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Seeing the forest for the trees: fertiliser increases tree growth but decreases understorey diversity in the Northern Jarrah Forest, southwest Australia

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Forestry science and practice suggests thinning and fertiliser increase the growth rates of individual trees. In a recent paper reporting on a long-term experiment conducted in the Northern Jarrah Forest, Bhandari *et al*. (2021) found positive effects of both thinning and fertilisation, and suggested these management practices will result in a shorter return interval for large trees within the population, which poses significant benefits at an ecosystem scale. We argue that whereas thinning alone may be beneficial, the application of fertiliser to native ecosystems within the South West Australian Floristic Region requires caution due to impacts on understorey plant diversity. Not only are the soils in the region generally deeply-weathered and highly nutrient-deficient, but the evolution of a suite of adaptations for nutrient-acquisition is implicated in both speciation and the maintenance of plant species diversity. Furthermore, recently published long-term experiments in restored jarrah forest indicate that applied fertiliser both reduces species diversity and increases fine fuel loads. In conclusion, thinning, but not fertiliser application, is an appropriate management strategy to improve tree growth in this global biodiversity hotspot.

Keywords: diversity; *Eucalyptus*; nutrients; phosphorus; thinning

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INTRODUCTION

A key motivation within silviculture is to maximise plant productivity and tree growth by applying a range of management strategies such as stand thinning. Bhandari *et al*.'s (2021) study on a long-term, large-scale experiment demonstrates the sustained benefits of stand thinning on jarrah (*Eucalyptus marginata*) tree growth. Their study builds on a significant body of knowledge on Northern Jarrah Forest (hereafter jarrah forest) silviculture developed from studies of forest re-growth post-logging (e.g. Abbott & Loneragan 1986 and references therein; Stoneman *et al*. 1997) and newly established stands in areas cleared for bauxite mining (e.g. Grigg & Grant 2009). Bhandari *et al*. (2021) also demonstrate, consistent with previous findings (e.g. Stoneman *et al*. 1997; Grigg & Grant 2009), that thinned jarrah stands exhibit a growth response to applied fertiliser, unlike dense jarrah stands, presumably because growth of the latter is more constrained by water than by nutrient availability. These studies suggest the combination of thinning and fertiliser application will result, over time, in a greater number of large trees per unit area of jarrah forest. However, there is increasing evidence that applying fertiliser, especially phosphorus (P) for jarrah and eucalypt forest restoration reduces floristic diversity, alters plant community structure and may increase fire fuel loads (Daws *et al*. 2013, 2015, 2019a, b; Grant *et al*. 2007; Spain *et al*. 2015; Standish *et al*. 2008; Tibbett *et al*. 2019, 2020). Consequently, we argue that Bhandari *et al*. (2021) have missed critical aspects of the ecology of the jarrah forest, particularly the well-recognised drawbacks of fertiliser application.

JARRAH FOREST ECOLOGY

The jarrah forest on the Darling Range of south-west Western Australia contains tall eucalypts dominated by jarrah, with *Corymbia calophylla* as a sub-dominant (Fig. 1). Unique among vegetation types in Mediterranean climates, the forest contains especially tall jarrah (up to 40 m) trees. Jarrah attains these heights due to its deep root system (up to 40 m; Abbott & Loneragan 1986) enabling access to water stored within the deep, highly weathered regolith. Some trees die due to competition for water, and their pursuit of nutrients and water is more important than any contest for light (Cowling *et al*. 1996). The canopy in the jarrah forest is comparatively open with projective cover rarely exceeding 50% (Abbott 1984) and self-thinning is slow (Stoneman *et al*. 1989).

Remarkable plant diversity on severely phosphorus-impoverished soils

A feature of the ancient deeply weathered nature of the landscape within the South West Australian Floristic Region, including the jarrah forest, is that soil nutrient concentrations, including P, are exceptionally low (Lambers *et al*. 2018; Tibbett *et al*. 2020). Understorey diversity is high, with 400–600 species per km^2 in the jarrah forest (Williams & Mitchell 2003). One factor that may have driven speciation and the maintenance of species diversity in this region is the suite of adaptations that species have evolved to enable growth given such low P concentrations (Lambers *et al*. 2018; Sander & Wardell-Johnson 2011). These adaptations for nutrient and P-acquisition include cluster roots, mycorrhizal symbioses and exudation of carboxylates and phosphatases (Lambers *et al*. 2008, 2018). However, many species are unable to down-regulate their P-uptake capacity when P is applied at concentrations just above the natural range in soils and display symptoms of P-toxicity including leaf necrosis and plant death (Shane *et al*. 2004; Fig. 2).

Returning large trees

From 1820 to the early 1900s, the jarrah forest produced sawlog quality trees of 150 cm diameter at breast height over bark (DBHOB) on an estimated rotation of 800–1000 years. However, almost all high-quality stands were logged prior to 1919, and most of the current forest has been cut two to three times (Abbott & Loneragan 1986). This history has largely transformed the jarrah forest from being dominated by a small number of widely spaced, large-diameter trees to a regrowth forest with relatively higher densities of small-diameter trees (Havel *et al*. 1989). The rapid return of large trees with old growth features has tangible economic benefits, given the logging legacy throughout the jarrah forest. There are few large old trees and many stumps. Tree hollows characteristic of large trees provide critical nesting habitat for threatened fauna such as black cockatoos. Assessing the implications of their findings, Bhandari *et al*. (2021) state that:

Large sized trees resulting from thinning and fertilizer application are likely to provide a greater volume of timber, forage and habitat for arboreal fauna and birds including threatened cockatoos, and more visually appealing forests.

Assuming the annual diameter growth increments reported by Bhandari *et al*. (2021) are maintained over time, their data suggest that the time to grow poles of 30 cm diameter at breast height under bark (DBHUB) into trees with a DBHUB of 80 cm (the average size of nest trees for threatened black cockatoos; Johnstone *et al*. 2013) is approximately 67 years for heavily thinned and fertilised stands, compared with 625 years for unfertilised stands not subject to thinning. However, applying fertiliser in combination with thinning only reduces this time frame to 51 years, so the growth benefits of thinning and fertiliser application (Bhandari *et al.* 2021) were almost entirely due to thinning. Nonetheless, this largely thinning-driven reduction in the time frame to grow trees of >80 cm DBHOB is a significant finding and could potentially make a difference to black cockatoo conservation (Bhandari *et al*. 2021), although the process of hollow formation likely reflects both time and tree age rather than simply being a function of tree size (Stoneman *et al*. 1997). For example, the lowest average age of nest trees recorded for local parrot species is 275 years, and 446 years for local threatened cockatoo species (Mawson & Long 1994).

EVOLVING BEST PRACTICE: THINNING AND FERTILISER APPLICATION

Multiple benefits may accrue from thinning in the jarrah forest. These include:
1) increased growth rates and hence timber production of retained trees (Stoneman *et al*. 1997; Bhandari *et al*. 2021);
2) reduced water use by thinned stands resulting in retained trees being more resilient to a drying climate (Grant *et al*. 2013);
3) reduced water use maintaining ground water levels and stream flows in the face of a drying climate (MacFarlane *et al.* 2010);
4) an increase in inflows to public drinking water dams (MacFarlane *et al.* 2010); and
5) more rapidly setting thinned stands on a trajectory towards developing large trees and a structure more similar to that in old-growth stands prior to European settlement and logging (pre-1820; MacFarlane *et al.* 2010; Bhandari *et al*. 2021). Perhaps this latter benefit is what Bhandari *et al* (2021) meant by 'more visually appealing forests'.

We suggest there are significant downsides associated with applying fertiliser. The earliest fertiliser research focused on the response of jarrah in the context of maximising timber production (e.g. Abbott & Loneragan 1986). The wider impacts of fertiliser on forest dynamics were not considered until jarrah forest restoration started in earnest in the 1980s (Fig. 1). Whereas fertiliser does increase tree growth in thinned stands, it is necessary to assess what impacts this strategy may have on the diverse and unique understorey flora species of the jarrah forest, many of which are long-lived, slow-growing plants with specialised adaptations for P-acquisition (Fig. 2). Research suggests a cautious approach to using P fertiliser in inherently P-impoverished systems is warranted. Research includes negative impacts on both native fungal communities (Hilton *et al*. 1989), and understorey diversity in jarrah forest restored after bauxite mining (e.g. Daws *et al*. 2013, 2015, 2019a; Tibbett *et al*. 2020). Moreover, fertiliser P persists in jarrah forest soils potentially affecting vegetation dynamics for decades after a single application (Daws *et al*. 2019b; Standish *et al*. 2008). These findings are consistent with findings for P-impoverished systems elsewhere in the region (e.g. Lambers *et al*. 2018), and declining species diversity in a range of global studies of nutrient effects on nutrient-limited ecosystems (e.g. Ceulemans *et al*. 2014; Isbell *et al*. 2013; Wassen *et al*. 2005). Multiple short- (<5 years) and long-term (20 years) studies of jarrah forest restoration unequivocally demonstrated that adding fertiliser, especially P, reduces understorey species diversity and alters community composition by stimulating the growth of some highly P-responsive N_2-fixing legume species which outcompete slower-growing species (Daws *et al*. 2013, 2015, 2019a, b; Standish *et al*. 2008; Tibbett *et al*. 2020) and increase fine fuel loads in the understorey (Daws *et al*. 2019a).

The understorey responses to applied fertiliser have not been assessed in the experiment reported by Bhandari *et al*. (2021). Consequently, we believe that this study presents a unique opportunity to further inform this debate, by enabling assessment of long-term fertiliser impacts on the understorey community in the severely nutrient-impoverished environment of the jarrah forest.

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Figure 1. The location of the Inglehope thinning experiment (Bhandari *et al*. 2021) as well as a range of experiments investigating fertiliser application to restored jarrah forest.

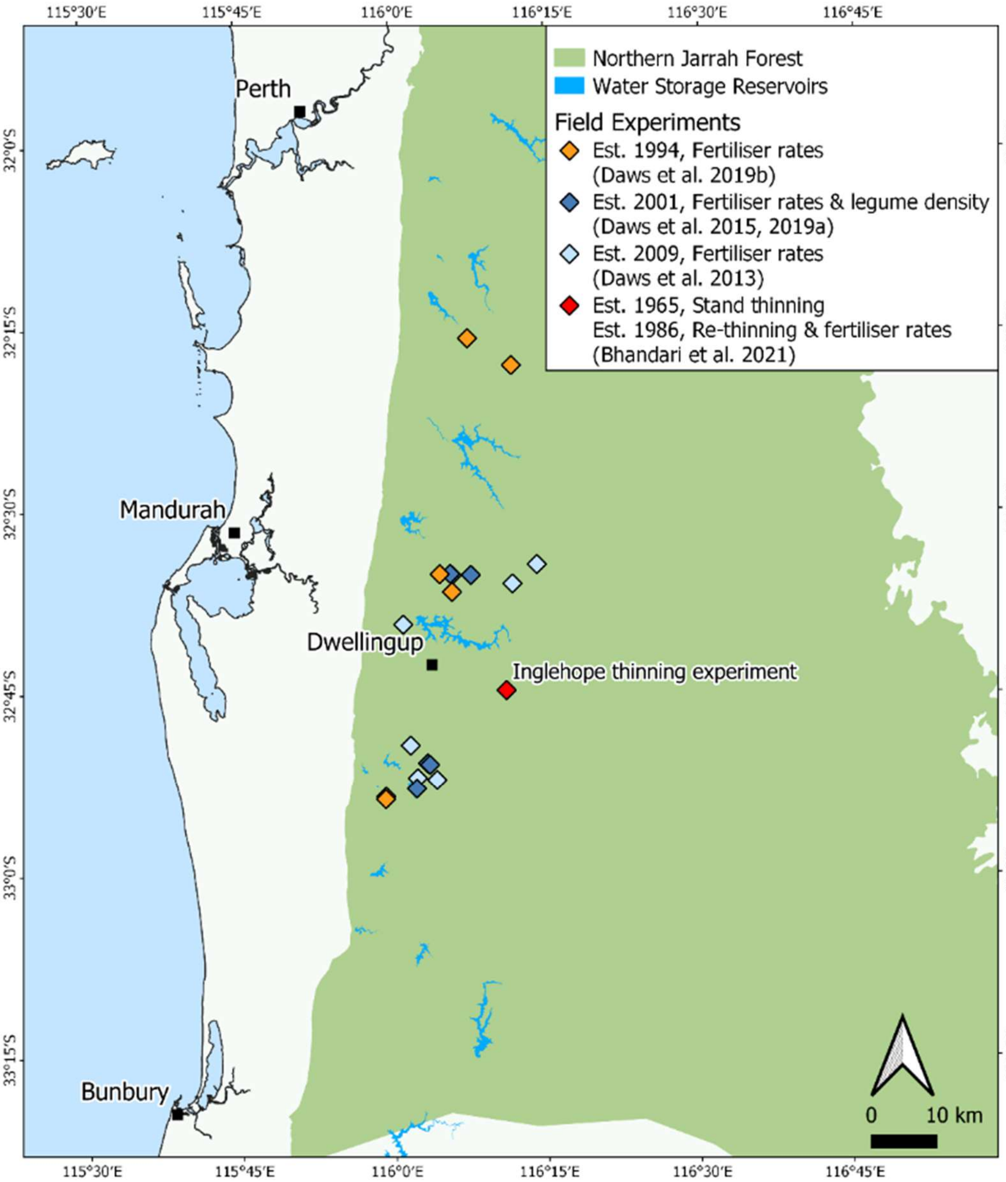

Figure 2. a) An example of the diverse understorey layer in the jarrah forest; b, c) *Banksia grandis* and *Hakea amplexicaulis*, respectively—two species that are sensitive to elevated soil phosphorus concentrations; and d) *Acacia pulchella* a legume that exhibits a vigorous growth response to applied P. Photo credits: a) & b) RJS; c) & d) MID.