

The cost of standing tall: wood nutrients associated with tree invasions in nutrient-poor fynbos soils of South Africa

MIRANDA D. REDMOND,^{1,†} TARYN L. MORRIS,² AND MICHAEL C. CRAMER²

¹Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colorado 80523 USA

²Department of Biological Sciences, University of Cape Town, Private Bag X1, Rondebosch 7701 South Africa

Citation: Redmond, M. D., T. L. Morris, and M. C. Cramer. 2019. The cost of standing tall: wood nutrients associated with tree invasions in nutrient-poor fynbos soils of South Africa. *Ecosphere* 10(9):e02831. 10.1002/ecs2.2831

Abstract. Tree invasions into native grasslands and shrublands are global phenomena, with alien tree invasions occurring on nearly every continent. We hypothesized that wood nutrient concentrations are a key trait to enable successful tree invasions in regions limited by soil nutrient availability, such as the fynbos vegetation of the Cape Floristic Region of South Africa. We sampled wood and bark of a height range of indigenous and alien woody species within the Cape Floristic Region. We used linear regression and phylogenetic analyses to assess associations between wood nutrients and tree height and analysis of variance to assess how wood nutrients vary across vegetation types. Alien trees had lower wood nutrient concentrations than many native trees, and nutrient concentrations, especially not only N and P, but also Mg and K, were negatively associated with tree height. These results suggest that recent tree invasions into the nutrient-poor fynbos shrublands may be a result of low wood nutrient concentrations that allow the alien trees to successfully overtop the native vegetation. This indicates that wood nutrient concentrations may be a useful trait to predict whether an alien tree species has a greater potential of becoming invasive in regions with limited soil nutrients.

Key words: *Acacia*; Afromontane; *Eucalyptus*; Fynbos; nutrient; *Pinus*; tree invasion; wood; wood density.

Received 27 June 2019; **accepted** 1 July 2019. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail: Miranda.Redmond@colostate.edu

INTRODUCTION

Globally, sparsely wooded grasslands and shrublands appear particularly prone to woody invasions (Richardson et al. 1994, Gordon 1998, Rundel et al. 2014). These alien tree invasions have been associated with reduced biodiversity (Richardson et al. 1989), altered fire regimes (Brooks et al. 2004, Mandle et al. 2011), and a loss in ecosystem services (Maitre et al. 1996, Richardson and van Wilgen 2004). One of the key elements for successful invasions worldwide is the ability of the introduced species to competitively dominate the native vegetation. This domination commonly results from the invasive species attaining a larger biomass than the native flora,

enabling both light exclusion and below-ground resource interception of water and nutrients (Morris et al. 2011). Less clear though is how these invasive woody species are able to invade previously non-forested ecosystems, particularly in regions where native tree species are present that have been unable to occupy the niche taken over by the alien invaders.

Major determinants of woody cover in these non-forested, open vegetation types such as savannas, grasslands, and shrublands fall into two categories: top-down and bottom-up controls (Weltzin and Coughenour 1990, Staver et al. 2011). Bottom-up controls include resource limitations such as water availability, soil nutrients, and access to light (Weltzin and Coughenour

1990), while top-down controls include herbivory and disturbances such as fire and windthrow (Bond 2008). Correlative analyses indicate that among other factors, such as water availability, low-nutrient soils are associated with the presence of open landscapes at the continental scale (Fisher et al. 2012). Yet, it is unclear whether low-nutrient soils in forests directly limit above ground biomass except in extreme cases (Vitousek and Sanford 1986, Kitayama and Aiba 2002). N_2 fixation has been an important trait to allow trees to invade previously non-forested ecosystems within areas of poor soil nutrients, such as in the fynbos biome of South Africa (Richardson and van Wilgen 2004), Mediterranean coastal dune ecosystems (Marchante et al. 2008), and dry scrub ecosystems of Hawaii (Vitousek and Walker 1989). Yet, non- N_2 -fixing species, particularly of the genus *Pinus* (Richardson et al. 1994, Nuñez et al. 2017) and *Eucalyptus* (Richardson and Rejmánek 2011), have also invaded previously non-forested areas with nutrient-poor soils across continents. As a result, multiple life history strategies have been identified to predict successful tree invasions, including enhanced seed production (Richardson et al. 1987), greater longevity (Kruger 1977), and production of nutrient-rich seeds (Mitchell and Allsopp 1984), in addition to N_2 fixation (Richardson and Cowling 1992).

We hypothesize that wood nutrients are another key trait that enables successful tree invasions in regions limited by soil nutrient availability. Wood contains significant concentrations of nutrients (Chave et al. 2009), and although these nutrients are much lower in concentration than leaf nutrients, when scaled by biomass the bulk of aboveground nutrients are associated with the wood (Bond 2010). Thus, regions with low-nutrient stocks may restrict the accumulation of woody biomass among species with high wood nutrients (Cramer 2012), suggesting that only trees with low wood nutrients or other nutrient adaptations (e.g., N_2 fixation) are able to establish and grow to overtop native vegetation.

This research focuses on the Cape Floristic Region (CFR) of South Africa where the shrubby fynbos biome has been heavily invaded by alien tree species, including Australian *Acacia* spp., *Hakea* spp., *Eucalyptus* spp., and *Pinus* spp.

(Mostert et al. 2017). A wide range of Afromontane native tree species are present, yet are very restricted in their distribution. On the contrary, invasive alien trees have been able to thrive in the adjacent shrubby (<2 m tall) areas, which were historically devoid of trees. This raises the question: Why are alien tree species able to thrive in areas that native tree species cannot? While the reasons for the invasive success of alien trees in shrublands are unclear and likely complex (Morris et al. 2011), it is possible that highly productive timber species such as *Pinus halepensis* Mill. produce nutritionally cheaper wood than slow-growing hard-wood indigenous species.

We sampled soil, bark, and wood of a height range of indigenous and alien woody species occurring within the CFR of South Africa to test the following hypotheses: (1) Bark and wood nutrient concentrations are inversely related to the height that species can achieve in the CFR, an area where nutrient limitations are common; (2) woody plants with high wood nutrient concentrations will only be able to grow tall in areas where soil nutrients are in adequate supply; and (3) alien invasive tree species will have lower wood nutrient concentrations than native Afromontane tree species. This raises the possibility that alien species that have lower concentrations of nutrients in wood than native species may be able to grow taller and consequently invade the native vegetation.

MATERIALS AND METHODS

This study was conducted in nature reserves in two study areas within the Western Cape, South Africa: the Jonkershoek and Orange Kloof study areas. The Jonkershoek study area comprises the Assegaaibosch Nature Reserve (-33.9693° S, 18.9232° E) and the adjacent Jonkershoek Nature Reserve (-33.9873° S, 18.9545° E). This study area contains the upper section of the Jonkershoek valley, surrounded by high Table Mountain Sandstone peaks overlying basement granite. The indigenous vegetation in the valley is Boland Granite Fynbos with patches of Cape Winelands Shale Fynbos and is dominated by Kogelberg Sandstone Fynbos on the upper slopes (Mucina and Rutherford 2006). Afromontane forests are present in riparian areas and in shallow soils on rocky scree slopes (Rebello et al. 2006). Large

sections of the valley are dominated by non-indigenous commercial plantations of *Pinus* species and also with *Eucalyptus cladocalyx*, *Hakea sericea*, *Paraserianthes lophantha*, and various *Acacia* and *Pinus* species invasions in the lower reaches of the valley.

The Orange Kloof Forest Reserve (33.9948° S, 18.3944° E) is a 285 ha region of the Table Mountain National Park in the Western Cape. The vegetation is Peninsula Sandstone Fynbos on west-facing valley slope, while the lower valley and large sections of the east-facing slope are dominated by indigenous Southern Afrotemperate Forest with patches of endangered Peninsula Granite Fynbos (Mucina and Rutherford 2006). Multiple invasive species are present in the lower sections of the reserve similar to Jonkershoek.

In each of the two study areas, we sampled all alien invasive (hereafter invasive) tree species, all alien non-invasive (alien) tree species, five common native fynbos (fynbos) shrub species, five common native forest edge (edge) tree species, and five common native Afromontane (forest) tree species (see Appendix S2: Table S1 for a list of all species sampled). We sampled a total of 32 woody evergreen species (154 individuals) across 18 sites in the Orange Kloof study area and 29 sites in the Jonkershoek study area. In order to minimize potential soil and climatic growth conditions between the different species sampled, we selected sites that contained a combination of indigenous forest, edge, and fynbos elements together with alien species, although due to challenges of finding sites with a mix of all four elements we often only had a subset present in any given site. For all species, three mature plants from each study species were selected for sampling within each of the two study areas, although only two individuals were sampled for some species (Appendix S2: Table S1). At any given site, we sampled as many species that were present, unless we had already sampled three individuals of that species at previous sites. We only sampled one individual of a species within a site to obtain a better representation of wood nutrient variability within a species. This was not possible for a few invasive species that were only present in one part of the study area (Appendix S2: Table S1).

The height of each woody plant >5 m was recorded using a hypsometer (Forestry Pro; Nikon, Tokyo, Japan) and with a ranging rod

when less than 5 m in height. Bark, sapwood, and heartwood samples (~5 g dry weight) were collected from each woody plant at a standard height of ~1 m above ground level. Bark samples (~5 × 5 cm) were collected using a hatchet to the cambial layer and thus include both the inner and outer bark. Wood samples were collected by taking 1–3 cores using a 4.5 mm diameter wood corer or by using a saw to collect a cross section. The volume of each sample was calculated by measuring the water volume displacement of the cylindrical core. Samples were dried for 48 h in a forced draft oven at 80°C, and the dry weight of the wood samples was divided by the associated volume to calculate the wood density of each plant. Three soil samples were collected and aggregated at each site and were all within 10 m of sampled trees. The organic layer was removed before collection, and soil was collected with an auger where possible or with a trowel in rocky locations. The samples were collected to a depth of 0.3 m. Bark, wood, and soil sampled were analyzed for total P, K, Ca, and Mg concentrations by the Institute for Plant Sciences (Department Agriculture: Western Cape, South Africa) and for total N by the Department of Archeometry (University of Cape Town) using mass spectrometry analyses (Appendix S1). All data used in this manuscript are available in Data S1.

Statistical analyses

We tested whether wood nutrient concentrations and density limit the height that a species can achieve in our study area by performing two separate sets of analyses: multiple linear regression analyses and quantile regression analyses. For the multiple linear regression analyses, the maximum height of each species measured was our response variable and mean wood nutrient concentrations for all macronutrients (N, P, K, Ca, Mg) and wood density were our predictor variables. We included wood density as a predictor variable because the total amount of nutrients in a given volume of wood is not only dependent on the concentrations of the nutrients but also dependent on the density of the wood. Predictor variables were not strongly correlated with one another (Pearson's $r < 0.49$), and the variance inflation factor was always <2. We performed model selection of the complete model using Akaike information criterion modified for small

sample sizes (AIC_c ; Akaike 1973). To do this, we compared the AIC_c of all possible model subsets of our complete model using the dredge function in the R package MuMIn and report the results of the model with the lowest AIC_c values.

We performed quantile regression analyses to test whether wood nutrients and density each place an upper constraint on the maximum tree height that a species can achieve in our study area. We used the *rq* function in the R package quantreg (Koenker 2015) and performed quantile regression analyses at the 90% quantile for each predictor variable with observed maximum tree height as our response variable. Confidence intervals were obtained using the rank inversion method with the default assumption of errors as independent and identically distributed (iid) and *P*-values were calculated using *se = iid*, which assumes errors are iid and computes an estimate of the asymptotic covariance matrix (Koenker 1994).

We performed similar analyses on bark nutrient concentrations (see Appendix S3 for bark results), but we focus here on wood (i.e., combined heartwood and sapwood) nutrient concentrations because the majority of nutrients are in the wood. We combined heartwood and sapwood as these were often difficult to distinguish and because wood nutrient concentrations were more strongly related to tree height. Sapwood nutrients and density were highly correlated with wood nutrients and density (Pearson's $r > 0.81$), and preliminary analyses suggest similar results when modeling the effects of sapwood nutrients and density as compared to the combination of sapwood and heartwood nutrient and density—largely because sapwood contains the majority of the nutrients (Appendix S2: Table S3).

We used mixed-effect modeling to test our hypothesis that trees with high wood nutrient concentrations will only be able to grow tall in areas where soil nutrients are in adequate supply. For these analyses, we focused on the wood nutrients identified from the analysis above that were important for influencing tree height: N, P, Mg, and K and we performed separate analyses for each of these nutrients. Woody plant height was our response variable and soil nutrient concentration (N, P [total and available], Mg, or K), mean species wood nutrient concentration (N, P,

Mg, or K), and their interactions were our predictor variables. To account for variability in height across species, we included a random intercept for species in each model. Similar to above, we performed model selection by comparing the AIC_c of all possible model subsets of our complete model and selected the model with the lowest AIC_c . Continuous predictor variables were z-scaled, and thus, standardized regression coefficients (β_{std}) are reported. Analyses were done in R version 3.1.1 (R Core Team 2014).

One-way ANOVAs were performed to compare differences in nutrient concentrations among the five woody species groupings (forest, fynbos, edge, native, invasive). We performed post hoc pairwise comparisons among the different groups using the Tukey HSD method to adjust *P*-values for multiple comparisons. We excluded all N_2 -fixing species (seven species) from the analysis of wood N concentrations. This is because for this analysis, we were comparing wood N concentrations between species groupings and hypothesized that N_2 -fixing species would have higher wood N concentrations, yet we only sampled N_2 -fixing species in the edge and invasive groups. Because of this, we performed a two-way ANOVA to assess how wood N concentrations varied based on N_2 -fixing status, species groupings (two levels: forest and edge, the only two groupings that N_2 -fixing species were sampled), and the interaction between N_2 -fixing status and species group.

Phylogenetic generalized least squares (PGLS) was conducted to test whether observed maximum tree height was significantly associated with bark and wood density and nutrient concentrations while controlling for phylogenetic structure. Family names were obtained using the *phylomatic_names* function (R package *brranching*) using the Angiosperm Phylogeny Group database (Chamberlain 2016). The phylogenetic tree was created using the *phylomatic* function based on Zanne et al. (2014). Phylogenetic generalized least squares was conducted using the generalized least squares in the package *nlme* with within-group correlation structure specified as Pagel's lambda. The significance of the PGLS model was assessed using the ANOVA function in the package *car* (Fox and Weisberg 2011).

RESULTS

Wood nutrient concentrations varied greatly across the 32 species sampled in the Western Cape of South Africa, with some species averaging over 10-fold higher wood nutrient concentrations than other species (Appendix S2: Table S2). Ordinary least squares (OLS) analyses revealed a negative relationship between wood N ($\beta_{\text{std}} = -4.1$, $P = 0.02$) and to a lesser extent wood P ($\beta_{\text{std}} = -2.9$, $P = 0.07$) and the maximum tree height observed at the two reserves sampled in the nutrient-poor soils of the Western Cape, South Africa (Fig. 1), supporting our hypothesis that wood nutrients limit tree height in an area where nutrient limitations are common. When controlling for phylogenetic structure (PGLS analyses), there was still a strong negative relationship between wood N and maximum tree height ($\beta = -1.8$, $P = 0.002$), but not wood P ($P = 0.48$), largely because more closely related species have more similar wood P concentrations (Appendix S3: Fig. S2). Our OLS model results suggest that the other wood nutrients examined (Ca, Mg, and K) and density were not associated with maximum tree height, as only wood N and P were in the most parsimonious (lowest AIC_c) model. Quantile regression analyses further suggest that wood N and P limit tree height (Fig. 1), as well as wood K and Mg (Fig. 1), although notably our sample size was small ($n = 32$) for upper quantile regression analyses, which limits our power to detect significant results and also leads to regression coefficients that are highly sensitive to a single data point and thus greater confidence intervals. Similar to OLS analyses, wood density and wood Ca were not associated with tree height with quantile regression (Fig. 1). Yet when controlling for phylogenetic structure, maximum tree height was positively associated with wood density ($\beta = 0.42$, $P = 0.003$; Appendix S3: Fig. S3) and, consistent with OLS results, not associated with wood K, Mg, or Ca ($P > 0.3$; Appendix S3: Table S1).

We found limited support for our hypothesis that trees with high concentrations of nutrients in wood will only be able to grow tall in areas where soil nutrients are in adequate supply. There was a weak, positive association between tree height and soil K ($\beta_{\text{std}} = 0.53$; $P = 0.07$) and soil Mg ($\beta_{\text{std}} = 0.74$; $P = 0.02$), but our model

results suggest that there was no interaction between those soil nutrients and wood K or Mg (Appendix S3: Table S2). Soil N, soil total P, and soil available P were not associated with tree height (Appendix S3: Table S2).

There were significant differences in wood nutrient concentrations between vegetation types for wood N (non-N₂-fixing species only; $P = 0.01$) and wood K ($P = 0.02$), and to a lesser extent for wood Mg ($P = 0.07$). Post hoc pairwise comparisons suggest that wood N and wood Mg of invasive species were lower than native forest edge species ($P < 0.09$; Fig. 2) and that invasive and alien species had lower wood K concentrations than native forest species ($P < 0.07$; Fig. 2). While not significant for all wood nutrients examined, invasive and alien species generally had lower wood nutrients than native forest and edge species, supporting our hypothesis that low wood nutrients have contributed to the success of recent tree invasions in the nutrient-poor fynbos soils. There was a significant interaction between N₂-fixing status and vegetation type (invasive vs. edge) on wood N ($P = 0.01$). Among invasive species, N₂ fixers had significantly higher wood N than non-N₂ fixers ($P = 0.007$), yet among edge species there were no differences in wood N ($P = 0.99$; Appendix S3: Fig. S4).

DISCUSSION

Two key findings emerged from our study: (1) Alien trees in the CFR of South Africa have lower wood nutrients than many native trees and (2) woody species with lower wood nutrients appear to be able to grow taller in a region characterized by nutrient-poor soils. Taken together, these results suggest that the successful alien tree invasions in the nutrient-poor fynbos shrublands may partially be a result of low wood nutrients that allow the alien trees to successfully overtop the open-canopy native vegetation. This indicates that wood nutrients, especially N and P, may be a useful trait to predict whether an alien tree species has a greater potential of becoming invasive in regions with limited soil nutrients.

The CFR comprises an extremely diverse assemblage of species with low-stature open-canopy vegetation juxtaposed with taller closed-canopy forests (Power et al. 2017). The co-existence of open- and closed-canopy vegetation across

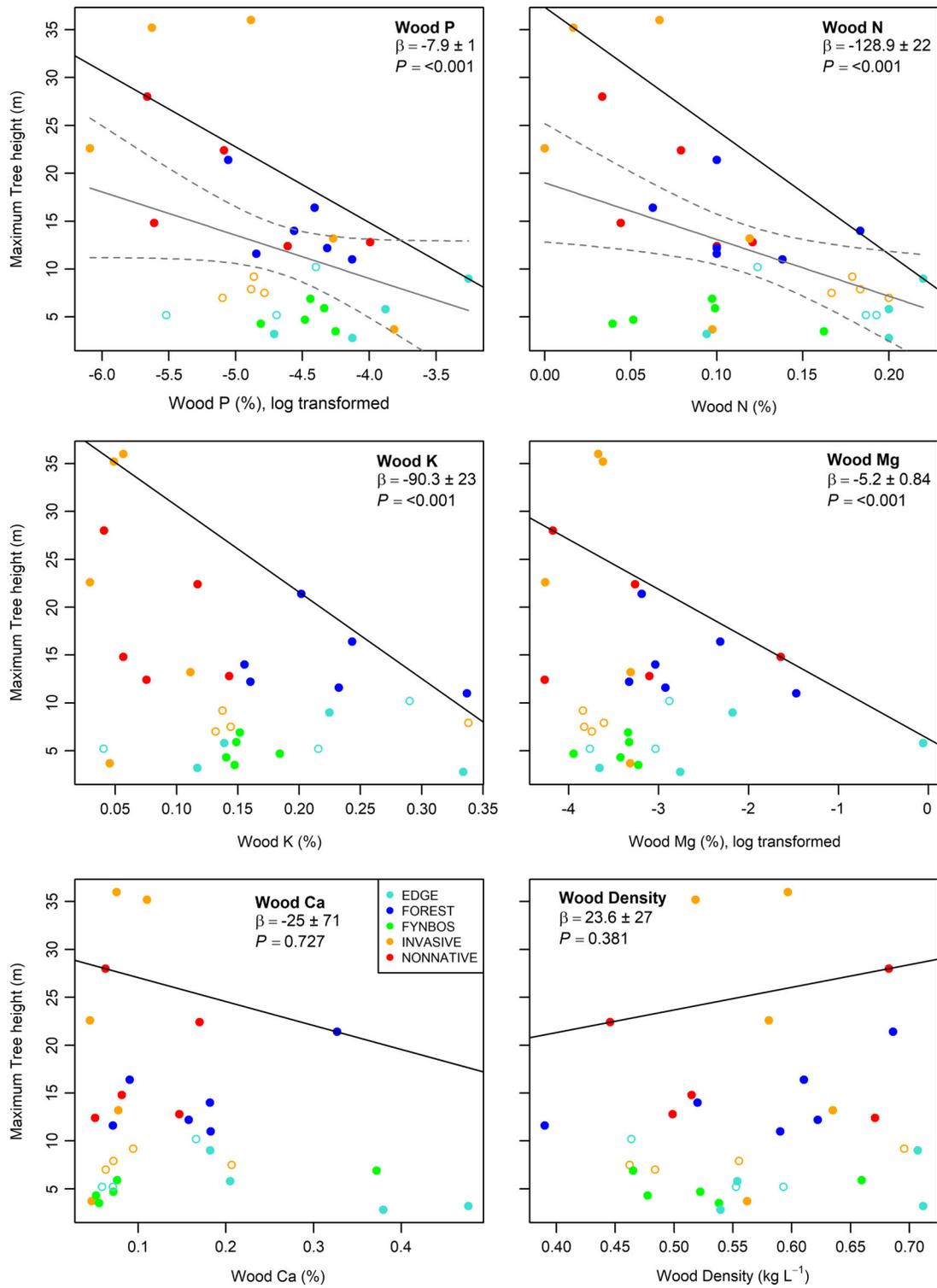


Fig. 1. Relationship between wood density and nutrient concentrations and observed maximum woody

(Fig. 1. *Continued*)

species height. Solid black lines are of the 90% quantile regression line, and the 95% confidence interval of the slope (β) of the 90% quantile regression line is provided in parentheses. Solid gray lines (N and P only) show the predicted mean effect (dashed gray lines show 95% CI) based on ordinary least squares analyses. Open circles are N₂-fixing species.

distinct boundaries in soil derived from the same geology and in the same climatic regime has been associated with the emergence of alternate stable states (Cramer et al. 2019). These alternate states are associated with distinct soil properties that are likely driven by nutrient accumulation in closed-canopy circumstances and depletion due to recurrent fires in the open-canopy (i.e., fynbos) vegetation. Afromontane forests seldom burn (Kraaij et al. 2013) and light limitation in these undisturbed forests exclude open-canopy species (Manders 1990), and likely also exclude alien woody species that have established in disturbed Afromontane forests. In contrast, many alien tree species successfully encroach in the low-nutrient open-canopy vegetation, suggesting either that nutrient availability does not limit tree establishment and growth (Bond 2010) or that these alien invasive trees can tolerate low-nutrient availability. Our data provide support for the ability of some alien invasive trees to tolerate nutrient limitations.

One of the abiding mysteries regarding the invasiveness of the CFR is why such a nutrient-poor ecosystem is so prone to invasion (Cramer et al. 2014). The flora of the CFR and fynbos in particular have an array of adaptations to enable survival in nutritionally poor environments. For example, many Proteaceae, Restionaceae, and Cyperaceae have cluster or cluster-like roots that improve nutrient access, particularly access to P (Lamont 1972, Lambers et al. 2006, Shane et al. 2006). Sclerophylly is also common in the CFR resulting in leaves that are long-lived and able to reduce nutrient costs by reducing leaf loss (Cramer et al. 2014). Despite these adaptations, our results suggest that wood nutrients limit tree height in the CFR and that soil nutrients limit the establishment of native Afromontane trees, which had generally higher wood nutrients, in fynbos soils (Power et al. 2017).

Our findings also suggest that low wood nutrients are a key trait to enable the successful establishment of alien trees in fynbos

shrublands, in addition to other commonly discussed traits, such as N₂ fixing and dispersal ability (Morris et al. 2011). This, however, leaves the intriguing question as to why indigenous open-canopy CFR species have not used nutritionally cheaper wood to enable height growth, and thus seize competitive advantage? This may be explained by the environmental circumstances that prevented the native flora from evolving to capitalize on the formation of nutritionally cheap wood. In particular, regular fires (Kraaij et al. 2013) may have prevented fynbos species from deriving benefit from overtopping their competitors. Reduced fire frequency as a result of fire suppression in the early to mid-1900s (Van Wilgen et al. 2010) may have allowed fire-adapted alien trees to successfully establish and overtop fynbos species. Although fynbos species do have relatively nutritionally cheap wood (Fig. 2), this has likely not been leveraged for height growth due to historic fire frequency.

Whereas our results suggest that wood nutrients can be a trait used to predict successful establishment of alien species in fynbos shrublands, it does not appear to be predictive of whether those species will become widespread invaders. This is likely because a suite of factors influences the invasibility of alien trees, including introduction history and human dispersal (van Wilgen et al. 2011), prolific seed production (Gibson et al. 2011) and resource access and conservation (Richardson and Cowling 1992, Morris et al. 2011), and more (see Richardson and Cowling 1992 for a review of common life history attributes of invasives in the fynbos shrublands). In our study, we only classified trees as invasive if established individuals were found throughout multiple areas of fynbos shrublands, rather than simply in planted regions. Yet, we did not take into account the time since planting of our alien vs. alien invasive species, which may have differed.

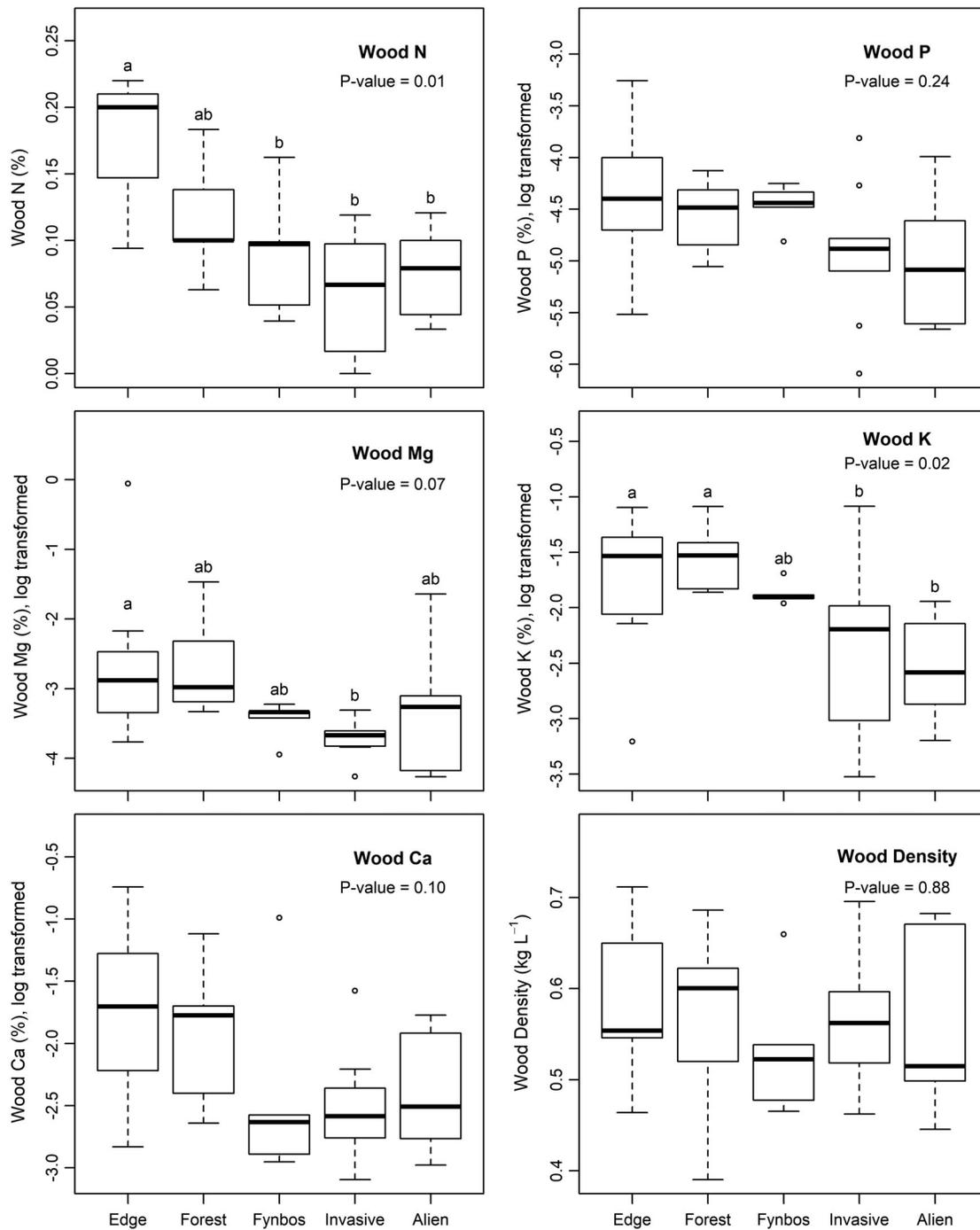


Figure 2. Average wood density and nutrient concentrations among the five different categories: indigenous forest (Forest), forest–fynbos boundary areas (Edge), fynbos (Fynbos), alien invasive (Invasive), and alien non-invasive (Nonnative) species. These data exclude all N_2 -fixing species (seven species). One-way ANOVA was performed to assess the effects of vegetation type on wood density and nutrient concentrations, and the P -value for each tree category is shown in the upper right corner of each panel. Different letters denote significant differences ($\alpha = 0.10$) between vegetation types based on Tukey’s HSD.

We found no relationship between tree height and soil N or P, even among trees with high wood nutrients. This was counter to our hypothesis and may be due to several possible reasons. First, we were unable to sample soil nutrients several meters deep, and as such our estimates of soil nutrients were from soil samples taken at a single time period and at a relatively shallow (10 cm) depth. Yet, these deeper soil layers are often a critical component of total soil nutrient stocks in these nutrient-poor ecosystems (Bond 2010). These samples were also only taken at a single point within 10 m of each tree. The lack of an association may thus be due to uncertainty in our estimates of soil nutrient availability.

The invasion of alien trees in open vegetation types across the globe has strongly altered ecosystem structure and function (Richardson et al. 1989, Brooks et al. 2004, Mandle et al. 2011) and led to reductions in important ecosystem services (Maitre et al. 1996, Richardson and van Wilgen 2004). The cause of these invasions is likely a result of a suite of factors, such as human introductions, reduced fire frequency, and changes in climate, yet the specific traits of these alien trees have allowed them to become highly prolific in the new environment. Traits often discussed in enabling successful invasions include drought tolerance, high growth rates, N₂-fixing ability, and long-distance dispersal (Richardson and Cowling 1992, Morris et al. 2011, Funk et al. 2016). Our data suggest not only that wood nutrients appear to limit tree height in nutrient-limited regions, but also that low wood nutrients are another key trait to allow for these alien trees to outcompete native vegetation by enabling these trees to grow taller under nutrient-poor conditions. Further research is needed to assess whether these relationships are found in other invaded regions of the globe characterized by poor soil nutrients, as well as planting experiments of species with similar traits but vary in wood nutrient concentrations.

ACKNOWLEDGMENTS

We are grateful to Simon Power, Edward Chirwa, and Rowan Gaffney for help in the field. This research was supported by a USAID Research and Innovation

Fellowship and an NSF Graduate Research Fellowship to M.D. Redmond (Grant No. DGE-1144083).

LITERATURE CITED

- Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* 39:641–659.
- Bond, W. J. 2010. Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. *Plant and Soil* 334:47–60.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677–688.
- Chamberlain, S. 2016. *branching: fetch "Phylogenies" from many sources*. R package version 0.2.0. <https://CRAN.R-project.org/package=branching>
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Cramer, M. 2012. Unravelling the limits to tree height: a major role for water and nutrient trade-offs. *Oecologia* 169:61–72.
- Cramer, M. D., S. C. Power, A. Belev, L. Gillson, W. J. Bond, M. T. Hoffman, and L. O. Hedin. 2019. Are forest-shrubland mosaics of the Cape Floristic Region an example of alternate stable states? *Ecography* 42:717–729.
- Cramer, M. D., A. G. West, S. C. Power, R. Skelton, and W. D. Stock. 2014. Plant ecophysiological diversity. Pages 248–272 *in* N. Allsopp, J. F. Colville, G. A. Verboom, and R. M. Cowling, editors. *Fynbos: ecology, evolution and conservation of a Megadiverse region*. Oxford University Press, Oxford, UK.
- Fisher, J. B., G. Badgley, and E. Blyth. 2012. Global nutrient limitation in terrestrial vegetation. *Global Biogeochemical Cycles* 26:GB3007.
- Fox, J., and S. Weisberg. 2011. *An R Companion to Applied Regression*. Sage, Thousand Oaks, California, USA.
- Funk, J. L., R. J. Standish, W. D. Stock, and F. Valladares. 2016. Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology* 97:75–83.
- Gibson, M. R., et al. 2011. Reproductive biology of Australian acacias: Important mediator of invasiveness? *Diversity and Distributions* 17:911–933.
- Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications* 8:975–989.
- Kitayama, K., and S. I. Aiba. 2002. Ecosystem structure and productivity of tropical rain forests along

- altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology* 90:37–51.
- Koenker, R. 1994. Confidence Intervals for Regression Quantiles. Pages 349–359 in P. Mandl and M. Hušková, editors. *Asymptotic Statistics*. Physica-Verlag, Heidelberg, Germany.
- Koenker, R. 2015. *quantreg: quantile Regression*. R package version 5.19. <http://CRAN.R-project.org/package=quantreg>
- Kraaij, T., R. M. Cowling, and B. W. Van Wilgen. 2013. Lightning and fire weather in eastern coastal fynbos shrublands: seasonality and long-term trends. *International Journal of Wildland Fire* 22:288–295.
- Kruger, F. J. 1977. Invasive woody plants in the Cape fynbos with special reference to the biology and control of *Pinus pinaster*. *Proceedings of the National Weeds Conference of South Africa* 2:57–74.
- Lambers, H., M. W. Shane, M. D. Cramer, S. J. Pearse, and E. J. Veneklaas. 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany* 98:693–713.
- Lamont, B. 1972. The effect of soil nutrients on the production of proteoid roots by *Hakea* species. *Australian Journal of Botany* 20:27–40.
- Maitre, D. C. L., B. W. V. Wilgen, R. A. Chapman, and D. H. McKelly. 1996. Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *Journal of Applied Ecology* 33:161–172.
- Manders, P. T. 1990. Fire and other variables as determinants of forest/fynbos boundaries in the Cape Province. *Journal of Vegetation Science* 1:483–490.
- Mandle, L., J. L. Bufford, I. B. Schmidt, and C. C. Daehler. 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. *Biological Invasions* 13:1815–1827.
- Marchante, E., A. Kjølner, S. Struwe, and H. Freitas. 2008. Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology* 40:210–217.
- Mitchell, D. T., and N. Allsopp. 1984. Changes in the phosphorus composition of seeds of *Hakea Sericea* (proteaceae) during germination under low phosphorus conditions. *New Phytologist* 96:239–247.
- Morris, T. L., K. J. Esler, N. N. Barger, S. M. Jacobs, and M. D. Cramer. 2011. Ecophysiological traits associated with the competitive ability of invasive Australian acacias. *Diversity and Distributions* 17: 898–910.
- Mostert, E., M. Gaertner, P. M. Holmes, A. G. Rebelo, and D. M. Richardson. 2017. Impacts of invasive alien trees on threatened lowland vegetation types in the Cape Floristic Region, South Africa. *South African Journal of Botany* 108:209–222.
- Mucina, L., and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria, South Africa.
- Núñez, M. A., et al. 2017. Ecology and management of invasive Pinaceae around the world: progress and challenges. *Biological Invasions* 19:3099–3120.
- Power, S. C., G. A. Verboom, W. J. Bond, and M. D. Cramer. 2017. Environmental correlates of biome-level floristic turnover in South Africa. *Journal of Biogeography* 44:1745–1757.
- R Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rebelo, A. G., et al. 2006. *Fynbos Biome. The vegetation of South Africa. Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria, South Africa.
- Richardson, D. M., B. W. Van Wilgen, and D. T. Mitchell. 1987. Aspects of the reproductive ecology of four Australian *Hakea* species (Proteaceae) in South Africa. *Oecologia* 71:345–354.
- Richardson, D. M., and R. M. Cowling. 1992. Why is mountain fynbos invulnerable and which species invade? Pages 161–181 in B. W. van Wilgen, D. M. Richardson, F. J. Kruger and H. J. van Hensbergen, editors. *Fire in South African Mountain Fynbos: ecosystem, community and species response at Swartboskloof*. Springer Berlin Heidelberg, Berlin, Heidelberg, Germany.
- Richardson, D. M., I. A. W. Macdonald, and G. G. Forsyth. 1989. Reductions in plant species richness under stands of alien trees and shrubs in the Fynbos Biome. *South African Forestry Journal* 149:1–8.
- Richardson, D. M., and M. Rejmánek. 2011. Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions* 17:788–809.
- Richardson, D. M., and B. W. van Wilgen. 2004. Invasive alien plants in South Africa: How well do we understand the ecological impacts? *South African Journal of Science* 100:45–52.
- Richardson, D. M., P. A. Williams, and R. J. Hobbs. 1994. Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *Journal of Biogeography* 21:511–527.
- Rundel, P. W., I. A. Dickie, and D. M. Richardson. 2014. Tree invasions into treeless areas: mechanisms and ecosystem processes. *Biological Invasions* 16:663–675.
- Shane, M. W., G. R. Cawthray, M. D. Cramer, J. Kuo, and H. Lambers. 2006. Specialized ‘dauciform’

- roots of Cyperaceae are structurally distinct, but functionally analogous with 'cluster' roots. *Plant, Cell & Environment* 29:1989–1999.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334: 230–232.
- Van Wilgen, B. W., G. G. Forsyth, H. D. Klerk, S. Das, S. Khuluse, and P. Schmitz. 2010. Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *Journal of Applied Ecology* 47:631–638.
- Vitousek, P. M., and R. L. Sanford. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17:137–167.
- Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica Faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 59:247–265.
- van Wilgen, B. W., et al. 2011. National-scale strategic approaches for managing introduced plants: insights from Australian acacias in South Africa. *Diversity and Distributions* 17:1060–1075.
- Weltzin, J. F., and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation Science* 1:325–334.
- Zanne, A. E., et al. 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506:89–92.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2831/full>