Are forests restricted by nutrient poor soils? An analysis of soil nutrient stocks and associated vegetation in the Fynbos Biome, South Africa

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ABSTRACT

The realized woody biomass of the Fynbos Biome in the Western Cape, South Africa falls below the climatic potential to support woody biomass. The lack of substantial tracts of woody forests has long puzzled ecologists, although patchy nutrient distribution and fire disturbance are thought to play a role. The issue has been confounded in the recent past by the invasion of non-indigenous woody plants into formerly low stature fynbos dominated areas. Despite low wood nutrient concentrations, a substantial proportion of nutrients are locked up in the wood of forests due to the large volume of wood. Nevertheless, nutrient stock analysis indicated that plant available nutrients in the poorest global soils (including fynbos soils) are sufficient to support forests (indigenous and alien). I hypothesized that soil nutrient stocks of the Fynbos Biome are sufficient in quantity to support closed canopy indigenous forests with a woody biomass greater than 225 000 kg ha^{-1} and that alien *Pinus* spp. and *Eucalyptus* spp. have lower nutrient stocks than indigenous fynbos species.

The study was conducted in the Orange Kloof Forest Reserve and Jonkershoek Nature Reserve within the Western Cape (South Africa). Soil, wood and leaf samples of representative species were collected from indigenous forest, fynbos, *E. globulus* and *P. halepensis* and assessed for nutrient contents. Estimates of potential woody biomass on four different soils indicated that indigenous forests would be limited by fynbos soil stocks to below the 225 000 kg ha^{-1}. Pine forest had lower wood nutrient concentrations (mg kg^{-1}, n=6) for N (2466), K (2433), Ca (383), and Fe (34) than indigenous forest species (n=11) N (3427), K (4254), Ca (1636) and Fe (140). The low nutrient stocks in pine wood may allow them to grow tall and be competitive in the shrubby fynbos biome where indigenous forests are limited by expensive wood costs.

Key words: Nutrient, Fynbos, forest, Afromontane, *Pinus*, *Eucalyptus*, wood

INTRODUCTION

Global vegetation models indicate that climate is a significant predictor of major vegetation types (Pearson & Dawson 2003). However, vegetation models fail to predict extensive regions of the globe dominated by 'open' vegetation types such as savannas, grasslands and shrublands (Bond *et al.* 2005). The Western Cape, South Africa, is a region in which realized woody biomass falls below the climatic potential. Forests of the Western Cape are embedded in a mosaic of Fynbos shrublands. Substantial areas of this Fynbos Biome receive high enough mean annual precipitation (MAP)and have warm enough temperatures throughout the year to support extensive closed canopy forest systems (Bond 2008; Bond *et al.* 2005; Bond *et al.* 2003). The lack of substantial woody forests in the fynbos region has long puzzled ecologists. The issue has been complicated in the recent past by the invasion of non-indigenous woody plants into areas previously devoid of significant woody biomass (Van Wilgen and Richardson 1985; Richardson *et al.* 1990). Major determinants of woody cover in these open systems fall into two categories: "top-down" and "bottom-up" controls (Staver *et al.* 2009; Weltzin and Coughenour 1990). The "bottom-up" controls include resource-limiting factors such as water availability, soil nutrients, and access to light (Weltzin and Coughenour 1990), while "top-down" controls describe disturbance regimes such as fire, herbivory and windthrow (Bond 2008). The limited extent of mammalian herbivory and sufficient mean annual precipitation (MAP) suggest that within the context of the Western Cape, limited woody cover is likely to be the result of interactions between fire disturbance and nutrient deficient soils (Bond 1997;Richards *et al.* 1997;Cowling *et al.* 1992;Manders 1990;Cowling and Campbell 1983; Manders and Richardson 1980;Moll *et al.* 1980).

Fire is a prominent feature of the landscape and it is argued that the presence of fire in the fynbos restricts the ability of forest species to recruit into areas dominated by fynbos vegetation (Bond *et al.* 2005; Bond 1997; Manders and Richardson 1980;Moll *et al.* 1980). Experimental burn plots indicate that fire limits woody biomass in savanna systems, a neighboring biome in which realized woody biomass falls below the climatic potential (Higgins *et al.* 2007; Bond and Archibald 2003;Silva *et al.* 1991, Sankaran *et al.* 2008). To date, similar experiments are lacking in the fynbos, although forest expansion in response to management exclusion of fire in Orange Kloof Forest Reserve may serve as an indication that fire disturbance limits forests in the Western Cape (Manders 1990, Masson and Moll 1987). However, the history of human intervention in this reserve is uncertain and might have included initial forest clearing prior to the declaration of the reserve, confounding the apparent encroachment of tees into low stature vegetation.

Fire as a limit to forest expansion is further complicated by the interaction with nutrient availability. Fire disturbance is limited by its inability to penetrate dense woody cover (Archibald et al. 2009). Thus in areas with high productivity, where woody cover is able to accumulate between fires, fire as a disturbance becomes limited (Higgins *et al.* 2007; Bond and Archibald 2003). In fynbos, fire return times range between 5-40 years, periods that in productive savanna systems result in shifts to closed canopy states (Higgins *et al.* 2007; Bond and Archibald 2003; Molls *et al.* 1980). However, the soils of the fynbos biome are generally defined as acidic, P deficient sandstones (Cowling *et al.* 1992). It has been argued that plant available nutrients in these soils are insufficient for forests to develop (Goodland and Pollard 1973). Thus, low nutrient stocks in the fynbos system may influence the accumulation of woody biomass between fires i.e. nutrient stocks may be too low for forests to develop and any trees that are able to grow are at low densities and vulnerable to fire (Manders 1990;

Cowling and Campbell 1980). It is therefore necessary to develop an understanding of nutrient dynamics within the fynbos system and particularly define any limitations that low nutrient fynbos soils may exert on indigenous forest.

The role of nutrients in open vegetation has been debated at the continental scale. Low nutrient soils have been partially associated with the presence of open landscapes at the global scale (Sankaran *et al.* 2005; 2008). However, globally there is little correlative evidence supporting the idea that low nutrient soils in forests directly limit above ground biomass except in extreme cases (Vitousek and Sanford 1986; Kitayama and Aiba 2002).It is probable that any correlative relationship between above ground production and soil nutrients in forests will be hidden by complexities related to other environmental factors such as soil moisture (Cramer, in press). Bond (2010) quantitatively assessed soil nutrient stocks and argued that soils in the Fynbos Biome have high enough nutrient contents to support low biomass forests with *ca.*225 000 kg ha^{-1}(the estimated woody biomass of a low biomass forest) of woody biomass. However, due to a lack of available wood and foliar data for the Fynbos region, this estimate was based on Amazon wood and foliage nutrient stocks. Supporting this conclusion, transplants of woody Afromontane species into fynbos soils have survived, suggesting enough nutrient stocks to support at least the early growth of individual trees in fynbos soils (Manders and Richardson 1980). The notion that fynbos soils are of sufficient quality for forests to grow is also supported by widespread invasion of woody species of *Pinus* and *Eucalyptus* throughout the Western Cape (LeMaitre *et al.* 1996, Bond 2010). However, highly productive timber species such as *P. halepensis* and *E. globulus* (blue gum) may produce nutritionally "cheaper" wood than slow growth, hard wood indigenous species.

Following the nutrient stock analysis of Bond (2010), I hypothesized that soil nutrient stocks of the Fynbos Biome are sufficient in quantity to support closed canopy indigenous forests with a woody biomass greater than 225 000 kg ha^{-1} and that alien *P. halepensis* and *E. globulus* have lower nutrient stocks in wood than indigenous fynbos species, facilitating their invasion into Fynbos areas. To address these hypotheses I estimated nutrient stocks in the leaves, wood and associated soils of indigenous and alien vegetation co-occurring in the Orange Kloof Forest Reserve and Swartboskloof Nature Reserve in the Western Cape. These estimates were based on nutrient analyses of leaves, wood and soil together with measures of standing woody biomass.

METHODS

Study sites

The study was conducted in two different nature reserves within the Western Cape, South Africa. Jonkershoek Nature Reserve (S33.58.225 E18.56.109) contains the upper section of the Jonkershoek valley, surrounded by high sandstone peaks. The weather is typical of the south-Western Cape with wet winters and hot dry summers. The indigenous element of the vegetation contains granite fynbos and cape winelands shale fynbos, but is dominated by sandstone fynbos (Rebelo et al. 2006). Afromontane forests are present in riparian areas and in shallow soils on rocky scree slopes (Rebelo et al. 2006). Large sections of the valley are dominated by non-indigenous commercial plantations of *Pinus halepensis*. In the lower reaches of the valley Australian *Eucalyptus globulus* has invaded and grows to substantial heights in the riparian zone. Soils in the Jonkershoek valley are derived from porphyritic granite and quartzitic sandstone. Soils are typically low pH and have low exchangeable cation capacities. Quartzite based soils are generally lower in organic matter, total N, P and pH than neighboring granite based soils (Manders 1990).

The Orange Kloof Forest Reserve (S34.00.624 E18.24.278) is a 285ha region of the Table Mountain National Park in the Western Cape. The Orange Kloof Reserve was set up to protect the Disa River catchment and has been intensely managed for over 50 years. Management practices have included the active prevention of fires in the area and fire has been excluded for over 30 years. The vegetation contains typical elements of Table Mountain fynbos on west facing valley slope while the lower valley and large sections of the east facing slope are dominated by indigenous Afromontane forest with patches of endangered peninsula granite fynbos (Rebelo *et al.* 2006). In addition to the indigenous vegetation, both European *P. halepensis* and Australian *E. globulus* are present in the lower sections of the reserve. Geologically the area is made up of the Table Mountain Series and Basement Granite. Table Mountain Sandstone forms the upper cliffs while the lower valley is dominated by granite based soils (Mckenzie *et al.* 1977). Soils of the former are shallow in depth (<0.5m) while granite based soils are deep (<2m) with greater total N and P (Mckenzie *et al.* 1977).

Species selection

Sites were selected due to the indigenous forest and fynbos elements combined with the presence of *P. halepensis* and *E. globulus*. Sampling was categorized into four 'vegetation types': indigenous forest; fynbos; *E. globulus* and *P. halepensis*. Indigenous forest included species generally considered to be Afromontane elements (*Podocarpus latifolius, Cunonia capensis, Olinia ventosa, Kiggelaria Africana, Olea europa*and, *Grewia occidentalis*). This wide range of the major species components were chosen to provide a broad analysis of the nutrient levels within an afromontane forest. Woody Fynbos species included *Protea neriifolia, Protea nitida, Widdringtonia nodiflora* and *Leucodendron conocarpadendron. P. halepensis* and *E. globulus* were selected as both are invasive in the South Western Cape and neither species is able to fix atmospheric nitrogen (Palgrave 1983) allowing for comparisons of nutrient content with non-leguminous indigenous species

Sample collection

Three mature, plants from each study species were selected for sampling within the two reserves. The height of each tree was recorded using an inclinometer and diameter at basal height (DBH) measured. why only heart wood. Heart wood samples (*ca.*5g dry weight) were collected from each study tree at a standard height of 1m above ground using a 4.5mm diameter wood corer. The volume of each sample was calculated by measuring the dimensions of the cylindrical core. The weight of the wood sample was then divided by the associated volume to calculate the wood density of each plant. Standard leaf area (SLA) was calculated from using the appropriate species from the GLOPNET data set of Wright *et al.* (2004).

Leaves were collected throughout the canopy of each tree to compensate for the effects of light variation on nutrient contents within leaves. To standardize this procedure a single leaf was taken from the lowest point of the canopy, then the middle and top using extendable secateurs. This process was repeated until sufficient leaf biomass for nutrient analysis was collected. A fresh mass of *ca.*10g of leaf material for each tree was dried for 24h and submitted for nutrient analysis.

Soil samples were collected on the soils associated with each tree i.e. within 5m of sample trees. The organic layer of was removed before and soil collected with a trowel down to a depth of 0.3 m where possible.

Tissue analysis

All leaf and wood samples were dried for 48h in an oven at 80°C. The dried samples were milled in a Wiley mill using a 0.5-mm mesh and analysed for N, P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn and B content by BemLab (Pty) Ltd. Total leaf N was determined through combusting pulverized leaf material on a FP-528 Nitrogen Analyser (Leco Corporation, St. Joseph, USA). Leaf P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn and B was determined through dry-ashing pulverized leaf material at a temperature of 480°C for 8 h and dissolving it in HCl (Kalra 1998). The solution was analysed using inductively coupled plasma atomic emission spectrometry (Varian Vista MPX ICP-AES, Australia).

Mass spectrometer analyses were run on the milled leaf and wood samples to determine the $\delta^{15}N$ and $\delta^{13}C$ values. The milled wood and leaf material (2.1-2.2 mg) were weighed into a tin capsule and combusted in a Thermo Flash EA 1112 series elemental analyser. The gasses were fed into a Delta Plus XP isotope ratio mass spectrometer. The results were calibrated using two in-house standards and one IAEA standard.

Soil analysis

Soil samples were dried in an oven at 80°C for 48 h. The dried samples were sieved (1mm mesh) and analyzed for N, P, K, Na, Ca and Mg content by Bemlab (Pty) Ltd. pH was measured by shaking 2 g soil in 20 mL 1 M KCl at 180 rpm (Hermle Z420, Gosheim, Germany) for 60 min, centrifuging at 10 000 g for 10 min and measuring the supernatant pH. Total nitrogen was determined by digestion with a FP-528 Nitrogen Analyzer (Leco Corporation, St. Joseph, USA). Soil was prepared for P analysis by extracting 6.6 g soil in Bray II solution (Bray and Kurtz 1945) before filtering and analysing using Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-OES, Varian Vista MPX, Australia). Exchangeable cations were displaced from 10 g soil with 25 mL of 0.2 M ammonium acetate. The samples were filtered through Whatman No. 2 filters and made to 200 mL, and K, Na, Ca and Mg were measured using ICP-OES analysis.

Mass spectrometer analysis used *ca.* 40 mg of soil from each sample placed into tin capsules (Elemental Microanalysis Ltd., Devon, U.K.) and combusted in a Thermo Flash EA 1112 series elemental analyser; the gasses were fed into a Delta Plus XP isotope ratio mass spectrometer (Thermo Electron Corporation, Milan, Italy). The C isotopic ratio of a sample was expressed versus the Pee Dee Belemnite standard (Ehleringer and Rundel 1989) and the N isotopic ratios expressed versus atmospheric nitrogen (Evans 2001).

Statistical analyses

One way ANOVA and Post-Hoc Tukey analyses were run to compare variance in the tree height, DBH, wood density and SLA between the four vegetation types (Zar 1999). Similar analyses were run on all nutrient data to compare variances between the two sites (Zar 1999). The same analyses were run separately on the wood and leaf nutrient contents with nutrient quantity as the dependent factor and vegetation type as the categorical predictor (indigenous forest, fynbos, *E. globulus* and *P. halepensis*). This method was also done for wood nutrient contents as a percentage of leaf nutrients after ARCSIN transformation (Zar 1999). Wood and leaf nutrient data were log transformed and correlated to assess plant bias in the allocation of nutrients.

Estimates of potential woody biomass

To quantify the ability of sampled soils to support forests, leaf, wood, and soil nutrient contents were used to calculate potential woody biomass of soils associated with the different vegetation types (Bond, 2010). The method of Bond (2010) was used for calculating potential woody biomass of all four vegetation types based on the soil nutrient stocks of sampled soils. Briefly, woody biomass (B^N, kg ha^{-1}) for each site was predicted for each nutrient (N) using $B^N = S_a^N / c_w^N / 100$, where S_a^N (kg ha^{-1}) was the total pool of individual available nutrient and c_w^N(%) the nutrient concentration in wood (Table 1). The total nutrient pool was calculated as $S_a^N = S_s^N$ -S_f^N, where $S_f^N = Fc_f^N / 100$ (Table 1). The soil nutrient stock (S_s^N, kg ha^{-1}) was calculated as $S_s^N = ND_b D/100$, where N is the soil nutrient concentration (kg ha^{-1}), D_b the soil bulk density (kg m^{-3}) and D the soil depth (m), set at 0.5 m. Soil bulk density was calculated using the equation of Benites *et al.*(2007) for a depth of 0-0.3 m (their Table 6). The predicted biomass (B^N) was compared with global wood estimates of 225000 kg ha^{-1} for low biomass forests to see whether soils were sufficient to support closed forest systems (Bond 2010).

RESULTS

Vegetative characteristics

The mean tree heights of *P. halepensis* and E. *globulus* were significantly greater (F=20.32, P<0.001) than indigenous forest. All other vegetation types were significantly taller than fynbos. Similarly, mean DBH was greatest (F=16.30, P <0.001) in *P. halepensis* and E. *globules* and significantly lower in fynbos than indigenous forest. There was no significant difference (F=0.50, P=0.68) in either mean wood density (F=0.50, P=0.68) or mean SLA (F=2.14, P=0.12) between the four vegetation types.

Table 1. Mean tree height, diameter at basal height, wood density and standard leaf area for the four different vegetation types (values calculated from Wright *et al.* 2004 data set*).

Vegetation type	Tree height (m)	Diameter at basal height (cm)	Wood density (kg m^{-3})	Standard leaf area (m^{-2} kg)	Sample size
Indigenous forest	6.9 (3.6)	24.8 (15.3)	964 (5.3)	8.5 (4.4)*	n=18
Fynbos	3.2 (0.9)	5.12 (3.4)	935 (7.8)	4.6 (0.7)*	n=12
E. globulus	15.0 (3.2)	51.67 (29.7)	880 (14.7)	6.9 (0.4)*	n=6
P. halepensis	16.6 (7.6)	56.67 (18.3)	842 (14.0)	7.9 (0.6)*	n=6

Soil nutrients

Soil stocks of total N (F=1.76, P=0.179) and exchangeable Na (F=1.69, P=1.92), Ca (F=1.93, P=0.150) and Mg (F=1.53, P=0.229) had no significant differences between the four vegetation types. Indigenous forest soils had significantly higher total P (F=12.27, P<0.001), K (F=4.05, P=0.01) and available P (F=9.17, P<0.001) stocks than the other soils. *E. globulus, P. halepensis* and fynbos soils had similar levels of all nutrient stocks (Table 2).

Table 2. Mean total soil stocks (kg ha^{-1}) for the four different vegetation types. These stocks were calculated from the soil nutrient concentrations averaged over the top 0.5 m of soil and with a bulk density of 1 300 kg m^{-3}.

Vegetaion type	Total N	Total P	Na	K	Ca	Mg	P Bray II
Indiginous forest	1487	76	38	91	581	152	9.0
Fynbos	1153	34	33	39	179	62	4.9
E. globulus	807	26	55	61	261	103	2.3
P. halepensis	824	25	54	55	253	97	2.5

Wood and foliar nutrients

Indigenous forests had no significant differences in mean wood nutrient concentrations compared to fynbos vegetation. It did have significantly higher tissue [N] (F=5.26, P=0.006), [K] (F=4.78, p=0.009), [Ca] (F=5.82; p=0.003), [Fe] (5.70; p=0.004) and [Cu] (F=3.25; p=0.03) wood contents than *P. halepensis* (Fig. 1). Mean total [P] in the wood of *P. halepensis* (16.67 mg kg^{-1}) was not significantly (F=2.41; p=0.09) lower than that in indigenous forests wood (127mg kg^{-1}) (Fig. 1). Mg showed no significant difference (F=1.75; p=0.182) in average wood quantities between vegetation types. E. globulus had significantly higher [Ca] (F=5.82; p=0.003) than *P. halepensis*.

Mean [P](F=2.92; p=0.053), [K] (F=2.11; p=0.124) and [Mg] (F=1.78; 0.177) nutrient concentration within leaves did not differ significantly ($P < 0.05$) between the four vegetation types (Fig. 2). However, leaf [N] was significantly lower (F=11.63; $p<0.001$) in fynbos leaves (8133mg kg^{-1}) than any other vegetation type. In contrast, leaf [Ca] was significantly higher (F=4.35; p=0.01) in indigenous forests (13409 mg kg^{-1}) than *P. halepensis* (4650 mg kg^{-1}) and [Fe] was highest in *P. halepensis* and significantly (F=4.23; p=0.01) lower in indigenous forests and *E. globulus* (Fig. 2).

The expression of wood nutrient concentration as a percentage of leaf concentrations indicates the proportion of foliar nutrients retained in wood and was used as an indication of the efficiency with which nutrients are withdrawn from wood. [P] retained in wood was significantly lower (F=3.85; p=0.02) in *P. halepensis* vegetation (1.33%) than indigenous forest (19.39%) (Fig. 3). *E. globulus* forest had the highest ratio of wood vs. leaf nutrient storage for [Ca] (F=5.92; 0.003), [Mg] (F=7.07; p=0.001) and [B] (F=5.57; 0.005). Total [N] was not significantly different between the four vegetation types, with all vegetation types retaining 20% and 30% of foliar N in wood (Fig. 3).

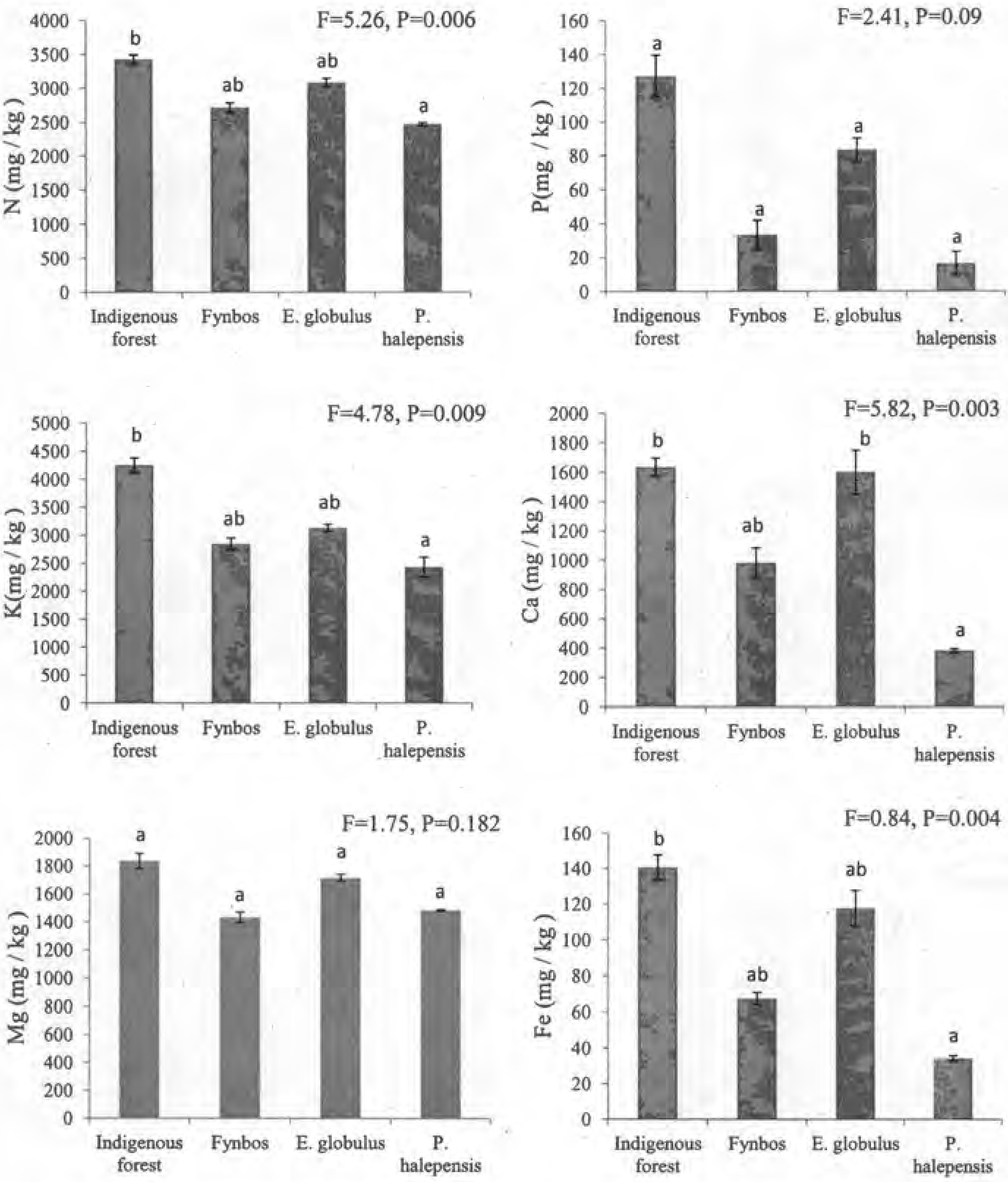

Figure 1. Comparisons of wood nutrient stocks (mgkg^{-1}) between vegetation types. Columns with the same letters (a) or (b) represent concentrations that are not significantly different, while those with different letters represent nutrient concentrations in wood that are significantly different (bars represent standard error).

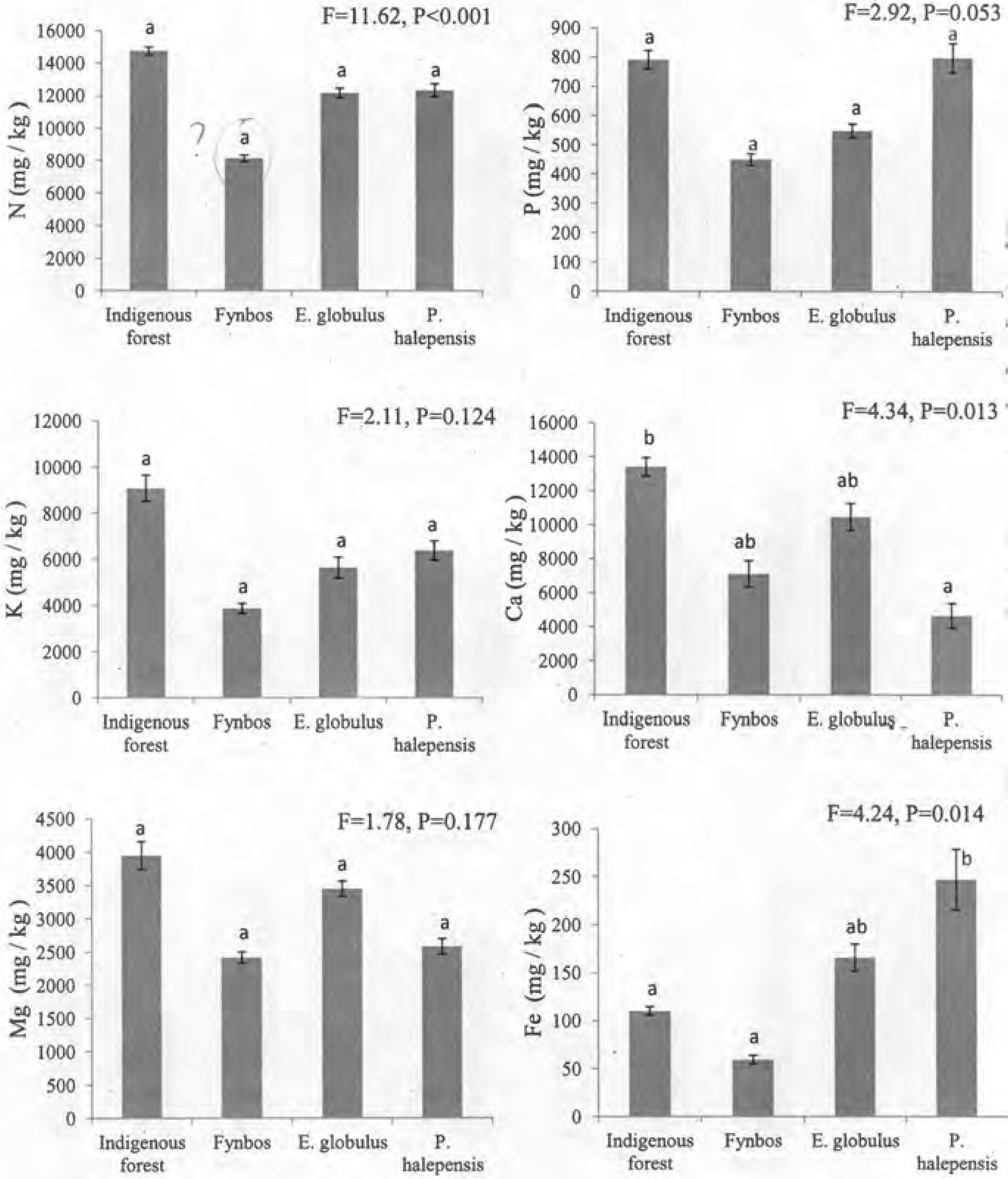

Figure 2. Comparisons of leaf nutrient stocks (mg kg^{-1}) between vegetation types. Columns with the same letters (a) or (b) represent concentrations that are not significantly different, while those with different letters represent nutrient concentrations in leaves that are significantly different (bars represent standard error).

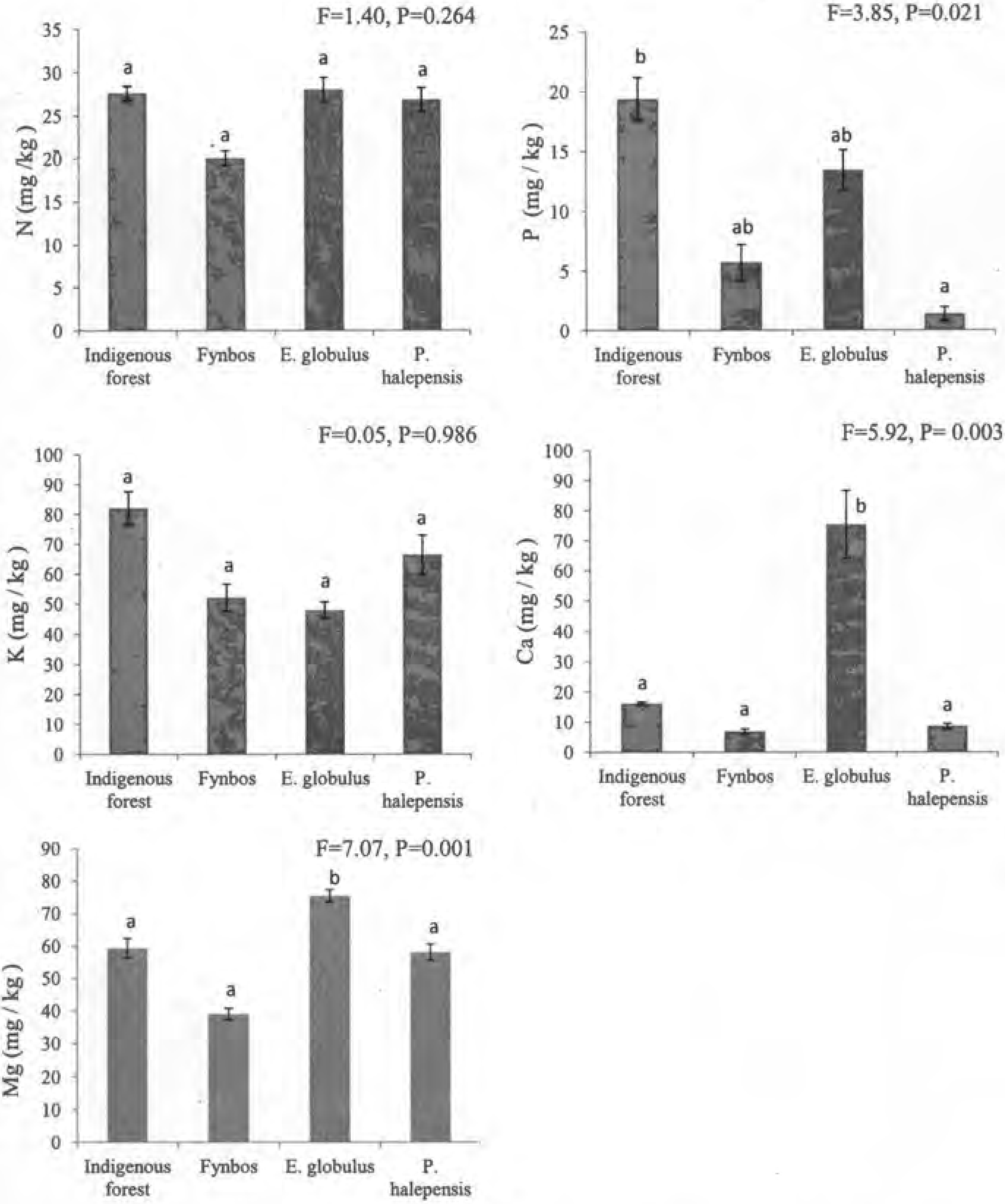

Figure 3. Comparisons nutrient stock in wood as a proportion leaf nutrient stock (%) between vegetation types. Columns with the same letters (a) or (b) represent wood as a percentage of leaf nutrients are not significantly different, while those with different letters represent percentages that are significantly different (bars represent standard error, data were arcsine transformed (Zar 1999) for ANOVA).

All vegetation types indicated that the average bias of nutrient allocation between leaf and wood tissue favoured greater leaf nutrient concentration. *P. halepensis* had the greatest inequality in nutrient concentrations between the two tissues, with the ratio of leaf nutrient concentration vs. wood nutrient concentration being highest in [P], [Mn], [Cu] and [B].

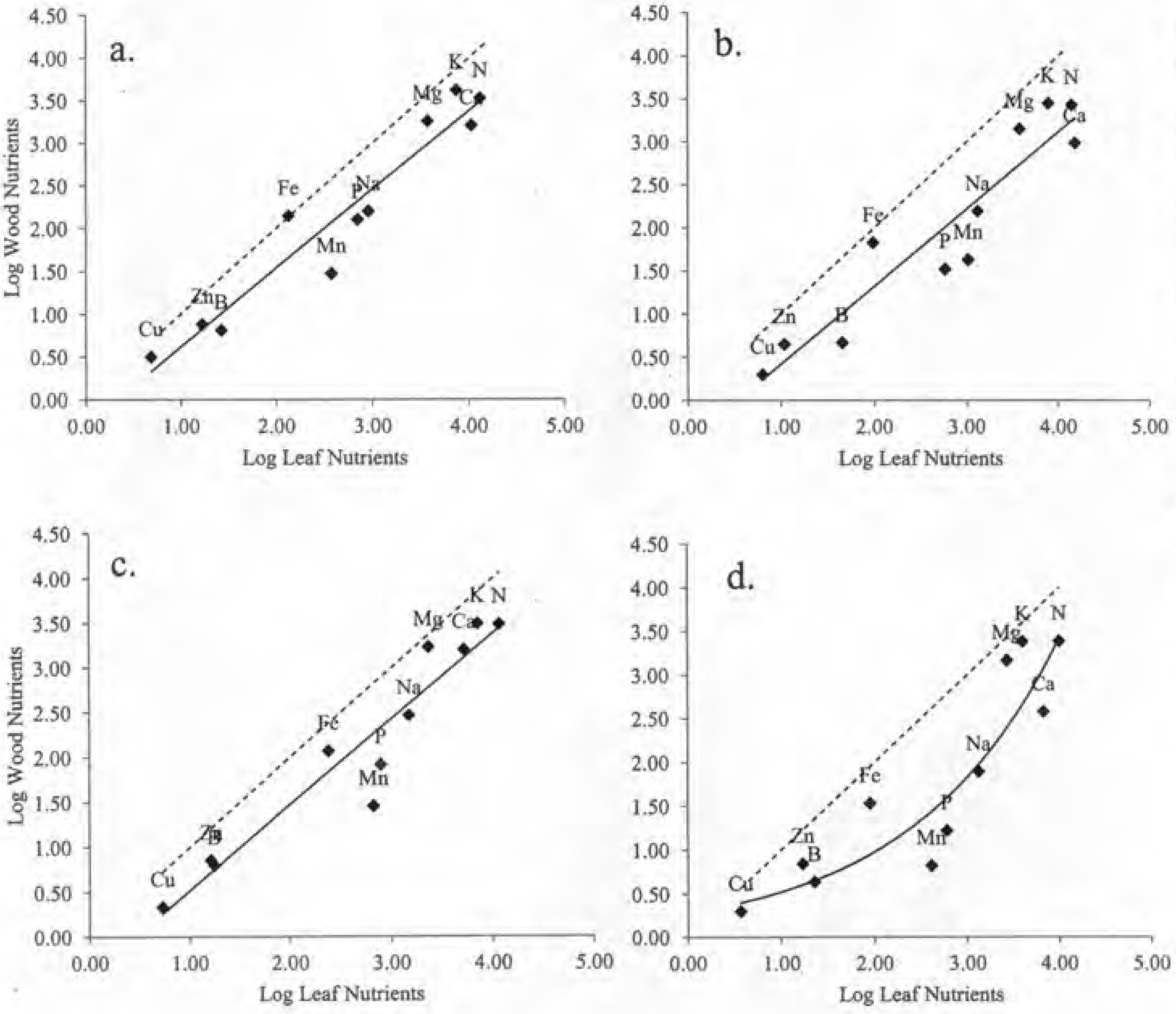

Figure 4. Relationship between quantities of N, P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn and B in wood and leaves for indigenous forest (a), fynbos (b), *E. globulus* (c) and *P. halepensis* (d). Dashed line represents 1:1 relationship. Data in mg kg^{-1} before log transformation. (a) $y = 0.920x - 0.299$ ($R^2 = 0.92$); (b) $y = 0.897x - 0.477$ ($R^2 = 0.89$); (c) $y = 0.955x - 0.436$ ($R^2 = 0.91$); (d) $y = 0.280e^{0.625x}$ ($R^2 = 0.84$).

The assessment of nutrient limited potential woody biomass based on relevant soil stocks indicates that K, Mg and available P are the most limiting nutrients across all vegetation types (Fig. 5). All three of these nutrients are well below the quantities required to build a low biomass forest. Soil stocks of total N and total P were large enough to support closed forests. Ca stocks in indigenous forest soils and pine forest soils were estimated to be sufficient to grow woody biomass over 225000 kg ha^{-1}, but were too low in fynbos and *E. globulus* soils to support this biomass.

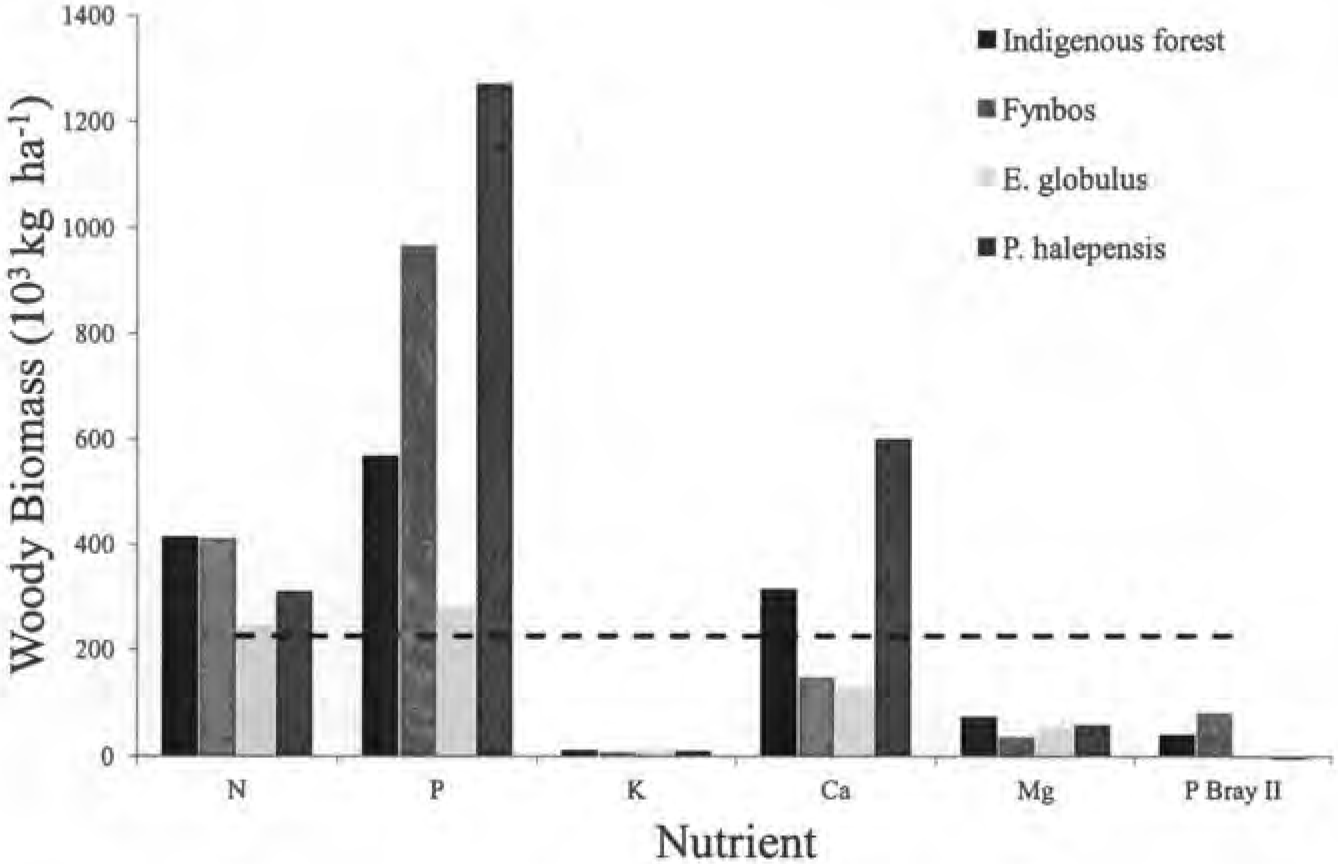

Figure 5. Nutrient limited potential woody biomass (10^3kg ha^{-1}) estimated for the four different vegetation types based on their respective soil stocks. Dashed line indicates the 225 000 kg ha^{-1} above ground woody biomass threshold assumed for a low biomass forest after Bond (2010).

The assessment of potential woody biomass for specific vegetation types on all soils indicated that soil nutrient stocks of K and Mg are likely the most limiting nutrients for woody growth in all vegetation types and all soils (Fig. 6 and 7). None of the soils had sufficient quantities of either K or Mg to support woody biomass of a low biomass forest (225000 kg ha^{-1}). The same is true of plant-available soil P (measured as Bray II P), except in the case of *P. halepensis* growing on indigenous forest soils, where soil stocks could potentially support over 300000 kg ha^{-1} of woody biomass (Fig. 7d). In the case of total N, P and exchangeable Ca,estimates indicate that indigenous forests can only grow on their own soils. The same nutrients are sufficient in quantity to support fynbos woody biomass up to 225000 kg ha^{-1}in all soils except their own soils (Fig. 6b). There are sufficient soil stocks of total N and P to support low biomass *E. globulus* in all soils (Fig. 7c). Exchangeable Ca quantities limit *E. globulus* in all but indigenous forest soils. Total N, P and exchangeable Ca stocks are sufficient in all soils to support over 240000 kg ha^{-1} of *P. halepensis* wood, with a potential woody biomass of over 570000 kg ha^{-1}(well above 350000 kg ha^{-1} estimated for high biomass forests) if growing on indigenous forest soils (Fig. 7d).

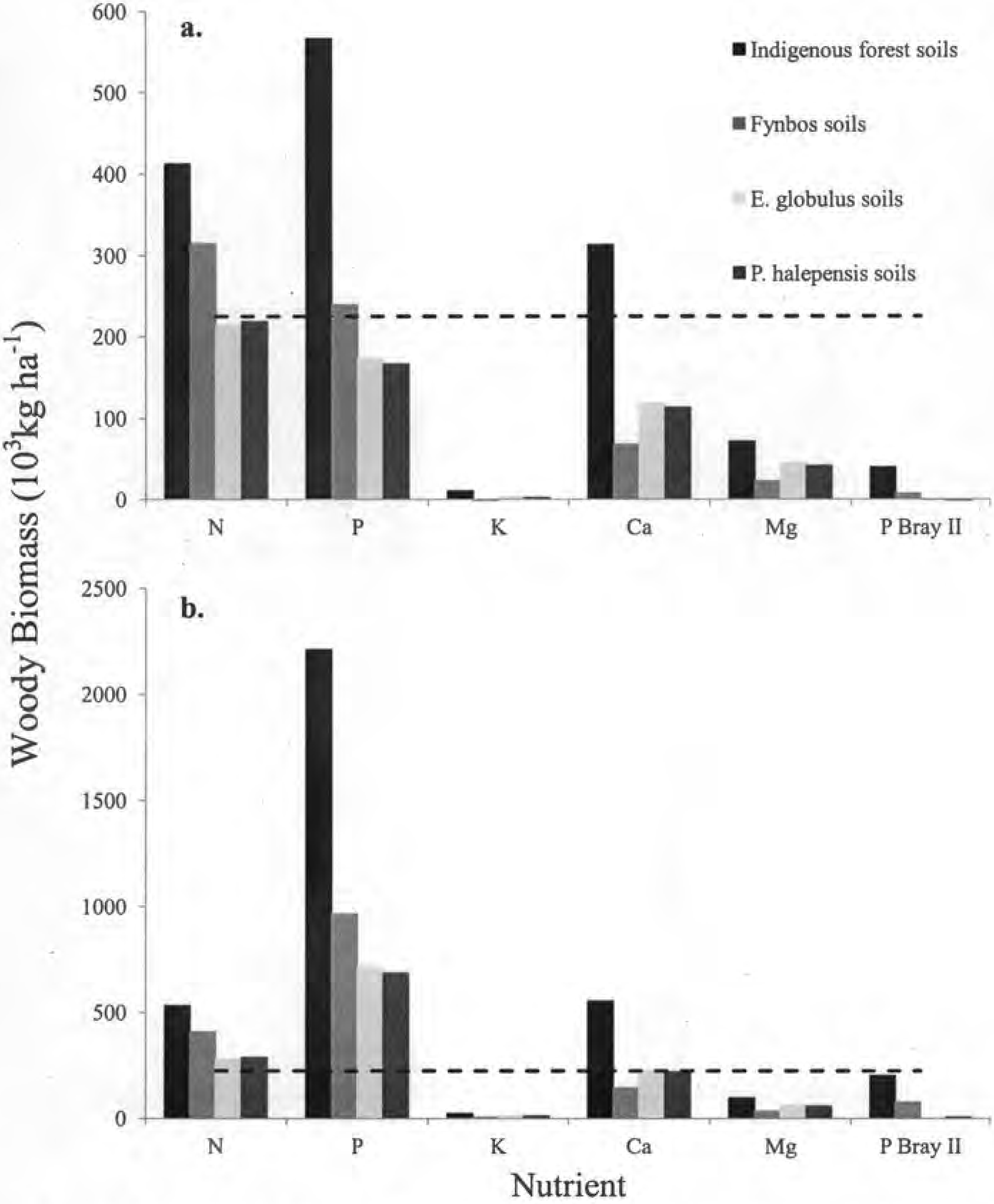

Figure 6. Nutrient limited potential woody biomass (10^3kg ha^{-1}) for the indigenous forest (a) and fynbos (b) using all soil stocks and indigenous forest (a) and fynbos (b) wood concentrations. Dashed line indicates 225 000 kg ha^{-1} above ground woody biomass as assumed necessary to construct a low biomass forest.

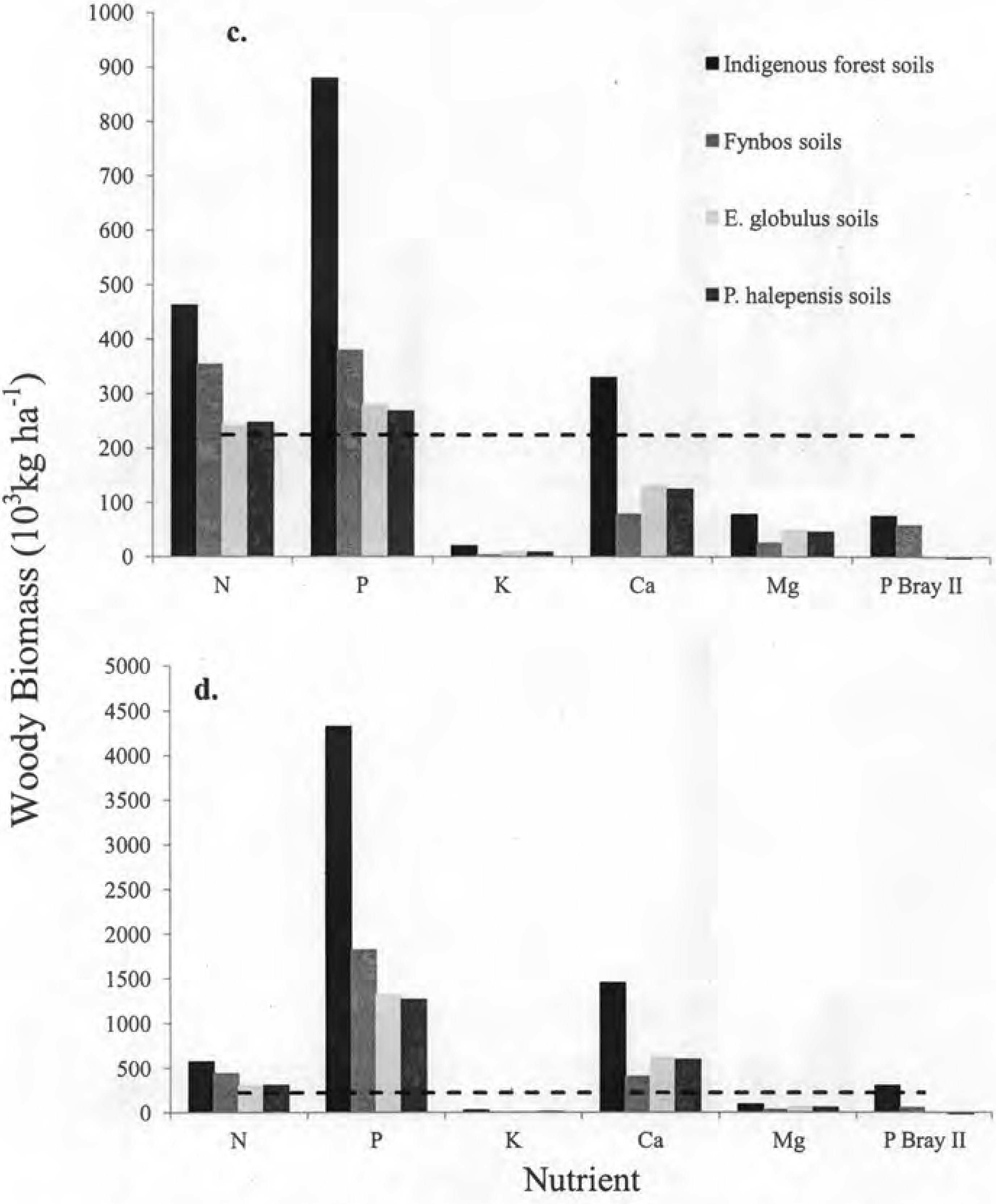

Figure 7. Nutrient limited potential woody biomass (10^3kg ha^{-1}) for the eucalyptus forest (c) and pine forest (d) using all soil stocks and *E. globulus* (c) and *P. halepensis* (d) wood concentrations. Dashed line indicates 225 000 kg ha^{-1} above ground woody biomass as assumed necessary to construct a low biomass forest.

DISCUSSION

The species chosen to represent fynbos and indigenous forest in this study were selected to give a broad picture of the nutrient characteristics within the tissue of related vegetation types. To achieve this woody species were selected that frequently occurred in the literature and have been recognised by Rebelo *et al.* (2006) as common elements of their related vegetation type. The selection of fynbos species was limited by the need for woody biomass in sufficient quantities to compare with forest tree species. To account for this species from the family Proteaceae and the genus *Widdringtonia* were selected as both contain species with woody stems that have been known to exceed 3m in height under certain conditions (Palgrave 1983). The data indicate that both the wood and leaf nutrient contents of the individual species are consistent with the broad overall trends observed in this study (Supplementary Table 2 a. and b.). Thus, it appears that the broad groupings of fynbos and indigenous forest are sufficiently representative of their constituent species and adequate for comparisons of nutrient trends in the associated vegetation.

Contrary to our hypothesis that the stock of nutrients in fynbos soils was sufficient to support indigenous forests, estimates showed that nutrients in fynbos soils were insufficient to support indigenous forests with a woody biomass exceeding 225000 kg ha^{-1}. These estimates indicated that fynbos soils were adequate for growth of *P. halepensis* forests of similar biomass to the trees in the indigenous forests. It has been suggested that the presence of alien invasive woody species in the Fynbos Biome indicates that soil nutrient stocks are not limiting to indigenous forests (Bond 2010). Contrary to this, my findings suggest that the invasive success of *P. halepensis* is the result of the low nutrient requirements involved in the construction of its heartwood. Plantation experiments have shown that after initial seedling establishment, *P. halepensis* growth rate is largely unaffected by variation in soil nutrient stocks and tree growth is only impacted by age (Peurtolas *et al.* 2003; Daskalakou and Thanos 1996). Thus, it appears this species is very nutrient efficient in its growth after successful seedlings recruitment (Peurtolas *et al.* 2003). The efficiency of this species after initial growth can be attributed to the low heartwood nutrient requirements. Other species of trees have been demonstrated to manipulate tissue concentrations with repercussions for growth (Kirshbaum *et al.* 1994) and this plasticity is linked to those species ability to grow tall (Kitayama 2005). Similarly, I suggest that the ability of *P. halepensis* to manipulate the recycling of nutrients in its heartwood, particularly [P] and [Ca], considered global limits to wood production, allows it to grow tall in nutrient poor fynbos soils (Fig. 2 and 3). Height in the shrubby vegetation of the fynbos is an advantage in respects to both competition and fire resistance (Witkowski 1991). Thus *P. halepensis* has a competitive advantage over indigenous, low growing fynbos species and slow growing, and nutrient expensive indigenous forests.

The difference in the amount of potential woody biomass of one vegetation type compared to another on the same soils indicated that the influence of soils on above ground woody biomass is determined by the particular species characteristics. Thus the question arises as to how one woody species may have the potential to develop more wood than another on the same soil? Leaf nutrient concentrations of *P. halepensis* forests were similar to those of other vegetation types (i.e. fynbos, indigenous forest and *E. globulus*) with only [Ca] being significantly lower and [Fe] significantly higher than the other vegetation (Fig. 2). Intraspecific variation in foliage nutrient concentrations (particularly N: P ratios) has been suggested as an adaptation to soil variation in the tropics (see Gusewell 2004 for review).

However, the similarity of leaf concentrations between vegetation types in this study and the relatively high SLA of *P. halepensis* indicates that variation in foliage nutrient concentrations does not explain the apparent invasive potential of *P. halepensis* on fynbos soils (Table 2). Instead it is the concentration of nutrients, specifically N, P, Ca, K and Fe, in the wood of *P. halepensis* that were consistently lower than in wood of the other vegetation types, particularly that of indigenous forests (Fig. 1). This combined with the high ratio of leaf vs. wood nutrient concentrations in *P. halepensis* when compared to the other vegetation types indicates that *P. halepensis* may be committing comparatively less of the overall available nutrients to heartwood construction than the other vegetation types. Attiwill (1980) found that nutrients recovered/re-sorbed from senescing plant material represented a significant source of nutrients for plant growth. In addition it has been shown that plant species with the ability to recover nutrients during the formation of heartwood from sapwood were able to maintain plant nutrient levels similar to trees occurring on richer soils (Andrews *et al.* 1999; Meerts 2002). Thus, it is suggested that the lower heartwood [P] and [Ca] as a percentage of leaf nutrients values indicates that *P. halepensis* is able to draw down wood nutrient concentration more than comparison species thus reducing the nutritional costs of woody biomass accumulation facilitating growth on nutrient poor fynbos soils.

Variability in heartwood nutrient content may play a role in the variations in realised tree height globally. Cramer (in press) suggested that the lack of correlation between soil nutrients and tree height is probably the result of other environmental factors particularly soil moisture. However, the difference in the amount of nutrient recovered during heartwood formation between different species possibly contributes to the variation in tree height. Furthermore, plasticity of wood nutrient concentrations in response to soil quality has been shown in white cedar (*Chamaecyparis thyoides*) with nutrient contents in sapwood 60-700% higher than adjacent heartwood of nutrient stressed plants (Andrew *et al.* 1999). Thus trees that are able to recover nutrients during heartwood formation could grow relatively tall even on low nutrient soils.

Soils are different between forest and fynbos vegetation (Table. 2). This is largely unsurprising and corresponds with the findings of Manders (1990) and Moll *et al.*(1980). Despite the difference in soil nutrient stocks there was no significant difference in the wood nutrient concentrations of fynbos and indigenous forest. It appears that none of the species sampled for either vegetation type has the same ability to recover nutrients as *P. halepensis*. If the cost of wood creation between indigenous forest and fynbos is similar, then low woody biomass fynbos vegetation will be favoured in low nutrient fynbos soils. This is supported by potential woody biomass estimates based on total N, P and exchangeable Ca, where the potential woody production of both vegetation types was high on forest soils but inadequate to produce 'forests' on nutrient poor fynbos soils. This would be an issue for indigenous trees where low densities and slow woody accumulation would leave any seedlings that did establish prone to fire. However, the shrubby structure of fynbos requires substantially less wood development than indigenous forest trees and therefore fynbos species would be able to mature and reproduce in the period between disturbances. Thus, the similar nutrient concentrations found in the heartwood of indigenous forests and fynbos vegetation combined with the regular disturbance (fire) regime plays a significant role in the exclusion of natural forests from fynbos soils. Manders (1990) suggested that the soils found under fynbos and indigenous forest were the result, not the cause of, the above ground vegetation. This is because, although afrotemparate forests in the cape floristic region (CFR) region do occur on similar geology to the fynbos vegetation, the soils are strikingly different. Soils on which indigenous forest occur may thus be the long-term consequence of fire-refugia protecting soil resources from volatilisation or mobilisation in ash thus facilitating the accrual of soil resources, rather than the regular displacement of those resources as might be the case in Fynbos. In addition the findings of Treydte *et al.* (2008) suggest that trees actively manipulate the soil under the canopy and improve the quality of soils in the local area. Thus, the nutrient concentrations required for wood construction in indigenous forests may limit them to soils that have been locally altered over a long period of time. This must significantly reduce the ability of indigenous forests to colonise fynbos areas on any significant scale.

The invasive ecology of *E. globulus* in the Fynbos Biome may be affected in a similar way to that of indigenous forests. *E. globulus* does not share the same low heartwood nutrient concentrations as *P. halepensis* and had higher concentrations of all nutrients, particularly Ca (Fig. 1). The estimates of potential woody biomass indicate that the nutrient concentrations in both the foliage and wood of *E. globulus* seem to restrict any substantial growth to indigenous forest soils (Fig. 7d). Established indigenous forests represent alight competitive environment and the height advantage exploited by *P. halepensis* in fynbos vegetation is not available to *E. globulus* in these systems. It is suggested that the substantially lower impact of *E. globulus* than *P. halepensis* as an invasive in the CFR is related to the higher nutrient requirements of E. globulus for the construction of heartwood.

CONCLUSION

The variability in heartwood nutrient concentrations has important explanatory power for global woody vegetation patterns and the observed lack of significant correlations between soil nutrient stocks and tree height. For example, the relatively nutrient expensive heartwood of indigenous forest species may constrain them to nutrient-rich soils due to interactions between slow woody growth and fire. Low heartwood stocks of [P] and [Ca] in the wood of *P. halepensis* gives it a competitive advantage over other species in the low nutrient soils of Fynbos Biome. This may be a major driver for the invasion of *Pinus halepensis* into nutrient poor fynbos areas where indigenous forests are absent.

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SUPPLMENTARY INFORMATION

Table 1. Study species and associated vegetation type.

Species	Vegetation type	Sample size
Cunonia capensis	Indigenous forest	n=4
Maytenus acuminata	Indigenous forest	n=3
Podocapus latifolius	Indigenous forest	n=3
Podocapus elongatus	Indigenous forest	n=1
Kiggelaria africana	Indigenous forest	n=3
Olea europaea -subsp. *africana*	Indigenous forest	n=1
Grewia occidentalis	Indigenous forest	n=1
Diospyros whyteana	Indigenous forest	n=1
Oliana ventosa	Indigenous forest	n=1
Protea nitiida	Fynbos	n=4
Widdringtonia nodiflora	Fynbos	n=4
Protea neriifolia	Fynbos	n=3
Leucodendron conocarpodendron	Fynbos	n=3
Eucalyptus globulus	*Eucalyptus globulus*	n=6
Pinus halepensis	*Pinus halepensis*	n=6

Table 2. Wood (a) and leaf (b) concentrations (mg kg^{-1}) for all species

2a Species	N mg/kg	P mg/kg	K mg/kg	Ca mg/kg	Mg mg/kg	Na mg/kg	Mn mg/kg	Fe mg/kg	Cu mg/kg	Zn mg/kg	B mg/kg	N:P
C. capensis	2850	100	3750	1350	1700	259	32	107	3	6	5	29
M. acuminata	4000	200	4800	1800	1700	246	31	224	4	10	8	20
P. latifolius	3900	50	3500	1550	1550	25	54	63	3	8	5	39
P. elongatus	4500	100	3300	2000	1500	20	41	80	3	7	5	45
K. africana	3700	500	5700	2500	1900	434	38	155	5	21	10	7
O. europaea	2400	100	2900	1000	1400	14	3	75	2	4	7	24
G. occidentalis	3300	100	6700	2900	3500	379	14	262	6	6	8	33
D. whyteana	3800	100	6200	1100	2300	61	15	172	3	6	8	38
O. ventosa	2500	0	2700	900	1400	33	14	242	2	4	6	25
P. nitiida	2450	50	3150	1400	1600	236	68	84	2	5	5	25
W. nodiflora	3100	0	2700	1300	1450	59	49	65	2	5	6	31
P. neriifolia	2600	100	3600	400	1500	295	16	63	3	8	4	26
L. conocarpodendron	2600	0	1800	100	1000	58	9	46	1	1	2	26
E. globulus	3083	83	3133	1600	1717	295	29	118	2	7	6	31
P. halepensis	2467	17	2433	383	1483	79	7	34	2	7	4	25

2b Species	N mg/kg	P mg/kg	K mg/kg	Ca mg/kg	Mg mg/kg	Na mg/kg	Mn mg/kg	Fe mg/kg	Cu mg/kg	Zn mg/kg	B mg/kg	N:P
C. capensis	14550	950	5400	12050	3900	1931	288	139	4	20	28	19
M. acuminata	14700	700	5200	10900	10300	421	92	68	5	11	34	21
P. latifolius	12950	950	12000	13800	2850	477	1826	86	6	13	18	17
P. elongatus	14600	800	6700	12700	3000	270	725	110	4	9	17	18
K. africana	14700	700	6800	15600	3000	712	766	148	5	12	49	21
O. europaea	16700	800	10800	7400	2900	143	83	177	6	21	17	21
G. occidentalis	13700	600	6500	15500	4600	1352	56	70	5	11	31	23
D. whyteana	12600	600	6500	16400	2900	1120	399	114	4	8	49	21
O. ventosa	15000	1400	7200	1900	2500	2896	215	209	4	32	19	11
P. nitiida	7400	350	4250	2850	2050	1331	209	50	3	4	14	21
W. nodiflora	9300	600	3900	12500	2700	552	932	67	4	7	18	16
P. neriifolia	6600	400	3900	3600	1900	923	39	23	3	4	14	17
L. conocarpodendron	8800	400	3000	8300	3100	2893	695	100	6	8	19	22
E. globulus	12183	550	5633	10467	3450	1202	981	166	7	20	36	23
P. halepensis	12367	800	6383	4650	2583	1580	217	247	5	23	23	17