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Journal of Arid Environments 227 (2025) 105308

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Leaf traits of the mistletoe *Erianthemum dregei* and its host tree *Sclerocarya birrea* vary across a rainfall gradient and levels of hemiparasite infection

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ARTICLE INFO

Keywords:
Acquisitive strategy
African savanna
Conservative strategy
Ecophysiology
Leaf traits
Marula
Mistletoes

ABSTRACT

Certain trees in semi-arid environments are surpassing their physiological thresholds because of erratic rainfall and rising global temperatures. Mistletoes (Loranthaceae) may also be making large trees more susceptible to the physiological stress imposed by climate change. Therefore, we examined intraspecific variations of selected leaf traits of the mistletoe, *Erianthemum dregei,* and *Sclerocarya birrea* host trees along a rainfall gradient at three levels of mistletoe infection. We measured seven leaf traits across five mistletoe-host pairs at low, medium, and high rainfall sites. Rainfall had significant effects on all measured traits, except host leaf succulence. Hosts were more resource-acquisitive at intermediate rainfall, but more conservative at high rainfall. The reverse is true for mistletoes. Mistletoe infection only had an effect on host leaf area, specific leaf area, and stomatal conductance, but most mistletoe leaf traits were significantly influenced by infection intensity. Uninfected hosts were more resource-conservative, but highly infected hosts were resource-acquisitive. Conversely, mistletoes on low-infected hosts were associated with high resource acquisition, while those on high-infection trees were resource-conservative. Therefore, the antagonistic response of host trees and mistletoes to infection and rainfall suggests the potential for resilience to environmental change.

1. Introduction

Species respond to environmental gradients through their functional traits, which are defined as quantifiable characteristics of a plant that influence its general fitness, reproduction, and function (Albert et al., 2010; Xu et al., 2020). Varying within and between species, plant functional traits help in understanding a species' adaptive strategy to environmental variation (Albert et al., 2010; Maponga et al., 2025). Many species across biomes exhibit intraspecific variation along various environmental gradients (Souza et al., 2018; Xu et al., 2020). As such, small environmental differences can cause intraspecific variance or phenotypic plasticity among individuals in the same population (Reich et al., 2003; de Cassia-Silva et al., 2017; Souza et al., 2018). Thus, intraspecific variation and phenotypic plasticity are crucial for the survival of plants, as they facilitate both short- and long-term protection and adaptation to environmental changes (e.g., rainfall, temperature, availability of soil resources, and soil texture, salinity, and compaction), especially in species with long lifespans such as trees (Albert et al., 2010; McLean et al., 2014; Araújo et al., 2021).

Heterogeneous environments often contain individuals within a species exhibiting greater genetic or phenotypic plasticity (Reich et al., 2003; de Cassia-Silva et al., 2017; Souza et al., 2018). For instance, Souza et al. (2018) show that higher inter-annual variation in rainfall resulted in greater phenotypic plasticity for both the morphological and physiological traits of a rainforest tree, *Copaifera langsdorffii* Desf (Fabaceae). In contrast, mesic habitats with more climatic homogeneity had lower phenotypic plasticity (Souza et al., 2018). Therefore, plant species employ different resource-use strategies in a number of varied environments. For example, ecosystems with elevated temperatures and light incidence, periodic droughts, frequent fires, and low soil fertility

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https://doi.org/10.1016/j.jaridenv.2024.105308
Received 30 January 2024; Received in revised form 10 December 2024; Accepted 13 December 2024
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often support plants with conservative resource-use strategies (de Cassia-Silva et al., 2017; Araújo et al., 2021). Plants with lower specific leaf areas (SLA) and higher leaf dry matter content (LDMC) are associated with a conservative resource-use strategy, while those with higher SLA and lower LDMC and leaf area (LA) are associated with a more acquisitive resource-use strategy (Cunningham et al., 1999; Pierce et al., 2013; Silva et al., 2019). Conservative resource strategies include high leaf water content to avoid desiccation and thick leaves to reduce leaf damage, and consequently, these plants tend to have greater intra-specific trait variation (Araújo et al., 2021). Plants that utilise the conservative resource-use strategy can often tolerate drought and photoinhibition. As such, their leaves have high nutrient use efficiency, slower tissue turnover, low photosynthetic rates, and are structurally resistant (Reich et al., 2003; Silva et al., 2019). In contrast, plants with resource-acquisitive strategies have high plant productivity, fast tissue turnover, high photosynthetic rates, and are more competitive (Reich et al., 2003; Silva et al., 2019). They promote higher growth rates, higher specific leaf area, thin leaves, and larger stomata sizes, which are linked to greater uptake of light, water, and nutrients (Araújo et al., 2021).

Like climate, hemi-parasitic plants, i.e., mistletoes, can impose physiological stress on semi-arid savanna trees that may even result in host tree mortality (Maponga, 2021). Mistletoes are hemiparasitic plants that acquire 60% of their carbohydrates from their hosts *via* a haustorium and photosynthesize the remainder (Watson, 2001; Barbu, 2010). The impact of the hemiparasites on their hosts depends on the host species (including its phenology), mistletoe sizes, infection intensity, host site quality (biotic and abiotic factors), and the host's ability to resist the mistletoes (Press and Phoenix, 2005; Glatzel and Geils, 2009; Scalon et al., 2016; Ozturk et al., 2022; Zhang et al., 2023). Infected trees often suffer changes to their chemical or metabolic profiles, have mineral and water deficiencies, and experience a reduction in their eco-physiological attributes, which can increase their vulnerability to pathogens (Bowie and Ward, 2004; Hosseini et al., 2007; Glatzel and Geils, 2009; Mellado et al., 2016; Scalon et al., 2017, 2017b; Maponga, 2021; Zhang et al., 2023).

Mistletoes are profligate water-users with higher stomatal conductance and transpiration rates and lower water use efficiency (WUE: trade-off between the amount of carbon assimilated and water released) compared to their hosts, and these impacts on the hosts are especially severe (including heat stress) during drought periods (Bowie and Ward, 2004; Okubamichael et al., 2011; Zweifel et al., 2012; Kubov et al., 2020; Ozturk et al., 2022; Wang et al., 2023). However, Küppers (1992) and Chen et al. (2013) report hosts having higher transpiration and WUE rates compared to their obligate mistletoes. Regardless, Ullmann et al. (1985) showed that for 18 different host/mistletoe pairs, mistletoe transpiration rates ranged between 1.4 and 8.9 times higher than their hosts. Similarly, Urban et al. (2012) found that the mistletoe *Loranthus europaeus* Jacq. transpired at least five times more than their oak hosts, thus negatively affecting the water potential of the host trees.

High transpiration rates are accomplished by maintaining a continuous flow of water and solutes from the host to the parasite, thus creating a negative water potential that is sustained by keeping mistletoe stomata open for extended periods of time (Glatzel and Geils, 2009; Okubamichael et al., 2011; Scalon and Wright, 2015; Scalon et al., 2017a; Queijeiro-Bolaños et al., 2020; Zhang et al., 2023). This is done to obtain sufficient nitrogen and mineral nutrition for biomass production (Ullmann et al., 1985; Küppers, 1992; Hosseini et al., 2007; Okubamichael et al., 2011; Wang et al., 2023). However, Zhang et al. (2023) found little evidence of transpiration-controlled nutrient acquisition for most nutrients except nitrogen.

The average global temperature, erratic rainfall, and frequency of extreme events are predicted to rise because of ongoing global climate change, creating even drier environments in currently arid places (Pachauri et al., 2014; Souza et al., 2018), which is likely to affect the availability of critical resources needed by plants (Souza et al., 2018). Further, an increase in extreme weather events such as droughts and heat waves will have a negative impact on the ecophysiological fitness of large trees (Araújo et al., 2021). Therefore, the capacity of a plant species to adapt their functional traits (through phenotypic plasticity) to changes in the environment and climate is important (Souza et al., 2018; Araújo et al., 2021; Maponga et al.). At a local scale or at the individual species level, functional traits of trees are mostly influenced by rainfall and temperature (Cunningham et al., 1999; Araújo et al., 2021). As such, investigating how large trees adapt to changes in the environment and climate is crucial (Souza et al., 2018; Araújo et al., 2021). In semi-arid savannas, large trees are keystone structures that play a critical role through understory species facilitation and providing foraging sites and shelter for animals, and thus they are important for the functioning of this ecosystem (Belsky et al., 1993; Ludwig et al., 2003). Moreover, large trees, such as our iconic study tree, *Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Marula), are important for both timber and non-timber forest products (NTFP) in the lowveld savannas of South Africa (Shackleton and Shackleton, 2002; Helm et al., 2011; Blair et al., 2021). Rainfall, drought, frequent fire, and mistletoes have been shown to have a significant influence on marula mortality rates (Dzerefos et al., 2003; Helm et al., 2011a; Helm and Witkowski, 2013). As such, all positive and negative factors that can potentially affect these large trees need to be investigated. Moreover, although mistletoe effects on understory plant community structures in semi-arid savannas have been well-studied (Ndagurwa et al., 2016, 2018; Maponga et al., 2021, 2024; Maponga et al. 2025), the variation of host and mistletoe functional traits due to varying mistletoe infection intensities still needs to be investigated. Mistletoes tend to have protracted longevity on trees; thus, understanding their effects on these keystone structures is important. Currently, little is known about the ecophysiological implications of rainfall gradient and mistletoe infection intensity on the functional traits of hemiparasites and their hosts in semi-arid savannas. Therefore, we sought to investigate the interaction of mistletoe infection intensity (uninfected, low, and high mistletoe infection) and rainfall gradient (low, medium, and high rainfall) on the inter- and intraspecific variation in plant resource use strategies and functional trait values of two plant species with contrasting life histories, i.e., the mistletoe *Erianthemum dregei* (Eckl. & Zeyh.) V. Tieghem (Loranthaceae) and its large tree host, marula, in a semi-arid savanna.

We predicted smaller, thicker leaves with low leaf water content, chlorophyll content, succulence, and stomatal conductance for host trees in low rainfall and under high mistletoe infection intensity as found elsewhere (Reich et al., 2003; Wright et al., 2004; Zweifel et al., 2012; de Cassia-Silva et al., 2017; Souza et al., 2018; Ozturk et al., 2022). We also predicted larger, thinner leaves with higher chlorophyll content, leaf water content, and stomatal conductance in areas of high rainfall and on trees with no or low mistletoe infection (Cunningham et al., 1999; Ozturk et al., 2022). Low rainfall and high demand for nutrients by the mistletoes can slow down growth, leading to less uptake of nutrients due to low availability of water. Water is crucial for nutrient uptake, and thus can lead to leaves that invest more in structural attributes than in high SLA (Ehleringer et al., 1985; Cunningham et al., 1999; Scalon et al., 2017; Souza et al., 2018; Araújo et al., 2021; Ozturk et al., 2022).

2. Materials and methods

2.1. Study area

This study was conducted in Bushbuckridge Local Municipality (31° 0' – 31° 35′ E; 24° 30' – 25° 0′ S), located in Mpumalanga Province in the savanna Lowveld region of South Africa (Shackleton, 2004; Dzerefos et al., 2003; Blair et al., 2021). Bushbuckridge is ~2417 km^2 (Shackleton and Shackleton, 2002). The mean annual temperature is 22 °C (Shackleton and Shackleton, 2002; Shackleton, 2004; Blair et al., 2021) and there is a west to east rainfall gradient. Woody vegetation is dominated by trees from the families Mimosaceae and Combretaceae

(Shackleton and Shackleton, 2002). Soil type varies with topography and nutrient deficiency, and shallow sandy soils dominate the upper slope while deep clay soils rich in resources are predominant at the base of the slope. The underlying parent rocks are granites and grandiorite (Shackleton and Shackleton, 2002; Dzerefos et al., 2003). Three sites in communal grazing areas selected according to Mean Annual Precipitation (MAP) were sampled, namely Seville (590 mm), Dumfries (655 mm), and Xanthia (695 mm) (Dzerefos et al., 2003). The study was done in communal areas where goats, cows, and sheep are the dominant herbivores.

2.2. Host tree

We chose *Sclerocarya birrea* (Marula), a locally abundant tree and preferred mistletoe host in the Bushbuckridge area (Dzerefos et al., 2003). Marula is a medium-to large-sized, widely distributed deciduous keystone tree species in the semi-arid savannas of southern Africa, (Shackleton and Shackleton, 2002; Helm et al., 2011; Blair et al., 2021). It is an important tree for both timber and non-timber forest products.

2.3. Mistletoe

Erianthemum dregei (Loranthaceae) was the only mistletoe species recorded on the sampled trees. It is a deciduous hemi-parasitic plant (Gairola et al., 2013), mainly dispersed by frugivorous birds (Dzerefos et al., 1998; Okubamichael et al., 2016). This mistletoe is known as a "wood flower" as it usually produces a woodrose when connecting to the xylem of its host *via* a haustorium (Dzerefos and Witkowski, 1997; Pooley, 1998; Gairola et al., 2013). *E. dregei* is also ubiquitous in its distribution and is somewhat euryxenous, growing on a wide range of host species (Dzerefos et al., 2003; Gairola et al., 2013). However, *E. dregei* tends to favour marula as one of its preferred hosts (Dzerefos et al., 2003).

2.4. Sampling design and field measurements

From the 2nd to the 15th of March 2023, we sampled host and mistletoe characteristics at the three sites. At each site, we randomly set up three 100 × 100 m plots within marula-dominated stands and recorded the GPS position, height, stem diameter, and canopy long (D_1) and short (90° of D_1; = D_2) of all the marula trees that were >3 m in height. The presence or absence and number of mistletoes per tree were recorded. The trees were then categorised into uninfected, low-, and high-mistletoe-infected trees. Low mistletoe-infected trees had <7 adult mistletoes covering <10% of host canopy, while high mistletoe-infected trees had >15 adult mistletoes covering >70% of host canopy (Maponga, 2021). Then, from all the marula trees recorded, we randomly selected five sample trees from each mistletoe infection category per site (n = five in each mistletoe-infection category per rainfall site, leading to n = 45 total trees sampled) for trait measurements. We chose trees that are not next (>50 m) to roadsides, rivers or streams, or on termite mounds, with at least 20 m between neighbouring replicate marula trees.

2.5. Leaf morphological and physiological trait measurements

The degree of phenotypic plasticity can be measured using different functional trait indices (Souza et al., 2018). Following Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2016), ten healthy (with no signs of herbivory or disease), fully expanded leaves directly exposed to full sunlight were randomly selected from each marula tree. Leaves were stored in a dark cooler box and transported to the Wits Rural Campus laboratory in Bushbuckridge, where measurements were done on the same day. Using the spreadsheet tool provided by Pierce et al. (2013) we calculated leaf area (LA, in mm^2), specific leaf area (SLA, ratio of fresh leaf area to leaf dry mass, in $mm^2\ g^{-1}$), leaf dry matter content (LDMC, ratio of leaf dry mass to leaf fresh mass, mg g^{-1}), leaf water content (LWC, % of fresh weight), leaf succulence (g water dm^{-2}), chlorophyll content, and stomatal conductance (mmol $m^{-2}\ s^{-1}$). Leaf wet and dry mass were measured using a precision balance (±0.001 g). Weighed leaves were placed in paper envelopes and oven-dried at 60 °C for 72 h before re-weighing for dry weight. Leaf area was measured by taking photographs of the leaves using a digital camera and Image J software (National Institute of Health, Bethesda, MD, USA). Chlorophyll content and stomatal conductance were measured on 20 leaves per tree using a SPAD-502-Plus chlorophyll meter (Spectrum Technologies, Inc., Plainfield, IL, USA) and an AP4 leaf Porometer (Delta-T Devices Ltd.), respectively. For mistletoe leaf trait measurements, we selected three different *E. dregei* plants per sampled tree that were more exposed to sunlight. Twenty mistletoe leaves were collected from each host tree. Leaf traits were measured as previously described.

2.6. Data analysis

Normality and homogeneity of variances were calculated using the Shapiro-Wilk test and the Levene statistic, respectively. General Linear models (GLM) were used to test the effects of rainfall site, infection intensity, and their interaction on leaf traits. Marula tree attributes and leaf trait measures for both the hosts and mistletoes were specified as response variables, while rainfall site and infection intensity were the explanatory variables. An ANOVA followed by a subsequent multiple comparison test (Tukey's honest significance test (HSD), $P < 0.05$) tested for differences across infection intensities within each rainfall site. All data were analysed using SPSS 28 for Windows (SPSS Inc., 2021; Armonk, NY: IBM Corp, USA). The relationship between marula host architecture, i.e., tree height, stem diameter, canopy area, and the number of mistletoes, was explored using regression analysis. Similarly, the association between host leaf traits and mistletoe leaf traits was analysed using regression analysis.

3. Results

3.1. Marula host tree attributes

Except for the number of mistletoes per tree, marula tree variables did not differ significantly with rainfall (site), infection (level), or their interaction ($P > 0.05$, Table 1, Fig. 1). The intermediate rainfall site had 2.17-fold significantly more living mistletoes per tree than the low rainfall site, but the intermediate and high rainfall sites were not different, however dead mistletoes did not vary with site (Fig. 2). Similarly, high mistletoe-infected trees had 2.33 and 4.64 times the number of live and dead mistletoes than low mistletoe-infected trees, respectively (Table 1).

Between rainfall sites, infection intensity did not have any significant effect on the marula host variables except for the number of mistletoes per tree which was significantly higher within high-than-low mistletoe-infected trees (Fig. 2). There was no relationship between marula tree

Table 1
F-ratio and level of significance of the general linear model (GLM) testing the effects of rainfall, infection intensity, and their interaction on marula host tree height, stem diameter, canopy area and number of living and dead mistletoes per tree. Significant P values appear in bold. For each variable, both Rainfall and Infection d.f. = 2,36, and Rainfall × Infection d.f. = 4,36.

Variables	Rainfall		Infection		Rainfall × Infection	
	F	*P*	F	*P*	F	*P*
Height (m)	1.01	0.37	0.83	0.45	1.46	0.23
Stem diameter (cm)	2.98	0.06	1.27	0.29	0.82	0.52
Canopy area (m^2)	2.11	0.14	0.57	0.57	0.01	0.99
Living mistletoes per tree	6.78	**0.003**	7.77	**0.002**	5.33	**0.002**
Dead mistletoes per tree	0.15	0.86	80.0	**<0.001**	0.60	0.67

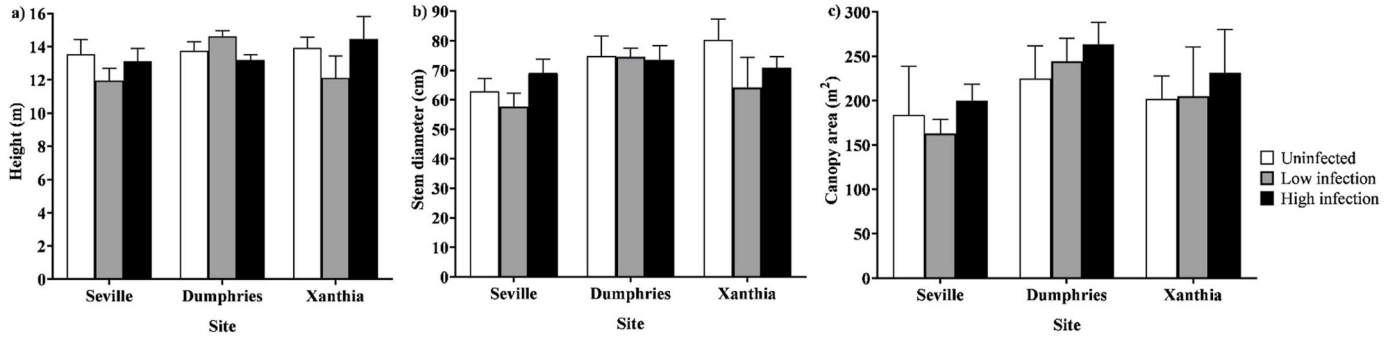


Fig. 1. Mean ± standard error (a) marula tree height, (b) stem diameter, and (c) canopy area, at Seville (590 mm), Dumfries (655 mm), and Xanthia (695 mm). There were no significant differences between sites (rainfall) and within site infection levels (uninfected, low, and high) (Tukey HSD test, $P < 0.05$), thus no superscripts are shown.

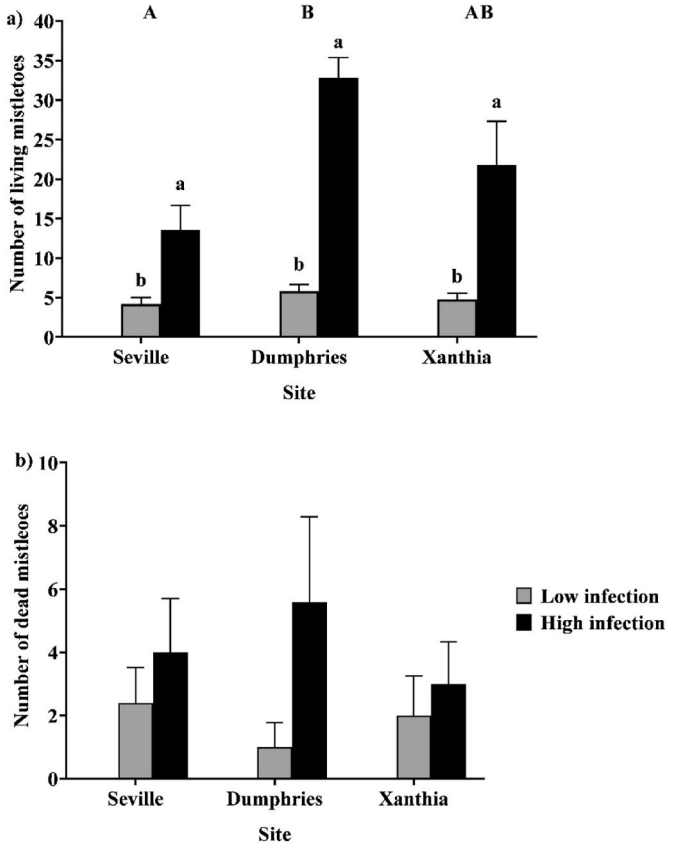


Fig. 2. Mean ± standard error (a) living or (b) dead mistletoe/trees at Seville (590 mm), Dumfries (655 mm), and Xanthia (695 mm). Capital letters show differences between sites (rainfall). Lower-case letters show differences within site infection levels (low and high) (Tukey HSD test, $P < 0.05$).

height ($R^2 = 0.01$), stem diameter ($R^2 = 0.04$), or canopy area ($R^2 = 0.06$), with number of mistletoes per tree.

3.2. Variation in host leaf traits

Rainfall had significant effects on all the marula host leaf traits except for succulence (Table 2). LA was up to 16% greater at the high rainfall site than at the low and intermediate rainfall sites (Fig. 3). The intermediate rainfall site had lower LDMC, but greater SLA, LWC, and stomatal conductance than the other sites (Fig. 3).

Marula host trees at the low rainfall site had higher chlorophyll content than those at high rainfall, but the chlorophyll content of hosts at intermediate rainfall did not differ with those at low and high rainfall sites (Fig. 3).

Table 2
F-ratio and level of significance of the general linear model (GLM) testing the effects of rainfall, infection intensity, and their interaction on Leaf area (LA), Leaf dry matter content (LDMC), Specific leaf area (SLA), succulence, Leaf water content (LWC), chlorophyll content, and stomatal conductance (g_{sw}) of marula host and mistletoe leaves. Significant *P* values appear in bold. For each variable, both Rainfall and Infection d.f. = 2,451, and Rainfall × Infection d.f. = 4,451.

Variables	Rainfall		Infection		Rainfall × Infection	
	F	*P*	F	*P*	F	*P*
Host						
LA (mm^2)	9.12	**<0.001**	15.59	**<0.001**	5.62	**<0.001**
LDMC (mg g^{-1})	25.63	**<0.001**	2.03	0.13	3.60	**0.01**
SLA (mm^2 mg^{-1})	8.46	**<0.001**	4.33	**0.01**	12.67	**<0.001**
Succulence (g water dm^{-2})	1.27	0.28	2.22	0.11	3.17	**0.01**
LWC (%)	25.63	**<0.001**	2.03	0.13	3.60	**0.01**
Chlorophyll content	4.75	**0.01**	2.76	0.06	7.67	**<0.001**
g_{sw} (mmol m^{-2} s^{-1})	64.14	**<0.001**	13.73	**<0.001**	2.95	**0.02**
Mistletoes						
LA (mm^2)	9.94	**<0.001**	1.04	0.308	0.37	0.69
LDMC (mg g^{-1})	36.48	**<0.001**	21.90	**<0.001**	10.27	**<0.001**
SLA (mm^2 mg^{-1})	7.71	**0.001**	4.45	**0.04**	2.36	0.10
Succulence (g water dm^{-2})	19.31	**<0.001**	1.29	0.26	12.08	**<0.001**
LWC (%)	36.48	**<0.001**	21.90	**<0.001**	10.27	**<0.001**
Chlorophyll content	6.25	**0.002**	4.17	**0.04**	3.44	**0.03**
g_{sw} (mmol m^{-2} s^{-1})	37.44	**<0.001**	11.61	**0.001**	2.17	0.12

Of all the measured marula host traits, only LA, SLA, and stomatal conductance varied with infection intensity (Table 2). Uninfected trees had up to 1.22-fold greater LA than low and high mistletoe-infected trees. In contrast, SLA was 1.07 times greater on high-than-low mistletoe-infected hosts. However, the SLA of uninfected trees was not different from that of low- and high-mistletoe-infected trees. Stomatal conductance increased with mistletoe infection and was up to 1.19 times significantly greater on high mistletoe-infected trees than on low mistletoe-infected and uninfected trees.

There was a significant interaction between rainfall and infection intensity for all marula host leaf traits (Table 2). However, site-specific infection interactions showed varying results (Fig. 3). In the low rainfall site, SLA declined, but succulence, and stomatal conductance increased with increasing mistletoe infection. However, marula host LA, LDMC, LWC, and chlorophyll content were not significantly different across the mistletoe infection categories ($P > 0.05$, Fig. 2).

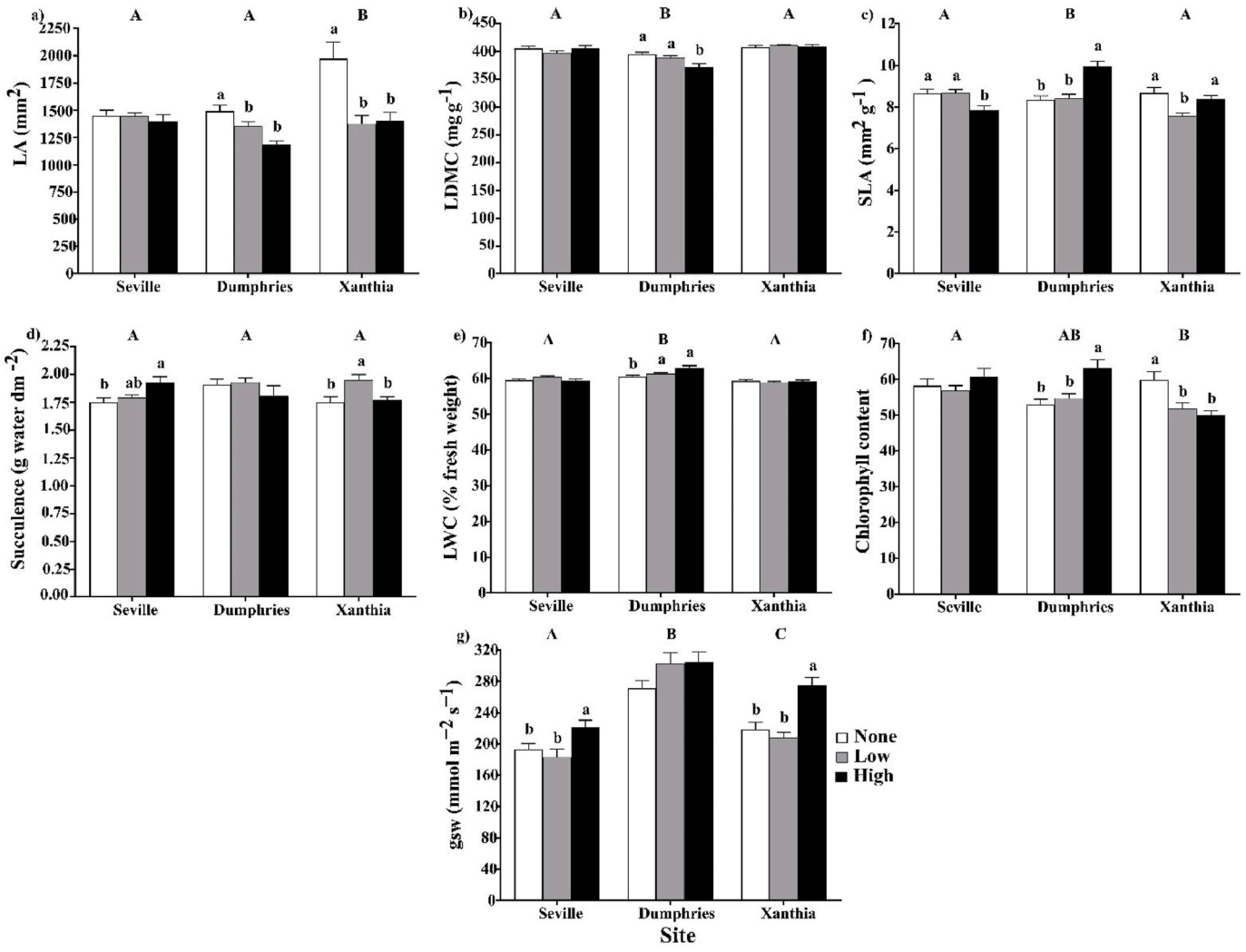


Fig. 3. Mean ± standard error (a) leaf area (LA), (b) leaf dry matter content (LDMC), (c) specific leaf area (SLA), (d) succulence, (e) leaf water content (LWC), (f) chlorophyll content, and (g) stomatal conductance (g_{sw}) of marula host leaves at Seville (590 mm), Dumfries (655 mm), and Xanthia (695 mm). Capital letters show differences between sites (rainfall). Lower-case letters show within site differences between infection levels (uninfected, low, and high) (Tukey HSD test, $P < 0.05$).

At the intermediate rainfall site, marula host leaf succulence and stomatal conductance did not differ across the infection intensities. Host LA and LDMC, decreased by up to 20%, while SLA, LWC, and chlorophyll content increased by 4%–16% with increasing mistletoe infection (Fig. 3). At the high rainfall site, host LDMC and LWC did not differ with mistletoe infection intensity (Fig. 3). Low mistletoe-infected trees had up to ~1.12-fold higher succulence than uninfected and high mistletoe-infected trees. Chlorophyll content decreased by up to 17% with increasing mistletoe infection. Low mistletoe-infected trees had a lower SLA than uninfected and high mistletoe-infected trees. Uninfected trees had a higher LA than low- and high-mistletoe-infected trees (Fig. 3). High-infected trees had higher stomatal conductance than uninfected and low mistletoe-infected trees (Fig. 3).

3.3. Variation in mistletoe leaf traits

Rainfall had a significant effect on all the mistletoe leaf traits (Table 2). Interestingly, mistletoe traits displayed an opposite trend from marula host leaves for the measured traits. Mistletoe LA declined, but succulence increased with increasing rainfall (Fig. 4). SLA was lower at intermediate than at low and high rainfall sites. LDMC peaked at intermediate rainfall, being lower at low and high rainfall sites. Mistletoes had higher stomatal conductance at intermediate rainfall sites than at low and high rainfall sites (Fig. 4). Chlorophyll content was 32% higher at intermediate rainfall sites than at low and high rainfall sites.

Mistletoe infection intensity had effects on most mistletoe leaf traits except for LA, and succulence (Table 2). The SLA, LWC, and stomatal conductance of mistletoes decreased by 1%–12% with an increase in mistletoe infection. In contrast, LDMC and chlorophyll increased by 8% with increasing mistletoe infection.

The interaction of rainfall site and infection had no effect on the LA, SLA, and stomatal conductance of mistletoes (Table 2). At low rainfall, LA, SLA, and chlorophyll content of mistletoes did not differ significantly with infection intensity ($P > 0.05$; Fig. 4). Mistletoe LDMC increased by 16% with an increase in mistletoe infection. However, succulence, LWC, and stomatal conductance decreased with increasing mistletoe infection by 6%–24%.

At intermediate rainfall, LA, SLA, and stomatal conductance did not differ between mistletoe infection categories. LDMC and chlorophyll content increased, but succulence and LWC decreased with increasing mistletoe infection (Fig. 4). At the high rainfall site, LA, LDMC, LWC, chlorophyll content, and stomatal conductance did not significantly differ with mistletoe infection intensity (Fig. 4). However, SLA decreased by 12%, while succulence increased by 16%, with increasing mistletoe infection. Lastly, there was no significant relationship between host leaf traits and mistletoe leaf traits (Appendix 1).

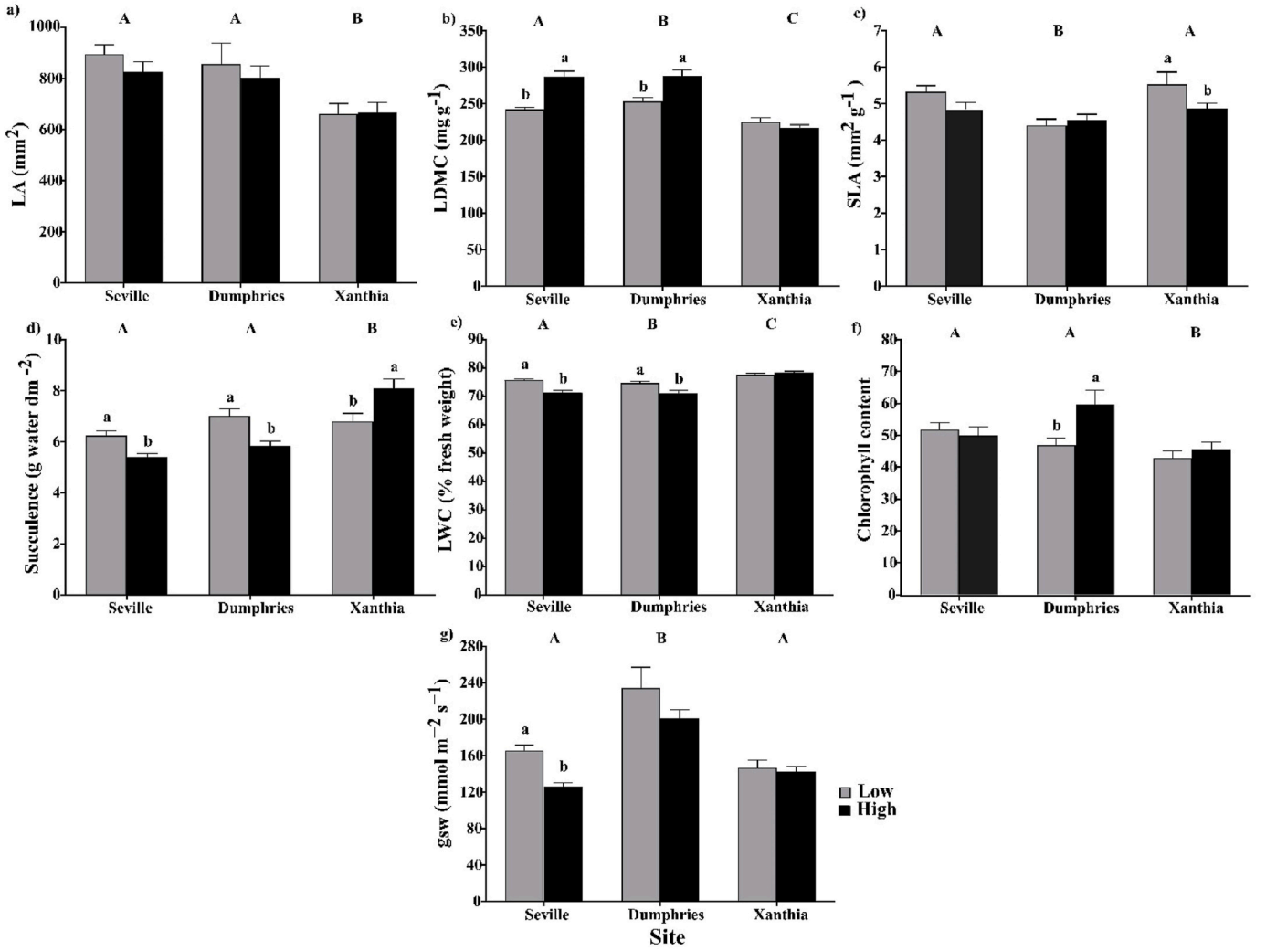


Fig. 4. Mean ± standard error (a) leaf area (LA), (b) leaf dry matter content (LDMC), (c) specific leaf area (SLA), (d) succulence, (e) leaf water content (LWC), (f) chlorophyll content, and (g) stomatal conductance (g_{sw}) of mistletoe leaves at Seville (590 mm), Dumfries (655 mm), and Xanthia (695 mm). Capital letters show differences between sites (rainfall). Lower-case letters show within site differences between infection levels (low and high) (Tukey HSD test, $P < 0.05$).

4. Discussion

In this study, we show that the functional leaf traits of marula host trees and mistletoes vary with levels of mean annual rainfall, mistletoe infection intensity, and their interaction. However, our tree characteristics (height, stem diameter, and canopy area) did not vary with rainfall or mistletoe-infection, thus any variations in the leaf traits are not attributed to differences in host size. Changes in leaf traits reveal how mistletoes and their marula hosts respond to variations in resource availability and stress from mistletoe infection. Mistletoe effects were far more subtle compared to rainfall impact. A summary of these strategies is shown in Table 3. We found that marula host trees were intermediary between being more conservative (in terms of water use) and highly acquisitive (in terms of nutrient resources) at low rainfall sites, while tending to be acquisitive and conservative at intermediate and high rainfall sites, respectively. Mistletoes were more conservative at low rainfall, but became more acquisitive with increasing rainfall. In terms of response to mistletoe infection intensity, uninfected marula trees were more conservative, while low and high mistletoe-infected trees tended to be highly acquisitive, indicating increased resource use with increasing mistletoe infection intensity. On the contrary, mistletoes were highly resource-acquisitive on low mistletoe-infected trees, but more conservative with an increase in mistletoe infection intensity. Our results show that *E. dregei* and marula are capable of leaf trait plasticity (rather than genetic variation) depending on rainfall and mistletoe infection intensity in their natural distribution areas.

4.1. Rainfall effects on host leaf traits

Contrary to findings elsewhere (Reich et al., 2003; Wright et al., 2004; Silva et al., 2019), the SLA of marula host trees declined with increasing rainfall, indicating resource retention and more investment in tissues relating to support and protection against herbivory and higher temperatures (Souza et al., 2018; Araújo et al., 2021). Marula host trees could also have adopted a highly conservative strategy to endure nutrient-poor soils (Reich et al., 2003; Wright et al., 2004; de Cassia-Silva et al., 2017; Silva et al., 2019), due to the depletion of soil nutrients through higher leaching at high rainfall. This indicates that marula hosts in the high rainfall site invest in a more conservative strategy wherein their leaves are more nutrient-use efficient and structurally resistant, thus potentially increasing their capacity to tolerate drought and photoinhibition (Silva et al., 2019).

Like McLean et al. (2014), marulas at intermediate rainfall sites had the largest SLA, suggesting that the moderate rainfall site had higher soil nutrients. Therefore, marulas in the intermediate rainfall site would likely have higher productivity and photosynthetic rates, and be more

Table 3
Summary of the differences in resource use strategy of host and mistletoe (↔, intermediate; ↓, lowest; ↑, highest) of the measured leaf traits shown only for traits with significant differences. Leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), succulence, leaf water content (LWC), chlorophyll content, and stomatal conductance (g_{sw}). The extent of variation (plasticity) is presented as a percentage of the difference (highest minus the lowest value) between uninfected, low mistletoe-infected, and high mistletoe-infected host trees and their respective mistletoes at three rainfall sites. In turn, traits are ranked according to their percentage variation with the highest variation being top ranked.

Variables	Rainfall site			Mistletoe infection			Plasticity	
	Seville (590 mm)	Dumphries (655 mm)	Xanthia (695 mm)	Uninfected	Low	High	Percentage (%)	Rank
Hosts								
LA (mm^2)	↓	↓	↑	↑	↓	↓	40	1
LDMC (mg g^{-1})	↑	↓	↑				10	5
SLA (mm^2 mg^{-1})	↓	↑	↓	↔	↓	↑	24	3
Succulence (g water dm^{-2})							10	5
LWC (%)	↓	↑	↓				6	7
Chlorophyll content	↑	↔	↓				21	4
g_{sw} (mmol m^{-2} s^{-1})	↓	↑	↔	↓	↓	↑	40	1
Strategy								
Water	Conservative	Acquisitive	Conservative	Conservative	Acquisitive	Acquisitive		
Nutrients	Intermediate	Acquisitive	Conservative	Conservative	Conservative	Acquisitive		
Mistletoes								
LA (mm^2)	↑	↑	↓				26	4
LDMC (mg g^{-1})	↔	↑	↓		↓	↑	25	5
SLA (mm^2 mg^{-1})	↑	↓	↑		↑	↓	20	6
Succulence (g water dm^{-2})	↓	↓	↑				33	2
LWC (%)	↔	↓	↑		↑	↓	9	7
Chlorophyll content	↑	↑	↓		↓	↑	28	3
g_{sw} (mmol m^{-2} s^{-1})	↓	↑	↓		↑	↓	46	1
Strategy								
Water	Conservative	Conservative	Acquisitive		Acquisitive	Conservative		
Nutrients	Intermediate	Acquisitive	Acquisitive		Acquisitive	Conservative		

competitive (Silva et al., 2019). These marulas will most likely be more competitive with their understory plants, whilst those at the high rainfall site will be more facilitative to their understory plants due to lower availability of resources. Trees tend to be more competitive when resource availability is higher and become more facilitative when resource availability is lower, reducing stressful conditions (Pugnaire and Luque, 2001; Dohn et al., 2013). As such, we anticipate that variations in the understorey species composition and functional traits due to the different impacts of the large trees, will further increase plant heterogeneity in this semi-arid savanna (Maponga et al., 2021; Maponga et al., 2025).

In support of our initial hypothesis, marulas in the intermediate and low rainfall sites had the smallest leaf areas relative to those in the high rainfall site, similar to findings in previous studies (Wright et al., 2004; McLean et al., 2014; Souza et al., 2018; Silva et al., 2019). Smaller leaf areas reduce canopy self-shading, thereby increasing light interception (Wright et al., 2004; Silva et al., 2019), leaf temperature control, and WUE (McLean et al., 2014; Silva et al., 2019; Moore et al., 2020). Consequently, marula host leaves in the intermediate and low-rainfall areas also had a higher chlorophyll content. In contrast, high-rainfall trees had the largest leaf areas, consistent with an increase in leaf size as mean annual precipitation increased (McLean et al., 2014). Indeed, rainfall is an important variable for leaf size in areas receiving <750 mm (Souza et al., 2018).

Stomatal conductance of marula host trees was lowest at the low rainfall site relative to the intermediate and high rainfall sites, in agreement with our hypothesis. The moderately-sized leaves in the low rainfall site had better WUE than the larger leaves in the high rainfall site (Queijeiro-Bolaños et al., 2020). Since water is one of the most limiting resources in semi-arid environments (Wilson and Witkowski, 1998), the lower stomatal conductance at low rainfall sites encourages isohydric behaviour, as shown by lower transpiration rates and increased WUE (Reich et al., 2003; Wright et al., 2004; Zweifel et al., 2012; de Cassia-Silva et al., 2017; Souza et al., 2018; Queijeiro-Bolaños et al., 2020; Wang et al., 2023). However, similar to McLean et al. (2014), marula host trees at the intermediate rainfall site had the highest stomatal conductance, possibly due to a high SLA, which increases transpiration rates and reduces WUE (Souza et al., 2018).

4.2. *Mistletoe-infection effects on host leaf traits*

We expected marula hosts to shift from being highly acquisitive (larger SLA, lower LDMC, and LA) when uninfected to being more conservative (lower SLA, higher LDMC, and LA) as infection severity increased (Cunningham et al., 1999; Hosseini et al., 2007; Pierce et al., 2013; Silva et al., 2019), due to water and nitrogen limitations (Ozturk et al., 2022). However, we found that marula host trees were more acquisitive (lowest LDMC, high SLA) at high mistletoe infection intensity. This could be a ploy by the marula hosts to increase their competitive capabilities to ensure survival against high mistletoe infection (Silva et al., 2019). Higher SLA could also be attributed to an increase in nutrient availability through increased litterfall of nutrient-enriched litter, particularly bird droppings (March and Watson, 2007, 2010; Ndagurwa, 2015; Ndagurwa et al., 2013, 2014, 2018, 2020), and improved soil water availability (Maponga, 2021) below high mistletoe-infected trees. Indeed, high understory species and functional diversity have been observed beneath high compared to low mistletoe-infected trees (Maponga et al., 2021) due to the significantly higher availability of limiting soil resources (Ndagurwa et al., 2016). Moreover, high mistletoe-infection microhabitats had higher herbivory and excreta compared to low-infected trees (Maponga, 2021). However, low mistletoe-infected trees had the lowest SLA, suggesting they could be responding to nutrient and water stress, which is attributed to the inception of mistletoe infection by being more scleromorphic (Scalon et al., 2017). At this stage, mistletoes may be more harmful, as they are directly acquiring dissolved carbon from the host (Zweifel et al., 2012). Nonetheless, low SLA could also be due to the low chlorophyll content of low mistletoe-infected trees relative to uninfected and high-infected trees. In contrast, uninfected marulas could be responding to lower soil nutrients while also utilising the shade-tolerant plant strategy to conserve resources and have longer leaf lifespans, thus their lower SLA and larger leaves (Reich et al., 2003). Regardless, this strategy may be more applicable to understorey plants, whose responses to light are more critical for their survival (Reich et al., 2003; Maponga et al., 2025).

Of interest, normally, trees that receive more hours of sunshine have large leaf areas (Souza et al., 2018); however, uninfected trees with full (denser) canopies had larger leaves compared to low and high mistletoe-infected trees with thinner crowns and lower leaf biomass (Mellado et al., 2016; Maponga, 2021; Douaihy et al., 2022). Shade-tolerant plants should also have a low leaf area per gram (Reich et al., 2003); therefore, the larger LA on uninfected marulas suggests that there could be other factors, e.g., herbivory by insects, that we did not measure but observed that could be influencing these leaf traits. Nonetheless, due to higher secondary compounds, herbivory by insects on mature marula leaves is not extensive, as mature leaves are less nutritious and digestible than more immature leaves (Msukwa et al., 2021). However, trees with smaller leaves are less frequently browsed (Wright et al., 2004); thus, small leaf areas may be a strategy in which infected trees avoid herbivory, pathogens, and mechanical damage (Reich et al., 2003; Araújo et al., 2021) compared to the larger leaves on uninfected marulas.

The short- and long-term effects of maintaining host water balance due to mistletoe infection includes a reduction in the hosts' transpiration rates and smaller leaf area (respectively), which both eventually lower the overall carbon gain of the host (Zweifel et al., 2012). Therefore, we hypothesised that the stomatal conductance of marula trees would decrease with an increase in mistletoe infection. However, our results showed that stomatal conductance significantly increased with the severity of infection, which could suggest reduced competition for water with co-occurring plants. These findings contradict decreased stomatal conductance recorded in *Acacia schaffneri* (*Vachellia schaffneri* (S.Watson) Seigler & Ebinger) with an increase in *Phoradendron brachystachyum* (DC.) Nutt. infection severity (Queijeiro-Bolaños et al., 2020). Similarly, Kubov et al. (2020) reported lower stomatal conductance in mistletoe-infected oaks than in uninfected sessile oaks. Thus, our results suggest increased water usage with increasing infection, thereby driving the host tree towards a more anisohydric behaviour (with low adjustment rates of stomatal conductance and photosynthetic rates), which can be detrimental to both the host and the mistletoes (Kubov et al., 2020). This may also have negative implications for the growth and productivity of other subordinate and less competitive plants within the high-infected trees' proximity, as water is already a limiting factor in semi-arid environments (Maponga et al., 2025). Regardless, increased stomatal conductance is positively associated with an increase in CO_2 assimilation, which is positive for the photosynthetic performance (Kubov et al., 2020) of high mistletoe-infected hosts, hence the higher SLA. As such, these infected large trees may persist for a few years, but at the detriment of other surrounding plants due to the higher competition for resources.

4.3. Rainfall effects on mistletoe leaf traits

Mistletoe leaves behaved in the opposite manner to the more conservative marula host leaves in the high rainfall area relative to the low and intermediate rainfall sites. Mistletoes were highly acquisitive at high rainfall and more conservative at intermediate rainfall. Since marulas at the high rainfall site are conservative, mistletoes could have opted to be more autotrophic to supplement the mineral resources by producing their own carbohydrates. However, despite high rainfall, mistletoes had the lowest chlorophyll contents. Regardless, mistletoes are adapted to shade, and they photosynthesize in low-light conditions (Nabity et al., 2021). In contrast, mistletoes in the intermediate rainfall site were more conservative and heterotrophic, and thus, they relied more on resources from their highly acquisitive hosts.

We had expected that under dry conditions, mistletoes would exhibit more controlled water use (Ullmann et al., 1985; Scalon and Wright, 2015; Zhang et al., 2023). Our results partially supported this, but they also show that mistletoes in the high- and low-rainfall sites had similar stomatal conductance. Low stomatal conductance in the low rainfall site may potentially be attributed to the resistance to cavitation (formation of tiny vapour bubbles within the xylem conduits attributed to a drop in pressure and strong suction, and these bubbles impede the flow of water (Tyree and Sperry, 1989) due to excessive tension within the xylem conduits, which leads to systematic failure in efficiently acquiring water, thus mistletoes close their stomata (Reich et al., 2003; Zweifel et al., 2012; Chen et al., 2013). In contrast, mistletoes in the high rainfall site are at a more optimum water supply, and they can acquire adequate water and dissolved nitrogen without having to increase their transpiration rates, subsequently reducing their stomatal conductance (Küppers, 1992; Chen et al., 2013). Therefore, mistletoes can show plasticity and adapt their physiological traits to increase WUE, depending on the prevailing environment (Scalon and Wright, 2015).

4.4. Mistletoe-infection effects on mistletoe leaf traits

Despite high resource availability within high-infected tree canopy patches (Ndagurwa et al., 2013, 2014; Ndagurwa, 2015; Maponga, 2021), mistletoes on low-infected marula hosts were acquisitive, while those on high-infected hosts were conservative. Usually, carbon acquisition decreases under increased proliferation of mistletoe infection (Zweifel et al., 2012). As such, high infection mistletoes restricted resource use to increase leaf longevity (Scalon et al., 2017), consequently increasing their competitive abilities against the acquisitive host and other surrounding subordinate understory plants that are also competing for soil resources within the hosts' proximity (Ndagurwa et al., 2016; Maponga et al., 2021). Similarly, the hemiparasite *Phoradendron californicum* Nutt. on the host *Prosopis velutina* Wooton shifted towards autotrophy when resources were scarce or when competition was high (Nabity et al., 2021). Furthermore, high-infection mistletoes could have been conservative to reduce intraspecific competition for host resources. Mistletoes recognise their kin and thus share resources between themselves while maintaining the integrity of their host (Nabity et al., 2021). This particularly occurs when host fitness is low; thus, to increase their survival and that of the host, mistletoes communicate to adequately share the resources. Therefore, depending on the extent of infection coupled with resource availability, the hemiparasite may trade off being autotrophic or heterotrophic, resulting in photosynthetic plasticity (Küppers, 1992; Nabity et al., 2021).

Similar to the mistletoe *Psittacanthus calyculatus* (DC.) G. Don, *E. dregei*'s stomatal conductance decreased with mistletoe infection intensity. Lower stomatal conductance on *E. dregei* on high-infection marula hosts supports efficient water use and the equitable sharing of water amongst the mistletoes through intraspecific facilitation (Queijeiro-Bolaños et al., 2020). Mistletoes tend to have water and nutrient control mechanisms to ensure the survival of both the host and the mistletoe (Ullmann et al., 1985; Bowie and Ward, 2004). Consequently, as aridity increases, mistletoes increase their WUE, which supports our findings (Scalon and Wright, 2015). Similar to Nabity et al. (2021), our results show that mistletoes increased their WUE on marula hosts that were profligate in their water use. This often occurs if the demand for supply from the mistletoe to the host critically exceeds the host capacity (Glatzel, 1983; Ullmann et al., 1985). In contrast, mistletoes parasitizing low-infection marulas had higher stomatal conductance due to low intraspecific competition. Further, with mistletoe infection inception, mistletoe water demands may not be detrimental to the host, thus mistletoe WUE is unimportant at this early growth stage.

5. Conclusion

Understanding the effects of environmental changes on ecosystem functioning was improved by including intraspecific trait variability in our investigations. This study contributes to knowledge on the intraspecific variability in plant resource use strategies and functional trait values of the host *S. birrea* (marula) and mistletoe *E. dregei* based on direct gradients, i.e., rainfall and mistletoe infection intensity. Our findings present rainfall and mistletoe infection intensity as important

filtering processes that influence mistletoe and host leaf traits. Rainfall effects on both mistletoe and marula leaf traits are more pronounced, while mistletoe-infection effects seem to be additive to both the host and the mistletoe. Moreover, there is a significant interaction between rainfall and infection for some leaf traits, thus further increasing this intraspecific variation. Marulas at different rainfall levels and with varying mistletoe infection intensities offer varying resources to their mistletoes based on their ecophysiology and prevailing environmental factors. As such, the performance of individual mistletoes is influenced by the availability of resources within each marula host. Consequently, the nutrient and competitive status of the host play an important role in the morphological traits that are exhibited by the mistletoes, thus further increasing intraspecific trait variability. Similarly, mistletoe effects on hosts are variable; they depend on the extent of mistletoe-infection intensity.

Variations were not always clear-cut, as shown by marula host leaves at the intermediate rainfall site showing acquisitive properties compared to leaves at high rainfall, which were more conservative. There may be other factors, such as soil nutrients and temperature, that were not included here that could be causing these differences. However, the broad range of leaf trait expression of marula hosts and mistletoes could ensure their survival in cases of stochastic events. Thus, we anticipate that high intra-specific variation will promote these species' persistence, establishment, and resilience, particularly in communal areas already facing other anthropogenic threats such as deforestation, overgrazing, and inappropriately applied fire. Moreover, these variations are expected to result in different understory species assemblages, functional and species diversity, and herbivore activity, thus further broadening plant and herbivore heterogeneity in this semi-arid savanna. Indeed, high phenotypic plasticity can increase the ability of a species to survive in the face of perturbations, and thus avoid local extinctions. Therefore, the heterogeneous rainfall in Bushbuckridge can support greater plasticity of both host and mistletoe traits, thus the persistence of these two populations. Our results further show that with an increase in scarcity of water in semi-arid savannas due to droughts, mistletoes and their hosts are likely to become more conservative and will regulate their water use to persist under a changing climate. However, increasing aridity, at least in isolation and because of plasticity in host and parasite, may not be an immediate threat. Therefore, understanding these adaptive strategies can help conservation managers predict future ecological patterns and trait syndromes of these species thus informing better conservation efforts for both species in different communal areas. This is particularly important for marulas that have been shown to be declining, which necessitate further monitoring, protection and conservation.

Since mistletoe impacts vary depending on host species, mistletoe size, infection intensity, and mistletoe species, other studies should also investigate the impact of different mistletoe species on various hosts. Soil resource availability, temperature, and megaherbivore impacts can also be incorporated into future studies. Further, measurements of soil moisture using more robust equipment, such as, isotopes, and long-term soil moisture measurements could be done to determine if these traits also show phenotypic plasticity in the same way.

Funding

This research was funded by the National Research Foundation Free Standing Post-doctoral Grant (138459) under the South African Environmental Observation Network. The study was also funded by the University of the Witwatersrand.

CRediT authorship contribution statement

Tsitsi Sithandiwe Maponga: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Hilton Garikai Taambuka Ndagurwa:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Dave Ian Thompson:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Justice Muvengwi:** Writing – review & editing, Methodology, Formal analysis. **Wayne Twine:** Writing – review & editing, Resources, Conceptualization. **Ed T.F. Witkowski:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Tsitsi Sithandiwe Maponga reports financial support was provided by National Research Foundation. Tsitsi Sithandiwe Maponga reports financial support was provided by University of the Witwatersrand Johannesburg. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the National Research Foundation - Free Standing Post-doctoral grant (grant 138459) through the South African Environmental Observation Network, and the University of the Witwatersrand for funding this research. We further thank the South African Environmental Observation Network for financial and logistical support. We also thank the Indunas at Dumfries, Seville, and Xanthia for allowing us to do research within their villages. We are grateful to Mightyman Mashele, Frank Nyathi, Tswarelo Ndlovu, Sandiso Dladla, Nic Venter, Una Manave, and Rivola Butibuti Khosa for assisting with data collection.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2024.105308.

Data availability

Data will be made available on request.

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