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Functional traits of *Ziziphus mucronata* below mistletoe-infected trees in a semi-arid African savanna

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ABSTRACT

Mistletoes are increasingly associated with elevated leaf litter, soil nutrients, and soil moisture, resources which influence variations in plant functional traits. Despite this recognition, variations in the functional traits of understorey plants with overstorey (host) tree mistletoe infection are yet to be examined. Here, we measured the different functional traits (height, stem diameter, canopy area, leaf area, specific leaf area, whole-leaf thickness, leaf dry matter content, and chlorophyll content) of *Ziziphus mucronata*, a dominant woody plant beneath mistletoe-infected *Vachellia karroo* trees in semi-arid savanna. Two-sample *t*-tests were used to compare host size, mistletoe infection intensity, and trait variables between low and high mistletoe-infected trees. The relationships between *Ziziphus mucronata* functional traits *vs.* host tree diameter and the number of mistletoes per tree were explored using regression analysis and visualized using a regression biplot based on a redundancy analysis (RDA). Host tree height, canopy area, and canopy volume were strongly positively ($r > 0.7$, $p < 0.05$) related to mistletoe infection intensity. While most of the traits did not vary with mistletoe infection, the chlorophyll content and leaf area of understorey *Z. mucronata* increased with host tree size, being greater beneath high than low mistletoe-infected trees. These variations are linked to changes in limiting resources such as light, soil nutrients, and soil moisture due to accumulation of mistletoes and increase in size as the host tree ages. As a result, the understorey plants shifted from being resource conservative to being acquisitive as limiting resources increased. The general lack of trait plasticity in understorey *Z. mucronata* suggests that plastic allocation responses may not be a general consequence of mistletoe infection.

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1. Introduction

Mistletoes are an important component of semi-arid savanna ecosystems primarily through their influence on the availability of often limiting resources such as soil moisture and nutrients (Ndagurwa, 2015; Maponga, 2021). Their effect on community or ecosystem properties is disproportionately large relative to their biomass, and thus they function as ecosystem engineers or keystone species in environments where they occur (Watson, 2001).

Mistletoes, due to low nutrient resorption, produce nutrient-rich litter, providing an additional source of nutrients beneath infected hosts (Ndagurwa et al., 2013, 2014a, 2016). The additional litter creates more persistent and deeper litter beds, which improve the diversity and abundance of litter-dwelling insects (Ndagurwa et al., 2014b), soil microbial communities (Bardgett et al., 2006), and the water holding capacity and infiltration rates of subcanopy soils (Maponga, 2021). Consequently, the understorey of mistletoe infected trees are associated with elevated rates of decomposition and nutrient release (Ndagurwa et al., 2015, 2020) and soil nutrient concentrations (March and Watson, 2007, 2010; Ndagurwa et al., 2013, 2014a, 2018; Muvengwi et al., 2015). Also, mistletoes suppress host performance and competitive ability, reduce host growth, modify canopy architecture (e.g., number of leaves), or cause host death (Spasojevic and Suding, 2011; Mathiasen et al., 2008; Mellado and Zamora, 2017) creating canopy and within-canopy gaps, which increase understorey light incidence, growth space, and soil temperatures and relative humidity (Mellado and Zamora, 2017; Maponga, 2021). These changes to the understorey properties increase the abundance, productivity, and functional diversity of understorey

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plants (March and Watson, 2010; Maponga et al., 2021; Spasojevic and Suding, 2011; Ndagurwa et al., 2016, 2018). In addition, the changes in understorey resource availability influence the physiological, morphological, and phenological attributes of each plant, resulting in intraspecific trait variability (Niu et al., 2016; Venâncio et al., 2016; Scalon et al., 2017; Cuma Mushagalusa et al., 2019). Hence, the functional traits of understorey plants are expected to vary following the resource gradients created by different mistletoe-infection intensities. However, variations in the functional traits of understorey plants with mistletoe infection in semi-arid savanna are yet to be examined.

Plant functional traits are quantifiable characteristics of a plant that influence its general fitness, reproduction, and function (Albert et al., 2010; Xu et al., 2020). They represent the ecological strategies of plants and show how plants respond to environmental factors (e.g., light, nutrients, water or temperature), enabling us to better understand ecological patterns and processes (Perez-Harguindeguy et al., 2016). The basic strategies range from conservative, where plants efficiently utilize limiting resources such as nutrients and water but grow slowly, to acquisitive where resources are used inefficiently to fuel rapid growth (Diaz et al., 2016). Conservative species have low leaf area, high leaf water content, and thick leaves to reduce leaf desiccation and damage (Araújo et al., 2021). In contrast, resource-acquisitive plant species retain thin large area leaves, with larger stomata for high light, water, and nutrient uptake (Araújo et al., 2021). As such, species that are widespread and exposed to varying environmental conditions often exhibit intraspecific trait variation following environmental gradients (Jung et al., 2010; Xu et al., 2020). Therefore, examination of the relationship between plant traits and their environment can help us understand plant responses to resource availability. Further, given the link between intraspecific trait variation and plant community structure, trait–environment relationships also enable the identification of the filtering processes that influence plant assemblages (Albert et al., 2010; Jung et al., 2010; Xu et al., 2020). However, despite the influence of mistletoes on resource availability and heterogeneity via their effects on host growth and performance as well as increased input of nutrient-rich litter (March and Watson, 2007, 2010; Ndagurwa, 2015; Maponga, 2021), the trait variation resulting from the resource gradients they create are yet to be examined. This limits our understanding of the broader ecological consequences of mistletoe infection on plant structure and function in semi-arid savanna.

In this context, we examined the variation in functional traits of *Ziziphus mucronata* Willd. subsp. *mucronata* (Rhamnaceae) in response to mistletoe-mediated resource heterogeneity by measuring plant traits (i.e., height, stem diameter, canopy area, chlorophyll content, leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), and whole leaf thickness (WLT)) of individuals beneath low compared with high mistletoe-infected *Vachellia karroo* trees. We hypothesized that *Z. mucronata* plants would have (i) greater height, diameter and canopy area, (ii) smaller leaf area and higher LDMC, SLA, and (iii) low chlorophyll content below high than low mistletoe-infected trees due to, for example, high soil nutrients, soil moisture, and light incidence in the former. The findings of this study will help to elucidate the effects of mistletoe-mediated resource heterogeneity on the plastic allocation patterns of understorey plants, and the potential implications for biodiversity conservation, savanna heterogeneity, and sustainable management.

2. Methods

2.1. Study area description

The study was carried out at the Matopos Research Station (MRS) (20° 31′S, 28° 31′E), southwest Zimbabwe. Long term mean annual rainfall averages 586 mm, mostly falling from November to March. Mean annual temperature averages 18 °C (Chirara et al., 1998). The vegetation on the predominantly medium-textured red clay soils (Dye, 1983) is Vachellia (formerly Acacia) tree-bush savanna dominated by *Vachellia karroo* Hayne, *Vachellia nilotica* (L.) Willd. ex Delile, *Vachellia gerrardii* Benth., *Vachellia rehmanniana* Schinz., *Senegalia nigrescens* Oliv. and *Maytenus senegalensis* (Lam.). The herbaceous layer is dominated by *Heteropogon contortus* L., *Themeda triandra* Forssk., and *Cymbopogon plurinodis* Stapf ex Burtt Davy with *Setaria incrassata* (Hochst.) Hack. Abh. *Erianthemum ngamicum, Plicosepalus kalachariensis* and *Viscum verrucosum* (Mapaura and Timberlake, 2004) are the most common mistletoes, but *Agelanthus subulatus* (Engl.) Polhill & Wiens and *Erianthemum dregei* (Eckl. & Zeyh.) also occur in the study area.

Ziziphus mucronata (buffalo thorn) is a deciduous, small to medium-sized, spinescent tree up to 9 m tall, with a dense spreading crown (Van Wyk and Van Wyk, 2013). The palatable leaves are ovate or broadly ovate, glossy dark green on top and pale and hairy on the bottom (Van Wyk and Van Wyk, 2013). *Z. mucronata* is a very hardy species, most common in dry areas with summer rainfall in sub-Saharan Africa (Van Wyk and Van Wyk, 2013). It is resistant to both frost and drought (Orwa et al., 2009). In addition to providing fodder, nectar, and firewood, *Z. mucronata* is an important medicinal plant in southern Africa (Orwa et al., 2009).

2.2. Research design and field measurements

Mistletoe-infected *V. karroo* trees were surveyed in the study site at the end of the growing season (end of February to early March of 2019; Maponga, 2021). The height, stem diameter at breast height (DBH), the number of adult mistletoes (those with several large axial branches with numerous side branches, Ndagurwa et al., 2012), and mistletoe species were recorded for each tree. We also recorded the canopy long (D_1) and short (90° of D_1; = D_2) diameters and used them to calculate the canopy area and canopy volume using Eqs. (1) and (2), respectively.

$$\textit{Canopy area}\ (m^2) = \pi\left(\frac{D1}{2} \times \frac{D2}{2}\right) \quad (1)$$

$$\textit{Canopy volume}\ (m^3) = \frac{4}{3}\pi\left(\frac{D1}{2}\right)\left(\frac{D2}{2}\right)\left(\frac{H}{2}\right) \quad (2)$$

where D_1, D_2, and H are canopy long (D_1) and short (90° of D_1; = D_2) diameters and canopy height, respectively.

We then assigned the trees to two mistletoe density categories based on mistletoe counts and canopy cover, low (< 10 % mistletoe canopy cover, < 7 number of mistletoes) and high (> 70 % mistletoe canopy cover, > 15 number of mistletoes) (n = 10 in each mistletoe density category) following (Maponga 2021; Maponga et al., 2021).

To investigate intraspecific trait variability, we compared the characteristics of *Z. mucronata* found below canopies of the low mistletoe-infected and high mistletoe-infected *V. karroo* trees. *Ziziphus mucronata* was selected because of its dominance below mistletoe-infected *V. karroo* trees, with ~36% cover relative to other species (Maponga, 2021; Maponga et al., 2021). We randomly sampled ±10 *Z. mucronata* individuals below each tree and recorded their height, stem diameter, and the canopy long (D_1) and short (90° of D_1; = D_2) diameters (Perez-Harguindeguy et al., 2016). The canopy area of each *Z. mucronata* individual was also calculated using Eq. (1).

Leaf traits were measured on ten fully expanded photosynthetically active leaves randomly selected on each *Z. mucronata* individual. The chlorophyll content (chlorophyll values which are proportional to the amount of nitrogen in the leaf) of each leaf was measured non-destructively using a SPAD-502-Plus chlorophyll meter (Spectrum Technologies, Inc., Plainfield IL, USA). To measure leaf area, the leaves were cut off, individually marked, and photographed using a digital camera, and then leaf area was calculated using ImageJ. Leaf fresh

and dry weight were respectively determined before and after oven drying at 70 °C for 72 h using a 0.0001 g precision scale. We then calculated specific leaf area (SLA), leaf dry matter content (LDMC), and whole leaf thickness following Perez-Harguindeguy et al. (2016) using Eqs. (3), (4), and (5), respectively.

$$Specific\ leaf\ area\ (SLA)(m^3\ kg^{-1}) = \frac{Fresh\ leaf\ area}{Oven\ dry\ mass} \quad (3)$$

$$Leaf\ dry\ matter\ content\ (mg\ g^{-1}) = \frac{Oven\ dry\ mass\ (mg)}{Water\ saturated\ fresh\ mass\ (g)} \quad (4)$$

$$Whole\ leaf\ thickness\ (\mu m) = \frac{1}{SLA\ \times\ LCMDC} \quad (5)$$

2.3. Statistical analysis

All data were tested for normality and heterogeneity of variances before analysis using Shapiro-Wilk test and Levene statistic, respectively. The data were normal, with homogeneous variances. Then we compared the differences in host variables (height, DBH, canopy area, and canopy volume), the number of mistletoes, and mistletoe canopy cover between low mistletoe-infected and high mistletoe-infected trees using an independent sample *t*-test. The differences in *Z. mucronata* leaf traits (height, stem diameter, canopy cover, chlorophyll content, leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), and whole leaf thickness (WLT)) between low mistletoe-infected and high mistletoe-infected trees was also tested using an independent two-sample *t*-test. Multicollinearity was tested for all variables using the variance inflation factor (VIF). Except for tree diameter and the number of mistletoes, all the other traits showed high multicollinearity, VIF > 5 (Table 1) (Logan, 2011). Thus, to avoid problems of multicollinearity and associated convergence failures, we excluded these variables from further analysis (Logan, 2011). The relationships between tree diameter and the number of mistletoes *vs*. the height, stem diameter, canopy area, chlorophyll content, leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), and whole leaf thickness (WLT) of understorey *Z. mucronata* were explored using regression analysis. These relationships were visualized using a regression biplot based on a redundancy analysis (RDA) performed using CANOCO version 4.5 (TerBraak and Smilauer, 2002). All other statistical tests were conducted in R v. 3.1.5 (R Core Team, 2020), and level of significance was set at 5 %.

3. Results

3.1. Host tree and mistletoe variables

High mistletoe-infected trees were taller, with larger canopies than low mistletoe-infected trees (Table 2). The canopies of high mistletoe-infected trees were twice as large as those of low mistletoe-infected trees. However, the stem diameter of low mistletoe-infected and high mistletoe-infected trees was not significantly different ($p > 0.05$). As expected, mistletoe canopy cover, the number of mistletoes, and the numbers of the mistletoe species, *Plicosepalus kalachariensis* and *Viscum verrucosum,* were greater in high mistletoe-infected than in low mistletoe-infected trees (Table 2). High mistletoe-infected trees had up to 10 times more mistletoes than low mistletoe-infected trees (Table 2). Mistletoe infection was positively related to tree height (number of mistletoes: $r = 0.71$, $p < 0.001$; mistletoe canopy cover: $r = 0.76$, $p < 0.001$), canopy area (number of mistletoes: $r = 0.51$, $p = 0.02$; mistletoe canopy cover: $r = 0.57$, $p = 0.001$), and canopy volume (number of mistletoes: $r = 0.58$, $p = 0.007$; mistletoe canopy cover: $r = 0.64$, $p = 0.002$), but not to tree stem diameter (number of mistletoes: $r = 0.11$, $p = 0.63$; mistletoe canopy cover: $r = 0.23$, $p = 0.34$).

Table 1
Multicollinearity statistics of host and mistletoe variables. VIF, Variance Inflation Factor.

Variable	Statistic	
	Tolerance	VIF
Height (cm)	0.053	18.95
DBH (cm)	0.829	1.206
Canopy area (cm^2)	0.009	107.7
Canopy volume (m^3)	0.007	153.7
Number of mistletoes	0.474	2.109
Mistletoe canopy cover (%)	0.101	9.921

Table 2
Mean ± standard error of mistletoe variables and dimensions of low and high mistletoe-infected *Vachellia karroo* trees. Significant *p* values (< 0.05) appear in bold.

Variable	Mistletoe density		*t*	*p value*
	Low	High		
Host tree variables				
Height (cm)	6.33 ± 0.23	9.53 ± 0.57	5.21	**0.001**
Stem diameter (DBH) (cm)	24.1 ± 2.15	28.0 ± 2.97	1.07	0.30
Canopy area (CA) (m^2)	71.3 ± 4.88	123 ± 15.2	3.25	**0.004**
Canopy volume (CV) (m^3)	300 ± 22	809 ± 131	3.83	**0.01**
Mistletoe variables				
Mistletoe canopy cover (%)	6.9 ± 2.57	78.5 ± 4.98	12.8	<**0.001**
Number of mistletoes per tree	3.0 ± 0.68	21.8 ± 2.91	6.35	<**0.001**
Viscum verrucosum	2.6 ± 0.64	17.7 ± 2.70	5.64	<**0.001**
Plicosepalus kalachariensis	0.4 ± 0.22	4.00 ± 1.37	3.46	**0.01**

3.2. Traits variations of understorey *Z. mucronata* plants

Ziziphus mucronata plants beneath high mistletoe-infected trees had significantly (~13 %) higher chlorophyll content than those below low mistletoe-infected trees (Table 3), but we found no significant differences in all the other measured traits of understorey *Z. mucronata* plants between high mistletoe-infected and low mistletoe-infected trees ($p > 0.05$; Table 3). The *Ziziphus mucronata* tree size measurements, as well as leaf area, specific leaf area, and leaf dry matter content, however, tended to be higher with high mistletoe infection intensity, corresponding with the reported higher chlorophyll content, even if they were not statistically different. Also, whole leaf thickness, which is often negatively correlated to leaf area and specific leaf area, showed a decline with mistletoe infection intensity suggesting a shift in traits with mistletoe infection.

The relationship between *Z. mucronata* traits and host tree diameter and the number of mistletoes visualized using a redundancy analysis (RDA) regression biplot is shown in Fig. 1. The model parameters

Table 3
Mean ± standard error trait measurements of *Ziziphus mucronata* plants beneath low and high mistletoe-infected *Vachellia karroo* trees. Significant *p* values (< 0.05) appear in bold.

Trait	Mistletoe density		*t*	*p* value
	Low	High		
Height (cm)	16.5 ± 1.88	23.0 ± 3.09	1.79	0.09
Stem diameter (cm)	0.32 ± 0.03	0.38 ± 0.04	1.02	0.57
Canopy area (CA) (cm^2)	182.2 ± 47.4	193.5 ± 47.0	0.17	0.74
Leaf area (LA) (cm^2)	6.60 ± 0.74	7.42 ± 0.83	0.74	0.47
Specific leaf area (SLA) ($m^2.kg^{-1}$)	1.77 ± 0.13	2.03 ± 0.14	1.39	0.18
Whole leaf thickness (μm)	328.1 ± 28.2	276.8 ± 17.5	1.19	0.14
Leaf dry matter content ($mg.g^{-1}$)	552.2 ± 15.3	543.2 ± 12.3	0.46	0.65
Chlorophyll content (%)	28.6 ± 0.74	30.7 ± 0.74	2.39	**0.01**

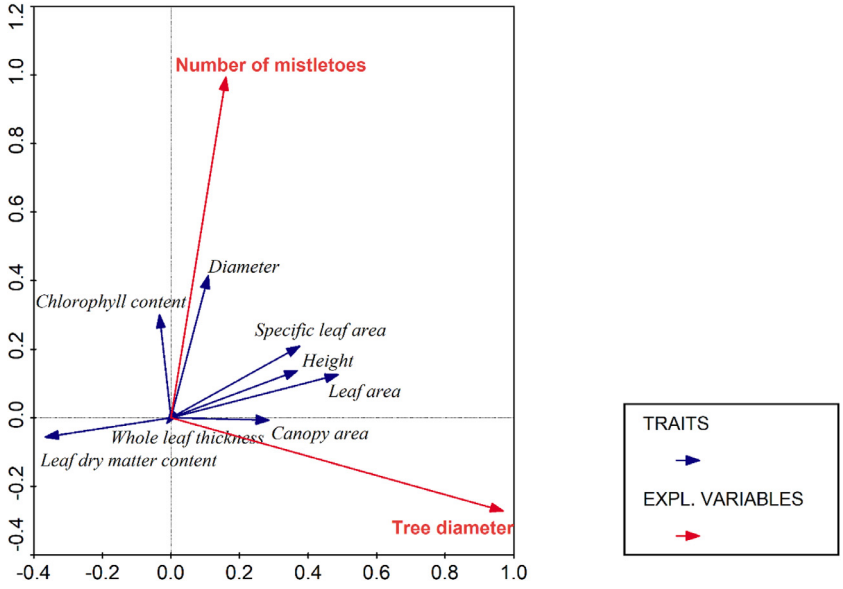


Fig. 1. Regression biplot based on redundancy analysis (RDA) showing the influence of the number of mistletoes per host tree and its stem diameter, on the leaf traits of understorey *Ziziphus mucronata* plants.

and significance of these relationships are shown in Table 4. The only significant relationships were observed between host tree diameter and the leaf area of understorey *Z. mucronata* plants (Table 4). The leaf area of understorey *Z. mucronata* plants increased with increasing host tree diameter (Table 4; Fig. 1). Although not statistically significant ($p > 0.05$; Table 4), host tree diameter and the number of mistletoes showed a positive influence on the height, stem diameter, canopy area, and leaf area of *Z. mucronata* (Fig. 1). In contrast, for whole leaf thickness and leaf dry matter content, the influence of host tree diameter and the number of mistletoes was negative (Table 4; Fig. 1). The number of mistletoes had a positive, while tree diameter had a negative influence on the chlorophyll content (Table 1; Fig. 1).

Table 4
Relationships (y = a + bx) between *Ziziphus mucronata* traits (height, stem diameter, canopy area, leaf area, specific leaf area, whole leaf thickness, leaf dry matter content and chlorophyll content; y) and host tree diameter, number of mistletoes (x).

Variable pair	Model parameters			Test statistic	
	r	r^2	Regression equation	t	p
Height *vs.*					
Tree diameter	0.34	0.12	$y = 10.4 \pm 0.36x$	1.55	0.14
Number of mistletoes	0.23	0.05	$y = 17.7 \pm 0.17x$	1.01	0.33
Stem diameter *vs.*					
Tree diameter	0.04	0.002	$y = 0.33 \pm 0.0006x$	0.18	0.86
Number of mistletoes	0.43	0.18	$y = 0.29 \pm 0.004x$	2.01	0.06
Canopy area *vs.*					
Tree diameter	0.28	0.08	$y = 57.5 \pm 5.00x$	1.25	0.23
Number of mistletoes	0.07	0.005	$y = 177 \pm 0.87x$	0.29	0.77
Leaf area *vs.*					
Tree diameter	0.46	0.21	$y = 3.42 \pm 0.14x$	2.21	**0.04**
Number of mistletoes	0.25	0.06	$y = 6.37 \pm 0.05x$	1.11	0.28
Specific leaf area *vs.*					
Tree diameter	0.34	0.11	$y = 1.45 \pm 0.02x$	1.52	0.15
Number of mistletoes	0.30	0.09	$y = 1.77 \pm 0.01x$	1.34	0.19
Whole leaf thickness *vs.*					
Tree diameter	−0.15	0.02	$y = 0.001 - 0.000005x$	−0.66	0.52
Number of mistletoes	−0.21	0.05	$y = 0.001 - 0.000004x$	−0.93	0.36
Leaf dry matter content *vs.*					
Tree diameter	−0.35	0.12	$y = 596 - 1.84x$	−1.60	0.13
Number of mistletoes	−0.15	0.02	$y = 554 - 0.55x$	−0.66	0.52
Chlorophyll content *vs.*					
Tree diameter	−0.08	0.02	$y = 34.3 - 0.03x$	−0.35	0.73
Number of mistletoes	−0.22	0.05	$y = 32.5 \pm 0.08x$	1.23	0.23

4. Discussion

In this study, mistletoe infection increased with host tree height, canopy area, and canopy volume, consistent with many previous studies (e.g., Aukema and Martínez Del Rio, 2002a, b; Ndagurwa et al., 2012, 2022; Overton, 1994; Reid and Stafford Smith, 2000). The strong ($r > 0.7$) correlation suggests the importance of host size in predicting mistletoe infection intensity. In terms of the understorey *Z. mucronata* plant responses, of the eight traits assessed, only chlorophyll content significantly changed as mistletoe infection intensity increased, with greater chlorophyll in *Z. mucronata* individuals below high mistletoe-infected than low mistletoe-infected trees. These findings suggest that plastic allocation responses may not be a general consequence of mistletoe infection.

4.1. Host tree and mistletoe variables

Mistletoe infection increased with tree height, canopy area, and canopy volume conforming to the general pattern of greater mistletoe abundances in large than small trees (Aukema and Martínez Del Rio, 2002a, b; Ndagurwa et al., 2012). Several possibilities underlie this general pattern including that mistletoe-seed-disperser birds prefer to perch and feed in larger than small trees (Aukema and Martinez del Rio, 2002a, b), or there is accumulation of mistletoes as the tree grows (Overton, 1994). Alternatively, mistletoes likely survive better on large than small trees because large trees can provide a more reliable water and nutrient supply. Here, the relationship between mistletoe infection and tree size parameters was very strong ($r > 0.7$) relative to other studies (e.g., $r = 0.03–0.13$, Ndagurwa et al., 2012, 2022), which suggests that the strength of size–intensity relationships may not be consistent across environments. These studies vary in terms of many factors including sampling scale, environmental conditions, mistletoe species, or host species, which shape mistletoe–host relations. Consequently, comparisons of size–intensity relationships within and between ecosystems should be interpreted with caution to avoid misleading conservation management. Additionally, there is need for standardization of mistletoe infection estimation methods.

4.2. Traits variations of understorey *Z. mucronata* plants

Mistletoes cause foliage loss, reduced host growth, and alter the canopy structure of their hosts (Press and Phoenix, 2005; Mueller and Gehring, 2006; Mathiasen et al., 2008; Bilgili et al., 2018), which increases the amount of light that penetrates through to the hosts' understorey (Mellado and Zamora, 2017). For example, Mellado and Zamora (2017) found that *Viscum album austriacum* reduced the canopy density of *Pinus nigra*, thereby resulting in an increase in the amount of light incidence penetrating to the understorey by up to 19 %. Likewise, Maponga (2021) also found higher soil temperatures below high than low mistletoe-infected trees, which was attributed to higher light incidence below high mistletoe-infected trees. Therefore, because of increased irradiance, the chlorophyll content of understory plants is expected to be lower beneath high than low mistletoe-infected trees. However, contrary to our hypothesis, the chlorophyll content of understorey *Z. mucronata* individuals was elevated beneath high compared with low mistletoe-infected trees, suggesting that instead of light intensity other factors could have influenced the high chlorophyll content beneath large mistletoe-infected trees. For example, because chlorophyll content is positively related to nitrogen supply, the high chlorophyll content of *Z. mucronata* beneath high mistletoe-infected trees could indicate better nitrogen availability within these patches (March and Watson, 2007; Ndagurwa et al., 2013; Muvengwi et al., 2015). Larger trees typically harbour older mistletoes with a diminishing leaf-to-stem ratio (Bilgili et al., 2020), indicating that more nutrient-rich mistletoe leaves are shed beneath heavily infested trees thereby increasing nitrogen supply (Ndagurwa et al., 2013, 2016). Although the host tree may acquire some of these additional nutrients, previous studies have shown that heavily infected trees have more soil nutrients than less infected trees (March and Watson, 2007; Ndagurwa et al., 2014a), which suggest that there is a consistent nutrient availability for understorey plants growing underneath heavily infected trees. This elevated nutrient supply enables understorey plants growing beneath heavily infected trees to increase their chlorophyll content.

Although the leaf area of understory *Z. mucronata* plants did not differ between low and high mistletoe-infected trees, we observed a significant increase in the leaf area with host tree diameter. Since high-radiation stress tends to select for relatively small leaves (Perez-Harguindeguy et al., 2016), leaf area should be low beneath heavily mistletoe-infected trees due to high irradiance. Thus, we suggest that the increase in leaf area with host tree diameter may be linked to a response to high soil resources beneath older, large host trees conforming with nurse protégé. Indeed, the nursing of younger plants by older plants is common in arid and semi-arid environments characterized by limiting resources such as water and nutrients (Maestre et al., 2009). Large trees through an efficient, deeper, and more extensive root system concentrate water and nutrients below their canopies (Dean et al., 1999; Mlambo et al., 2005). In addition, mistletoes in the canopy of these large trees through addition of nutrient-rich litter and their effects on host performance and growth also increase below-canopy litterfall, decomposition, soil nutrients, and soil moisture (March and Watson, 2007, 2010; Ndagurwa et al., 2013, 2014a; Muvengwi et al., 2015; Maponga, 2021). This enables understorey plants to proliferate and grow rapidly, hence the increase in leaf area of *Z. mucronata* with host diameter. Therefore, as light and soil resources increase there is simultaneously less competition for them, allowing understorey plants to shift towards resource acquisition rather than resource conservation (Zheng et al., 2015; Scalon et al., 2017; Cuma Mushagalusa et al., 2019). However, a large leaf area may increase water loss through high transpiration. Therefore, *Z. mucronata* may have begun to trade-off between limiting water losses and having higher photosynthetic yield (productivity) by making larger leaves (Venâncio et al., 2016).

The direct (consumption) or indirect (trampling, excretion) effects of variable numbers of herbivores visiting mistletoe-infected trees could also mediate the differences in light and nutrient availability between low and high mistletoe-infected trees. Many mammals and arthropod herbivores consume mistletoe leaves, flowers, stems or fruit (Watson 2001; Burns and Watson, 2013), which further opens up the sparse crowns of heavily infected trees thereby increasing light availability. Indeed, higher soil temperatures and relative humidity beneath high than low mistletoe-infected *V. karroo* canopy patches indicate high light incidence beneath heavily infected trees (Maponga, 2021). Also, herbivory/grazing/trampling (proxy for animal visits) tend to increase with mistletoe infection (Mellado and Zamora, 2017; Maponga, 2021), which may affect nutrient input beneath mistletoe-infected trees. Many other animals also use mistletoes and the understorey host tree canopy patches for shade, forage, or shelter (Watson, 2001). These animals increase nutrient and organic matter inputs through dung, urine, and other debris (e.g., frass, seeds) increasing nutrient availability beneath parasitized trees (Watson, 2001; Mellado et al., 2016; Mellado and Zamora, 2017). As a result, considering these biotic interactions tend to increase with mistletoe load (e.g., Mellado and Zamora, 2017; Maponga, 2021), there is an expected increase in the spatial heterogeneity of light and nutrient availability between low and high mistletoe-infected trees. We suggest that these direct or indirect effects of mistletoes on light and nutrient availability could also have contributed to the differences in the chlorophyll content and leaf area of understorey *Z. mucronata* plants.

Unlike the chlorophyll content and leaf area, all the other understorey *Z. mucronata* traits did not significantly change with increase in mistletoe infection or tree size parameters, suggesting that plastic allocation responses to changes in environmental conditions may be trait-specific (e.g., Ndagurwa et al., 2016) or dependent on other factors acting alone or in interaction. Alternatively, it is also possible that the changes in understorey environmental conditions or host competitive ability were not strong enough to trigger plastic allocation responses in understorey *Z. mucronata*. Here, we considered traits related to plant size (height, stem diameter, and canopy area) and leaf structure (leaf area, specific leaf area, whole leaf thickness, and leaf dry-matter content) because they are universally at the core of the plant life history (Grime et al., 1997; Westoby, 1998), and they show how plants respond to changes in environmental conditions e.g., soil nutrients, moisture, or light intensity. With only chlorophyll content and leaf area, we were able to show the mechanisms with which mistletoes can alter understorey plant functional traits. However, the measurement of more traits may not only reveal trait variations that we may have missed, but will also help elucidate mistletoe-induced trait variations related to regeneration, dispersal or response to disturbances, among many others (*see* Cornelissen et al., 2003). Therefore, we suggest that future studies should be long-term and focus on a wider range of plant species to capture trait variations occurring at different temporal and spatial scales.

In conclusion, while most traits were not related to host size or the number of mistletoes, chlorophyll content and leaf area showed variations with mistletoe infection and host tree size, respectively. This trait plasticity was attributed to changes in limiting resources i.e., light intensity, soil fertility, and soil moisture due to increase in size and accumulation of mistletoes as the host tree ages. These findings show that when resources are limited, understorey *Z. mucronata* is resource conservative, but as resources become more readily available, the species becomes more resource acquisitive. Thus, understorey *Z. mucronata* respond differently to heterogeneous environments, resulting in greater variability in plant community structure and function. Thus, if in principle other understorey species follow the same strategies, there is likely greater inter- and intraspecific variation, thereby increasing ecosystem resilience and reinforcing the patch dynamics of this semi-arid savanna system. In the

future, we suggest more trait measurements on a wide range of plant species under different mistletoe infection intensities (e.g., none, low, moderate, high) to have a broader scale appreciation of how mistletoe infection intensity influences understorey plant traits.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Tsitsi S. Maponga: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Hilton G.T. Ndagurwa:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Ed T.F. Witkowski:** Writing – review & editing, Methodology, Conceptualization.

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