Plant and Soil **155/156**: 269-272, 1993

Why are hairy root clusters so abundant in the most nutrient-impoverished soils of Australia?

BYRON B. LAMONT
School of Environmental Biology, Curtin University, GPO Box U1987, Perth 6001, Western Australia

Key words: proteoid roots, organic matter, nodules, mycorrhizas, phosphorus uptake, root hairs, Proteaceae, seasonal climates

Abstract

Rootlets, covered in long root hairs, are aggregated into distinct clusters in many groups of Australian plants. They are almost universal in the family Proteaceae, and some members of the Papilionaceae, Mimosaceae, Casuarinaceae, Cyperaceae, Restionaceae and Dasypogonaceae. These families have their centres of distribution in the oldest, most leached sands and laterites of the continent. Root clusters are almost confined to the uppermost 100 mm of the soil profile, often penetrating into the raw litter. These horizons are the major sources of mineral nutrients which are mobilized when these soils become moist. I argue that root clusters are an ideal solution for maximizing nutrient uptake in extremely impoverished soils, especially in seasonal climates.

Introduction

Root clusters were first recognized in the large Australian family, Proteaceae, where they were given the name of proteoid roots (Purnell, 1960). Proteoid roots consist of clusters of longitudinal rows of contiguous, extremely hairy rootlets. All but a few primitive members of this family of about 1 800 species are now considered to produce them, including those in South Africa and South America (Grinsbergs et al., 1987; Lamont, 1981; 1983a). Homologous structures have been identified in a range of legumes, including Acacia (Mimosaceae), nine genera in the tribe Podalyrieae of the Papilionaceae, some Casuarinaceae and the related (non-Australian) Betulaceae and Myricaceae (Louis et al., 1990; Pathamaranee, 1974; Reddell, 1986; Sward, 1978). These root clusters are not as tightly packed as proteoid roots.

Analogous root clusters have been recognized in other families. This includes most members examined in the tribes Cariceae and Rhynchosporeae of the Cyperaceae both in Australia and elsewhere (Davies et al., 1973; Lamont, 1974; Phillips and Weste, 1984). The rootlets are swollen (dauciform) with obvious gaps between them but appear even hairier than proteoid roots. Another grass-like family well-represented in the Southern Hemisphere is the Restionaceae. Although not as well known, its surface rootlets are similar to dauciform roots but are not swollen (Campbell, 1964; Gullan, 1975; Lamont, 1982). The grass-tree, *Kingia australis* (Dasypogonaceae), has concealed aerial roots whose root clusters proliferate among the persistent leaf-bases (Lamont, 1981a).

I will explore the hypothesis that root clusters exploit nutrients in the humus and decomposing litter layers and provide an adaptive advantage in nutrient-impoverished soils on which litter accumulates.

Soil profile distribution

The first task is to show that root clusters are distributed where organic matter levels are greatest. While roots are absent from the raw litter in *Hakea laurina*, proteoid roots account for over 80% of the roots in the decomposing litter (A_0 horizon), followed by the humus layer (A_1) and are absent from the depositional layers (B) (Lamont, 1984). The compound proteoid roots (groups of clusters) of the important genera, *Banksia* and *Dryandra*, in scrub-heath and woodland are so dense that they form a continuous mat, 20-50 mm wide, enmeshed among the litter and humus particles (Jeffrey, 1967; Low and Lamont, 1990). A similar pattern exists for other proteaceous genera and root cluster types (Davies et al., 1973; Lamont, 1974, 1982, 1983, 1984; Lamont et al., 1984).

By shifting the position of the organically-rich layer through the profile it was shown that there is a causal relationship for *H. laurina* (Lamont, 1973): A_1 soil placed at a depth of 240-360 mm resulted in 227 proteoid roots per gram of root whereas normally there would only be 8. This pattern was even more extreme for the South African *Leucadendron laureolum* (Lamont et al., 1984). This could be due to the well-established effect of local nutrient enrichment but it may occur even in the absence of a substantial increase in general root growth (Lamont, 1973). A more likely cause is the effect of the abundant soil bacteria: in a way still not understood, these stimulate the production of proteoid roots (Gardner et al., 1982; Lamont and McComb, 1974; Malajczuk and Bowen, 1974). The antibiotic, chloromycetin, decreased proteoid root numbers substantially without altering normal root growth or nutrient availability in *L. laureolum* (Lamont et al., 1984). The causal organisms do not invade the roots and mycorrhizal fungi are not normally present (Lamont, 1972a,1982). There have been no experimental studies for other cluster types but aerobic conditions at the surface may be important, especially in waterlogged soils.

Inorganic nutrient effects

If root clusters enhance nutrient uptake as a response to poor soils they should form preferentially in those soils. Provided base levels of nutrients are suffiently low, the contribution of proteoid and dauciform roots to the plant rises from nil as the external supply of N or P is increased from zero, peaking before total plant growth is at a maximum (Gardner et al., 1982; Handrick, 1991; Lamont, 1972b, 1974; Louis et al., 1990). Cluster root production falls away to nil again as total root and then shoot growth peak. At higher base levels of other nutrients, proteoid roots may be present only in the absence of added N or P (Lamont, 1986). Seedlings grown in fertile soils (high in clay or humus) may attain maximum shoot size but they lack proteoid roots (Lamont, 1972b; Siddiqi and Carolin, 1976). In *Banksia ericifolia*, proteoid roots are eliminated at about 0.5% leaf P (Handreck, 1991).

Function of root clusters

Support for my hypothesis requires demonstration that root clusters have a superior capacity over unmodified roots for absorption of nutrients from the soil surface horizons. Early work showed that uptake of ^{32}P and Rb from solution by proteoid roots may be up to 13 times greater than by unclustered roots (reviewed in Lamont, 1982). The aerial root clusters of *Kingia* readily absorbed ^{32}P inserted among the dead leaf bases (Lamont, 1981b). Calculations show the surface area to weight ratio may be up to 25 times that of the parent root (Dell et al., 1980; Lamont, 1983b). More importantly, the clusters of *L. laureolum* may explore 32.5 times the volume of soil as an equivalent weight of parent root (Lamont, 1983b). In addition, proteoid roots have a strong reducing, acidifying and chelating capacity for poorly-soluble sources of P, Fe and Mn (Gardner et al., 1982, 1983; Grierson and Attiwell, 1989). Secreted citrate appears to have a central role in enhanced Fe and P uptake in the non-native *Lupinus albus*. These effects can be attributed to the greater surface area and compaction which raise the concentration of exudates in the rhizosphere. Further, uptake is facilitated by adhesion of the long, abundant root hairs to soil particles and the presence of copious mucigel (Davies et al., 1973; Dell et al., 1980; Lamont et al., 1984). The unsubstantiated evidence of enhanced phosphatase activity by proteoid roots (Lamont,

1982) indicates a possible role in organic matter decomposition.

Soil nutrient levels

It is now necessary to show that species with root clusters are best represented in the most impoverished soils and that the most fertile part of these soils is in the organically-rich surface horizons. For the non-arid parts of Australia, the least fertile soils are the deeply leached, acid sands, sandstones and laterites widespread in southern Australia. Agricultural crops require the addition of P, N, K, S and trace elements (Cu, Zn, Mn, Mo) to these soils (Williams and Raupach, 1983). There is increasing evidence that some of these, especially in south-western Australia, may be among the world's least fertile soils (Lamont, 1993; Lindsay, 1985). It is here (and to a lesser extent, the sands and sandstones of the Cape, South Africa) that species with root clusters have their centres of distribution (Lamont, 1982; Lamont, et al., 1985). This is especially so for the Proteaceae, restios and sclerophyllous legumes which are concentrated in the poorest sands and laterites of south-western Australia (Lamont et al., 1984). Given adequate moisture, these soils are sub-optimal for growth of species normally restricted to them (Lamont, 1972a). It is in these soils that most nutrients derive from the decomposing litter, so that their concentration is greatest at the soil surface (Froend, 1987 for N; Lamont, 1973 for N, Mg, Ca, K). P is more likely to be an exception: although it is stored in, and released from, the litter and humus, it is sorbed in the B horizon. The dead leaf bases of *Kingia* are a much better source of nutrients than the soil (Lamont, 1981b).

Discussion

I have demonstrated that root clusters contribute most to the root system under sub-optimal nutrient conditions and that species possessing root clusters are most likely to occur naturally in such soils. As nutrient-impoverished soils are characteristic of much of temperate Australia, we find that species with these structures often dominate the landscape. Root clusters enhance the release and uptake of nutrients and they form preferentially in that part of the profile which is the main source of nutrients in leached soils: the decomposing litter. The highly sclerophyllous vegetation and prolonged summer drought ensure substantial litter build-up between fires (Low and Lamont, 1990). Nevertheless, evidence that root clusters assist the decomposition process has yet to be obtained. Certainly, the dense cover of long root hairs ensures good contact with the soil and litter particles, enabling immediate uptake of nutrients as they are released. The A_0 horizon is most prone to sudden and prolonged drying out, an environment more suited to root hair formation than to mycorrhizal fungal growth (Baylis, 1972; Reid and Bowen, 1979). The strength of the root hairs and the abundant mucigel may even provide a better link with the nutrient source under fluctuating moisture conditions than fungi and competitive uptake between the partners, an important issue only in extremely poor soils, is irrelevant. In this respect it is worth noting that species with root clusters are rarely mycorrhizal (though legumes are still nodulated) which implies a similar function (Lamont, 1982). There may therefore be some significance in the characteristic clustering of ectomycorrhizas. Nevertheless, root clusters appear to have an adaptive advantage in the least fertile, seasonally dry soils.

References

Baylis GT 1972 Search 3, 257-259.

Campbell EO 1964 Trans. Roy. Soc. New Zeal., Bot. 2, 219-227.

Davies J, Briarty LG and Rieley JO 1973 New Phytol. 72, 167-174.

Dell B, Kuo J and Thomson GJ 1980 Aust. J. Bot. 28, 27-37.

Gardner WK, Barber DA and Parbery DG 1982 Aust. J. Bot. 30, 303-309.

Froend RH 1987 Investigations into species richness patterns in the northern sandplain region of Western Australia. Thesis, Univ. West. Aust., Perth.

Gardner WK, Parbery DG and Barber DA 1982 Plant Soil 68, 19-32.

Gardner WK, Parbery DG and Barber DA 1983 Plant Soil 70, 107-124.

Grinbergs JM, Valezuela EF and Ramirez CG 1987 Agro Sur 15, 1-9.

Gullan PK 1975 Vegetation at Ganbourne Vol. 2. Thesis, Monash Univ., Vic.

Handreck KA 1991 Aust. J. Bot. 39, 373-384.

Jeffrey DW 1967 Aust. J. Bot. 15, 403-411.

Lamont B 1972a Aust. J. Bot. 20, 155-174.

Lamont B 1972b Aust. J. Bot. 20, 373-384.

Lamont B 1973 Aust. J. Bot. 21, 165-187.

Lamont B 1974 New Phytol. 73, 985-996.

Lamont B 1981 *In* Heathlands and Related Shrublands of the World. B Analytical Studies. Ed RL Specht. pp 183-195. Elsevier, Amsterdam.

Lamont B 1981a Aust. J. Bot. 29, 81-96.

Lamont B 1981b Physiol. Plant. 52, 181-186.

Lamont B 1982 Bot. Rev. 48, 597-689.

Lamont B 1983a J. S. Afr. Bot. 49, 103-123.

Lamont B 1983b Plant Soil 74, 149-152.

Lamont BB 1984 *In* Kwongan: Plant Life of the Sandplain. Eds JS Pate and JS Beard. pp 126-145 Univ. West. Aust. Press, Perth.

Lamont BB, Hopkins AJM and Hnatiuk RJ 1984 In Kwongan: Plant Life of the Sandplain. Eds JS Pate and JS Beard. pp 27-50 Univ. West. Aust. Press, Perth.

Lamont BB 1986 Acta Hort. 185, 163-170.

Lamont BB 1993 *In* Mediterranean-type Ecosystems of the Pacific Basin: Similarities and Differences. Springer-Verlag, NY (*in press*)

Lamont BB and McComb AJ 1974 Aust. J. Bot. 22, 681-688.

Lamont BB, Brown G and Mitchell DT 1984 New Phytol. 97, 381-390.

Lindsay AM 1985 Proc. Ecol. Soc. Aust. 14, 83-97.

Louis I, Racette S and Torrey JG 1990 New Phytol. 115, 311-317.

Low AB and Lamont BB 1990 Aust. J. Bot. .38, 351-359.

Malajczuk N and Bowen GD 1974 Nature 251, 316-317.

Pathmaranee N 1974 Observations on proteoid roots. Thesis, Univ. Sydney, N.S.W.

Phillips D and Weste G 1984 Aust. J. Bot. 32, 339-352.

Purnell HM 1960 Aust. J. Bot. 8, 38-50.

Reddell P 1986 Soil and plant factors affecting nodulation and nitrogen-fixation in Casuarinaceae-Frankia symbiosis. Thesis, Univ. West. Aust., Perth.

Reid CP and Bowen GD 1979 *In* The Soil-Root Interface. Eds JL Harley and RS Russell. pp 211-219. Academic Press, London.

Sward RJ 1978 Studies on VA mycorrhizas of some Australian heathland plants. Thesis, Monash Univ., Vic.

Williams CH and Raupach M 1983 *In* Soils: An Australian Viewpoint. pp 777-794. Academic Press, London.