Do tissue chemical components and the effect of vegetation on soil properties contribute to the invasiveness of lippia (*Phyla canescens*)? – indications from soil moisture and plant calcium concentration

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Summary Invasive plants often have different physiological properties, chemical components and nutrient element dynamics from native vegetation, which can contribute to their invasiveness and change soil properties. Lippia (*Phyla canescens* (Kunth) Greene; family: Verbenaceae) is a perennial herb of South American origin. In Australia, lippia replaces desired species in native and improved pastures and is causing serious environmental and pastoral problems in the Murray-Darling Basin. However, the effect of lippia invasion on the water, carbon and nutrient dynamics of pasture soil is not known. In this study, we compared the carbon and nitrogen stable isotope ratio, soil moisture, organic carbon, and nutrient elements in the plant-soil system on lippia infested land and adjacent native and improved pasture. Comparisons were made at three sites, at Somerset Dam (SE QLD), near Leyburn (Eastern Darling Downs, QLD) and near Maitland (the Hunter Valley, NSW). We tested two hypotheses: (1) that lippia displays different stable isotope signature and nutrient element components to the major pasture grasses; and (2) that soil infested by lippia will be substantially different from soil under native pasture in soil moisture, stable isotope signature and nutrient dynamics.

Consistent differences between lippia and grass pastures were detected across all three sites, despite large differences between sites in soil, vegetation, and climate conditions.

The plant tissue of lippia had a much higher calcium concentration (up to 4% w/w) than pasture grass species regardless of the concentration of soil exchangeable Ca^{2+}. This observation, together with chemical analysis which shows more than 65% of calcium in leaf tissue is not soluble to 80% acetic acid, suggests the existence of calcium oxalate, although crystals were not observable under a light microscope. If present, these crystals are likely to inhibit feeding by cattle and other potential herbivores, thereby benefiting lippia in heavily grazed pasture. In addition, calcium carbonate crystals were found in the lithocyst on the leaf surface, which may also contribute to herbivore defence.

Compared with soil under native pasture, soil invaded by lippia displayed: (1) significantly decreased soil moisture (16–30% w/w lower); (2) generally lower soil pH and higher electrical conductance, which may be mediated by the increment of Na^+ in infested soil; and (3) lower nitrate-based soil nitrogen. Also, invasion by lippia (a C_3 plant) significantly changed the carbon isotope signature of the pasture soil organic carbon pool, which was previously determined by the more ^{13}C-enriched C_4 grass biomass. In lippia infested soil (compared to the control soil), organic carbon ^{13}C was depleted (1.5–2.2‰), but there was no significant difference in soil $\delta^{15}N$. Based on the carbon stable isotope ratio, we estimate that the input of lippia biomass into the soil has substituted 23.6%, 69.7% and 42.9% of the surface soil organic carbon pool (0–20 cm) at Somerset Dam, Leyburn and Maitland sites respectively.

The soil moisture decrement on lippia infested land may be caused by two mechanisms. First, as a C_3 plant, lippia has lower water use efficiency than C_4 grasses, so the vegetative transpiration rate is higher on lippia infested land. Second, the aboveground biomass productivity of lippia is lower than for grasses, while decomposition rates appear higher (due to the low C:N ratio). As a consequence, the lippia invaded land is covered by a thinner litter layer than native or improved pastures, which might be causing higher evaporation at the surface soil. Field observations suggest that lippia may remain photosynthetically active even in very dry conditions, and grow better than pasture grasses, so decreased soil moisture may facilitate the competitiveness of lippia over pasture grasses. Further studies are warranted to compare the drought tolerance of lippia and grasses.

We conclude that lippia may benefit from its high tissue calcium concentration and its apparent ability to drain soil moisture when invading Australian pastures.

Keywords *Phyla canescens*, soil moisture, nutrient element, stable isotope, calcium oxalate, competitiveness.