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REGULAR ARTICLE

Iron and phosphorus fertilizations and the development of proteoid roots in macadamia (*Macadamia integrifolia*)

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Abstract Proteoid roots are reportedly an adaptation to soils with either low phosphorus (P) or iron (Fe) or both. Since macadamia (*Macadamia integrifolia*, a member of the family Proteaceae) is an important crop in Hawaii, a factorial experiment with soil P levels of 0, 150, and 500 mg/kg and Fe levels of 0, 5, and 10 mg/kg was conducted to evaluate the effects of P and Fe fertilizations and possible Fe x P interactions on proteoid root development and macadamia growth. The soil was a highly weathered Oxisol having 0.015 mg P/L and 0.03 mg Fe/L in the soil solution in its unamended state. Proteoid roots were reduced in number and as a percentage of the total root mass at the highest levels of P and Fe. Phosphorus, however was a major controlling factor. Optimum dry matter associated with at least 10% proteoid roots, corresponding to a P concentration approximately of 0.035 mg/L in soil solution and 0.10% P in leaves. Total Fe in leaves or the amount of Fe applied was not a good predictor of plant growth. In contrast, chlorophyll content, a surrogate of biologically active Fe, was. Soil-solution ratio of Fe $^{1/3}$/ P (molar basis) could be used to predict the response of macadamia growth to P and Fe fertilizations.

Keywords Proteoid roots · Macadamia · Iron · Phosphate · Fertilization

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Introduction

Proteoid roots were first described in detail by Purnell (1960) as "dense clusters of rootlets of limited growth" in the family Proteaceae to which macadamia (*Macadamia integrifolia*) belongs. Because such roots have subsequently been found in other plant families (e.g., Casuarinaceae, Cucurbitaceae, Fabaceae, and Myricaceae) they are now often called cluster roots (Lamont 1993; Watt and Evans 1999; Shane and Lambers 2005; Lambers and Shane 2007). Their morphology is variable (classified as simple, compound, dauciform, capillaroid), but commonly large numbers of determinate branch roots develop over very short distances of main root axes giving a bottlebrush appearance (Lambers and Shane 2007). Proteoid roots develop in nutrient-poor soils and are assumed to be an adaptation for nutrient acquisition from such soils (Lamont 1993; Liang and Li 2003).

Production of proteoid roots is commonly associated with phophorus (P) deficiency, implying that plant resources are diverted to expanding root surface area and releasing organic compounds to facilitate P uptake where P limits growth (Dinkelaker et al 1995;