

Competitive resistance of a native shrubland to invasion by the alien invasive tree species, *Acacia cyclops*

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Abstract Biotic resistance is infrequently considered when investigating the potential spread of invasive woody species. In this study, we determined whether native vegetation of Mediterranean-climate shrublands in the Cape Floristic Region of South Africa constrains woody invasive seedling establishment and performance through above- and below-ground competition for resources. Seedlings of the invasive tree, *Acacia cyclops*, were transplanted into native shrubland vegetation in a three-way factorial design where light availability, below-ground root competition and soil nutrient availability were manipulated. Survival, growth, biomass allocation, water use efficiency, foliar nutrients and $\delta^{15}\text{N}$ were assessed after ca. 7 months. Control seedlings had a ca. 20 % survival, which increased to a maximum of ca. 80 % depending on treatments. Root exclusion tubes increased seedling survival and heights by ca. 1.6-fold and total biomass by ca. 4.8-fold. In contrast, above-ground availability of light did not influence seedling survival or height, although seedlings grown under the lowest light availability (0–20 %) had

biomass ca. threefold lower than seedlings grown under the highest light availability (80–100 %). Competition from native vegetation, particularly below-ground competition, impedes survival, growth and biomass accumulation of these woody invasives, presumably constraining invasion spread. We conclude that the maintenance of intact, native ecosystems is important in limiting woody invasion spread and also suggest that biotic components should be included in invasion distribution and spread models in order to aid in optimization of scarce management resources.

Keywords Cape Floristic Region · N_2 -fixation · Root exclusion · Strandveld

Introduction

Predictions of exotic plant invasion seldom incorporate measures of biotic resistance and instead focus primarily on abiotic factors such as climate and soil geochemistry (e.g. Higgins et al. 1999; Thuiller et al. 2005). Models that combine both abiotic niche suitability of the invader as well as susceptibility of different landscape patches to invasion are, however, more appropriate tools to predict the rate and magnitude of invasion spread (Caplat et al. 2012). Thus, there is a clear need to quantify and understand the competitive resistance of native plant communities to alien plant invasion.

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Competitive resistance refers to the reduction in establishment and performance of alien plant invaders as a result of competition from the established resident plant community for the essential resources of water, nutrients and light. While competitive resistance of native ecosystems to grassy and/or herbaceous invaders has been illustrated in numerous examples, far fewer have explored competitive resistance to woody invaders (reviewed in Levine et al. 2004). Two notable exceptions include Mazia et al. (2001) who found that removal of above-ground grassland competition, increased seedling survival of the invasive tree species *Gleditsia triacanthos* from 36 to 78 %, and of *Prosopis caldenia* from 0 to 58 % within the first 3 months of emergence. While, Siemann and Rogers (2003) found that a reduction in above-ground grassland competition, increased the survival and biomass of the invasive tree species *Sapium sebiferum*.

Globally, woody invasions have increased in recent decades, largely due to intensive and continuing introductions of thousands of species for horticulture, forestry, agriculture and agroforestry (Richardson and Rejmánek 2011; Richardson et al. 2014). Sparsely wooded ecosystems, including grasslands, semi-arid riparian areas and shrublands, appear particularly prone to woody invasions (Rundel et al. 2014). In such ecosystems, woody invaders are recognized to be important ecosystem engineers partly attributable to their greater size relative to native species (Richardson et al. 2014; Rundel et al. 2014) but also often associated with the introduction of novel traits such as N₂-fixation (Vitousek and Walker 1989; Richardson and van Wilgen 2004; Marchante et al. 2008). A prime example is the widespread invasion of several Australian *Acacia* tree species from the subgenus *Phyllodineae* into Mediterranean-climate shrublands of the world (Rundel et al. 2014) and particularly those found in the Cape Floristic Region (CFR) of South Africa (Henderson 2007), a region renowned for its high floral diversity and endemism (Goldblatt 1997).

In these shrublands invasive *Acacias* often form dense mono-specific stands leading to long-lasting ecosystem impacts including reductions in water availability, alteration of fire regimes, modifications of soil biogeochemistry and reductions in biodiversity (Le Maitre et al. 2011). Management of these invasions is challenging due to the intensive and costly efforts associated with woody species removal (van Wilgen et al. 2011) as well as due to socio-economic

conflicts of interest associated with newly derived benefits of many of the introduced invasive *Acacia* species (Kull et al. 2011; van Wilgen et al. 2011). Complete eradication is thus often unrealistic and management strategies are instead focused on slowing invasion spread and containment of invasions. Understanding the role native vegetation can play in limiting *Acacia* invasions could thus be useful to aid in development of management strategies, to inform post-invasion ecological restoration efforts and to strengthen current models of invasion spread.

The predominantly winter-rainfall climate of the CFR shrublands results in access to water during the drier summer months to being a key barrier to woody seedling establishment (Frazer and Davis 1988; Lamont et al. 1989; Lamont and Bergl 1991; Enright and Lamont 1992; Vilà and Sardans 1999). In addition, nutrient-poor soils are also known to strongly regulate plant establishment and growth (Kruger 1983; Specht and Moll 1983). To establish in native vegetation, invasive *Acacia* seedlings must be able to compete with the already established and highly adapted native vegetation for the scarce resources of water and nutrients. Furthermore, to succeed under the canopy of established native vegetation patches, invasive tree seedlings must either be shade tolerant, enabling persistence beneath the canopy until sufficient growth is reached or until light conditions become more conducive to growth (e.g. through disturbance, or canopy leaf abscission), or alternatively invasive seedlings must exhibit rapid growth to be able to emerge quickly from the native canopy (Funk 2013).

Several ecophysiological traits have been suggested to enhance resource acquisition and use by invasive Australian *Acacias*, including rapid and substantial allocation to below-ground biomass, strong N₂-fixation abilities, and the trait of heteroblasty, whereby the high specific leaf area (SLA) bipinnate leaflets produced by seedlings that confer high relative growth rates, later modify into lower SLA long-lived nutrient conserving phyllodes (Morris et al. 2011). While these traits have often been shown to increase competitive success of the invasive seedlings when growing against similar sized native seedlings (e.g. Witkowski 1991; Peperkorn et al. 2005), whether such traits would still be advantageous when competing against established native vegetation is uncertain.

In this study we determined whether competition from native shrubland vegetation constrains establishment of the invasive tree species *Acacia cyclops*. *Acacia cyclops*, native to western Australia, is widely invasive in several Mediterranean-climate shrublands across the globe (Webber et al. 2011). Originally introduced into the CFR for dune stabilization in the mid-1800's through the early-1900's (Poynton 2009), *A. cyclops* has become one of the most widespread and abundant invasives in the CFR particularly in the coastal shrublands (Henderson 2007), commonly known as the "strandveld" vegetation type. Here, dense monospecific *A. cyclops* stands are often associated with disturbance such as land-use change and fire. However, the persistent spread of *A. cyclops* seeds into native vegetation patches by several indigenous bird species that consume the seeds (Gibson et al. 2011; Glyphis et al. 1981; Fraser 1990) makes invasion of *A. cyclops* into undisturbed native vegetation a management concern (Stirton 1980; Richardson et al. 1997). This invasion scenario provides an ideal context in which to investigate the role of native vegetation in constraining woody invasion. To do so, above- and below-ground competition and soil nutrient availability were manipulated in a three-way factorial design and the effects on early seedling survival, growth, biomass allocation, water use efficiency, foliar nutrients and ^{15}N were assessed.

Methods

Study sites

Research sites were located in Koeberg Nature Reserve (33.65287 S, 18.43725 E) and Vergaderingskop Nature Conservancy (34.55466 S, 19.37298 E) in the Cape Floristic Region of the Western Cape Province, South Africa. At Koeberg, daily temperatures range between 7.1 and 26.5 °C, with a mean annual temperature (MAT) of 16.5 °C and at Vergaderingskop daily temperatures range between 6.9 and 26.2 °C, with a MAT of 17.1 °C. Mean annual precipitation (MAP) is 500 and 533 mm at Koeberg and Vergaderingskop, respectively. At Koeberg, 45 % of MAP falls within the coldest quarter of the year, while only 10 % falls within the hottest quarter. At Vergaderingskop rainfall is less seasonal with 28 % of the MAP falling in the coldest quarter and 20 % falling in the hottest quarter ("Appendix 1").

The sites are both situated in the strandveld vegetation type, with Koeberg classified as Cape Flats Dune Strandveld while Vergaderingskop is Blombos Strandveld (Mucina and Rutherford 2006). Strandveld vegetation is 1–2 m in height and is dominated by broad-leaved, sclerophyllous shrubs interspersed with succulents, bulbs and grasses (Mucina and Rutherford 2006). Vergaderingskop is more densely vegetated than Koeberg as illustrated by differences in normalized difference vegetation indices (NDVI) of 0.69 and 0.54, calculated using MODIS LIB Terra surfaces reflectances, corrected for molecular scattering, ozone absorption, and aerosols using MODIS Science Team algorithms. The eMODIS 10-day maximum-value composite NDVI images at 250 m spatial resolution were averaged using the QGIS raster calculator to obtain the annual average NDVI. Disturbance through fire is not as common in strandveld systems in comparison to the surrounding CFR vegetation types (e.g. fynbos), and fire return intervals are estimated to be 50–200 years (Rebelo et al. 2006). The soils of the CFR are known to be low in nutrients, especially N and P (Kruger 1983). Strandveld soils, however, have been shown to have higher nutrients than soils of the rest of the CFR (Witkowski and Mitchell 1987), possibly attributable in part to atmospheric deposition of marine derived aerosols (Nyaga et al. 2013).

Experimental design

Above- and below-ground competition as well as soil nutrient availability were manipulated in a three-way factorial design to assess the effects of native plant competition on early seedling establishment and performance of *A. cyclops*. Five plots (ca. 60 × 60 m) were established at each of the two study sites and within each plot four subplots (ca. 15 × 15 m) at Koeberg (20 total replicates) and three subplots at Vergaderingskop (15 total replicates) were established 20–40 m from each other ("Appendix 2"). The lower number of subplots at Vergaderingskop was due logistical issues arising from the relatively remote location of this study site.

Within each experimental subplot, ten sets of two *A. cyclops* seedlings were planted (0.5 m apart) under five categories of light availability: 0–20, 20–40, 40–60, 60–80 and 80–100 % based on the amount of light diffusion through vegetation canopy measured using a LAI-2000 ceptometer (LI-COR Inc., Lincoln, NE, USA) with the sensor placed at seedling height.

One of the two sets planted under each light availability category was treated with ca. 100 g (50 g N, 10 g P, 40 g K, 3.5 g Mg) slow-release fertilizer (Haifa group: Multicote [8] 15N – 3P – 12K + Mg + trace elements), placed in a 10 cm radius away from each seedling, directly into the soil at a depth of ca. 5–10 cm. This slow release fertilizer (8-month release) was used to provide increased nutrient availability throughout the growth period. Additionally, in each of the seedling sets (both fertilized and unfertilized), one seedling was protected from below-ground competition using a PVC root exclusion tube 0.2 m diameter \times 0.4 m long to separate roots of *A. cyclops* seedlings from root competition of surrounding native vegetation. The PVC tubes were driven into the soil ca. 2 months before seedlings were planted to diminish disturbance effects on seedling growth. The exclusion tubes were also weeded of other vegetation throughout the duration of the study. All seedlings were protected from vertebrate herbivory by enclosure in 0.2 m diameter \times 0.3 m high diamond mesh (1.3 cm) cages.

Acacia cyclops A.Cunn. ex G.Don (Miller et al. 2011) seedlings were grown from seeds collected at Vergaderingskop. Seeds were scarified with sandpaper and grown in trays of sand/potting soil mix in the University of Cape Town greenhouse in June 2012. Seeds were watered daily until germination occurred. After germination, seedlings were watered every second day in order to harden them in preparation for transplant into the field experiment. On appearance of the second set of bipinnate leaflets, ca. 14 days after sowing, seedlings were transplanted into the field, which took place on 26–27 June 2012 at Koeberg and 10–11 July 2012 at Vergaderingskop, corresponding to natural germination timing in the wet winter season. Seedlings were watered every second day for 10 days and any individuals that died during this time were replaced. Seedling survival was assessed 40 days later. Of the total seedlings, 28 % died within this period, but this mortality was not correlated to any of the treatments. Mortality during this period was thus assumed to be due to transplant shock or damage (particularly of roots) and these seedlings were excluded from further analyses. Seedlings were then allowed to grow for ca. 7 months and were harvested at the end of January 2013. This growth period encompassed the driest summer months after which seedlings were considered to be successfully established.

Seedling performance

Seedling survival, height, biomass gain, and biomass allocation were assessed at the end of January 2013. Above-ground biomass of seedlings was removed at the soil surface and below-ground biomass was excavated from within the root exclusion tubes. For seedlings not planted in root exclusion tubes, rooting systems were followed and excavated from approximately the same soil volume as the root exclusion tubes. All plant material was dried at 70 °C for 48 h and weighed.

Foliar $\delta^{13}\text{C}$, an integrated measure of C_i/C_a , was used as a measure of water use efficiency (WUE) as suggested by Farquhar et al. (1982), while, foliar N concentrations, N_2 -fixing nodule biomass relative to plant biomass and foliar $\delta^{15}\text{N}$ values were measured as indicators of N_2 -fixation activity. N_2 -fixing nodules were collected from roots, and dried and weighed as above, while foliar N, foliar $\delta^{15}\text{N}$ and foliar $\delta^{13}\text{C}$ were measured using mass spectrometry (Department of Archaeometry, University of Cape Town, South Africa). Since some seedlings had already lost all bipinnate leaves at harvest, only phyllodes were used for foliar analysis. Phyllodes were ground in a Wiley mill to pass through a 1 mm sieve. Milled samples were weighed into tin capsules and combusted in a Thermo Flash EA 112 series elemental analyzer coupled with a Delta Plus XP isotope ratio mass spectrometer (Thermo Electron Corporation, Milan, Italy). An International Atomic Energy Authority standard was used to calibrate results.

Soil analysis

To assess the effects of below-ground treatments (fertilization and root exclusion tubes) on soil fertility, surface soil cores (0–10 cm deep \times 8 cm diameter) were collected at the end of the study (end January 2013) from twenty transplant locations selected from across subplots. Cores were taken from locations where seedlings did not survive initial transplant, so that soil samples were representative of overall soil nutrient availability over time, rather than residual soil nutrient availability after seedling uptake and growth. Cores were taken from both inside and outside root exclusion tubes of both fertilized and unfertilized soils. Soils were air dried for 72 h and passed through a 1 mm sieve to remove rocks and coarse organic

matter. Soil concentrations of total N, NH_4^+ , NO_3^- , available P (Olsen et al. 1954), and K, were analyzed by the Institute for Plant Production (Department of Agriculture: Western Cape, South Africa) following standard protocols (The non-affiliated soil analysis work committee 1990).

Data analysis

Linear mixed-effects models were used to assess treatment affects using the *lmer* function in the *lme4* package (Bates et al. 2013) in R (R Core Team 2013). For analysis of below-ground treatment effects on soil nutrient measures, fixed effects were specified as a three-way interaction between site (Koeberg and Vergaderingskop), root treatment (no exclusion vs. root exclusion) and fertilization treatment (unfertilized vs. fertilized), while subplot was specified as a random effect. For analysis of treatment effects on seedling performance variables, models were specified with fixed effects as a four-way interaction between site (Koeberg vs. Vergaderingskop), light availability (0–20, 20–40, 40–60, 60–80 and 80–100 %), root treatment (no exclusion vs. root exclusion) and fertilization treatment (unfertilized vs. fertilized), while subplot was specified as the random effect.

Best-fit models were derived by the deletion of fixed effect variables one at a time from the full model as described in Buckley et al. (2003). Significance of variables retained in the final best-fit model were determined using the Wald χ^2 statistic with the *Anova* function in the Applied Econometrics package (AER; Kleiber and Zeileis 2008). Post-hoc differences were determined by comparing contrasts of least-squares means using the *lsmeans* function in the package *lsmeans* (Lenth 2014). Plots of fitted and observed values and residuals were examined to ensure deviations from homoscedasticity and normality did not occur, as described by Pinheiro and Bates (2000). Data were log transformed if assumptions of normality were not met.

Results

Soil nutrients

Soil nutrient pools were higher at Vergaderingskop than Koeberg for all soil nutrients both before and after

fertilization, except for NH_4^+ , which was only greater after fertilization (Tables 1, 2). At Koeberg, Fertilization increased total N ca. 1.5-fold, NO_3^- ca. 70-fold, available P ca. 1.5-fold and K ca. fivefold. At Vergaderingskop, fertilization increased NH_4^+ ca. eightfold, NO_3^- 80-fold, available P ca. 2.4-fold and K ca. fivefold (Tables 1, 2). Root exclusion tubes had no effect on soil nutrient availability at either site (Table 1).

Seedling performance

Seedling survival varied between ca. 20 and 80 % across the different sites and treatments (Fig. 1). Neither increases in light availability nor fertilization affected seedling survival (Table 3). Protection of seedlings from below-ground competition through root exclusion tubes, however, increased seedling survival ca. 1.8-fold and ca. 1.4-fold at Koeberg and Vergaderingskop, respectively (Table 3; Fig. 1). Average seedling survival differed between the sites with a ca. 1.5-fold greater survival at Vergaderingskop (61 ± 3.6 %) than at Koeberg (42 ± 4.1 %) (Table 3; Fig. 1).

Seedling growth, measured as height and biomass accumulation over the 6 months, was strongly influenced by the below-ground treatments of root exclusion tubes and fertilization (Table 3). Plants in root exclusion tubes grew ca. 1.6-fold taller and accumulated 4.8-fold greater biomass than those not in root exclusion tubes, while fertilized seedlings had ca. 1.2-fold greater height and ca. 2.3-fold greater total biomass than unfertilized seedlings (Table 3; Fig. 2a, b).

Seedlings at Vergaderingskop were ca. 1.5-fold taller than seedlings at Koeberg, while seedlings at Koeberg had ca. 2.3-fold greater below-ground biomass than those at Vergaderingskop. This translated to site-level differences in shoot:root allocations which also responded differently to treatments at each site (Table 3). At Koeberg, shoot:root allocations of biomass remained consistent across all treatments, whereas at Vergaderingskop fertilization yielded seedlings with greater shoot:root ratios than unfertilized seedlings (Table 3; Fig. 2c).

In contrast to below-ground treatments, variations in the above-ground availability of light did not influence seedling height or shoot:root ratios (Table 3), and differences in biomass were only

Table 1 The effects of site (S), fertilization (F), and root exclusion (R) on soil nutrient concentrations

Fixed effects	Total N χ^2	NH_4^+ χ^2	NO_3^- χ^2	Available P χ^2	K χ^2
S	25.0 ***	9.9**	17.0***	42.1***	250.0***
F	17.1***	17.8***	403.5***	102.7***	108.4***
R	NS	NS	NS	NS	NS
S \times F	6.5*	11.4***	NS	31.4***	NS
S \times R	NS	NS	NS	NS	NS
F \times R	NS	NS	NS	NS	NS
S \times F \times R	NS	NS	NS	NS	NS

Wald χ^2 test statistics and significance were derived from linear mixed effects models with site (S), fertilizer treatment (F) and root exclusion treatment (R) specified as fixed effects and subplot as the random effect. Fixed effect variables that did not significantly effect predictions of the soil nutrient concentration were removed from the best-fit model and are thus indicated as not significant (NS)

NS no significance

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; + $P < 0.1$

Table 2 Soil nutrient concentrations (mean \pm SE) of unfertilized and fertilized surface soils at each site, measured 6 months after slow release fertilizer addition

Soil nutrient (mg kg ⁻¹)	n	Koeberg		Vergaderingskop	
		Unfertilized	Fertilized	Unfertilized	Fertilized
Total N	10	236 \pm 76 ^a	351 \pm 82 ^b	1327 \pm 157 ^c	1542 \pm 221 ^c
NH_4^+	6	2.0 \pm 0.1 ^a	3.0 \pm 0.2 ^a	3.0 \pm 0.1 ^a	24.2 \pm 8.1 ^b
NO_3^-	6	0.32 \pm 0.05 ^a	22.8 \pm 6.7 ^b	0.77 \pm 0.09 ^c	61.4 \pm 9.4 ^d
Available P (Olsen)	10	2.4 \pm 0.2 ^a	3.5 \pm 0.3 ^b	4 \pm 0.4 ^b	9.5 \pm 0.5 ^c
K	10	10 \pm 1 ^a	47 \pm 7 ^b	45 \pm 2 ^b	204 \pm 20 ^c

Different letters indicate significant differences ($P < 0.05$) of the soil nutrient concentration between treatments determined by comparing contrasts of least-squares means

Fig. 1 Survival of unfertilized and fertilized *Acacia cyclops* seedlings with and without root exclusion tubes, 6 months after planting, at Koeberg and Vergaderingskop study sites. Bars represent the mean \pm SE and different letters above bars indicate significant differences ($P < 0.05$) between treatments determined by comparing contrasts of least-squares means

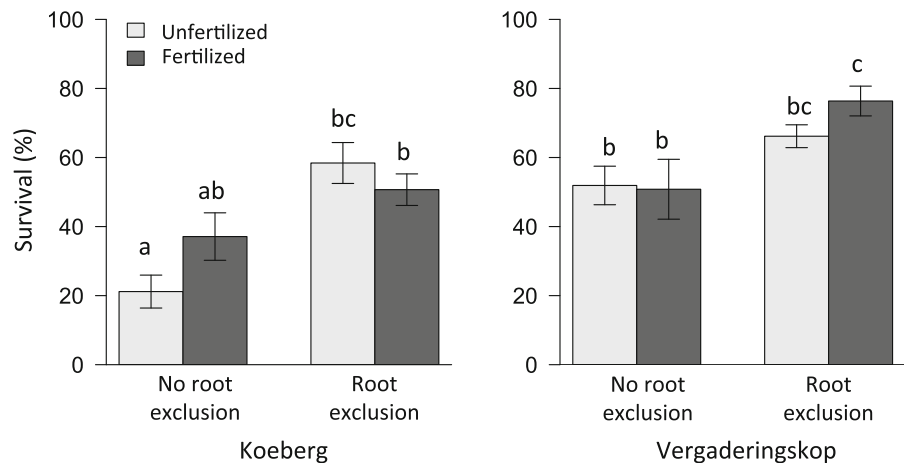


Table 3 The effects of site (S), fertilization (F), root exclusion (R) and light availability (L) on measured seedling response variables

Fixed effects	Seedling response variables									
	Survival	Height	Above-ground biomass	Below-ground biomass	Total biomass	Shoot:root	$\delta^{13}\text{C}$	Foliar N	Nodule mass: total biomass	$\delta^{15}\text{N}$
S	14.6***	17.9***	NS	10.5**	NS	18.4***	323***	25.4***	13.1***	46.6***
F	NS	15.4***	49.8***	22.4***	48.22***	19.2***	123***	54.8***	182.4***	NS
R	34.8***	62.4***	89.9***	104.5***	106.5***	NS	4.3*	42.3***	3.9*	4.2*
L	NS	NS	16.4**	16.9**	17.9**	NS	NS	NS	NS	NS
S \times F	NS	NS	NS	NS	NS	4.6*	9.0**	NS	18.4***	NS
S \times R	NS	NS	NS	NS	NS	7.4**	NS	NS	NS	4.0*
S \times L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
F \times R	NS	NS	NS	NS	NS	NS	6.3*	5.3*	6.1*	NS
F \times L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
R \times L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S \times F \times R	NS	NS	NS	NS	NS	NS	NS	NS	NS	5.2*
S \times F \times L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S \times R \times L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
F \times R \times L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S \times F \times R \times L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Wald χ^2 test statistics and significance were derived from linear mixed effects models with S, F, R, and L specified as fixed effects and subplot as the random effect. Fixed effect variables that did not significantly effect predictions of the response variable were removed from the best-fit model and are thus indicated as not significant (NS)

NS no significance

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

significant between the most extreme differences in light availability where seedlings under 0–20 % light availability had biomass ca. threefold lower than seedlings grown under 80–100 % light availability (Table 3; Fig. 3).

Response of foliar $\delta^{13}\text{C}$ values to below-ground treatments differed at each site (Table 3). At Koeberg, unfertilized seedlings had lower foliar $\delta^{13}\text{C}$ than fertilized seedlings but there was no effect from root exclusion tubes. At Vergaderingskop, unfertilized seedlings also had lower foliar $\delta^{13}\text{C}$ than fertilized seedlings, but in addition, root exclusion tubes yielded seedlings with lower foliar $\delta^{13}\text{C}$. Overall, foliar $\delta^{13}\text{C}$ was ca. 1.2-fold lower at Vergaderingskop than at Koeberg (Table 3; Fig. 4).

Seedling foliar N concentrations were similar for all seedlings at Koeberg, aside from fertilized seedlings grown in root exclusion tubes, which had ca. 1.4-fold greater foliar N. At Vergaderingskop, seedlings in root exclusion tubes had ca. 1.3-fold and

1.5-fold greater foliar N concentrations for unfertilized and fertilized seedlings, respectively (Table 3; Fig. 5a). Overall, seedling foliar N concentrations were ca. 1.2-fold greater at Vergaderingskop than at Koeberg (Table 3; Fig. 5a). Average nodule mass of fertilized seedlings was negligible at both sites indicating minimal N_2 -fixation capacity in comparison to unfertilized seedlings. When grown without root exclusion tubes unfertilized seedlings had ca. 1.4-fold and twofold greater nodule mass:plant mass ratios than seedling without root exclusion tubes at Koeberg and Vergaderingskop respectively (Table 3; Fig. 5b), as well as ca. 1.3-fold and 4.5-fold more negative foliar $\delta^{15}\text{N}$ (Table 3; Fig. 5c). These results indicate greater N_2 -fixation of seedlings not growing in root exclusion tubes. Overall, nodule mass:plant mass ratios were ca. twofold greater at Koeberg than at Vergaderingskop, while $\delta^{15}\text{N}$ was 1.5 to 17-fold more negative, depending on the treatment (Table 3; Fig. 5b, c).

Fig. 2 Final values after 6 months for height (a), above- and below-ground biomass (b), and shoot:root biomass ratios (c) of unfertilized and fertilized *Acacia cyclops* seedlings with and without root exclusion tubes at Koeberg and Vergaderingskop study sites. Bars represent the mean \pm SE and different letters above bars indicate significant differences ($P < 0.05$) between treatments determined by comparing contrasts of least-squares means

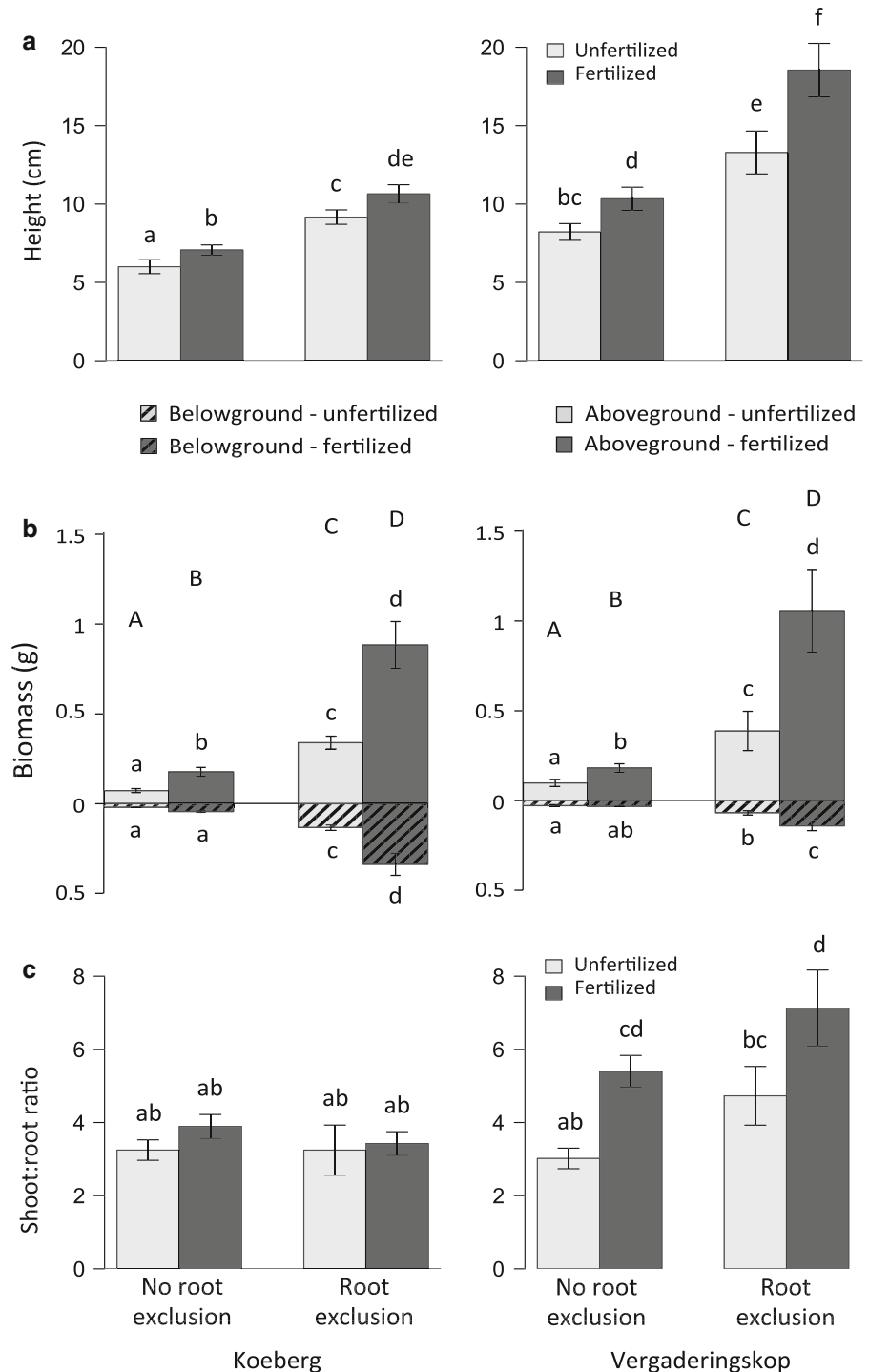


Fig. 3 Above- and below-ground biomass of *Acacia cyclops* seedlings under the range of light availabilities at Koeberg and Vergaderingskop study site. Bars represent mean \pm SE. Bars represent the mean \pm SE and different letters above bars indicate significant differences ($P < 0.05$) between treatments determined by comparing contrasts of least-squares means

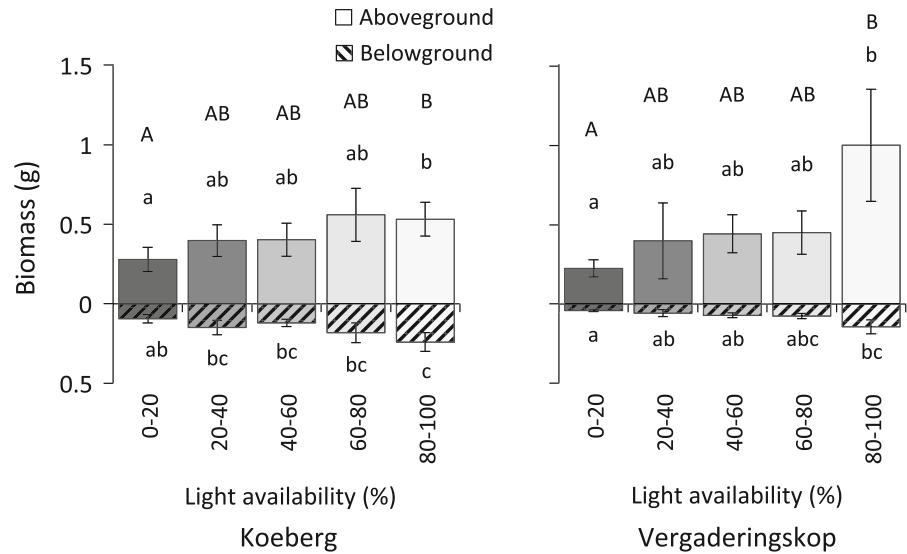
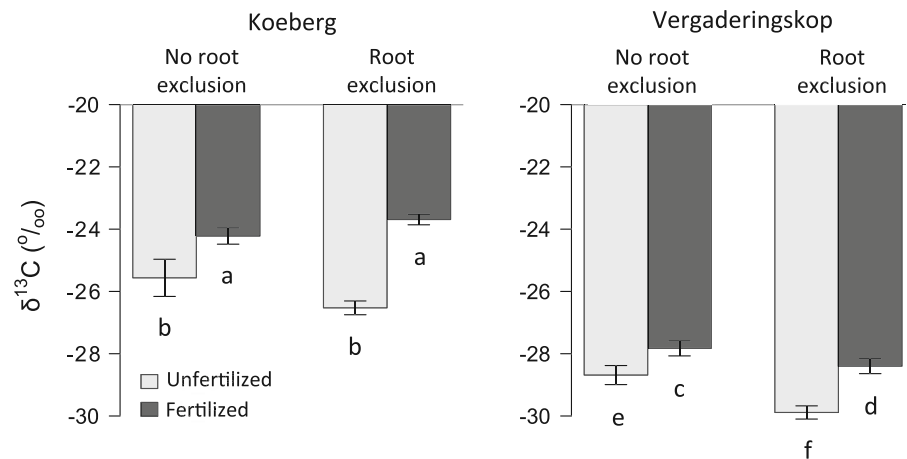


Fig. 4 Foliar $\delta^{13}\text{C}$ of unfertilized and fertilized *Acacia cyclops* seedlings with and without root exclusion tubes at Koeberg and Vergaderingskop study site. Bars represent the mean \pm SE. Different letters above bars indicate significant differences ($P < 0.05$) between treatments determined by comparing contrasts of least-squares means



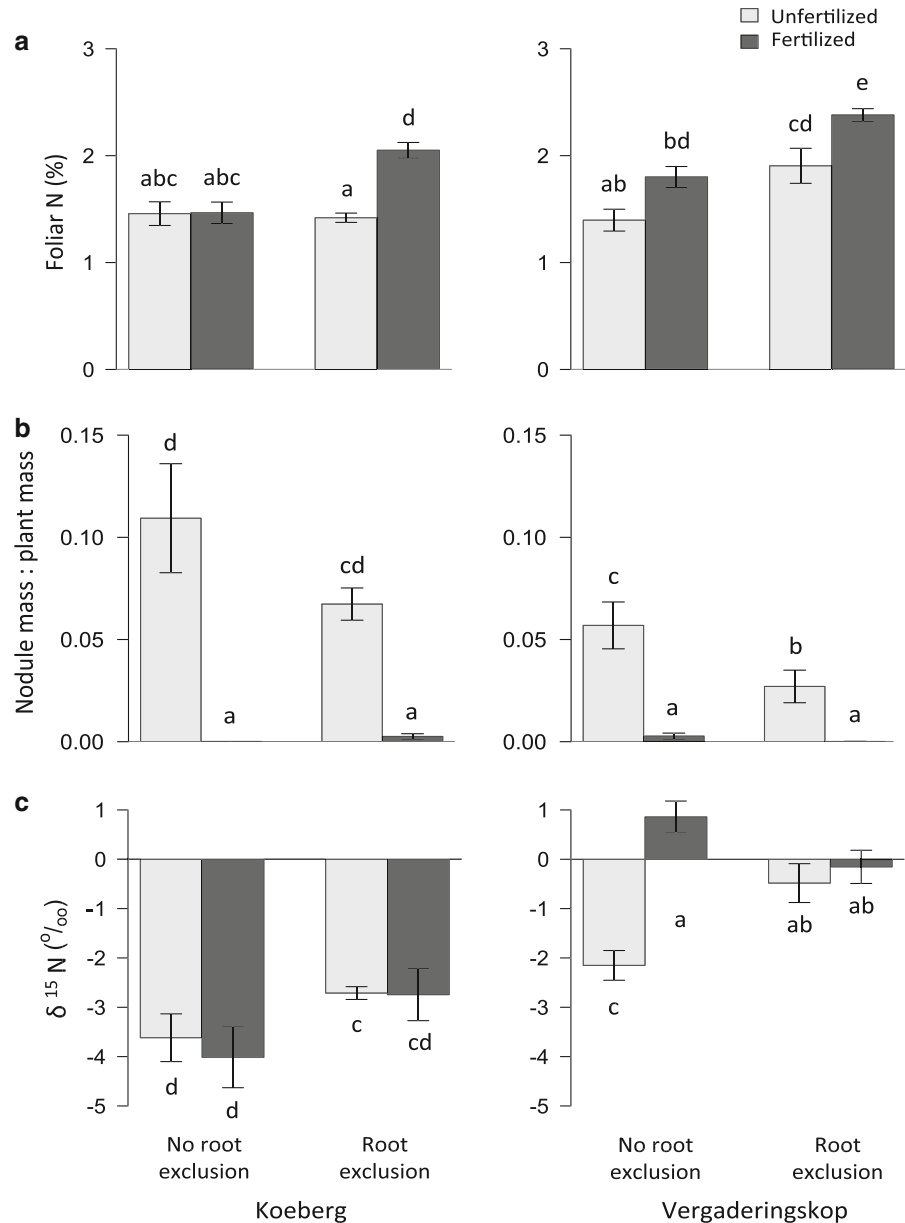
Discussion

We found that below-ground competition placed greater limitations on woody invasive seedling establishment and early growth than above-ground competition in Mediterranean-climate shrublands. Although the shrublands were not completely resistant to invasion, competition by native vegetation is likely to impede survival, growth and biomass accumulation of woody invasives. This suppression of seedling growth may delay reproductive maturation and output and hence can contribute to constraining invasion spread.

Below-ground competition from the established native vegetation reduced both survival and growth of

the woody invasive seedlings. These reductions occurred even when nutrient limitations were reduced through fertilization indicating competition for water as a potential constraint on seedling establishment. Such competitive effects would be likely to increase seedling susceptibility to drought-induced mortality, particularly in the drier summer season, when access to water is a major constraint on woody seedling establishment (Vilà and Sardans 1999). Alternatively, competitive reductions on fertilized seedlings, may indicate that fertilization only partially ameliorated nutrient limitation and hence competition for nutrients still occurred. Fertilized seedlings exhibited greater height and biomass indicating that nutrient limitation constrained seedling performance. Reduced

Fig. 5 Foliar N (a), nodule mass relative to total plant mass (b) and $\delta^{15}\text{N}$ (c) of unfertilized and fertilized *Acacia cyclops* seedlings with and without root exclusion tubes at each site. Bars represent the mean \pm SE and dissimilar letters above the bars indicate significant differences ($P < 0.05$) between treatments determined by comparing contrasts of least-squares means



performance of seedlings exposed to root competition was likely to thus be partly due to competition for nutrients. This potential importance of water and nutrient availability for seedling survival is reinforced by the overall lower seedling survival at Koeberg, which receives significantly less summer rainfall and has lower soil nutrient availability, particularly of N, than Vergaderingskop.

At all sites, fertilization repressed N_2 -fixing nodule development indicating that nodules served to at least partially meet the N requirements of unfertilized

plants. This is further supported by both greater nodule development and lower foliar $\delta^{15}\text{N}$ of seedlings at the Koeberg study site, which had considerably lower soil N concentrations than Vergaderingskop. Furthermore, seedlings exposed to root competition had higher nodule biomass and more negative foliar $\delta^{15}\text{N}$ than seedlings protected from root competition, indicating that N_2 -fixation may aid in alleviating N constraints induced by native competition. Although, foliar $\delta^{15}\text{N}$ results at both sites were lower (-4 to -2 ‰) than values generally assumed to indicate N_2 -fixation in

land plants (close to or just below zero; Lajtha and Marshall 1994), the values were not dissimilar from other foliar $\delta^{15}\text{N}$ of N_2 -fixing *A. cyclops* in the CFR (-2 and 0 ‰; Stock et al. 1995; -4 and 1 ‰; Morris 2014) and fall within ranges of globally reported $\delta^{15}\text{N}$ values (-5 and 2 ‰; Amundson et al. 2003). These results are thus congruent with several other studies and support the suggestion that N_2 -fixation is an important trait contributing to the success of invasive Australian *Acacias* (Morris et al. 2011) especially when growing in nutrient poor environments (Rodríguez-Echeverría et al. 2009).

Higher foliar $\delta^{13}\text{C}$ values of seedlings exposed to root competition at Vergaderingskop compared to those growing in root exclusion tubes suggest that when exposed to competition, invasive seedlings may exhibit higher WUEs, presumably associated with constraints on water availability caused by below-ground competition. The lack of effect of root exclusion on $\delta^{13}\text{C}$ at Koeberg may indicate that root exclusion was insufficient to improve water relations at that site. This could be due the likelihood of consistently greater water limitations of seedlings at Koeberg than at Vergaderingskop due to more severe summer drought periods, which is also suggested by higher overall foliar $\delta^{13}\text{C}$ of seedlings at Koeberg than at Vergaderingskop. At both sites, regardless of the level of root competition, foliar $\delta^{13}\text{C}$ was consistently greater in fertilized seedlings than in unfertilized seedlings. This may be explained by greater total photosynthesis in fertilized seedlings, as indicated by greater total biomass, which is known to lead to reduced discrimination against $\delta^{13}\text{C}$ (Sparks and Ehleringer 1997). Alternatively, foliar $\delta^{13}\text{C}$ may be reduced in unfertilized seedlings due to increased stomatal conductance and transpiration as a means of nutrient acquisition via the mechanism of mass flow (Cramer et al. 2009). There are thus several potential explanations for the variation in $\delta^{13}\text{C}$ with root exclusion and fertilization that are not mutually exclusive.

Effects of light availability on plant performance were only evident between seedlings grown in fully shaded versus open environments resulting in a ca. threefold reduced biomass accumulation in the shaded condition. The strength of these biomass reductions were, however, weaker than those induced by below-ground competition (ca. fivefold), supporting suggestions that in Mediterranean-climate shrublands,

above-ground competition for light is less intense than below-ground competition for nutrients and water (Vilà 1997). Furthermore, since variations in light availability did not differentially affect seedling survival, height or shoot:root ratios, it would suggest that *A. cyclops* seedlings tolerate low light conditions, although they do not thrive under these conditions. It thus appears that the invasive seedlings are able to establish and persist under a range of light conditions and that above-ground competition is at least a contributing constraint on invasive seedling establishment and growth.

The ability of seedlings to persist under a range of light conditions may be associated with the capacity for production of the two different leaf types with the higher specific leaf area (SLA) bipinnate leaflets, that are produced during early growth, suggested to be advantageous for shade tolerance (Pasquet-Kok et al. 2010). This is supported by observations of the closely related *A. koa* and *A. implexa* to retain leaflets for longer under low light conditions as well as the ability of phyllode-bearing *A. koa* individuals to revert back to leaflet production when returned to shady conditions (Walters and Bartholomew 1990; Forster and Bonser 2009a, b). On the other hand, the low SLA, sclerophyllous phyllodes, which develop as seedlings mature, are suggested to be better adapted for heat and water stress, which would be likely under more exposed conditions. This suggestion is largely as a consequence of phyllodes possessing a relatively greater proportion of mesophyll with large-celled water storage tissue in comparison to bipinnate leaflets (Pasquet-Kok et al. 2010). This is associated with greater water mass per area, greater relative capacitance at full turgor as well as greater absolute capacitance per leaf area at full turgor and turgor loss, which would delay mesophyll desiccation after stomatal closure. In addition, phyllodes also exhibit a more rapid and complete stomatal response to VPD (reviewed in Pasquet-Kok et al. 2010). Thus, the trait of heteroblasty may be important for conferring tolerance to above-ground competition since seedlings can use both light-use efficient, shade-tolerant bipinnate leaves when growing under vegetation canopies as well as sclerophyllous phyllodes when exposed to high irradiance conditions. Furthermore, negative effects that shading can have on seedling growth may be offset with potential benefits that over-story canopies can have in Mediterranean-climate shrublands such as

reductions of air temperature, beneficial changes in soil conditions and protection from herbivory (Vilà and Sardans 1999) influencing seedling survival and growth.

The ability of seedlings to tolerate above-and below-ground competition, to some extent, explains the presence of these invasive trees even in undisturbed native vegetation patches. While the overall success of invasive seedlings would be regulated by native competition, the overall density of invasives in a system is likely to largely depend on propagule pressure into the uninvaded systems. *Acacia cyclops* can produce ca. 1200 seeds m⁻² of canopy in invaded ranges (Gibson et al. 2011). These seeds are favoured by several bird species. When seeds are available, *A. cyclops* seeds form up to 95 % of pellets regurgitated by native bird species (e.g. redwinged starlings, *Onychognathus morio*; Fraser 1990). There is thus likely to be an abundant dispersal of seeds into native vegetation patches that can remain dormant in the seedbank for 50–100 years or more and retain a seed viability of up to 99 % (Gibson et al. 2011). However, both invasive *Acacia* seeds and seedlings are destructively consumed in strandveld ecosystem by several native fauna including the highly abundant small rodent, *Rhabdomys pumilio*, which would also constrain seedling establishment and densities (Holmes 1990; Mokotjomela and Hoffman 2013; Morris 2014). This highlights the importance of integrated control efforts, which should include monitoring and removal of satellite establishments, continued reductions of propagule pressure through biological control (Impson et al. 2011, Rouget and Richardson 2003) and preservation of native fauna and flora with the purpose of increasing overall biotic resistance.

Conclusion

Competition, particularly below-ground, constrains invasive *A. cyclops* seedling survival in Mediterranean-climate shrublands. If seedlings are able to survive, competition from native vegetation further impedes growth and biomass accumulation, potentially reducing the rate of maturation, seed output and hence spread potential of the invasive tree species. This indicates that maintenance of intact, undisturbed native ecosystems is important in limiting invasive establishment. Although invasion is highly species and ecosystem dependent, it is likely that the vegetation structure and density is an important biotic determinant of invasive success, suggesting that climatic and edaphic variables alone are not sufficient in predicting invasion spread (e.g. Rouget et al. 2004). We suggest that indicators of biotic variation, for example NDVI, be included in invasion distribution and spread models in order to aid in optimization of scarce management resources.

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Appendix 1

See Table 4.

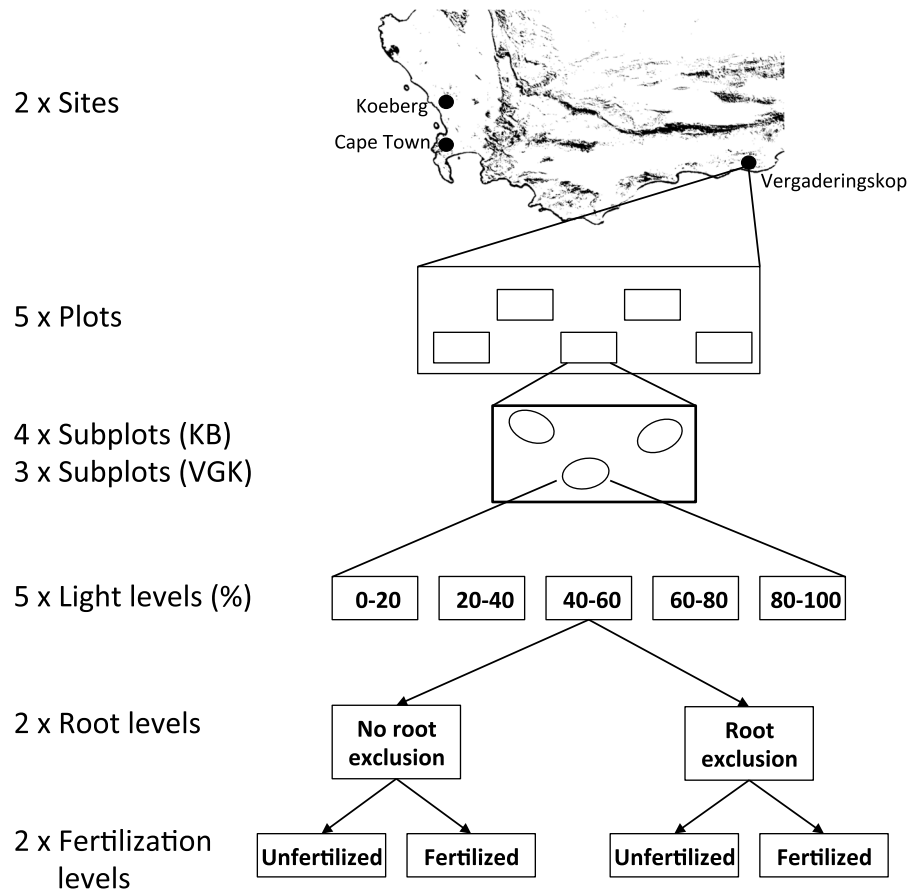
Table 4 Study site locations and climatic characteristics derived from data of Hijmans et al. (2005)

Site characteristic	Koeberg	Vegaderingskop
Coordinates	33.65287 S 18.43725 E	34.35790 S 21.56873 E
Mean annual temp. (°C)	16.5	17.1
Minimum temp. in coldest month (°C)	7.1	6.9
Maximum temp. in warmest month (°C)	26.4	26.2
Mean annual precipitation (mm)	533	500
Precipitation in coldest quarter (mm)	238	137
Precipitation in warmest quarter (mm)	54	99

Appendix 2

See Fig. 6.

Fig. 6 Graphic representation of the experimental design. Two sites were sampled (*KB* Koeberg, *VGK* Vergaderingskop) and at each site 5 plots with 3–4 subplots were selected resulting in 20 replicates at *KB* and 15 replicates at *VGK*. In each replicate (subplot), 20 *Acacia cyclops* seedling were planted according to the three-way interaction of the light, rooting, and fertilization treatments



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