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## STRUCTURE AND FUNCTIONING OF CLUSTER ROOTS AND PLANT RESPONSES TO PHOSPHATE DEFICIENCY

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### Introduction

Phosphate readily binds to cations and particles in the soil forming sparingly soluble precipitates and making P the least accessible macronutrient for plants. Its availability frequently limits plant growth in both natural and agricultural systems. Fertiliser P is acquired from non-renewable resources, and it is anticipated that readily available sources of P sediments will be depleted by the end of this century. This will cause P-fertiliser prices to rise, increasing the incentive to develop new crops that are better able to access P in soil. This is particularly relevant in large parts of the world where the major part of applied fertiliser is extensively immobilised, and, therefore, unavailable to most traditional crops, e.g., wheat.

Plant roots are now viewed as active "miners" rather than simply passive accumulators of soil minerals. This 'mining' activity is realised through symbiotic associations with mycorrhizal fungi (Fransson et al., 2003; Solaiman and Abbott, 2003), root-hair formation (Bates and Lynch, 1996) and other morphological responses (De Groot et al., 2003; He et al., 2003); and chemical and physical modification of the substrate (Jones et al., 2003). There is also evidence that crops that are very good at accessing sparingly available P can have a favourable effect on plants with which they are intercropped (Horst and Waschkiel, 1987; Li et al., 2003) and on the following crop (Kamh et al., 1999). The mechanisms that are responsible for these effects (Zhang and Li, 2003) remain to be further

explored (2003). Although all plant roots are, to some extent, capable of chemical and physical 'mining' of the soil, the highly branched and specialised roots of certain plant species, known as 'proteoid' or 'cluster' roots, are extremely effective in mobilising sparingly soluble minerals (Wan and Evans, 2003). It has been proposed that the present-day soil characteristics of some regions are, in fact, the result of millennia of cluster-root 'mining' activity (Pate et al., 2001; Verboom and Pate, 2003).

Although the morphology of cluster roots has been known since Engler described them at the end of the 19th century for Proteaceae growing in the Leipzig Botanic Gardens (cited in Skene, 1998), there has recently been renewed interest in cluster-rooted plant species. This renewed interest has, to some extent, been driven by the recognition of the role of cluster roots in P acquisition in some crop plants (e.g., *Lupinus albus*) (Gardner et al., 1982). The importance of cluster roots to the survival of P-limited native flora, especially the Proteaceae growing on highly leached soils (e.g., regions of Australia and Southern Africa), has also been increasingly recognised (Lamont, 2003). Proteaceae occur at their highest frequency in the southwest of Western Australia and South Africa (Pate et al., 2001). Almost all Proteaceae have 'proteoid' or 'cluster' roots. The enormous diversity of plant species in the flora of the southwest of Western Australia and South Africa (Myers et al., 2000) occurs on the most nutrient-impovertised soils in the world (Pate and Dell, 1984; Specht and Specht, 1999), suggesting

**Cover Photo:** Cluster roots of *Hakea prostrata* R.Br., grown in nutrient solution with 1  $\mu$ M phosphate. Cluster roots occur in most species of the Proteaceae and in a range of other species. They release inorganic anions, such as citrate and malate, into the rhizosphere and mobilise and absorb sparingly available phosphate. Cluster roots allow plants to grow in nutrient-impovertised or phosphate-fixing soils. Photograph by Michael W. Shane.