International Scholars Journals

African Journal of Botany ISSN: 2314-9825, Vol. 13 (1), pp. 001-010, February, 2025. Available online at www.internationalscholarsjournals.org © International Scholars Journals

Full Length Research Paper

Seriphium Plumosum Encroachment's Ecological Drivers: Management and Conservation Implications

Kungawo

University of Cape Town, Rondebosch, Cape Town, 7700, South Africa

Accepted 3 February, 2025

In South Africa's grassland and savanna biomes, Seriphium plumosum is known to be a strongly invasive plant, especially in places that have been degraded. This study examined the effects of biotic and abiotic factors on S. plumosum density, height, and population structure at two locations—Klipiviersberg Nature Reserve (KNR, Gauteng) and Amathole Hogsback Plantation (HP, Eastern Cape), both of which experience significant disturbances. 928 plants were found at each site through field sampling along 9 (100 m) transects using the Point-Centered Quarter technique. Recently burned middle slopes at the HP site had the highest density of S. plumosum, followed by less recently burned top and bottom slopes. On the other hand, at KNR, the middle slope with intermediate grazing had the highest shrub density, followed by the slopes with heavy and minimal grazing, respectively. The HP site showed large numbers of juveniles and young adults, suggesting recent disturbances promoting shrub development, while the KNR population structure was primarily composed of mature plants with few juveniles. Our results demonstrate how disturbances, such as fire and grazing, significantly affect S. plumosum distribution patterns by establishing advantageous "open niches." Site-specific biotic and abiotic variables on shrub proliferation were highlighted by structural equation modeling, which found that disturbance and tree cover were important determinants at HP whereas grass biomass predominated at KNR. Effective land management techniques aimed at reducing shrub encroachment and maintaining biodiversity in similar habitats depend on the valuable insights this study offers into the dynamics of S. plumosum in response to changing environmental conditions.

Keywords: Bush encroachment, Disturbance, Point centered quarter method, Reproduction, Size structure

INTRODUCTION

Formerly known as Stoebe vulgaris, Seriphium plumosum L. (Asteraceae) is a renowned encroacher in the savanna and grassland biomes of South Africa (Jordaan and Jordaan, 2007; Snyman, 2012a). Often referred to as the "Bankrupt bush" because of its link to farmers' financial difficulties (Snyman, 2010; Baltimore et al., 2017; Marquart et al., 2023), S. plumosum is a serious hazard to ecosystems and farmers' livelihoods (Jordaan and Jordaan, 2007; Marquart et al., 2023). Due of persistent concerns over the last 20 years, S. plumosum has been classified as an encroacher under the Conservation of Agriculture Resources Act (CARA) (Regulation 16 of the Conservation of Agriculture Resources Act 43; Snyman, 2010). It has been demonstrated that a number of conditions, including uncontrolled veld fires, soil erosion, and poor land management, encourage the growth of this encroaching shrub (Baltimore et al., 2017; Marquart et al., 2023). Although farmers and landowners have attempted to prevent the spread of S. plumosum through management measures, these efforts have mostly failed (Snyman, 2012a).

Up to 80% of the grazing capacity in impacted regions is drastically reduced when S. plumosum is present (Marquart et al., 2023). This is partly explained by S. plumosum's capacity to release volatile oils, which act as a defense mechanism and make the shrub inedible to animals (Snyman, 2010; 2012b). Via allelopathy, these substances also prevent the spread of new propagules from the nearby co-occurring plants as well as the germination and growth of their own seedlings (Dakshini et al., 2023; Mar-quart et al., 2023; Snyman, 2010). For up to five years, the seeds of this shrub may lie dormant in the ground, waiting for favorable circumstances to allow them to germinate (Snyman, 2012a; Dakshini et al., 2023). Additionally, it is well known that the seedlings are extremely vulnerable to extreme weather and direct sunshine (Cohen, 1935; Snyman, 2010). To protect itself from direct sunlight until it reaches maturity, the shrub usually develops under the shade of other shrubs or grasses once the seedlings have established (Snyman, 2010; Dubula et al., 2016).

Many studies have been conducted on S. plumosum's preferred slope positions (Snyman, 2010; 2012a). The plant grows best in rocky, severely disturbed areas with rainfall between 620 and 750 mm (Snyman, 2012a). New research by Adepoju et al. (2020) indicates that S. plumosum tends to proliferate in areas with low rainfall, high diurnal temperature variation, and heavy grazing pressure, although previous studies by Davidson (1962) and Hattingh (1953) attributed the encroachment more to low soil fertility than to overgrazing. Notwithstanding these variations, disturbed slopes seem to offer this shrub growth prospects. Although S. plumosum can flourish on clay soils with adequate drainage, it seems to favor sandy soils with a low pH (Snyman, 2012a) (Wepener et al., 2007). Rarely found in moist, fertile regions, the shrub usually grows on rocky hill sides. It first appears on southern slopes, which are usually colder and have higher soil fertility, before moving into the valleys (Snyman, 2010; 2012b; Pule et al., 2018). As is typical of many Asteraceae weeds and wind-pollinated plants (Burgoyne et al., 2005), S. plumosum eventually establishes dense stands.

Due to its lack of natural enemies, S. plumosum's widespread expansion presents serious problems for South African farmlands (Marquart et al., 2023). Wide-ranging effects result from this encroachment, particularly for areas that depend on animal farming. In addition to reducing grazing capacity, the invasion has an impact on the impacted areas' economic viability (Snyman, 2012a). Effective control strategies that balance ecological integrity and economic viability are therefore desperately needed. Numerous research have investigated management strategies for the shrub, but none have been completely successful (Snyman, 2012a; Marquart et al., 2023). Herbicides can stop the growth of the shrub, but it usually grows back even after treatment, and they usually have negative, non-target impacts on the plant community (Goodall et al., 2022). Because dormant seeds can sprout after a fire, studies have demonstrated that fires do not totally destroy S. plumo-sum (Snyman, 2012a). Fire's ability to suppress this shrub is still up for debate, though, since some research indicates that fire and livestock grazing may work together to lower the shrub's height and canopy cover (Clark et al., 2020). Although there has been some success with manual removal of S. plumosum, there are still obstacles because of the risk of leftover plant remnants growing in favorable conditions and economical limitations (Marquart et al., 2023). Woody shrubs like S. plumosum are also frequently controlled with chemical treatments, but they can be costly and have unforeseen environmental effects (du Toit, 2012; du Toit and Sekwadi, 2012). Therefore, it is essential to identify long-term measures to reduce this shrub's encroachment in order to safeguard South Africa's environmental stability and economic interests.

The uncontrolled expansion of this aggressive invading shrub could result in major financial losses for the farming sector as well as the displacement of native vegetation if effective monitoring and management are not implemented. The possible effects of S. plumosum encroachment, such as reductions in biodiversity and disturbances to ecosystem functioning, have been emphasized in studies by Snyman (2010; 2012a). Thus, the purpose of this study is to (i) evaluate the density, size (height) structure, and distribution of S. plumosum on various slopes and (ii) pinpoint the main biotic and abiotic variables influencing the variance in shrub density, height, and distribution. Given that middle slopes frequently have more favorable conditions for shrub growth, such as moderate soil moisture, improved drainage, and low nutrient availability, we hypothesized that (i) S. plumosum density and height would be higher on middle slopes as compared to bottom and top slopes. Additionally, we hypothesized that (ii) abiotic factors—like rock cover and disturbance—have a greater influence on shrub density than biotic factors—like competition from grass and trees. The development of more efficient shrub control strategies that farmers and landowners might use could be facilitated by these ecological findings.

2. Materials and methods

2.1. Study area

Two locations in South Africa were used to get the data. The Amathole Hogsback Plantation (HP) is situated in the Eastern Cape Province's Amathole Mountains, while the first location, Klipriviersberg Nature Reserve (KNR), is situated in Gauteng. Johannesburg's largest nature reserve, KNR, is 680 hectares in size and is at an elevation of 1712 meters above sea level (26.289467° S, 28.011° E; van Rooyen and van Rooyen, 2014). Because of its well-known extensive grazing, this reserve was chosen as a study location. Within the Andesite Mountain bushveld of the central bushveld bio-region of the Savanna Biome, the vegetation at KNR is classified as Themeda triandra-Acacia karroo microphyllous woodland (Mucina and Rutherford, 2006; Cousins et al., 2014). Hills, rocky ridges, valleys, grassy plains, and drainage lines are all features of the terrain (van Rooyen and van Rooyen, 2014). With a dry season from June to August, the average annual rainfall is 660 mm (with a range of 550 to 750 mm) and mostly falls between October and March (van Rooyen and van Rooyen, 2014). From April to October, frost is frequent and temperatures range from 5.6 °C to 35 °C (Cousins et al., 2014).

On the other hand, HP (32.5833° S, 26.9500° E) was selected because of the frequent fires connected to timber harvesting, and it has a large concentration of non-native tree plantings. Intentional fires are used to clear the remaining vegetation for new plantation cycles when certain slopes are targeted for timber harvests. The plantation cycles and frequent fires are disturbances that probably have a major impact on the spread of S. plumosum in this region. Within the Maputa-land—Pondoland—Albany major biodiversity conservation region, HP has both naturally occurring and man-made slopes that are primarily covered in alpine grasslands and native Afro-montane Forest vegetation (Mucina and Rutherford, 2006). With a total area of 1378 hectares and an elevation of 1200–1300 meters above sea level, HP has been a hub for the South African timber industry for more than a century and experiences major human disturbances from tourists (Xulu et al., 2019). Non-native timber plantations make up 50% of the land, with 43% eucalyptus, 50% pine (including other conifers like Cedrus and Cupressus species), and 7% wattle (commercial plantations of Acacia mearnsii and minor amounts of other foreign Acacia species) (Xulu et al., 2019). According to some studies, herbicides have an even greater impact on soil pollution (Marin-Morales et al., 2013; Singh et al., 2020), and the use of fertilizers and herbicides in these areas damages native species and contaminates the natural forest ground cover and soil (Xulu et al., 2019). As a result, these tree plantations cause significant environmental disturbances. According to Mucina and Rutherford (2006), Hogsback experiences temperatures ranging from below freezing in June through August to over 30 °C on hot summer days in February. An average of 974 mm of rain falls on the region each year, primarily in the summer, when thunderstorms are common.

2.2. Field sampling

2.2.1. Plant density

One slope was selected from each site where S. plumosum was shown to be plentiful in order to create a preliminary framework for our sampling strategy. In order to provide different sampling locations within each study region, the slopes were then further separated into three main slope positions: top, middle, and bottom. The Point Centered Quarter method (PCQ) was the primary sampling approach, and field sampling consisted of nine (100 m) transects parallel to the slope at each site (3-top ridge, 3-middle ridge, and 3-bottom ridge). At the HP site, transects were set up inside plantations with different fire histories.

The distance between the PCQ point and the center of the nearest S. plumosum within each quarter was measured. PCQ sites were positioned every 5 m along each 100 m transect. Red tags were used to identify the plants that were sampled, and each quarter had a restriction distance of 10 meters from the transect's placement.

Despite the fact that this should produce 80 plants each transect, several plants that were more than 10 meters away were reported as blanks (Warde and Petranka, 1981). In order to account for the empty quar- ters where individuals were absent, a correction factor was used, and the density of S. plumosum was calculated as:

Total density plant.ha—1
1 X CF no X 10 000 1
mean distance (m)2 nk

where nk was the total number of sample quadrants, CF was the correction factor, and n0 was the number of quadrants with missing data (Warde and Petranka, 1981). Table 1 of Warde and Petranka (1981) provides values for the correction factor (CF), which is based on the proportion of quarters with missing data.

2.2.2. Canopy area and reproductive stage

Every plant under consideration had its height and canopy diameter measured (using a measuring tape) at each 5-meter position along the 100-meter transect within each quarter of the PCQ. Additionally, the stage class of each plant was determined. Growth was evaluated by measuring the canopy sizes in order to ascertain the stage and size structures of the S. plumosum populations.

symbolized substantial rock and tree cover or disturbance (Supplementary Material). The presence of animal excrement, human litter, animal trails, and any indication that plants had been trampled or rooted out were specifically used to calculate the disturbance levels (Supplementary Material). As for the tree cover level, we took into account the proportion of S. plumosum covered by tree shade, with 0 denoting no trees surrounding S. plumosum and 5 denoting complete tree shade. For the rock cover assessment, we took into account the composition of soil and rocks, with scores ranging from 0 (very fine soils, with no rocks) to 5 (mainly large rocks) (Supple-mentary Material). While fire history was divided into three categories—recently burned, less recently burned, and longest time since burned—grazing was divided into three categories: low, middle, and heavy (Supplemental Material). The major disturbances on each slope were identified using these criteria. The site management provided these facts.

Disc Pasture Meter (DPM) height readings were used to estimate herbaceous biomass in accordance with Zambatis et al. (2006)'s technique. In order to supplement the DPM height readings and guarantee precise height measurements for cross-site comparison, grass height was also measured in situ using a measuring tape. Those who measured less than 26 cm and those who measured more than 26 cm were the two categories into which the DPM height readings were divided. For DPM measurements below or equal to 26 cm, biomass was calculated using the following formula:

Grass Biomass kg ha—1 = 431.7176@0.3218x
Ax0.28345
r2 = 0.951; P < 0.0005

Each site's stage classes were divided into three categories: juveniles, young adults, and mature adults. Juveniles exhibited a green stem base, whereas mature adults had a woody, grey stem base, indicating that they had survived at least one winter (Avenant, 2015). Young adults, on the other hand, had a slender, semi-green stem and a comparatively small percentage of a grey base, making them neither mature nor juvenile plants. The following 0.2 m2 increments were used to define the canopy area size classes: 0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.0, 2.2, 2.4, and finally >2.4. Mature plants were predicted to have larger canopy areas, whereas juveniles had smaller canopies, and young adults were in the middle.

2.2.3. Biotic and abiotic factors promoting the density of S. plumosum

In addition to the density and canopy area of S. plumosum, the level of disturbance, rock cover, grass biomass and tree cover at each 5 m point along the transect were determined. To determine the dis- turbance levels, a scale ranging from 0 to 5 was utilised, where 0 indi- cated no disturbance or minimal tree and rock cover, and 5 r2 = 0.882; P < 0.0005
Where x is the mean DPM height in cm of a site.

2.3. Data analysis

R Studio version 4.0.5 was used to analyze the data (Team, 2015). To ascertain whether the distributions of S. plumosum in various slopes varied within and between sites, a Kolmogorov-Smirnov test was performed on canopy area size classes. A chi-squared test was used to determine whether there was a significant correlation between the observed frequencies under the assumption of independence between the two categorical variables (slope position and stage class distribution) in order to evaluate the relationship between slope position and the distribution of various stage classes within each site. A one-way analysis of variance (ANOVA) with p < 0.05 was used to look at any variations in grass height and S. plumosum between sites.

To investigate the impacts of site and slope position on disturbance, tree cover, and rock cover, we ran two-way ANOVAs. In order to investigate possible combination effects on each variable, the model incorporated the interaction term between slope and site. The effects of slope, site, and degree of disturbance (fire intensity and grazing pressure) on S. plumosum density were further examined using a factorial ANOVA, which included interaction terms for possible combination effects. Last but not least, a structural equation model (SEM) was carried out using the "piecewiseSEM" library (Lefcheck, 2016) in order to determine the biotic and abiotic elements that encourage S. plumosum growth at the Amathole Hogsback Plantation and Klipriviersberg Nature Reserve. The density of S. plumosum was the dependent variable, whereas the percentage of rock cover, disturbance, biomass of grass, and percentage of tree cover were the independent variables. The model also looked at how disturbance and rock cover affect the model's intermediate variables, tree cover and grass biomass. This was done in order to evaluate how these biotic and abiotic factors affected S. plumosum density directly and indirectly. Prior ecological understanding about the major determinants of S. plumosum density served as the foundation for the development of the SEM. The associations between rock cover and disturbance and grass biomass and tree cover were not calculated since, according to earlier research, these relationships were deemed to be less ecologically significant. AIC values were used to choose models based on their overall goodness of fit.

3. Results

Different prevailing disturbance patterns were seen at the two sites (Table 1). Burning was the main disturbance element at the HP site, and different patterns were seen depending on the slope position. The longest duration without a controlled burn occurred on the top slope, which was followed by a recent middle-slope burn and a less recent bottom-slope burn (Table 1). At KNR, on the other hand, grazing intensities were more significant, with low grazing at the bottom slope, medium grazing in the middle, and heavy grazing at the summit (Table 1). The significance of taking into account both biotic and abiotic elements in ecosystem management and conservation efforts is highlighted by these findings, which indicated that different factors influenced the ecological dynamics at each location.

3.1. Patterns of population structure

Significant variations in the distribution of S. plumosum across and within locations were found using chi-squared analyses. Slope location and the distribution of various stage classes at the HP site were highly significantly correlated (x2 = 231.1, df = 4, p < 0.001; Table 1). This showed that there were significant differences in the percentages of juveniles, young adults, and mature adults on the top, middle, and bottom slopes. Compared to the top slope (juveniles: x2 = 37.1, df = 1, p < 0.001; young adults: x2 = 68.1, df = 1, p < 0.001), which burnt more than five years ago, the bottom slope, which had burned less than three years ago, had a notably higher prevalence of young adults and juveniles (Table 1). Though juveniles were still significantly more common at the bottom than the middle slope (x2 = 37.1, df = 1, p < 0.001) that had burned less than a year ago, there was no discernible difference in the prevalence of young adults between the bottom and mid-dle slopes (x2 = 1.43, df = 1, p = 0.23). Slope position and stage class distribution also showed a significant, albeit weaker, correlation at the KNR site (x2 = 13.719, df = 4, p = 0.008). Due to heavy grazing, there was no discernible variation in the distribution of young adults between the middle and top slopes at this location (x2 = 0.018, df = 1, p = 0.89). However, compared to the lowest slope, which had lower levels of grazing, the proportions of young adults on the top and middle slopes were higher ($x2 = 26.103$, df = 2, $p < 0.01$). Additionally, the top slope had more juveniles than the bottom ($x2 = 15$, df = 1, $p < 0.001$). These results indicated a variation in the stage class distribution at the HP and KNR sites throughout the three slope positions. At the HP site, however, stage classes were more strongly correlated with slope position. While juveniles were primarily dispersed among the lower and middle slopes at the HP site, with young adults exhibiting a predilection for the bottom slope, adults were primarily found in the higher-lying sections. On the other hand, juveniles were only linked to the top slope at the KNR site, while mature adults and juveniles were more prevalent in the top and middle slopes. Overall, the findings showed that the distribution of S. plumosum stage classes was impacted by slope position and disturbance level, with a larger correlation observed at the HP site (Table 1).

Additional data demonstrated the impact of slope and disturbance on the distribution and dynamics of S. plumosum populations in addition to the population structure (Fig. 1). An inverse-J size class distribution (SCD), which is frequently linked to high levels of recent recruitment, was demonstrated by the left-skewed distributions of all populations both within and across the sites. According to this pattern, each site showed an inverse-J distribution, however the degree of this distribution can vary depending on the particular slope features and disturbance history. The size class distributions of several KNR slopes and their matching HP slopes differed significantly, according to the findings of the Kolmogorov-Smirnov (KS) tests. Significant differences were seen in the compositions of the top slopes at the KNR and HP sites ($D = 0.28205$, $p = 0.04859$) and the bottom slopes at both sites ($D = 0.28205$, $p = 0.009954$), suggesting that the size class distributions at these respective sites varied significantly. Notable variations were also noted among the KNR slopes. At the KNR site, there was a difference between the middle and bottom slopes ($D = 0.23077$, $p = 0.03659$) and the top and middle slopes ($D = 0.33333$, $p = 0.009863$). The difference between the top and bottom slopes was the most noticeable ($D = 0.53846$, $p < 0.001$), indicating a significant variation in the size class structure. The HP slopes, on the other hand, showed comparable size class distributions, as evidenced by the non-significant findings of comparisons (top and middle slopes: $D = 0.20513$, $p = 0.1565$; middle and bottom slopes: $D = 0.076923$, $p = 0.937$; bottom and top slopes: $D = 0.17949$, $p = 0.2646$). These results demonstrate that whereas the general recruitment pattern of S. plumosum was inverse-J, small variations in the size-class distributions indicated population structure differences by site.

Populations in the KNR had a high percentage of mature adults and a notable juvenile recruitment rate (Fig. 1). In general, the HP site had a greater percentage of juveniles than the KNR site ($x2 = 350.59$, df = 1, $p < 0.001$). With constant recruitment and a larger percentage of juveniles at the HP site compared to the KNR site, this balanced distribution of mature and juvenile individuals suggested a robust and well-established community. The finding that topography and disturbance levels had a major impact on stage class distribution and population dynamics at both sites was further corroborated by this pattern.

3.2. Impact of biotic and abiotic factors

Biotic and abiotic factors both generally impacted the distribution of S. plumosum. Among the biotic factors analysed, grass height posi- tively correlated with the height of S. plumosum at both the HP and KNR sites. The results showed a statistically significant difference in grass height between the sites ($F(1,254) = 36.78$, $p < 0.001$), with HP having taller grasses than KNR (Fig. 2A). Additionally, regression analyses revealed that the competition between S. plumosum and grasses was higher at KNR ($R2 = 0.63$, $p < 0.001$) compared to HP ($R2 = 0.19$, $p = 0.03$; Fig. 2A). These findings indicate that the height of S. plumo- sum at both sites did not suppress grass height. Tree cover, another biotic factor analysed, was measured as the proportion of S. plumosum covered by tree shade. Similar to grass height, tree cover also

The distribution of S. plumosum was generally influenced by both biotic and abiotic causes. At both the HP and KNR sites, there was a positive correlation between the height of S. plumosum and the grass height, one of the biotic parameters examined. HP had taller grasses than KNR, according to the data, which indicated a statistically significant difference in grass height between the sites ($F(1,254) = 36.78$, $p < 0.001$) (Fig. 2A). Furthermore, the rivalry between S. plumosum and grasses was greater in KNR ($R2 = 0.63$, $p < 0.001$) than at HP ($R2 = 0.19$, $p = 0.03$; Fig. 2A), according to regression analyses. These results show that grass height was not suppressed by S. plumosum height at either location. The percentage of S. plumosum covered by tree shadow was used to calculate tree cover, another biotic component that was examined. Like grass height, tree cover varied significantly between sites ($F(1,254) = 5.877$, $p = 0.016$) and across slope positions ($F(2,254) = 14.257$, $p < 0.001$), with KNR having more tree cover than HP. Tree cover within HP was very low at the other two slope positions (<1%; $p < 0.05$; Fig. 2D) and highest at the top (12%). However, there was no discernible change in tree cover between the top (7.7%), middle (6.7%), and bottom (100.7%) slopes inside KNR ($p = 0.99$; Fig. 2D). This suggests that tree cover had no discernible influence on S. plumosum at KNR but had a negligible effect at HP. Additionally, abiotic variables had conflicting impacts on S. plumosum distribution. There were notable differences in rock cover, an important abiotic characteristic that is primarily linked to the prevalence of S. plumosum, between the sites ($F(1,254) = 279.01$, $p < 0.001$) and among the three slopes ($F(2,254) = 15.49$, $p < 0.001$). The bottom slope in HP had the largest rock cover (25 percent; $p < 0.01$), but the middle and top slopes (4.23% and 0.034 percent, respectively) did not differ significantly ($p > 0.05$; Fig. 2C). The huge quantity of juveniles discovered in the bottom slope of HP was mostly related to the high rock cover there (Fig. 2C). On the other hand, in the KNR site, the top slope had more rock cover (49.2%; $p < 0.001$) than the mid-dle (24.2%) and bottom slopes (24.8%), which did not differ significantly ($p > 0.05$; Fig 2C). The observed high development of S. plumosum in KNR was likewise closely linked to the high rock cover at the top slope (Fig. 2). The shrub's prevalence was also impacted by the degree of disturbance seen at each slope. As an abiotic factor, the degree of disturbance differed significantly between locations ($F(1,254) = 31.162$, $p < 0.001$) and slopes ($F(2,254) = 4.982$, $p < 0.01$). There was little variation in the levels of disturbance within HP, with the top slope having comparatively higher levels (21.8%), followed by the middle (21.4%), and the bottom slope (20%; $p < 0.05$; Fig. 2B).

The disturbance levels on the slopes at the KNR site did not change significantly ($p > 0.05$; Fig 2B). Therefore, the prevalence of S. plumosum was not significantly impacted by the local disturbance within each slope. Among the sites, HP, which is frequently burned, had a much higher degree of disturbance than KNR, which is greatly influenced by grazing pressure ($p < 0.001$).
As a result, S. plumosum was variably stimulated to proliferate across slope positions and sites by both biotic and abiotic variables.
Depending on the primary disturbance, the density of S. plumosum also varied considerably between sites ($F(1,254) = 22.342$, $p < 0.0001$) and between slope positions ($F(2,254) = 4.088$, $p = 0.0179$) (Fig. 2E). Slope position and location had a significant interaction ($F(2,254) = 4.436$, $p = 0.0128$). While there was no difference in density between the top and bottom slopes ($p = 0.94$), the middle slope within the HP site had a considerably greater mean density than the bottom and top slopes ($p < 0.001$). The top, middle, and bottom slopes did not significantly differ in density at KNR ($p = 0.57$, $p = 0.09$, and $p = 0.971$, respectively). These results showed that the density of S. plumosum was not significantly impacted by variations in abiotic variables across slopes. The type of disturbance, however, had a major impact on S. plumosum density; higher densities were seen at HP, where prior burns were implemented, while lower densities were seen at KNR, where grazing was the primary disturbance.
The effects of biotic and abiotic factors on the distribution of S. plumosum among the sites were examined using structural equation modeling (SEM) (Fig. 3). Rock cover at the HP site had a detrimental impact on tree cover ($p < 0.005$) and grass biomass ($p < 0.001$), but it had no discernible effect on S. plumosum density ($p = 0.08$; Fig 3).

At the HP site, on the other hand, the degree of disturbance had a negative impact on grass biomass ($p < 0.001$) but a positive impact on tree cover ($p < 0.005$) and S. plumosum density ($p < 0.001$). This suggested that the density of the shrub was positively correlated with the degree of disturbance. The impact of biotic variables on S. plumosum density was comparable. Although the density of the shrub was adversely impacted by grass biomass, this effect was not statistically significant ($p > 0.05$). On the other hand, shrub density was significantly positively impacted by tree cover ($p < 0.005$). The positive correlation between disturbance and tree cover indicated possible indirect effects on S. plumosum growth, even though there were no clear direct correlations between shrub density and either rock cover or grass biomass. Only grass biomass had a significant impact on S. plumosum density in the KNR site ($p < 0.01$).
The density of the shrub was not significantly impacted by the amount of disturbance ($p > 0.05$), rock cover ($p > 0.05$), or tree cover ($p > 0.05$). These results demonstrated the intricate relationships between biotic and abiotic elements that affect S. plumosum distribution and recommended that site-specific circumstances be taken into account when developing management plans.

4. Discussion

With an emphasis on how these variables change depending on the slope position, this study evaluated the impact of biotic and abiotic factors on the density, height, and population structure of S. plumosum. Our research showed clear distinctions between HP and KNR in terms of the variables influencing shrub growth. We found short, dense S. plumosum at the HP site, together with tall grasses, heavy rock cover, and significant levels of disturbance. The KNR site, on the other hand, featured taller, less dense S. plumosum and short grasses. This implied that diverse development patterns of S. plumosum at various sites are caused by different combinations of environmental variables. The most important factors influencing shrub density at the HP site, according to the structural equation model, were disturbance and tree cover. This highlights the critical role that both biotic and abiotic factors play in determining the population structure of S. plumosum. However, the model showed that grass biomass was the only significant component at the KNR site, indicating that biotic variables had a dominant influence. Our second hypothesis, according to which biotic factors would have less of an impact on shrub density than abi-biotic ones like rock cover and disturbance, was not supported by our data. Rather, we discovered that S. plumosum slope preferences were influenced by both biotic and abiotic factors, with biotic factors—such as tree cover and grass biomass—having a larger overall effect. More significantly, although shrub density was influenced by both kinds of influences, their impacts varied depending on the site. Building on previous discoveries, our findings offered important new information about how biotic and abiotic variables influence S. plumosum population structure, density, and height. Higher grass biomass had a negative effect on shrub density in the KNR site, most likely as a result of competition for nutrients and water. This finding is consistent with that of Snyman (2012a), who attributed the high link between S. plumo-sum density and grass phytomass output to resource competition. Furthermore, Sny-man (2010; 2012a) found that S. plumosum seedlings establish more readily in shade, potentially as a result of less stress from the sun. Our results at the KNR site, where there was more tree cover, however, indicate that although shading might help seedlings establish, it does not encourage the growth of dense shrubs. Whereas the HP site had shorter, denser clumps of the shrub due to lower tree cover and disturbance, the KNR site had less dense bushes that grew much taller. This trend implies that while tree cover might initially promote the establishment of seedlings, other elements including resource constraints and grass competition might eventually limit shrub density.

Additionally, protective microhabitats that promote juvenile establishment and growth are probably created by abiotic variables including increased rock cover and disturbance levels at the HP site (Pule et al., 2018). This is corroborated by our data, which showed that regions with higher rock cover and disturbance at the HP site had higher juvenile establishment; high rock cover is linked to fire protection (Arena et al., 2015; Kremer-Kohne et al., 2020). The disparity in environmental circumstances between the HP and KNR sites emphasizes how crucial site-specific elements are in influencing S. plumo-sum development patterns. Whereas the KNR site fosters taller and more mature plants, the HP site encourages the establishment of more juveniles and young adults. This indicates that grazing pressure (KNR site) has less of an impact on juvenile establishment than regular fires (HP site). The plant's resilience is demonstrated by its capacity to adapt to a variety of environments. In order to guide targeted management options, such as regulating grass biomass by minimizing grazing pressure and eliminating land disturbances that encourage the spread of S. plumosum, it is imperative to comprehend these dynamics.

Both sites showed an inverse J-shaped population structure, suggesting high recruitment rates and favorable circumstances for juvenile plants, despite variations in biotic and abiotic parameters. According to Cousins et al. (2014), a distribution that is left-skewed indicates that there were more people in the younger stage groups—such as juveniles and young adults—than in the older classes. A rising population is frequently characterized by this distribution, which indicates that the population has just gone through a phase of effective recruitment or high levels of seedling establishment (Cousins et al., 2014; Helm and Witkowski, 2012; Mwavu and Witkowski, 2009). The population is expected to grow if the young individuals live to adulthood and procreate (Cousins et al., 2014). If the environmental conditions stay favorable and the individuals successfully mature and reproduce, the population with a large base of young individuals has the potential to grow significantly and densify. Because of the frequent fires that disrupt the soils and native vegetation, the population at the HP site is therefore expected to grow. Heavy grazing pressure will also encourage the growth of this shrub if management techniques at the KNR site do not improve.

At the HP site, the middle slope—which had just been burned—had the highest shrub densities, followed by the bottom slope and the top slope, which had the longest interval between burns. At the KNR location, the top slope had considerable grazing, whereas the middle slope had the maximum shrub density and intermediate grazing. The density of shrubs was lowest on the bottom slope, where there was less grazing. These findings suggest that the distribution and occurrence of shrubs are significantly influenced by topography as well as the primary disturbance factors present at a site, such as fire and grazing. Similar results were reported by Snyman (2012b), who observed that S. plumosum initially established on ridges before spreading to valley bottoms, indicating a significant predilection for steep slopes and rocky terrain. Furthermore, according to Snyman (2010), S. plumosum prefers infertile soils with low levels of organic matter, therefore stony ridges with low levels of nutrients (Huang et al., 2023) are better suited for its dominance than the comparatively fertile slopes. Our results support these observations by emphasizing the preference for higher, less nutrient-rich ridges, which help shrubs dominate certain slopes.

According to earlier observations by Snyman (2012a), S. plumosum grows best in disturbed environments where open niches with little competition offer ideal growing and spreading conditions. This opportunistic distribution pattern implies that the plant frequently inhabits regions where "empty" niches free from competition are accessible due to overgrazing or other land disturbances (Pule et al., 2018). Therefore, by establishing or preserving these open niches, our work contributes to the increasing amount of evidence showing that both fire and grazing have a significant impact on shrub distribution patterns. The complexity of putting management techniques in place to control this shrub is highlighted by the combination of S. plumosum's adaptability to a variety of environmental conditions, including its preference for disturbed, nutrient-poor settings and its capacity to establish in regions with less competition. This implies that in order to successfully manage the spread of S. plumosum across South Africa, landowners and farmers need to carefully evaluate the effects of disturbance (such as fire and grazing).

5. Conclusion

Due to prior major disturbances, both study sites showed high densities of S. plumosum, supporting the idea that the shrub grows best in severely disturbed habitats. Mature plants made up the majority of the population structure in the KNR site, while youngsters were noticeably scarce. On the other hand, the HP site had significant concentrations of juveniles and young adults, suggesting that the shrub had proliferated due to recent disturbances. These findings highlight how disturbance regimes affect S. plumosum population demography. Juve-niles are common at the HP site, which emphasizes how high disturbance levels—like periodic fires—help the plant grow and spread. This study reveals the main perturbations that encourage S. plumosum's growth and offers useful baseline data on the population structure. Our findings highlight the fact that frequent fires and excessive grazing are the main causes of S. plumosum invasion. The need for better land management practices to prevent shrub encroachment and maintain current biodiversity is highlighted by this research. This study aids in the creation of solutions meant to lessen the negative impacts of these disturbances on the structure of plant communities by providing guidance for management suggestions for farmlands and comparable rangelands.

Declaration of competing interest

The authors affirm that none of the work described in this publication may have been influenced by any known conflicting financial interests or personal ties.

Acknowledgements

For help with fieldwork and other requirements needed to sample in the Klipriviersberg Nature Reserve, we are grateful to the crew there. We are grateful for permission to conduct research on the Amathole Hogsback Plantation (permits 14311 and 14319). Additionally, we would like to sincerely thank Professor Craig Peter for his persistent support and ongoing advise.

References

Adepoju, K., Adelabu, S., Mokubung, C., 2020. Mapping Seriphium plumosum encroach- ment and interaction with wildfire and environmental factors in a protected mountainous grassland. Environ. Monit. Assess. 192, 1–15. https://doi.org/ 10.1007/s10661-020-08253-x.
Arena, G., Witkowski, E.T., Symes, C.T., 2015. Growing on rocky ground: microhabitat predictors for site-occupancy of Aloe peglerae, an Endangered endemic species with a restricted range. South African J. Botany 100, 174–182. https://doi.org/ 10.1016/j.sajb.2015.05.022.
Avenant, P., 2015. Report On the National Bankrupt Bush (Seriphium plumosum) Survey (2010-2012). Department of Environmental Affairs, pp. 1–47.
Baltimore, M.Mokou, Jordaan, Jorrie.J., Mafeo, Tieho.P., Potgieter, Martin J., 2017. The effect of root and shoot extracts of Seriphium plumosum as allelopathic agents. Insights Forest Res. 1, 42–49. https://doi.org/10.36959/948/460.
Burgoyne, P.M., van Wyk, A.E., Anderson, J.M., Schrire, B.D., 2005. Phanerozoic evolu- tion of plants on the African plate. J. African Earth Sci. 43, 13–52. https://doi.org/ 10.1016/j.jafrearsci.2005.07.015.
Clark, M.D., Wonkka, C.L., Kreuter, U.P., Rogers, W.E., 2020. Interactive effects of pre- scribed fire and livestock grazing on Seriphium plumosum in South African sour bushveld. Afr. J. Range Forage Sci. 37, 278–285. https://doi.org/10.2989/ 10220119.2020.1751287.
Cohen, C., 1935. Stoebe sp. A contribution to its ecology. J. South African Botany 171– 175 URL https://archive.org/details/biostor-28677.
Cousins, S., Faiola, J., Vermaak, V., 2014. Klipriviersberg - Johannesburg's green jewel of the south. Veld Flora 100, 68–71.
Cousins, S.R., Witkowski, E.T.F., Pfab, M.F., 2014. Elucidating patterns in the population size structure and density of Aloe plicatilis, a tree aloe endemic to the Cape fynbos, South Africa. South African J. Botany 90, 20–36. https://doi.org/10.1016/j.sajb.2013.09.012.
Dakshini, K.M.M., Foy, C.L., Inderjit, 2023. Allelopathy: one component in a multiface- ted approach to ecology. Principles and Practices in Plant Ecology: Allelochemical Interactions, pp. 3–14. https://doi.org/10.1201/9780203742181-2.
Davidson, R.L., 1962. The influence of edaphic factors on the species composition of early stages of the subsere. J. Ecol. 50, 401–410. https://doi.org/10.2307/2257451.
du Toit, J.C.O., Sekwadi, K., 2012. Tebuthiuron residues remain active in soil for at least eight years in a semi-arid grassland, South Africa. Afr. J. Range Forage Sci. 29, 85–90. https://doi.org/10.2989/10220119.2012.705325.
Dubula, B., Tefsamichael, S.G., Rampedi, I.T., 2016. Assessing the potential of remote sensing to discriminate invasive Seriphium plumosum from grass. South African Journal of Geomatics 5, 201–213. https://doi.org/10.4314/sajg.v5i2.8.
Goodall, J., Witkowski, E.T.F., Morris, C., 2022. Patterns of persistence demonstrate the vulnerability of the root hemiparasite Thesium utile A.W.Hill (Santalaceae) to weed control measures. South African J. Botany 151, 481–484. https://doi.org/10.1016/j. sajb.2022.10.016.
Hattingh, E.R., 1953. Observations on the ecology of stone vulgaris Levyns. Empire J. Experiment. Agricult. 309–321 URL https://www.cabidigitallibrary.org/doi/full/ 10.5555/19540700813.
Helm, C.V., Witkowski, E.T.F., 2012. Characterising wide spatial variation in population size structure of a keystone African savanna tree. For. Ecol. Manage 263, 175–188. https://doi.org/10.1016/j.foreco.2011.09.024.
Huang, L., Hu, H., Bao, W., Hu, B., Liu, J., Li, F., 2023. Shifting soil nutrient stoichiometry with soil of variable rock fragment contents and different vegetation types. Catena (Amst) 220, 1–10. https://doi.org/10.1016/j.catena.2022.106717.
Jordaan, D., Jordaan, F.P., 2007. Probleemplante in die Suidwes-gebied. Ons Eie, pp. 38–40. URL https://scholar.google.com/scholar_lookup?title=Probleemplante%20in%20die %20Suidwes-gebied&publication_year=2007&author=D.%20Jordaan&author=F. P.%20Jordaan.
Kremer-Ko€hne, S., Witkowski, E.T.F., Steffens, F.E., Thompson, D.I., 2020. Hanging in there: aloe lettyae populations in Critically Endangered grassland fragments. South African J. Botany 131, 33–42.
Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol. Evol. 5, 573–579. https://doi. org/10.1111/2041-210X.12512.
Marin-Morales, M.A., Ventura-Camargo, B.C., Hoshina, M.Y., 2013. Toxicity of herbi- cides: impact on aquatic and soil biota and human health. Herbicides - Current Research and Case Studies in Use, pp. 399–443. https://doi.org/10.5772/55851.
Marquart, A., Slooten, E., Jordaan, F.P., Vermeulen, M., Kellner, K., 2023. The control of the encroaching shrub Seriphium plumosum (L.) Thunb. (Asteraceae) and the response of the grassy layer in a South African semi-arid rangeland. Afr. J. Range Forage Sci. 40, 316–321. https://doi.org/10.2989/10220119.2022.2086620.
Mucina, Rutherford, 2006. The Vegetation of South Africa. Lesotho and Swaziland. South African National Biodiversity Institute.

Mwavu, E.N., Witkowski, E.T.F., 2009. Population structure and regeneration of multi- ple-use tree species in a semi-deciduous African tropical rainforest: implications for primate conservation. For. Ecol. Manage 258, 840–849. https://doi.org/10.1016/ j.foreco.2009.03.019.

Pfab, M.F., Witkowski, E.T.F., 1999. Contrasting effects of herbivory on plant size and reproductive performance in two populations of the critically endangered species, Euphorbia clivicola R. A. Dyer. Plant Ecol. 145, 317–325. https://doi.org/10.1023/ A:1009869011237.

Pule, H.T., Tjelele, J.T., Tedder, M.J., 2018. The effects of abiotic factors in South African semi-arid grassland communities on Seriphium plumosum L density and canopy size. PLoS. One 13, 1–14. https://doi.org/10.1371/journal.pone.0202809.

Singh, M.K., Singh, N.K., Singh, S.P., 2020. Impact of herbicide use on soil microorgan- isms. Plant Responses to Soil Pollution, pp. 179–194. https://doi.org/10.1007/978- 981-15-4964-9_11.

Snyman, H.A., 2012a. Control measures for the encroacher shrub Seriphium plumosum. South African J. Plant Soil 29, 157–163. https://doi.org/10.1080/02571862.2012.745905.

Snyman, H.A., 2012b. Habitat preferences of the encroacher shrub, Seriphium plumo- sum. South African J. Botany 81, 34–39. https://doi.org/10.1016/j.sajb.2012.05.001.

Snyman, H.A., 2010. Allelopathic potential, seed ecology and germination of the encroacher shrub Seriphium plumosum. Afr. J. Range Forage Sci. 27, 29–37. https:// doi.org/10.2989/10220111003718482.

Warde, W., Petranka, J.W., 1981. A correction factor table for missing point-center quarter data. Ecology. 62, 491–494. https://doi.org/10.2307/1936723.

Wepener, J., Kellner, K., Jordaan, D., 2007. The Control of Stoebe vulgaris Encroachment in the Hartbeesfontein Area of the North West Province. Student Thesis pp. 1–130.

Witkowski, E.T.F., Garner, R.D., 2008. Seed production, seed bank dynamics, resprout- ing and long-term response to clearing of the alien invasive Solanum mauritianum in a temperate to subtropical riparian ecosystem. South African J. Botany 74, 476–484. https://doi.org/10.1016/j.sajb.2008.01.173.

Xulu, S., Gebreslasie, M.T., Peerbhay, K.Y., 2019. Remote sensing of forest health and vitality: a South African perspective. Souther Forests 81, 91–102. https://doi.org/ 10.2989/20702620.2018.1512787 South For.

Zambatis, N., Zacharias, P.J.K., Morris, C.D., Derry, J.F., 2006. Re-evaluation of the disc pasture meter calibration for the Kruger National Park, South Africa. Afr. J. Range Forage Sci. 23, 85–97. https://doi.org/10.2989/10220110609485891.

Table 1
Numbers (and % per stage class) of *Seriphium plumosum* individuals per habitat with transect sampling at Amathole Hogsback Plantation (HP) and the Klipriviersburg Nature Reserve (KNR), with altitude and dominant disturbance.

Site	Habitat	Mature adults (n)	Young adults (n)	Juveniles (n)	Total plants sampled (n)	Altitude (m.a.s.l)	Dominant disturbance
HP	Top	202 (96)	7 (3.5)	1 (0.5)	210	1187	Burned (>5 years)
	Middle	176 (84.2)	3 (1.4)	30 (14.4)	209	1166	Burned (<1 year)
	Bottom	78 (38.1)	87 (42.4)	40 (19.5)	205	1140	Burned (<3 years)
KNR	Top	179 (80.6)	28 (12.6)	15 (6.8)	122	1780	Heavy grazing
	Middle	122 (79.7)	29 (19.0)	2 (1.3)	153	1612	Medium grazing
	Bottom	28 (96.6)	1 (3.4)	0 (0)	29	1542	Low grazing

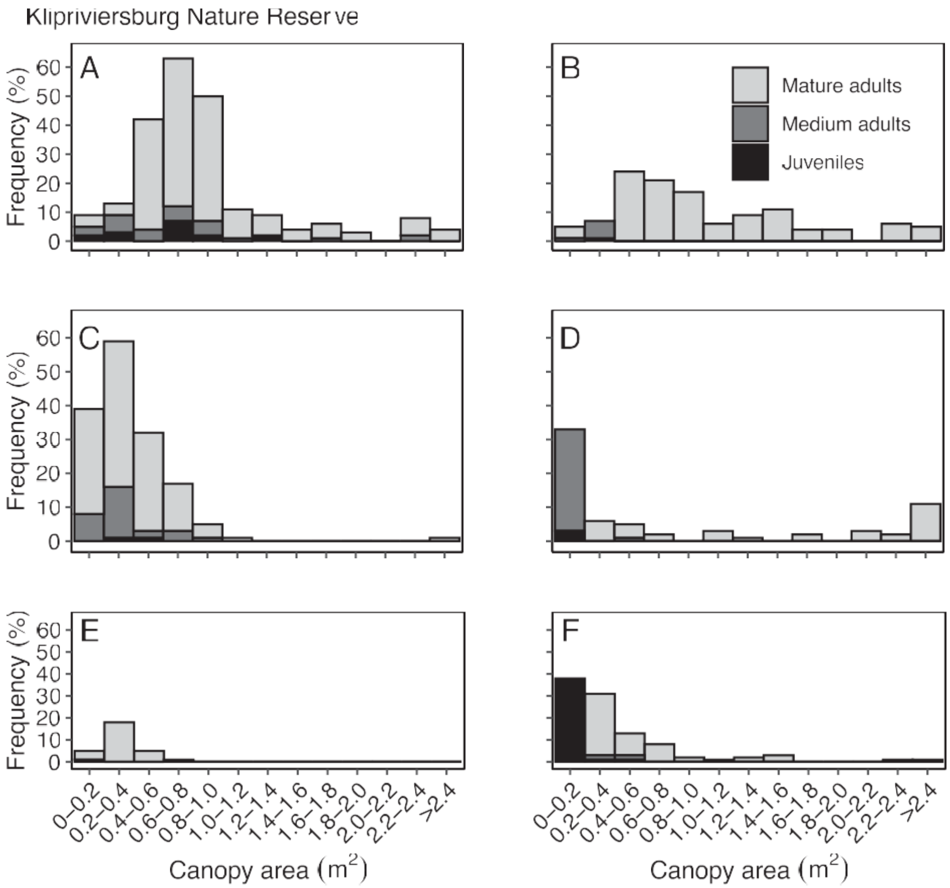

Fig. 1. Canopy area (m^2) size frequency distribution of *Seriphium plumosum* at the top (A, B), middle (C and D) and bottom (E and F) ridge at the Klipriviersburg Nature Reserve (A, C and E) and Amathole Hogsback plantation (B, D and F).