

A Test of Nutrient Limitation in Two Tropical Montane Forests Using Root Ingrowth Cores¹

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TROPICAL MONTANE FORESTS DIFFER FROM LOWLAND FORESTS in overall stature, physiognomy, species composition, and overall productivity (Richards 1952, Grubb 1977). They appear to be more similar to temperate forests in many aspects of their structure and function than to lowland tropical forests (Vitousek & Sanford 1986, Tanner *et al.* 1998). Most frequently, the physical determinants of the reduced productivity in tropical montane forests appear to be persistent cloudiness and low temperatures (Bruijnzeel & Veneklaas 1998). Decomposition rates, soil nutrient availability, and soil pH tend to be low in these forests, and interactions between soil and climatic factors tend to promote increased leaf thickness, coriaceousness, and longevity, which helps to maintain slow litter decomposition. In their recent review of the available information, Tanner *et al.* (1998) concluded that tropical montane forests are commonly deficient in one or more nutrients, with consistent trends in decreasing availability of N, P, and K with elevation. Their review suggested a tendency toward N-limitation in montane forests, in contrast to more likely P-limitation in tropical lowland forests while K, Ca, and Mg may be secondarily limiting in poorer lowland sites with highly leached and weathered soils (Cuevas & Medina 1988, Burslem *et al.* 1994).

True tests of nutrient limitation necessitate laborious fertilization experiments, which may be expensive, slow to yield results (particularly when overall productivity is low), or inappropriate, in sites such as protected national parks (Raich *et al.* 1994). Proliferation of roots in nutrient-enriched soil microsites, however, is a widely reported phenomenon; 71 percent of 49 published experiments (for potted plants) examining root responses to patches enriched in N, P, or K showed significantly increased growth rates relative to untreated soils (Robinson 1994). The responsiveness of roots to patches of enriched nutrients (decaying organic matter) also has been demonstrated in field situations (*e.g.*, St. John 1983). In certain tropical lowland forests, a root mat is formed in decomposing matter above the mineral layer, which plays an important role in the rapid reabsorption of minerals in the litter and helps prevent leaching of nutrients (Jordan & Escalante 1980, Jordan & Herrera 1981). In some cases, roots grow up the trunks of other trees, even reaching into the canopy to intercept the nutrients borne in stemflow before they enter the soil solution where other roots might compete for them. Sanford (1987) showed that roots of trees in a nutrient-starved Amazon forest grew higher on plastic trunks "baited" above ground with bags of litter or manure than on unbaited trunks.

This property was employed as the basis of an alternative test of nutrient limitation by Cuevas and Medina (1988) who made the crucial additional assumption that roots specifically respond to limiting nutrients. In theory, root ingrowth cores enriched with limiting nutrients should accumulate greater fine root biomass and provide a relatively easy test of nutrient limitation at a particular site. Raich *et al.* (1994) showed that results from root ingrowth cores paralleled results from stand-level fertilization experiments; they demonstrated a response to N but not to P, both in ingrowth cores and their large-scale fertilization trials.

In this study, the root ingrowth technique was applied to two forests of contrasting stature and soil types in the Blue Mountains of Jamaica, where the nutrient relations of the trees were well known from previous investigations. The aim of the study was to clarify certain contradictions in the available evidence for these forests. A series of bioassays with potted plants suggested that N was not a growth-limiting factor in one study (Tanner 1977a) but was so in a second bioassay (Healey 1989); P was found to limit growth in both these bioassay tests. Some reservations, however, have been voiced as to the validity of studies on potted plants relative to field trials, because pot size may affect the relative availability of nutrients with different mobility in the soil (Peace & Grubb 1982). The highly mobile nitrate ion would tend to limit growth when the ratio of soil volume (and thus exchange sites) to root surface area is low, whereas the nearly immobile P ion would tend to limit growth when the ratio is high. When Tanner *et al.* (1990) conducted an unreplicated broadcast fertilizer experiment *in situ* at the Mull Ridge site (see below), N addition substantially increased trunk diameter growth (*ca* 80%), strongly suggesting N-

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