Foliar chemistry of tallowwood – patterns of anti-herbivore defence in a *Eucalyptus* species

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The concept of a direct link between soil fertility, plant defence and animal abundance has been an important driver of the conservation of arboreal marsupials in southern Australia. In the forests of south-eastern Australia, for example, it has been shown that high densities of mammals occur where eucalypts with high foliar nutrients and low concentrations of phenolics grow on fertile soils (*1, 2*). The foliar chemistry of *Eucalyptus* is complex however, and includes terpenoids, phenolics and formyl phloroglucinol compounds (FPCs) all of which influence herbivory to differing extents. In particular, FPCs, such as sideroxylonal, have recently been shown to explain most of the variation in palatability of eucalypt foliage to vertebrate herbivores where they occur (*3*). This study aimed to assess the degree and type of variation in chemical defences for a single eucalypt species' and to ask how the variation was influenced by environmental factors.

A stratified design was used to sample foliage from 12 individual trees of *Eucalyptus microcorys* (tallowwood) growing at each of 42 sites from 7 drainage regions in northern NSW. Sites were distributed from Newcastle to the Queensland border, from sea level to 1000 m and encompassed a range of soil types and forest types. We took advantage of the capacity of residual maximum likelihood (REML) theory to incorporate the regional and site structure of our survey into statistical models and investigated ways in which variation in foliar constituents could be attributed to measured site and tree variables. These included measures of tree morphology, vegetation structure, topography, terrain, and a broad suite of climatic variables. We also classified most sites according to site quality, a measure that reflected site productivity and which was judged on the basis of soil chemical fertility, forest height, understorey type and density and tree species composition.

Sideroxylonal concentrations were greater in trees growing at higher, colder sites and in trees with lower foliar nitrogen (fig. 1). Although the relationship with nitrogen initially appears to match the predictions of carbon-nutrient balance (CNB) theory, when we summarised variables as site means, a generalised linear model indicated that, in fact, mean site sideroxylonal concentrations were greater at higher elevation sites and sites with *higher* mean nitrogen levels. Our analyses showed opposite effects of foliar nitrogen at two different scales because most variation in nitrogen occurred within sites, obscuring between-site differences in the full REML analysis. The analysis explaining most variation in sideroxylonal concentration showed that concentrations increased as site quality improved (fig. 2). Concentrations of foliar sideroxylonal measured in tallowwood are relatively high, and given the strong responses previously observed in captive common ringtail (*Pseudocheirus peregrinus*) and common brushtail possums (*Trichosurus vulpecula*) and koalas (*Phascolarctos cinereus*) to this compound, the patterns of plant defence reported here are expected to have profound implications for communities of marsupial herbivores. Indeed, patterns of faecal pellet occurrence indicated that the variation in foliar chemistry measured in this study influenced

herbivory by koalas (fig. 3). The patterns of variation in sideroxylonal concentration observed in this study suggest that the high levels of available nutrients in many trees growing on fertile soils may not be accessible to most folivores because they are highly defended. Further work is required to establish whether the patterns of chemical defence exhibited by tallowwood (the sole member of its subgenus) are representative of eucalypts in general. Certainly, large-scale patterns of chemical defence in the genus *Eucalyptus* appear to present a fascinating set of contrasts, as the two largest subgenera differ qualitatively in that the subgenus *Symphyomyrtus* produces FPCs and the subgenus *Eucalyptus* (formerly *Monocalyptus*) does not (*4*). The results of this study raise many important issues, for example, is it reasonable to generalise about the nutritional quality of an ecosystem on the basis of eucalypt species composition? And do current models of habitat quality for arboreal mammals identify the best habitat for all or only some species?

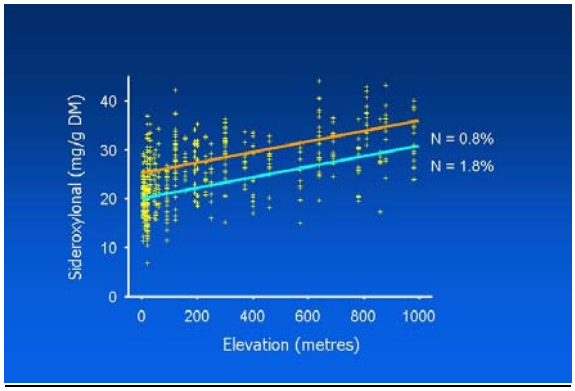

Fig. 1. This REML analysis shows that trees have higher sideroxylonal at higher sites ($P < 0.001$) and when foliar nitrogen concentrations are lower ($P < 0.01$). The two lines model sideroxylonal concentrations at fixed levels of nitrogen.

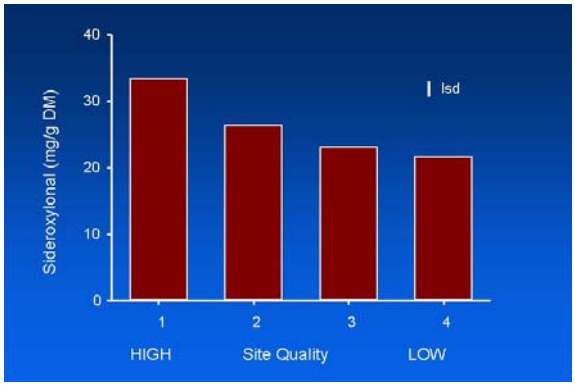

Fig. 2. This REML analysis indicates that higher sideroxylonal concentrations occurred in trees at higher quality sites (site quality Δdev. = 33.4, $P < 0.001$)

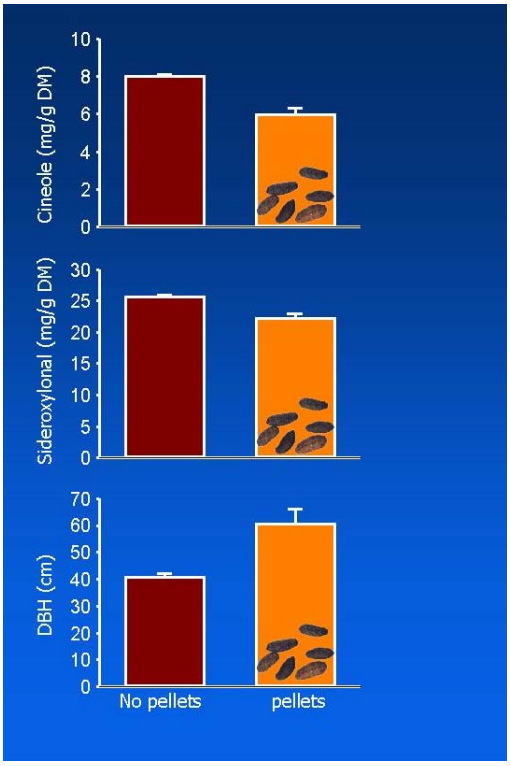

Fig. 3. Trees with koala faecal pellets found at their base were bigger and had lower mean concentrations of sideroxylonal and cineole than trees without pellets.

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