Searching for David within the Goliath of alien woody plant invasions in the Western Cape Province

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Despite a few victories in which biocontrol has contained some species of invasive alien woody plants, the war to contain alien invasions and to prevent them from threatening the exceptional plant diversity of the Cape Floristic Region is largely being lost.[1-8] Indeed, these invading plants are estimated to be expanding their range at an average rate of 7% per year.[9]

Apart from releasing more biocontrols and trying to chop out the plants where feasible, are there any other options available? Perhaps inadvertent experiments have been performed by land managers which could provide insights into new ways of managing this alien woody scourge? In densely invaded landscapes, patches of land are on occasion encountered which are mysteriously free of the alien woody invaders. Have these patches been cleared meticulously by land managers, or are there other forces at play? Perhaps the soil conditions are not suitable for the germination of the woody plants' seeds, or there are specific seed predators present in the patches, but not in the surrounding landscape? Or perhaps the plants in these patches are more competitive than the invading woody plant seedlings and prevent them from recruiting by smothering them above ground, strangling their roots below ground, releasing toxins in the soil that damage them, or taking up nutrients faster than them?

Taking these questions into account, we searched for sites in and around the southwestern Cape Floristic Region where there were sizeable patches (at least several hectares) of non-invaded land within densely invaded landscapes. We found seven such sites where there were no plausible reasons for why alien woody plants had not invaded certain patches of land. Land use histories of the sites are provided in Table 1. Three of these tree-free patches (at the Blaauwberg, Rooshook and Vergelegen sites) were old agricultural lands, with mixes of herbaceous alien weeds, alien grasses and ruderal fynbos. The other four patches (at the Bothasig, Dassenberg, Klein Dassenberg and Joostenbergkloof sites) were in previously uncultivated vegetation i.e. intact fynbos. We analysed the chemistry of topsoils in the non-invaded patches and the surrounding invaded landscape.

Table 1: Land history and vegetation type (by Mucina and Rutherford[25]) of the seven study sites

Site	Sub-sites (*n*)	Land history	Vegetation type
Blaauwberg[1]	N-En (20) Mod (17) En (20)	N-En sub-sites were previously cultivated and left fallow since the late 1980s. En sub-sites were uncultivated.	Cape Flats Sand Fynbos
Bothasig[2]	N-En (5) En (5)	Before 2010, the entire site was managed as a municipal park and mowed extensively. All sub-sites were uncultivated.	Cape Flats Sand Fynbos
Dassenberg[3]	N-En (20) En (20)	The site was historically used for grazing. All sub-sites were uncultivated.	Atlantis Sand Fynbos
Joostenbergkloof[4]	N-En (20) En (20)	All sub-sites were uncultivated.	Swartland Shale Renosterveld
Klein Dassenberg[5]	N-En (18) En (20)	The site was historically used for grazing. All sub-sites were uncultivated.	Atlantis Sand Fynbos
Rooshook[6]	N-En (18) En (21)	N-En sub-sites were fallow lands last cultivated 15 years ago. En sub-sites were uncultivated.	Swartland Shale Renosterveld and Swartland Alluvium Fynbos
Vergelegen[7]	N-En (20) ModAg (10) ModP (10) En (20)	N-En and ModAg sub-sites were last cultivated 15 years ago. ModP sub-sites were recently felled pine plantations. En sub-sites were uncultivated.	Boland Granite Fynbos

[1]Blaauwberg Nature Reserve; [2]Bothasig Fynbos Nature Reserve; [3]Dassenberg Coastal Catchment Partnership; [4]Joostenbergkloof Farm; [5]Dassenberg Coastal Catchment Partnership – Klein Dassenberg Section; [6]Rooshook Farm; [7]Vergelegen Wine Estate

N-En, non-encroached plots, free of alien woody plants or seedlings; En, encroached plots, densely invaded with alien woody plants; Mod, moderately encroached plots, scattered with alien woody plants; ModAg, moderately encroached and historically cultivated; ModP, moderately encroached and historically pine plantations

Although it is feasible that certain soil physical or organic chemical properties had prevented germination of the alien woody plant seeds, or certain seed predators had consumed the seeds before they germinated at our study sites, we focused our research on soil inorganic nutrients, which we consider to be a more likely explanation for the constraint of the woody plants. In particular, we tested the explanatory power of what is known as the Catabolic Theory.[10-12] This theory holds that short plants (namely herbs, grasses and shrubs) will outcompete tree seedlings when demand for catabolic nutrients (e.g. P, Cu and Zn) is met by supply – with this demand being

partly dependent on the availability of anabolic nutrients (e.g. B, Mg and Mn).[13-15] The reasoning underpinning the theory is that if a soil nutritional regime favours the production over the metabolism of photosynthates, then a photosynthate surplus arises, which will be used for synthesising wood. The concept of short plants outcompeting tree seedlings is not new[16], and the Catabolic Theory has been corroborated by studies on treeless vegetation surrounded by treed vegetation in both Australia and South Africa[14,15].

The results of our investigation support the Catabolic Theory. Although many nutrients are likely to be involved in the interplay between the short plants in the non-invaded patches and the alien woody invaders, two nutrients were particularly noteworthy: phosphorus (P) and boron (B). Old agricultural lands were consistently enriched in P, compared with the adjacent invaded landscapes (Figure 1). This observation suggests that an ample amount of P allows the ruderal herbaceous species to outcompete the alien woody plants. Moreover, in the case of B, all of the non-encroached sites, with the exception of Joostenbergkloof, had significantly lower concentrations of B than did the surrounding invaded landscape (Figure 2). This finding suggests that a scarcity of B favours fynbos plants over woody plant invaders.

What are the management implications of our findings? Although soil amendments are not traditional weapons in the arsenal of conservationists, they could be used to manipulate the availability of certain nutrients, ultimately constraining the invasion of woody plants into fynbos. For example, clay minerals such as illite and vermiculite are strong binders of B.[17-19] Based on the findings of our study, their application could potentially increase the competitive strength of fynbos plants relative to woody alien invaders. In certain farming environments, the application of P fertilisers may be appropriate for constraining woody plant invasions by increasing the competitive strength of grasses and herbs. Plot-scale experiments would be needed to determine the efficacy of such treatments before landscape interventions could be recommended. Soil amendments on a landscape-scale may not even be necessary to halt woody plant invasions – there may be opportunities to create strips of land resilient to woody plants around heavily infested landscapes. Such strips could be used to contain the infestations in much the same way that firebreaks are used to contain fires.

Although soil amendments would be a radical approach to conserving fynbos, the current threat from woody alien invaders is so grave that all options need to be put on the table and carefully scrutinised, no matter how startling. Furthermore, new ideas and new experiments are needed to develop a deeper understanding of why the woody alien invaders are so pervasive in the first place. Without such an understanding, it is difficult to pioneer new options for management in a coherent, systematic manner.

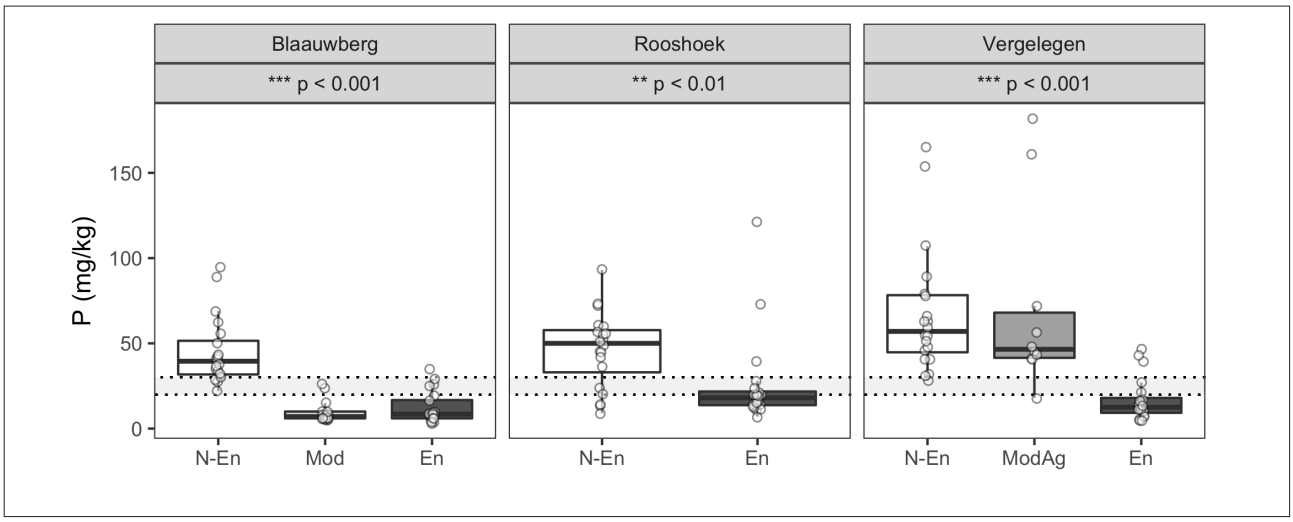

Figure 1: Phosphorus concentration (mg/kg) of encroached (En), moderately encroached (Mod), non-encroached (N-En), and moderately encroached historically cultivated (ModAg) patches at the four previously cultivated study sites. Horizontal grey bars indicate critical deficiency ranges (20–30 mg/kg).

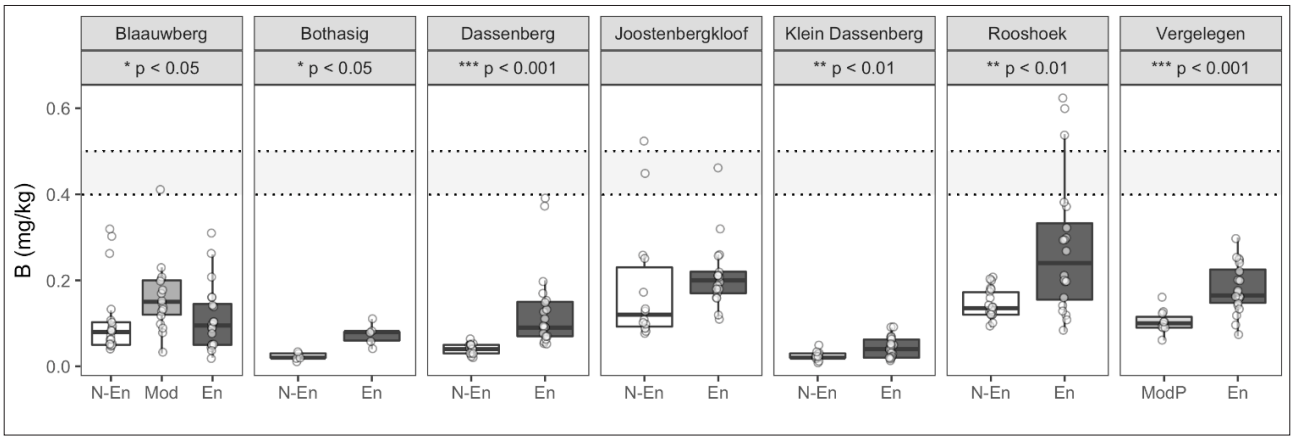

Figure 2: Boron concentration (mg/kg) of encroached (En), moderately encroached (Mod), non-encroached (N-En), and moderately encroached historically pine plantation (ModP) patches at the seven study sites. Horizontal grey bars indicate critical deficiency ranges (0.4–0.5 mg/kg). Fertilisation of agricultural lands at Vergelegen (N-En and ModAg) greatly increased B concentrations. These fertilised sites are consequently excluded from the graph.

The simple explanations of a lack of natural predators[20-22] and carbon dioxide fertilisation[23,24] are surely just valuable chapters in a complex story. A long-term fertilisation experiment in a South African savanna has shown conclusively that changes in soil nutrient regimes can either promote or entirely constrain woody plant encroachment.[15] It is highly probable that soil nutrients exert similar strong controls on woody plants in all biomes globally, not only in South African savannas. There are 13 plant nutrients which have the potential to affect the competitive interplay between fynbos plants and their woody alien invaders. It is high time that we started understanding these effects.

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