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Seed germination of cultivated, naturalised and floristically traded *Cortaderia* species in South Africa

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ABSTRACT

Cortaderia species (commonly known as pampas grass), *C. jubata* and *C. selloana,* have become invasive in South Africa. The National Environmental Management: Biodiversity Act (NEM:BA) (Act 10 of 2004, updated 2020): Alien and Invasive Species regulations (A&IS regs) forbids the trade of pampas grass. The growing popularity of pampas grass inflorescences for home décor and events is a concern. This study aimed to test the seed viability of cultivated, naturalised, and traded inflorescences of *Cortaderia* in South Africa to determine whether the trade in inforescences might lead to viable seeds being dispersed and thereby increasing opportunities for these species to invade. Seeds were collected from inflorescences of cultivated and naturalised populations from across nine provinces, and traded inflorescences were bought from retail and informal traders. Seed viability and germination of seeds of both species, cultivated, naturalised, formal and informally traded inflorescences were assessed using: (1) triphenyl tetrazolium stain, (2) germination trials in a growth chamber (triplicate repeats, randomised placement), and (3) germination trials in potting soil in a greenhouse (randomised complete plot design). There was no significant difference between *C. selloana* (71.67 %, 68.89 %, 79.15 %) and *C. jubata*'s (57.00 %, 52.62 %, 62.54 %) ($P = 0.277$, $P = 1.00$, $P = 0.362$) seed viability and germination across triphenyl tetrazolium stain, growth chamber and greenhouse trials, respectively. Seed viability of cultivated and naturalised *Cortaderia* inflorescences differed significantly to formally traded inflorescences ($P = 0.022$ and $P = 0.018$, respectively). Naturalised populations of both *Cortaderia* species had a significantly higher germination (65.69 %, 74.35 %) than the formally (25.00 %, 5.33 %) and informally traded populations (28.75 %, 35.56 %) under growth chamber and greenhouse experiments, respectively. These results suggest that traded inflorescences of *Cortaderia* might often not be sterile, as evident from the observed seed viability and germination success of seeds from traded inflorescences and thus promote invasion and further spread of *Cortaderia* species. Effective management of *Cortaderia* species must focus on enforcing legislation to stop this pathway of spread, and reduce new seed recruitment, particularly during their short flowering season, and also explore more options to effectively treat inflorescences.

1. Introduction

The success of invasive alien plant (IAP) species depends largely on the biological attributes of the species, appropriate environmental conditions (Lonsdale, 1999; Gioria et al., 2018) and human factors related to introduction pathways (Pyšek et al., 2020). Seed germination, large seed production and the ability to germinate and grow in a broad range of environmental conditions can lead to successful establishment, growth and further expansion of many successful invaders (Van Kleunen et al., 2016). Production of large quantities of seeds by alien plants results in a greater number of individual colonisation opportunities (Lake and Leishman, 2004). Understanding the dispersal mechanisms of these seeds is crucial to effective management (Leung et al., 2002). Wind dispersed species commonly have light structures on their seeds that can

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act as wings, plumes or balloons, allowing them to travel long distances and land in a wide range of new habitats (Thomson et al., 2011; Planchuelo et al., 2016). Soomers et al. (2013) reported that plants whose primary dispersal method is wind may also be effectively dispersed by water. All these traits confer weediness and dispersal success for IAPs.

The global ornamental horticultural trade has expanded significantly since the 1950s (Hammond et al., 2023) and is characterised by the deliberate introduction of alien species to many areas outside their native range (Mack, 2003). Mack and Enberg (2002) found that 65 % of IAPs introduced into Australia between 1971 and 1995 were ornamentals. In addition, Dehnen-Schmutz et al. (2007) showed that plant nurseries generally sell more alien than native species and that prices for alien species are often significantly lower than those of native species. This has resulted in the plant trade being a key pathway for the introduction of IAPs (Faulkner et al., 2020). In Africa, the ornamental plant trade has also been shown to be a leading cause of alien plants escaping cultivation (Faulkner et al., 2016, 2020), and as a result the number of IAPs naturalising in native ecosystems is steadily increasing (Faulkner et al., 2020; Van Wilgen et al., 2020; IPBES 2023). The ornamental horticultural industry recognises the need for action against the negative impacts of IAPs and has developed techniques to induce sterility for certain popular ornamentals with a high risk of spreading (Freyre et al., 2016; Datta et al., 2020; Chetty et al., 2024). For example, the triploid *Hibiscus syriacus* L. cultivar "Diana" sets very little fruit, which contrasts with the diploid species that sets a large amount of fruit (Niemiera and Holle, 2009). Efforts to breed sterile plant cultivars are still rare; therefore, there is still a limited number of ornamental alien species for which sterile cultivars have been developed (Bechtloff et al., 2019).

Poaceae is arguably the most successful graminoid family in terms of its global occurrence in almost all open ecosystems with angiosperms, its ecological dominance in many ecosystems, and high species richness (Macphail and Hill, 2002; Blair et al., 2014). Linder et al. (2018) suggested that the success of grasses is best understood in the context of their capacity to colonise, persist, and transform environments. There have been attempts to develop sterile cultivars of invasive ornamental grasses. According to Dorner (2002) and Granite (2007), a combination of an annual growth form and sterility can result in plants that survive only one growing season. However, such sterility is not always permanent. For example, Beyers (2008) documented the sterile annual hybrid grass variety Regreen (*Triticum aestivum* L. × *Elytrigia elongata* (Host) Nevski) persisting into a second growing season after failing to die at the end of the first season. Both *T. aestivum* × *E. elongata* and Quickguard (*Triticum* sp. × *Secale* sp.) are described as "sterile", yet it was noted that they both produce viable seed when exposed to pollen from wheat (*T. aestivum*) or other *Tritosecale* spp. respectively (Granite, 2007). Mooris and Schupp (2009) also investigated whether the sterile annual hybrid cereal grasses were sterile. They found that both types of grass produced viable seeds under greenhouse conditions, indicating a lack of true sterility, which may contradict management goals.

Cortaderia jubata (Lemoine) Stapf and *C. selloana* (Schult. & Schult. f.) Asch. & Graebn. have been widely cultivated around the world through the nursery trade, and their plumes are commonly sold as decorative dried flower arrangements (Oakes, 2012; Roldão Almeida et al., 2023). They were the only *Cortaderia* species introduced into South Africa and were cultivated for several purposes, including for ornamental trade, erosion control, creating windbreaks and mine dump stabilisation (Henderson, 2020; Sutton et al., 2021). However, they have long since escaped cultivation and now invade a range of habitats including grasslands, roadsides, wastelands, rivers and seasonally wet habitats (Henderson, 2020; Sutton et al., 2021). The leaves of *Cortaderia* species are very abrasive with sharp and cutting edges, making it undesirable as food or shelter to birds and other wildlife as they can cause physical harm to those animals (DiTomaso et al., 2010). *Cortaderia* abundantly produce small wind-dispersed seeds which are also well-suited to dispersal by water (Parsons and Cuthbertson, 2001; DAISIE, 2009). For *C. jubata* and *C. selloana*, germination generally occurs in spring and seedlings will establish if there is adequate moisture and light (DiTomaso et al., 2010; Lázaro-Lobo et al., 2024). Once naturalised, *Cortaderia* develops strong tussocks with vigorous basal growth. There have been sterile cultivars of pampas grass developed such as Pumila (*Cortaderia selloana* Schult. 'Pumila') (Robacker, 1993; Ahmad et al., 2006). However, this cultivar is now known to produce many viable seeds (Ahmad et al., 2006). *Cortaderia jubata* and *C. selloana* are very similar in appearance and can be difficult to distinguish morphologically by non-experts, particularly when not in flower (DiTomaso et al., 2010). The primary physiological difference between *C. jubata* and *C. selloana* is their reproductive strategy. *Cortaderia jubata* is apomictic, having only female flowers that are able to set viable seed without fertilisation (Stanton and DiTomaso, 2004). *Cortaderia selloana* reproduces sexually and is functionally dioecious, and can also reproduce asexually by spreading through rhizomes and tillers (Stanton and DiTomaso, 2004). Little information is known about the seed biology and germination characteristics of *Cortaderia* species in South Africa. Understanding the characteristics of *Cortaderia* species' reproductive biology is important because seeds are the primary pathway for spread (DiTomaso et al., 1999). In addition, knowledge of seed germination of IAPs is crucial for predicting future spread and developing control measures (Gioria et al., 2018). Few control strategies are available for *Cortaderia* in South Africa and no biological control programmes have yet been initiated. The available control strategies include mechanical removal and herbicide applications. However, these control strategies are only effective for restricted or small populations as they are costly and need repeated treatments (Lázaro-Lobo et al., 2024).

In the past, exemptions were made to allow both species to be traded, under the condition that the cultivars sold in nurseries were sterile (Department of Environmental Affairs 2014). Two cultivars of *Cortaderia*, Silver Stripe and Gold Band, were listed on the National Regulations as sterile (Chetty et al., 2024) and were exempted to allow for trade. However, this trade was recognised as problematic as there was a rapid increase of *Cortaderia* species populations between 2000 and 2016 and no formal process for proving sterility (Henderson and Wilson, 2017). When the National Regulations were updated in 2020, the trade of both species was banned in South Africa (Wilson and Kumschick, 2024) and nurseries complied by stopping all sales of the plants. Although the national regulations forbid the trade of *Cortaderia*, the continuing popularity of *Cortaderia* inflorescences for home decorations and special events is of concern, and the inflorescences are still being sold through retail and vendors (Sutton et al., 2021). Many suppliers often acknowledge the environmental risk of selling *Cortaderia* inflorescences by communicating to customers that they sterilise the seeds; providing statements such as, 'our pampas has been heat-bleached, which kills the seeds (preventing it from propagating or spreading)' (Bloom Space, 2024). However, other suppliers are often unaware of these National Regulations and therefore do not take any steps to reduce the spread of seeds.

The aim of this study was to explore seed viability in inflorescences from cultivated, naturalised and traded populations of *Cortaderia* species in South Africa. Understanding seed viability in these different populations will give insight into how the species are spreading and whether the trade of inflorescences is another pathway of introduction to new habitats. Lastly, the historical trade of supposedly 'sterile' *Cortaderia* cultivars will be explored to ascertain whether any populations exhibit such sterility.

2. Material and methods

2.1. Site and sample collection

Naturalised populations refer to populations that are self-sustaining in habitats that have no signs of having been intentionally planted. For naturalised populations, inflorescences of two *Cortaderia* species were collected from 21 populations across the nine provinces of South Africa

(Eastern Cape, Free State, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, North West, Northern Cape and Western Cape) from February 2023 to May 2024 (see supplementary information Fig. 1). Inflorescences were collected from mature plants (basal diameter > 1 m) with more than two inflorescences. The inflorescences were kept in separate paper bags until seed removal. Each inflorescence bag was initially categorised into species according to their inflorescence colour (white for *C. selloana* and pink for *C. jubata*) and later verified using genetic analyses (Mbele, 2024). A total of 73 inflorescences, for both species, were collected from naturalised populations. From the 73 inflorescences, only 28 had seeds, seven *C. jubata* and 21 *C. selloana* inflorescences. Similar to collections from naturalised populations, inflorescences of the two *Cortaderia* species were collected from private properties to represent cultivated populations across the nine provinces of South Africa. Cultivated populations thus refer to plants that were intentionally planted in private properties such as home gardens. Since cultivated populations were in private properties, the main challenge was access, and only 11 inflorescences from cultivated populations were collected. From the 11 inflorescences, only four had seeds and all were *C. selloana* (Table 1).

Formally traded inflorescences refers to inflorescences that were sold in commercial stores, including florists, online shops and through social media platforms, which often claimed to have bleached flowers, but this was not always stated. Formal traders were identified by carrying out an exhaustive search of online trade by searching the words 'pampas' and/or 'cortaderia' using online search engines. All search results relevant to South Africa were checked and inflorescences were purchased from 15 known retailers. In addition, inflorescences were purchased from florist shops according to availability. No nurseries were found to be selling pampas grass flowers.

Informal traders refer to traders selling pampas inflorescences on the streets and who did not claim to treat the flowers but generally collected from naturalised populations themselves. Informal traders were identified on the streets or roadsides where they were observed selling pampas grass. For both formally and informally traded *Cortaderia* inflorescences, a population is represented by a supplier (Table 1). A minimum number of one inflorescence was bought per supplier and species, depending on how they were sold (i.e. some suppliers did not sell individual inflorescences but grouped them into a bouquet). The prices of these inflorescences ranged from R50 to R595, depending on whether its from an informal or formal trade, formal traders being more expensive than informal traders. In total, inflorescences were bought from nine informal traders and ten formal traders, however only eight and five inflorescences contained seeds respectively. Inflorescences were bought from Gauteng and KwaZulu-Natal because we could not find any traders in the other provinces. However, seeds were only found on inflorescences bought from traders in Gauteng. For both naturalised and traded populations, all inflorescences had no seeds outside of the flowering season.

As a control of our methods for testing seed viability and germination, an alternative grass species was used as there are no commercially sold seeds of *Cortaderia* in South Africa. Lemongrass, *Cymbopogon citratus* (DC.) Stapf., acted as a control for experiments because it was commercially sold under the established brand MayFord and, therefore, ensured to be viable. In addition, *C. citratus* has seeds similar in size to *Cortaderia*, is also a tall-statured grass and germinates under the same temperatures as *Cortaderia* (Francisco et al., 2011).

The seeds of all *Cortaderia* inflorescences were removed from the panicles using a sieve with 0.5 cm diameter holes and stored at room temperature in seed envelopes. As in other experiments for the *Cortaderia* genus, the seeds were not stored longer than one year (Stanton and DiTomaso, 2004; Drewitz and DiTomaso, 2004); experiments were carried out four months after collection. The experiments were carried out in Spring when the average temperature in Qwaqwa is 23 °C and relative humidity is 25 %. The viability of seed collected from each plant was assessed through three methods: using a stain specific for testing the

Table 1
The *Cortaderia* inflorescences included in this study collected from naturalised populations or bought from commercial (formal) and informal traders in South Africa. Only inflorescences that had mature seeds are included here.

	Source	Species	GPS coordinates/ trade	Town/ supplier
Cultivated	Cultivated	*1. C. selloana*	−32.2197; 25.7114	Cradock, Eastern Cape
	Cultivated	2. *C. selloana*	−26.1537; 27.9823	Johannesburg, Gauteng
	Cultivated	3. *C. selloana*	−26.1889; 27.9562	Johannesburg, Gauteng
	Cultivated	4. *C. selloana*	−34.05481; 18.43293	Tokai, Western Cape
Naturalised	Naturalised	*5. C. selloana*	−33.7285; 25.7654	Port Elizabeth, Eastern Cape
	Naturalised	6. *C. selloana*	−33.7285; 25.7654	Port Elizabeth, Eastern Cape
	Naturalised	7. *C. selloana*	−33.7285; 25.7654	Port Elizabeth, Eastern Cape
	Naturalised	8. *C. selloana*	−33.7285; 25.7654	Port Elizabeth, Eastern Cape
	Naturalised	9. *C. jubata*	−26.153; 27.9823	Johannesburg, Gauteng
	Naturalised	10. *C. jubata*	−261,533; 27.9821	Johannesburg, Gauteng
	Naturalised	11. *C. selloana*	−26.153; 27.9825	Johannesburg, Gauteng
	Naturalised	12. *C. selloana*	−26.154; 27.9825	Johannesburg, Gauteng
	Naturalised	13. *C. selloana*	−26.1681; 27.9612	Johannesburg, Gauteng
	Naturalised	14. *C. jubata*	−26.1533; 27.9821	Johannesburg, Gauteng
	Naturalised	15. *C. jubata*	−26.1711; 27.9023	Johannesburg, Gauteng
	Naturalised	16. *C. jubata*	−26.1712; 27.9025	Johannesburg, Gauteng
	Naturalised	17. *C. selloana*	−26.1709; 27.9023	Johannesburg, Gauteng
	Naturalised	18. *C. selloana*	−26.1017; 27.9526	Johannesburg, Gauteng
	Naturalised	19. *C. jubata*	−26.1312; 27.9116	Johannesburg, Gauteng
	Naturalised	20. *C. jubata*	−26.1011; 27.9571	Johannesburg, Gauteng
	Naturalised	21. *C. selloana*	−26.1315; 27.9118	Johannesburg, Gauteng
	Naturalised	22. *C. selloana*	−26.189; 27.9562	Johannesburg, Gauteng
	Naturalised	23. *C. selloana*	−29.2006; 27.4635	Ladybrand, Free State
	Naturalised	24. *C. selloana*	−29.2008; 27.4635	Ladybrand, Free State
	Naturalised	25. *C. selloana*	−29.201; 27.4634	Ladybrand, Free State
	Naturalised	26. *C. selloana*	−29.2012; 27.4632	Ladybrand, Free State
	Naturalised	27. *C. selloana*	−29.2013; 27.4632	Ladybrand, Free State
	Naturalised	28. *C. selloana*	−29.2015; 27.4631	Ladybrand, Free State
Traded	Informal	29. *C. selloana*	−26.2056; 28.0222	Fordsburg, Gauteng
	Informal	30. *C. jubata*	−26.2056; 28.0222	Fordsburg, Gauteng
	Informal	31. *C. selloana*	−26.20227; 28.04363	Johannesburg, Gauteng
	Informal	32. *C. selloana*	−26.195246; 28.034088	Johannesburg, Gauteng
	Informal	33. *C. selloana*	−26.204103; 28.047305	Johannesburg, Gauteng
	Informal	34. *C. selloana*	−26. 179,356; 28.03673	Johannesburg, Gauteng
	Informal	35. *C. selloana*	−26.2348; 28.1766	Germiston, Gauteng

(*continued on next page*)

Table 1 (*continued*)

	Source	Species	GPS coordinates/ trade	Town/ supplier
	Informal	36. *C. jubata*	−26.2348; 28.1766	Germiston, Gauteng
	Formal	37. *C. selloana*	−26.2842; 28.2378	Germiston, Gauteng
	Formal	38. *C. jubata*	−26.2842; 28.2378	Germiston, Gauteng
	Formal	39. *C. selloana*	Truffle	Online, website
	Formal	40. *C. selloana*	−26.1841; 28.1956	Marlands, Germiston, Gauteng
	Formal	41. *C. jubata*	−26.1841; 28.1956	Marlands, Germiston, Gauteng

viability of embryos in seeds (tetrazolium test); radicle protrusion in vitro in a controlled growth chamber (rapid germination); and seedling emergence in greenhouse conditions (germination in greenhouse).

2.2. Seed germination trials and data collection

2.2.1. Tetrazolium tests

To test viability, ten seeds per plant sampled (Table 1) were soaked in distilled water for 24 h, then soaked in a 1 % solution of 2,3,5 triphenyl tetrazolium chloride for 24 h. The seeds were then examined using a dissecting microscope to observe staining. The seeds were considered viable if the entire embryo was stained red and the endosperm remained unstained (see supplementary information Fig. S2). The seeds were considered non-viable if the embryo did not stain, only a part of the embryo stained, the stain was light pink, or the endosperm stained red in addition to or instead of the embryo (Drewitz and DiTomaso, 2004). Ten replicates of ten seeds from the control species were used for comparison to the seeds of the two *Cortaderia* species.

2.2.2. Rapid germination in a growth chamber

For the rapid germination tests, 20 seeds per plant, including the control, were placed in petri dishes on top of a disc of Munktell Filtrak™ paper saturated with 5 ml of distilled water. The petri dishes were replicated three times ($n = 60$ seeds per plant) and placed in an in vitro PROLAB incubator in a randomised placement. The temperature was set at 27 °C but would drop down to 26 °C on cold days or go up to 28 °C on hot days. Water was added to the dishes in 2 ml increments as needed to keep the filter papers moist. Seeds were considered germinated when the radicle was clearly visible (see supplementary information Fig. S3; Domènech and Vilà, 2008). Germination was recorded daily until seeds stopped germinating, and seeds were removed from the petri dishes once germinated.

2.2.3. Germination in a greenhouse

Germination pots (ranging from 8 – 18 cm) with drainage holes at the bottom were half-filled with Culterra® professional potting mix soil, and the seeds were buried at the surface of the soil in each pot (see supplementary information Fig. S4A). For each plant, three pots (replicates), with 15 seeds per pot, including the control, were established ($n = 129$ pots). Germination pots were placed in a greenhouse with a temperature of 27 °C, following a randomised complete block design at the University of the Free State, Qwaqwa campus. The pots were re-randomised every two days to avoid greenhouse position effects. Pots were watered daily with 50 ml of distilled water. Germination was also monitored and recorded daily, until seeds stopped germinating. Seeds were considered germinated when leaf emergence was clearly visible but were not removed from the pots (see supplementary information Fig. S4B).

2.3. Data analysis

All statistical analyses were performed using IBM SPSS version 29, and graphics were produced in IBM SPSS or in R (version 4.3.1, R Core Team, 2023) using the package "ggplot2" (Wickham, 2016). For the tetrazolium test, the number of stained seeds observed under a dissecting microscope was recorded as the proportion of viable seeds for each plant for each of the three species. The proportion data were arcsine-squareroot transformed and tested for normality using Shapiro Wilk's Normality test. The data for comparing species were not normally distributed ($P = 0.03$) and thus a Kruskal Wallis H-test with pairwise comparison post-hoc tests with Bonferreni correction was used to test for significant differences between species. The species were treated as the predictor (independent) variable and the response (dependant) variable was the transformed proportion of viable seed. For comparing seed viability with source as the predictor (cultivated, naturalised, formal and informally traded inflorescences), the data were transformed and tested for normality as described above. The data were normally distributed ($P = 0.118$) and tested using Levene's test for homogeneity of variance (variances were equal, $P > 0.05$), and sources compared using a one-way ANOVA with a Tukey HSD post-hoc test.

For germination in the growth chamber and greenhouse, the daily average germination was calculated from the three replicates for each inflorescence, and the cumulative average and standard error proportion of seeds germinated over all inflorescences of each species or source (cultivated, naturalised, formally and informally traded) plotted over time. The averaged overall proportions of germinated seeds per inflorescence were compared statistically using proportional data that were arcsine-squareroot transformed and tested for normality using Shapiro Wilk's Normality test. The data for comparing species and source (cultivated, naturalised, formally and informally traded) for both growth chamber and greenhouse were not normally distributed (species: $P = 0.020$; source: $P = 0.044$ and species: $P < 0.001$; source: $P < 0.001$, respectively) and thus non-parametric statistical tests were performed on these data. The species/ source was treated as the predictor (independent) variable and the response (dependent) variable was the transformed proportion of germinated seed using Kruskal-Wallis H-tests with pairwise comparison post-hoc tests with Bonferreni correction to test for significant differences.

3. Results

Under all three experiments, cultivated, naturalised and traded *Cortaderia* seeds showed viability, except for one naturalised *C. jubata* population. Under greenhouse conditions, germination of traded *Cortaderia* seeds was greatly reduced. Timing to find matured seeds still attached on the inflorescences is very narrow. Seeds of *C. jubata* are mature from late February to early March, while *C. selloana* seeds are mature from late March to early April. The short period to find mature seeds for each species resulted in a low number of seeds being collected (Appendix).

3.1. Tetrazolium tests

The control (*C. citratus*) had an average ± SE of 79.10 ± 8.90 % seed viability while *C. jubata* and *C. selloana* had an average of 57.00 ± 8.57 % and 71.67 ± 6.58 % seed viability, respectively. Seed viability differed significantly among species ($H = 7.387$; df = 2; $P = 0.025$) with seed viability of the control significantly higher compared to *C. jubata* ($P = 0.020$) but not significantly different to *C. selloana* ($P = 0.493$) (Fig. 1). There was no significant difference in the average seed viability between *C. selloana* and *C. jubata* ($P = 0.277$). Seed viability differed significantly among sources ($F = 4.904$; df = 3, 37; $P = 0.006$); with cultivated and naturalised *Cortaderia* inflorescences having a significantly higher average ± SE seed viability (80.00 ± 10.80 % ($P = 0.022$) and 64.17 ± 5.86 % ($P = 0.018$), respectively) compared to the formally traded

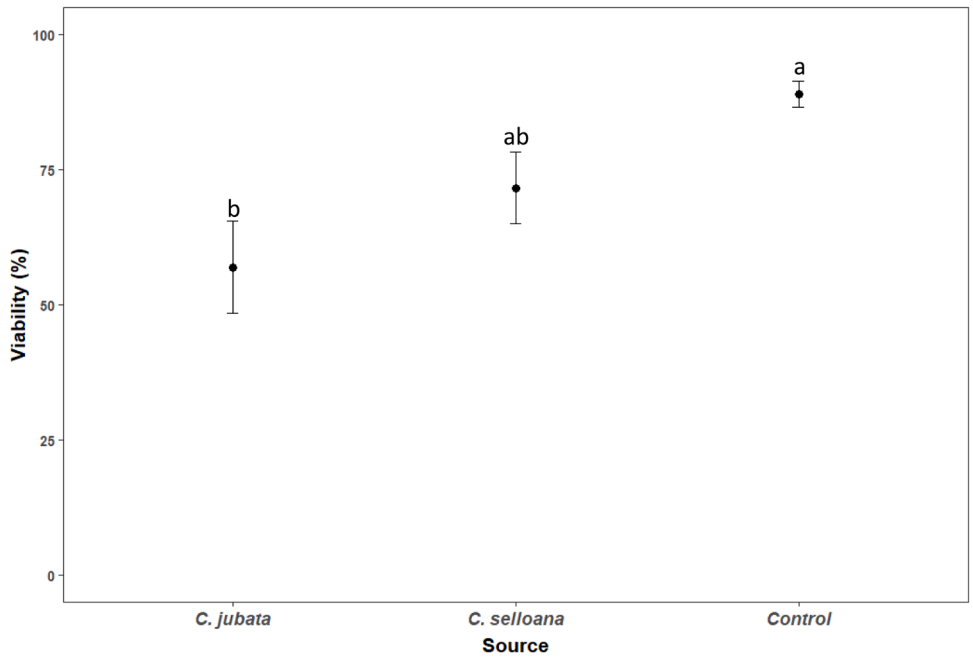

Fig. 1. Mean ± SE seed viability following tetrazolium staining of two *Cortaderia* species (*C. jubata* and *C. selloana*) ($n = 10$) present in South Africa. The dots represent the mean. Seed viability was compared using a Kruskal Wallis Test followed by a pairwise comparison posthoc test with a Bonferroni correction ($P = 0.025$); different letters above the bars represent significant differences.

Cortaderia inflorescences (20.00 ± 5.48 %) but not significantly different to the informally traded inflorescences (42.50 ± 11.30 %) (Fig. 2).

3.2. Rapid germination in a growth chamber

For rapid germination, the control (*C. citratus*) started germinating on day three while the two *Cortaderia* species started germinating on day four, and all seeds of all species stopped germinating after 44 days (Fig. 3). The control had an average ± SE of 93.33 ± 3.33 % seed germination while *C. jubata* and *C. selloana* had an average of 52.62 ± 9.55 % and 68.89 ± 4.45 %, respectively. Average germination differed significanty among species ($H = 8.086$; df = 2; $P = 0.018$), with average germination of the control significantly higher compared to *C. jubata* ($P = 0.015$) and *C. selloana* ($P = 0.041$), but there was no statistical difference between the two *Cortaderia* species ($P = 1.00$) (Fig. 3). Cultivated and naturalised *Cortaderia* populations had an average ± SE of 59.58 ± 6.91 % and 65.69 ± 2.97 % germination, respectively, while

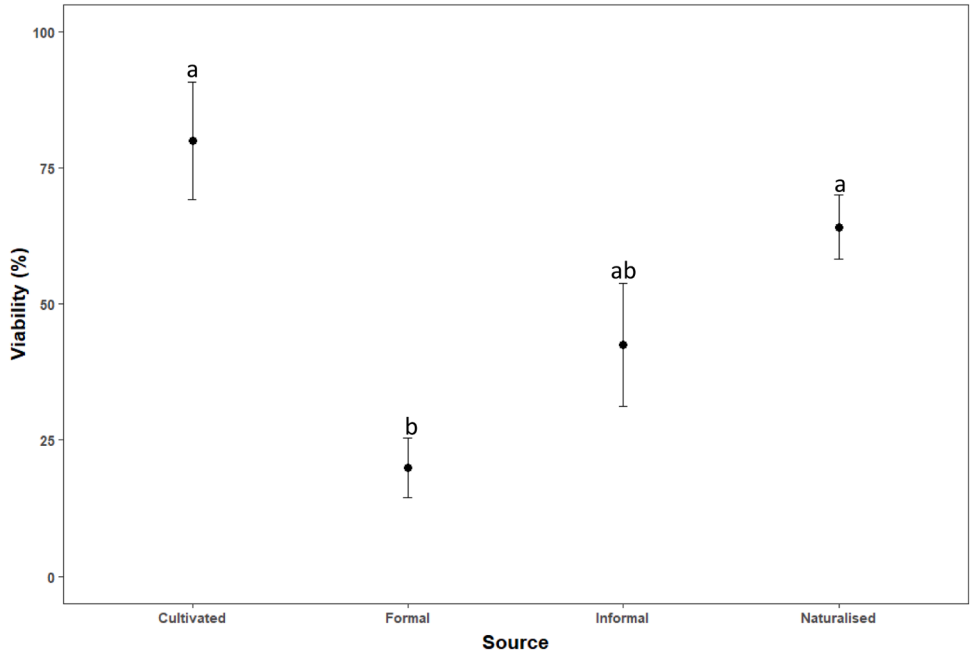

Fig. 2. Mean ± SE seed viability of the cultivated, naturalised, formally and informally traded *Cortaderia* species in South Africa ($n = 10$). The dots represent the mean. Seed viability was compared using an Analysis of Variance followed by a Tukey HSD posthoc test ($P = 0.006$); different letters above the bars represent significant differences.

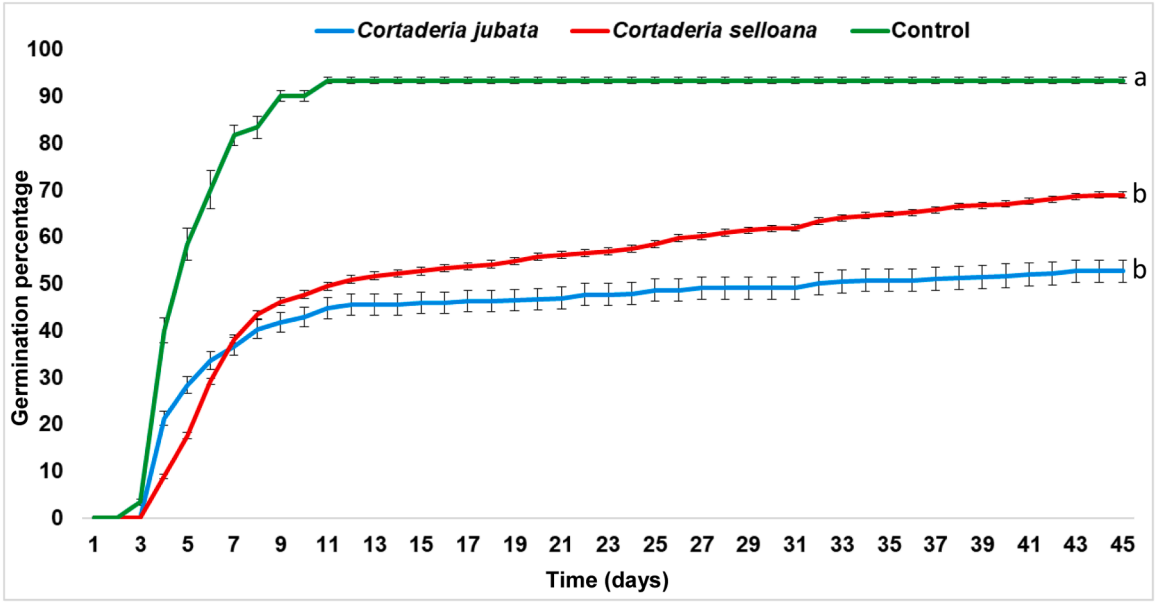

Fig. 3. Mean ± SE rapid cumulative seed germination of *Cortaderia jubata* and *C. selloana* present in South Africa. Germination rate was compared using a Kruskal Wallis Test followed by a pairwise comparison posthoc test with a bonferroni correction ($P = 0.018$); different letters on the side represent significant differences.

formal and informally traded *Cortaderia* populations had a germination of 25.00 ± 5.60 % and 28.75 ± 4.89 %, respectively, with germination differing significantly among the different sources ($H = 23.030$ df = 3; $P < 0.001$; Fig. 4). The average seed germination from naturalised *Cortaderia* populations was significantly higher compared to the formally ($P = 0.003$) and informally traded *Cortaderia* populations ($P = 0.001$). There was no statistical difference between cultivated and naturalised ($P = 1.00$), informally traded ($P = 0.293$) and formally traded *Cortaderia* populations ($P = 0.286$).

3.3. Germination in a greenhouse

For germination trials under greenhouse conditions, *C. citratus* (control) started germinating on day six while the two *Cortaderia* species started germinating on day seven. All seeds of the control, *C. jubata,* and *C. selloana* stopped germinating after 11, 26, and 29 days, respectively. The control had an average of 48.89 ± 5.88 % seed germination while *C. jubata* and *C. selloana* had an average of 62.54 ± 13.51 % and 79.15 ± 3.74 %, respectively. The seed germination was statistically similar for all three species ($H = 5.575$; df = 2; $P = 0.062$; Fig. 5). Cultivated and naturalised *Cortaderia* populations had 78.89 ± 5.56 % and 74.35 ± 5.14 % seed germination, respectively, while formal and informally traded *Cortaderia* populations had a germination of 5.33 ± 3.19 % and 35.56 ± 9.06 %, respectively. Germination differed significantly among sources ($H = 19.841$; df = 3; $P < 0.001$; Fig. 6). The average seed germination from cultivated *Cortaderia* populations was significantly higher compared to the formally ($P = 0.002$) and informally traded *Cortaderia* populations ($P = 0.007$). There was no statistical difference

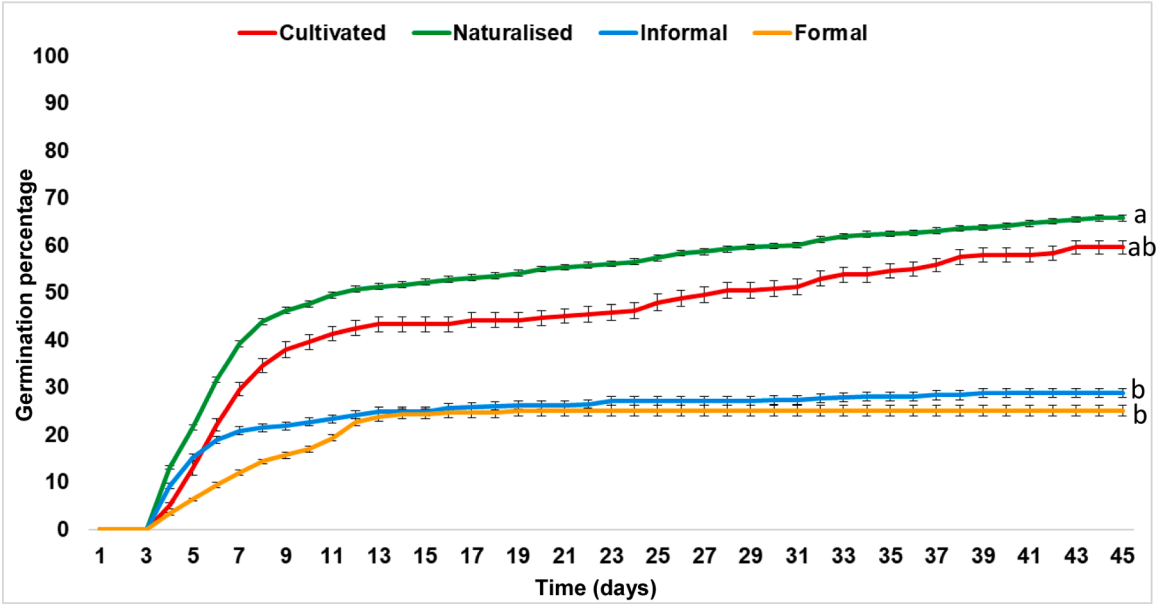

Fig. 4. Mean ± SE rapid cumulative seed germination of cultivated, naturalised, formally and informally traded inflorescences of *Cortaderia* in South Africa. Germination rate was compared using a Kruskal Wallis Test followed by a pairwise comparison with a Bonferroni correction ($P < 0.001$); different letters on the side represent significant differences.

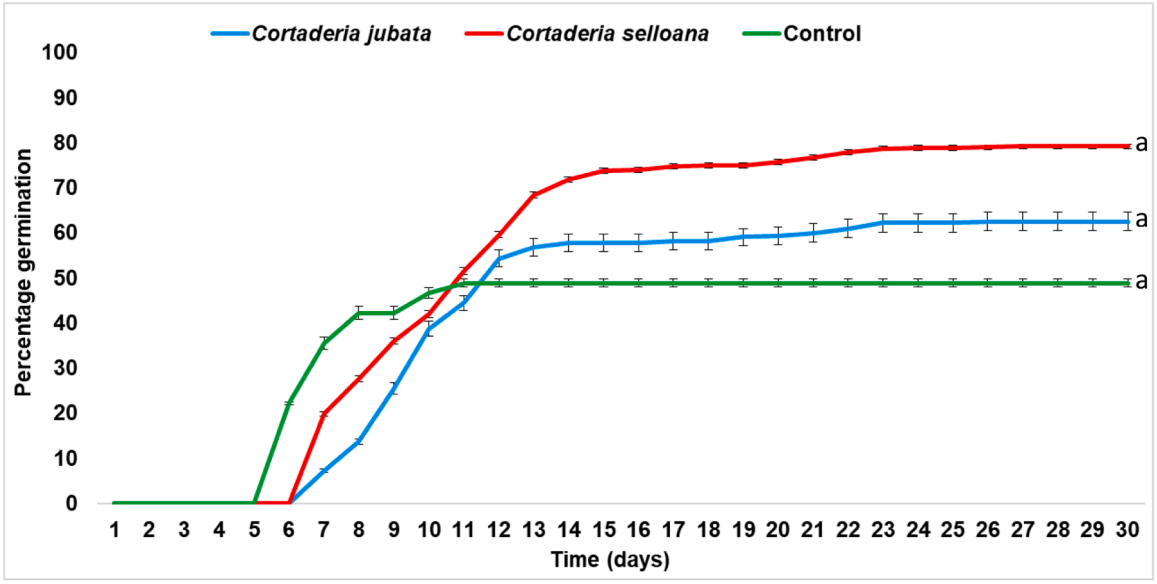

Fig. 5. Mean ± SE cumulative seed germination (in a greenhouse) of *Cortaderia jubata* and *C. selloana* present in South Africa. Germination rate was compared using a Kruskal Wallis Test followed by a pairwise comparison posthoc test with a Bonferroni correction ($P = 0.062$); different letters on the side represent significant differences.

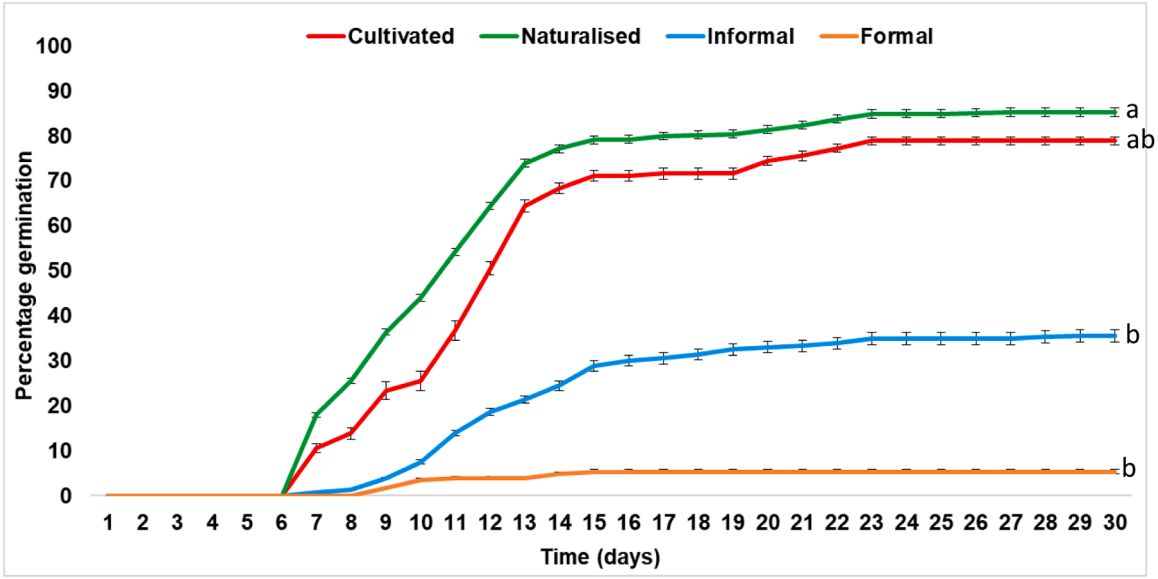

Fig. 6. Mean ± SE cumulative seed germination (in a greenhouse) of cultivated, naturalised, formally and informally traded inflorescences of *Cortaderia* in South Africa. Germination rate was compared using a Kruskal Wallis Test followed by a pairwise comparison posthoc test with a Bonferroni correction ($P < 0.001$); different letters on the side represent significant differences.

between cultivated and naturalised ($P = 1.00$), informally traded ($P = 0.254$) and formally traded *Cortaderia* populations ($P = 0.080$).

4. Discussion

Overall, some inflorescences that were tested that are sold as 'sterile' had significant numbers of viable seeds and germination, showing not enough evidence of seed sterility. However, one naturalised population of *C. jubata* had zero seed viability and germination and some inflorescences collected did not have seeds. The seed viability and germination of *C. selloana* was higher than that of *C. jubata* for all three experimental methods. Cultivated and naturalised *Cortaderia* populations showed higher seed viability and germination than the formally and informally traded *Cortaderia* across all three experimental methods. In addition, an average of 69.24 %, 70.02 %, 32.16 % and 15.17 % seeds from cultivated, naturalised, informally and formally traded populations, respectively, germinated, indicating that the threat of *Cortaderia* spreading is not only from wind-dispersed seeds from naturalised populations but from trade as well. Based on these results, seed viability and germination of *C. selloana* is higher than that of *C. jubata* under different germination methods. This finding may provide an explanation for its more widespread distribution in South Africa compared to *C. jubata*. The role of germination traits as determinants of species invasiveness indicates that 'germination rate' is positively associated with the 'establishment/spread' and/or 'abundance/impact' of invasive species (Colautti et al., 2006). A study by Bacchetta et al. (2010) found that *C. selloana* seeds germinated at a variety of incubation temperatures (i.e., 15 °C, 20 °C, 25 °C, 30 °C). Lázaro-Lobo et al. (2024) showed that

the minimum temperature for *C. selloana* to germinate is 10 °C, showing a high tolerance for low temparatures, which might also contribute to its high germination and invasion. This observation together with diverse environmental conditions in South Africa leads to the conclusion that *C. selloana* has high invasion potential. In contrast, *C. jubata* occurs mainly to the northern areas of the country and is spreading by producing wind dispersed seeds, of which only 20 to 30 % germinate when exposed to light (Drewitz and DiTomaso, 2004). In addition, *C. jubata* seeds do not persist under natural conditions after six months (Drewitz and DiTomaso, 2004). Populations of *C. jubata* consist of entirely female plants that produce seeds asexually, resulting in seeds that are genetically identical to the parent plant (Stanton and DiTomaso, 2004). A study by Drewitz and DiTomaso (2004) found no significant differences between the percentages of germinable and viable seeds, indicating that *C. jubata* does not have primary dormancy. Roldão Almeida et al. (2024) studied the morphological and reproductive traits in female and hermaphrodite plants of *C. selloana* and found significant differences regarding reproductive traits of female and hermaphrodite plants but no significant differences in morphological traits. Their results also found that female plants are largely responsible for the dispersal of the species, while hermaphrodite plants primarily serve as pollen donors, which might explain the germination success of *Cortaderia* species in South Africa.

There has been an increasing focus on trying to develop cultivars and hybrids of many ornamental plants that are less invasive (Datta et al., 2020). Until recently, sterile cultivars of *Cortaderia* were permitted to be sold in nurseries. As such, cultivated plants in gardens were expected to have zero to very little germination, as it was assumed they were grown from sterile cultivars. Naturalised populations were expected to have viable seeds as they are self-sustaining populations that likely would have had to have established from seeds due to a lack of intentional planting. However, there was no evidence of complete sterility in cultivated populations. Cultivated plants, collected from gardens, were found to have viable seeds suggesting that if these plants were bought from nurseries, it is unlikely that the cultivar was sterile. Hulme et al. (2018) and Van Kleunen et al. (2018) have shown that the introduction of alien plants as ornamentals in the horticulture industry is a major pathway for the introduction of IAPs globally. Results from these previous studies and the current study shows that the flower trade presents a route into South Africa for alien species and a potential mechanism for their spread within the country. These results also show that sterile cultivars in grasses needs to be clearly defined (Chetty et al., 2024), and hence banning of permits for sterile cultivars was a good management decision.

Seeds of traded inflorescences showed viability and germination across tri-phenyl tetrazolium stain, growth chamber, and greenhouse conditions. This suggests that the trade of inflorescences is an important pathway for the spread of these species in South Africa. Formal traders often indicated that they are aware of the problem of *Cortaderia* invasions in the country. Therefore, some traders outline that they use sterilising techniques such as bleaching methods to prevent them from propagating or spreading (Bloom Space, 2024; Happy Home, 2024). Furthermore, formal traders generally preserve flowers and keep them past their flowering season. Therefore, most seeds are likely to be lost during transportation and out of season storage. In contrast, informal traders are unlikely to take such measures to treat the seeds because they are not informed about the threat of these species and the legislation. They generally collect from naturalised populations and sell them directly, and only during the flowering period. The window period to find mature seeds on inflorescences is very short and seeds are easily blown by the wind, hence, seeds do not stay on inflorescences for long. According to Roldão Almeida et al. (2024), seeds of female plants are mature for 3 – 4 weeks from the onset of seed development and are dispersed by wind up to four months, but timings are influenced by weather conditions. This study also did not find any viable seeds attached to the inflorescences after three weeks of seed maturity. Therefore, this could explain why informal trade is more likely to be spreading viable seeds. Lastly, one of the main issues that came up during conversations with informal traders was that they are not aware of the legislation forbidding them from selling pampas grass. Roldão Almeida et al. (2023), when studying the public perceptions about invasive *Cortaderia* in Portugal and Spain, also found that few people were aware of the legislation that limits its use. Therefore, it is recommended that information on legislation be shared with traders to ensure they are aware of the threats of *Cortaderia* and what native alternatives could be used to trade instead to protect their livelihoods.

5. Conclusion

Overall, *Cortaderia* inflorescences had viable seeds within the flowering season in both naturalised and traded populations. This study established that despite the legislation being updated and forbidding the trade of *Cortaderia* species, the trade is continuing and is the most important pathway for their spread. Some inflorescences that are sold as 'sterile' showed seed viability and should be viewed as posing a risk and regulated as such. Moreover, this study found that informal traders need to be made aware of the current legislation prohibiting them from selling *Cortaderia.* Discovering this pathway of spread has important implications for the management of these alien species. Management should focus on enforcing legislation to stop the pathway of spread and encouraging florists to use native options. This study also recommends creating public awareness of the current legislation, as well as the risks of *Cortaderia* invasions. This study provides an important way to understand seed sterility of *Cortaderia* species in South Africa. However, the overall reproductive output of these different species and populations still need further assessment.

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Compliance with ethical standards

The study was approved by the Environmental and Biosafety Research Ethics Committee of University of the Free State (UFS-ESD2023/0041). Permits for restricted activities of alien species or listed invasive species in this research were approved by the Department of Forestry, Fisheries and the Environment (permit number: 50742230302103605).

CRediT authorship contribution statement

Thembelihle J. Mbele: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Sandy-Lynn Steenhuisen:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Stephanie L. Payne:** Writing – review & editing, Supervision, Formal analysis, Data curation. **Kim Canavan:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2025.09.009.

Appendix: The *Cortaderia* inflorescences of *C. jubata* and *C. selloana* collected from naturalised populations and bought from commercial and informal traders in South Africa

	Species	Town/ supplier	Source/ trade	Seeds
Naturalised	*C. jubata*	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	Seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. jubata	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. jubata	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. selloana	Cradock, Eastern Cape	Naturalised	No seeds
	C. jubata	Cradock, Eastern Cape	Naturalised	No seeds
	C. jubata	Cradock, Eastern Cape	Naturalised	No seeds
	C. jubata	Cradock, Eastern Cape	Naturalised	No seeds
	C. jubata	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	Seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	Seeds
	C. jubata	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. jubata	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	Seeds
	C. jubata	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	No seeds
	C. selloana	Port Elizabeth, Eastern Cape	Naturalised	Seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	Seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	No seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	Seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	Seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	No seeds
	C. jubata	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Johannesburg, Gauteng	Naturalised	Seeds
	C. selloana	Bultfontein, Free State	Cultivated	No seeds
	C. selloana	Bultfontein, Free State	Cultivated	No seeds
	C. selloana	Ladybrand, Free State	Naturalised	Seeds
	C. selloana	Ladybrand, Free State	Naturalised	Seeds
	C. selloana	Ladybrand, Free State	Naturalised	Seeds
	C. selloana	Ladybrand, Free State	Naturalised	No seeds
	C. selloana	Ladybrand, Free State	Naturalised	Seeds
	C. selloana	Ladybrand, Free State	Naturalised	Seeds

(*continued on next page*)

(*continued*)

	Species	Town/ supplier	Source/ trade	Seeds
	C. selloana	Ladybrand, Free State	Naturalised	Seeds
	C. selloana	Ladybrand, Free State	Naturalised	No seeds
	C. selloana	Clarens, Free State	Cultivated	No seeds
	C. selloana	Clarens, Free State	Cultivated	No seeds
	C. selloana	Durbanville, Western Cape	Naturalised	No seeds
	C. selloana	Durbanville, Western Cape	Naturalised	No seeds
	C. selloana	Durbanville, Western Cape	Naturalised	No seeds
	C. selloana	Simonstown, Western Cape	Naturalised	No seeds
	C. selloana	Stellenbosch, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	Seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Tokai, Western Cape	Naturalised	No seeds
	C. selloana	Spier, Western Cape	Naturalised	No seeds
	C. selloana	Spier, Western Cape	Naturalised	No seeds
	C. selloana	Bloemfontein, Free State	Cultivated	No seeds
	C. selloana	Bloemfontein, Free State	Cultivated	No seeds
	C. selloana	Bloemfontein, Free State	Cultivated	No seeds
Traded	*C. selloana*	Anonymous 1	Informal	Seeds
	C. jubata	Anonymous 1	Informal	Seeds
	C. selloana	Vendor 1	Informal	Seeds
	C. selloana	Vendor 2	Informal	Seeds
	C. selloana	Vendor 3	Informal	Seeds
	C. selloana	Vendor 4	Informal	Seeds
	C. selloana	Anonymous 2	Informal	Seeds
	C. jubata	Anonymous 2	Informal	Seeds
	C. selloana	Anonymous 3	Formal	No seeds
	C. selloana	Anonymous 4	Formal	Seeds
	C. jubata	Anonymous 4	Formal	Seeds
	C. selloana	Anonymous 5	Formal	Seeds
	C. selloana	Anonymous 6	Formal	Seeds
	C. jubata	Anonymous 6	Formal	Seeds
	C. selloana	Anonymous 7	Formal	No seeds
	C. selloana	Anonymous 8	Informal	No seeds
	C. selloana	Anonymous 9	Formal	No seeds
	C. selloana	Anonymous 10	Formal	No seeds
	C. selloana	Anonymous 11	Formal	No seeds

Data availability

The data presented in this study are available on request from the corresponding author.

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Supplementary data



Fig. 1. The distribution of the *Cortaderia* samples across South Africa included in this study, including inflorescences that did not have mature seeds.



Fig. 2. (A) A viable and (B) non-viable *Cortaderia selloana* seed under a microscope after treatment with tetrazolium stain.



Fig. 3. Laboratory monitoring of rapid germination in a petri dish (nine cm diameter) incubated in a growth chamber, showing the developed radicles from seeds of *Cortaderia selloana*.

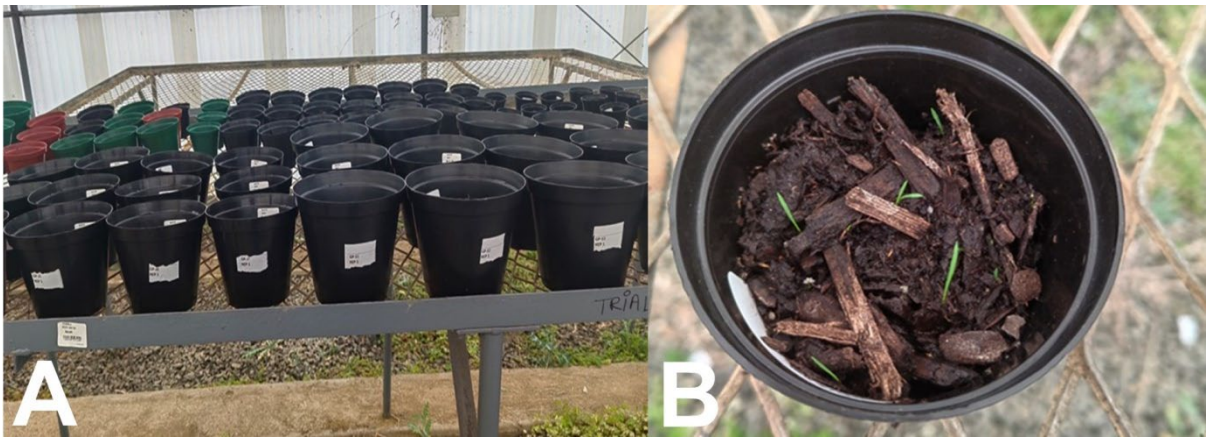

Fig. 4. (A) Complete block design of the germination pots in a greenhouse and (B) Leaf emergence indicating germination of *Cortaderia selloana* seeds.