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Comparison of nutrient cycling abilities between the invasive *Acacia mearnsii* and the native *Virgilia divaricata* trees growing sympatrically in forest margins in South Africa

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ABSTRACT

Australian acacias have significant impacts on the habitats that they invade. For example, they can increase nutrient input and alter natural nutrient cycles. Here we assessed how the invasive *Acacia mearnsii* and native *Virgilia divaricata*, both nodulating legume trees with similar growth forms and general ecologies, compared in terms of N and P nutrient content, nutrient resorption and their Biological Nitrogen Fixation (BNF) capacities where they co-occur within forest margins in South Africa. Fresh and senesced leaf samples were collected in sympatric populations and analysed for N and P concentrations. We also measured the δ15N/δ14N isotope ratio, and used it to calculate percentage nitrogen derived from the atmosphere. The two species were very similar in their total nutrient content, but *V. divaricata* showed strong dependence on available P which determined its dominant source of N. It had a higher use of BNF, an energetically-expensive process, than the invasive species. *Acacia mearnsii* was also more efficient in N resorption than the native species. Our results highlight nutritional economy differences between these two ecologically similar species and provide further data on reasons for the success of *A. mearnsii* compared to native tree species.

1. Introduction

Invasion is recognized as the second largest threat to biodiversity (Mooney and Hobbs, 2000; Secretariaton the Convention on Biological Diversity, 2001) and invasive alien plant species have a significant impact on the environments that they invade (Pimentel et al., 2001). They can alter nutrient cycling (Witkowski, 1989; Le Maitre et al., 2011), impact water resources (Dye and Jarmain, 2004; Naude et al., 2011) and can be very costly to control (Pimentel et al., 2001). Australian acacias are among the most devastating groups of invasive species around the world where they are planted for commercial purposes, but have subsequently escaped from plantations (Searle, 1997; Kull and Rangan, 2008).

Acacia mearnsii De Wild. is classified as an invasive alien plant (IAP) in South Africa (IAP) (Henderson, 2007) as it has overcome all barriers proposed by the unified framework for biological invasion (Blackburn et al., 2011). It is the fifth most widespread IAP in the country and has a large ecological and economic impact (Pimentel et al., 2001; Dye and Jarmain, 2004; Henderson, 2007; Naude et al., 2011). It has invaded all habitats except the very arid Karoo (Henderson, 2007) and dense natural forest with changing the natural fire regime (Geldenhuys, 2004). Forest margins, an ecotone between forests and fire prone fynbos vegetation (Low and Rebelo, 1996), is more vulnerable to invasion with changing the natural fire regime (Geldenhuys, 2004). While in Australia, in its native range, *A. mearnsii* is not restricted to any specific habitat or soil type but flourishes in soil with high moisture content. Many Australian soils have extremely low nutrient content and *A. meansii* is naturally adapted to have a high tolerance for infertile soils (Searle, 1997). It is also a pioneer species, which dominates the forest after disturbance and later becomes an understory species (Searle, 1997).

Virgilia divaricata Adamson is a native forest pioneer tree species associated with Afromontane forest margins (Low and Rebelo, 1996; Goldblatt and Manning, 2000). It is ecologically similar to *A. mearnsii* in being a short-lived, fast growing and woody perennial (Phillips, 1928; Searle, 1997). Both species belong to the Fabaceae, but are grouped into different subfamilies (Searle, 1997; Goldblatt and Manning, 2000). *Acacia mearnsii* has invaded Afromontane forest margins, the ecotone between forest and fynbos, with its' invasion originating in the fynbos (Geldenhuys, 2011) and now co-occurs with *V. divaricata* over extensive areas of its native range. Both tree species are nodulating legumes that can acquire N via Biological Nitrogen Fixation (BNF) (Joubert, 2003; Beukes et al., 2011; Rodrìguez-Echeverrıa et al., 2011). Each species has its own unique compliment of rhizobial associates (Rodrìguez-Echeverrıa et al., 2011) that enable them to

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acquire nitrogen (N) from both the soil and the atmosphere. Nitrogen derived from the atmosphere (NDFA) is converted from N_2 gas into mineral NH_4^+ by these nodular rhizobia, and made available to the plant as alternative source of nitrogen (Allen and Allen, 1981). This ability of legumes may be viewed as both beneficial (sustainable N source) and harmful (adding to the success of invaders) to plantations and/or ecosystems (Brockwell et al., 2005). However, BNF is an energetically expensive process (Pate and Layzell, 1990) and plants often rely on N-recycling from abscising leaves in nutrient poor environments along with other adaptations such as reducing nutrient content in fresh leaves (Hobbie, 1992; Vergutz et al., 2012).

Nutrient cycling in natural environments is very complex and influenced by many interacting factors (Magdoff et al., 1997; Huber and Hanekleus, 2007). New methods focused on nutrient economies have been developed to aid our understanding of how ecosystems function. For example, the δ15N isotope method is widely used within botanical ecology and agriculture to help understand and predict the nature of nutrient limitation to net primary production in a changing world (Isaac et al., 2012). The stoichiometric approach to resorption efficiency (Reed et al., 2012) is useful and informative, because nutrients that are reabsorbed before leaf abscission are directly and immediately available to the plant (Clark, 1977; Turner, 1977) and relates directly to its nutrient use efficiency (Vitousek, 1982; Aerts and Chapin, 2000; Franklin and Agren, 2002). It is currently not known how differences in nutrient reabsorption may affect the mineral nutrition of invasive and indigenous legumes in ecosystems, but determining this may contribute to the understanding of the success of invasive legumes over native competitors.

The aim of this research was to investigate the role of nutrient reabsorption in the mineral nutrition of *A. mearnsii* and *V. divaricata* in Afromontane forest margins where these species grow sympatrically. We determined differences in foliar N and P concentrations, nutrient resorption, and their reliance on biological N_2 fixation. We also assessed soil N and P levels to determine its possible influence on the nutrient economies of these plants. We predicted that, since the invasive tree is well-adapted to nutrient limiting environments in its native range, it would have a competitive advantage over the native tree in terms of its nutrient economy (e.g. higher resorption efficiency and lower dependence on BNF), and in so doing makes use of a cheaper N source.

2. Materials and methods

2.1. Study area

Study sites were located within the Garden Route National Park in the Western and Eastern Cape Provinces of South Africa (Fig. A-1) and stretched from Gouna forest near Knysna (33.9804° S, 23.04642° E) in the west to Stormsriver near the Tsitsikamma National Park in the east (33.9901° S, 23.8978° E). Sites were selected ±20 km apart to prevent pseudo-replication and were selected based on the shared presence of *A. mearnsii* and *V. divaricata*. The rainfall varies from an average of 500 mm to 1200 mm per year, with the highest rainfall during autumn and early summer and the lowest during December. Temperatures are mild, ranging from of 7 °C to 19 °C during June and 15 °C to 26 °C during January (Bond, 1981). Soils are largely derived from quartzitic sandstone of the Table Mountain Group. All sites were located within the ecotone between Fynbos and Afromontane biomes. Data collection was conducted in December 2013.

2.2. Foliar nutrient content

Five ca. 7 m tall individual trees (per species) were chosen at random at each of the six sites. Leaf traps, constructed from folded 0.09 m^2 mesh netting (2 mm), were placed in each of these trees to capture foliar litter as outlined in Reed et al. (2012). Four weeks later, material in these traps were collected and samples of fully sunlight exposed canopy leaves were taken from the focal trees. Litter was sorted to remove any foreign material, where after both the litter and the fresh leaves were respectively oven dried at 80 °C for 48 h, milled and analysed for N and P content.

Phosphorous concentration was determined by an external laboratory (Elsenburg, Stellenbosch) using inductively coupled mass spectrometry (ICP-MS). N content and N isotope content were determined

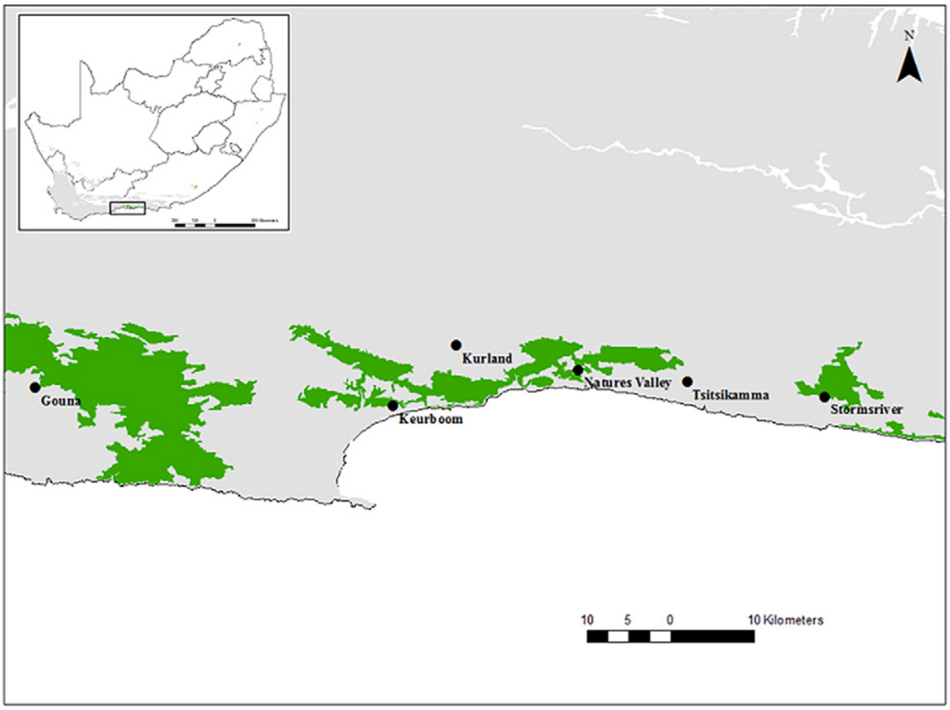

Fig. A-1. Sampling sites for *Virgilia divaricata* and *A. mearnsii* where these grow in sympatry in ecotones between the Fynbos biome (grey) and the Forest biome (green) along the southern Cape coastal belt in South Africa.