

# Biotic resistance affects growth and reproduction, but not survival of a high-impact woody invader in African savannas

Mariska te Beest<sup>1,2,3</sup>  | Nokukhanya J. Mpandza<sup>4</sup> | Han Olff<sup>3</sup>

<sup>1</sup>Resource Ecology Group, Wageningen University, Wageningen, The Netherlands

<sup>2</sup>Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

<sup>3</sup>Community and Conservation Ecology Group, University of Groningen, Groningen, The Netherlands

<sup>4</sup>Scientific Services, South African National Parks, Skukuza, South Africa

## Correspondence

Mariska te Beest, Department of Environmental Sciences, Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, The Netherlands.  
Email: mariskatebeest@hotmail.com

## Funding information

Nederlandse Organisatie voor Wetenschappelijk Onderzoek, Grant/Award Number: NWO-PIONIER; Marie Skłodowska-Curie Actions of the European Union Horizon 2020 Programme, Grant/Award Number: IF-655761-EXTREME

Co-ordinating Editor: Jodi Price

## Abstract

**Question:** Biotic resistance is defined as the reduction in invasion success caused by the native community through competition, herbivory and/or pathogens. Biotic resistance has mostly been studied during the initial stages of invasion. However, to what extent biotic resistance hampers survival, or persistence, of invaders in the longer term is often not known. We studied how native grassland communities affected growth, reproduction and survival during the adult life stage of the high-impact woody invader *Chromolaena odorata* under different water availability treatments.

**Location:** Hluhluwe-iMfolozi Park, South Africa.

**Methods:** We performed a 2-years full-factorial field experiment in a savanna grassland where we manipulated water availability and neighbouring vegetation; in one-third of the plots vegetation was cleared and planted with *C. odorata* monocultures, in one-third *C. odorata* shrubs were planted in grasslands, and one-third were unplanted grassland controls.

**Results:** Growth and reproduction of adult *C. odorata* were greatly reduced due to competition with native grasses, but not survival of *C. odorata*. Shrub survival was high and did not differ in plots with and without grass. Water availability did not affect growth, reproduction and competitive ability of *C. odorata*, but higher water availability did increase the competitive ability of the grasses. Soil moisture levels were lower in grasslands planted with *C. odorata* compared to unplanted controls, independent of the water treatment, suggesting higher water use of *C. odorata* compared to native grasses.

**Conclusions:** Savanna grasslands have a strong competitive effect on invasion by the exotic woody shrub *C. odorata*, reducing growth and reproduction, but not survival of the shrub. We found no evidence that biotic resistance was stronger under more unfavourable abiotic conditions, as *C. odorata* was equally impacted in all water treatments. The high survival rates of *C. odorata* suggest that competitive interactions are not likely to prevent invader persistence in the landscape. Invader persistence is important in determining longer-term invasion success as well as invader impact, and the concept of persistence should not be overlooked in studies on invasive species.

## KEYWORDS

*Chromolaena odorata*, colonization, drought, exotic species, experiment, grassland, impact, invasion, moisture, persistence, water availability

## 1 | INTRODUCTION

Biotic resistance from the native community is a key factor controlling invasion success via competition, herbivory and/or pathogens (Elton, 1958; Levine, Adler, & Yelenik, 2004). Many studies on biotic resistance focus on the effect of competition during the early life stages (Cano, Escarre, & Sans, 2007; Eskelinen & Harrison, 2014; Hierro, Lortie, Villarreal, Estanga-Mollica, & Callaway, 2011; te Beest, Mpandza, & Olff, 2015; Thomsen, Corbin, & D'Antonio, 2006; Thomsen & D'Antonio, 2007). However, to what extent competition from resident communities affects survival and persistence during later life stages of long-lived woody plants is much less known. The role of competition in the establishment stage of invasion differs considerably from its role in the later stages of invader spread and impact (Levine et al., 2004; Vila & Weiner, 2004). For example, a study on the population dynamics of *Prunus serotina* in European forests shows that the effect of competition on invasion success decreases with the life-history stage of this woody species (Closset-Kopp, Chabrerie, Valentin, Delachapelle, & Decocq, 2007). Woody species have different requirements during their life history and, therefore, resident communities may only be able to reduce invasion success during certain stages in their life history, e.g. hamper seedling establishment (Barger, D'Antonio, Ghneim, & Cuevas, 2003; Sheppard, Hodge, Paynter, & Rees, 2002) or reduce population growth (Levine, 2001). Competitive interactions with the resident community rarely completely repel invasions, but rather constrain their spread and impact (Levine et al., 2004).

Biotic resistance is inherently context-dependent and varies depending on abiotic conditions (D'Antonio & Thomsen, 2004; Stotz, Pec, & Cahill, 2016). Several studies have shown that interactions with abiotic conditions alter the strength and direction of competitive interactions between invaders and the resident community and determine the net outcome of biotic resistance (Barger et al., 2003; Eskelinen & Harrison, 2014; Going, HilleRisLambers, & Levine, 2009; Stotz et al., 2016; Thomsen & D'Antonio, 2007). For example, in California, nutrient addition lowers biotic resistance to annual grass invasions in serpentine grasslands (Eskelinen & Harrison, 2014; Going et al., 2009), but not in coastal prairie (Thomsen et al., 2006). Similarly, in South African renosterveld, a type of mediterranean shrubland, N enrichment lowers biotic resistance and increases invasions of annual grasses (Sharma, Muhl, Esler, & Milton, 2010). In old-field grasslands in Cedar Creek stochastic water pulses temporarily reduce competition and increase community invasibility (Davis & Pelsor, 2001). These studies show that in many cases, more benign abiotic conditions or the addition of a limiting resource increase invasion success, due to reduced resource competition (Davis & Pelsor, 2001; Barger et al., 2003; Going et al., 2009; Eskelinen & Harrison, 2014).

We studied how competition from resident grassland communities in a mesic savanna in South Africa interacts with abiotic conditions to determine community resistance to the invasion of the shrub *Chromolaena odorata* (L.) King and Robinson (Asteraceae) during its adult life stage. *Chromolaena odorata* is a high-impact shrub from tropical America that has invaded most (sub-)tropical regions of the Paleotropics (te Beest et al., 2017; Gaertner et al., 2014; Raimundo, Fonseca, Schachetti-Pereira, Peterson, & Lewinsohn, 2007). Its

invasion success is thought to depend on its high relative growth rate (Ramakrishnan & Vitousek, 1989; te Beest, Esler, & Richardson, 2015) and its high reproductive capacity, whereby a single shrub can produce as many as 800,000 apomictic wind-dispersed seeds (Gautier, 1992; Ramakrishnan & Vitousek, 1989; Witkowski & Wilson, 2001). Also, its ability to effectively shade out native vegetation (Honu & Dang, 2000; te Beest, Esler, et al., 2015) and to survive severe disturbances, such as fire, by re-sprouting from the basal stems (te Beest, Cromsigt, Ngobese, & Olff, 2012) contributes to its success. The species behaves like a herbaceous plant during the early life stages, grows into a semi-lignified multi-stemmed shrub of around 2 m in height at an older age and can reach a maximum height of 6 m as a scrambler on trees (Witkowski & Wilson, 2001). In a previous study we showed that survival of *C. odorata* seedlings is low when grown in undisturbed savanna grasslands, indicating strong biotic resistance during the early life stages (te Beest, Mpandza, et al., 2015). However, it is unknown how competitive interactions change when these seedlings grow into adult shrubs and how abiotic factors influence the outcome of competition. In southern Africa *C. odorata* preferably invades moist environments in broad-leaved woodlands, along rivers and forest margins, suggesting that water availability is an important factor controlling the distribution of *C. odorata* (Goodall & Erasmus, 1996; te Beest, Elschot, Olff, & Etienne, 2013).

We designed a full-factorial field experiment to study the interactive effect of competition and water availability on growth, reproduction and survival of adult *C. odorata* shrubs in a protected savanna reserve in South Africa. We tested for biotic resistance of native grasslands to shrub invasion by transplanting *C. odorata* shrubs into plots with and without resident grassland communities. We included an unplanted grassland control to be able to test for potential impact of *C. odorata* on native grassland communities. The transplanted shrubs were followed for 2 years. We hypothesize that *C. odorata* growth, reproduction and survival will be reduced under competition with native grasses (biotic resistance). We expect biotic resistance to be stronger under lower water availability due to the stronger competition for the limiting resource.

## 2 | METHODS

### 2.1 | Site description

The experiment was performed in Hluhluwe-iMfolozi Park, a protected savanna reserve in South Africa, situated between 28°00'–28°26'S and 31°43'–32°09'E. The experimental site was situated in a savanna grassland in the northern section of the park with mean annual precipitation of 900 mm. The vegetation was dominated by the tall bunchgrass species *Cymbopogon excavatus*, *Panicum maximum*, *Themeda triandra*, *Hyparrhenia filipendula*, *Eragrostis curvula* and *Chloris gayana*, with some native forbs, woody species and *Chromolaena odorata* present. The forb species formed a minor component of total native biomass, but were high in diversity, with 46 species present. Common forbs included *Acalypha villicaulis*, *Berkheya bergiana*, *Thunbergia natalensis*, *Solanum panduriforme*,

*Commelina africana* and *Pelargonium luridum*. Native woody species included *Dombeya burgessiae*, *Dichrostachys cinerea*, *Rhus pentheri*, *Diospyros dichrophylla* and *Gymnosporia senegalensis*.

## 2.2 | Experimental design

The experiment was set up in March 2005 according to a randomized block design, with four replicate blocks and nine treatment plots per block ( $n = 4$ , see Figure 1). We removed all large woody species and *C. odorata* plants from the experimental area and established 3 m x 4 m plots that were spaced 1 m apart to avoid interaction effects and allow easy access. Each plot was subjected to one of three competition treatments and one of three water availability treatments in a full-factorial design.

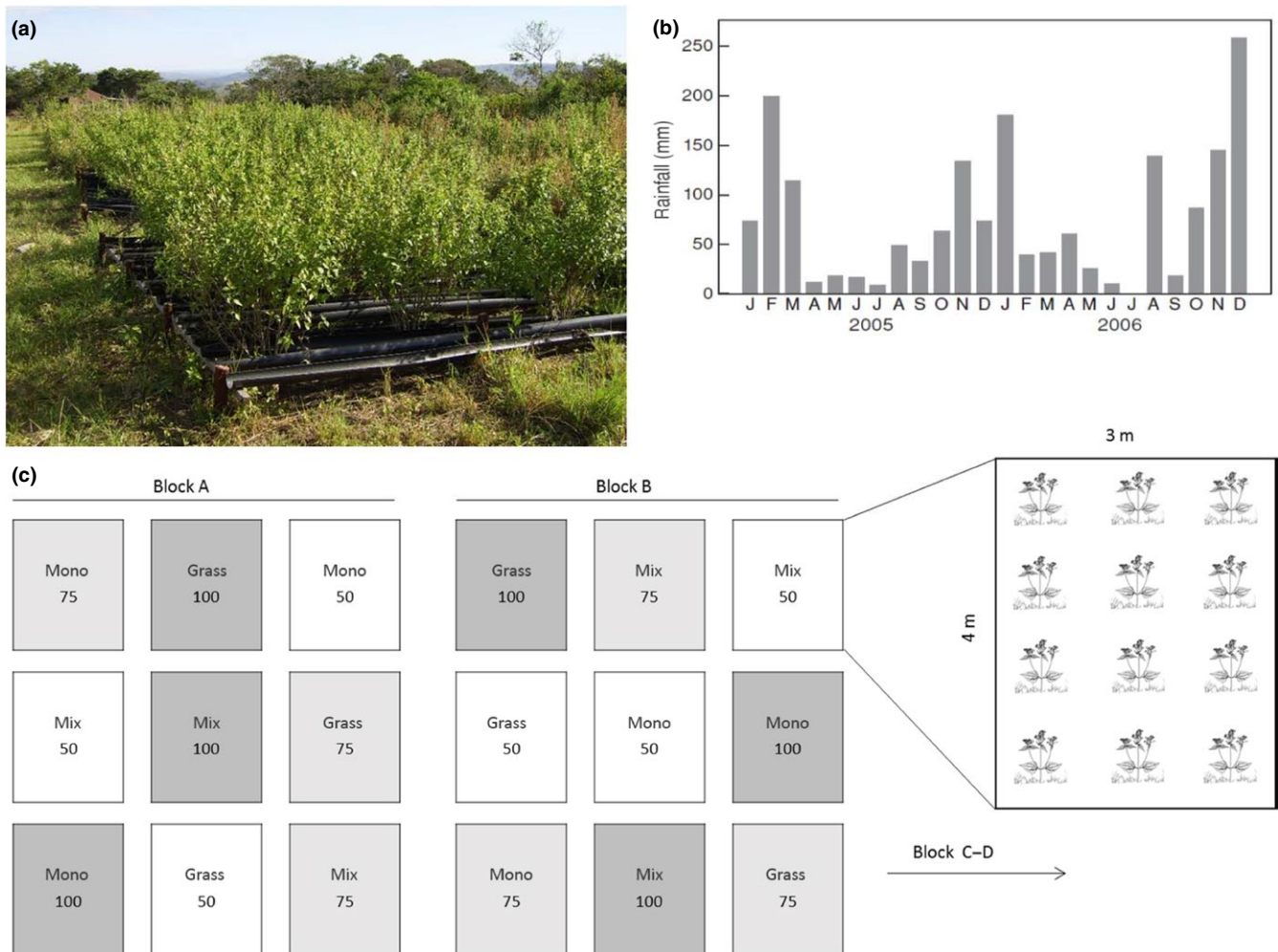
The competition treatment consisted of three levels. One third of the plots were cleared of all vegetation, including roots, and planted with *C. odorata* monocultures. In one-third of the plots we planted *C. odorata* in the grassland (mixtures) and in one-third of the plots the grassland remained unplanted. In the shrub monocultures and mixtures we planted 12 adult *C. odorata* shrubs per plot that were obtained from the direct vicinity of the experiment. We chose plants of similar age (>1 year) that were approximately 1 m in height with a single lignified stem. Plants lost their leaves shortly after transplantation due to water stress and additional water was supplied for the first month to enable the plants to recover. There was little regrowth of native vegetation in the shrub monocultures, due to placing of the gutters and shading of the *C. odorata* shrubs. Regrowth consisted mostly of annual weeds and grasses growing in from the sides and was maintained by hand-weeding for the duration of the experiment. The water availability treatment consisted of three levels: 100% of ambient rainfall (0% reduction), 75% of ambient rainfall (25% reduction) and 50% of ambient rainfall (50% reduction). To achieve the reduction in ambient rainfall we installed a system of rain gutters in the grass canopy (Figure 1). By covering half of the area of the plot with gutters we aimed to prevent 50% of precipitation penetrating the soil. To account for the effect of the gutters on the vegetation, we placed equal amounts of gutters in all treatments. For the 100% water treatment all gutters contained holes, allowing rain to penetrate into the soil. For the 75% water treatment half of the gutters had holes, and for the 50% treatment none of the gutters had holes. To increase run-off in the 75% and 50% water treatments, we tilted the gutters at a 45° angle. The gutters in the 100% water treatment were placed flat on the soil surface. We collected the run-off in a perpendicular-placed gutter that was attached to a barrel that was emptied regularly outside the experiment.

The experiment ran for 2 years from Mar 2005 to Feb 2007. Plants were allowed to acclimatize for 2 months and were subsequently monitored from May 2005 to Feb 2007 for 650 days. We measured height, diameter of the canopy at breast height and number of flowering shoots of individual *C. odorata* shrubs once per month for the whole duration of the experiment. Every second

month we measured stem diameter for each shrub. Ambient rainfall was measured continuously for the duration of the experiment. Volumetric soil water content was measured once per month for the first year using a Thetaprobe ML2x (Delta-T Devices, Cambridge, UK). Six replicate measurements were taken per plot. In Feb 2007, all *C. odorata* shrubs were harvested and separated into leaves, stems and roots. Roots were washed and all plant parts were dried at 70°C for 48 hr and weighed. Subsequently, all above-ground grass biomass was harvested per plot and weighed. A sub-sample was dried at 70°C for 48 hr and weighed to estimate dry weight of the whole plot.

## 2.3 | Data analyses

We used a LMEM to test if the competition and water availability treatments and their interaction affected soil moisture levels. Competition and water availability were treated as fixed effects and date and block were included as random effects. We analysed the effects of competition and water availability and their interaction on growth and reproduction of *C. odorata* with a similar LMEM, with block included as a random effect. Response variables included total biomass, height and canopy diameter of *C. odorata* at breast height at the time of harvest, and number of flowering shoots per m<sup>2</sup>. Total biomass was log-transformed to meet assumptions of normality. The number of flowering shoots per m<sup>2</sup> was calculated by dividing the number of flowering shoots per plant during a 4-month flowering period (June–Sept 2006) by the surface area of the plant. The latter was estimated by considering the shrub as a cylinder and calculating the surface area of this cylinder using canopy diameter and height. In order to measure differences in allocation between individual *C. odorata* plants, we calculated leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR) by dividing the biomass of each plant part by the total biomass and tested this with the same LMEM as used for *C. odorata* growth and reproduction. Leaf, stem and root weight ratios were square root-transformed to meet assumptions of normality. Mortality was excluded in the analyses on growth, reproduction and allocation parameters, so as not to confound the growth and allocation response with survival. We analysed the effects of competition and water availability on *C. odorata* survival using Cox regression. To quantify the effect of competition we calculated the relative performance as the ratio between above-ground biomass in mixture vs above-ground biomass in monocultures,  $P_{\text{mix}}/P_{\text{mono}}$  (Weigelt & Jolliffe, 2003). We tested for differences between relative performance of *C. odorata* and native grasses with independent *t*-tests with unequal variances. To determine whether plants were hampered by inter-specific competition we performed one-sample *t*-tests to test the relative performance against 1, which is the point where biomass in the mixtures equals biomass in the monocultures and there is no effect of competition. The survival analysis and *t*-tests were performed in SPSS 14.0 (SPSS, Chicago, IL, USA). For the LMEM we used the statistical environment R v 3.0.1 (2013-05-16; R Foundation for Statistical Computing, Vienna, Austria).



**FIGURE 1** Experimental design of the study, where we tested the effect of competition with native grasses on growth, reproduction and survival of the woody invader *C. odorata* under three different water availability treatments. The study took place in Hluhluwe-iMfolozi Park, South Africa. (a) image of a monoculture plot planted with 12 *C. odorata* plants, (b) monthly rainfall (mm) for the duration of the study (2005–2007), and (c) the layout of the randomized block design ( $n = 4$ , only the first two blocks are shown), indicating the position and size of each plot, as well as the 12 plants planted in the mixtures (mix) and shrub monocultures (mono). The grass treatments (grass) remained unplanted. The numbers and the grey shading indicate the different water availability treatments: 50% (white), 75% (light grey) and 100% (dark grey) of ambient rainfall [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 3 | RESULTS

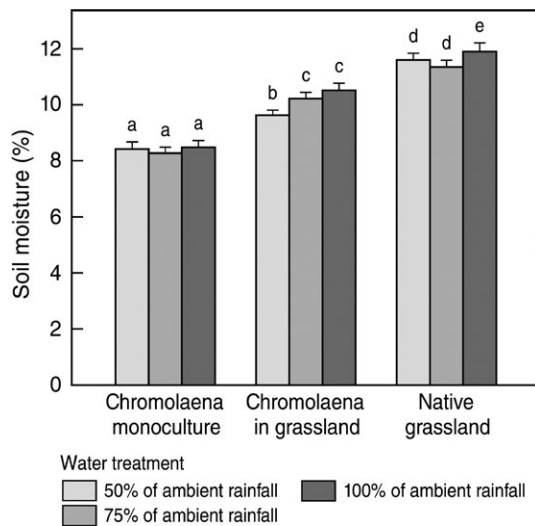
Ambient rainfall for 2005 and 2006 at the experimental site was 800 and 1,000 mm, respectively (Figure 1). Soil moisture did not differ between the 50% and 75% water availability treatments, but was significantly higher in the 100% water availability treatment ( $F_{2,24} = 4.8$ ,  $p = .02$ ; Figure 2). The competition treatment had a stronger effect on soil moisture than the water availability treatment ( $F_{2,24} = 42.4$ ,  $p < .001$ ; Figure 2). All competition treatments significantly differed from each other in soil moisture, whereby the *C. odorata* monoculture had the lowest moisture levels and the unplanted grassland the highest (Figure 2). There was no significant interaction between the competition and water availability treatments ( $F_{4,48} = 1.7$ ,  $p = .2$ ).

Competition with native vegetation had a negative effect on *C. odorata* performance, while the effect of the water treatments was limited (Table 1). *Chromolaena odorata* shrubs planted in native

grassland had lower total biomass (Figure 3a), lower canopy diameter (Figure 3c) and fewer flowering shoots per  $m^2$  (Figure 3d), but were equal in height (Figure 3b) compared to plants in the shrub monocultures. Also, the relative allocation to leaves, stems and roots was altered by the competition treatment (Figure 3e–g). Stem and root allocation increased, whereas relative allocation to leaf mass decreased when *C. odorata* was grown in competition with grasses as compared to the shrub monocultures. The water treatment did not affect total biomass (Figure 3a), nor the number of flowering shoots per  $m^2$  (Figure 3d). Height (Figure 3b) and canopy diameter (Figure 3c) tended to decrease under higher water availability. The overall mixed-effects model did not show a significant response of biomass allocation to the water availability treatments. However, when *C. odorata* was grown in native grasslands, plants invested significantly more in leaves in the lowest water availability treatment (Figure 3e).

Survival of adult *C. odorata* shrubs was high; 80% of the shrubs survived in the monocultures and even a slightly higher percentage (87.5%) survived when growing in native grassland. Accordingly, competition did not affect survival nor did the water availability treatments (Competition: Wald = 2.8,  $p = .10$ ; Water: Wald = 0.5,  $p = .48$ ; Figure 4).

Resident grasses have a strong competitive effect on *C. odorata* independent of the water availability treatment, as indicated by a lower relative performance of *C. odorata* compared to resident grasses (Figure 5). The relative performance was consistently lower for *C. odorata* compared to the resident grasses, with an average ratio of 0.42, indicating a 58% reduction in *C. odorata* biomass in mixtures relative to monocultures. *Chromolaena odorata* was equally impacted in all water availability treatments, as indicated by relative performance  $<1$  (50%:  $t = -7.1$ ,  $p < .01$ ; 75%:  $t = -9.4$ ,  $p < .01$ ; 100%:  $t = -8.0$ ,  $p < .01$ ). The effect of competition on native grasses shows a clear trend with water availability; in the 50% water treatment, native grasses were negatively impacted, meaning that grass biomass



**FIGURE 2** Average soil moisture (%) per experimental treatment. Competition treatments are shown on the x-axis, water availability treatments are indicated in different shades: 50% (light grey), 75% (grey) and 100% (dark grey) of ambient rainfall. Different letters denote significant differences after SNK post-hoc tests

**TABLE 1** Results of the LMEM testing the effects of water availability and competition on total biomass, height, canopy diameter, number of flowering shoots per  $m^2$  and biomass allocation, expressed as leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR) of *Chromolaena odorata*. Statistically significant effects ( $p < .05$ ) are marked in bold, near-significant effects ( $p < .1$ ) are marked in italic

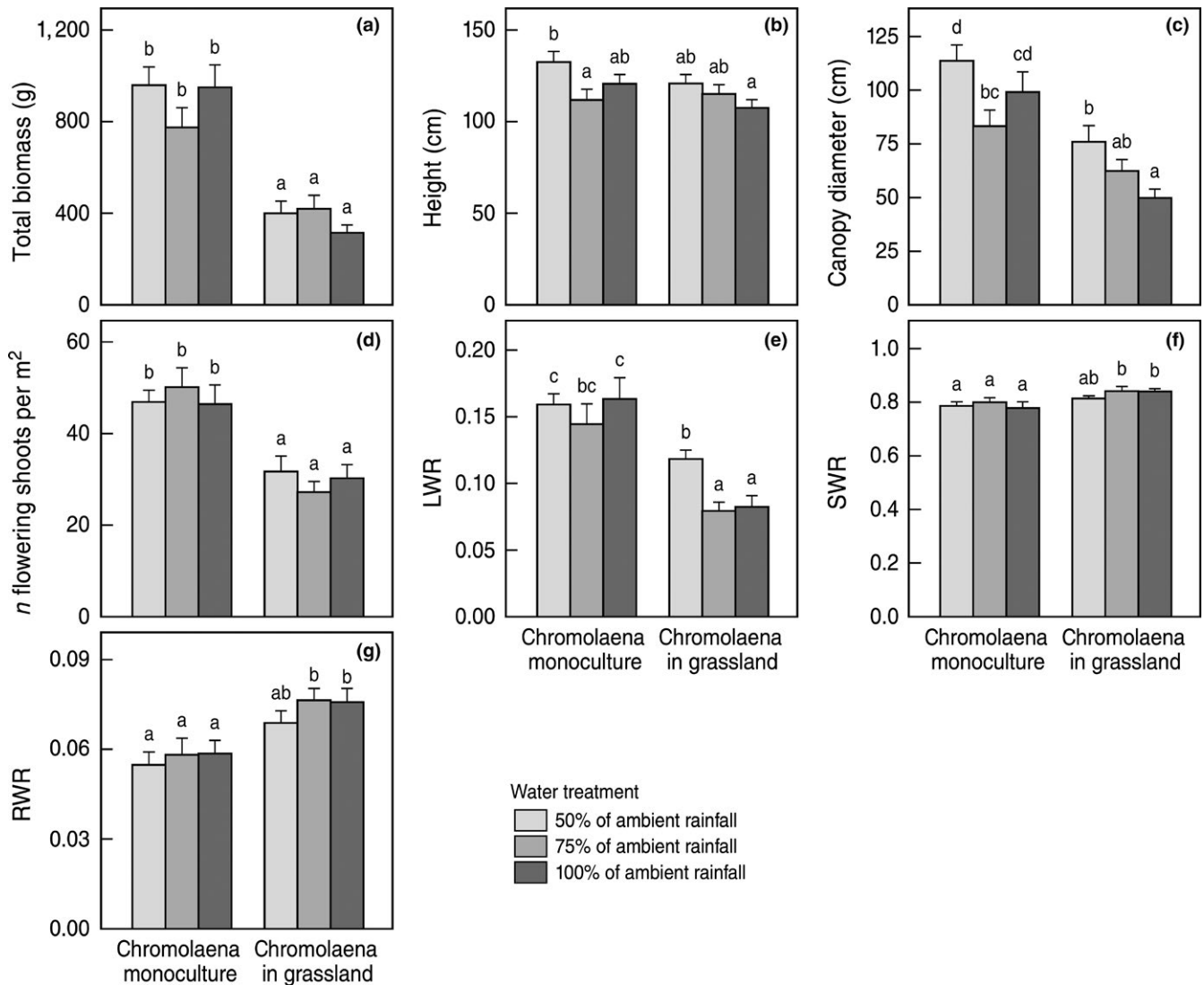
	df	Biomass		Height		Canopy diameter		N flowering shoots per $m^2$		LWR		SWR		RWR	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p
Water availability	2	0.7	.49	3.5	.057	<b>5.3</b>	<b>.018</b>	0.2	.83	1.6	.23	0.8	.47	1.1	.35
Competition	1	<b>93.4</b>	<b>&lt;.001</b>	2.1	.17	<b>28.4</b>	<b>&lt;.001</b>	<b>31.1</b>	<b>&lt;.001</b>	<b>22.9</b>	<b>&lt;.001</b>	<b>9.8</b>	<b>.007</b>	<b>23.4</b>	<b>&lt;.001</b>
Water:Competition	2	2.3	.14	1.3	.30	1.78	.20	0.6	.59	0.5	.62	0.4	.68	0.2	.85
Residuals	15														

was lower in the mixtures than in the unplanted controls ( $t = -9.1$ ,  $p < .01$ ). In the 75% water treatments grasses were not impacted ( $p = -1.2$ ,  $p = .31$ ) and in the 100% water treatment grasses show a trend towards positive interaction or facilitation ( $t = 2.5$ ,  $p = .09$ ; Figure 5).

## 4 | DISCUSSION

Competition with the resident community reduced the growth and reproduction of *C. odorata* in savanna grasslands, but did not affect survival and, hence, persistence of *C. odorata* in these grasslands during the 2 years of our study. Biomass of adult *C. odorata* shrubs was halved when grown in competition with grasses, and the number of flowering shoots was reduced by one third. However, contrary to our expectations, adult shrub survival did not differ between plots with and without grass competition. In the long term, the outcome of competition is mostly determined through effects on survival and reproduction, rather than effects on growth (Aarssen & Keogh, 2002). Therefore, even though biotic resistance from the resident grassland community constrains the abundance and spread of *C. odorata* due to reduced growth and reproduction, competitive interactions are not expected to reduce adult persistence in terms of survival rates, at least in the short term.

Competition with native grasses had stronger effects on growth and reproduction of *C. odorata* than changes in water availability. Contrary to our hypothesis, that biotic resistance would be stronger under more unfavourable abiotic conditions, we found that growth of *C. odorata* was equally impacted in all water availability treatments. Although this result seems to contrast with previous studies showing that more stressful abiotic conditions, such as nutrient or water limitation, decrease invasion success (Davis & Pelsor, 2001; Eskelinen & Harrison, 2014; Goings et al., 2009; Sharma et al., 2010), it probably rather reflects that the level of the water treatments in our experiment were not extreme enough to induce drought stress in *C. odorata*. This is further supported by the fact that in a previous experiment we did observe a negative growth response in *C. odorata* seedlings under lower water availability (te Beest et al., 2013). In contrast to *C. odorata*, native grasses responded strongly to the experimental

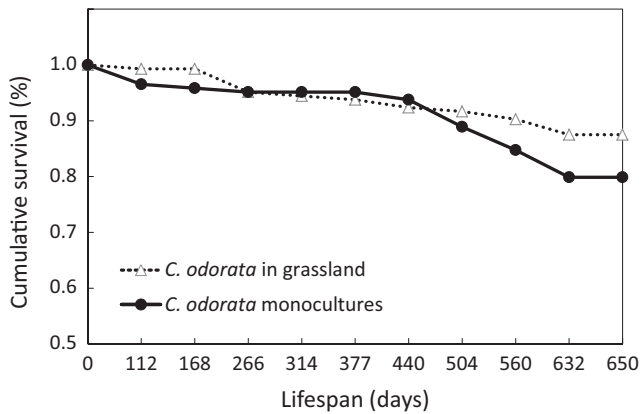


**FIGURE 3** Growth, reproduction and biomass allocation of *C. odorata* plants growing in monoculture or in competition with native grasses under different water availability treatments. Growth of *C. odorata* is expressed as (a) total biomass, (b) height and (c) average diameter of the canopy at breast height. Reproduction is expressed as (d) average number of flowering shoots per m<sup>2</sup>. Biomass allocation is expressed as (e) relative allocation of biomass to leaves (leaf weight ratio), (f) relative allocation of biomass to stems (stem weight ratio) and (g) relative allocation of biomass to roots (root weight ratio). Bars show mean values  $\pm$ SE per treatment. Competition treatments are shown on the x-axis, water availability treatments are indicated in different shades: 50% (light grey), 75% (grey) and 100% (dark grey) of ambient rainfall. Different letters denote significant differences after SNK post-hoc tests

water gradient. Under high water availability grasses performed better in the presence of *C. odorata* shrubs than without shrubs, as indicated by a higher relative performance. This could suggest positive grass–shrub interactions related to hydrological processes (Cavaleri & Sack, 2010; Goldstein & Suding, 2014; Joffe & Rambal, 1993; Syktus & McAlpine, 2016). However, this increase in relative performance of native grasses did not decrease the relative performance of *C. odorata*, which further supports the strong ability of this species to persist despite competition from the resident community.

In our experiment, water availability in terms of soil moisture was determined more by modification of the vegetation in the competition treatments than by the water availability treatment itself, with

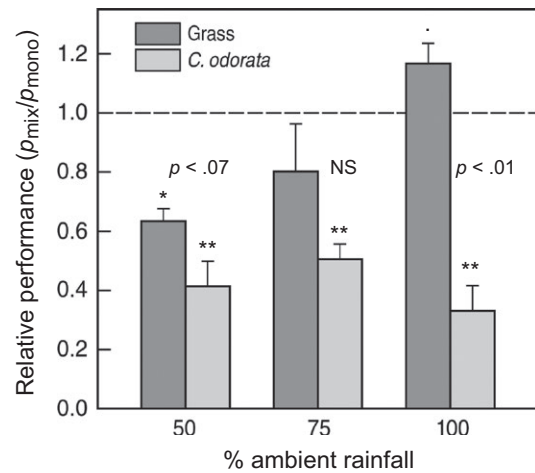
the unplanted grassland controls having the highest soil moisture levels and the shrub monocultures the lowest. Butterfield, Bradford, Armas, Prieto, and Pugnaire (2016) show that the effect of plants on soil moisture can be predicted based on precipitation, evaporation and transpiration. Since altering precipitation had limited effect on soil moisture, the lower soil moisture in the *C. odorata* monocultures can be ascribed to increased bare soil evaporation and higher transpiration rates due to a larger canopy and a higher investment in leaves (Butterfield et al., 2016; Craine & Dybzinski, 2013). Of these two processes, transpiration often dries soils faster than evaporation (Craine & Dybzinski, 2013). Higher transpiration rates could also explain the lower soil moisture in grasslands planted with *C. odorata* compared to unplanted controls, which suggests higher water use



**FIGURE 4** Cumulative percentage survival of *C. odorata* (y-axis) against the life span in days (x-axis) for *C. odorata* planted in grassland (dashed line with open triangles) and *C. odorata* planted in monocultures (solid line with solid circles). Survival did not significantly differ between the two treatments

of *C. odorata* compared to grasses. A study by Cavaleri and Sack (2010) confirms that at several scales, invasive species have higher water use than natives in terms of stomatal conductance and sap flow rates. However, the authors also show that these processes strongly depend on differences in growth form. For example, woody species invading into herbaceous vegetation always showed higher ecosystem-scale evapotranspiration than the native vegetation, whereas native–invasive species pairs of the same growth form did not show this difference (Cavaleri & Sack, 2010). This suggests that our results are similar to eco-hydrological processes between native trees and grasses across the world, whereby woody species generally increase evapotranspiration rates (Cavaleri & Sack, 2010; Goldstein & Suding, 2014; Joffre & Rambal, 1993; Syktus & McAlpine, 2016).

Our study adds to the limited number of case studies that experimentally manipulated the presence of native vegetation together with environmental factors to evaluate the effect on invasive species (Stotz et al., 2016). For example, similar to Bakker and Wilson (2001) and Ekelinen and Harrison (2014), we found that manipulating neighbouring vegetation had much greater effects on growth and reproduction of the invasive species than manipulating rainfall or water availability. However, there are also some potential caveats to our work. Our study lasted only a fraction of the adult life span of this shrub (10–15 years), therefore it is difficult to extrapolate our results to the long-term invasion dynamics of the species. For example, the negative effects we found on *C. odorata* growth could accumulate over time and affect resource acquisition and thus potential survival of the species in the longer term. Furthermore, we do not know if the observed mortality rate of 12.5% over 2 years is cumulative or not. If it is, then few individuals might remain after a decade. However, the fact that mortality rates were similar for *C. odorata* shrubs planted in monocultures vs those planted in grasslands would suggest that factors other than competition with grasses determine adult shrub mortality. Also, several studies have shown a very high tolerance



**FIGURE 5** The effect of competition calculated as relative performance (RP): ratio between above-ground biomass in mixtures ( $P_{mix}$ ) divided by above-ground biomass in monocultures ( $P_{mono}$ ) on the y-axis for native grasses (dark grey bars) and *C. odorata* (light grey bars) in each of the water availability treatments (50%, 75% and 100% of ambient rainfall) on the x-axis. Bars show mean values  $\pm$ SE. The species or community with the larger ratio has the higher competitive effect. The dotted line through 1 indicates the point where there is no effect of competition (biomass in mixtures equals biomass in monocultures).  $RP < 1$  indicates a reduction in biomass due to competition.  $RP > 1$  indicates facilitation: an increase in biomass in the presence of the competitor.  $p$ -Values show significant differences in RP between native grasses and *C. odorata*. Asterisks denote significant deviations from 1 ( $< .1$ ,  $* < .05$ ,  $** < .01$ )

to severe disturbances, such as fire or cutting (Goodall & Erasmus, 1996; te Beest et al., 2012), which would confirm low mortality rates of adult shrubs. A second caveat is the treatment of the soil in the shrub monocultures. Because of the grass removal in the shrub monoculture plots, the soil was disturbed, which would potentially lead to better soil aeration and less compaction compared to the intact grass turf. This could have positively affected the growth of *C. odorata* independent of the effect of competition and, therefore, (partly) confounded our results. In a previous study, we indeed showed that small-scale soil disturbances greatly increased growth and survival of *C. odorata* seedlings (te Beest, Mpandza, et al., 2015). Hence, it is likely that this positive growth response would hold true for adult shrubs as well, but further studies are needed to confirm this.

In conclusion, we found evidence that native savanna grasslands have a strong competitive effect on invasions by the exotic woody shrub *C. odorata*, reducing growth and reproduction, but that competitive interactions are not likely to prevent its persistence in the landscape. This is consistent with other studies on biotic resistance that show that resistance mostly acts to slow down the invasion process and is effective at regulating the spread and impacts of invaders, but often cannot completely repel invasions (Levine et al., 2004). Our results also explain why *C. odorata* preferably invades woodlands, forest margins and river courses, and occurs much less in grasslands (te Beest et al., 2017). In conjunction with

our previous study on biotic resistance during the seedling stage (te Beest, Mpandza, et al., 2015), this study illustrates how biotic resistance may differ between early and later life stages, similarly to results found for other woody invaders, such as *Prunus serotina* in European forests (Closset-Kopp et al., 2007). Particularly when long-lived woody species invade grasslands, this may lead to dominance in the longer term and a negative impact on biodiversity and ecosystem functioning, despite initial biotic resistance. With our study, we contribute to the mechanistic understanding of biotic resistance and warrant the importance of persistence in determining invasion success.

## ACKNOWLEDGEMENTS

We thank the Ezemvelo KZN Wildlife research and management staff of Hluhluwe-iMfolozi Park for providing support for the study. We thank the many people who collected data for this study, notably M. van Hoppe, J. Herder, N. Mbatha, T. Gumede, J.P.G.M. Cromsigt, N. Stevens, A. van Erk, E.H.E.M. van de Wal, R. Mhlaba and M. Khumalo. We thank the 'Dungbeetle' research community for creating an excellent working place and Dick Visser for drawing the figures. We also thank the co-ordinating editor and two anonymous reviewers, whose comments much improved the manuscript. MtB acknowledges financial support from the Dutch Scientific Organisation (NWO-PIONIER to HO) and Marie Skłodowska-Curie Actions of the European Union Horizon 2020 Programme (IF-655761-EXTREME).

## ORCID

Mariska te Beest  <http://orcid.org/0000-0003-3673-4105>

## REFERENCES

- Aarssen, L. W., & Keogh, T. (2002). Conundrums of competitive ability in plants: What to measure? *Oikos*, *96*, 531–542. <https://doi.org/10.1034/j.1600-0706.2002.960314.x>
- Bakker, J., & Wilson, S. (2001). Competitive abilities of introduced and native grasses. *Plant Ecology*, *157*, 117–125.
- Barger, N. N., D'Antonio, C. M., Ghneim, T., & Cuevas, E. (2003). Constraints to colonization and growth of the African grass, *Melinis minutiflora*, in a Venezuelan savanna. *Plant Ecology*, *167*, 31–43. <https://doi.org/10.1023/A:1023903901286>
- Butterfield, B. J., Bradford, J. B., Armas, C., Prieto, I., & Pugnaire, F. I. (2016). Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems. *Functional Ecology*, *30*, 10–19. <https://doi.org/10.1111/1365-2435.12592>
- Cano, L., Escarre, J., & Sans, F. X. (2007). Factors affecting the invasion success of *Senecio inaequidens* and *S. pterophorus* in Mediterranean plant communities. *Journal of Vegetation Science*, *8*, 281–288.
- Cavaleri, M. A., & Sack, L. (2010). Comparative water use of native and invasive plants at multiple scales: A global meta-analysis. *Ecology*, *91*, 2705–2715. <https://doi.org/10.1890/09-0582.1>
- Closset-Kopp, D., Chabrierie, O., Valentin, B., Delachapelle, H., & Decocq, G. (2007). When Oskar meets Alice: Does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? *Forest Ecology & Management*, *247*, 120–130. <https://doi.org/10.1016/j.foreco.2007.04.023>
- Craine, J. M., & Dyzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, *27*, 833–840. <https://doi.org/10.1111/1365-2435.12081>
- D'Antonio, C. M., & Thomsen, M. (2004). Ecological resistance in theory and practice. *Weed Technology*, *18*, 1572–1577. [https://doi.org/10.1614/0890-037X\(2004\)018\[1572:ERITAP\]2.0.CO;2](https://doi.org/10.1614/0890-037X(2004)018[1572:ERITAP]2.0.CO;2)
- Davis, M. A., & Pelsor, M. (2001). Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters*, *4*, 421–428. <https://doi.org/10.1046/j.1461-0248.2001.00246.x>
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. London, UK: Methuen. <https://doi.org/10.1007/978-1-4899-7214-9>
- Eskelinen, A., & Harrison, S. (2014). Exotic plant invasions under enhanced rainfall are constrained by soil nutrients and competition. *Ecology*, *95*, 682–692. <https://doi.org/10.1890/13-0288.1>
- Gaertner, M., Biggs, R., te Beest, M., Hui, C., Molofsky, J., & Richardson, D. M. (2014). Invasive plants as drivers of regime shifts: Identifying high-priority invaders that alter feedback relationships. *Diversity and Distributions*, *20*, 733–744. <https://doi.org/10.1111/ddi.12182>
- Gautier, L. (1992). Taxonomy and distribution of a tropical weed: *Chromolaena odorata* (L.) R. King & H. Robinson. *Candollea*, *47*, 645–662.
- Going, B., HilleRisLambers, J., & Levine, J. (2009). Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia*, *159*, 839–847. <https://doi.org/10.1007/s00442-008-1264-y>
- Goldstein, L. J., & Suding, K. N. (2014). Applying competition theory to invasion: Resource impacts indicate invasion mechanisms in California shrublands. *Biological Invasions*, *16*, 191–203. <https://doi.org/10.1007/s10530-013-0513-0>
- Goodall, J. M., & Erasmus, D. J. (1996). Review of the status and integrated control of the invasive alien weed, *Chromolaena odorata*, in South Africa. *Agriculture, Ecosystems and Environment*, *56*, 151–164. [https://doi.org/10.1016/0167-8809\(95\)00647-8](https://doi.org/10.1016/0167-8809(95)00647-8)
- Hierro, J. L., Lortie, C. J., Villarreal, D., Estanga-Mollica, M. E., & Callaway, R. M. (2011). Resistance to *Centaurea solstitialis* invasion from annual and perennial grasses in California and Argentina. *Biological Invasions*, *13*, 2249–2259. <https://doi.org/10.1007/s10530-011-0037-4>
- Honu, Y. A. K., & Dang, Q. L. (2000). Responses of tree seedlings to the removal of *Chromolaena odorata* Linn. in a degraded forest in Ghana. *Forest Ecology and Management*, *137*, 75–82. [https://doi.org/10.1016/S0378-1127\(99\)00315-1](https://doi.org/10.1016/S0378-1127(99)00315-1)
- Joffe, R., & Rambal, S. (1993). How tree cover influences the water balance of Mediterranean rangelands. *Ecology*, *74*, 570–582. <https://doi.org/10.2307/1939317>
- Levine, J. M. (2001). Local interactions, dispersal, and native and exotic plant diversity along a California stream. *Oikos*, *95*, 397–408. <https://doi.org/10.1034/j.1600-0706.2001.950304.x>
- Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, *7*, 975–989. <https://doi.org/10.1111/j.1461-0248.2004.00657.x>
- Raimundo, R. L. G., Fonseca, R. L., Schachetti-Pereira, R., Peterson, A. T., & Lewinsohn, T. M. (2007). Native and exotic distributions of siamweed (*Chromolaena odorata*) modelled using the genetic algorithm for rule-set production. *Weed Science*, *55*, 41–48. <https://doi.org/10.1614/WS-06-083.1>
- Ramakrishnan, P. S., & Vitousek, P. M. (1989). Ecosystem-level processes and the consequences of biological invasions. In J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, & M. Williamson (Eds.), *Biological Invasions – a global perspective* (pp. 281–300). New York, NY: John Wiley & Sons.
- Sharma, G., Muhl, S., Esler, K., & Milton, S. (2010). Competitive interactions between the alien invasive annual grass *Avena fatua* and indigenous herbaceous plants in South African Renosterveld: The role of



- nitrogen enrichment. *Biological Invasions*, 12, 3371–3378. <https://doi.org/10.1007/s10530-010-9730-y>
- Sheppard, A. W., Hodge, P., Paynter, Q., & Rees, M. (2002). Factors affecting invasion and persistence of broom *Cytisus scoparius* in Australia. *Journal of Applied Ecology*, 39, 721–734. <https://doi.org/10.1046/j.1365-2664.2002.00750.x>
- Stotz, G. C., Pec, G. J., & Cahill, J. F. (2016). Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis. *Basic and Applied Ecology*, 17, 377–387. <https://doi.org/10.1016/j.baae.2016.04.001>
- Syktus, J. I., & McAlpine, C. A. (2016). More than carbon sequestration: Biophysical climate benefits of restored savanna woodlands. *Scientific Reports*, 6, 29194. <https://doi.org/10.1038/srep29194>
- te Beest, M., Cromsigt, J. P. G. M., Ngobese, J., & Olf, H. (2012). Managing invasions at the cost of native habitat? An experimental test of the impact of fire on the invasion of *Chromolaena odorata* in a South African savanna. *Biological Invasions*, 14, 607–618. <https://doi.org/10.1007/s10530-011-0102-z>
- te Beest, M., Elschot, K., Olf, H., & Etienne, R. S. (2013). Invasion success in a marginal habitat: An experimental test of competitive ability and drought tolerance in *Chromolaena odorata*. *PLoS ONE*, 8, 1–8.
- te Beest, M., Esler, K. J., & Richardson, D. M. (2015). Linking functional traits to impacts of invasive plant species: A case study. *Plant Ecology*, 216, 293–305. <https://doi.org/10.1007/s11258-014-0437-5>
- te Beest, M., Howison, O., Howison, R., Dew, L. A., Mgobozi Poswa, M., Dumalisile, L., ... Terblanche, C. (2017). Successful control of the invasive shrub *Chromolaena odorata* in Hluhluwe-iMfolozi Park. In J. P. G. M. Cromsigt, S. Archibald & N. Owen-Smith (Eds.), *Savanna ecology and management. Conserving Africa's mega-diversity in the Hluhluwe-iMfolozi Park* (pp. 358–382). Cambridge, UK: Cambridge University Press.
- te Beest, M., Mpandza, N. J., & Olf, H. (2015). Fire and simulated herbivory have antagonistic effects on resistance of savanna grasslands to alien shrub invasion. *Journal of Vegetation Science*, 26, 114–122. <https://doi.org/10.1111/jvs.12208>
- Thomsen, M. A., Corbin, J. D., & D'Antonio, C. M. (2006). The effect of soil nitrogen on competition between native and exotic perennial grasses from northern coastal California. *Plant Ecology*, 186, 23–35. <https://doi.org/10.1007/s11258-006-9109-4>
- Thomsen, M. A., & D'Antonio, C. M. (2007). Mechanisms of resistance to invasion in a California grassland: The roles of competitor identity, resource availability, and environmental gradients. *Oikos*, 116, 17–30. <https://doi.org/10.1111/j.2006.0030-1299.14929.x>
- Vila, M., & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? evidence from pair-wise experiments. *Oikos*, 105, 229–238. <https://doi.org/10.1111/j.0030-1299.2004.12682.x>
- Weigelt, A., & Jolliffe, P. (2003). Indices of plant competition. *Journal of Ecology*, 91, 707–720. <https://doi.org/10.1046/j.1365-2745.2003.00805.x>
- Witkowski, E. T. F., & Wilson, M. (2001). Changes in density, biomass, seed production and soil seed banks of the non-native invasive plant, *Chromolaena odorata*, along a 15-year chronosequence. *Plant Ecology*, 152, 13–27. <https://doi.org/10.1023/A:1011409004004>

**How to cite this article:** te Beest M, Mpandza NJ, Olf H. Biotic resistance affects growth and reproduction, but not survival of a high-impact woody invader in African savannas. *J Veg Sci*. 2018;29:532–540. <https://doi.org/10.1111/jvs.12633>