Pushing the boundaries: *Virgilia oroboides* (Keurboom) facilitated expansion of forest into fynbos

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ABSTRACT

The boundary between forest and fynbos vegetation in the Southern Cape of South Africa present a dynamic ecotone in which forest has previously been noted to have expanded into fynbos territory. Forest colonization of fynbos has been shown to be primarily a function of nutrients and light environments in the understory which may or may not be conducive for the growth of forest species. Additionally, it is understood that fire regime is the primary agent in determining forest/fynbos boundaries. *Virgilia oroboides* is a fast-growing leguminous tree confined to the margin between forest and fynbos. It has long been thought to facilitate the growth of forest species through the heavy shading and nutrient enrichment of soils; both of which facilitate the growth of forest seedlings. Furthermore, *V. oroboides* is predicted to reduce fuel loads and as a result prevent fire penetration of forests. These possible functions were tested by sampling soils, nutrient content of leaves and the shade cast by plants 18 months after a burn on a forest margin near Swellendam, Southern Cape. In addition, the effects of varying density of *Virgilia* on surrogates for fuel biomass, and forest seedling growth, were observed at Silvermine on the Cape Peninsula. Shaded environments produced by *V. oroboides* are shown to have detrimental effects on the growth of fynbos, while facilitating the growth of forests. *V. oroboides* had the highest soil nutrient enrichment potential of all species investigated and is therefore predicted to produce nutrient cycling processes conducive to the growth and regeneration of forests. Estimates of fuel in the understory of *V. oroboides* are predicted to reduce fynbos fire severity upon reaching the margin. These results suggest that *Virgilia* does indeed facilitate forest tree species more than light-demanding fynbos species so that its presence should result in greater stability or slow expansion of forests into fynbos. If supported by further work, this facilitative role of *Virgilia* has management implications for the conservation of fynbos and forests in the Southern Cape of South Africa.

INTRODUCTION

Natural forests in South Africa are the smallest, most vulnerable vegetation type in the country (Van der Merwe, 2011). The distribution of forests in the southwestern Cape conforms to the worldwide pattern of plant communities along watercourses differing in species composition (Miller and Johnson 1986). This has been interpreted as watercourse areas offering zones of amelioration in reducing harsh environmental

factors of adjacent vegetation which are unfavorable for forest growth. In addition to this, watercourses in the Cape also act as fire refugia, protecting forest species from burning. Covering approximately half a million ha of South Africa (0.5%), potential forest distributions have been shown to be limited by environmental factors such as rainfall and substrate composition; however, actual forest distribution is largely determined by the prevailing fire regime as a function of the dominant winds during the dry summer periods and the terrain physiography (Geldenhuys, 1994). Heath-like vegetation, locally known as fynbos, forms a matrix with forests and is highly adapted to fire, as highlighted by the widespread fire-stimulated recruitment of fynbos species. Post-fire recruitment is caused by fire-stimulated flowering, fire-stimulated germination by heat or smoke as well as from serotiny- the fire-stimulated release of seeds (Manders, *et al* 1992). Furthermore, forest succession has been noted in the absence of fire at various sites, for example; significant areas of Orange Kloof near Cape Town have been converted to forest after 50 years of fire suppression, as well as at Swartboskloof valley after only 28 years of no fire (Masson & Moll 1987; Manders et al. 1992). Therefore, it would appear that forests in the southwestern Cape are capable of invading adjacent fynbos vegetation, but are limited by their inability to withstand frequent fires in this region. This results in an ecotone tension at the margin between the two vegetation types in which forests seem to have a competitive advantage over fynbos, but boundaries with fynbos are kept relatively constant by the presence of fire.

Other factors which may prevent fynbos colonization by forest species are lack of perches for birds which limits seed dispersal, the inability for seedlings to survive summer droughts, high light intensity and low soil nutrients (White, 1978; Campbell & Killick 1985; Manders 1990; Manders & Richardson, 1992). Although soil moisture is important for forest growth, it has been shown to have very little influence on controlling the dynamics of the forest/fynbos ecotone (Van Daalen, 1981; Masson & Moll 1987). The majority of forest species in the southwestern Cape (40%) are ornithochorous and a large proportion of the remainder (32%) is anemochorous (Knight, 1988). Masson & Moll (1987) hypothesized that forest seed dispersal into fynbos is limited by the availability of suitable perches for birds as well as the fruit type of the species providing the perch. Manders *et al* (1992), however -rejected this hypothesis and concluded that colonization of fynbos by forest cannot be limited by dispersal as seeds of ornithochorous and anemochorous forest species were found immediately after fire in fynbos, irrespective of branch/fruit type of the surrounding vegetation. A dispersal-linked limitation of fynbos colonization by forest may be that forest recruitment has no link to local disturbance, whereas fynbos seeds generally recruit after fire. In occupying the correct ‘recruitment window’, this may allow for fynbos to establish before forest can take advantage of the post-fire habitats. Manders (1990) noted that heavy shading resulted in mortality of fynbos plants and that high light intensity in the fynbos region is a limiting factor to forest development.

Furthermore, Manders & Richardson (1992) showed how colonization of fynbos by forest species is expedited with increased soil nutrient levels. Given that fynbos plants are generally adapted to low-nutrient environments (Stock & Allsopp 1992; Lambers, *et al* 2010), high nutrients would appear to favour the competitive ability of forest over fynbos. The colonization of fynbos by forest may therefore be inhibited by low nutrients and high light intensities. Moreover, high nutrient levels and low light in the forest region would appear to preclude the colonization of forest by fynbos.

Manders and Richardson (2002) propose that fynbos colonization by forest involves a successional mechanism of facilitation. Precursor forest species establish and act as 'nurse plants' for recruitment of forest species by protecting them from excessive radiation and wind, ameliorating the effects of summer droughts through a mulching effect of litter as well as decreasing competition by reducing cover of herbaceous species beneath the 'nurse' plants. Establishment of forest patches within fynbos is a process called 'nucleation' (Janzen, 1988), with patches which are proposed to coalesce to form stable forest ecosystems (Yarranon & Morrison, 1974). The ability of an organism to alter an environment has been termed 'niche construction' or 'ecosystem engineering (Laland *et al.* 1999; Crain & Bertness 2006). Other examples of ecosystem engineering include changes in soil chemistry and nutrient cycling processes, temperature, fertility, humidity, acidity and salinity of soils as well as the light environment of a particular environment (Laland *et al.* 1999).

Virgilia oroboides, locally known as Keurboom, is a legume tree species limited to forest margins and riparian habitats (Philips, 1926) *V. oroboides* has taken a disturbance-linked recruitment strategy in that its seeds need high temperature fires in order to germinate and can maintain viability for up to 230 years (Geldenhuys, 1994). The ability of *V. oroboides* to grow incredibly fast and in high light conditions coupled with the large seed-bank in the barren post-fire habitats results in dense stands shortly after fires. In common with the large majority of members of *Fabaceae*, Palgrave (1981) reported on the presence of root-nodules containing nitrogen (N) fixing bacteria in *V. oroboides*. The invasive N-fixing alien *Acacia saligna* has been found to increase the nutrient content of the soils after it invades fynbos, ultimately resulting in the exclusion of indigenous species (Stock *et al.* 1995; Yelenik *et al.* 2004). Forest species can commonly be found growing in the understory of 5-10 year old *V. oroboides* stands (Geldenhuys, 1994), and have been shown to have accelerated growth rates when compared to that of seedling growth under typical climax forest habitats (Phillips, 1926). Phillips (1926) however, did not investigate the causes of this accelerated growth and proposed that the understory light conditions offered by *V. oroboides* was more favorable for growth.

I tested the hypothesis that *V. oroboides* along forest margins acts as an ecosystem engineer by creating more favorable conditions for forest growth and ultimately resulting in forest expansion. I tested three possible ways in which *Virgilia* could alter the environment to favour forest rather than fynbos:

1) *V. oroboides* could so alter the light environment that it would shade out light-demanding fynbos species but promote the growth of shade-tolerant forest species.
2) *V. oroboides* could enrich the soil through adding large quantities of nitrogen (and phosphorus)-rich leaf litter in a manner similar to that described by Yelenik *et al* (2004) for invasive Australian acacias
3) *V. oroboides* could reduce fire severity as fires approach the forest margin as a result of reduced fuel in the understory of the margin because of the elimination of fynbos species by shading.

METHODS & MATERIALS

Study sites

The elected study sites are all situated in the Western Cape province of South Africa. Marloth Nature reserve (Fig. 1 A & C) (33°05'16''S, 20°27'19''E) is situated in the Overberg, just north of the town of Swellendam. The two ecotones used at this site comprise of one exemplary ecotone (Fig. 1 C/A green polygon) and another smaller stand of *V. oroboides*. The fynbos region between the two sites in this area burnt in February 2012, approximately 18 months prior to this study. The second site used for this study is situated in the Silvermine section of the Table Mountain National Park (34°05'15''S, 18°25'07''E), where there is an extensive stand of *V. oroboides*.

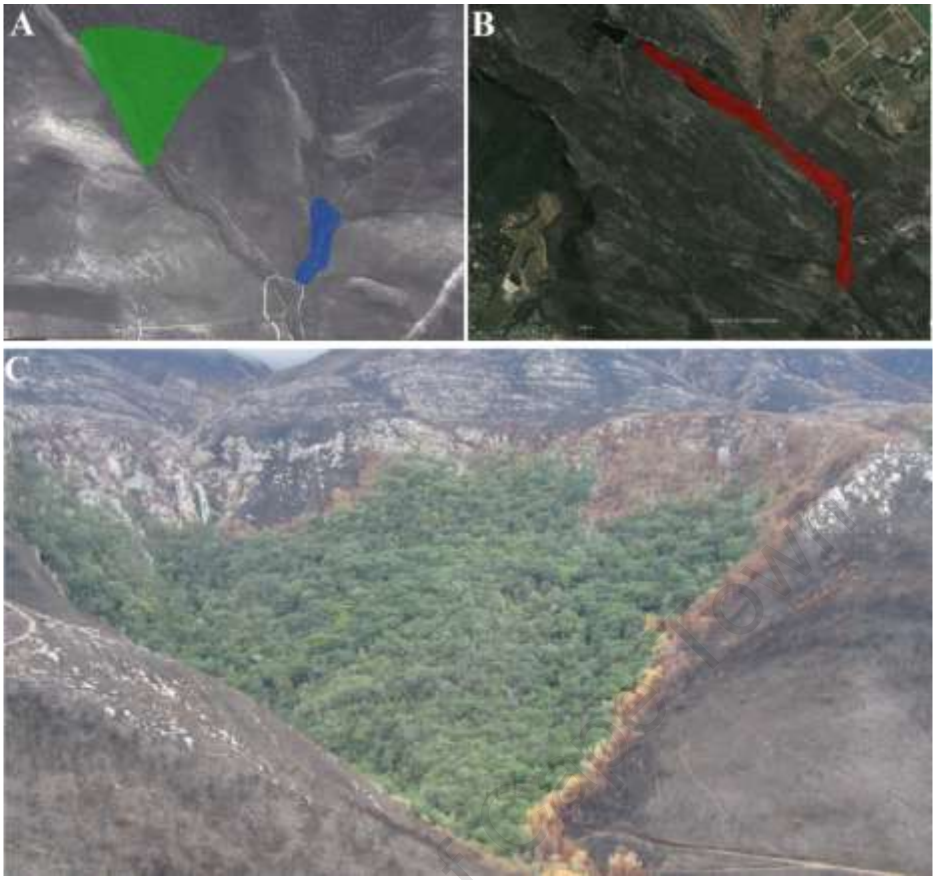

Figure 1: Study sites in A) Marloth Nature Reserve, Swellendam, B) Silvermine, Table Mountain National Park, and C) image of the Marloth study site in February 2012 shortly after a burn. Polygons represent different forest/fynbos margins. Photograph (C) taken of post-fire burn of Koloniesbos margin (green polygon).

Light

In order to test the effect of varying light intensity on the growth of fynbos and forest species, two of the most common species in the Marloth study area growing under shaded and open canopy light environments in the post-burn vegetation were investigated (Fig. 2) *V. oroboides* saplings that had established post-fire created a large amount of shading. *Protea mundii* and *Hartogiella schinoides* were chosen to represent the light responses of fynbos and forest respectively. Five 10 x 2 m transects were set out perpendicular to the length of the margin in which *P. mundii* and *H. schinoides* were recorded. *P. mundii* stem diameter was measured using Vernier calipers as well as plant height. Height and two diameter measurements were recorded for *H. schinoides.*, after which canopy area was estimated using a πr^2 relationship. Physical condition was noted for *P. mundii* growing in shaded and open canopy environments. Plants were assigned a binary condition classification of ‘good’ and ‘bad’ (Fig. 3) which was based on leaf and structural rigidity.

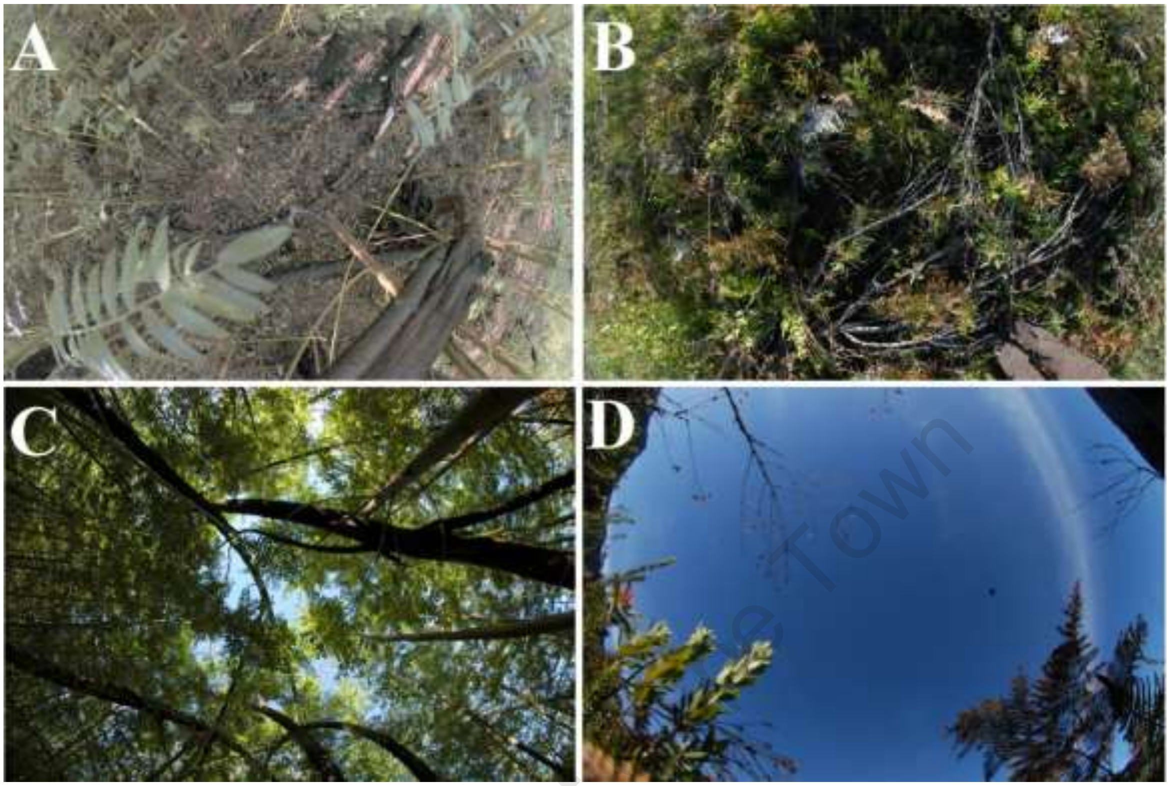

Figure 2: Fish-eye photographs illustrating undergrowth (A) and (B) of shaded (C) and open (D) canopy environments respectively. Litter production and canopy cover in photographs A & C respectively are entirely from *V. oroboides*.

Nutrients

Soil samples were collected at Marloth using a soil auger approximately six months after the fire. Three forest soil samples were collected parallel to the length of the margin approximately ten meters from one another. Four and five soil samples were collected from the margin and fynbos respectively, both perpendicular to the length of the margin. Soil samples were air-dried for five days after which soils were sieved using a 2mm mesh and sent for analysis of %N, %C, %K, total P, δ15N and δ13C. In order to determine nutrient content of various species, leaf samples were collected from the species accounting for most of the biomass in the forest, margin and fynbos regions. Three thirty-meter transects were set out in the forest parallel to the margin and all species within one meter either side of the transect were counted and added to a cumulative total. Tree sizes were categorized into size classes of 0-2m, 2-5m and >5m and assigned a value of 1, 2 and 3 respectively. Individuals were multiplied by the assigned size value and a total was recorded for each species in order to obtain estimations of relative biomass contributions. Similar transects were conducted in the margin , however resprouting individuals were multiplied by four rather than having size class separations as differences in size appeared to not have as much of an influence on biomass contributions as resprouting. The same 30 x 2 m meter transects were conducted parallel to the margin in the fynbos region. However due to the relatively recent fire, the size of plants was similar across species and as a result, cumulative totals of species were used to estimate biomass contribution. The five, seven and eight top ranking species in terms of biomass contribution for the forest, margin and fynbos region respectively were chosen for leaf collections. Species were identified by using previous species community reports of Marloth (McDonald, 1993) as well as the Guthrie Herbarium at the University of Cape Town (UCT). More species were chosen in the fynbos region than the forest as there were far fewer species in the forest transect. Leaf samples were dried in an oven for 120 hours at 60°C. Once dried, leaf samples were ground to a powder and sent off for analysis at the University of Cape Town (UCT) Archaeology department's mass spectrometry unit and Elsenburg institute for plant production. Leaf samples were analysed for %C, %N, $\delta^{13}C$, $\delta^{15}N$ and %P. A Principal Components Analysis (PCA) was conducted on all the species using all nutrient variables previously mentioned. The remainder of the leaf samples were measured for leaf area using a leaf area meter and dry mass in order to calculate specific leaf area (SLA) for each species. Nutrient input from litter is a function both of litter quality and quantity (e.g. Yelenik et al. 2004). Litterfall could not be measured for logistic reasons; however leaf productivity is related to SLA (Poorter & Van der Werf, 1988; Van der Werf, *et al.* 1988). As a simple index of relative nutrient contribution from litter, I therefore calculated the product of SLA and P and N nutrient content for each species *Metalasia densa* and *Gnidia galpinii* were removed from SLA measurements because their area was difficult to measure due to their leaf shape.

Figure 3: Image illustrating "good" (A) and "bad" (B) condition *P. mundii*

Leaf samples were collected from a further 20 *Protea mundii* individuals; ten from a stand previously occupied by *V. oroboides* which was burnt in the fire, and ten from a fynbos patch which had no evidence of pre-burn or post-burn *V. oroboides* occupancy. *P. mundii* was used here as a phytometer to note the leaf nutrient content effects of growing in soils previously occupied by *V. oroboides* compared with fynbos soils.

Fire

At the Silvermine site (Fig. 1, B), the extensive *V. oroboides* offered stands varying in density. Seven 12-meter transects were conducted through each of the *V. oroboides* stands of high, medium and low density (Fig. 4). Each transect consisted of six foliage profiles, three left and three right of the transect (Bond et al. 1983; MacArthur and MacArthur 1968). Foliage profiles were assigned height increments of 0.25m, 0.5m, 0.75m, 1m, 1.5m and 2m. Foliage profiles provide a proxy for fuel estimates and could be compared for various *V. oroboides* densities. Three densitometer readings were taken in each transect which were converted to percentage canopy cover. Basal area of *V. oroboides* was estimated once per transect using a Bitterlich wedge. Furthermore, forest seedlings within one meter either side of the transect were recorded.

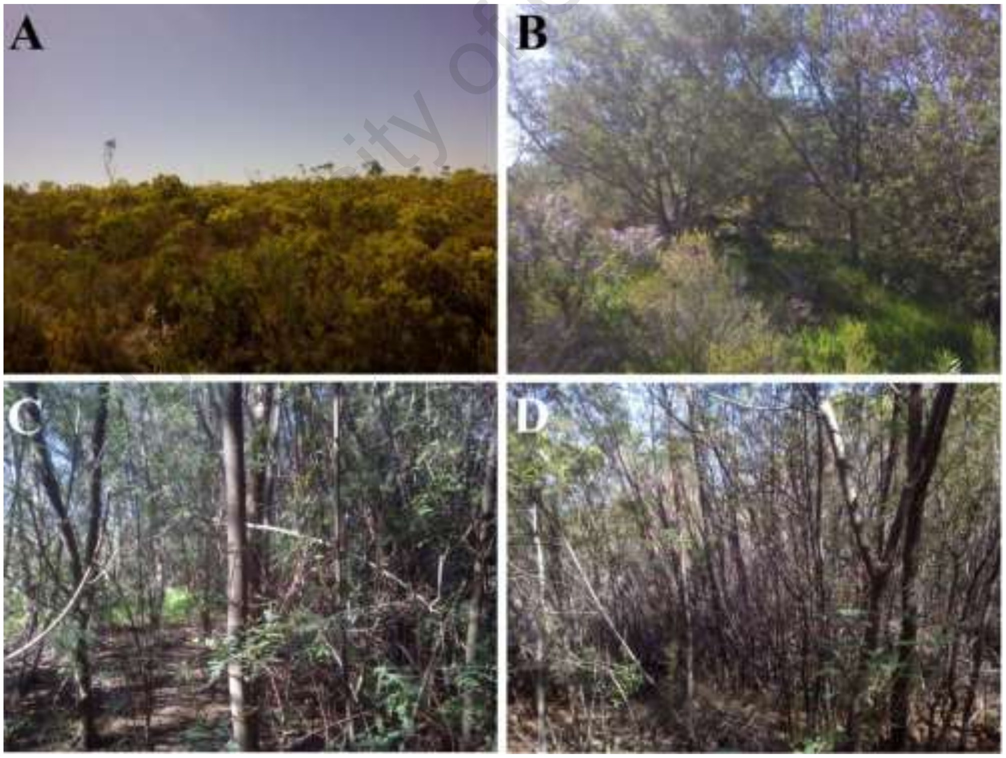

Figure 4: Images showing open fynbos (A), low density (B), medium density (C) and high density (D) *Virgilia oroboides* stands.

Statistical Analysis

All statistics were performed using the statistical analysis package Statistica. T-tests were used to determine statistical differences between two means, whereas Analysis of Variance (ANOVA) was used to determine differences between three or more means. Additionally, post-hoc HSD-Tukey tests were used at the 95% confidence level to determine where differences between three or more means arise; differences are indicated by lower case letters plotted above histogram bars. A principle components analysis (PCA) was performed in order to determine patterns of variation in leaf nutrient variables. All presented error bars represent 95% confidence intervals as a function of standard deviation and sample size.

RESULTS

Light

P. mundii had thinner stems in shaded conditions (beneath 18 month old *Virgilia* saplings) when compared to plants in the open (p<0.01, t=3.29, df=38). There were, however, no differences in the height/diameter relationship of *P. mundii* in the different light environments. Plants growing in shady environments beneath *Virgilia* were in significantly poorer condition based on the binary classification of ‘good’ and ‘bad’ (Fig.3) (Fisher’ exact test p<0.0001).

Hartogiella plants were taller in the shade than in the sun (μ=162.5 vs. μ=131, respectively) but the difference was only significant at the 10% level (p=0.057, t=-.196, df=38). There were no significant differences in canopy area between closed and open canopy environments but plants in the open had larger canopy areas for a given height than plants growing in the shade (Fig. 4).

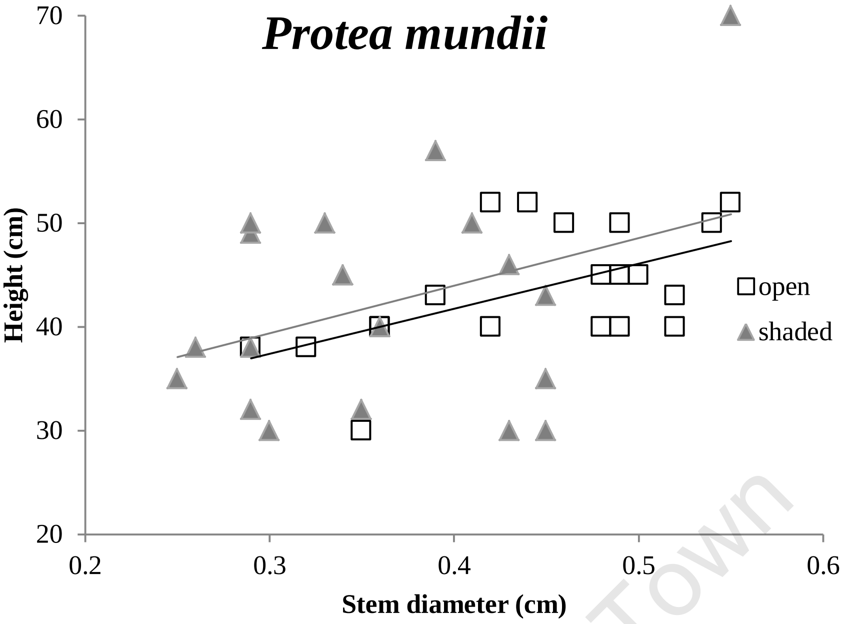

Figure 3: Stem diameter versus height relationship of *P. mundii* in shaded and open canopy light environments

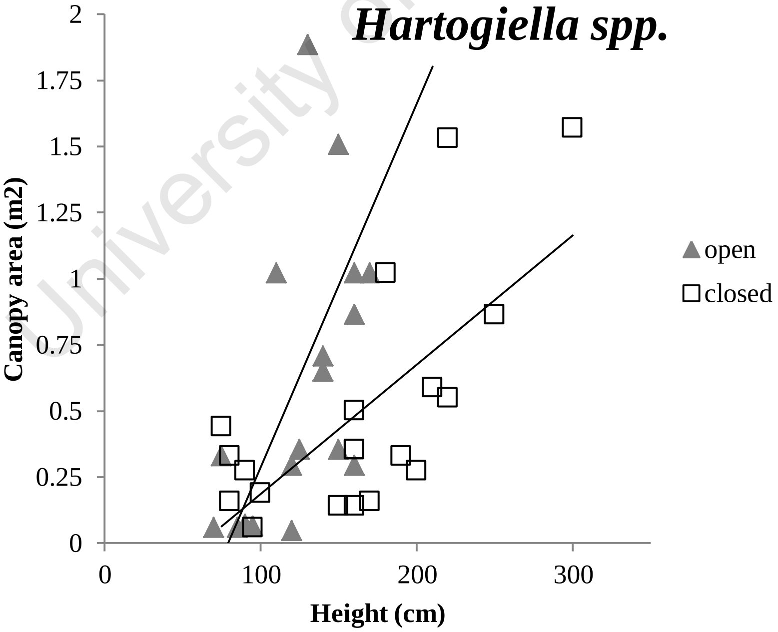

Figure 4: Height (cm) versus canopy area (m^2) relationship of *Hartogiella* in shaded and open canopy light environments.

Nutrients

All soils collected in Marloth are shale-derived. Soils did not differ much in morphology or texture, although fynbos soils were somewhat shallower than margin soils. The forest showed some evidence of podsolization with grey sandy elements in the A horizon. A, B and C horizons had depths of 0-60cm, 60-120cm, >120cm, respectively. The margin had sandy-clay to clay type soils with horizons of 50cm, 50-120cm, >120cm. The fynbos vegetation was growing on the shallowest soils with A, B and C horizons of 35cm, 35-75cm, >75cm which consisted of >40% clay, and was classified as sandy-clay. The C horizon here contained large amounts of weathered bed rock.

Figure 8 is a histogram showing the differences in major soil nutrients across the three vegetation types approximately 6 months after the fire. Different letters indicate statistical differences computed using post-hoc HSD-Tukey tests at the 95% confidence level. The forest had significantly higher % N and % C than the margin and fynbos sites, which did not statistically differ from one another. The fynbos soils, however, had far lower levels of Total P than the forest and margin regions, which did not statistically differ from one another. %K, δ15N (‰) and δ13C (‰) did not show any statistical differences between the three soils analyzed.

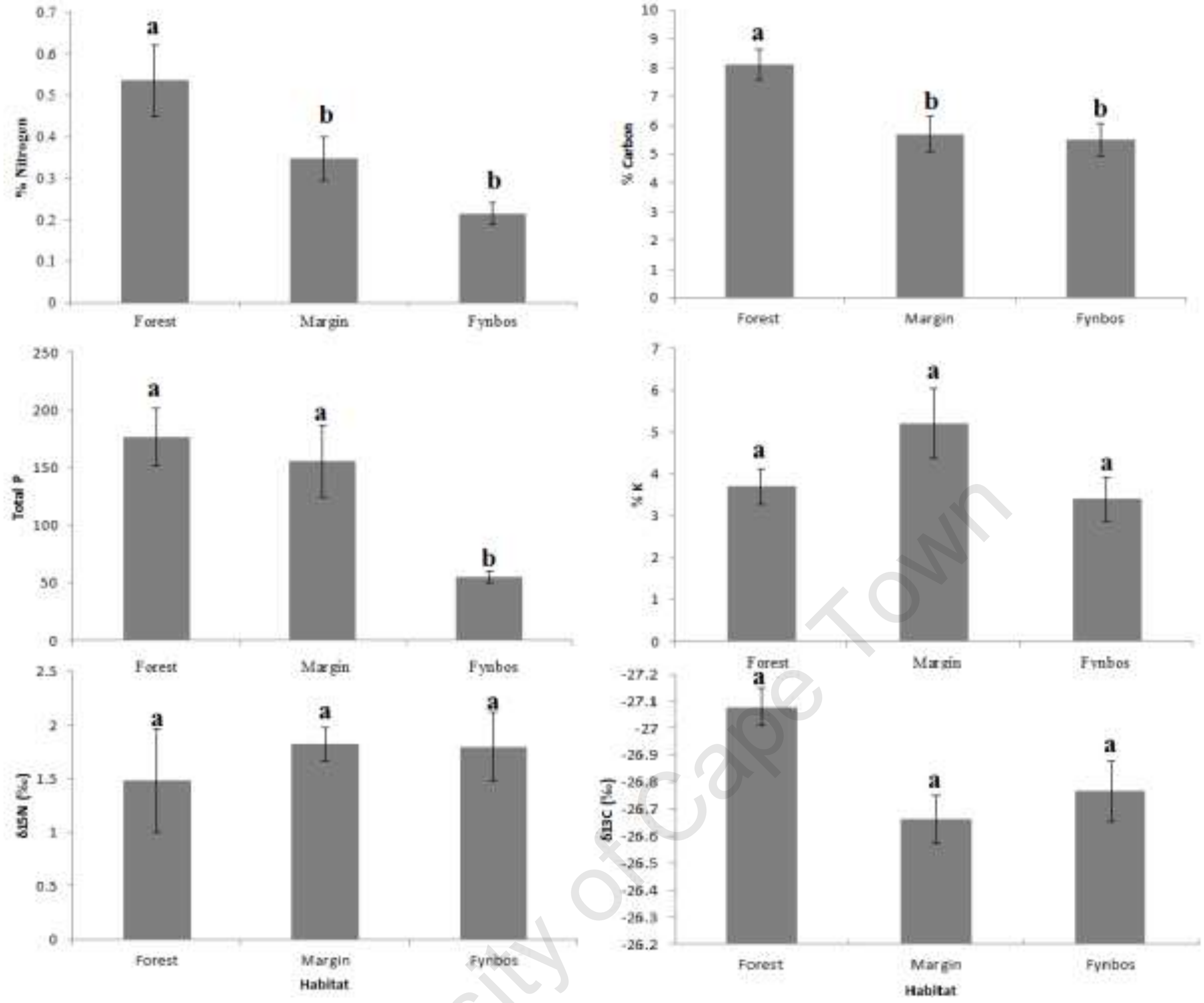

Figure 8: Major soil nutrients (N, C, P, K) and δ13C (‰) δ15N (‰) across the forest, margin and fynbos vegetation types. The margin and fynbos sites had been burnt approximately six months before sampling. Letters indicate statistical differences (HSD-Tukey 95% confidence).

The PC1 axis of the PCA (Fig. 9) described 43% of the variation in leaf nutrients. This axis had extremely high loadings for %N (-0.90) and %P (-0.92) resulting in most of the explained variance within this axis arising through these two nutrients. PC2 accounted for a further 25% of the variance explained with high loadings in the δ15N (0.72) and %C (-0.71) variables. Species from the different vegetation types were generally separated in ordination space with margin species typically at the high nutrient end of PC1, whereas fynbos species were located at the opposite end of the axis indicating low nutrient contents. Most forest species occurred at the intermediate positions along PC1.

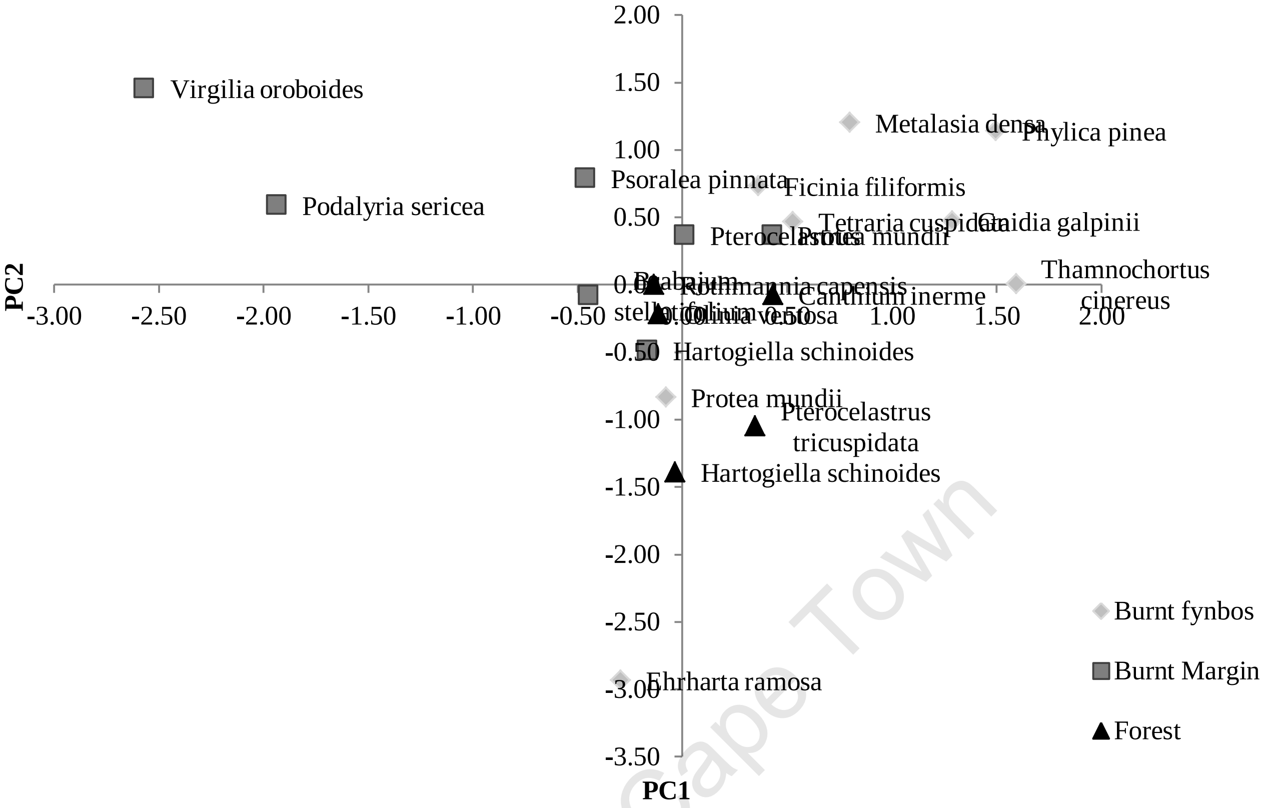

Figure 9: Principal Component Analysis (PCA) based on measures of leaf nutrients. PC1 (x-axis) explains 43 % of the variation and PC2 (y-axis) explains a further 25% of the variation.

Table 1: Principal components (PC1&2) Eigen value correlations with leaf variables

Variables	PC1	PC2
%N	-0.90	0.17
d 13C/12C	0.46	-0.35
d 15N/14N	0.35	0.72
%C	-0.42	-0.71
%P	-0.92	0.26
Expl.Var	2.17	1.24
Prp.Totl	0.43	0.25

There was a strong relationship between N enrichment and P enrichment (R^2=0.84). Fynbos and margin species separated themselves on an enrichment gradient where fynbos are predicted to have very little effect on enriching the soils, whereas the margin species appear to be more likely to add nutrients to the soil, which is indicative of their large values on the enrichment axes. Interestingly, *V. oroboides* growing in the margin is predicted to have the highest addition of nitrogen and phosphorus to the soils. Forest species did not appear to have any segregation along the enrichment axes.

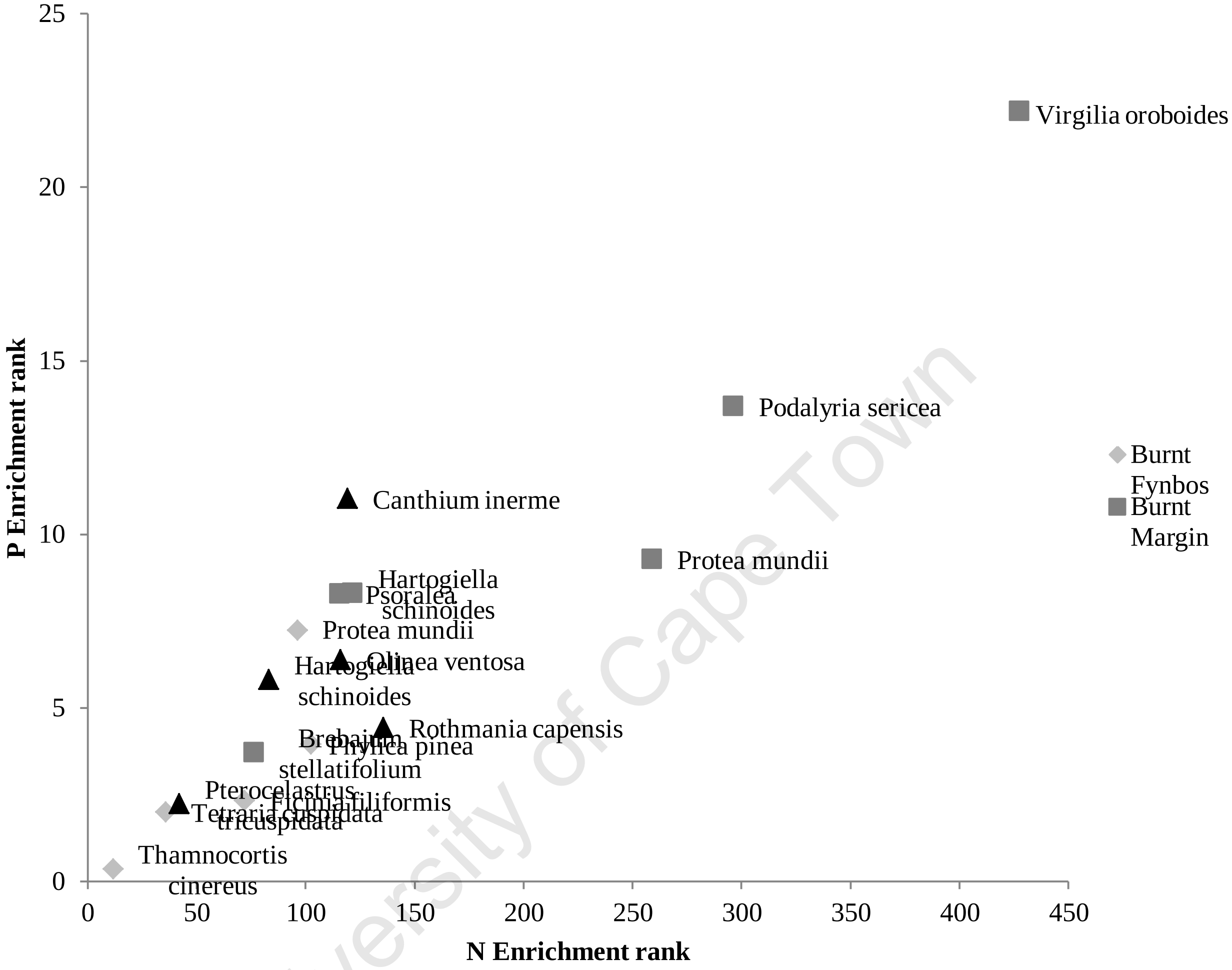

Figure 10: Species enrichment relationship between Nitrogen (N) and Phosphorous (P). Higher values represent higher enrichment potentials.

P. mundii growing in the burnt margin had higher % N and %P when compared with individuals growing in burnt fynbos (p<0.01).

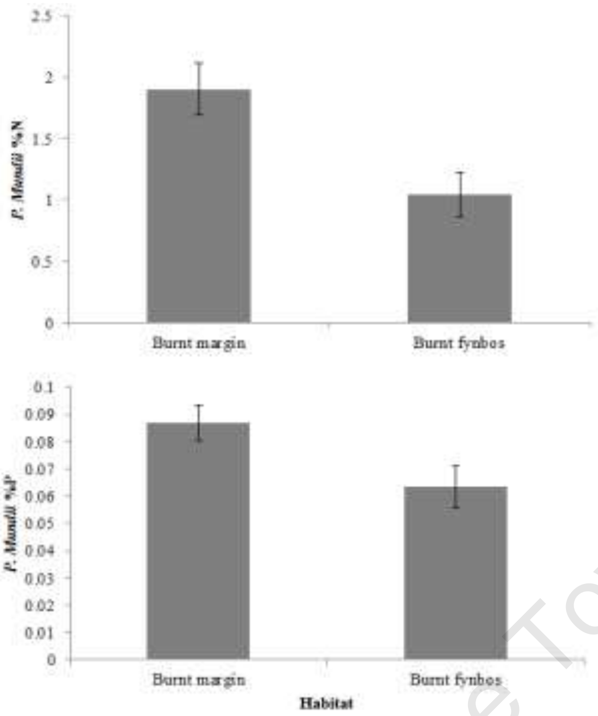

Figure 11: %P and %N of *P. mundii* growing in previously occupied *V. oroboides* stands and fynbos stands with no evidence of *V. oroboides* pre or post-fire.

The C: N ratios of leaves differed significantly between the fynbos and the margin ($p<0.01$), however, forest did not differ from either of the other vegetation types ($p=0.23$). The differences in this ratio is almost entirely due to differences in nitrogen content, as there was very little statistical difference between the % C for each of the vegetation types. Interestingly, *V. oroboides* had the lowest C:N ratio of all species investigated (*Virgilia* C:N = 11.5)

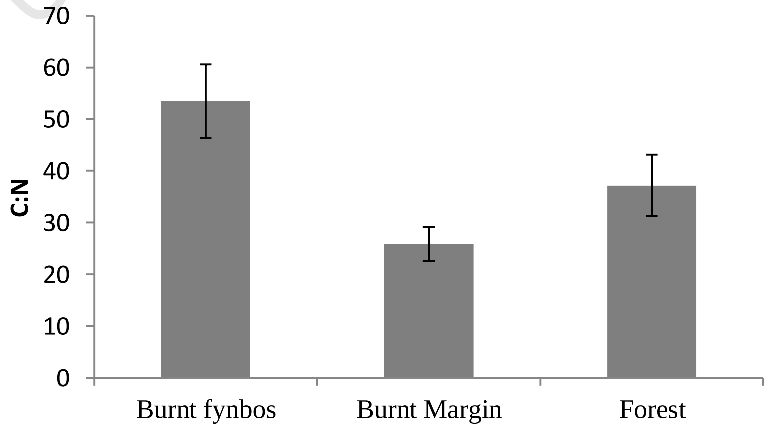

Figure 12: C:N ratios of species from the fynbos, margin and forest vegetation types.

Fire

Figure 14 shows typical foliage profiles for differing densities of *V. oroboides*. Low density *V. oroboides* stands (µ =7.8m^2/ha) provided larger amounts of fuel as indicated by foliage profile estimates. This is due to low density stands allowing for the understory growth of fynbos, whereas the foliage under medium (µ=13.2m^2/ha) and high density (µ=20.4m^2/ha) stands came entirely from debris from *V. oroboides* itself. Medium density *V. oroboides* stands generally produced the lowest amounts of fuel as fynbos understory growth was prevented and there was minimal self-originating debris/fuel.

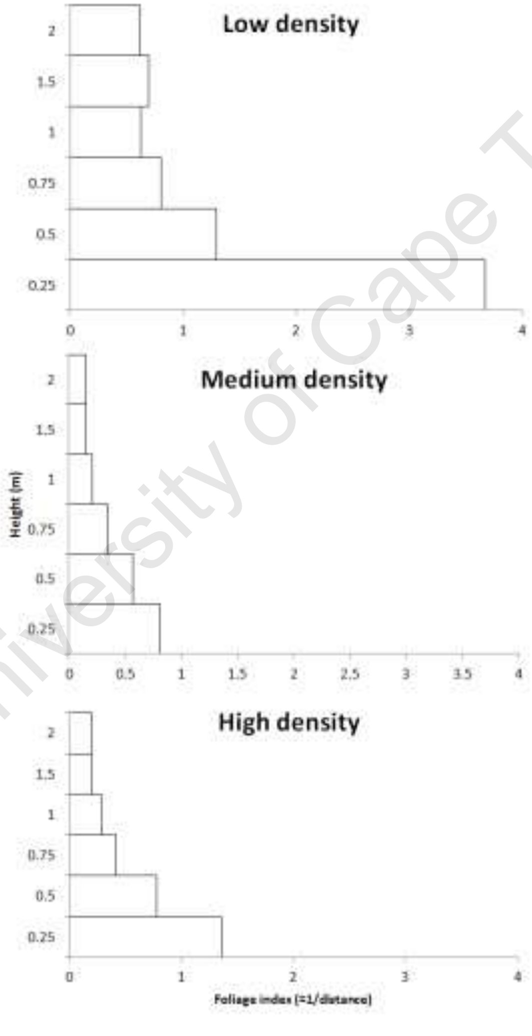

Figure 14: Typical foliage profiles from the low, medium and high density *V. oroboides* stands

Once *V. oroboides* basal area begins to exceed approximately 10 m^2/ha, understory biomass begins to decline. At high basal areas, branch and litter fall from *V. oroboides* can produce significant fuel in some stands or create an open understory, free of fuel.

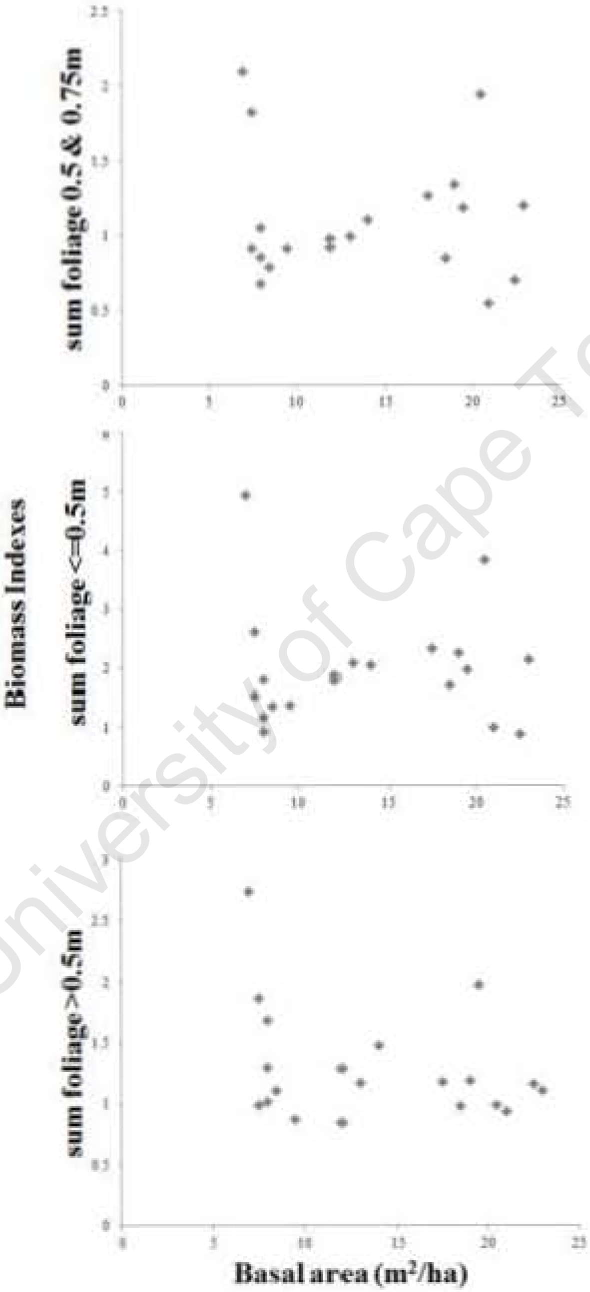

Figure 13: Basal area (m^2/ha) relationship with cumulative fuel estimates (0.5m & 0.75m), (<=0.5m) and (>0.5).

V. oroboides basal area (density) had a humped relationship with the number of forest seedlings growing in the understory (Fig. 4). Tree seedlings increased with increasing basal area of *V. oroboides* to a maximum of $15m^2$/ha, but thereafter declined with no seedlings in dense stands with basal area >20 m^2/ha. The number of seedlings per transect counted within medium density (μ=11.14) stands was significantly higher than that of the low (μ=6) and high (μ=0.86) density stands (p<0.01, F=19.87, df= 2).

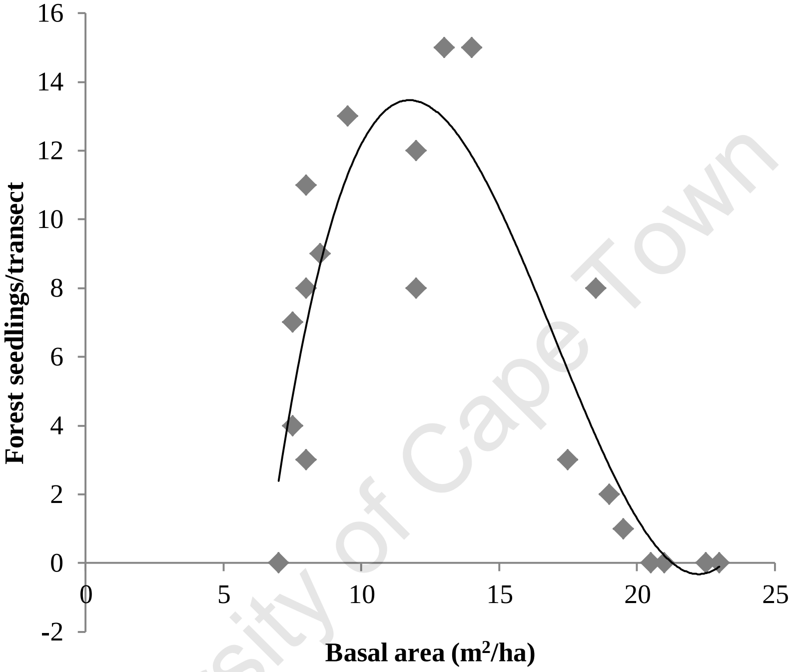

Figure 4: Scatterplot of *V. oroboides* basal area relationship with forest seedling counts per transect. The fitted line is a polynomial of order 3. R^2=0.77

DISCUSSION

Light

This study was aimed at determining whether or not *V. oroboides* has a facilitative effect on the expansion of forest into fynbos. The first way in which *V. oroboides* is predicted to promote forest expansion is through the reduction in understory. Regrowth of forest, fynbos and margin species after fire will appear along the burnt margin region as well as into parts of the burnt fynbos (Manders, *et al* 1992) and it is predicted that the rapid post-fire growth of *V. oroboides* produces a shaded light environment that will suppress the growth of fynbos species. *P. mundii* appears to have compromised growth when in shaded environments; although not in terms of their height but rather in their stem diameters. Fynbos species in general are known to be shade intolerant (Manders, 1990) and the thin stems of *P. mundii* growing in low light environments found in this study appear to be an etiolated response light consistent with shade intolerance. The healthier condition of plants growing in high light environments (Fig. 3) further suggest that post-fire shaded environments produced by *V. oroboides* ultimately inhibits the sympatric growth of fynbos in the understory as supported by Manders (1990).

While plant competition for light has received considerable attention, the facilitative effect of shading on forest species has not (Semchenk, *et al.* 2012). *Hartogiella schinoides,* a broad-leaved forest species, had similar growth rates in the sun and shade in post-burn environments. It is however, difficult to extrapolate these findings to the growth of seedlings as growth rates investigated in this paper were that of post-burn resprouting individuals. Nevertheless, Manders (1990) recognized forest species of South Africa as shade-tolerant and suggested that high light intensities might be a limiting factor for the establishment of forest species in fynbos regions. Therefore, in an opposite effect to that of fynbos species, shade produced by rapid regeneration of *V. oroboides* in post-fire environments would appear to facilitate the growth of forest species rather than fynbos.

Walters & Reich (1996) recognized shade tolerance as a primary mechanism for the succession of northern deciduous forests. It would appear that there is a similar case for that of forests of the Southern Cape. The shade created by *V. oroboides* allows for the sympatric understory growth of forest and fynbos species. However, due to the shade-tolerance of forest species, forest establishment would appear more likely than fynbos.

Nutrients

Fynbos vegetation grows on some of the most nutrient poor soils in the world, with particularly low levels of N & P (Stock & Lewis, 1986; Witkowski & Mitchell 1987, Stock *et al*, 1995). Fynbos plants have adaptations to cope with low nutrients such as cluster roots (eg, proteioid, capillaroid, dauciform) which help with P uptake, as well as mycorrhizal associations for the assimilation of N (Lamont, 1982; Allsop & Stock, 1993). There is, however, a debate on whether or not the lower nutrients found in fynbos, when compared with forest, is the cause of fynbos growth or simply the result. Manders (1990) noted these differences in soil nutrients between forest and fynbos growing on the same parent material within a few meters of each other which provides solid evidence that these differences arise from their associated nutrient cycling processes. Van Daalen (1981) showed no regeneration of forest individuals in fynbos and attributed this to the dependence of forests on a ‘closed’ system of nutrient cycling characteristic of established forests where nutrients are tightly and efficiently cycled within the rooting zone. In addition to this, although fynbos soils are low in N and P, Van Daalen (1984) has shown that forests are capable of establishing on most soils and that forest and fynbos soils rarely differ in parent material and therefore ascribed any differences in soil nutrients as an artifact of the vegetation. The establishment and maintenance of forest in fynbos would therefore appear to be dependent on appropriate niche construction through rapid nutrient enrichment of soils by litter from forest species that is maintained through cycling processes.

The effect of vegetation feedbacks on soil fertility has recently been recognized at a key mechanism for the establishment of forest species on nutrient poor soils (Vitousek & Walker 1989; Vitousek 1990; Wedin & Tilman 1990). The ability for one species to significantly alter soil fertility is not uncommon; for example, alien *Acacia* species recover rapidly after fire (Milton & Hall, 1981) and elevate soil fertility, particularly N, as a result of high leaf-litter inputs (Stock *et al*, 1995; Yelenik *et al.* 2004). Furthermore, Witkowski (1991b) found no differences in the resorption of nutrients between the invasive acacias and indigenous fynbos, which suggests that the acacias had a high net input of nutrients into the soil when compared to fynbos species. It would appear that *V. oroboides* acts in the same way. In addition to its rapid post-fire recover, the PCA (see Fig. 9) showed that *V. oroboides* had the highest leaf nutrient content in terms of N and P of all species investigated in this study. Yelenik *et al.* (2004) suggest that soil nutrient enrichment is a function of leaf nutrient content and leaf productivity. Given that SLA can be used as a proxy for leaf productivity (Poorter & Van der Werf, 1988; Van der Werf, et al. 1988) it would appear that the input of nutrients by *V. oroboides* is extremely high. Furthermore, the C: N ratio, often used as an indication of how well leaf material will decompose (Enriquez *et al.* 1993), was lowest in *V. oroboides*, suggesting that the nutrients from these leaves will be easily converted to available nutrients in the soil. In contrast to *V. oroboides*, forest species were found to have lower leaf productivity (as indicated by lower SLA) and are generally sclerophyllous (Van Daalen, 1981); as a result, forest species would have lower soil nutrient enrichment capabilities. The establishment of forests in nutrient poor fynbos in my study sites would therefore depend on *V. oroboides* as a precursor species to establish the necessary nutrient cycling process prior to seedling development. Given that fynbos can show reduced growth rates with the elevated N and P soil concentrations (Witkowski, 1989), the inputs of nutrients by *V. oroboides* would appear to promote the growth of forest species in the understory at the expense of fynbos. Furthermore, the ability of *V. oroboides* to reestablish rapidly after fire may increase nutrients in ways other than through the addition of leaf litter; these include a) accessing nutrients from deep soils and redepositing these in shallow root layers through root exude or litter (Kellman, 1979; Belsky 1994; Scholes & Hall 1996; Jobbagy and Jackson 2004), b) increasing canopy leaching by acting as a dust trap

(Escuderi *et al.* 1985; Bernhard-Reversat 1988) and c) adding nutrients through droppings by attracting birds and mammals through the addition of perches and shelter (Giorgiadis 1989; Belsky 1994).

It would appear that *V. oroboides* performs a similar role to that of the *Acacia* in its rapid addition of nutrients and as a result would act as an ideal precursor species for the establishment of forest in fynbos. In support of this is the phytometer results (see Fig. 11); *P. mundii* growing in soils previously occupied by *V. oroboides* had higher N and P concentrations than plants growing in soils which had no evidence of pre-fire or post-fire *V. oroboides* occurrence. Therefore, we might expect the persistence of nutrients added by *V. oroboides,* even after its local disappearance, and that higher nutrients would favour the growth of forest over fynbos.

Fire

Fire has been identified as one of the key mechanisms for determining forest distributions in the Cape (Geldenhuys 1994). Forests themselves however, rarely burn and are only significantly diminished by severe fires, rather than frequent fires (Van Wilgen, *et al.* 1992). This study investigated whether or not the presence of *V. oroboides* along the margin of forests would reduce fuel and as a result prevent fires from entering the forest. Medium density *V. oroboides* stands resulted in the lowest fuel estimates. Fuel estimates in the low density stands was entirely attributable to the fynbos growth in the understory, whereas high density stands were devoid of any fynbos growth (see Fig. 4). However, low density stands occupied by fynbos are more likely to burn as the result of one or more of the following factors; i) higher moisture content of live foliage in trees than fynbos, ii) higher proportion of flammable crude fats in fynbos, iii) higher heat yields of fynbos and iv) differences in the packing ratio of fuel parts and the ratio of live to dead plant material (Van Wilgen *et al.*1992). Fynbos has been reported to have higher flammability than Chilean mattoral, but lower flammability than Californian chaparral or Australian *Eucalyptus* woodlands. Therefore, high fuel loads in low density stands are far more likely to produce severe fires when compared to the fuel in high density stands.

In order for *V. oroboides* to significantly reduce understory fuel, stands need to have a basal area of approximately 10m^2/ha, which is approximately the density mid-point between low and high density stands investigated in this study (see Fig. 4). Van Wagner (1977) recognized that for fires to be damaging to forests, crown fires need to form from surface fires, which necessitates the presence of 'bridging fuels'. Furthermore, Van Wilgen *et al.* (1992) noted that the spatial distribution of fuel is a major determinant of whether fynbos fires will penetrate the forest or not. The low and patchy fuel estimates of *V. oroboides* stands therefore suggests that surface fynbos fires approaching the margin are unlikely to penetrate and spread into forests due to their inability to convert to crown fires. In addition to this, *V. oroboides* generally had concentrated litter layers, sparse side branches and sparse crowns, a fuel arrangement described to be unconducive to the spread of fire (Van Wilgen *et al* 1992).

Forest expansion has been shown to be determined by the fire regime (frequency, intensity and season of burn) rather than individual fires (Manders, 1990). Although it would seem that the complete absence of fire would favour the expansion of forest, this may not be the case; prolonged absence of fire will result in the build of up fuel in adjacent fynbos, which once burnt will produce a fire of such high intensity, fire penetration of the forest may be powerful enough to destroy the forest entirely, after which recruitment of fynbos will occur at the expense of the forest (Manders, 1990). In saying this, if fire is absent from a forest/fynbos ecotone for long enough, the expansion of forest might consume the entire adjacent fynbos (as in the case of Orangekloof), in which further fires will be highly unlikely. Such long-term fire suppression is, however, unlikely without anthropogenic influence.

CONCLUSIONS

The effects of light, nutrients and fire all seem to play important roles in the ecotone dynamic between forest and fynbos in the Southern Cape; however I predict that their effects on facilitating forest are temporally separated. Rapid post-fire growth of *V. oroboides* produces dense stands that produce heavily shaded understory unconducive to growth of shade sensitive fynbos, as well as through interspecific competition for space. Once established, *V. oroboides* stands thin out through natural processes (such as ring barking of caterpillars of the *Leto venus* moth and intraspecific competition) and establish a nutrient cycling environment that allows the for the stable growth of forest species. However, it appears that the presence of fire is the overriding agent in controlling the position of the forest/fynbos ecotone. Currently, fynbos in the Southern Cape burns every 10-20 years (Van Wilgen, *et al* 1992) similar to recommended frequencies of 9-15 years for sufficient maintenance of fynbos (Kruger & Bigalke, 1984). Given that *V. oroboides* readily burns but prevents fire sustenance, and that forest seedlings can generally be found growing in the understory of *V. oroboides* stands only after 5-9 years after fire (Geldenhuys 1994), it would seem highly unlikely that in natural fire regimes, forest seedlings would be able to out-grow the "fire trap", as described by Bond *et al.* (2005).

In the absence of fire, I predict that forest development in fynbos seems likely through the facilitative effects of *V. oroboides*. The expansion of forest into fynbos in the absence of fire has been noted at various sites previously mentioned. In saying this, it is difficult to entirely attribute the expansion of forest through the facilitative effects of *V. oroboides*, this study does however provide clarity on the role of this margin species on these effects. Furthermore, it seems unlikely that fynbos conversion into forest in the Southern Cape conforms to the coalescence of scattered ‘nucleation’ sites within fynbos, as proposed by Yarranon & Morrison (1974). Van Daalen (1981) proposed that forest species would be unable to act as precursor species due to their inability to establish suitable environments for growth of following generation. The dependence of *V. oroboides* as a precursor species for these nucleation sites seems to be essential. Furthermore, *V. oroboides* may be limited to the nutrient rich margin given the poor P-acquisition strategies and high P requirements of fynbos legumes. This would suggest that *V. oroboides* meets its phosphate requirements by accessing nutrients from adjacent forests, and would therefore cease to be found in low phosphate soils in fynbos and nucleation patches within this vegetation type are therefore unlikely. Forest boundaries with fynbos are kept relatively constant under natural fire regimes, however, in reduced fire frequency I predict that forest expansion into fynbos occurs in a ‘two steps forward, one step back’ manner; some forest seedlings in the margin will survive fires as a result of reduced frequencies allowing for them to escape the “fire trap” (Bond *et al*. 2005), and dense stands of *V. oroboides* will form slightly further into fynbos after each infrequent fire. This hypothesis, however, is not supported by any data here and further studies investigating the mechanisms behind forest expansion into fynbos in more detail are encouraged.

This study strongly suggests that *V. oroboides* has the ability to restore nutrient cycling processes and may provide a way to aid forest regeneration. However, maintaining the correct fire regime has been outlined to be of most importance in producing the correct micro-climate for fynbos vegetation. Frequent fires disrupt the nutrient cycles which favour forest growth, creating low nutrient conditions in which fynbos plants have a competitive advantage over forest species, but frequent fires are also important in reducing the build-up of fuel in fynbos which may lead to severe fires capable of eradicating adjacent forest vegetation. These results, however, should be used conservatively when extrapolating to all forest margins, whether *Virgilia* grows along them or not. Furthermore, this study lacks site replications of nutrient, light and fuel analyses and these results would be supported with data on the ecotone dynamics of the forest/fynbos boundary in which *Virgilia* is absent. Nearly 100 years ago foresters questioned whether or not *Virgilia* would promote forest expansion, and although this study does not confidently answer this question, solid evidence is provided that this may in fact be the case.

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