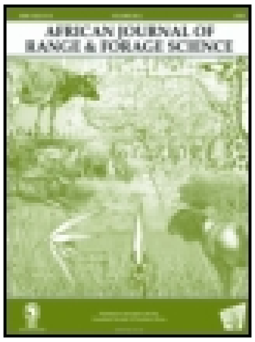

African Journal of Range & Forage Science

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tarf20

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To cite this article: Kiersten McMahon & David Ward (2021): The effects of tree canopies on invasive *Lantana camara*: a follow-up study 18 years later, African Journal of Range & Forage Science, DOI: 10.2989/10220119.2020.1850522

To link to this article: https://doi.org/10.2989/10220119.2020.1850522

African Journal of Range & Forage Science 2021: 1–5
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This is the final version of the article that is published ahead of the print and online issue

AFRICAN JOURNAL OF RANGE & FORAGE SCIENCE
ISSN 1022-0119 EISSN 1727-9380
https://doi.org/10.2989/10220119.2020.1850522

Research Note

The effects of tree canopies on invasive *Lantana camara*: a follow-up study 18 years later

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***Lantana camara* is primarily a bird-dispersed invasive plant species that has spread quickly across South Africa in disturbed areas. We re-examined the distribution of *Lantana* at Rodger and Twine's (2002) study site (R&T) in a highly grazed communal area and an adjacent conserved area in 2019. R&T found that *Lantana* was more common in the communal area than in the conserved area. Glyphosate herbicide was sprayed to suppress *Lantana* from 2016 to 2019 in the conserved area only. We re-examined the bird-dispersal hypothesis by surveying subcanopy and intercanopy environments. We found more *Lantana* in the subcanopy than in the intercanopy. There were more *Lantana* plants in the conserved area, but there were virtually none in the communal area. Most concerning was the apparent resprouting of *Lantana* despite herbicide application. We used sequential aerial photographs and found that there has been an increase in woody cover in the conservation area since 2013, which may exacerbate the problem with this invasive plant. We conclude that it is not communal grazing *per se* that causes the encroachment of *Lantana*, and that it has more do with the woody cover of native plants, as concluded by R&T.**

Keywords: bird dispersal, communal land-use, conservation, invasive species, woody cover

Supplementary material: available at https://doi.org/10.2989/10220119.2020.1850522

The invasive shrub *Lantana camara* (hereafter *Lantana*) is widespread in subtropical areas of the world (Taylor et al. 2012a; Vardien et al. 2012; Niphadkar et al. 2017). *Lantana* frequently occurs in disturbed lands (Vardien et al. 2012; Dube et al. 2020), but also occurs in forest and woodland understoreys (Niphadkar et al. 2017). In South Africa, this species has spread quickly, replacing native species in more than two million hectares (Bromilow 1995; Versfeld et al. 1998; Bhagwat et al. 2012; Shackleton et al. 2017). This species has also been planted by local people for aesthetic and medicinal purposes, which has led to dispersal into adjacent habitats (Shackleton et al. 2017; Amoateng et al. 2018).

Lantana is toxic to livestock (Sharma et al. 1981). As a consequence of this toxicity, differences in grazing pressure provide *Lantana* with less competition in heavily grazed areas (Shackleton et al. 2017). An additional factor of its life history that affects its dispersion is that *Lantana* is primarily dispersed by birds. Bird defaecation primarily occurs in subcanopy environments (Green et al. 2009), resulting in higher *Lantana* density than in intercanopy environments (Rodger and Twine 2002).

Rodger and Twine (2002) (hereafter, R&T) examined the dispersion and abundance of *Lantana* in a conserved area (Wits Rural Facility) and an adjacent highly populated communal area (Timbavati) near Acornhoek, Mpumalanga, South Africa (24°31' S, 31°06' E). They found that *Lantana* density was higher under subcanopy than intercanopy environments primarily because of bird dispersal. The large numbers of domestic livestock in the communal area resulted in higher disturbance, resulting in a higher density of *Lantana* than in the conserved area where there are few wild herbivores and no livestock. High levels of tree felling in the communal area have caused a low density of trees in the communal lands (Shackleton 1993; R&T). We performed a follow-up study in 2019 to ascertain whether there were any significant changes in the dispersion and abundance of *Lantana*. Subsequent to R&T's study, *Lantana* was sprayed with a glyphosate herbicide (Springbok 360 SL, Arysta LifeScience) at six-monthly intervals from 2016 to 2019 in the conserved area, but not in the communal area (W.C. Twine, Wits Rural Facility, pers. comm.). Accordingly, we anticipated that there would have been a dramatic decline or absence of *Lantana* in the conserved area in 2019.

We formulated the following predictions:

1. *Lantana* will remain more common in the communal area because of the higher disturbance than in the conserved area.
2. *Lantana* will be absent or very rare in the conserved area because of the application of herbicide subsequent to R&T.
3. *Lantana* would be more common in subcanopy environments than in intercanopy environments due to *Lantana* being primarily bird dispersed.

The study area was located in the Bushbuckridge Lowveld, which is broadly classified as Granite Lowveld Bushveld (Mucina and Rutherford 2006). The tree layer is dominated by *Sclerocarya birrea*, *Terminalia sericea* and *Combretum collinum* on the sandy slopes, with species, such as *Dichrostachys cinerea* and *Acacia swazica*, on the clayey sodic bottomlands (Colgan et al. 2012; Twine and Holdo 2016). Mean annual rainfall has declined from 670 mm (R&T) to 535 mm over the past 20 years with high interannual variation, with most rain falling between November and February. The environment is subtropical, with a mean annual temperature of 22 °C.

Both the communal and conserved areas observed have similar topography, geology, and climate. Therefore, differences in vegetation between the two study areas are the result of the differences in previous and current land-use practices (R&T). Two 180 m transects were surveyed by us in the conserved area, each at least 150 m apart, running downslope toward the riparian area, as in the previous study, although R&T performed three 250 m transects. To ensure a fair comparison, we obtained the original data from James Rodger (Stellenbosch University, pers. comm.), and used two transects only. Twenty 3 m × 3 m quadrats were randomly placed along the transect and the habitat type (subcanopy/intercanopy) recorded. We spaced each quadrat 9 m apart to ensure that there were 20 quadrats on the transect, as R&T did. Where a 9 m interval fell on a subcanopy position, we performed an intercanopy quadrat nearby, as R&T did, and *vice versa*. We also recorded the number and stem diameters of *Lantana* plants. In our study, we could not survey transects in the communal area, because of the low density of *Lantana* plants found (n = 5) after surveying an area of several square kilometres. Similar to R&T, we recorded four classes of herbaceous cover (estimated visually in a single 1 m × 1 m quadrat) as: 0–25%, 26–50%, 51–75% and 76–100%. All other details followed those described by R&T.

A contingency table test was conducted to compare the percentage of quadrats with *Lantana* for cover (low, medium, high, very high) with the different biomass class categories as recorded in R&T. We used a Kolmogorov–Smirnov test to compare size distributions of *Lantana* plants from the 2002 study with ours.

In the communal area (Timbavati), R&T found 479 *Lantana* stems, whereas we found virtually none (n = 5), despite searching a very broad area (Table 1). In the conserved area of the Wits Rural Facility, R&T found eight *Lantana* stems (in three transects), whereas we found 60 *Lantana* stems in two transects.

Unlike the R&T study, which found that *Lantana* was significantly more abundant in the lowest herbaceous cover class (56.3%), *Lantana* was more frequent in the highest cover class (77.8%) (Tables 1 and 2). *Lantana* stem diameters were significantly larger in the R&T study than in 2019 (Kolmogorov–Smirnov test: Z = 2.157, p < 0.001) (Figure 1), although this may have been due to resprouting subsequent to herbicide application.

R&T found a decline in the percentage of quadrats containing *Lantana* as herbaceous biomass class increased, whereas we recorded the opposite (Table 1). We were unable to perform a statistical test for intercanopy comparisons between R&T's data and our 2019 data, because of the large number of zeros within the table. However, there was a higher percentage frequency of quadrats with *Lantana* in the low biomass class in our study (3.7) compared with R&T (0.9), but this difference was not significant (χ^2 = 1.64, p = 0.200) (Table 1). We found a significant difference in the R&T subcanopy data, compared with our 2019 subcanopy data (χ^2 = 150.2, p < 0.001) (Table 2).

Table 1: Frequency of *Lantana* within classes according to land use, cover and canopy position in 2002 (Rodger and Twine 2002) and 2019 (this study); n/a indicates that *Lantana* was absent

Factor	Class	Percentage of quadrats with Lantana	
		2002 (%)	2019 (%)
Land-use	Communal	30.5	n/a
	Conservation	2.5	23.8
Biomass class	Low	23.4	1.1
	Medium	8.8	22.7
	High	7.9	30.0
	Very high	0.0	70.0
Canopy position	Subcanopy	47.5	45.0
	Intercanopy	0.6	2.5

We also used sequential aerial photographs taken from Google Earth® to explore the possibility that there had been an increase in woody cover with time since the R&T study. We used *ImageJ* (Rasband 2018) to measure the reciprocal of the mean grey value of the conserved and the communal area, with high values indicating dense vegetation. There was a significant positive correlation between the reciprocal of mean grey values and year since 2013 for the conservation area (r = 0.96, F = 59.346, p <0.001) (Supplementary Figures S1 and S2). However, there was no significant change in the reciprocal of mean grey values and year since 2013 for the communal area (r = 0.15, F = 0.107, p = 0.756). This indicates that there was an increase in woody cover in the conservation area and no significant change for the communal area, the latter result perhaps being consistent with tree felling.

There are very few long-term follow-up studies on invasive plants (Strayer et al. 2006; Bhagwat et al. 2012; Sundaram and Hiremath 2012; Shackleton et al. 2017; Verheyen et al. 2017). In the previous *Lantana* study at Acornhoek (R&T), abundance of *Lantana* was highest in the communal lands and nearly non-existent in the conserved lands, but the reverse was true in this study. There was an attempt to manage the *Lantana* invasion in the conserved area by applying herbicide (2016 to 2019), but not in the communal area. Most of the *Lantana* stems found in the 2019 study had a small diameter, which may have resulted from resprouting, although we recognise that some individuals may have developed from seeds. Nonetheless, this suggests that the invasion management in the conserved lands is not effective. Follow-up studies on invasive plant abundance and distribution are crucial to the proper management of species invasions (Shackleton et al. 2017).

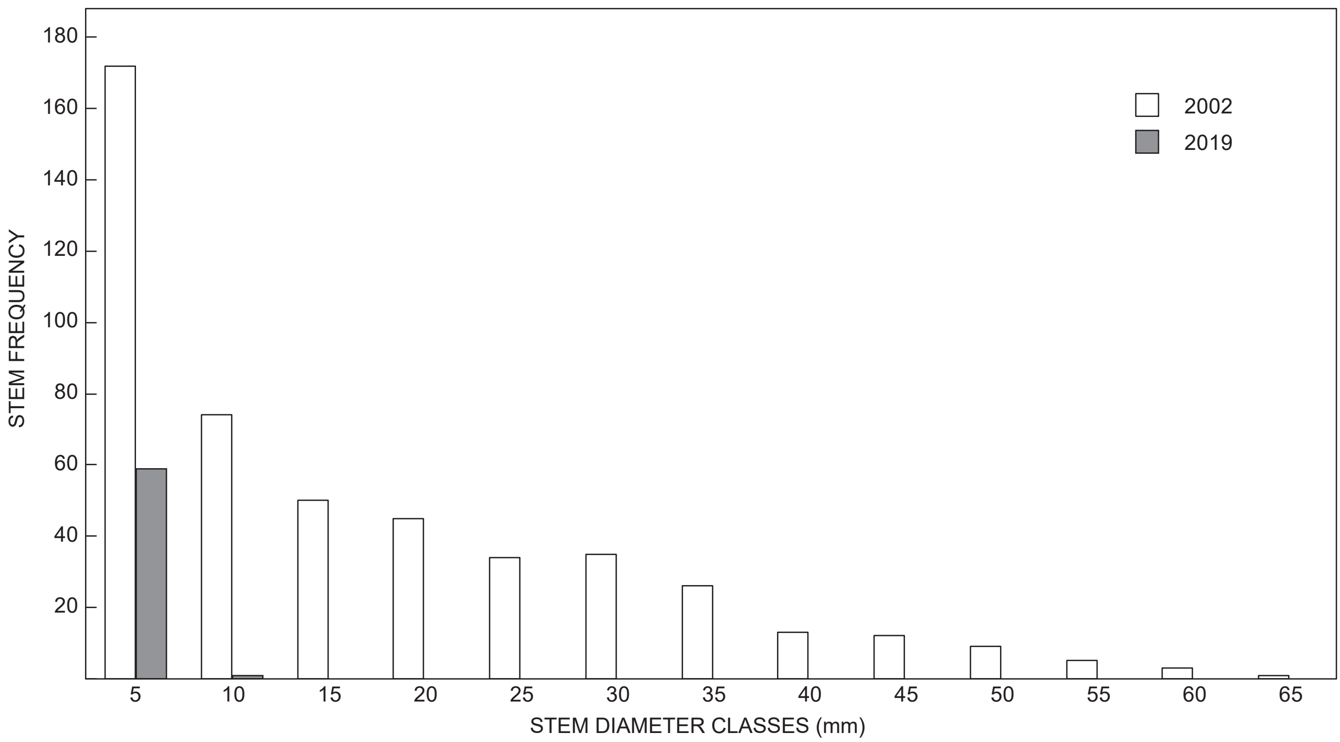

Figure 1: Stem diameter class distribution of *Lantana* in 2002 (Rodger and Twine 2002; not collected only along transects) and 2019 in the conservation area (Wits Rural Facility). There were insufficient *Lantana* (n = 5) in the communal area to record them in 2019. The values on the x-axis represent the upper limits of their respective size classes. Most of the individuals recorded in our 2019 study were resprouts

Table 2: Percentage frequency of quadrats with *Lantana* in subcanopy and intercanopy positions, within different herbaceous biomass classes for Rodger and Twine's (2002) study and our 2019 data in the conserved Wits Rural Facility. Numbers in parentheses indicate values based on two transects only from the communal area (arbitrarily chosen), as we did in 2019

Cover	Subcanopy		Intercanopy	
	2002	2019	2002	2019
Low	56.3 (60.6)	9.1	0.9 (1.7)	3.7
Medium	15.2 (81.0)	38.5	0	0
High	0.04 (48.3)	42.9	0	0
Very high	0.0 (42.9)	77.8	0	0

Lantana is primarily dispersed by birds (R&T; Vardien et al. 2012). This explains why many *Lantana* in the current study were found under the subcanopies of large trees (Tables 1, 2). This clumping pattern has been observed in other plant species, which further supports this claim (Rey and Alcántara 2000; Green et al. 2009; Merow et al. 2011; Ramaswami et al. 2016).

We found more quadrats containing *Lantana* at higher densities of herbaceous cover within the conserved area, whereas R&T found the reverse pattern (Table 1). We also found more *Lantana* on the conserved area and virtually none in the communal area, *contra* R&T. It is unlikely that tree felling on the communal area has contributed to the decline of *Lantana*, because this species is avoided by fuel-gatherers (Shackleton 1993), although the possibility remains that livestock have changed their dietary preferences and are consuming this species now that there is little else to eat (Chritz et al. 2016), despite the fact that it induces photosensitivity in cattle (Shackleton et al. 2017). Use for fencing is another possibility (Kannan et al. 2013), but it was not apparent at Timbavati. We spoke to communal farmers and they were unclear as to the reason for the large-scale disappearance of *Lantana*.

We found that *Lantana* was more abundant in the conserved area where there was greater woody cover. The same result has also been recorded in Indian forests (Niphadkar et al. 2017). The increasing woody cover in the conserved area over time (Supplementary Figure S1) suggests that *Lantana* might continue to benefit from the increased cover (see also Vardien et al. 2012). Possible reasons for increased *Lantana* cover include increased probability of bird dispersal and improved microsite conditions, such as increased shade, greater nutrient availability (mostly because of nitrogen fixation by *Vachellia*/*Senegalia* (formerly *Acacia*) and *Dichrostachys* species; Kambatuku et al. 2013), and/or hydraulic lift (Richards and Caldwell 1987; Schleicher et al. 2011). Woody plant encroachment is also ascribed to increasing global CO_2 concentrations that benefit C_3 woody plants over the C_4 grasses that predominate in this subtropical environment (Ward 2010; Ward et al. 2014). We note that our results are not contradictory with those of R&T; both show that *Lantana* responds positively to vegetation cover.

In our literature survey, we noticed that *Lantana* is still cited as occupying the same area (2 million ha) of South

Africa in later studies (e.g. Vardien et al. 2012; Shackleton et al. 2017), as was re-recorded in earlier studies (e.g. Bromilow 1995; Versveld et al. 1998). We deem this unlikely. Dube et al. (2020) used remote sensing to study *Lantana* in neighbouring Agincourt (Mpumalanga, South Africa) and predicted that this species would expand into higher precipitation areas under future climate-change scenarios. Taylor et al. (2012b) used a global process-based niche model, CLIMEX, to predict that *Lantana* could expand its distribution inland in South Africa where the subtropical zone is likely to occur. Vardien et al. (2012) also predicted that dispersal along rivers, especially by birds, would be an important driver of invasion at large spatial scales in South Africa. Our data, especially those indicating increasing woody cover that *Lantana* favours (Supplementary Figure S1), supports the above-mentioned predictions, and indicates that management of *Lantana* is imperative, if we are to control this problematic invader. We believe that it is primarily bird dispersal that is problematic and that microsite conditions promote the abundance of *Lantana* under subcanopies, regardless of land ownership. These results are supported by Vardien et al. (2012), indicating dispersal along rivers with high canopy cover and the observation of Dube et al. (2020) that *Lantana* would increase in density with high precipitation. Our earlier studies on the positive effects of increased woody cover with increasing global CO_2 levels (Ward 2010, Ward et al. 2014) also suggest that controlling *Lantana* is likely to prove highly problematic.

Acknowledgments — We thank Carol Baker, Justice Mosuma and Nature Shabangu for assistance in the field and the laboratory. We are grateful to Wayne Twine and James Rodger for providing data and insights. This study was funded in part by the Herrick Trust of Kent State University.

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Manuscript received: 23 June 2020, revised: 28 October 2020, accepted: 10 November 2020
Associate Editor: L Trenchard