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Prionium serratum (Thurniaceae): Evaluation of chlorophyll and influence of waterlogging and heavy metals on flowering in the Palmiet River, KwaZulu-Natal.

Phakamani Linda Masuku [1], Himansu Baijnath [1], and Ajay Bissessur [2]

[1] *School of Agriculture and Science, Discipline of Life Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag X54001, Durban 4000, South Africa.*

[2] *School of Agriculture and Science, Discipline of Chemistry, University of KwaZulu-Natal, Westville Campus, Private Bag X54001, Durban 4000, South Africa.*

ABSTRACT

Background:

Prionium serratum (Thurniaceae), a South African endemic plant, thrives in oligotrophic soils where it flowers and produces seeds. However, KwaZulu-Natal populations show declining numbers and lack flowering or seeding, prompting conservation efforts. This study examined the influence of temperature, waterlogging, and heavy metals on flowering and population decline of *P. serratum*.

Methods:

The chlorophyll content was recorded from 10 mature, randomly sampled leaves using the SPAD-502 chlorophyll meter to assess the influence of temperature on flowering in *P. serratum*. *P. serratum* on one site was subjected to drought, and the observations with *P. serratum* growing on two waterlogged habitats. *P. serratum* samples were also taken for heavy metal analysis with ICP-OES, and data were analyzed with One-Way ANOVA in IBM SPSS version 28.

Results:

Temperature did not stress *P. serratum* as chlorophyll levels indicated healthy photosynthesis and growth across all sampled sites (≥ 30 SPAD units, $p > 0.05$). *Prionium serratum* in constantly waterlogged habitats did not flower, while *P. Serratum* exposed to alternating wet and dry conditions produced flowers. Investigation of the levels of heavy metal accumulation showed the existence of Al, Ca, Cu, Fe, Pb, Mg, Hg, Se, and Si. Despite elevated levels of these metals, flowering was not hindered ($p > 0.05$). Observations of stunted growth of *P. serratum* in Mhlanga River may be attributed to frequent flooding disturbances, not metal toxicity, and historical herbarium records confirm past flowering there.

Conclusion:

Sunlight or shade (temperature) and heavy metal exposure did not hinder flowering in *P. serratum*. Waterlogging inhibited and delayed flowering, and drought triggered and prompted flowering in this species.

Recommendation:

For successful restoration, *P. serratum* should be propagated from seedlings or plantlets in sandy, well-drained soil with periodic wet-dry cycles to prevent waterlogging. Conservation efforts should focus on riverbank planting rather than ponds or floodplains to ensure successful establishment.

Keywords: *Prionium serratum; Restoration; Conservation; Waterlogging; Flowering; Extirpation; Heavy metals; Phytoremediation.*

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Corresponding author: *Phakamani Linda Masuku.*

Email: *212539683@stu.ukzn.ac.za*

School of Life Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag X54001, Durban 4000, South Africa.

INTRODUCTION

The restoration and conservation of biodiversity are essential to maintaining the ecological balance and resilience of ecosystems (Huang, 2011; Huang et al., 2013). Within this context, attention must be given to the conservation of endemic, vulnerable, and endangered plant species, as they play a crucial role in supporting diverse habitats and promoting overall ecosystem health (Huang, 2011; Huang et al., 2013). *Prionium serratum* (L.f.) Drège ex E. Mey., a member of the family Thurniaceae (Munro and Linder, 1997; Munyai, 2013), is one such plant species that requires urgent attention,

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restoration, and conservation efforts within the PR system in Durban, KZN, South Africa.

Prionium serratum is an ecologically significant plant species found in riparian zones, wetlands, and marshes (Boucher and Withers, 2004; Sieben, 2012; Munyai, 2013; Rebelo et al., 2018a; Rebelo et al., 2018b). Also known as the river sedge, *P. serratum* plays a crucial role in stabilizing riverbanks, preventing erosion, and providing habitats for numerous species within the CFR (Johnson, 2012). However, due to harsh environmental events, habitat degradation, and anthropogenic activities, the population of *P. serratum* has experienced a decline, making restoration and population conservation imperative in the PR system and KZN region.

The restoration and conservation of *P. serratum* are essential for maintaining the ecological integrity and biodiversity of the PR system. Riparian ecosystems, where *P. serratum* thrives, are recognized for their vital functions in water filtration, nutrient cycling, flood buffering, and habitat provision (Brookes, 1997). *Prionium serratum* contributes to the structural integrity and stability of these ecosystems, benefiting both aquatic and terrestrial species (Mendelssohn and McKee, 1988). Therefore, restoring the population of *P. serratum* is essential for the overall health and resilience of the PR system.

In addition to its ecological significance, the conservation of *P. serratum* holds socio-economic importance. Riparian areas, including the PR system, often attract tourism and recreational activities and provide ecosystem services such as flood control and water purification (Rebelo et al., 2018a; Rebelo et al., 2018b; Tanner et al., 2019; Rebelo et al., 2020; Rebelo et al., 2022). The preservation of *P. serratum* in the PR system can thus contribute to local economies and sustainable development.

To address the conservation challenges faced by *P. serratum*, a comprehensive understanding of its distribution, population dynamics, and ecological requirements is necessary. Studies on the reproductive biology, habitat preferences, and interactions with other species will guide restoration strategies of *P. serratum* (Johnson and Brown, 2010). Monitoring population size, seed dispersal, and germination or recruitment patterns will inform conservation efforts focused on population recovery and long-term sustainability (Hagger et al., 2022).

Furthermore, engaging with local communities, stakeholders, and policymakers is crucial for effective restoration and population conservation initiatives. Collaboration and knowledge exchange foster a sense of ownership, enhancing success and long-term commitment to conservation efforts (Rebelo, 2012; Rebelo and Cowling, 2013; Rebelo et al., 2018b). Involving local communities in restoration activities and raising awareness of the importance of *P. serratum* can cultivate a culture of environmental stewardship.

This research seeks to investigate the restoration and population conservation of *P. serratum* in the PR system by synthesizing existing knowledge, conducting ecological assessments, and engaging stakeholders. The findings will contribute to evidence-based conservation strategies that ensure the ecological integrity and socio-economic sustainability of the region.

Prionium serratum, once found in the PR system between the 1960s and 1970s (Scott-Shaw, 1999), has largely disappeared, with small populations remaining in the UKZN-Westville and PNR ponds. About 50% of its populations in KZN is extirpated (Scott-Shaw, 1999; Munyai, 2013; Rebelo et al., 2018b), highlighting an urgent need for conservation. The causes of *P. serratum* decline in the PR and KZN are unknown, and no restoration efforts have been made.

Additionally, the species is failing to flower in KZN, including in PNR and UKZN-Westville ponds, which threatens its reproduction, genetic diversity, and long-term survival (Basey et al., 2015). Flowering and seed production are crucial for the persistence of *P. serratum*; research is necessary to understand the factors and causes contributing to the decline of this species. Without intervention, the loss of *P. serratum* could negatively impact communities relying on it for medicine, livestock fodder, and food.

MATERIALS AND METHODS

Study design

A study was conducted in 2020 and 2021 at UKZN-Westville Pond, PNR Pond, and Mhlanga River to evaluate the influence of temperature, waterlogging, and heavy metals accumulation on the flowering of the endemic plant *P. serratum* in the PR system of KZN, South Africa.

The pH concentrations of water in *P. serratum*-inhabited sampling sites were recorded using a calibrated digital pH meter (Extech, SKU: PH210). The metal rod was dipped into water for 2 minutes, and then the pH reading was recorded. The pH in the UKZN-Westville Pond, PNR Pond, and Mhlanga River was compared with the pH in *P. serratum* sites in KZN through EC to the WC, which was obtained from the literature (**Tables 1** and **2**). A slightly acidic soil environment (low pH < 6 but > 2) is one of the requirements for normal growth and development of *P. serratum* (Munyai, 2013).

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Table 1: The water pH recorded in *Prionium serratum* sampling sites.

Site	UKZN-Westville Pond	PNR Pond	PR	Mhlanga River
pH	6.8 – 7.8	6.2 – 7.2	7.2 – 7.6	6.5 – 7.8

Table 2: The comparison of pH in other *Prionium serratum* sites as reported by Munyai (2013).

Site	pH
Citrusdal (WC)	4.50
Tsitsikamma National Park (EC/WC)	4.50
Napier (WC)	5.43
Mpenjati Nature Reserve (KZN)	4.60
Hermanus (WC)	3.27
Prince Alfred Pass (WC)	3.50
Grahamstown (EC)	3.63

Recording leaf chlorophyll content in *Prionium serratum* using SPAD-502.

To determine the influence of temperature on the flowering of *P. serratum*, the chlorophyll content was recorded from 10 mature (n = 10), randomly sampled leaves using the SPAD-502 chlorophyll meter, Konica Minolta Inc., Japan, in UKZN-Westville Pond, PNR Pond, and Mhlanga River (N = 30). Due to the long length of *P. serratum* leaves, the chlorophyll content was recorded at three points along the leaf length (leaf base, midway, and apex), and the average of the three points was recorded. The chlorophyll content was recorded during the coldest three winter months (June, July, and August) and the hottest three summer months (December, January, and February) of 2020 and 2021.

The chlorophyll content data in winter 2020 and 2021 and summer 2020 and 2021 were analyzed by performing the One-Way ANOVA on IBM SPSS version 28 because there were more than two groups (UKZN-Westville Pond, PNR Pond, and Mhlanga River). The chlorophyll content of ≥ 30 SPAD units was indicative of good health and photosynthesis for *P. serratum*. Studentized Residuals were used to perform the One-Sample Kolmogorov-Smirnov test to assess data normality for the chlorophyll data in winter 2020 and 2021 and summer 2020 and 2021. The chlorophyll data for winter 2020 and 2021 were normally distributed, respectively ($Z = 0.113$, p = 0.200 and $Z = 0.132$, p = 0.193). The One-Sample Kolmogorov-Smirnov test also showed that Studentized Residuals for chlorophyll data in summer 2020 and 2021 were normally distributed, respectively ($Z = 0.177$, p = 0.078 and $Z = 0.098$, p = 0.200). Levene's test showed that the variances between the chlorophyll data in winter 2020 were equal (p = 0.192), while in winter 2021 were not equal (p = 0.014). Then, the chlorophyll data for winter 2021 were log-transformed using the Log_{10} of the arithmetic test in SPSS, and the data conformed to normality (Z = 0.114, p = 0.109). Levene's test showed that the variances between the chlorophyll data in summer 2020 and 2021 were equal, respectively (p = 0.507 and p = 0.070).

Assessing the influence of waterlogging on the flowering of *Prionium serratum*.

The investigations into the influence of water availability on the flowering of *P. serratum* were conducted from the UKZN-Westville Pond. Observations were also conducted on *P. serratum* in the PNR Pond and naturally occurring populations inside the Mpenjati Nature Reserve swampy forest and the Mhlanga River. Study sites were the Mhlanga River (control site), UKZN-Westville (experimental site), and PNR Ponds (observation). During the study period, the Mhlanga River experienced repeated flooding events during the summer of 2020 and 2021, which disrupted the normal growth of *P. serratum*. Tall shrubs of *P. serratum* were washed away with floods in the summer of 2020, seedlings and plantlets grew, but had not reached maturity when the next flooding event occurred in the summer of 2021. Thus, only herbarium specimens with flowers from the Mhlanga River are shown because *P. serratum* did not flower during the study period due to flooding.

In the determination of the influence of water availability on the flower setting of *P. serratum*, this species was stressed by inducing drought or removing water from the UKZN-Westville Pond (experimental), and morphological changes were compared with *P. serratum* growing in a waterlogged site in the PNR Pond. There were five clumps of *P. serratum* in the UKZN-Westville Pond with ten or more individuals. All the mud was removed from the UKZN-Westville Pond to deprive *P. serratum* of water so that the roots would not absorb water for over 33 days (**Figure 1A – E**). Observations were conducted during the 33 days of water stress, after which water was returned to the pond (**Figure 2A – D**). Then, observations were conducted for the entire duration of the study period.

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Within 2.5 – 3 months after water was returned to the UKZN-Westville Pond, *P. serratum* produced an inflorescence and flowers. The flowers were harvested for seed viability analysis and to quantify reproductive output. The flowers were shaken so that the seeds would fall onto the paper towel. Some seeds were poured into the glass jar for three months to test for viability. If the seeds sank to the bottom of the jar, they would have indicated viability, but those that remained suspended on top of the water were not viable. All the seeds remained suspended on top of the water in the glass jar after three months. Some of the seeds were decanted onto a paper towel and enclosed with two layers of paper towel. Then, the seeds were placed on top of the soil bed in a greenhouse and irrigated every single day for three months. However, the seeds did not germinate, thus the results were omitted.

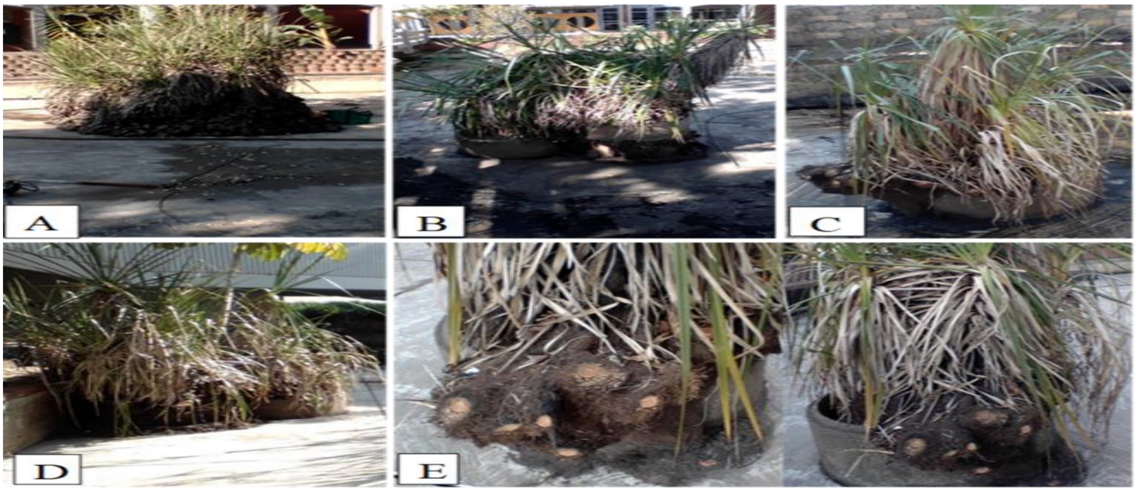

Figure 1: *Prionium serratum* is subjected to water scarcity stress in the UKZN-Westville Pond. Water (**A**) and mud (**B**, **C**, **D**, **E**) were removed for 33 days so that this species would not absorb water or have moisture.

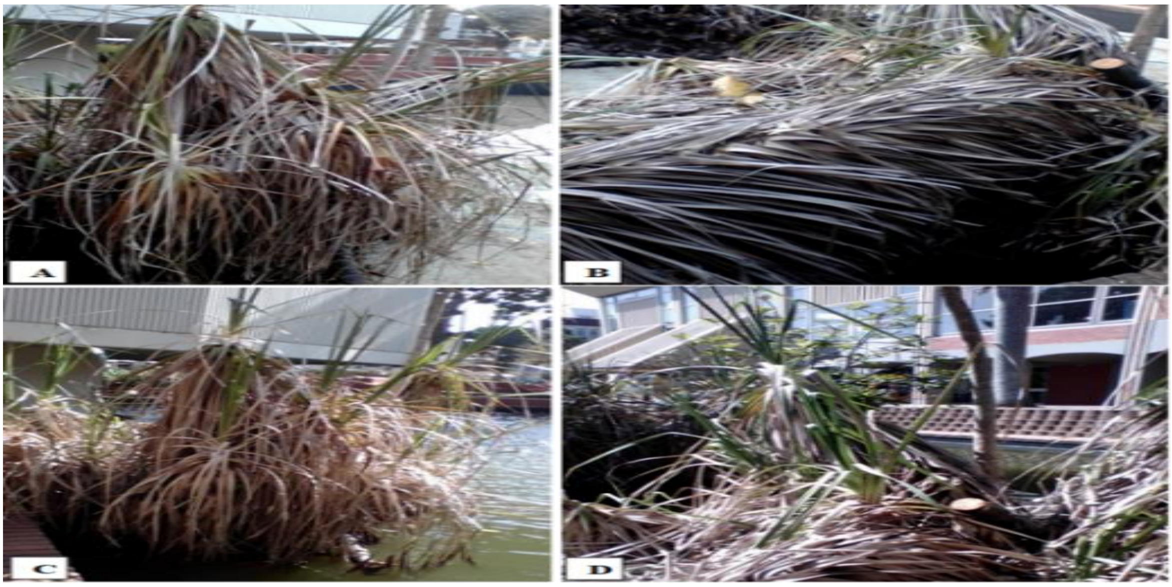

Figure 2: *Prionium serratum* wilting and drying (**A – B**) during the 33 days of water scarcity stress in the UKZN-Westville Pond and greening (**C – D**) a few days after water was returned to the pond.

Identification of heavy metal accumulation in *Prionium serratum*.

In the determination of the influence of heavy metals on the flower setting of *P. serratum*, the Inductive Coupled Plasma-Optical Emission Spectrometry (ICP-OES) technique (Perkin Elmer 5300, Germany) was followed to

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identify the heavy metals that were present in plant samples and their quantities. For the screening of elemental analysis present in *P. serratum*, ten (10) random leaves (**Figure 3A**), roots (**Figure 3B**), and rhizomes (**Figure 3C**) were sampled at UKZN-Westville and PNR Ponds. Each leaf was approximately 1.5–2m long. The leaves, roots, and rhizomes were brought to the University of KwaZulu-Natal laboratory for preparation.

Leaves, roots, and rhizomes of *P. serratum* were also sampled from the naturally occurring populations in the Mhlanga River (control), Margate, on the south coast of KZN. It was ensured that the plant and three water samples were randomly collected along the Mhlanga River. The same methodology for sample preparation, digesting, and filtering that was applied to *P. serratum* samples from UKZN-Westville and PNR Ponds was followed for the Mhlanga River samples.

Figure 3: Example of *Prionium serratum* leaves (**A**), roots (**B**), and rhizomes (**C**) sampled for heavy metal analysis.

Sample preparation

The leaves, roots, and rhizomes were washed with distilled water to remove dirt, damaged and rotten parts, foreign substances, and contaminants. The plant samples were oven-dried at 85 °C for 48 hours, and charring was avoided. After 48 hours of drying, the leaves, roots, and rhizomes were ground to a fine powder using a coffee grinder.

A mass aliquot of 14.79g of fine-ground powdered leaves, roots, and rhizomes of *P. serratum* was stored in a sterile container for subsequent analysis. Thereafter, 0.15g of dried powdered leaf, root, and rhizome was digested with 5ml of nitric acid and by gentle boiling and stirring for 10 minutes on a hot plate magnetic stirrer unit in a fume hood. Then, the acid-digested sample of the dried powdered leaf mass was diluted to exactly 25ml with Millipore® water and filtered using a 0.2µm sterile Acrodisc® filter. The same procedure was followed for dried, powdered roots and rhizomes. Three water samples from the Mhlanga River, UKZN-Westville, and PNR Ponds were prepared following the same procedure. Samples were analyzed for heavy metal content using Inductively Coupled Plasma-Optical Emission Spectrometry (ICP-OES) with a Perkin Elmer 5300 spectrophotometer.

An ICP-OES scan of the plant samples (leaves, roots, and rhizomes) was performed for the identification of the heavy metal composition. Upon processing and perusal of the ICP intensities, there were nine (9) common heavy metals that were identified in *P. serratum* and water samples (**Table 3**). A 1000 ppm solution of magnesium (Mg), silicon (Si), calcium (Ca), selenium (Se), aluminium (Al), lead (Pb), iron (Fe), copper (Cu), and mercury (Hg) was prepared. A series of multi-element standards was prepared to establish a standard linear series for each element. Lower concentrations were diluted by serial dilution. The analysis of metals was carried out in triplicate, and the calculations were performed using the average values. Data were analysed by performing the Tukey HSD (equal number of samples) and multiple comparisons in the One-Way ANOVA. The One-Sample Kolmogorov-Smirnov test for data normality could not be performed on single values of each heavy metal; hence, not shown.

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Table 3: Common heavy metals that were absorbed and accumulated by *Prionium serratum* in UKZN-Westville Pond, PNR Pond, Mhlanga River, and were present in water samples.

Heavy metals	
Aluminium (Al)	Calcium (Ca)
Copper (Cu)	Iron (Fe)
Lead (Pb)	Magnesium (Mg)
Mercury (Hg)	Selenium (Se)
Silicon (Si)	

Study sites

The samples for *P. serratum* were collected in the UKZN-Westville and PNR Ponds. The UKZN-Westville Pond is located inside the UKZN, Westville campus, while the PNR Pond is in the PNR. The results from *P. serratum* in the UKZN-Westville and PNR Ponds were compared with the control site (Mhlanga River), Margate, and the south coast of KZN (**Figure 4**).

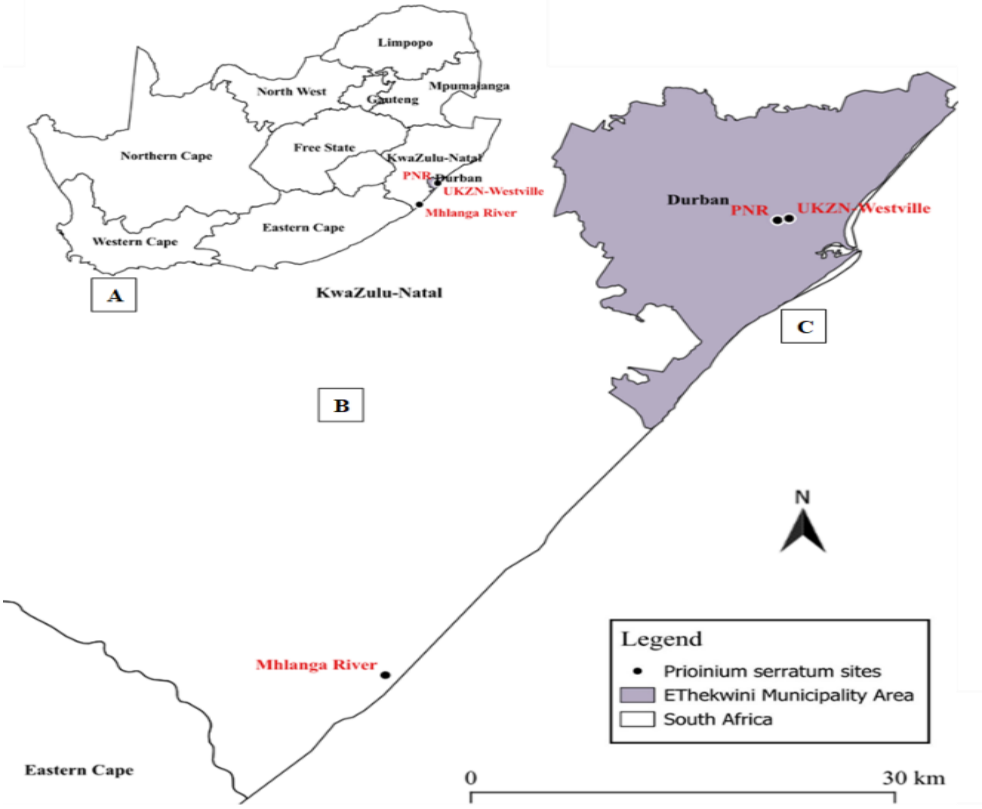

Figure 4: A map of South Africa (**A**) showing KZN (**B**) and Durban (**C**) with *P. serratum* localities in the UKZN-Westville Pond, PNR Pond, and Mhlanga River. Image source: Created using QGIS version 3.40.7 by Masuku PL.

University of KwaZulu-Natal Westville Pond

The UKZN-Westville Pond is situated within the Westville campus in front of T-Block (-29°49'05"S, 30°56'38"E; **Figure 5A – D**). There are five clumps of *P. serratum* in the pond; none have been flowering for the last decade. The pond is artificial with concrete underneath, and plants are waterlogged annually. In this pond, *P. serratum* is exposed to the sun for most of the day (around 10 a.m. in the morning to 16 p.m. in the afternoon), with a few other companion plants in the pond. There is no human interference in the pond, except for feeding the pond's fish and birdlife.

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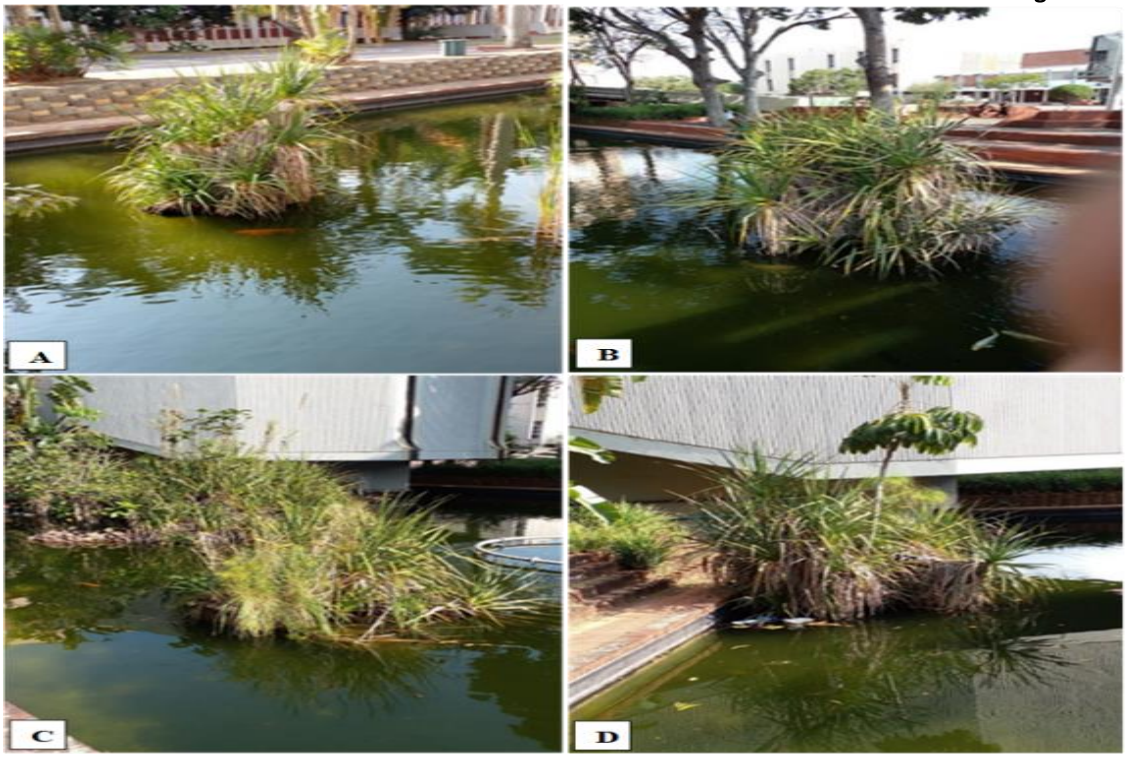

Figure 5: *Prionium serratum* in the UKZN-Westville Pond, annually waterlogged and exposed to full sunlight. Clumps grow on underlying concrete surfaces and have never produced flowers since the late 1970s.

Palmiet River locality

The PR is situated northwest of Durban, Republic of South Africa, and is a 26-kilometer (km) tributary of the uMngeni River (**Figure 6**). The PR is a 37-square-kilometer (km^2) drainage catchment area (Du Preez and De Villiers, 1987) that is continuously polluted by different sources of anthropogenic waste that affect its physicochemical composition (Chetty, 2016). The obvious pollution in the PR comes from industrial and residential inputs, classifying it as an industrial-residential river (Chetty, 2016).

The source of the PR is located northwest of Durban in Kloof and runs through the high-income residential areas, the Pinetown and New Germany industrial complexes, the PNR, UKZN-Westville, the Rainbow Ridge informal settlement, and the QRW informal settlements (Chetty, 2016; Vogel et al., 2016). In the end, the PR flows into the uMngeni River just below the Quarry Road West informal settlements (Vogel et al., 2016). This river is heavily polluted from the catchment or source upstream near Kloof to the mouth below QRW informal settlements and is continuously subjected to regular flooding during heavy rainfalls, which feed pollutants into the uMngeni River and subsequently into the ocean (Vogel et al., 2016). The Pinetown-New Germany industrial complex is the region where most toxic and harmful pollutants from plastic, metal, motor, and vehicle parts washing and cleaning, chemical manufacturing, and processing industries enter the PR (Chetty, 2016).

The selection of study sites was exclusively for *P. serratum* ponds in the PNR and UKZN-Westville, where this species is located. In both locations, *P. serratum* is not flowering and is not influenced by anthropogenic activities from industrial or residential input. However, the chemical composition of the water where *P. serratum* grows is unknown. Understanding various plant growth factors in both the PR system and pond, where *P. serratum* is currently growing, will provide insights into identifying the factors that cause the decline of this species and the lack of flower setting.

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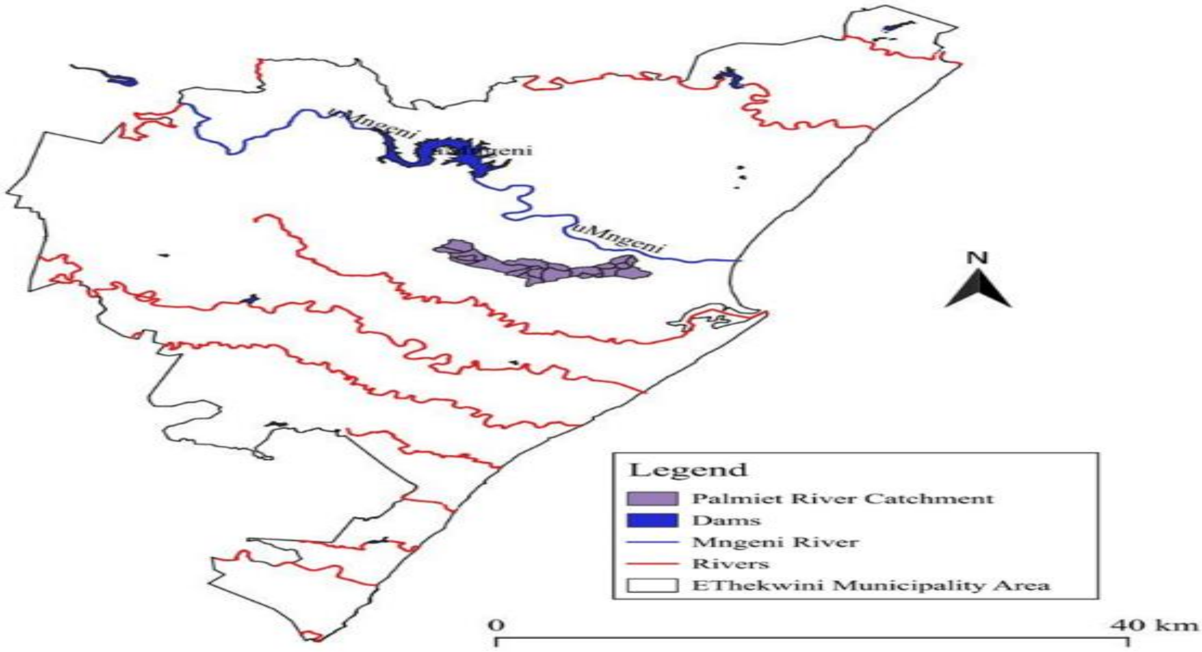

Figure 6: The PR tributary feeds into the Mngeni River and flows into the Indian Ocean. Image source: Created using QGIS version 3.40.7 by Masuku PL.

Palmiet Nature Reserve Pond

The pond on which *P. serratum* grows is located inside the PNR (-29°49'30" S, 30°55'37" E; **Figure 7A – B**), next to the parking lot, in front of or northwest of the offices. The pond is artificial (underlined with concrete at the bottom), always waterlogged, has a variety of fish species and vegetation, and *P. serratum* is waterlogged throughout the year. The pond receives minimal disturbance from anthropogenic activities, such as research activities. No other disturbance has been recorded. The pond is surrounded by vegetation and canopy trees, which provide shade for an entire photoperiod with minor sun flecks (brief, intermittent periods of increased solar irradiance or high photon flux density that can significantly improve carbon gain in shaded forest understories and lower canopies of trees). This is due to the movement of the sun during the day or moving branches due to blowing wind (Way and Pearcy, 2012). The pond does not mix with PR water, except for rainwater during heavy rainfall or the rainy season. There have been no flowers or inflorescences observed in *P. serratum* in this pond for the last ± five decades.

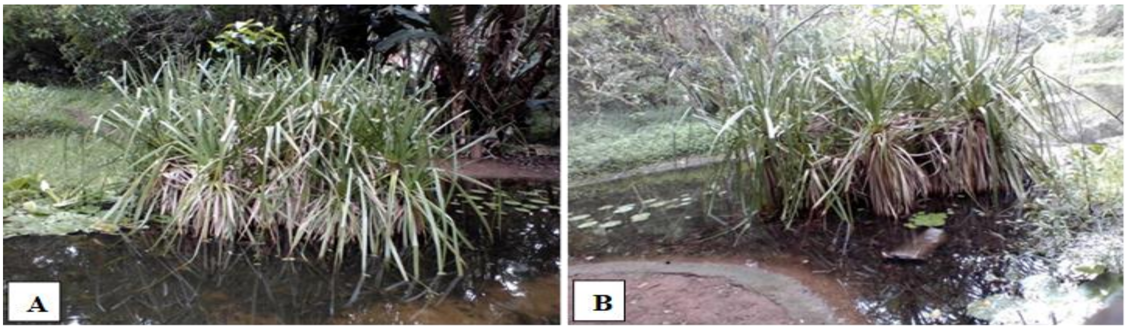

Figure 7: *Prionium serratum* growing in the pond inside the PNR is waterlogged all year round, shaded all day in summer and winter due to the tree canopy, and receives sun flecks in winter after the abscission of tree leaves. Clumps grow on a concrete surface and do not produce flowers.

The size and depth of the UKZN-Westville and PNR Ponds.

A 100-meter (100 m) Grip tape was used to measure the size (length and breadth) of the UKZN-Westville and PNR Ponds. A 5-meter Grip steel tape was used to

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measure the height of the ponds and the depth of the water in the UKZN-Westville and PNR Ponds. This was carefully done to prevent stepping into the pond and disturbing the ecosystem. The length of the pond referred to how long the pond was, the height referred to how deep the pond was, and the depth referred to how shallow or deep the water was from the surface to the bottom of the pond. In the UKZN-Westville Pond, the tape was dipped into the water until it reached the bottom of the shallow pond and recorded the depth from the bottom to the top of the pond. The length of the UKZN-Westville Pond is 45 m, and the breadth is 23.9 m. The height of the UKZN-Westville Pond is 1.10 m (110 cm), and the depth of water from the surface to the bottom of the pond is 0.60 m (60 cm). The length of the PNR Pond is 28 m, and the breadth is 21 m. The height of the PNR Pond is 0.60 m (60 cm), and the depth of the water is 0.45 m (45 cm). The UKZN-Westville Pond was bigger, longer, and deeper than the PNR Pond. These measurements were recorded to measure the depth to which *P. serratum* was submerged.

Mhlanga River (sampling site)

The Mhlanga River (**Figure 8**) is situated within Ray Nkonyeni Local Municipality in Margate (-30°48'20.9" S, 30°23'31.1" E) and originates from the Nsimbini Area, northeast (NE) of INkulu Primary School, and runs through the low and high-income settlements to the Nsangwini Area. Eventually, it passes through the intensive and extensive commercial agricultural fields from Qina-About to the Mhlanga River and R61 crossing, where there is a mixing of freshwater and seawater. The Mhlanga River passes through large agricultural fields, possibly serving as a primary source of pollution, such as the adjacent sugarcane and banana fields that border the river, as well as sewage outbursts from high- and low-income settlements upstream of the river. There are numerous sewage manholes along the river that overflow into the Mhlanga River when blocked or congested. The Mhlanga River eventually meets the St. Michael's on Sea estuary.

Figure 8: *Prionium serratum* sampled site in the Mhlanga River (-30°48'20.9" S, 30°23'31.1" E), Ugu District Municipality, southwest of South Coast Mall. There is no *P. serratum* growing upstream and in salty waters towards the St. Michael on Sea Estuary. (**Image source:** Google Earth Pro, 2023).

RESULTS

Evaluation of chlorophyll content in the leaves of *Prionium serratum*.

The chlorophyll content differed significantly between *P. serratum* sampled at UKZN-Westville, PNR, and Mhlanga River in winter 2020 (F = 1.787, df = 2, p = 0.049), except winter 2021 (F = 2.158, df = 2, p = 0.135; **Table 4**). The univariate multiple comparison showed that the chlorophyll content differed significantly between *P. serratum* sampled at UKZN-Westville and PNR in winter 2020 ($p < 0.05$), except for the rest of the samples ($p > 0.05$; **Table 5**). Leaf chlorophyll content at UKZN-Westville Pond was high relative to PNR Pond and Mhlanga River in winter 2020 (62.53 ± 3.75 SPAD units, 56.55 ± 2.81 SPAD units, and 56.06 ± 1.95 SPAD units, respectively; **Figure 9**). However, *P. serratum* sampled at Mhlanga River in winter 2021 showed slightly higher chlorophyll content compared to UKZN-Westville and PNR, respectively (52.96 ± 5.90 SPAD Units, 50.06 ± 5.41 SPAD Units, and 49.10 ± 1.90 SPAD Units; **Figure 9**).

The chlorophyll content did not differ significantly between sampled sites in summer 2020 and 2021 (F =

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1.721, df = 2, p = 0.198 and F = 1.501, df = 2, p = 0.241; **Table 6**). The univariate multiple comparisons also showed that the chlorophyll content between sampled sites did not differ significantly (p > 0.05; **Table 7**). *Prionium serratum* in UKZN-Westville had a higher chlorophyll content in summer 2020 compared to PNR and Mhlanga River, respectively (56.06 ± 6.15 SPAD Units, 55.29 ± 6.39 SPAD Units, and 52.77 ± 5.90 SPAD Units; **Figure 10**). In summer 2021, the chlorophyll content in UKZN-Westville was also higher compared to Mhlanga River and PNR, respectively (52.96 ± 5.90 SPAD Units, 51.10 ± 3.33 SPAD Units, and 47.94 ± 3.38 SPAD Units; **Figure 10**).

Table 4: One-Way ANOVA descriptive statistics comparing the significance of chlorophyll content in the leaves of *Prionium serratum* sampled at UKZN-Westville, PNR, and Mhlanga River in the winter of 2020 and 2021.

Season	F	df	p
Winter 2020	1.787	2	0.049
Winter 2021	2.158	2	0.135

Table 5: One-Way ANOVA Multiple comparisons for the significance in chlorophyll content in the leaves of *Prionium serratum* between samples from UKZN-Westville, PNR, and Mhlanga River in winter 2020 and 2021.

Season	(I) Site	(J) Site	p
Winter 2020	UKZN-Westville	PNR	0.041
		Mhlanga River	0.373
	PNR	Mhlanga River	0.184
Winter 2021	UKZN-Westville	PNR	0.978
		Mhlanga River	0.227
	PNR	Mhlanga River	0.161

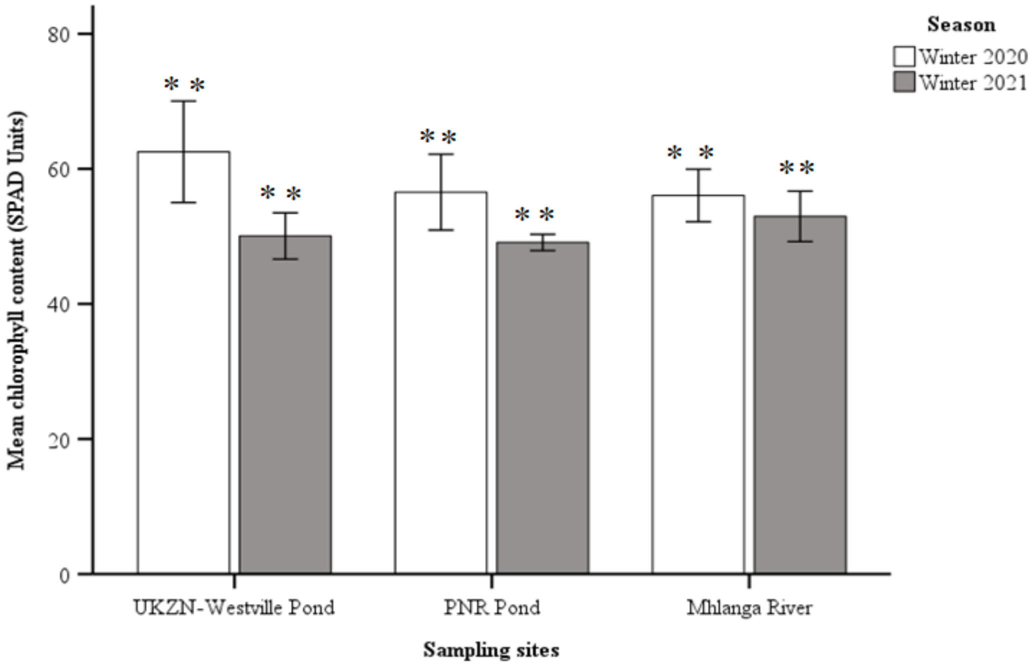

Figure 9: The average chlorophyll content (mean ± S.E) of ten randomly sampled leaves for *Prionium serratum* in the UKZN-Westville Pond, PNR Pond, and Mhlanga River in winter 2020 and 2021 (n = 30). Two asterisks (**) indicate significantly high chlorophyll content (values above 30 SPAD units), while one asterisk (*) indicates significantly low chlorophyll content with values below 30 SPAD units and an unhealthy plant.

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Table 6: One-Way ANOVA descriptive statistics comparing the significance of chlorophyll content in the leaves of *Prionium serratum* sampled at UKZN-Westville, PNR, and Mhlanga River in the summer of 2020 and 2021.

Season	F	df	p
Summer 2020	1.721	2	0.198
Summer 2021	1.501	2	0.241

Table 7: One-Way ANOVA Multiple comparisons for the significance in chlorophyll content in the leaves of *Prionium serratum* between samples from UKZN-Westville, PNR, and Mhlanga River in summer 2020 and 2021.

Season	(I) Site	(J) Site	p
Summer 2020	UKZN-Westville	PNR	0.338
		Mhlanga River	0.210
	PNR	Mhlanga River	0.951
Summer 2021	UKZN-Westville	PNR	0.498
		Mhlanga River	0.843
	PNR	Mhlanga River	0.224

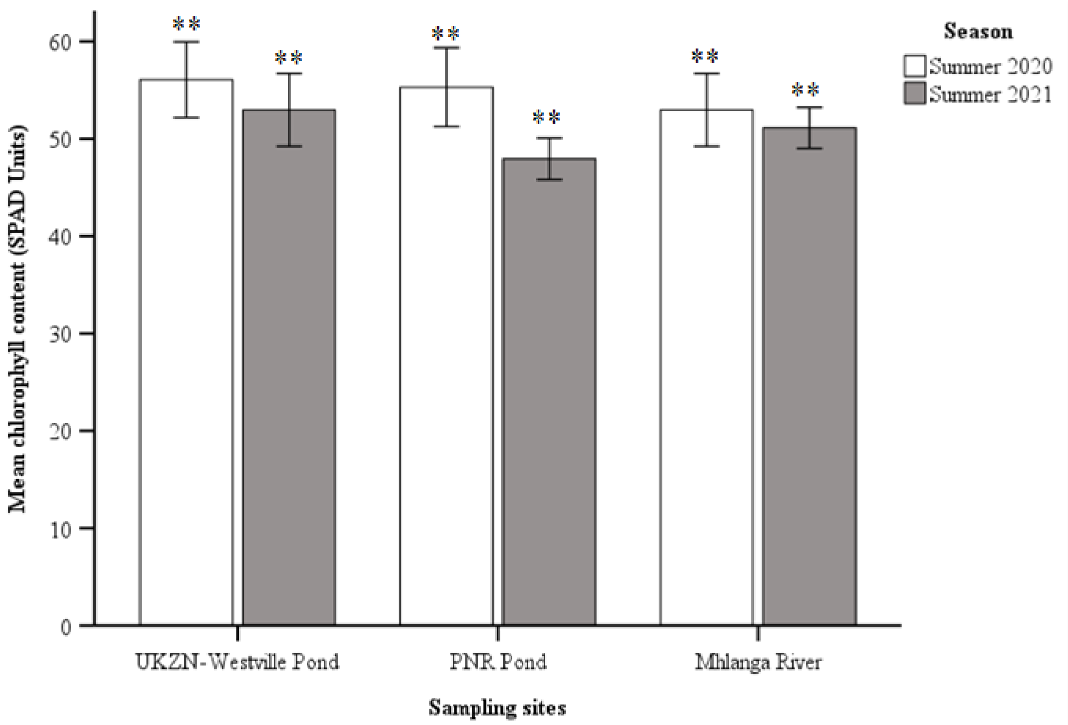

Figure 10: The average chlorophyll content (mean ± S.E) of ten randomly sampled leaves for *Prionium serratum* in the UKZN-Westville Pond, PNR Pond, and Mhlanga River in the summer of 2020 and 2021 (n = 30). Two asterisks (**) indicate significantly high chlorophyll content (values above 30 SPAD units), while one asterisk (*) indicates significantly low chlorophyll content with values below 30 SPAD units and an unhealthy plant.

Influence of waterlogging on the flowering of *Prionium serratum*.

Water scarcity stimulated flowering in *P. serratum*. After 2.5 – 3 months, water was returned to the UKZN-Westville Pond, *P. serratum* produced a large inflorescence, and later flowers and seeds (**Figure 11A – B**). This species did not set flowers in the same season during the following years (September 2021–February 2022). During the same study period and flowering season, *P. serratum* in the PNR Pond and Mpenjati Nature Reserve swampy forest did not produce flowers due to waterlogging.

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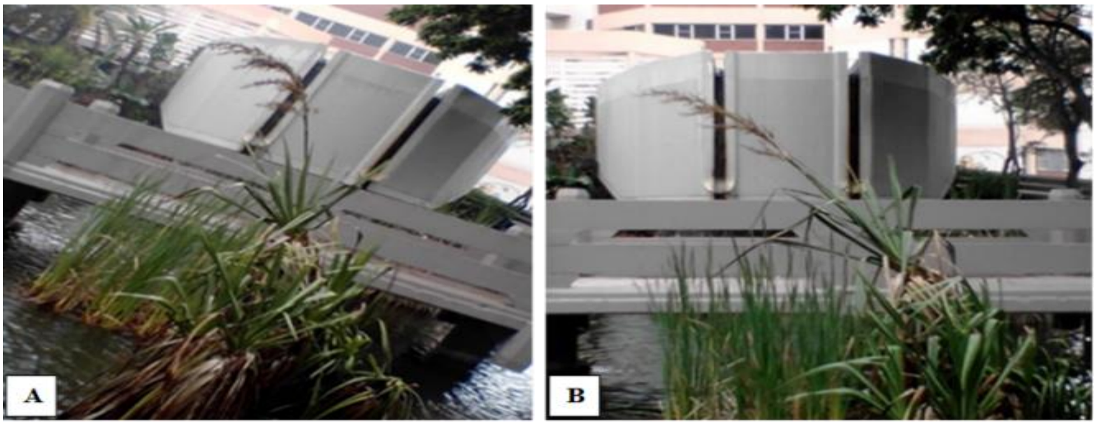

Figure 11: *Prionium serratum* produced an inflorescence with flowers between 2.5 and 3 months after water was returned to the UKZN-Westville Pond.

Evaluation of heavy metal (HM) levels accumulated in *Prionium serratum* samples (leaves, roots, rhizomes).

Aluminium (Al)

Aluminium levels in the leaves, roots, and rhizomes of *P. serratum* sampled at the three sites showed a significant difference ($p = 0.002$; **Table 8**). The leaves and roots in the Mhlanga River showed high Al levels relative to PNR and UKZN-Westville Ponds (**Figure 12**). Aluminium levels in the leaves, roots, and rhizomes of *P. serratum* between PNR and UKZN-Westville Ponds showed no significant difference ($p > 0.05$; **Table 9**). The leaves, roots, and rhizomes showed relatively low Al levels in the PNR and UKZN-Westville Ponds (**Figure 12**). Aluminium levels in the leaves, roots, and rhizomes of *P. serratum* sampled in the Mhlanga River showed significant differences ($p < 0.05$, **Table 9**). Roots for *P. serratum* sampled at the Mhlanga River showed the highest level of Al ions relative to the rest of the samples from UKZN-Westville and PNR Ponds (174.67 ± 55.33 ppm; **Figure 12**). Roots sampled in the Mhlanga River showed high levels of Al ions relative to leaves, rhizomes, and water samples in all three sites (**Figure 12**). The roots of *P. serratum* are seen as effective hyperaccumulators of aluminium ions compared to leaves and rhizomes.

Calcium (Ca)

Calcium (Ca) is abundant in nature and is present in any plant species due to requirements in chlorophyll maintenance, growth, and strengthening of the cell wall. This is evident in the roots and leaves of *P. serratum* sampled at UKZN-Westville, PNR, and Mhlanga River, respectively. Roots of *P. serratum* are seen as effective hyperaccumulators of calcium ions (**Figure 13**). The roots in the Mhlanga River showed the highest Ca level relative to the rest of the samples from the three sites (**Figure 13**). The roots sampled in the Mhlanga River showed the highest Ca level relative to water samples from all three sites. The roots are seen as effective hyperaccumulators of Ca ions compared to leaves and rhizomes.

Calcium levels in the leaves, roots, and rhizomes of *P. serratum* sampled at the PNR, UKZN-Westville, and Mhlanga River showed a significant difference ($p = 0.005$; **Table 8**). The roots in the Mhlanga River showed the highest Ca levels relative to the rest of the samples (**Figure 13**). Calcium levels between leaves and rhizomes and roots and rhizomes sampled in the PNR and UKZN-Westville Ponds showed a significant difference ($p < 0.05$; **Table 9**). The leaves and rhizomes in the PNR Pond showed high Ca levels relative to roots, while leaves and roots in the UKZN-Westville Pond showed high Ca levels relative to rhizomes (**Figure 13**). The Ca level between leaves and roots in PNR and UKZN-Westville Ponds showed no significant difference ($p = 0.129$ and $p = 0.165$, respectively; **Table 9**). Calcium levels between leaves and roots, roots and rhizomes sampled in the Mhlanga River showed a significant difference ($p < 0.05$), while the Ca level between leaves and rhizomes in the Mhlanga River showed no significant difference ($p = 0.450$; **Table 9**).

Copper (Cu)

Copper (Cu) is generally abundant in the Earth's crust and is an essential micronutrient that is required by plants for many physiological and biochemical processes. Copper is expected to be present in high levels in the roots and rhizomes of all plants. This can be seen in **Figure 14**, where the roots and rhizomes of *P. serratum* sampled at Mhlanga River showed high levels of Cu ions relative to PNR and UKZN-Westville Ponds. However, the leaves sampled at the Mhlanga River are seen as effective hyperaccumulators of copper ions compared to the rest of the samples from the sampled sites (**Figure 14**). The leaves, roots, and rhizomes sampled at the Mhlanga River also showed high levels of Cu ions relative to water samples at all three sites.

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Copper levels in the leaves, roots, and rhizomes of *P. serratum* sampled at the PNR, UKZN-Westville, and Mhlanga River showed a significant difference ($p = 0.015$; **Table 8**). The leaves, roots, and rhizomes of *P. serratum* sampled at the Mhlanga River showed high levels of Cu ions relative to PNR and UKZN-Westville Ponds (**Figure 14**). Copper levels between the leaves, roots, and rhizomes of *P. serratum* sampled at PNR, UKZN-Westville, and Mhlanga River showed no significant difference ($p > 0.05$; **Table 9**).

Iron (Fe)

Iron is the most abundant element on Earth and in the Earth's crust and is an essential micronutrient for plant development. The Fe is expected to be present in any plant species due to its role in chlorophyll synthesis, photosynthesis, and enzymatic and metabolic processes in plants. The Fe levels in the leaves, roots, and rhizomes of *P. serratum* between PNR, UKZN-Westville, and Mhlanga River showed a significant difference ($p = 0.005$; **Table 8**). The roots and leaves sampled from the Mhlanga River showed the highest Fe levels relative to the rest of the samples from the three sites (**Figure 15**). The Fe levels between the leaves, roots, and rhizomes of *P. serratum* sampled from PNR and UKZN-Westville Ponds showed no significant difference ($p > 0.005$; **Table 9**).
The Fe levels between the leaves and roots, leaves and rhizomes, and roots and rhizomes of *P. serratum* sampled at the Mhlanga River showed a significant difference ($p < 0.05$; **Table 9**). The roots sampled from the Mhlanga River showed the highest Fe levels relative to leaves and rhizomes (108 ± 32 ppm, 39.33 ± 7.67 ppm, and 0.00 ± 0.00 ppm, respectively; **Figure 15**). The roots of *P. serratum* are seen as effective hyperaccumulators of Fe ions. The roots and leaves sampled from the Mhlanga River also showed high Fe levels relative to water samples at all three sites. The roots and leaves of *P. serratum* sampled at Mhlanga River showed the highest levels of Fe ion accumulation (108 ± 32 ppm and 39.33 ± 7.67 ppm, respectively) relative to the rest of the samples from the three sites. Roots of *P. serratum* are seen as effective hyperaccumulators of Fe ions compared to the leaves and rhizomes (**Figure 15**).

Mercury (Hg)

Mercury is a volatile substance and is expected to be present in high levels in the leaves of plants growing around areas where the burning of Hg-containing products, such as paints and municipal, construction, and medical waste, occurs. This can be seen in the leaves of *P. serratum* sampled at PNR Pond, which showed the highest levels of Hg ions (0.24 ± 0.00 ppm) relative to the rest of the samples from the three sampled sites (**Figure 16**). Leaves of *P. serratum* are seen as effective hyperaccumulators of Hg ions compared to the roots and rhizomes. Mercury ion accumulation was not detected in the rhizomes of *P. serratum* sampled at UKZN-Westville Pond. The Hg levels in the leaves, roots, and rhizomes of *P. serratum* sampled at all three sites showed a significant difference ($p = 0.005$; **Table 8**). The leaves sampled from the PNR Pond showed the highest Hg levels relative to the rest of the samples at all three sites (**Figure 16**). The Hg levels between leaves and rhizomes sampled at PNR Pond showed a significant difference ($p = 0.005$) relative to the rest of the sampling from all three sites ($p > 0.05$, **Table 9**). Water samples sampled at the Mhlanga River showed the highest Hg levels relative to *P. serratum* samples.

Magnesium (Mg)

Magnesium (Mg) is also an abundant element in the Earth's crust and is present in any plant due to its roles in chlorophyll production, photosynthesis, and plant growth. Roots for *P. serratum* sampled at the Mhlanga River showed the highest Mg ion levels relative to the rest of the samples in all three sampling sites (**Figure 17**). Roots of *P. serratum* are seen as effective hyperaccumulators of magnesium ions compared to the leaves and rhizomes. Magnesium levels in the leaves, roots, and rhizomes of *P. serratum* sampled at the PNR, UKZN-Westville, and Mhlanga River showed a significant difference ($p = 0.005$; **Table 8**). The roots of *P. serratum* sampled at the Mhlanga River showed the highest Mg level relative to the rest of the samples at all three sites (**Figure 17**). Mg levels between the leaves and roots, leaves and rhizomes, and roots and rhizomes sampled from the Mhlanga River showed a significant difference ($p < 0.05$; **Table 9**). The roots showed the highest level of Mg ions relative to leaves and rhizomes, respectively (**Figure 17**). Roots sampled from the Mhlanga River also showed the highest Mg level relative to water samples in all three sites.

Lead (Pb)

Lead (Pb) is the most widely distributed non-essential element in plants. Lead is expected to be present in high levels in plants due to similarities with phosphorus and is easily absorbed by plants through phosphate transport. Phosphorus is an essential nutrient for the growth and development of plants. Roots for *P. serratum* sampled at UKZN-Westville and PNR Ponds showed the highest levels of Pb ions relative to the rest of the samples in all three sampling sites (**Figure 18**). The leaves, roots, and rhizomes of *P. serratum* are seen as effective hyperaccumulators of Pb ions. Pb levels in the leaves, roots, and rhizomes between *P. serratum* sampled at the PNR, UKZN-Westville, and Mhlanga River showed no significant difference ($p > 0.05$; **Tables 8** and **9**). The leaves, roots, and rhizomes showed relatively low Mg levels in all three sampling sites (**Figure 18**).

Selenium (Se)

Selenium (Se) is widely distributed in nature, in the soil and rocks, and is required by plants for photosynthesis and growth, protection from extreme temperatures, and heavy

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metal stress. The importance of Se in photosynthesis is evident in the leaves of *P. serratum* sampled at PNR, UKZN-Westville, and Mhlanga River, which showed the highest levels of Se ions relative to the roots and rhizomes sampled from all three sites (**Figure 19**). Leaves of *P. serratum* are seen as effective hyperaccumulators of Se ions compared to the roots and rhizomes. Selenium levels in the leaves, roots, and rhizomes of *P. serratum* sampled at the PNR, UKZN-Westville, and Mhlanga River showed a significant difference ($p = 0.005$; **Table 8**). The leaves showed the highest Se levels relative to the rest of the samples at all three sites (**Figure 19**). Selenium levels between leaves and roots and between leaves and rhizomes sampled at PNR and UKZN-Westville showed a significant difference in all three sampling sites ($p < 0.05$; **Table 9**).

Silicon (Si)

Silicon (Si) is highly abundant and is the second most widely distributed element in the Earth's crust as a silicate mineral. Silicon is expected to be present in high levels in plants and is absorbed for its role in resistance to abiotic stresses. Roots for *P. serratum* sampled at the Mhlanga River showed the highest Si ion levels relative to the rest of the samples in all three sampling sites (**Figure 20**). The roots are seen as effective hyperaccumulators of Si ions compared to the leaves and rhizomes. Silicon levels in the leaves, roots, and rhizomes of *P. serratum* between PNR, UKZN, and the Mhlanga River showed a significant difference ($p = 0.014$; **Table 8**). The roots sampled at the Mhlanga River showed the highest Si levels relative to the rest of the samples at all three sites (**Figure 20**).

Si levels between leaves and roots, leaves and rhizomes, and roots and rhizomes sampled at PNR and UKZN-Westville Ponds showed no significant difference ($p > 0.05$; **Table 9**). The samples from both sites showed relatively low Si levels. Silicon levels between leaves and roots, leaves and rhizomes, and roots and rhizomes sampled at the Mhlanga River showed a significant difference ($p < 0.05$; **Table 9**). The roots showed the highest Si level relative to leaves and rhizomes, respectively. The roots also showed a high Si level relative to the water sample at all three sites.

Table 8: The One-way ANOVA descriptive statistics comparing the significance of different heavy metal levels identified in the leaves, roots, and rhizomes of *Prionium serratum* sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River.

Level (ppm)	F	df	p
Aluminium (Al)	9.612	27	0.002
Calcium (Ca)	48.037	27	0.005
Copper (Cu)	3.392	27	0.015
Iron (Fe)	11.161	27	0.005
Mercury (Hg)	113.588	27	0.005
Magnesium (Mg)	921.220	27	0.005
Lead (Pb)	82.524	27	0.205
Selenium (Se)	51.759	27	0.005
Silicon (Si)	16.132	27	0.014

Note: *The analysis of metals was carried out in triplicate, and the calculations in Tables 8 and 9 were performed using the average value.*

Table 9: The One-way ANOVA Multiple Comparisons descriptive statistics showing the significance of different heavy metal levels in the leaves, roots, and rhizomes of *Prionium serratum* sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River.

HM	Site	(I) Plant part	(J) Plant part	p
Al	PNR	Leaves	Roots	0.155
			Rhizomes	0.375
		Roots	Rhizomes	0.0761
	UKZN-Westville	Leaves	Roots	0.150
			Rhizomes	0.077
		Roots	Rhizomes	0.568
	Mhlanga River	Leaves	Roots	0.030
			Rhizomes	0.005
		Roots	Rhizomes	0.019
Ca	PNR	Leaves	Roots	0.129
			Rhizomes	0.003
		Roots	Rhizomes	0.030

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	UKZN-Westville	Leaves	Roots	0.165
			Rhizomes	0.002
		Roots	Rhizomes	0.010
	Mhlanga River	Leaves	Roots	0.022
			Rhizomes	0.450
		Roots	Rhizomes	0.005
Cu	PNR	Leaves	Roots	0.196
			Rhizomes	0.726
		Roots	Rhizomes	0.818
	UKZN-Westville	Leaves	Roots	0.201
			Rhizomes	0.736
		Roots	Rhizomes	0.087
	Mhlanga River	Leaves	Roots	0.116
			Rhizomes	0.099
		Roots	Rhizomes	0.222

***Table 9** continues …*

HM	Site	Plant part	(J) Plant part	p
Fe	PNR	Leaves	Roots	0.287
			Rhizomes	0.281
		Roots	Rhizomes	0.300
	UKZN-Westville	Leaves	Roots	0.762
			Rhizomes	0.754
		Roots	Rhizomes	0.825
	Mhlanga River	Leaves	Roots	0.008
			Rhizomes	0.012
		Roots	Rhizomes	0.005
Hg	PNR	Leaves	Roots	0.999
			Rhizomes	0.005
		Roots	Rhizomes	0.982
	UKZN-Westville	Leaves	Roots	0.933
			Rhizomes	0.582
		Roots	Rhizomes	0.439
	Mhlanga River	Leaves	Roots	0.628
			Rhizomes	0.398
		Roots	Rhizomes	0.941
Mg	PNR	Leaves	Roots	0.860
			Rhizomes	0.985
		Roots	Rhizomes	0.330
	UKZN-Westville	Leaves	Roots	0.296
			Rhizomes	0.976
		Roots	Rhizomes	0.812
	Mhlanga River	Leaves	Roots	0.005
			Rhizomes	0.012
		Roots	Rhizomes	0.019
Pb	PNR	Leaves	Roots	0.788
			Rhizomes	0.949
		Roots	Rhizomes	0.636
	UKZN-Westville	Leaves	Roots	0.304
			Rhizomes	0.966
		Roots	Rhizomes	0.998
	Mhlanga River	Leaves	Roots	0.911
			Rhizomes	0.354
		Roots	Rhizomes	0.844
Se	PNR	Leaves	Roots	0.006
			Rhizomes	0.003
		Roots	Rhizomes	0.680

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	UKZN-Westville	Leaves	Roots	0.036
			Rhizomes	0.024
		Roots	Rhizomes	0.352
	Mhlanga River	Leaves	Roots	0.337
			Rhizomes	0.134
		Roots	Rhizomes	0.118

***Table 9** continues …*

HM	Site	Plant part	(J) Plant part	p
Si	PNR	Leaves	Roots	0.370
			Rhizomes	0.606
		Roots	Rhizomes	0.354
	UKZN-Westville	Leaves	Roots	0.587
			Rhizomes	0.884
		Roots	Rhizomes	0.971
	Mhlanga River	Leaves	Roots	0.005
			Rhizomes	0.015
		Roots	Rhizomes	0.005

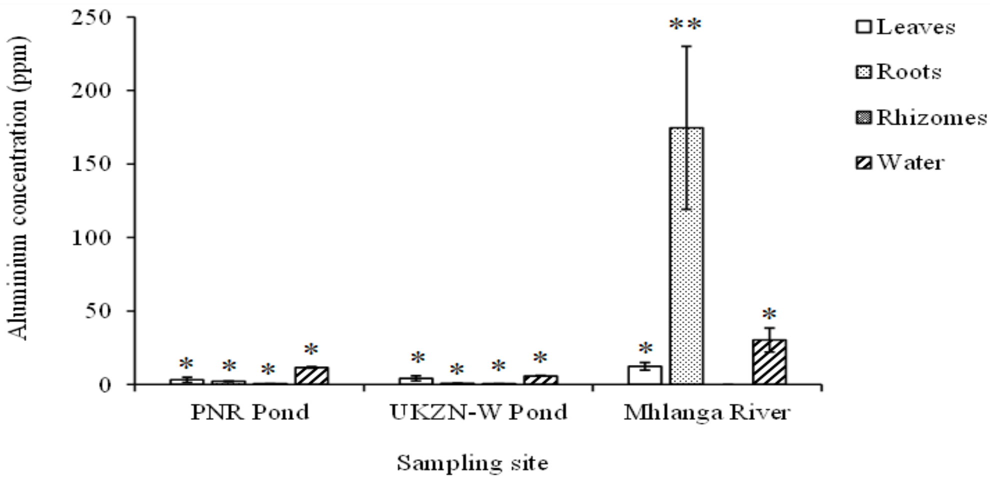

Figure 12: Levels of aluminium accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in the water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Al levels ($p < 0.05$), and a single asterisk indicates significantly low Al levels ($p > 0.05$).

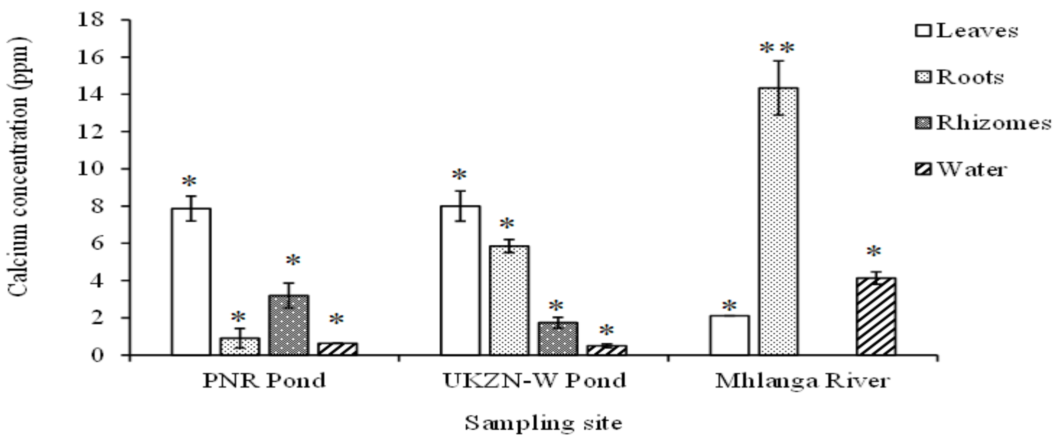

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Figure 13: Levels of calcium accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Ca levels ($p < 0.05$), and a single asterisk indicates significantly low Ca levels ($p > 0.05$).

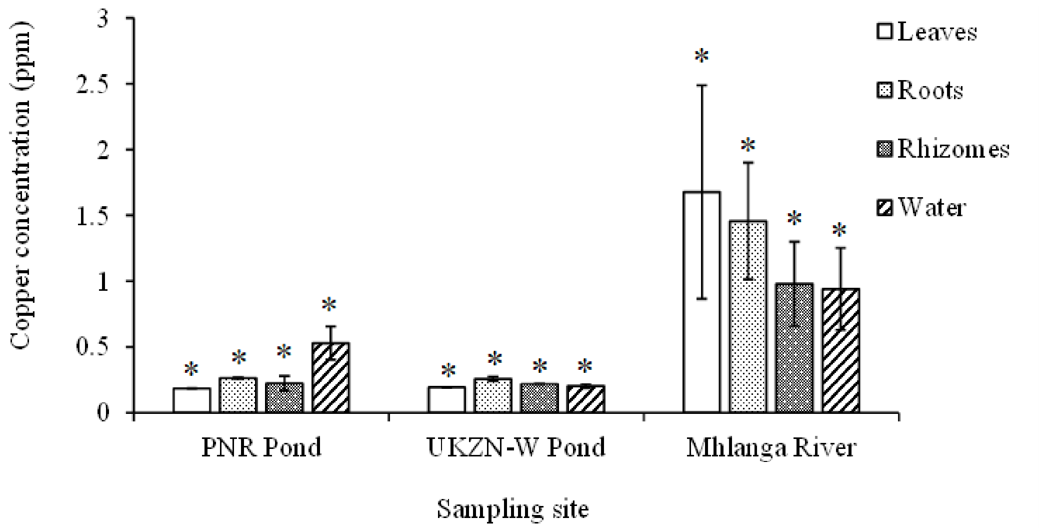

Figure 14: Levels of copper accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in the water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Cu levels ($p < 0.05$), and a single asterisk indicates significantly low Cu levels ($p > 0.05$).

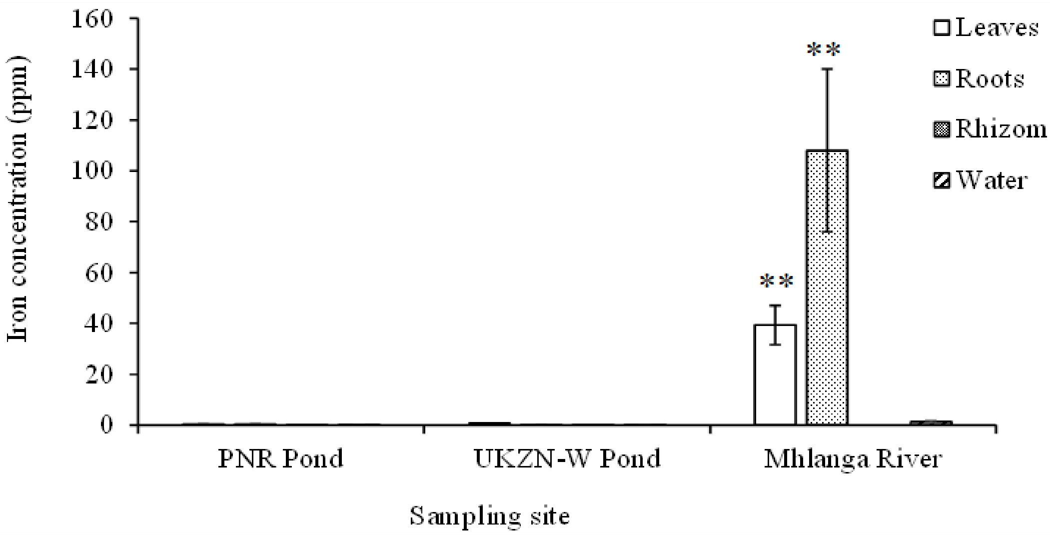

Figure 15: Levels of Fe accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in the water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Fe levels ($p < 0.05$), and a single asterisk indicates significantly low Fe levels ($p > 0.05$).

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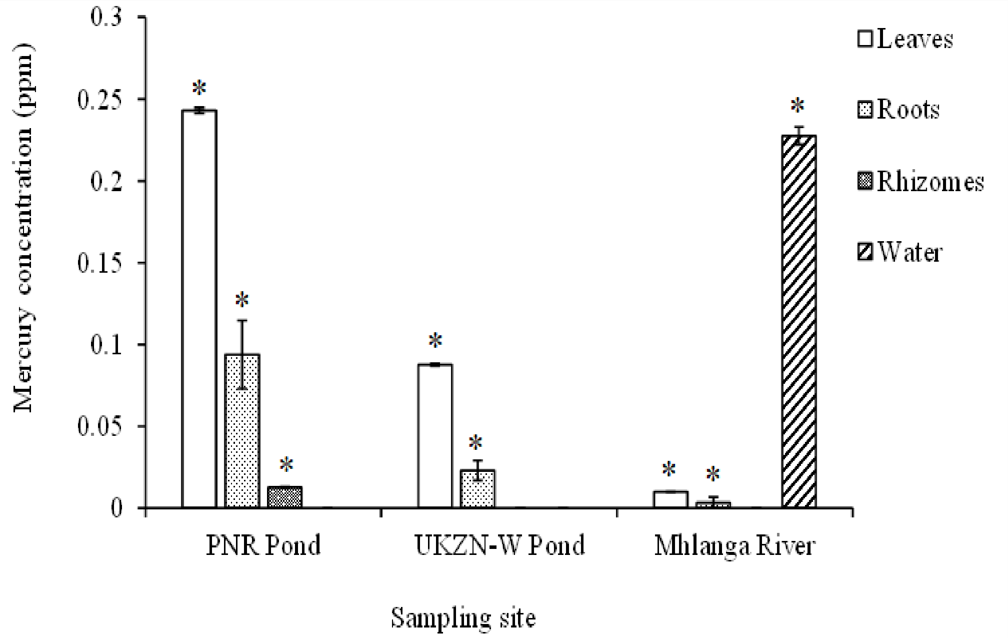

Figure 16: Levels of mercury accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in the water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Hg levels ($p < 0.05$), and a single asterisk indicates significantly low Hg levels ($p > 0.05$).

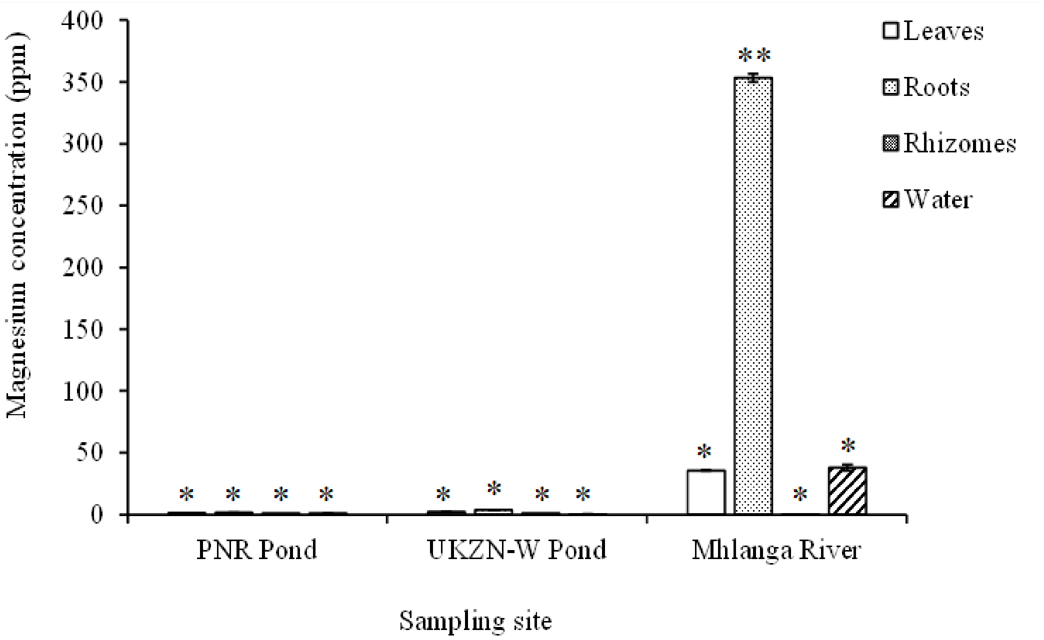

Figure 17: Levels of magnesium accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Mg levels ($p < 0.05$), and a single asterisk indicates significantly low Mg levels ($p > 0.05$).

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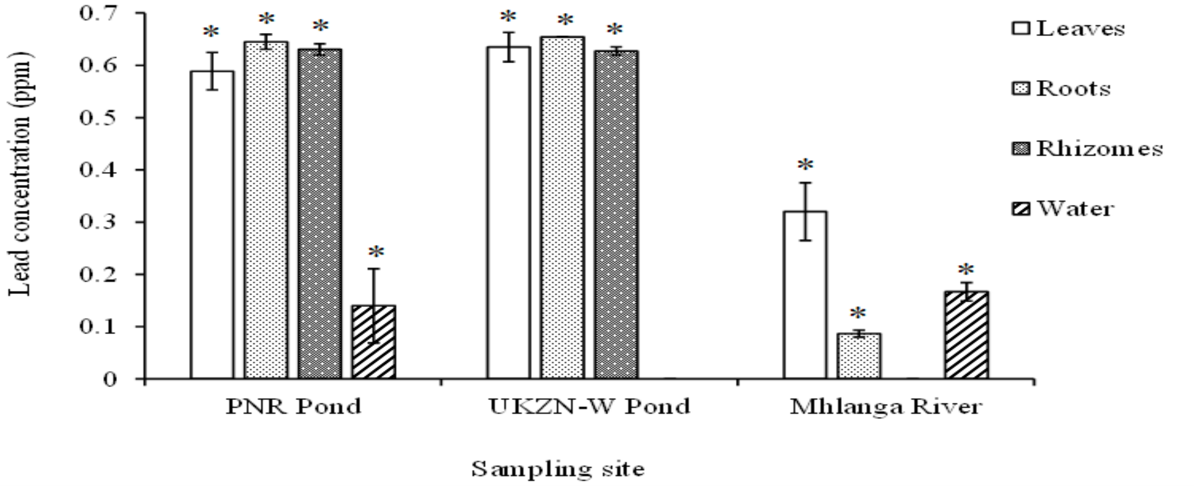

Figure 18: Levels of lead (Pb) accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in the water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Pb levels ($p < 0.05$), and a single asterisk indicates significantly low Pb levels ($p > 0.05$).

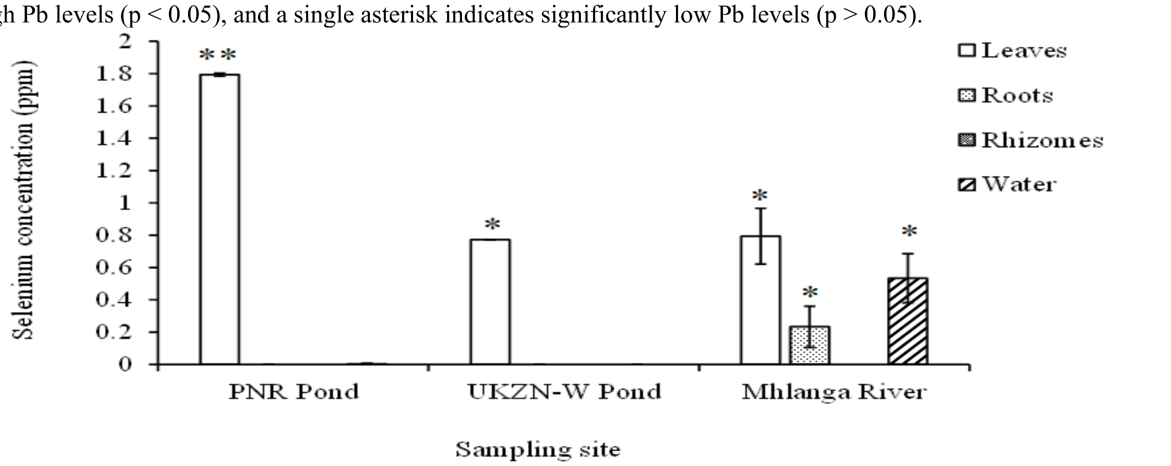

Figure 19: Levels of selenium accumulated in the leaves, roots, and rhizomes (n = 30) of *Prionium serratum* and in the water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Se levels ($p < 0.05$), and a single asterisk indicates significantly low Se levels ($p > 0.05$).

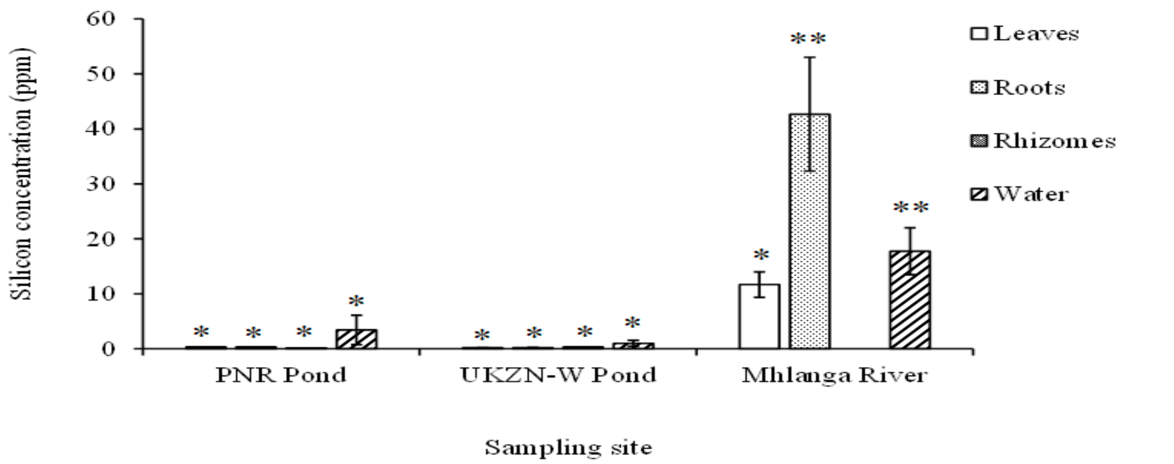

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Figure 20: Levels of silicon accumulated in the leaves, roots, and rhizomes (n = 30*)* of *Prionium serratum* and in the water (n = 9) sampled at PNR Pond, UKZN-Westville Pond, and Mhlanga River. Two asterisks indicate significantly high Si levels ($p < 0.05$), and a single asterisk indicates significantly low Si levels ($p > 0.05$).

DISCUSSION

The results of the chlorophyll content and heavy metals analyses, and water availability are discussed and evaluated to determine their influence on the lack of flowering in *P. serratum*. The chlorophyll content is indicative of the health and stress in plants (Talebzadeh and Valeo, 2022). Low chlorophyll levels (< 30 SPAD Units) may suggest poor photosynthetic efficiency, weaken the plant, and reduce energy available for reproduction, such as flowering (Islam et al., 2014; Zandonadi et al., 2016; Shah et al., 2017). Environmental stressors such as pollution, drought, and nutrient deficiency can impair chlorophyll production, indirectly affecting flowering capacity (Abbas et al., 2021; Seleiman et al., 2021; Mareri et al., 2022).

Heavy metals are potentially toxic and can disrupt physiological plant functions (Rai et al., 2016; Goncharuk and Zagoskina, 2023). The accumulation of heavy metals like magnesium (Mg), silicon (Si), calcium (Ca), selenium (Se), aluminium (Al), lead (Pb), iron (Fe), copper (Cu), and mercury (Hg) can cause toxicity that may damage cellular processes, impair growth and reproduction (oxidative stress), and nutrient uptake interference which can lead to deficiencies that may inhibit flowering (Asati et al., 2016; Kalaivanan and Ganeshamurthy, 2016; Goncharuk and Zagoskina, 2023). *Prionium serratum* exposure to contaminated water or soil can lead to reproductive failure. Moreover, altered hydrological requirements may reduce turgor pressure, which limits nutrient transport (Gonzalez-Dugo et al., 2010; Bitterlich et al., 2018). This may induce stress responses that prioritize survival over reproduction, like flowering, disrupting pollination mechanisms. Identifying whether heavy metals, poor plant health (chlorophyll), or hydrological changes are causing the lack of flowering can guide targeted restoration strategies. If heavy metals hinder flowering in *P. serratum*, water remediation may be needed. If chlorophyll levels are low due to nutrient deficiencies, soil or water enrichment could help. If water scarcity is the problem, habitat management (maintaining water availability) may be critical.

Evaluating the influence of temperature on *Prionium serratum* flowering.

The monitoring of the chlorophyll content is geared towards acting as an effective biomarker to give an indication of the impact of contaminants, borne mainly out of anthropogenic factors, on plant development and can be a biomarker of the effects of exogenous factors, such as increased temperature, on the growth, physiology, and biochemical processes in plants (Cortazar et al., 2015). A chlorophyll content greater than 30 SPAD units is indicative of good plant health, low stress, and sufficient chlorophyll to support photosynthetic functions and flowering (Massa et al., 2015). Due to temperature stress and other environmental stresses, such as the interaction of heavy metals with temperature, plant leaves may become pale yellow (chlorosis) because of reduced chlorophyll content below 30 SPAD units. Reduced chlorophyll concentration to the level of chlorosis may delay or inhibit flowering depending on the affected plant species (Boldt, 2018).

Data collated inferred a generally high chlorophyll content (> 50 SPAD units) in the Mhlanga River, UKZN-Westville, and PNR Ponds from 2020 to 2021. This suggests that chlorophyll, the green pigment in the chloroplasts, was able to capture light energy to facilitate the photosynthetic process, and *P. serratum* leaves were able to carry out photosynthetic functions, including flowering. Leaves are the primary sites of photosynthesis, and they play a vital role in supporting the overall health of the plant, which, in turn, affects its ability to flower (De Bang et al., 2020). Chlorophyll and other photosynthetic pigments are essential for capturing the specific wavelengths of light required for photosynthesis (De Bang et al., 2020). Adequate light is crucial for photosynthesis, and light availability can influence flowering initiation and development (Rai, 2016).

The high chlorophyll content showed that, through photosynthesis, *P. serratum* may have produced carbohydrates, which are essential for resource allocation within the plant. Carbohydrates serve as the building blocks for the formation of flower buds and the production of pollen and nectar in some species (Borghi and Fernie, 2017). This suggests that *P. serratum* may have had adequate carbohydrate availability to support the energy-intensive processes associated with flowering. The production of these sugars through photosynthesis may have signalled to *P. serratum* that it had sufficient resources to invest in flowering and reproduction, suggesting that the flowering of this species may not be inhibited by exposure to the sun or shade. However, photosynthesis, along with other environmental cues such as day length and temperature, did not play a role in the timing of flowering, except for waterlogging. Waterlogging may have played a significant role in the timing of flowering and delayed the production of flowers due to stress linked to hypoxic conditions.

Prionium serratum in the Mhlanga River showed good health, with an average chlorophyll content of > 50 SPAD Units despite exposure to full sunlight. This may suggest that *P. serratum* is adapted to both shaded and sun-exposed environments. If the temperature had affected *P. serratum*, the leaf chlorophyll content would be reduced

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to below 30 SPAD units in the UKZN-Westville Pond and Mhlanga River due to the exposure to full sunlight. In the natural environment, plant species with an average chlorophyll concentration of 30 SPAD units and below are considered chlorophyll-deficient and inefficient at photosynthesis (Johnson et al., 2005; Zhang et al., 2016). This possibly suggests that temperature is not a limiting factor for flowering in *P. serratum* in the UKZN-Westville Pond, PNR Pond, and Mhlanga River and that this species may be efficient at photosynthesizing despite growing under the shaded and sun-exposed areas.

Evaluating the influence of water availability on *Prionium serratum* flowering.

Observations showed that water scarcity stimulated inflorescence growth and flowering in *P. serratum*. However, during the same study period and flowering season, *P. serratum* in the PNR Pond and Mpenjati Nature Reserve swampy forest did not produce flowers due to waterlogging.

The results showed that waterlogging inhibited flowering in *P. serratum*. This was consistent with *P. serratum* populations, which show reproductive failure in swampy habitats in the Mpenjati Nature Reserve. In contrast, *P. serratum* populations growing on well-drained, periodically wet, and dry habitats showed reproductive success. These results contradict the hypothesis by Munyai (2013), which stated that *P. serratum* populations in KZN are not flowering. *Prionium serratum* growing on well-drained sandy loam and sandstone alluvium produces flowers (**Figure 23A–D**). However, it can be noted that herbarium voucher specimens in the Schweickerdt Herbarium (uMtamvuna Nature Reserve), SANBI-KZN Herbarium (NH), Ward Herbarium (UKZN Westville campus), Bews Herbarium (UKZN Pietermaritzburg campus), Killick Herbarium (Ezemvelo KZN Wildlife), and Moss Herbarium (University of the Witwatersrand) collected from swampy grounds, swampy forests, and waterlogged habitats in KZN south coast did not produce flowers (**Figure 24A-B**).

Waterlogging may have resulted in energy deficiency due to the lack of oxygen (anoxia) in the root system of *P. serratum* in the Mpenjati Nature Reserve swampy forests, UKZN-Westville, and PNR Ponds, resulting in the lack of flower production (Millar et al., 2011). However, this species was able to respire through the horizontally creeping stems and adventitious roots, which get exposed above water to absorb O_2 and assimilate CO_2, which in turn assisted in photosynthesis (Millar et al., 2011; Tan et al., 2018). Oxygen absorption is aided by aerenchyma tissues, which allow plant parts that are submerged in water to receive oxygen from non-submerged parts of the plant above water, allowing *P. serratum* to adapt and remain submerged for long periods (Millar et al., 2011; Tan et al., 2018). *Prionium serratum* does not die in a waterlogged environment but is not sexually active, suggesting that this species is adapted to inundated soil and maintains plant-water relations.

Waterlogging may have induced stress, which may have activated stress-response pathways in *P. serratum* to divert resources away from reproductive processes like flowering in favour of survival and recovery mechanisms (Kumar et al., 2020). Anoxia due to waterlogged soil may have disrupted the balance of *P. serratum* hormones, including those involved in flowering regulation, such as auxins, gibberellins, and cytokinins, resulting in reproductive failure (Tan et al., 2018). These results correlate with other plant studies, such as the findings by Ahmed et al. (2002), who noted that waterlogging decreased the yield and inhibited the flowering and seeding of cotton. A study by Wada and Takeno (2010) also found that *Pharbitis nil* and *Perilla frutescens* var. *crispa* produced flowers in response to long days of poor nutrition or low-light intensity. Additionally, the living specimen of *P. serratum* in the Royal Botanic Gardens, Kew, which had been grown in a pot that stood on a pan of water since 1857, never produced flowers (Hooker, 1868), suggesting that *P. serratum* may be supersensitive to waterlogging.

Evaluating the influence of heavy metals on *Prionium serratum* flowering.

Aluminium (Al)

There was a high accumulation of Al levels in the roots relative to the leaves and rhizomes. Aluminium (Al) may have stimulated root growth and promoted the absorption of essential macronutrients such as nitrogen (N), phosphorus (P), and potassium (K) for *P. serratum* growth and development (Bojórquez-Quintal et al., 2017). Aluminium may have increased tolerance to abiotic stress induced by other heavy metals, nutrient deficiency, and pathogen attacks (Panda et al., 2009; Kaur et al., 2016). However, the bioavailability of Al, especially Al^{3+}, depends on a low pH of about 4.3 (Bojórquez-Quintal et al., 2017). The water pH in the Mhlanga River ranged from 4.5 to 7.8, with some patches of mud ponds on the river edges averaging a pH of 4.5 and 7.8 in the middle of the river. This pH range may have facilitated the absorption of Al ions in this habitat. *P. serratum* roots are seen as effective hyperaccumulators of Al ions, as shown by high Al levels in the roots.

Prionium serratum may have absorbed low levels of Al ions because, at low concentrations, Al has roles in the growth and biomass of plants, such as stimulating root and shoot growth (Bojórquez-Quintal et al., 2017; Rahman et al., 2018). Aluminium ions at low concentrations could also indirectly influence flower setting in plants as it enhances metabolism and modulate flower colour (Rahman et al., 2018). Khan et al. (2021), Katz et al. (2021), and Pavlovic et al. (2021) said that Al is one of the

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essential micronutrients for plant growth and development after nitrogen (N), phosphorus (P), and potassium (K), which could also explain high Al ion accumulation by roots in the Mhlanga River. Thus, *P. serratum* possibly absorbed Al by the roots and translocated it to the shoot system as a nutrient to assist in the growth of this species.

Moreover, the accumulation of low Al levels in UKZN-Westville and PNR Ponds could possibly be due to amino acids, chelation, and compartmentalization mechanisms as an adaptation strategy to tolerate stress. Through the avoidance mechanism, plants prevent toxic heavy metal ions from travelling through the plasma membrane (Tong et al., 2004; Yang et al., 2005; Thakur et al., 2016). Amino acids such as histidine, serine, aspartic acid, and isoleucine increase in the xylem as a tolerance to heavy metals (Krämer et al., 1996; Callahan et al., 2006). During the chelation and compartmentalization mechanisms, Al is converted to non-toxic Al-oxalate in roots and translocated to leaves (Ma, 2007). In the leaves, excess phytotoxic Al ions were possibly translocated into old leaves, which became pale yellow and senesced during natural leaf shedding, which was supported by observations by Ernst et al. (1992) and Thakur et al. (2016).

Calcium (Ca)

There were the highest Ca levels in the roots of *P. serratum* sampled at the Mhlanga River. This may have resulted from the abundance of this element in nature and thus found in every plant in large concentrations due to its importance in growth (Van der Hoven and Quade, 2002). White and Broadley (2003) noted that plants also absorb Ca through the symplastic movement of water, which is aided by plasmodesmata through the cytoplasmic cells or through the apoplast movement (spaces between cells). Therefore, this element is always present in every plant and is required by plants in low to large concentrations for growth, maintenance of photosynthetic chlorophyll content, strengthening of the cell wall, and protection from heavy metal stress (Kumar et al., 2010; Chang et al., 2012; Oloo-Abucheli et al., 2016; Ahmad and Rab, 2019). Calcium's roles in photosynthesis are evidenced by the accumulation of high levels of Ca ions in the leaves of *P. serratum* sampled at UKZN-Westville and PNR Ponds. The roots and rhizomes possibly served as storage organs to maintain the presence of calcium for strengthening the cell wall and the general growth of *P. serratum* in all three sites, especially in the Mhlanga River. This possibly highlights that the Mhlanga River had high Ca levels, which could also be attributed to anthropogenic and enrichment factors such as fertilizers, wastewater, and weathering of rocks and minerals from the soil.

The lack of flower setting in non-flowering *P. serratum* may not be attributed to Ca toxicity. Plants, like *P. serratum,* require Ca for chlorophyll and photosynthesis. Most of the calcium was possibly stored in the roots and translocated into the leaves to maintain chlorophyll content and effective photosynthesis for growth and development. This is evidenced by the high Ca levels in the roots sampled at the Mhlanga River. Moreover, Ca is one of the essential micronutrients for plant growth and development after nitrogen (N), phosphorus (P), and potassium (K), hence its high accumulation by roots (Khan et al., 2021; Katz et al., 2021; Pavlovic et al., 2021). Therefore, this element may not necessarily inhibit the flowering of *P. serratum*.

Copper (Cu)

Copper was accumulated in relatively low concentrations in all three sites, probably due to requirements in low concentrations by plants for normal growth and development (Lindsay and Norvell, 1978; Puri and Kumar, 2012; Ramlal et al., 2021). Low Cu concentrations are sufficient to enhance photosynthesis, growth, and flower setting in plants (Yruela, 2005). Copper is generally an essential micronutrient that is required at low levels for many enzymatic activities, including chlorophyll, flower, and seed production, as well as enhanced yield (Printz et al., 2016). Therefore, the lack of flower setting in non-flowering *P. serratum* in the UKZN-Westville and PNR Ponds may not be attributed to Cu toxicity in these sites. The roots and rhizomes possibly serve as storage organs to maintain and control low levels of Cu in the shoot system to prevent phytotoxicity. However, Cu toxicity rarely occurs in plants (Pietrini et al., 2019), which may also suggest that the lack of flower setting in no-flowering *P. serratum* in the UKZN-Westville and PNR Ponds may not be attributed to Cu toxicity. The lack of Cu, which was not observed in *P. serratum* in all three sites, causes deficiency syndrome, which affects the chlorophyll of young leaves and reproductive organs and consequently lacks flower setting (Yruela, 2005).

Iron (Fe)

There were low levels of Fe in the leaves, roots, and rhizomes of *P. serratum* sampled in the UKZN-Westville and PNR Ponds. The roots sampled at the Mhlanga River showed the highest Fe levels. This possibly shows the essential roles of Fe in plants, such as the production of chlorophyll for enhanced photosynthesis and the production of high biomass (Xing and Liu, 2011). Iron (Fe) is expected to be present in any plant species due to its roles in chlorophyll synthesis and enzymatic and metabolic processes (Schmidt et al., 2020). Iron is one of the essential micronutrients for plant growth and development after nitrogen (N), phosphorus (P), and potassium (K), hence the high accumulation by roots and leaves sampled at the Mhlanga River (Khan et al., 2021; Katz et al., 2021; Pavlovic et al., 2021).

Moreover, Fe is among the essential heavy metals for plants due to its role in helping plants tolerate environmental stress, assisting in chloroplast and deoxyribonucleic acid (DNA) synthesis, respiration, and photosynthesis (Wintz et al., 2002; Schmidt et al., 2020; Rout and Sahoo, 2015; Marzorati et al., 2022). However, Fe is toxic to plant physiology and metabolic processes in acidic soils or water (Rout and Sahoo, 2015). The excess Fe accumulation above optimal levels usually occur in acidic soils and damages cell membranes through lipid peroxidation due to high levels of hydrogen peroxide (H_2O_2), causing reactive oxygen species (ROS), necrosis, chlorosis, and complications in plant metabolism related to stress (Laan et al., 1991; Minina et al., 2013; Rout and Sahoo, 2015; Zahra et al., 2021).

Therefore, Fe possibly did not inhibit flowering or cause toxicity to *P. serratum* in these pH ranges but served as a source of nutrients. Thus, the lack of flower setting in non-flowering *P. serratum* in UKZN-Westville and PNR Ponds may not be attributed to Fe toxicity. The accumulated Fe levels in the leaves, roots, and rhizomes of *P. serratum* were possibly optimal to improve chlorophyll content, photosynthetic rate, stomatal conductance, transpiration rate, carbon dioxide (CO_2) sequestration, nutrient uptake, and growth (Schmidt et al., 2020; Wang et al., 2022). However, more studies should be conducted on the effect of Fe on the growth, development, and flowering of *P. serratum*.

Mercury (Hg)

Anthropogenic activities such as the burning of medical and municipal waste, paint, and Hg-containing products, and electronic waste may have resulted in the observed Hg levels in the leaves of *P. serratum* in the PNR Pond (Driscoll et al., 2013). This is because Mercury (Hg) is a volatile substance at room temperature $\geq 25\ ^{\circ}C$ (Hojdová et al., 2015; Saturday, 2018).
The accumulation of atmospheric Hg can be seen by the high levels of Hg shown in the leaves sampled in the PNR Pond. The water samples showed high Hg levels relative to leaves, roots, and rhizomes in the Mhlanga River and possibly accumulated naturally occurring and atmospheric Hg. Mercury has no physiological or metabolic benefits for plants and is accumulated in relatively low concentrations to prevent its phytotoxicity (Asati et al., 2016; Gworek et al., 2020). This was evidenced by low Hg levels in a range between 0.01 and 0.24 ppm in all three sample sites. The lack of flower setting in non-flowering *P. serratum* may not be attributed to Hg phytotoxicity.

Magnesium (Mg)

The roots sampled at the Mhlanga River accumulated the highest Mg levels relative to the rest of the samples at UKZN-Westville and PNR Ponds. The high Mg levels in the roots sampled at the Mhlanga River could be attributed to natural rock weathering, overland flow through agricultural fields, and sewage water flow (Kumar et al., 2022). Magnesium is one of the essential micronutrients for plant growth and development after nitrogen (N), phosphorus (P), and potassium (K), hence its high storage and accumulation by roots (Khan et al., 2021; Katz et al., 2021; Pavlovic et al., 2021).
Magnesium (Mg^{2+}) serves as a central component of chlorophyll, which plants depend on to capture photosynthetic sunlight for CO_2 assimilation (Cakmak and Kirkby, 2008; Cakmak and Yazici, 2010; Hauer-Jákli and Tränkner, 2019; Ye et al., 2019). Magnesium is involved in a plethora of cellular activities, such as protein synthesis, cell proliferation, DNA synthesis and repair, and mitotic spindle formation (Hermans et al., 2013). Moreover, Mg is a core essential element for chlorophyll production and has crucial roles in a myriad of physiological and biochemical processes throughout plant growth and development (Ishfaq et al., 2022). Plants secrete Mg in root cells for energy generation, enzyme activation or inactivation, nucleic acid synthesis, and numerous other fundamental biochemical processes (Niu et al., 2014). This is evidenced by the high Mg levels in the roots sampled at Mhlanga River relative to the leaves and rhizomes, suggesting that *P. serratum* possibly secreted Mg in the roots and translocated small concentrations of Mg to the shoot system for chlorophyll synthesis. Moreover, *P. serratum* may have secreted Mg in the roots to enhance the resistance of root tissues to pathogen attacks and rotting (Huber and Jones, 2012). Thus, *P. serratum* roots are seen as effective hyperaccumulators of Mg ions.

With a deficiency in Mg, the plant cannot perform cell membrane stabilization, and the leaves would become pale yellow due to chlorosis and subsequently be inefficient for photosynthesis (Ishfaq et al., 2022). There are no specific magnesium levels required by plants for growth and development. Thus, even at low concentrations, Mg promotes high flowering intensity and high fruit setting in plants (Alcaraz-Lopez et al., 2003). Moreover, Mg is required for physiological processes, and the accumulated concentrations in *P. serratum* may have been sufficient for such processes as flowering, fruiting, or seed setting. Thus, the high accumulation of Mg by roots could be related to the benefits that magnesium provides to *P. serratum*.

Lead (Pb)

Lead (Pb) joins chromium (Cr) with unknown biological functions in plants (Aziz et al., 2015; Collin et al., 2022). Lead is widely distributed in the soil and is the second most phytotoxic heavy metal after arsenic, even at lower concentrations (Pourrut et al., 2011; Zulfiqar et al., 2019; Collin et al., 2022). The leaves, roots, and rhizomes of *P. serratum* possibly absorbed low Pb levels to prevent toxicity in all three sampled sites. Sources of Pb in sampled sites could include natural weathering, Pb-based

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paints, and atmospheric Pb from gasoline or exhaust fumes. The Pb concentrations from these sources are expected to be low and range between 0.1 and 10 ppm, with no negative effects on plant growth (Khatik et al., 2006). Therefore, the recorded Pb concentration range of 0.09–0.65 ppm in *P. serratum* in all three sampled sites was between the acceptable concentrations in plants. Thus, the lack of flower setting in non-flowering *P. serratum* in the UKZN-Westville and PNR Ponds may not be attributed to Pb toxicity. However, the interacting effects of Pb with other heavy metals, temperature, and waterlogging on *P. serratum* are unknown.

Selenium (Se)

The sources of selenium (Se) may include the soil, weathering of rocks, deposition during precipitation, and runoff from land when it rains, especially in the PNR Pond. Plants generally confuse Se with Sulphur due to structural similarities (Hasanuzzaman et al., 2010). However, Se ions are absorbed in low concentrations via Sulphur transporters within the roots and transported to the shoot system (Hasanuzzaman et al., 2010; Gupta and Gupta, 2017). Selenium increases photosynthetic pigments at optimal levels, which in turn protects the chlorophyll from sunlight and has important roles in photosynthesis and the growth of plants (Lanza and Reis, 2021). This is possibly shown by the accumulation of high Se levels in the leaves of *P. serratum* in all three sampled sites. Selenium not only assists in the physiological and biochemical processes of plants but also in the mitigation of abiotic stresses such as elevated temperature, hence the high accumulation in the leaves relative to roots and rhizomes (Lanza and Reis, 2021).

Germ and Stibilj (2007) and Lanza and Reis (2021) noted that selenium accumulation inhibits damage related to extreme sunlight intensity or UV-induced oxidative stress, balances plant-water relations, improves tolerance to heavy metal and salinity stress, and delays senescence. However, senescence could be important for *P. serratum* in reducing phytotoxic ions of Se from the leaves. This would protect chlorophyll for effective photosynthesis and plant growth. The lack of flower setting in non-flowering *P. serratum* in the UKZN-Westville and PNR Ponds may not be attributed to Se due to concentrations below 6 ppm. Selenium concentrations lower than 6 ppm are beneficial to plant growth and development and enhance flower settings (Shekari et al., 2019). The accumulated Se levels in the leaves of *P. serratum* in all three sampled sites were generally low, ranging between 0.23 and 1.79 ppm. Additionally, Se levels in the leaves could be due to translocation to the shoot system as an adaptation strategy to reduce Se toxicity through transpiration or the removal of leaves with high Se concentrations during senescence.

Silicon (Si)

Construction materials such as sand and rocks may be the main sources of silicon (Si) in the UKZN-Westville and PNR Ponds. Silicon in the Mhlanga River may be naturally occurring. Si has no known essential benefits for physiological and biochemical processes in plants (Fiala et al., 2021; Khan et al., 2021; Pavlovic et al., 2021). However, Si may not assist plants at a physiological or biochemical level but may be involved in environmental stress resistance (Pavlovic et al., 2021). This was evidenced by the accumulation of high Si levels in the roots sampled at the Mhlanga River, which possibly assisted parenchyma tissues in the root system to store and assimilate unused heavy metals released as waste products, thereby reducing their phytotoxicity. Silicon assists plants to adapt and enhance resistance to environmental stress such as salt, drought, and heavy metal stress, with no known direct physiological benefits to flower setting or growth (Cavins et al., 2010; Janislampi, 2012; Luyckx et al., 2017; Daoud et al., 2018). Therefore, the accumulated Si levels in the roots may assist *P. serratum* in adapting to abiotic stress conditions other than growth or flowering. This allows normal plant growth and development, which may indirectly contribute to flowering.

There are numerous reports that the accumulation of Si ions promotes root growth, water uptake, optimal growth, and the development of plants (Ma, 2005; Ma, 2009; Ma et al., 2011; Fiala et al., 2021; Katz et al., 2021; Zhou et al., 2021). Frantz et al. (2011) and Khan et al. (2021) reported that Si competes with essential elements in the soil that are assimilated by plants, such as Al, Fe, Ca, Mg, N, P, and K, which results in the accumulation of Si ions together with essential elements. This is evidenced by the high Si levels in the roots sampled at Mhlanga River relative to the rest of the samples at all three sites. Likewise, since Si has no physiological or biochemical benefits to plants, this could explain the accumulation of low Si levels in the range between 0.19 and 0.34 ppm in the UKZN-Westville and PNR Ponds. Therefore, the lack of flower setting in non-flowering *P. serratum* in all three sampled sites may not be potentially attributed to silicon toxicity.

Evaluation of the possible drivers of *Prionium serratum* decline in KZN.

Heavy metals may not have inhibited flower setting in non-flowering *P. serratum*. Although live flowering *P. serratum* specimens were not observed during the study period, herbarium specimens of *P. serratum* in the South African National Biodiversity Institute-KwaZulu-Natal Herbarium (SANBI-KZN Herbarium, or NH) that were collected by various researchers from 1937 to 1986 in the Mhlanga River, including the Ifafa River, Mbizana River, Oribi Gorge Flats, Oribi Gorge District, Uvongo River

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crossing, The Valleys Farm, St. Michael's on Sea, Mr. D. E. Mitchell's farm near South Broom, Port Edward in the swampy ground along the rivers, uMtamvuna River, uMtamvuna Nature Reserve, the greater Port Shepstone District, and up to Kromrivier wetlands (periodically wet and dry) along R62 and Krugersland in Eastern Cape, have flowers.

Moreover, current *P. serratum* populations on the south coast of KZN and greater Eastern Cape are also flowering (**Figures 21A – B** and **23A – D**), except for those populations that are growing in swamp forests and waterlogged soils and habitats in Mpenjati Nature Reserve, in swampy grounds along the Zolwane and Sandlundlu Rivers in Port Edward, and in stagnant water bodies in which this species is cultivated in dams and ponds, such as in UKZN-Westville and PNR (**Figures 21C – D**, **22A – B** and **24A – C**). This shows that naturally occurring populations of *P. serratum* in well-drained soils produce flowers in the KZN coastal regions. These results are contrary to the findings of Munyai (2013), who stated that *P. serratum* populations in KZN lack flower setting. However, only waterlogged and growing in a swamp forest, *P. serratum* populations that do not produce flowers. Heavy metals possibly provided a primary source of nutrients for the growth of *P. serratum*. However, these results agree with the fast decline of *P. serratum* populations in KZN, which was mentioned by Sieben (2012), Munyai (2013), and Job (2014). Heavy metals are possibly not the cause of the decline of *P. serratum* in KZN's south coast, except harvesting for medicine (**Figure 25A – F**), consumption by the homeless and locals (**Figure 26**), erosion during flooding (**Figure 27A – C**), living land expansion, the building of malls, housing development, waterlogging, and harvesting for a pigsty.

Figure 21: *Prionium serratum* growing naturally along the Mtentweni River (30°42'21.1" S, 30°28'54.0" E), Port Shepstone, south coast of KZN, approximately 100 m from the Mtentweni River mouth, and producing flowers (**A** – **B**). *Prionium serratum* growing in the PNR (**C**) and UKZN-Westville ponds (**D**) in a waterlogged concreted area and not producing flowers. Image credit: Lee D'Eathe (**A**, **B**) and Linda Masuku (**C**, **D**).

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Figure 22: *Prionium serratum* growing in a stagnant pond under tree canopy shade inside the PNR.

Figure 23: Herbarium voucher specimens showing *Prionium serratum* producing flowers in the Port Shepstone area from the Mbizane River (**A**), St. Michael's on Sea (**B**), the Uvongo River crossing (**C**), and Umtamvuna Nature Reserve (**D**). In these localities, *Prionium serratum* grows on riverbanks and well-drained riverbeds.

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Figure 24: Herbarium voucher specimens showing the lack of flowering in *Prionium serratum* growing in riverbeds with stagnant water in the Mhlanga River towards St. Michael's on Sea (**A**), swampy low-lying ground in Port Shepstone, north of Port Edward (**B**), and swampy forests inside Mpenjati Nature Reserve (**C**).

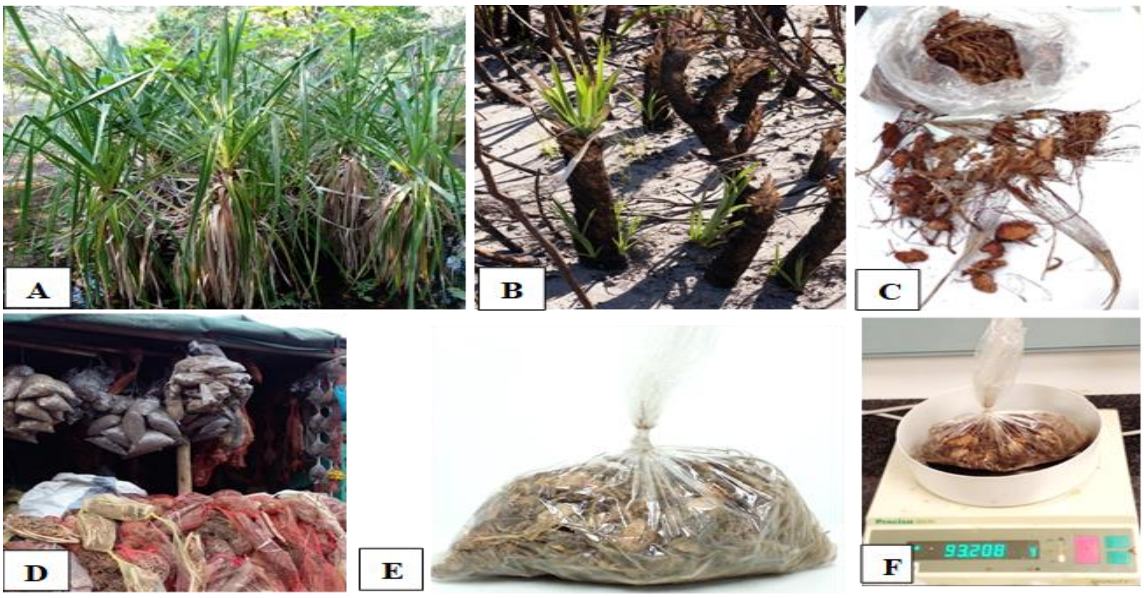

Figure 25: *Prionium serratum* (**A**) stems are harvested from the wild (**B**), dried (**C**), and cut into small pieces for usage in traditional medicines and traded in the Muthi markets (**D**). A 93.208 g packet of *Prionium serratum* dried stem chops sells for R20 each in the Victoria Street Muthi market, eThekwini Municipality (**E** – **F**). Source for image (**B**): Carina Lochner, 2019. Palmiet (*Prionium serratum*). Access on 25 March 2023. Available on iNaturalist at https://www.inaturalist.org.

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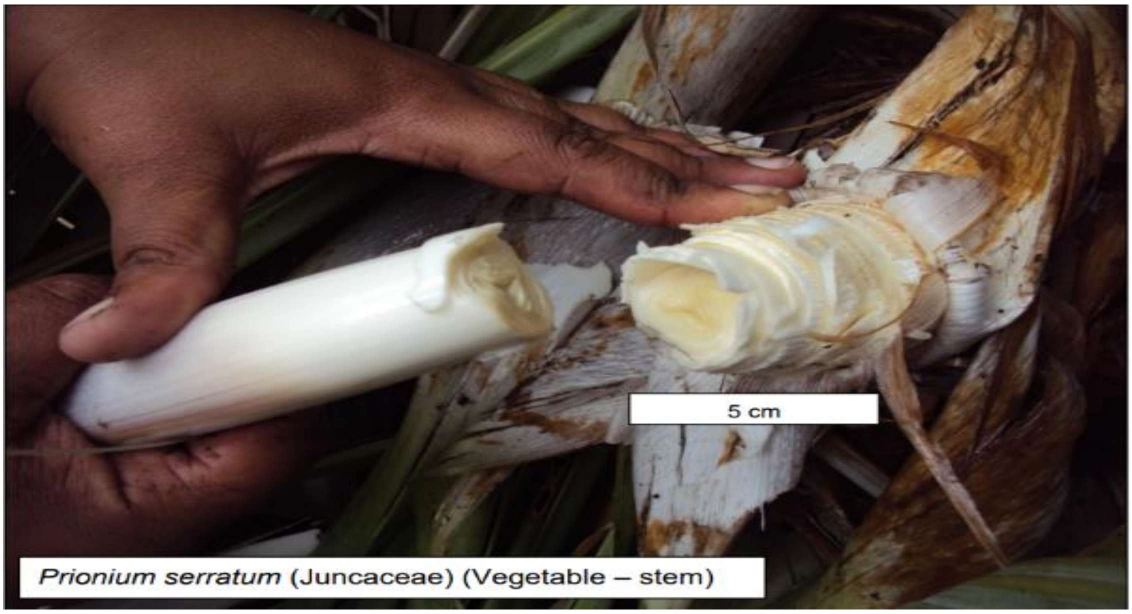

Figure 26: The edible inner part of *Prionium serratum* stem is most consumed by the homeless and locals on the south coast of KwaZulu-Natal. **Source:** De Vynck (2014).

Figure 27: Naturally occurring *Prionium serratum* plantlets or seedlings in the Mhlanga River, Ugu District Municipality. In all cases, individuals are leaning towards the direction of the water flow.

Restoration of *Prionium serratum* and Conservation in the Palmiet River system.

The populations of *Prionium* are morphologically similar across their habitats (Munyai, 2013). The complexity of plant population genetic structure is driven by gene flow and selection processes (microevolutionary forces), mating systems, modes of dispersal, reproduction, and the phylogenetic history of populations (Hamrick et al., 1992; Schaal et al., 2003; Munyai, 2013). The role of these forces is unknown in *Prionium,* as other factors may account for the lack of genetic variability. Moreover, the uniform morphology and the lack of genetic diversity in *P. serratum* are not well understood. Munyai (2013) mentioned that the lack of DNA sequence variability may be linked to the *Prionium* life form, but it is bizarrely low for a lineage with an Oligocene stem age. However, *P. serratum* is presumed to have high genetic diversity between populations and low diversity within populations (Munyai, 2013). Thus, there is a low level of gene flow within the populations of *P. serratum* due to a lack of genetic exchange and dispersion of favourable alleles between populations (Munyai, 2013).

This low genetic diversity may be restricting the range of *P. serratum* and resulting in habitat specialization, such as oligotrophic environments and wetlands. Additionally, *P.*

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serratum populations are adapted to periodically wet and dry habitats, hence, a history of occurrence in the PR system (**Figure 28**). *Prionium serratum* establishment in the PR system is not limited by genetic diversity, which may affect the survival in *in-situ* conditions. Re-introduction is the main factor limiting the restoration and conservation of this species. *Prionium serratum* does not occur in the PR system because it has not been reintroduced. *Prionium serratum* and other species of Thurniaceae are associated with both entomophilous (insect) and anemophilous (wind) pollination due to flower characteristics (Cook, 1988; Silva et al., 2020). However, during this study, the thick-billed weaver (*Amblyospiza albifrons*) was also observed dispersing the seeds and frequently visiting *P. serratum* flowers in the early mornings and late afternoons. This suggests that *P. serratum* distribution may not be limited by pollination, reproductive success rates, or seed dispersal vectors. The seedlings of this species can establish in both disturbed and natural habitats, such as in PNR and UKZN-Westville Ponds.

The PR receives heavy metal pollution and myriads of water pollutants from the Pinetown-New Germany industrial area. The inputs from sewage, industrial effluents, and solid waste may lead to reduced population densities. However, the correlation between pollutant loads to *P. serratum* health and regeneration capacity has never been explored. *Prionium* and all Juncaceae members, apart from the genus *Juncus*, lack silica bodies in vascular bundle sheath cells (Prychid et al., 2004). However, silica bodies are present in the genus *Thurnia* (Thurniaceae) as small, spherical bodies (Cutler, 1965; Prychid et al., 2004). Silica bodies control and regulate the uptake of toxic heavy metals, which allows for photosynthesis, growth, and development of plant species in stressed environments (Dabney et al., 2016). This makes *P. serratum* vulnerable to heavy metal exposure, which possibly contributed to the decline of this species in the PR system due to the absence of silica bodies (Dabney et al., 2016).

Adaptations such as high silica content may not be a limiting factor to *P. serratum* growth and positive response to environmental stressors due to the presence of other adaptations like thick stems and flexible shoots, which suggest resilience to flooding and fire. The physiological response of *P. serratum* to fluctuating water regimes, drought, and fire suggests adaptation to periodically wet and dry environments. During this study, this species produced inflorescence and flowers when subjected to drought but not in waterlogged conditions. In Palmiet wetlands in Krugersland, and along the Kromrivier in the EC, there are die-backs of *P. serratum* after fires (own observations, **Figure 29**), suggesting adaptation to such stressors.
Prionium serratum reduces erosive damage and retains water in floodplains, such as in Palmiet wetlands (Boucher and Withers, 2004; Sieben, 2012; Rebelo and Cowling, 2013; Rebelo, 2018). However, in the Mhlanga River system, variation in soil water content affected the distribution and influenced the patchiness of *P. serratum*. High groundwater level and waterlogged soils (highly saturated with water) resulted in the washaway of this species during heavy rains and flooding, which may affect the restoration success in the PR system. This species has a fibrous root system instead of a tap root (Boucher and Withers, 2004).

Alien woody species invasion may outcompete *P. serratum* due to its fibrous root system. Land misuse and increased stormwater runoff contribute to habitat degradation and hydrological alterations affecting *P. serratum* habitats. Concrete surfaces are primary contributors to the large water volumes entering the PR during rainy days and seasons (Naidoo, 2005). Increased area of concreted surfaces increases stormwater runoff, which may result in the erosion and washaway of this species due to its fibrous root system. *Prionium serratum* populations are declining in KwaZulu-Natal due to harvesting for plant medicines, food, flooding and waterlogging, and habitat degradation from frequent fires and overgrazing. Nonetheless, this species is listed as Least Concern (LC) due to localized declines (KZN).

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Figure 28: The last living specimen of *Prionium serratum* that was observed along the PR inside the PNR, northwest of the main entrance. This species was formerly abundant along the PR system; this was the last and only observed specimen in 1979, which the public was urged to protect. Image credit: Lee D'Eathe.

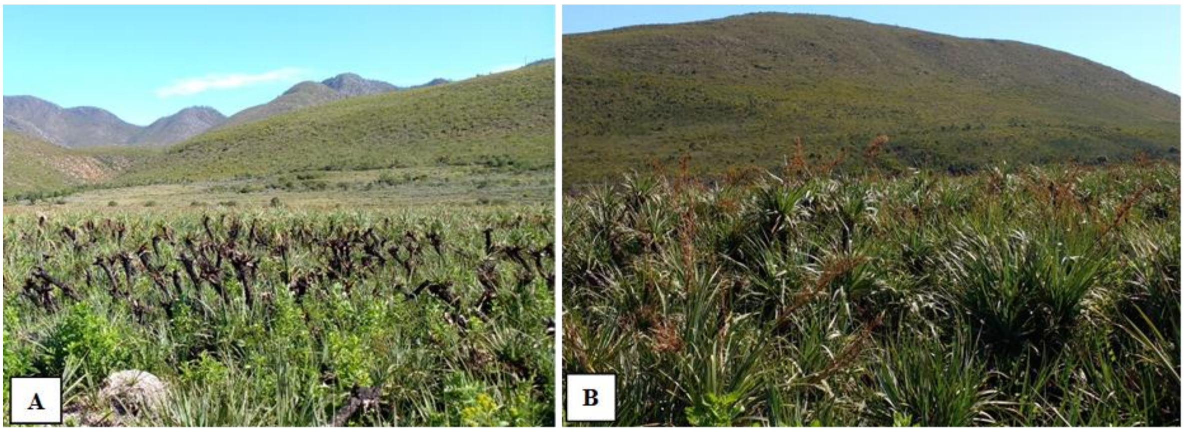

Figure 29: *Prionium serratum* subjected to fires (**A**) as an environmental stressor in Palmiet wetlands and later dying-back and producing inflorescence and flowers (**B**) in Krugersland, Eastern Cape.

CONCLUSIONS

The chlorophyll content of *P. serratum* was greater than 30 SPAD units in all sampled sites, which was indicative of good health, low stress, and sufficient chlorophyll to support photosynthetic functions and flowering. The lack of flowering in *Prionium serratum* was not influenced by exposure to sunlight or shade, as shown by high chlorophyll content, which suggested that this species was efficient at photosynthesis, including the production of flowers under these conditions. Thus, flowering in this species may not be inhibited by exposure to the sun or shade. The null hypothesis, which stated that temperature has no influence on the flowering of *P. serratum,* was therefore accepted.

Waterlogging inhibited and delayed flowering in *P. serratum* at PNR Pond. Water scarcity and drought triggered and promoted flowering in *P. serratum* at UKZN-Westville Pond. Waterlogging also inhibited the flowering of naturally occurring *P. serratum* populations in swampy forests in Mpenjati Nature Reserve. *Prionium serratum* growing in riverbanks and periodically wet and dry habitats produced flowers. Waterlogging has emerged as a significant factor influencing flower setting in *P. serratum*. Prolonged waterlogging periods disrupt the hormonal regulation required for flower initiation and development, ultimately leading to reduced reproductive success. However, this was not explored in relation to *P. serratum* and is an avenue that needs to be investigated further, along with the genetic aspects of flowering. Understanding the implications of waterlogging on flower setting in *P. serratum* is vital for informing wetland management, restoration, and conservation strategies

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aimed at preserving the ecological integrity of these important ecosystems.

Prionium serratum was unaffected by heavy metals; it is possible that heavy metal toxicity does not prevent flowering in this species. The null hypothesis, which claimed that heavy metals have no effect on flower bud development and flowering of *P. serratum*, was accepted. However, *P. serratum* might be sensitive to exposure to heavy metals, and its range might be constrained close to the sources of industrial contamination and heavy metal pollution. The absence of silica bodies, which absorb and convert heavy metals into a non-toxic form in *P. serratum*, is particularly noteworthy. However, *P. serratum* has parenchyma tissues in the root system that store and digest unneeded heavy metals released as waste products, lowering their phytotoxicity. This species has the potential to adapt physiologically to situations that are acidic and polluted with heavy metals.
The hypotheses which stated that neither temperature nor heavy metals has an influence on the flower setting of *P. serratum* were accepted; only water availability influenced flowering in this species.

Successful restoration of *P. serratum* requires a periodically wet and dry environment throughout the year, not an inundated or waterlogged habitat, for growth and development as well as flower setting. Waterlogging creates an anaerobic soil condition that disrupts the physiological metabolism of *P. serratum,* resulting in the inhibition of flowering. *Prionium serratum* is adapted to a range of soil and habitat types with varying pH levels, suggesting no special soil requirements. This species may not occur in non-*P. Serratum* habitats are limited by dispersal and have not been introduced to new or former habitats, nor by environmental factors such as soil type, salinity, or acidity. This species can grow in clay soil, any soil type, and waterlogged soils. This is the case for the two Durban populations that grow in waterlogged scenarios. However, *P. serratum* cannot sexually reproduce under these conditions, provided the soil is well-drained.

LIMITATIONS

While this study provides valuable insights into the conservation, propagation, and initial establishment of *P. serratum*, findings are constrained by the short-term nature of the project relative to the life cycle of this species. There may be a lack of comprehensive historical data on the original extent, density, and health of *P. serratum* populations in the PR system, making it challenging to set accurate restoration targets. The precise hydrological requirements, such as ideal water depth in the habitat, flow velocity tolerance, and scour tolerance for different life stages of *P. serratum,* might not be fully known, leading to trial and error. The study was also limited by a stochastic event, catastrophic flooding in the Mhlanga River, which severely impacted the study as it may have scoured out all mature members of *P. serratum* that were ready to flower during the study period; hence, no sightings of flowering individuals.

RECOMMENDATIONS

Future studies should include results reflecting the translocation factor, indicating the ability of *P. serratum* to move heavy metals from roots to shoots and leaves. This will provide insights into compartmentalization and storage of heavy metals by this species, which is important in phytoremediation. For successful restoration, *P. serratum* should be propagated from seedlings or plantlets in sandy, well-drained soil with periodic wet-dry cycles to prevent waterlogging. Conservation efforts should focus on riverbank planting rather than ponds or floodplains to ensure successful establishment. It is crucial to understand the optimal soil pH range for seed germination and plantlet growth when propagating *P. serratum*. Studies should be conducted on pollen, seed, and embryo viability to assess their viability and germinability and gain insights into whether *P. serratum* can be propagated through seeds or seedling transplant.

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SOURCE OF FUNDING

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CONFLICT OF INTEREST

The authors declare that there was no conflict of interest or any known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

ETHICAL CONSIDERATION

This study did not require ethical clearance. The sampled clumps of *P. serratum* did not require ethical consideration. The study of *P. serratum* in Mpenjati Nature Reserve was based on observations only and did not require permit applications.

AUTHOR CONTRIBUTIONS

Mr. Masuku PL was responsible for research conceptualization, investigations/research, writing the original draft, data analysis, methodology, laboratory analysis, review, and editing. Professor H. Baijnath assisted with conceptualization, review, and editing. Dr.

A. Bissessur assisted with the conceptualization of the analytical chemistry method, review, and editing.

ABBREVIATIONS

One-Way ANOVA	Univariate analysis of variance
D'RAP	Durban Research Action Partnership
KZN	KwaZulu-Natal
CO_2	Carbon dioxide
O_2	Oxygen
CFR	Cape Floristic Region
P. serratum	*Prionium serratum*
PNR	PNR
SANBI	South African Biodiversity Institute
SPAD	Special Product Analysis Division
UKZN	University of KwaZulu-Natal
SPSS	Statistical Package for Social Sciences
IBM	International Business Machines
ICP-OES	Inductive Coupled Plasma-Optical Emission Spectrometry
PR	Palmiet River
QRW	Quarry Road West
EC	Eastern Cape
WC	Western Cape

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