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Research Article

Effects of herbicide and water availability on the bulbils of the invasive terrestrial plant *Furcraea foetida*

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Abstract

Invasive terrestrial plant, *Furcraea foetida* (Mauritius hemp) originates from central and South America and is invasive in South Africa. The species predominantly reproduces asexually by producing copious bulbils that facilitate spread (especially down slopes). In this study, we investigated the efficacy of a herbicide (viz. fluroxypyr/picloram), both *in situ* and *ex situ*, to control bulbils of *F. foetida*. Additionally, given the increasing evidence that suggests that climate change could alter the growth and physiology of invasive alien plant species, and hence their management, we also investigated bulbil responses to reduced water availability. For the *in situ* herbicide investigation, three study sites were selected along the coast of KwaZulu-Natal (South Africa) and seventy herbicide-treated and seventy untreated bulbils (per site) were monitored. There was 0–13% bulbil survival in herbicide-treated bulbils compared to 100% survival in control bulbils *in situ* after four weeks. In bulbils that survived, the herbicide appeared to limit rooting, which might also limit recruitment. For the *ex situ* experiment, we planted herbicide-treated bulbils, that were subjected to different durations of herbicide exposure, in a shade house and found that all herbicide-treated bulbils died after 28 days. The irrigation experiment showed no negative physiological effects on root length, plant height, chlorophyll content and leaf area in bulbils subjected to a water deficit. However, it should be noted that the final biomass was significantly higher in water-deficit treated plants (2.83 g) compared to the normally irrigated plants (0.82 g) indicating that the species may be adapted to arid climates. This study found that [2.5%] fluroxypyr/picloram is effective against *F. foetida* bulbils, suggesting that chemical control by targeting the bulbils is a potential management option to minimise spread and invasiveness. The study also suggests that *F. foetida* has the potential to tolerate drought conditions in subtropical KwaZulu-Natal, which advocates for the prioritisation of managing populations in arid regions of South Africa.

Key words: chemical control, climate change, succulent, invasive alien plants, reduced water availability

Introduction

In South Africa (SA), *Furcraea foetida* (L.) Haw. (Agavaceae) is currently a target for nationwide eradication [Category 1a under the National Environmental Management: Biodiversity Act Alien and Invasive Species Regulations (Department of Forestry, Fisheries and the Envrionment 2020)].

The species may have been introduced to SA in the early 1880s for horticultural purposes (Crouch and Smith 2011) but became economically important as it was subsequently intensively farmed for its fibre which is used in ropes and cordage (Wood 1907; Crouch and Smith 2011). This species, commonly known as the "Mauritius hemp" is a succulent monocotyledonous species native to the Caribbean and northern parts of South America, and is invasive outside its native range (Crouch and Smith 2011; Barbosa et al. 2017a, 2018; Verloove at al. 2019; da Silva Machado et al. 2020). In its native range, the species is generally found in tropical and subtropical areas with infrequent frosts and grows well on rocky terrain, lava, sand and drained soil, making it very drought-tolerant (Francis 2004). This implies that its invasiveness could be promoted in areas that are subjected to climate change-induced drought in the future. Further, *F. foetida* can successfully occupy a wide range of climates, mainly due to its crassulacean acid metabolism (CAM) photosynthetic pathway and succulent leaves (Barbosa et al. 2017b).

Furcraea foetida predominantly spreads via the prolific production of bulbils (ca. 1250 new bulbils per individual in a single reproductive cycle) that are genetically identical to the parent plant and which develop roots once they fall to the ground (Crouch and Smith 2011). These bulbils can form monotypic thickets allowing populations to spread (Crouch and Smith 2011; Barbosa et al. 2017a). Additionally, *F. foetida* can reproduce via seeds (very rarely) and the plant is considered to be monocarpic, i.e. dies after flowering (Crouch and Smith 2011; Francis 2004). The flowering process can take between 7–10 years (Crouch and Smith 2011) and commences once the plant attains sufficient vigour and size, which can support the large inflorescence (Francis 2004). The bulbils of *F. foetida* are the primary target of the herbicide because if these can be effectively controlled by limiting root emergence, recruitment of new individuals is prevented and spread will be reduced.

Herbicides afford effective chemical control for some invasive or weedy plants globally (Vitelli et al. 2009; Tran et al. 2016; Weidlich et al. 2020). Such control efforts will benefit from research associated with the control of invasive alien plants. Several studies have evaluated the costs of different herbicide applications on invasive species (Oneto et al. 2010; Afonso et al. 2022), and cost can be a major factor when deciding which method of application or herbicide to use. Various types of herbicides have been used to examine their efficacy on invasive alien plants (Vitelli et al. 2009; Oneto et al. 2010) and different methods of application have been implemented (Uremis et al. 2004; Talaviya et al. 2020; Bilodeau et al. 2023). For example, in Brazil, triclopyr, glyphosate, and the combination of triclopyr/fluroxypyr herbicides have been shown to be lethal when applied to cuts in the stem of *F. foetida* plants (Dechoum and Ziller 2013). Thus, in the present study a fluroxypyr/picloram herbicide, which is an auxin herbicide with a combination of aryloxyacetates (fluroxypyr) and pyridine-2-carbohydrates (picloram), was tested for efficacy against *F. foetid*a bulbils. However, it is also worth noting that *F. foetida* has also been controlled by ecological restoration and by utilising cattle to feed on small plants in New Zealand and Puerto Rico, respectively (Francis 2004; West and Thompson 2013).

Management of invasive alien plants is influenced by various factors, including climate change which can alter their growth and physiology (Bäurle et al. 2023) and influence their distribution patterns (Mengistu et al. 2023; Bazzato et al. 2024; Sanders et al. 2024). However, the effects of climate change on invasive alien plant species are multifarious and often context and species-specific (Merow et al. 2017; Mengistu et al. 2023). For example, Hoveka et al. (2016) provided evidence for contrasting species distribution shifts for five freshwater invasive alien plants under future climate change scenarios in SA. Additionally, Kumschick et al. (2024) predicted that the overall climate suitability will decrease for invasive Australian *Acacia* species in SA but warned that the fynbos biome will remain at high risk in terms of these invasive tree species. There are also studies which predict that invasive alien species will acclimatize more easily to new environments due to climate change (Polce et al. 2011; Klonner et al. 2017; Xian et al. 2023). Therefore, understanding the potential effects of climate change on the growth, physiology and distribution of invasive alien plants is crucial (Pyšek and Richardson 2010; Bäurle et al. 2023) for the development of proactive, effective and climate-smart management strategies for invasive alien plant species (Crossman et al. 2011; Lozano et al. 2024).

To contribute towards developing an effective management option for *F. foetida*, we assessed the efficacy of a [2.5%] fluroxypyr/picloram herbicide on the bulbils of different populations of *F. foetida* along the coast of KwaZulu-Natal (KZN), SA. Additionally, in an effort to understand the potential response of *F. foetida* to climate change, we investigated the physiological responses of the species to different levels of water availability (as a proxy for altered rainfall regimes).

Materials and methods

The study was conducted in the KwaZulu-Natal province of South Africa. The efficacy of a [2.5%] fluroxypyr/picloram herbicide application on the bulbils of *F. foetida* was assessed both *in situ* and *ex situ* by recording the survival percentage of the bulbils after exposure (Figure 1). In this aspect of the study, we considered bulbils (small bulbs that develop from aerial buds) as propagules. Additionally, the physiological effects of altered water availability (irrigation) which simulated altered rainfall regimes were investigated on *F. foetida* plants (grown from bulbils) in a greenhouse.

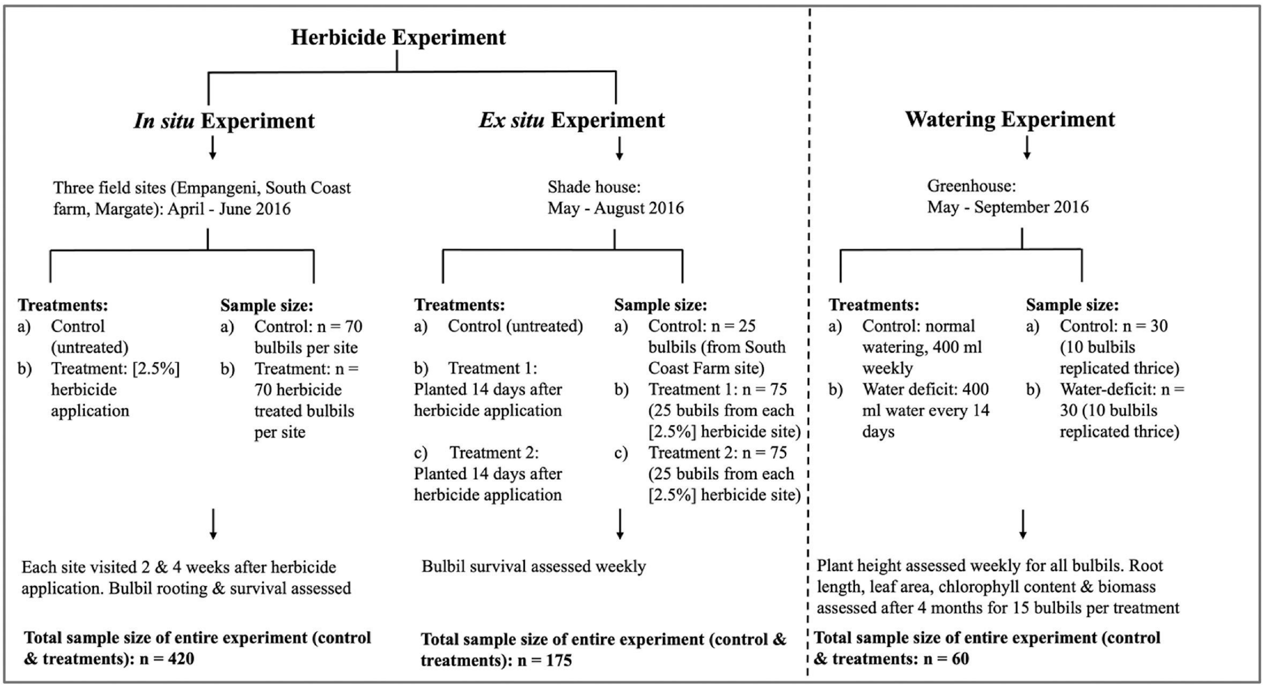

Figure 1. Experimental design for the *in situ*, *ex situ* and watering experiment conducted in the study.

Table 1. Details of the *F. foetida* sites used in this study. Vegetation types follow Mucina and Rutherford (2006).

Sites	GPS coordinates	Altitude above sea level	Vegetation	Population size	Other
Empangeni	28°44′14.5″S, 31°49′8.0″E	150 m	Maputaland Coastal Belt	103 plants	Site is found in an open area exposed to a lot of animal disturbance
South Coast Farm	30°49′30.6″S, 30°21′12.4″E	110 m	KwaZulu-Natal Coastal Belt	1481 plants	Site is within a sugar farming area
Margate	30°50′57.8″S, 30°21′51.6″E	42 m	KwaZulu-Natal Coastal Belt	145 plants	Site is near outskirts of a wastewater treatment site
Shelly Beach	30°47′23″S, 30°22′32″E	43 m	KwaZulu-Natal Coastal Belt	750 plants	Site found off road within a sugar farming area

Study site selection and in situ experimental design

Study sites

Four experimental sites were established at different geographical locations (Empangeni, South Coast Farm, Margate, Shelly Beach) along the east coast of SA (in KZN); these locations all hosted well-established *F. foetida* populations but these varied in size (Table 1). At each site, inflorescences of *F. foetida* were mechanically cut down to release the attached bulbils, and a sub-sample of these bulbils was used for each of the experimental components of the study.

In situ experiment

Seventy bulbils were collected and tagged at each site during the period of April–June 2016 (Autumn-Winter season). These bulbils were left in the field and were not subjected to any herbicide treatment (control). An additional 70 bulbils were tagged, placed in plastic bags and sprayed with approximately 200 ml of [2.5%] fluroxypyr/picloram (herbicide) to minimize the amount of herbicide entering the environment, and to ensure that all bulbils were evenly treated. The bulbils were then placed haphazardly (though trying to ensure they were distributed similar to how they would have been if they had fallen directly from a flower stalk) on the ground. The experimental set-up at each site was marked off with red barrier tape, to avoid any unwanted interference and to facilitate future visitation. The remainder of the bulbils from trimmed inflorescences at each site were collected, placed in plastic bags and sprayed with the herbicide (in the same manner as for the experiment), those bulbils were then left in a pile on the ground away from the experimental set-up and used for the *ex situ* experiment. Each site was then revisited two and four weeks after the herbicide treatment and root emergence, and survival of the tagged bulbils was recorded. Root emergence was considered successful if the emerging root of the bulbil reached 2 mm in length (Walck et al. 2010).

Bulbil survival (*ex situ* experimental design)

During the first (two weeks after herbicide exposure) and second post-treatment site visits (four weeks after herbicide exposure), 25 (of the untagged) herbicide-treated bulbils were collected (from the pile away from the experimental site) and carefully placed in separate plastic bags. An additional 25 untagged and untreated random bulbils were collected from the South Coast Farm site during the initial visit, and these were used as the control for the *ex situ* experiment. All the collected untagged, herbicide-treated bulbils from South Coast Farm, Margate and Empangeni (i.e. 2.5% herbicide-treated sites) were sown one per bag (n = 25 per site) in 25 l black plastic bags filled with topsoil. The entire experiment was repeated thrice with each site as a replicate [n = 75 (25 × 3)]. Bulbils for the control and treatment groups were sown such that the bottom half of the bulbil was buried in the soil and was watered to field capacity to ensure sufficient moisture. The planted bulbils were then left in a shade house during the months of May-August 2016 (Autumn-Winter season) for the duration of the experiment. Bulbils were watered once a week with 400 ml of water (per bag). At the end of every week, bagged bulbils were assessed for survival and data were recorded. Bulbils were considered dead once they turned black in colour with no signs of green (living) tissue remaining.

Watering experiment

Experimental design

Sixty untagged and untreated bulbils were collected from the Empangeni site to be used in the watering experiment (Figure 1). Three replicates of 10 bulbils each were set up for both the control and treatment (n = 60). Bulbils were sown in 25 l black plastic bags filled with topsoil, such that the bottom half of the bulbil was buried in the soil, and all bags were watered to field capacity to ensure sufficient moisture. Thereafter, the control group of bulbils (n = 30) were watered once a week with 400 ml of water. To simulate water scarcity conditions (at least in a scenario representative for coastal KZN) the remaining bulbils (treatment, n = 30) were watered once in fourteen days with 400 ml of water per bag. This watering regime was guided by a previous study which used the same greenhouse conditions and bag size but used a different species, propagule (seeds) and soil profile (Ramlall et al. 2015). In that study, control plants performed well with a 400 ml per week watering regime (albeit after three months), with no visible signs of stress. Consequently, in this study, a 400 ml per 14-day watering regime was used for the water-deficit treatment noting that drought conditions might involve higher levels of water stress used in the present study. Both control and water-deficit treated bulbils were left to grow in a greenhouse for a four-month period during May–September 2016 (Autumn, Winter and Spring seasons). As bulbils were considered propagules in this study, the initial fresh or dry weights were not considered prior to the commencement of this experiment in much the same way that the fresh and dry weight of a seed or geophytic organ are not considered in a growth experiment.

Measurements of vegetative traits

The planted bulbils (in both the control and treatment groups) only showed signs of growth after three months. From that point onwards, plant height was measured weekly for five consecutive weeks. Four months after planting, the bulbils were harvested and assessed for vigour using various parameters described below. A sub-sample of five bulbils was randomly selected for harvesting from each treatment of all three trials (n = 15 per treatment), and care was taken not to break the root system. Plants were rinsed with water to remove excess soil on the roots. These plants were then measured for root length, leaf area and chlorophyll content. Thereafter, the plants were individually separated into roots, bulbs and leaves. Leaf area was measured, and biomass was compared for dry weights between treatment and control bulbils.

Leaf area

It has been shown that plants which are sensitive to water stress can suffer from a reduction in leaf area (Bangar et al. 2019; Leuschner 2020; Nansamba et al. 2022). Thus, to assess leaf area in this study, entire leaves of each bulbil were carefully placed flat on a leaf area meter (C1-202 Area Meter, CID Inc., USA), and leaf area measurements were taken twice, but only the mean was used in analyses.

Chlorophyll content

Two days prior to harvest, five randomly selected bulbils from each treatment were measured for chlorophyll content each day using a hand-held chlorophyll absorbance meter (Minolta SPAD-502, Minolta Camera Co. Ltd.). Readings were taken at two separate points on the leaf and the average was taken.

Biomass (dry weight)

Leaves, roots and bulbs were then wrapped in foil, and dried in an oven at 80 °C for a 72 h period. Thereafter, individual organs (leaves, roots and bulbs) were weighed.

Statistical analysis

The effect of herbicide application on the bulbils was tested, using repeated measures ANOVA, on control and treatments for the *ex situ* survival experiment. Vigour data (root length, leaf area, chlorophyll content and biomass) for the water availability experiment were analysed with an independent sample T-Test to determine the effectiveness of treatments on all variables measured. All the relevant assumptions were met for the statistical analyses except for the repeated measure ANOVA whereby Mauchly's test indicated that the assumption for sphericity had been violated ($p = < 0.001$), therefore the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.643$). All statistical analyses were done using International Business Machines (IBM) Corporation SPSS (Version 24) (IBM 2021; Hinton et al. 2014).

Results

Herbicide efficacy

Bulbils only developed roots at the South Coast Farm in both the control and herbicide-treated groups (Table 2). Root emergence was 51.25% in the herbicide-treated bulbils at this site after two weeks, with no further rooting recorded after four weeks (Table 2), but survival decreased. The untreated bulbils had a very high root emergence of 82.25% and 92.25% after two and four weeks, respectively. Despite root emergence in herbicide-treated bulbils, the bulbils generally could not survive longer than four weeks *in situ*.

Survival of the herbicide-treated bulbils was 100% at all sites after two weeks but declined dramatically to 0% (at the Empangeni and Margate sites) and to 12% (at South Coast Farm site) after four weeks. Conversely, the untreated (control) bulbils had 100% survival at all sites at both time intervals *in situ* (Table 3).

The *ex situ* experiment had treatments that comprised of planting bulbils within 5 (T1) and 14 (T2) days after herbicide application. The T1 set of bulbils declined in survival percentage for every interval sampled (i.e. seven days) with the sharpest decline observed from days 21–28 (Figure 2). The entire T2 set of bulbils only managed to survive a maximum of 14 days. In contrast, the untreated bulbils had significantly higher survival (100%) for the full duration of the experiment (Figure 2). The results showed that there was a significant effect of the herbicide on the survival of *F. foetida* bulbils over time ($p < 0.001$, Repeated Measure ANOVA; df = 4.329; test statistic =

Table 2. Percentage root emergence *in situ* of bulbils of *F. foetida* at three study sites in KwaZulu-Natal, South Africa. Data were recorded at two and four weeks after initial herbicide exposure [n = 140 (70 control; 70 treated) per site].

Weeks after exposure	Empangeni (%)		South Coast Farm (%)		Margate (%)	
	Control	Treatment [2.5%] herbicide	Control	Treatment [2.5%] herbicide	Control	Treatment [2.5%] herbicide
2	0	0	81.25	51.25	0	0
4	0	0	92.25	[a] 51.25 [b] 67.67	0	0

[a] Total percentage of bulbils that showed root emergence after four weeks of experimental period. [b] No further root emergence was observed, as bulbils began to die, as such total percentage of mortalities are recorded here (see survival results).

Table 3. Percentage survival of *in situ* bulbils of *F. foetida* at three study sites over four weeks. Data were recorded at two and four weeks after initial experiment set up and herbicide exposure [n =140 (70 control; 70 treated) per site].

Weeks after exposure	Empangeni (%)		South Coast Farm (%)		Margate (%)	
	Control	Treatment [2.5%] herbicide	Control	Treatment [2.5%] herbicide	Control	Treatment [2.5%] herbicide
2	100	100	100	100	100	100
4	100	0	100	12	100	0

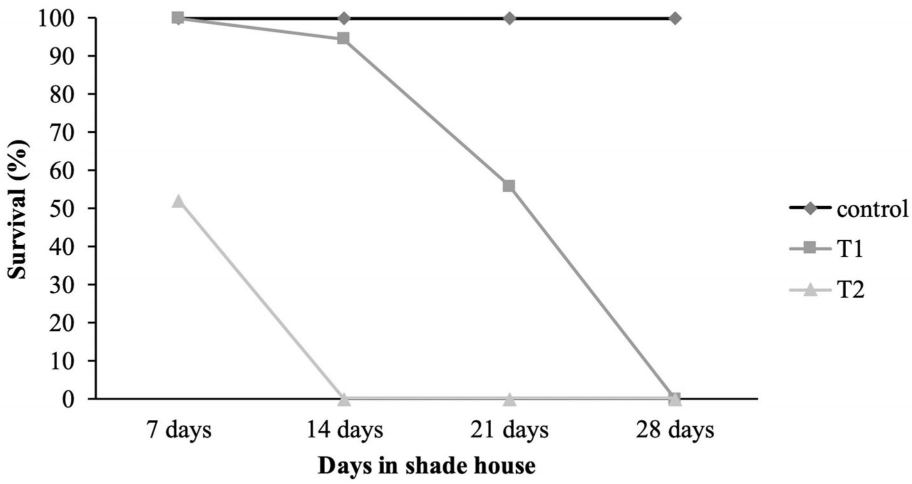

Figure 2. *Ex situ* survival (%) of untreated (control) and herbicide-treated *F. foetida* bulbils planted within 5 (T1) and 14 (T2) days after herbicide application inside a shade house for four weeks. Bulbils were considered dead once they turned black in colour with no signs of green (living) tissue remaining. Bulbils that survived (presumably retaining regrowth ability) were recorded every seven days (weekly). Values represent the means ± SD for (n = 175, ($p < 0.001$, df = 4.329 test statistic = 47.173, Repeated Measure ANOVA).

47.173). These results suggest that bulbils treated with the herbicide cannot survive longer than 14 days even under favourable conditions.

Effect of water availability

For both groups, bulbils showed signs of growth after 13 weeks (Figure 3) indicating a possible dormancy period for the bulbils. Upon harvesting, there were no significant differences ($p > 0.05$) between the control and treatment groups for plant height (Figure 3, $p > 0.05$, df = 58, test statistic = 3.469), root length (Figure 4A, $p > 0.05$, df = 28, test statistic = 0.175), leaf area (Figure 4B, $p > 0.05$, df = 28, test statistic = 2.510) and chlorophyll content (Figure 4C, $p > 0.05$, df =18, test statistic = −2.241). The biomass of roots was comparable between the treatment and control, however, leaves, bulbils and total biomass of the water-deficit treated plants were significantly

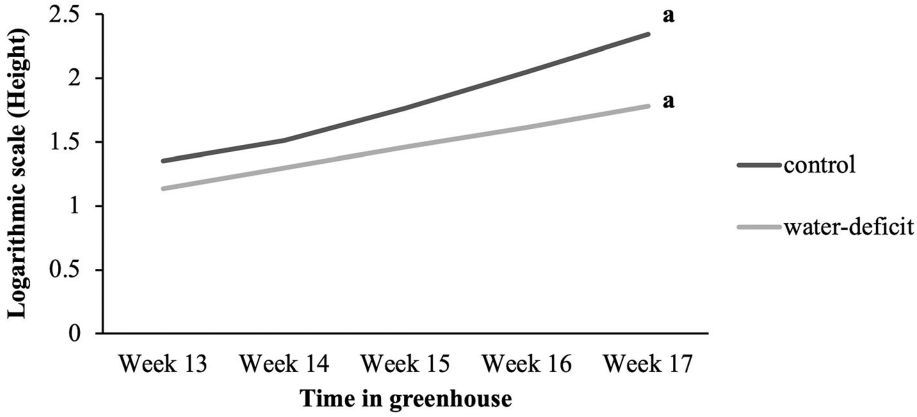

Figure 3. Plant height of *F. foetida* seedlings, subjected to normal (control) and water-deficit conditions. Measurements were taken 13 weeks after bulbils were sown in soil when bulbils showed first signs of growth. Height was recorded each week for the next five consecutive weeks. Values represent mean ± SD ($n = 60$, $p > 0.05$ where final values were tested for inter-treatment differences, $df = 58$, test statistic = 3.469, Independent sample T-Test). Different letters denote statistical significance.

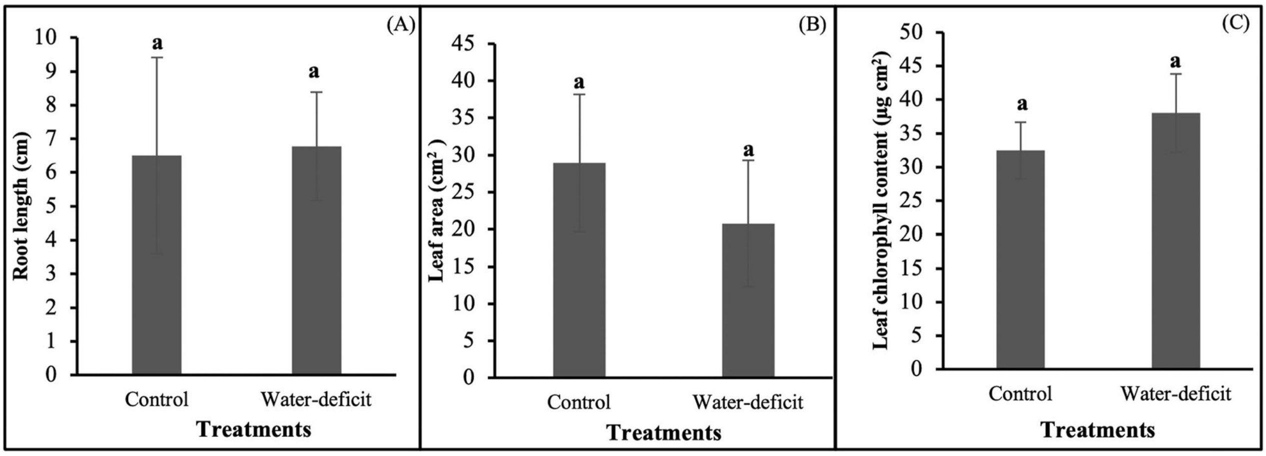

Figure 4. A) Root lengths (values represent means ± SD, $n = 30$, $p > 0.05$, $df = 28$, test statistic = 0.175); B) leaf area (values represent means ± SD $n = 30$, $p > 0.05$, $df = 28$, test statistic = 2.510); and C) chlorophyll content (values represent means ± SD, $n = 20$, $p > 0.05$, $df = 18$, test statistic = −2.241) of *F. foetida* seedlings, subjected to normal and water-deficit conditions after 17 weeks). Independent sample T-test used to calculate statistical differences between means and bars with different letters denote statistical significance.

higher (leaves = 0.48 g, bulbs = 2.3 g, total biomass = 2.83 g) compared to the untreated plants (leaves = 0.29 g; bulbs = 0.48 g, total biomass = 0.82 g) (Figure 5, leaves $p < 0.05$ $df = 28$, test statistic = −2.105; bulb $p < 0.05$, $df = 28$, test statistic = −13.632; total biomass $p < 0.05$, $df = 22.4$, test statistic = −12.402) indicating a positive physiological response of the species to the water-deficit conditions over short time frames which may create complications in eradication efforts under a changing climate.

Discussion

Main findings

Our study shows that a fluroxypyr/picloram herbicide at a concentration of 1–2.5% is efficient at terminating the propagules (bulbils) of *F. foetida* and

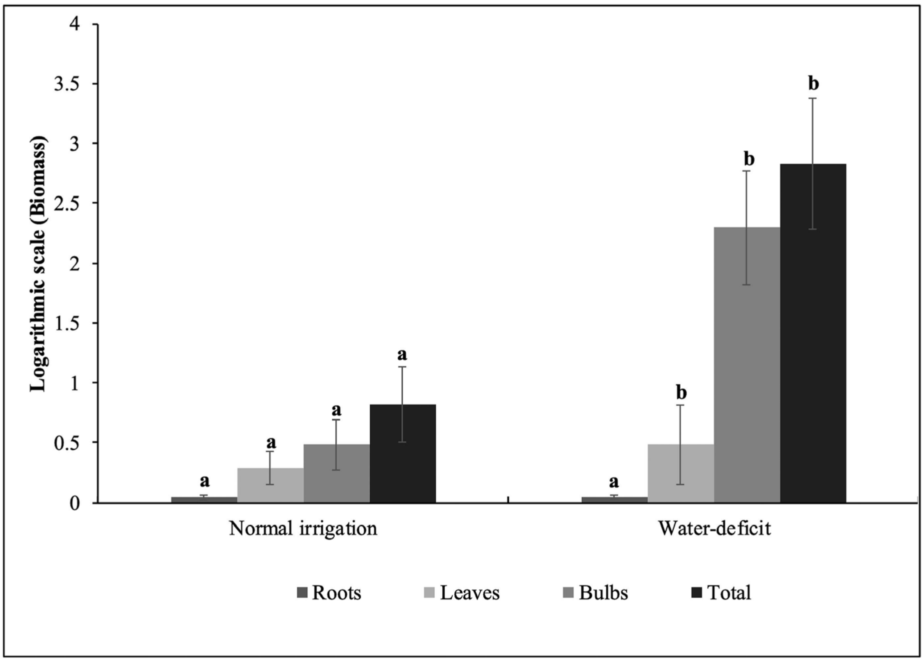

Figure 5. Biomass in *F. foetida* seedlings subjected to normal and water-deficit conditions after 17 weeks sown in soil. Values represent means ± SD (n = 30, root biomass $p > 0.05$; df = 28, test statistic = -1.201; leaves $p < 0.05$ df = 28, test statistic = -2.105; bulb $p < 0.05$, df = 28, test statistic = -13.632; total biomass $p < 0.05$, df = 22.4, test statistic = -12.402. Independent sample T-test used to calculate statistical differences and bars with different letters denote statistical significance.

could also play a role in limiting the rooting of the bulbils. However, given that the bulbils are produced on the top of the tall stalks of the species, a combination of mechanical control (physically cutting down the stalks) coupled with chemical control (which targets the bulbils) is recommended. However, management efficacy could be affected by the effects of climate change, such as altered rainfall patterns or drought. The results of the water-availability component of our study suggest that *F. foetida* could have positive physiological responses to water-deficit conditions, and this should be considered for current and future management plans of the species.

Bulbil survival and root emergence

Bulbils treated with [2.5%] of the tested herbicide were unable to survive longer than four weeks *in situ* (Table 2). Further, herbicide-treated bulbils from the South Coast Farm site showed signs of life *ex situ* up to and until two weeks (Table 2). In support of our findings, Dechoum and Ziller (2013) showed that triclopyr/fluroxypyr herbicide concentrations were lethal to *F. foetida* plants when applied at a cut stump. Moreover, picloram-based herbicides produced the most effective results by controlling and limiting root regrowth of *Solanum elaeagnifolium*, an invasive alien plant species in Australia (Wu et al. 2016). Additionally, a small-scale (pilot experiment) was conducted in the present study (but not included in results) where bulbils were treated with a lower concentration [1%] of the herbicide *in situ* at one site (Shelly Beach, Table 1). The herbicide was still lethal at this lower concentration; however, the bulbils were able to survive for up to six weeks (with 13% survival at four weeks). This is two weeks longer than the higher [2.5%] concentration used in this study. Thus, in situations where time is not a major limiting factor in the control strategy, spraying with a lower dose of [1%] may still be highly effective. However, this should be investigated in more detail to make a conclusive recommendation. Although the results of this study indicate that herbicide efficacy is similar across all study sites, seasons of high rainfall could dilute the concentration of herbicide especially if applied in spring/summer when *F. foetida* is reproductively active (flowers present) and produces bulbils. Therefore, other complementary management strategies could be employed for the species, such as the introduction of cattle, in suitable sites, as a biological control agent to feed on smaller plants before reaching reproductive maturity (Francis 2004). Additionally, ecological restoration practices could also be applied in invaded sites, as this has been effective in other regions invaded by *F. foetida* and other invasive alien species (West and Thompson 2013).

The South Coast Farm site had larger bulbils than other sites (author's qualitative observation) which could have been a contributing factor in the root emergence of the bulbils at this site, indicating that a size-dose response relationship may have to be investigated. Although distantly related, garlic bulb size was correlated with seedling emergence and quality (Jimenez-Vazquez et al. 2014), and this could apply to bulbils of *F. foetida*. Moreover, the South Coast Farm site had the largest population size (Table 1) which could mean that the population was older and better established (i.e. with larger plants). The lack of bulbil rooting observed could also be related to dormancy (Okagami and Nagao 1971; Kim et al. 2003; Sanada et al. 2018). Germination studies on bulbils suggest that bulbils from temperate regions have a dormancy period that requires after-ripening to germinate (Stritzke and Peters 1970; Ronsheim 1994). In contrast, bulbils from tropical regions are unlikely to have a dormancy period and may germinate rapidly after dispersal (Wang and Cronk 2003). As *F. foetida* is native to tropical regions, the possibility of bulbil dormancy in this study is low. However, Kim et al. (2003) showed that endogenous gibberellin content was higher in larger bulbs, which led to longer dormancy. The larger bulbils observed at the South Coast Farm site could indicate higher gibberellin content. Moreover, the *ex situ* water-availability component of this study (discussed later), which was conducted with bulbils collected from the Empangeni site, showed that bulbils only began growing after three months, suggesting a possible dormancy period in the bulbils from that site as well. Whilst the herbicide could have an impact on rooting, the effect of dormancy also needs to be investigated in more detail.

Effect of reduced water availability on F. foetida*: a proxy for a future climate change induced scenario*

The effect of water availability on the bulbils of *F. foetida* was also investigated as understanding these ramifications can assist in prioritizing eradication. If the species responds in a favourable manner to simulated drought conditions this necessitates immediate eradication or stronger control measures, especially during drought periods. The results of the water-availability study indicated no significant differences in most of the parameters measured (except biomass; Figures 4–5) between the control and water-deficit treated bulbils. In plants, leaf chlorophyll content is closely related to chlorophyll density (Jangpromma et al. 2010; Ruttanaprasert et al. 2012) which affects photosynthetic capacity (Silva et al. 2013; Wang et al. 2020). Plants that are drought tolerant will perform better under water-deficit conditions, by increasing photosynthetic capacity (Silva et al. 2013; Wang et al. 2020) which may occur due to increased leaf chlorophyll content (Puangbut et al. 2017). *Furcraea foetida* is suggested to be drought tolerant (Francis 2004), thus in the present study, the predicted trend was for leaf chlorophyll content to be higher in *F. foetida* plants grown under water-deficit conditions compared to control conditions. This prediction was not observed but the emerging trend of higher leaf chlorophyll content in plants under water-deficit conditions was observed (Figure 4C), suggesting that higher leaf chlorophyll content could emerge under severe and prolonged water deficit conditions (i.e. drought). In terms of leaf area, it has been shown that plants which are sensitive to water stress induced by drought can suffer from a reduction in leaf area (Bangar et al. 2019; Leuschner 2020; Nansamba et al. 2022), however, this trend was not observed for *F. foetida,* indicating that this species may not be sensitive to water stress levels tested in this study. The result of root length (Figure 4A) and root biomass (Figure 5) being similar for the control and the water-deficit treated bulbils was inconsistent with a meta-analysis that showed drought generally significantly increases root biomass (Eziz et al. 2017). However, another meta-analysis that focussed on the effect of drought on roots only showed that drought significantly decreased root length (Zhou et al. 2018). Hence, the effect of drought on the root length of plants may vary. The statistically similar root lengths, leaf area and chlorophyll content (Figure 4A–C) between both groups suggest that the timeframe or the water-deficit conditions of the study were not long enough for differences to be apparent and/or the consequences of drought in a subtropical climate is inconsequential.

Interestingly, it was observed that the leaf, bulbil, and therefore total biomass were significantly higher in the water-deficit treated bulbils compared to the control group of bulbils (Figure 5), which is in contrast to the findings of Eziz et al. (2017). This links to the emerging trend observed in the leaf chlorophyll content results (Figure 4C) which suggests that photosynthetic capacity was increased, which could have led to the higher total biomass in water-deficit treated bulbils. In this context, our results support the notion that *F. foetida* is able to perform well under short term drought conditions. Other studies have found that *F. foetida* can adapt quickly and thrive in various climatic conditions which is most likely a consequence of morphophysiological traits, such as the CAM metabolism, salinity resistance of the succulent leaves, and rapid and abundant propagule production (Barbosa et al. 2017a, b, 2019).

However, this needs to be interpreted in the context of the study area, which has a subtropical climate. For example, Durban had a mean annual precipitation of 1007 mm and a mean annual temperature of 16.75/23.8 °C in 2022 (WWO 2023). In its native range, *F. foetida* prefers a tropical savanna climate with < 100 mm mean annual precipitation and a mean annual temperature of 16 °C/34 °C (CABI 2023). Drought conditions in subtropical coastal KZN may represent (close to) optimal or normal growth and reproductive conditions as in the native range of *F. foetida* which are consistent with the description of this species (see Ramana et al. 2015).

Irrespective of the parameters that constitute a drought scenario for *F. foetida*, the somewhat localised results are concerning. Climate change may result in more drought conditions in the future (Ogunrinde et al. 2023), which are predicted to affect many native species negatively and influence invasion dynamics of invasive alien plant species (Bäurle et al. 2023; Orbán et al. 2021; Sanders et al. 2024). However, *F. foetida*, which is adapted to such arid conditions, might perform optimally and thrive in a subtropical coastal drought, possibly increasing its distribution and invasive potential. Moreover, another study suggests that this species will perform better in climate change-induced scenarios (Barbosa et al. 2017b).

South Africa has been susceptible to episodic drought over the past four decades (Mahlalela et al. 2020; Walz et al. 2020). In terms of agricultural risk, the Northern Cape, North West and Limpopo and Eastern Cape provinces were the most susceptible to drought (Meza et al. 2021). Further, the Eastern Cape (Mahlalela et al. 2020), Free State and North West provinces are often hard hit by droughts (Botai et al. 2016). Currently, *F. foetida* is abundantly distributed in the coastal areas of the Western Cape, Eastern Cape and KZN provinces, and occurs much less frequently in Limpopo, Gauteng and Mpumalanga (GBIF 2023). *Furcraea foetida* already has a wide and abundant distribution in the Eastern Cape, possibly as a consequence of this drought tolerance. Furthermore, it is important to note that *F. foetida* is not currently found in the North West, Northern Cape and Free State provinces, which are susceptible to drought but is found in neighbouring provinces. Therefore, the species can easily spread into and thrive in drought-prone areas, potentially increasing its naturalisation (and subsequent invasive) potential.

Concluding remarks and recommendations

The bulbils of *F. foetida* are chiefly responsible for its invasiveness and treating the bulbils with fluroxypyr/picloram at a 2.5% concentration proved to be lethal, suggesting that chemical control can be used for the eradication and/or control of this invasive alien species. Additionally, the results suggest that *F. foetida* may be unaffected under water scarce or altered rainfall conditions associated with climate change. This could lead to the species displaying a competitive advantage over native species in arid and semi-arid environments, or regions experiencing drought and greater tolerance to herbicides. The future management of *F. foetida* should include early detection to prevent their establishment and spread; rapid response efforts, such as targeted removal or herbicide treatments in the early stages of invasion; integrated management approaches such as a combination of mechanical removal, herbicides, and biological control agents; and restoration of native plant communities.

The collective findings advocate for prioritisation for the eradication and control of this species in line with Category 1a control measures in SA. A combination of cutting down the stalk and then spraying the bulbils that detach or remain on the stalk, with a repeat application after a few week or month is likely to be an effective control strategy, as this would very likely prevent bulbil survival, and restrict root growth which is an essential requirement for plant recovery and recruitment. As alluded to above, the use of biological control or ecological restoration might also be viable options to be used in conjunction with the herbicide-based method established in this study, or as alternate strategies in situations where chemical control is not feasible or desirable.

Future studies should assess the feasibility and environmental implications of the herbicide application and use data from induced drought experiments to inform species distribution models in predictive studies on invasiveness under different climate change scenarios. One of the limitations of the present study was the relatively short (four months) drought experiment which is somewhat restrictive as water availability fluctuates more dynamically over years. Future studies on *F. foetida* and other invasive alien plant species that have the potential to thrive in water-limited habitats should include more long-term data on water availability effects, to capture the full extent of drought resilience/sensitivity.

Authors' contribution

DC: original draft, investigation, field work and data collection, data analysis and interpretation, writing – review and editing; RL: writing – review and editing, investigation, field work and data collection; NS: writing – review and editing, investigation, field work and data collection; Sershen: research conceptualization, sample design and methodology, writing – review and editing; SR: research conceptualization, sample design and methodology, writing – review and editing.

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