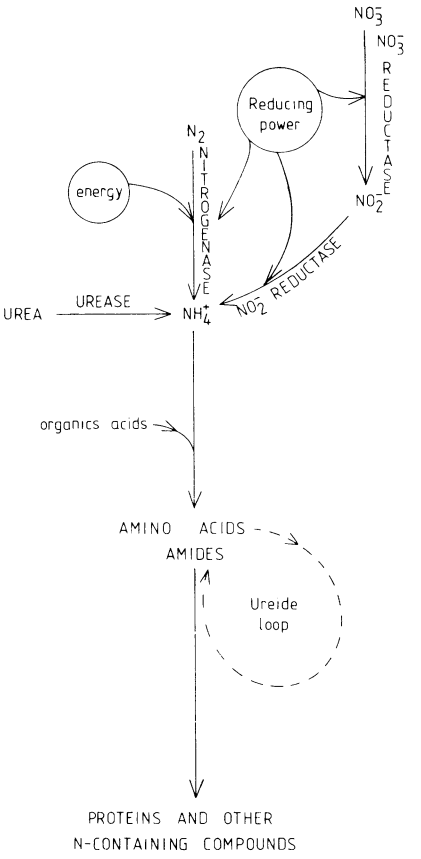

Figure 16.1 Outline of the processes whereby various nitrogen sources are incorporated into plant cells. Those from ammonium to protein are the same for all N sources, apart from the ureide loop which is largely confined to certain tropical legumes and then only when they are fixing nitrogen.

into account the differences may not be very great (Raven 1984). However, the nitrogen fixing reaction is much slower than the alternative processes and more expensive in terms of iron and molybdenum, which may be limiting in some soils (see Table in Sprent & Raven 1985). Thus in evolutionary terms it has been argued that selection pressures only favoured nitrogen fixation when supply of combined nitrogen was the major limiting factor (Sprent & Raven 1985). The same arguments can be applied to arid environments. Here water deficit is the major factor limiting plant growth. The supply of nutrients in the soil may or may not be adequate to