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3.1??Root system architecture

3.1.1??Introduction

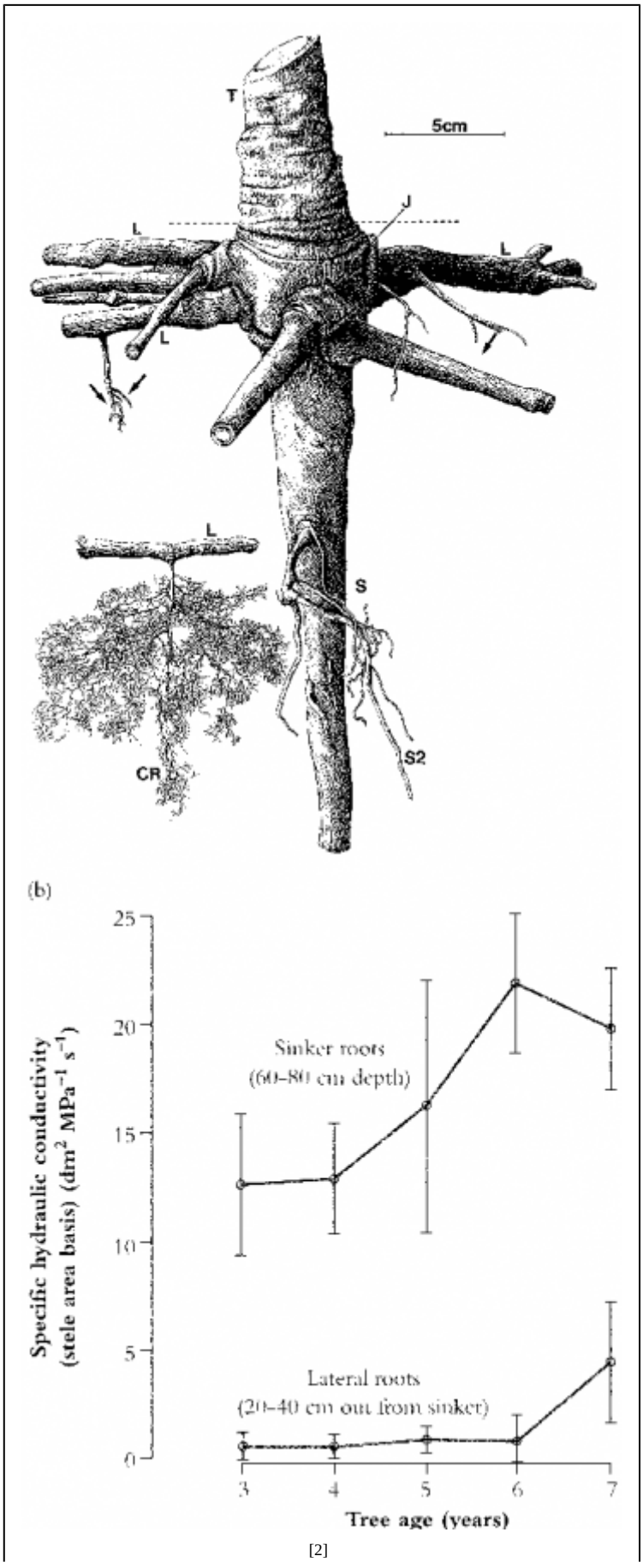


[1]

Figure 3.1 Root systems of young (a) wheat and (b) lupin plants. Wheat, a monocotyledon, has a dual root system. Seminal roots emerge from the seed and nodal roots (thicker roots on the outside of the picture) emerge from the crown, a group of closely packed nodes from which tillers emerge. Lupin, a dicotyledon, has a tap root from which lateral roots emerge and which thickens with time as continued cambial activity leads to secondary growth

Roots keep shoots anchored and supported. A great diversity of overall architecture among root systems is fashioned as much by soil conditions as by genotype; hard subsoils, for example, restrict roots to surface soil layers. Root systems of monocotyledons and dicotyledons are genotypically distinct (Figure 3.1). Dicotyledons frequently develop tap roots from a single radicle that emerges from a seed. This tap root plus primary lateral roots emerging from it form a framework on which higher-order lateral roots are formed. Such a framework strengthens due to secondary thickening as a plant matures, leading to massive roots that are often seen radiating from the base of a tree trunk (Figure 3.2a). Monocotyledons such as grasses do not have a facility for secondary thickening and develop a ?brous root system comprised of one to several seminal roots, which emerge from the seed, plus nodal or adventitious

roots, which emerge from lower stem nodes. Monocotyledonous stems are typically anchored by these nodal roots, which are much stronger and more numerous than seminal roots.



[2]

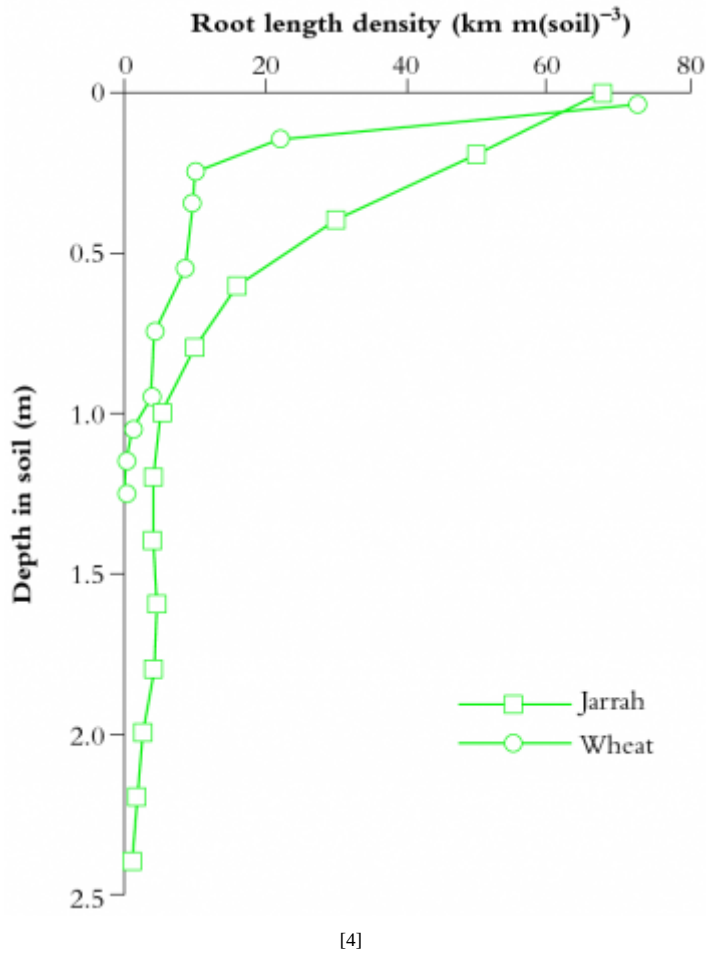
Figure 3.2 (a) Dimorphic root system of a six-year-old *Banksia prionotes* tree growing in Yanchep, Western Australia, on a deep sand with dominant winter rainfall. The lower trunk (T) is connected through a swollen junction (J) to the root system. A system of lateral roots (L) emerge horizontally from the junction, some bearing smaller sinker roots (arrows). Other laterals give rise to ephemeral cluster roots (CR) as described in Case study 3.1. The remainder of the root system comprises a dominant sinker root (S) which gives rise to smaller sinkers (S2). (b) Sinker roots penetrate up to 2.6 m into the sand and extract water through a low-resistance (high hydraulic conductivity) xylem pathway. Xylem in lateral roots is significantly narrower, raising axial resistance to water flow by at least one order of magnitude (Based on Jeschke and Pate 1995; reproduced with permission of *Journal of Experimental Biology*)

Roots do much more than anchor a plant. In addition to their obvious role in taking up water and nutrients (Section 3.6), they are also a source of hormones such as gibberellins, abscisic acid and cytokinins, which modify shoot physiology (Chapter 9). Concentrations of some hormones respond to soil conditions, allowing roots to act as sensors of soil conditions which might affect overall plant performance. Roots also act as storage organs; examples from the Australian flora are found in the Proteaceae (*Clematis pubescens*, *Stirlingia latifolia*), Portulaceae (*Calandrinia* spp.), Juncaginaceae (*Triglochin procera*) and even the bladderwort, *Utricularia menziesii*. Also very importantly for native vegetation, roots fashion soil pro?les, creating niches (biopores) which can be colonised afresh each season and which enable roots to traverse otherwise inhospitable subsoils to gain access to water at depth. Complex physical and biological interactions between roots and soil occur in the rhizosphere (Section 3.3), where bacterial activity and root exudates stabilise biopores and modify soil chemistry.

3.1.2??Root architecture and uptake of nutrients

Table 3.1 Densities of root systems of some annual and perennial plants expressed as root length per unit volume of soil at different depths within soil profiles. Grasses are equipped with an abundance of fine roots in surface layers that penetrate little beyond 1 m. Trees commonly have sparser root systems in surface layers than grasses but with thick axes that penetrate deeply into soil profiles. Depth of penetration is enhanced by high-density planting and can result in reduced root length densities in upper layers (see E. grandis *agroforest)*

Species	Soil depth (cm)	Root length density (km m (soil)$^{-3}$)
Pinus radiata	0–10	1.5
	10–20	3.2
	40–50	0.3
Pinus silvestris	0–15	52.5
	15–30	12.5
	45–60	3.4
	90–105	0.8
Eucalyptus grandis[a] (agroforest)	0–20	30 (dense planting)
	0–20	95 (medium density)
	0–20	110 (sparse planting)
Eucalyptus grandis[b] (trial plantation)	0–10	81
	10–20	21
	20–30	18
	30–40	14
	40–50	8



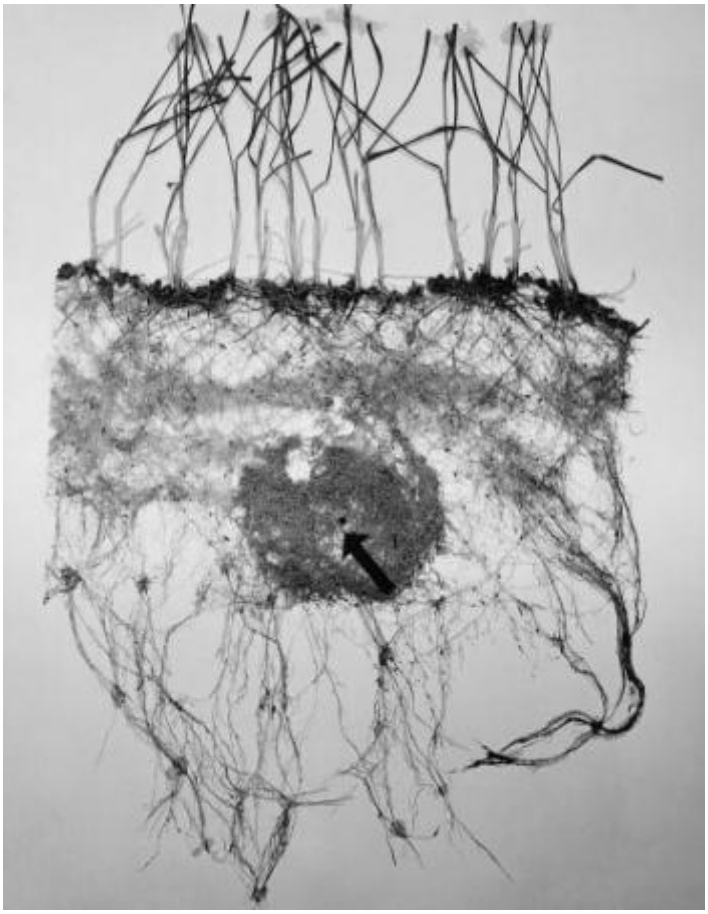
[4]

Figure 3.3 Root length density in relation to depth in the soil for a wheat crop (circles) and a jarrah (*Eucalyptus marginata* Sm.) forest (squares). Both have a dense population of roots near the surface but wheat roots barely penetrate below 1 m, whereas jarrah roots penetrate to well below the 2.5 m shown here, often to 20 m (Based on Carbon *et al.* 1980 (jarrah); and F.X. Dunn, unpublished data (wheat))

Total length of root per unit volume of soil (root length density, L, expressed in km m^{-3}) is often large in surface layers of the soil and typically decreases with increasing depth. Commonly, hundreds of kilometres of root per cubic metre of soil are observed near the soil surface (Table 3.1). Figure 3.3 shows L as a function of depth in a wheat crop in early spring, and under a *Eucalyptus* stand, also in spring. Dense root proliferation near the soil surface probably reflects an adaptation of plants to acquisition of nutrients such as phosphorus, potassium and cationic micronutrients such as zinc and copper. Such nutrients do not move readily in soil, hence roots branch proli?cally to ensure close proximity (a few millimetres) between adsorbing surfaces and these soil-immobile ions. Roots of jarrah are also concentrated near the soil surface (Figure 3.3) but some roots penetrate very deeply to tap subsoil moisture. Such water escapes the wheat roots and ?nishes up as groundwater.

Many plants are mycorrhizal (Section 3.4). They form symbioses (mycorrhizas) with certain fungi which obtain ?xed carbon from the host plant, in turn supplying the host with poorly mobile nutrients, especially phosphorus. This is achieved by proliferating their hyphae to provide a much greater surface area for nutrient uptake than could be provided by roots alone. Another adaptation, common in the Proteaceae, and also occurring in some species of lupin, is proteoid roots, clusters of tiny rootlets that greatly enlarge the available surface area for ion uptake and which are inducible by low levels of

phosphorus (see Case study 3.1).



[5]

Figure 3.4 Excavated root system of wheat plants whose roots were provided with a concentrated band of ammonium sulphate fertiliser at the head of the arrow. This band is toxic at first but roots start to proliferate in its vicinity and eventually form a dense cylindrical cluster as they progressively take up the fertiliser (Photograph courtesy J.B. Passioura)

Nutrients are distributed unevenly in soil, generally being concentrated in the topsoil and also dispersed elsewhere in pockets. Surface enrichment arises from diverse sources such as dead fauna, urine patches and localised application of fertiliser. Root systems respond to enriched zones of nutrients by proliferating in their vicinity. Figure 3.4 shows an example of such a proliferation; the dense cluster of roots in the centre of the ?gure is a response by the row of wheat plants to application of a large pellet of nitrogen fertiliser (see arrow). Such proliferations ensure plants garner nitrogen ahead of loss to competing plants or as leachate into subsoil.

Young roots absorb nutrients more rapidly than old roots. New roots supply annual plants with abundant sites for nutrient uptake, especially during establishment. A feature of the roots of perennials is that they have a large turnover of the ?ne, high-order lateral roots that emerge from the secondarily thickened framework each year. This turnover draws heavily on photoassimilate, equivalent to between 40 and 90% of the standing biomass of temperate forests and half the CO_2 ?xed in desert succulents (cited in Waisel *et al*. 1996). Production of ?ne (and often ephemeral) roots ensures uptake of nutrients over many years.

3.1.3??Root architecture and uptake of water



[6]

Figure 3.5 Sample of dense subsoil containing a biopore occupied by a root. Such biopores are passages for roots through otherwise almost impenetrably dense soil

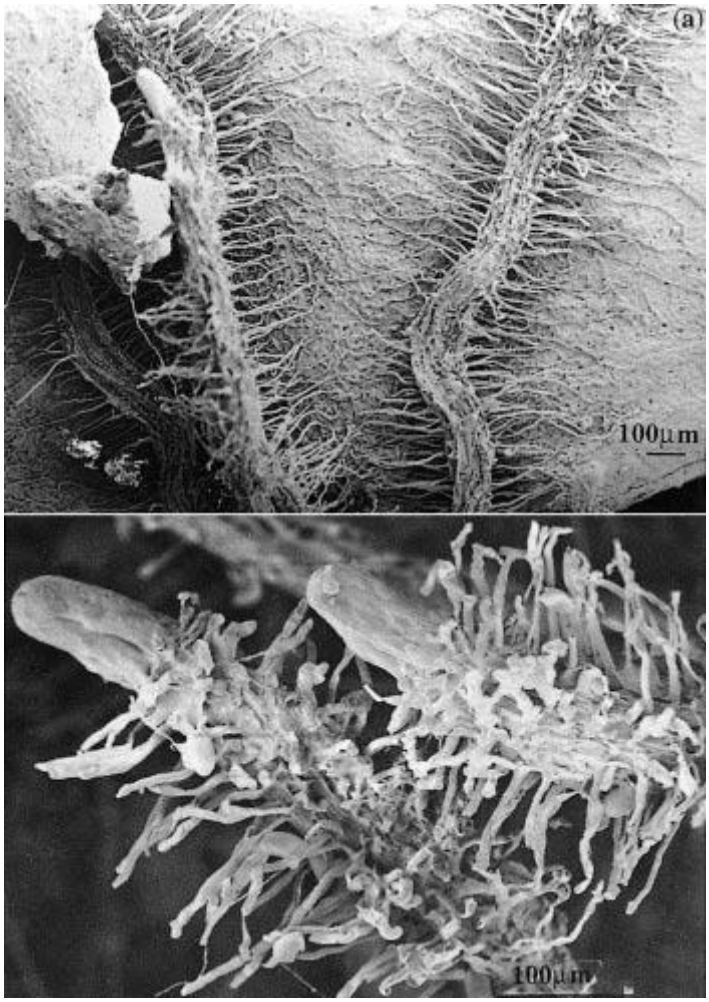
The dense root systems common in topsoils (Table 3.1) extract water effectively from surface soil layers. Extracting water from subsoil layers is more dif?cult. Australian subsoils are typically inhospitable to roots. They are dense, have a large resistance to penetration and are often sodic, that is, sodium dominates the exchange complexes on soil particles, affecting structure and water availability. Moreover, subsoils can be acutely de?cient in some nutrients that are required locally by roots (e.g. zinc) or poisonously high in others (e.g. boron). Native vegetation overcomes these dif?culties by forming biopores in the subsoil — highways that enable roots to create and maintain a path to water deep in the subsoil, possibly even as far as a water table 20 m below the surface, as in the jarrah forests in Western Australia. Clearing native vegetation for agriculture has disconnected subsoil biopores from the topsoil, and the roots of crops may have trouble in ?nding them. Nevertheless it is common for roots of crops to colonise biopores; a particularly clear example is given in Figure 3.5 which shows dozens of roots clustered together in a pore about 5 mm in diameter that traverses a soil core collected from subsoil under a wheat crop.

Clearing native perennial vegetation for agriculture has generally replaced deep-rooted perennials with shallow-rooted annuals. These annuals, whether crop or pasture, do not have time to grow their deep roots into the subsoil, and consequently considerable amounts of rain may percolate beyond the reach of roots. Such water moves slowly through the deep subsoil, moving laterally as well as vertically, and in so doing often transports salt to lower parts of a landscape, discharging at the surface and leading to

dryland salinity. A major challenge facing Australian agriculture is to prevent long-distance movement of this escaped water. Any long-term solution will depend on manipulating root-system architecture. Replanting agricultural landscapes with trees sometimes helps but is not a universal solution because water will not move to roots through the unsaturated zone of the soil over distances greater than about 1 m. Effects from trees are therefore quite local unless tree roots can reach a water table where lateral movement of water is rapid.

CASE STUDY 3.1??Cluster (proteoid) roots

M. Watt



[7]

Figure 1 Cluster roots in *Banksia serrata* growing on Hawkesbury Sandstone hillslopes in the Sydney region. (a) Roots that have grown across a dead eucalypt leaf extract nutrients remaining in the decaying leaf. (b) Clusters of fine rootlets at the tips of roots increase the surface area for nutrient extraction from surrounding soil. Scale bar = 100µm

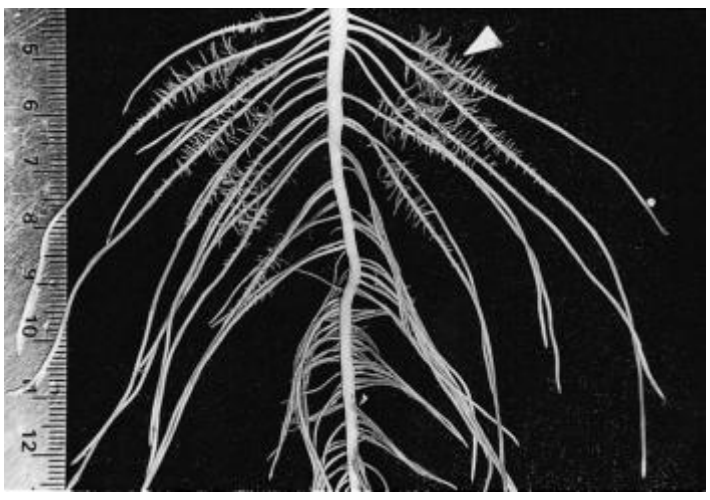
(Scanning electron micrograph courtesy S. Gould)

Cluster roots (Figure 1) are found worldwide in species from nutrient-de?cient soils (Dinkelaker *et al*. 1995). In these soils, cluster roots enhance uptake of nutrients, especially phosphate, and help prevent soil erosion. Many species which develop cluster roots, including members of the Proteaceae where they were ?rst described by Purnell (1960), are native to Australia. Other families such as the Casuarinaceae, Cyperaceae, Mimosaceae and Restionaceae also have heavily branched root systems (Lamont 1993); similarities in function between capillaroid roots of the Restionaceae and cluster roots of the Proteaceae might be expected as they are both major Gondwanan families. Signi?cantly, few species with cluster roots are mycorrhizal, implying that root clusters ful?l a similar role to mycorrhizal fungi.

Australian soils generally contain low concentrations of plant-available phosphate, much of it bound with iron–aluminium silicates into insoluble forms or concentrated in the remains of decaying plant matter. Because very little of this phosphate is soluble, most roots extract it only slowly. Plants with cluster roots gain access to ?xed and organic phosphate through an increase in surface area and release of phosphate-solubilising exudates (Section 3.3). Hence plants with cluster roots grow faster on phosphate-?xing soils than species without clusters, supporting claims that cluster roots are an adaptation to phosphate de?ciency.

Cluster roots have a distinct morphology. Intense proliferation of closely spaced, lateral ‘rootlets’ occurs along part of a root axis to form the visually striking structures. Root hairs develop along each rootlet and result in a further increase in surface area compared to regions where cluster roots have not developed (e.g. 26 times in *Leucadendron laureolum*; Lamont *et al*. 1984).

Factors driving cluster root formation in relation to overall morphology of a root system remain a matter for conjecture. In the Proteaceae, clusters generally form on basal laterals so that they are abundant near the soil surface where most nutrients are found. For example, *Banksia serrata* produces a persistent, dense root mat capable of intercepting nutrients from leaf litter and binding the protecting underlying soil from erosion (Figure 1). New clusters differentiate on the surface of this mat after ?res and are well placed to capture nutrients. In contrast, *Banksia prionotes* forms ephemeral clusters which export large amounts of nutrients during winter (Jeschke and Pate 1995). *Lupinus albus* has more random clusters which appear on up to 50% of roots (Figure 2).



[8]

Figure 2 Basal roots of a two-week-old *Lupinus albus* plant grown in nutrient culture with 1 µM phosphate. Proteoid roots have emerged along the primary lateral roots (arrowhead) and the oldest proteoid rootlets have reached a determinate length of 5 mm. As rootlets approach their final length, they exude citrate for 2-3 d. (mm scale on left side) (Photograph courtesy M. Watt, Research School of Biological Sciences, ANU)

Rootlets not only represent an increase in surface area but also exude protons and organic acids, solubilising phosphate and making it available for uptake. Exudates from cluster roots represent up to 10–23% of the total weight of an *L. albus* plant, suggesting that they constitute a major sink for photoassimilates. However, not all this additional carbon comes from photosynthesis because approximately 30% of the carbon demand of clusters is met by dark CO_2 ?xation via phosphoenolpyruvate carboxylase (Johnson *et al*. 1994). Because cluster roots form on roots of *L. albus* even when phosphate supply is adequate, growth of *L. albus* in soils with low phosphate availability is not restricted by an additional carbon 'drain' to roots. On the other hand, the great many species which produce cluster roots in response to environmental cues like phosphate de?ciency (Dinkelaker *et al*. 1989) or seasons (e.g. *Banksia prionotes*) might experience a carbon penalty to support these roots.

Cluster roots on *L. albus* are ef?cient with respect to carbon consumption by generating citrate on cue. Most of the citrate exuded by clusters is released during a two to three day period when the cluster is young (Watt *et al*. 1997). A large root surface area in clusters works in concert with this burst of exudation to solubilise phosphate before it is re-?xed to clay surfaces or diffuses away (Gardner *et al*. 1981).

Form and function are thus coordinated in time and space, so that cluster roots can mine a pocket of phosphate-rich soil which would otherwise not yield its nutrients. Cluster roots are an elegant adaptation of root structure and biochemistry to nutrient-poor soils.

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