



Responses to warming and low soil moisture provide insights into vulnerability of key plant species of Southern Africa

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Abstract

The study evaluated whether common bulbous (*Eucomis autumnalis*, *Bulbine natalensis*, *Agapanthus praecox*), herbaceous perennial (*Pelargonium* sp.), palm (*Dypsis lutescens*, *Neodypsis decaryi*), shrub (*Barleria greenii*, *Carissa macrocarpa*) and succulent (*Portulacaria cafra*, *Crassula ovata*) functional groups of Southern Africa differed in biomass and physiological stress responses under warmer (2 °C above ambient midday temperature) and drier future climates. We set a species × warming × soil moisture factorial experiment in a completely randomised design, with five replicates of each treatment combination. Warming and soil moisture interacted in influencing plant biomass across different species. Biomass in bulbous plants significantly dropped by 33%. At low soil moisture, total biomass significantly dropped in bulbous and herbaceous plants. Under a warmer microclimate, shrubs and herbaceous plants prioritised their biomass towards belowground organs. The ambient temperatures were close to what the bulbous and herbaceous functional groups could tolerate. Long term field monitoring studies of bulbous and herbaceous functional groups are therefore recommended.

Keywords Biomass · Climate warming · Soil moisture

Introduction

Southern Africa is known for its unique plant biodiversity, especially in biodiversity hotspots, which harbour many rare plant species that make the area ecologically unique (Myers et al. 2000). It is home to the Cape Floristic Region, the Succulent Karoo, and the Maputaland-Pondoland-Albany. These areas have high plant species richness, which is associated with extensive evolutionary radiations and sharp environmental gradients (Linder 2003; Klak et al. 2004; Goldblatt and Manning 2002; Verboom et al. 2015). The exceptional plant diversity and ecological importance

of Southern African plant communities highlight the urgent need for their conservation in the face of climate change-induced warming and drought. While the impacts of global warming on vegetation have been extensively modelled for Southern Africa (Lawal et al. 2019), empirical studies simulating future climatic scenarios, including warmer climates and droughts, on local plant species remains limited. These studies have focussed on the impacts of warming and precipitation changes on dwarf succulents in the Succulent karoo (Musil et al. 2005, 2009; Young et al. 2016) as well as the monitoring of vegetation changes (Schmiedel et al. 2023). Understanding these ecosystem responses is essential, both for their intrinsic value and for safeguarding vital ecosystem services and supporting global biodiversity. Strategies for mitigation and adaptation, along with scientific research and conservation efforts, are crucial for the resilience and survival of these important plant communities. South African plant communities are increasingly threatened by warming and drought caused by climate change (Milton et al. 2022).

Rising temperatures and changing precipitation patterns pose significant challenges to the delicate balance of these ecosystems (Scholes 2020; Thuiller et al. 2008; Milton et al. 2022). Drought events are becoming frequent and severe, alongside extended heatwaves, disrupting plant physiology,

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phenology, and ecosystem functioning (Cui et al. 2022; Brodribb et al. 2020; Crous et al. 2022; Choat et al. 2018). Climate change affects plant communities, leading to significant consequences (McDowell et al. 2022; Altwegg et al. 2014). Changes in species distribution, altered flowering and fruiting patterns, and shifts in species interactions can disrupt ecosystem dynamics and threaten the survival of endemic and specialized plant species (Bentley et al. 2018; Milton and Dean 2000; Thuiller et al. 2008; Altwegg et al. 2014). Disruptions can lead to cascading effects on other organisms dependent on these plant communities for food, habitat, and pollination services (Thuiller et al. 2008; Altwegg et al. 2014; Melin et al. 2014; Settele et al. 2016). While climate change-induced habitat loss is thought to increase the risk to plant species (Giam et al. 2010; Altwegg et al. 2014), no studies have experimentally shown the effects of anticipated climatic warming and drought on key plant functional groups in Southern Africa.

Climate change-induced warming and drought may increasingly threaten several plant functional groups in South Africa, such as bulbous plants, herbaceous perennials, shrubs, and succulents. In a changing climate, these plant functional groups are vulnerable, potentially affecting their distribution, phenology, and overall survival (Geissler et al. 2023). Rising temperatures and droughts can affect the growth, flowering patterns, and reproductive success of bulbous plants (Schmiedel et al. 2011). Herbaceous flowering plants can experience changes in flowering time (Snyman and Fitchett 2022), pollinator interactions, and changes in species composition. Herbaceous perennials are sensitive to changes in temperature and water availability (Compagnoni et al. 2021), impacting their growth rates, physiological processes, and species composition. Shrubs, important components of South African ecosystems, may experience reduced growth, changes in phenology, and altered competitive dynamics under climate-induced stress (Milton and Dean 2000). Succulents, known for their capacity to store water, may face difficulties as severe droughts increase in frequency, affecting their water-use efficiency, growth rates, and overall resilience (Musil et al. 2005, 2009). These findings highlight the need for empirical research to inform conservation measures and adaptive strategies that protect these plant functional groups against escalating climate threats.

This study examined the impacts of changing climatic conditions on selected common species representing various functional groups to offer insights into their adaptive strategies, and potential implications for regional ecosystems and conservation efforts. The study examined species of bulbous plants, herbaceous perennials, shrubs, palms, and succulents. We hypothesized that bulbous plants (*Eucomis autumnalis*, *Bulbine natalensis*, *Agapanthus praecox*), herbaceous perennial (*Pelargonium sp.*), shrubs (*Barleria*

greenii, *Carissa macrocarpa*), palms (*Dypsis lutescens*, *Neodypsis decaryi*) and succulents (*Portulacaria afra*, *Crassula ovata*) differ significantly in their growth and physiological responses to both climatic warming and availability of soil moisture, in a way that favours those species with better drought and temperature escape strategies. Succulents and bulbous plants with water storage tissues are likely to be more resilient, while woody shrubs may prioritize their photoassimilates towards root development. This study aimed to enhance understanding of climate change impacts on Southern African plant functional groups, and offer insights for land managers, conservation practitioners, and policymakers.

Materials and methods

Plant culture

Two hundred PVC 3-litre pots were filled with a mixed substrate comprising 40% v/v of grade 30/10 sand (Consol Minerals, Cape Town, RSA), 30% v/v of Garden Master® premium potting soil (Builders Express, Durban, RSA), and 30% v/v of Garden Master® compost (Builders Express, Durban, RSA). Twenty replicates of rooted bulbous plants (*Agapanthus praecox* Willd., *Eucomis autumnalis* (Mill.) Chitt), herbaceous plant (*Pelargonium sp.*), palms (*Dypsis lutescens* (H. Wendl.) Beentje & J. Dransf., *Neodypsis decaryi* Jum.), succulents (*Crassula ovata* (Miller) Druce, *Portulacaria afra* Jacq., *Bulbine natalensis* Baker) and shrubs (*Carissa macrocarpa* (Eckl.) A. DC., *Barleria greenii* M. & K. Balkwill) were each transplanted to the PVC pots and acclimatized under humid ambient environmental conditions for 14 d, with consistent irrigation frequency. All plants were relocated to an open area and maintained for 18 months under consistent irrigation prior to the start of the experiment. A 2 × 2 factorial arrangement in a completely randomised design, with five replicates per species was established at the Durban University of Technology Nursery (−29.852417 °, 31.009267 °) to test the hypothesis. The factors were two climatic environments (hereafter termed ‘Ambient’ and ‘Warmer’) and two levels of watering (high- and low-moisture). Ambient plants were grown in a naturally ventilated tunnel clad with a 200-micron mesh, with all doors and vents kept open, while Warmer plants experienced an approximate 2 °C increase above ambient conditions at midday (Fig. 1). Air temperature, and relative humidity were monitored at hourly intervals using thermocouples and relative humidity sensors connected with miniature data loggers in ventilated radiation shields (Watch Dog 1000, Spectrum Technologies Inc., Plainfield, Illinois, USA). Vapour pressure deficits (VPD) were calculated from

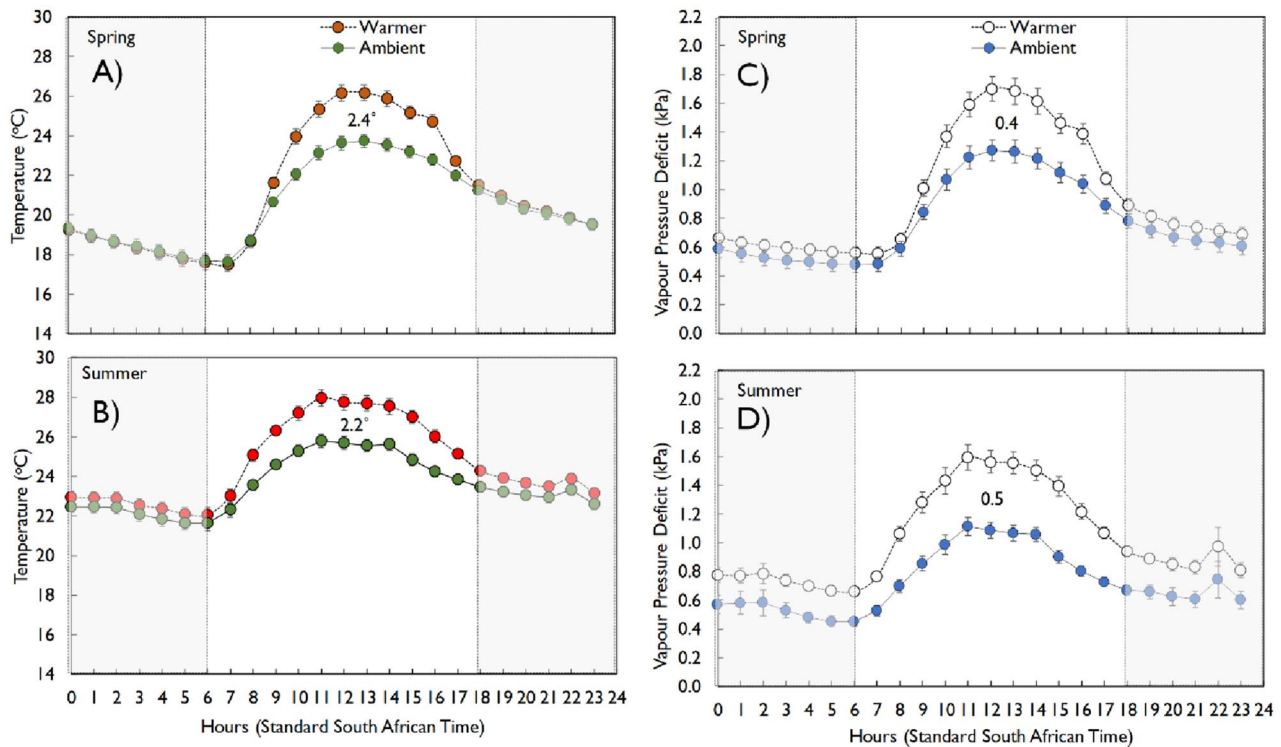


Fig. 1 Diurnal (A) spring and (B) summer season air temperatures (mean $\pm$ se) and (C) spring and (D) summer vapour pressure deficits of current ambient climatic conditions (Ambient) and at a simulated warmer climate (Warmer). The respective midday temperature differ-

ences between Ambient and Warmer scenarios for Spring (August) and Summer (October) were 2.4 °C and 2.2 °C respectively. The midday vapour pressure deficit was consistently higher by ca. 0.4–0.5 kPa in the Warmer compared to the Ambient microenvironment

air temperature and relative humidity measurements using the functions outlined by Snyder and Paw (2006); Monteith and Unsworth (2013):

$$e = 0.6108 \exp \left(\frac{17.27T}{T + 265.5} \right) \quad (1)$$

$$es = \frac{100e}{RH} \quad (2)$$

$$VPD = es - e \quad (3)$$

where e is vapour pressure (kPa), T denotes air temperature (°C), es indicates saturation vapour pressure (kPa), RH stands for relative humidity (%), and VPD signifies vapour pressure deficit (kPa).

We simulated the 30–55% decrease in precipitation that is projected for southeastern Africa (15° S to 40° S, 30° E to 40° E) for 2050s under A2 (medium-high) emissions scenario (Nakicenovic et al. 2000; Hulme et al. 2001). The high-moisture plants received 200 ml twice a week (on day 1 and day 4), while low-moisture plants received 200 ml plant⁻¹ once every week. In this experiment, 400 mL returned soil moisture to field capacity, whereas the droughted plants

received half that volume of water. All plants were monitored for 150 d.

Chlorophyll measurements

Chlorophyll content indices (SPAD readings) were measured after 150 d to assess plant vulnerability to warming and drought stresses. A SPAD 502 Plus chlorophyll meter (Konica Minolta, Osaka, Japan), was utilised as a non-destructive method. SPAD readings indirectly estimate chlorophyll content. Measurements were conducted on the third fully expanded apical leaf exposed to natural light. *Crassula ovata* was excluded from the analysis as could not be measured with a SPAD 502 Plus due to its thick succulent leaves.

Biomass measurements

To quantify the biomasses of the species, *A. praecox*, *C. ovata*, *D. lutescens*, *B. natalensis*, *N. decaryi*, *Perlagonium sp.*, *C. macrocarpa*, *B. greenii*, *E. autumnalis*, and *P. afra* plants were gently excavated under water in 90-Litre ‘No Ash’ bins to remove any soil media or compost particles without damaging the roots. The wet plants were blotted with paper towel, then separated into below ground (roots)

and above ground (shoots) parts using secateurs and placed in clearly labelled paper bags. Each plant had one bag for roots and another for shoots to determine the shoot to root biomass ratio. All plants were dried at 70 °C for 48 h in an oven (Ecotherm, Labotec, RSA) or until their weights stabilized (approximately 72 h for *B. natalensis*). The oven-dried samples were weighed using a 0.01 g Radwag Precision Balance (Lasec, Cape Town, RSA) to determine their dry masses. Shoot: root ratios were calculated by dividing the shoot mass by the root mass.

Statistical analyses

Data were analyzed using R version 4.3.2 (R Core Team 2023). Linear mixed effects models were fitted to predict the impact of the warming scenario, soil moisture and species (or functional groups), and the possible interactions on SPAD, shoot: root ratios, and total biomass. The *MuMIn* package's *dredge* function was utilized to select the most parsimonious model by ranking the models according to their Akaike Information Criterion (AIC) values. Tukey's HSD post-hoc test for treatment differences were determined by comparing treatment means using the *emmeans* package.

Results

Ambient and warmer microenvironments

The average daily maximum air temperatures at 13H00 in the Ambient microenvironment were 23.7 °C in spring and 25.6 °C in summer. The highest average midday air temperatures in the Warmer microenvironment during spring and summer were 2.2 °C and 2.4 °C higher than those in the Ambient microenvironment (Fig. 1a and b). The Ambient and Warmer microenvironments exhibited different vapour pressure deficits (VPD) (Fig. 1c and d). The Warmer VPD, was consistently higher by approximately 0.4–0.5 kPa during midday compared to the Ambient microenvironment.

Plant stress response to warming and soil moisture differences

After 150 d from planting, a highly significant interaction ($p < 0.001$) was observed between the warming scenario and the species for chlorophyll content (supporting Table S1). Chlorophyll content, as inferred from SPAD index readings, was highest in the shrub *C. macrocarpa* in warmer microenvironments (67.2) and lowest in the herbaceous perennial *Perlagonium sp.* (28.4) (Fig. 2, supporting Table S1). Only *C. macrocarpa* and *Perlagonium sp.* exhibited higher SPAD

Fig. 2 Total biomass, shoot: root biomass ratios and chlorophyll content indirectly estimated as SPAD index of bulbous plants (*Agapanthus praecox*, *Bulbine natalensis*, *Eucomis autumnalis*), herbaceous perennial (*Pelargonium sp.*), palms (*Dypsis lutescens*, *Neodypsis decaryi*), shrubs (*Barleria greenii*, *Carissa macrocarpa*) and succulents (*Crassula ovata*, *Portulacaria cafra*) at ambient climatic conditions and at a simulated warming (2 °C above the ambient temperatures) with either low soil moisture (200 ml plant⁻¹ once a week) or high soil moisture (200 ml plant⁻¹ twice a week). Different letters show significant differences across treatment combinations for each species after an analysis of variance (ANOVA) and Tukey HSD test at $p = 0.05$

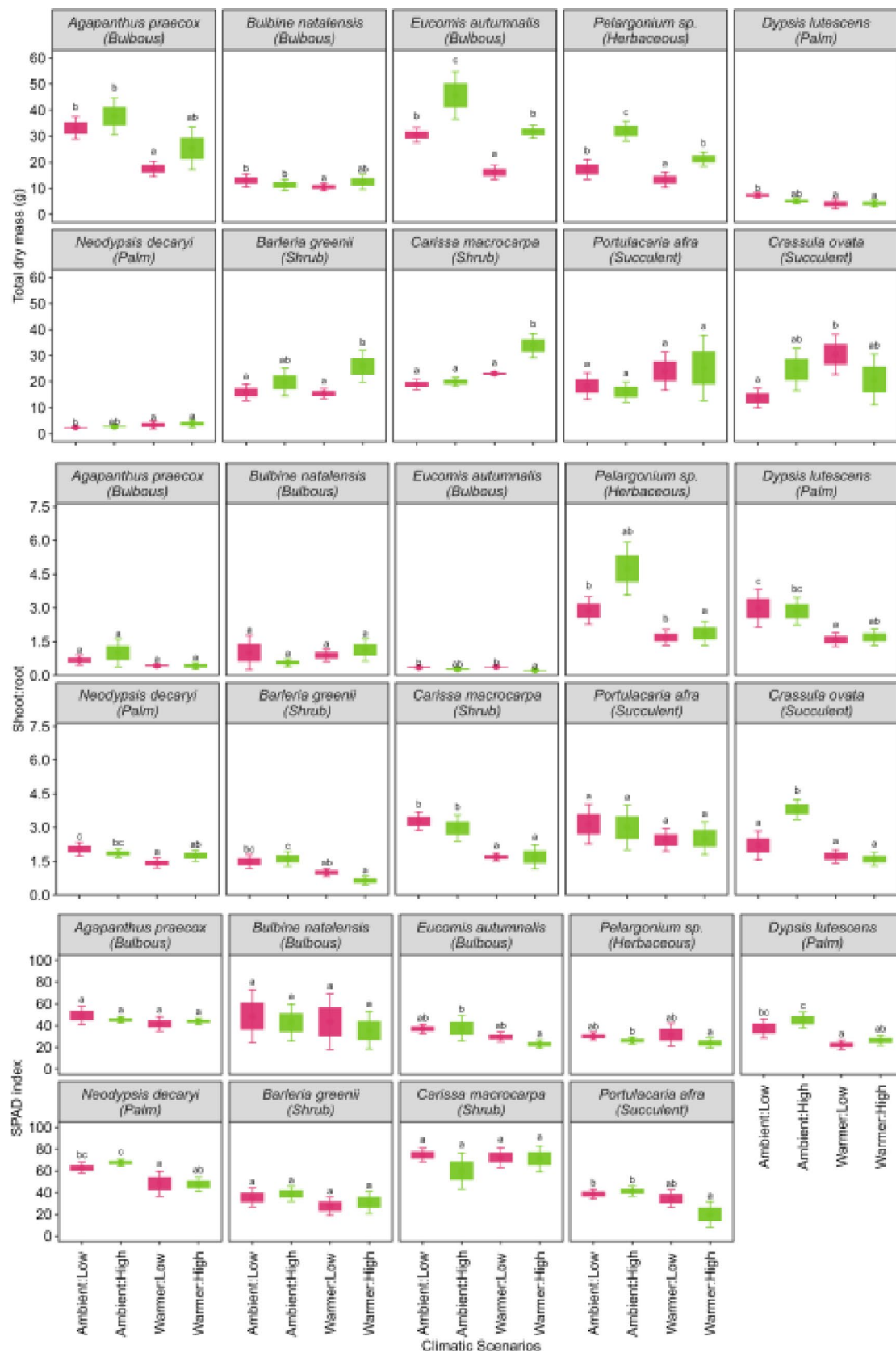
indices under a Warmer scenario compared to the Ambient scenario, whereas other species showed lower values under Warmer conditions.

Biomass allocation under ambient and warmer scenarios

The most parsimonious model (supporting Table S2) predicted total dry mass based on warming scenario, soil moisture and species. The model demonstrated significant explanatory power ($R^2 = 0.62$). There were no significant interactions between climatic scenarios and soil moisture on the total plant biomass (supporting Table S3). Although all species were propagated at the same time, *A. praecox* and *E. autumnalis* exhibited the highest total biomasses under both ambient and high soil moisture conditions (Fig. 2, supporting Table S2), whereas the palm *N. decaryi* produced the least dry biomass. Total dry biomasses in both the bulbous and herbaceous plants were significantly lower in the 2 °C warmer and low moisture microenvironments (Fig. 2). Other functional groups (palms, shrubs, and succulents) showed no significant differences in dry biomasses across the different climatic scenarios.

The warming scenario had insignificant effects on total plant biomass, while soil moisture significantly impacted plant biomasses. Very large effect sizes (Cohen's $d \geq 1.3$, Fig. 4) of soil moisture on total biomasses were observed in *E. autumnalis*, *B. greenii* and *Perlagonium sp.*, while large effect sizes (Cohen's $d \geq 0.8$) were noted for *C. macrocarpa*.

Carissa macrocarpa, *Pelargonium sp.* and *P. afra* exhibited reduced shoot: root ratios in conditions of low soil moisture and warmer microenvironments (supporting Table S3, Fig. 2). When species were grouped into their functional groups, only herbaceous plants and the shrubs showed significantly lower shoot: root ratios in warmer compared to ambient conditions (Fig. 3). Effect sizes (Cohen's d) of warming on shoot: root ratios were very large and positive for most species (Fig. 4), except for *C. ovata*, *B. natalensis* and *E. autumnalis*.



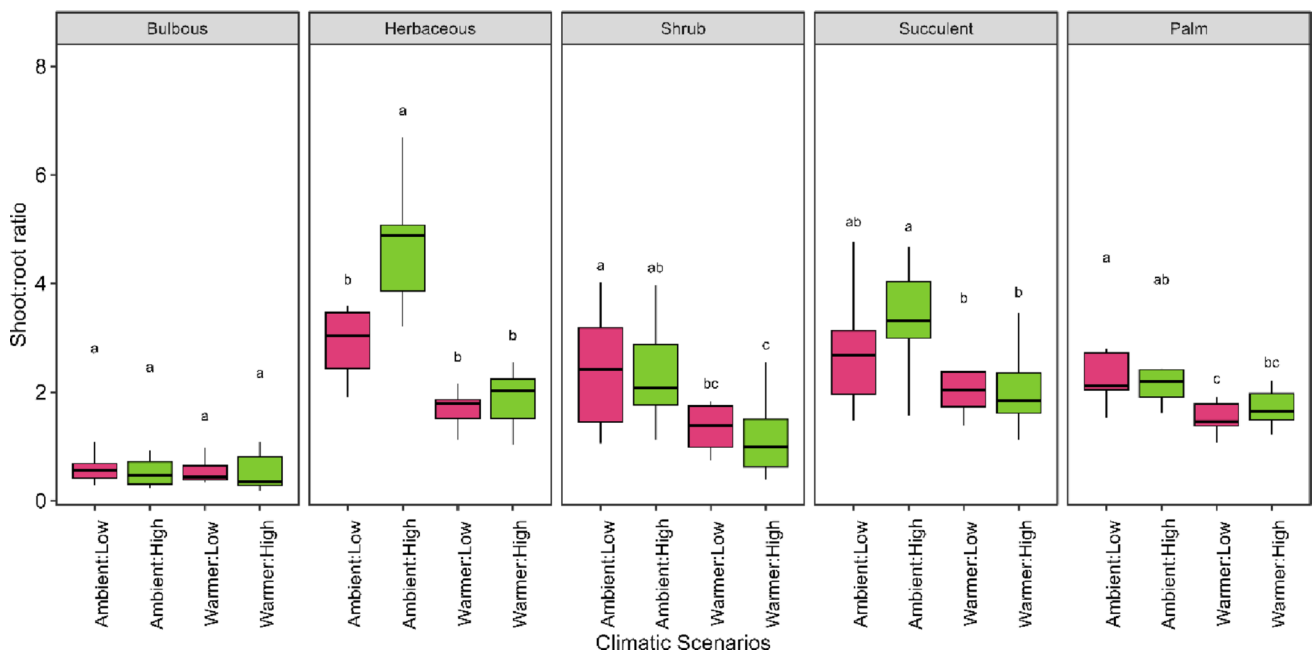


Fig. 3 Ratio of shoot: root biomasses of ten species, belonging to five functional types, for two warming and two soil moisture treatments. The species, functional types and treatments are described in

Fig. 2 Different letters show significant differences across treatment combinations for each functional group after an analysis of variance (ANOVA) and Tukey HSD test at $p=0.05$

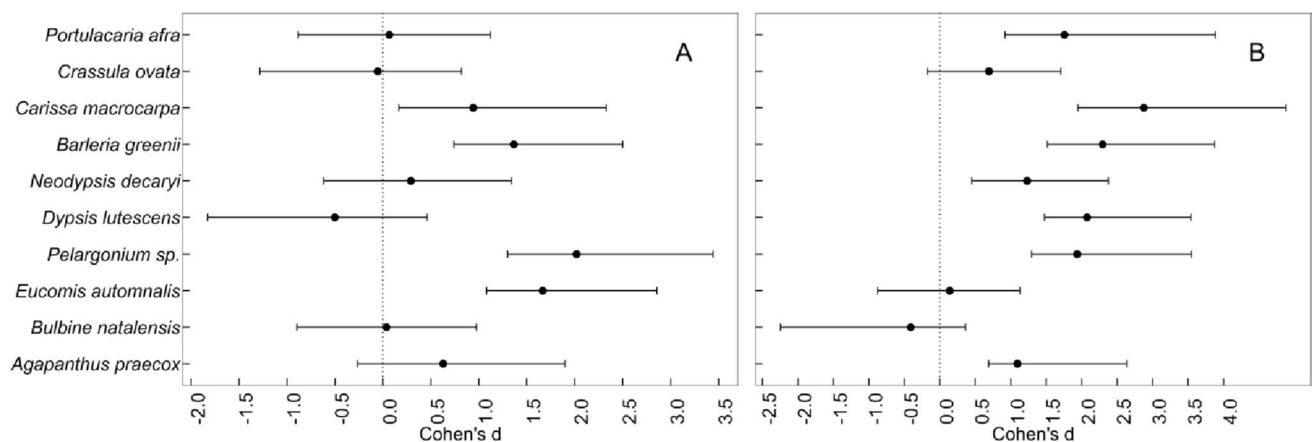


Fig. 4 Effect sizes (estimated using Cohen's d) of (a) soil moisture on plant biomasses and (b) warming on shoot: root ratios of bulbous (*Agapanthus praecox*, *Bulbine natalensis*, *Eucomis autumnalis*), herbaceous perennial plant (*Pelargonium sp.*), palm (*Dypsis lutescens*, *Neodopsis decaryi*), shrub (*Barleria greenii*, *Carissa macrocarpa*) and

succulent (*Crassula ovata*, *Portulacaria afra*) grown either at ambient climatic conditions or at a simulated warmer climatic scenario (2 °C above the ambient temperatures). Effect sizes were interpreted as small ($d=0.2$), medium ($d=0.5$), large ($d=0.8$) and very large ($d=1.3$)

Discussion

Ambient air temperatures at our study site during the 150-day period reflected the average climatic conditions for the area. This was supported by the similar range of average daily maximum air temperatures at the Durban Wentworth Weather Station, South Africa. Average daily maximum air temperatures at Durban South Wentworth Station (−29.9340° 30.9880°) located 11.5 km away, were 24.0 °C in spring and 26.9 °C in summer. The higher midday

maximum temperatures in the warmer microenvironment during spring and summer by 2.2 °C and 2.4 °C respectively, confirm the warming of ambient temperatures. The temperature increases and rainfall decrease align with A2 (medium-high) emissions scenario projections for 2050s, based on the median of seven GCM experiments for the coordinates 15° S to 40° S, 30° E to 40° E (Hulme et al. 2001). Under this A2 (medium-high) emissions scenario precipitation is expected to drop by 30–55%. The warmer microenvironments had 33–34% higher VPD (ca. 0.4–0.5

kPa) at midday than ambient, indicating that the plants in the warmer microenvironment were exposed to increased warming.

This study shows that species may respond differently to future climatic scenarios of warming and limiting soil moisture in their biomass allocation, favouring those with superior drought and temperature escape strategies. However, warming and limiting soil moisture did not influence chlorophyll concentrations as inferred from SPAD measurements. Succulents, characterized by thick waxy cuticles and water storage tissues (Griffiths and Males 2017), demonstrated greater resilience to warming and water stresses, as indicated by minimal responses to warming and moisture treatments. *Crassula ovata* exhibited no significant differences in shoot: root biomass allocation in response to warming and moisture scenarios. Shrubs in warmer, drier conditions allocate biomass to extensive root systems to manage moisture stress, which concurs with Li et al. (2024). In contrast, herbaceous species with shorter life cycles evade extreme drought by growing and reproducing before its onset (Kooyers 2015). This applied to the herbaceous perennial *Pelargonium sp.* and the shrubs *C. macrocarpa*, and *B. greenii*. Bulbous species (*E. autumnalis* and *B. natalensis*) and succulent (*C. ovata*) with water storage organs did not show significant variation in their shoot: root ratios under low soil moisture. Two lines of evidence indicate that bulbous and herbaceous plant species may be more vulnerable to warming and drought conditions in the future. Bulbous plants exhibited lower total biomass in warmer conditions compared to ambient microenvironments. In warmer and drier climates, bulbous plants are more vulnerable to drought and warming due to their dependence on stored water, shallow roots, and sensitivity to temperature changes (Kumar et al. 2021). Conversely, the other plant species showed no significant differences in total biomasses between warmer and ambient microenvironments, indicating that bulbous plants are the most vulnerable to warming. The interaction between soil moisture and functional groups indicates that these groups are likely to respond differently to future climates for south-eastern Africa. Both bulbous and the herbaceous plant exhibited greater biomass under high soil moisture compared to low soil moisture conditions. This indicates that extreme droughts and warmer temperatures are expected to impact herbaceous and bulbous plants more severely than the other functional groups.

Shoot: root ratios indicate biomass allocation and show that species may vary in their allocation of photoassimilates under warmer climates and varying soil moisture levels. Although the Ambient and Warmer microenvironments exhibit the same total biomass in the herbaceous plant and shrubs (Fig. 4), the reduced shoot: root ratios in Warmer microenvironment for these functional groups (Fig. 3)

indicate a focus on root development in stressed shrubs and herbaceous plants. Recent studies indicate trade-offs in the allocation of recent photosynthate carbon to roots under warmer conditions (Li et al. 2024). The study indicated a notable decrease in photosynthates directed to shoots, coupled with an increase in root allocation, similar to our findings in shrubs and herbaceous species. A global synthesis of changes in plant phenology due to climate change (Liu et al. 2021) indicates that mismatches between above- and below-ground phenology may account for variations in shoot: root ratios. Their study revealed that climate warming in woody plants did not impact aboveground phenophases but did extend the belowground growing season, leading to observed mismatches. While their study found no changes in biomass allocation in herbaceous plants, our research indicated that the herbaceous *Perlagonium sp.* prioritised belowground biomass in warmer microenvironments. Our findings indicate that the herbaceous *Perlagonium sp.* exhibited greater sensitivity to drought compared to woody plants, as supported by Eziz et al. (2017). Plant root biomass across various biomes showed a negative correlation with mean annual temperature (Qi et al. 2019), corroborating our findings (Fig. 2). Liu et al. (2021) emphasize the need for further examination of biomass allocation, particularly regarding belowground phenological changes, to accurately project plant responses to warming and drought.

This study demonstrated that warming and soil moisture changes interact to influence plant biomass. Warmer microclimates subjected plant groups to increased stress, particularly under limited soil moisture, indicating that the predicted warmer, drier conditions in parts of Southern Africa may limit plant productivity across the represented plant species. This is supported by findings that soil moisture is a critical factor for plant growth, particularly in semi-arid and arid regions (Su et al. 2021; Xu et al. 2022). This study indicates that total biomass of the species belonging to the bulbous and herbaceous groups may decrease when soil moisture is limited. In areas where warming increases without a notable reduction in soil moisture, the representatives of shrubs and the herbaceous plants will be significantly affected. Experimental warming reduces aboveground biomass growth and long-term survival of the shrub species (Cuartero et al. 2024). The ambient conditions during the study period were likely near tolerable extremes for bulbous and herbaceous functional groups. Consequently, climate warming may significantly exceed these temperature thresholds, exacerbated by the decline in soil moisture. Studies indicate that herbaceous plants can exhibit notable physiological and phenological responses to temperature changes. Warming has lengthened the growing season and advanced flowering times for several herbaceous species (Rice et al. 2018). Responses are often species-specific and influenced

by environmental factors such as soil moisture (Ishioka et al. 2013; Olivera-Viciedo et al. 2021).

In conclusion, soil moisture had a significant effect on plant biomasses, whereas warming did not affect total plant biomass. No significant interactions were observed between warming and soil moisture on total plant biomass. *Carissa macrocarpa* and *Pelargonium sp.* showed lower shoot: root ratios under limiting soil moisture and warmer conditions, likely to enhance their root water and nutrient acquisition. The herbaceous plant and shrubs exhibited reduced shoot: root ratios in warmer compared to ambient conditions. This study's findings can improve projections of vegetation dynamics in Southern Africa for current and future climate scenarios. Long term field monitoring of common plant species, in larger sample sizes, is recommended to determine their range shifts, distribution patterns, biomass partitioning, stress vulnerability, and whether the observed complex interactions between warming, soil moisture and plant species are consistent under field conditions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11258-026-01604-7>.

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Author contributions Both IM and MM contributed to the study conception and design and conducted the experiments and data collection. IM analysed the data and wrote the first draft. Both authors read and approved the final manuscript.

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Data availability Data from this study are available from the authors upon request.

Declarations

Competing interests The authors declare no competing interests.

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