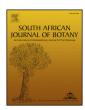
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Landscape degradation may contribute to large-scale die-offs of *Euphorbia ingens* in South Africa



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ABSTRACT

Euphorbia ingens, a large succulent tree species native to southern African savanna ecosystems, has died in large numbers in recent years in some areas of South Africa. A previous study found that changes in climate (higher temperatures and lower or more variable rainfall) likely play an important role in causing mortality. However, anecdotal evidence suggests that stress due to habitat degradation may also contribute to E. ingens die-offs. In this study, we evaluated E. ingens die-offs in South Africa at 10 sites. Specifically, we aimed to examine the roles of both climate and landscape degradation in causing the die-offs. We used a combination of climate data, estimates of tree mortality and ratings of die-off symptoms (categories of grey discoloration and rotting associated with moth attacks), and proxies for landscape degradation associated with livestock grazing. We assessed which sites exhibited greater mortality and die-off associated symptoms, and whether they exhibited spatial auto-correlation (did distance between sites correlate with severity of E. ingens die-off?). We also used correlation analysis to compare tree mortality to proxies of savanna ecosystem degradation. These proxies were dung counts (livestock), woody debris counts, plant and bare soil cover, soil nutrients, and density of Dichrostachys cinerea (Fabaceae), a savanna plant that dominates when disturbance is high. Minimum and maximum temperatures as well as precipitation were compared among sites. There was no spatial auto-correlation between distance and die-off severity among sites, and sites with greater levels of tree mortality were associated with proxies indicating degradation. This suggests that die-offs of E. ingens are likely due to a complex of stressors, including both changes in climate and poor land-use practices. Our results indicate that sustainable rangeland practising of South African savannas may aid in conserving *E. ingens* and retaining this iconic tree on the landscape. © 2017 SAAB. Published by Elsevier B.V. All rights reserved.

1. Introduction

Euphorbia ingens E. Meyer: Boissier is native to southern Africa where it is found primarily in savanna ecosystems (Van Wyk and Van Wyk, 1997; Palgrave et al., 2002). It is a large succulent tree with a branching crown and a main woody stem supported by a shallow, widely-spread root system (Van Wyk and Van Wyk, 1997; Palgrave et al., 2002; Gildenhuys, 2006). Several animals rely on this tree for moisture and nutrients (most notably nitrogen), especially during periods of drought (Dudley, 1997; Brown et al., 2003; Heilmann et al., 2006). Culturally, the tree is important to local human communities that use the chemically complex latex it produces to stun or kill fish allowing easy capture and to produce an array of traditional medicines (Dudley, 1997; Brown et al., 2003; Gildenhuys, 2006; Heilmann et al.,

* Corresponding author. E-mail address: jolanda.roux@fabi.up.ac.za (J. Roux). 2006). The tree is also one of the most iconic examples of convergent evolution in the world (Bennici, 2002; Horn et al., 2012).

Unfortunately, rapid localized die-offs of *E. ingens* are increasingly reported. The first reports of high levels of mortality of the tree were from the Limpopo Province of South Africa (Malan, 2006; Roux et al., 2008, 2009). The main symptoms exhibited by dying trees were a gray discoloration of the succulent branches and the rotting of branches associated with feeding by the larvae of a moth in the genus *Megasis* Guenée (Lepidoptera: Pyralidae) (Malan, 2006; Roux et al., 2008, 2009; Van der Linde et al., 2011a). Subsequent studies revealed that various beetles and fungi were associated with diseased and dying *E. ingens*, but none were clear primary causal agents of mortality (Van der Linde et al., 2011b, 2011c, 2016).

Van der Linde et al. (2012) found evidence that changes in climatic conditions (higher temperatures and lower or more variable rainfall) were involved in *E. ingens* die-offs. Changes in local climate could result in stress to *E. ingens*, allowing insects and pathogens, that are otherwise relatively benign, to contribute to tree mortality. However, anecdotal

observations also suggested that die-offs may be triggered by locally-induced stressors such as poor land-use practices, including intensive grazing. However, the hypothesis that land degradation plays a role had not been investigated.

The savanna ecosystem in which E. ingens occurs covers approximately 35% of South Africa (Scholes, 1997; Scholes and Archer, 1997). Savanna ecosystems are maintained by interactions among fire, herbivory and precipitation (Backéus, 1992; Scholes, 1997; Scholes and Archer, 1997; Van Langevelde et al., 2003; Archibald et al., 2005; Van Wilgen, 2009). Two types of savanna systems occur in South Africa; mesic savanna and xeric savanna which are differentiated by mean annual precipitation (Scholes, 1997). Mesic savanna landscapes generally have a higher woody component compared to xeric savannas due to higher rainfall (Scholes, 1997; Scholes and Archer, 1997). Xeric savannas are drier with a lower woody plant to grass ratio (Scholes, 1997). Historic fire regimes maintain both grasses and trees in savannas (Bond et al., 2003). A lack of fire or reduction in mean fire intervals, due to fire suppression, can lead to increased woody vegetation and a loss of grass cover especially in mesic savanna (Bond et al., 2003; Sankaran et al., 2005; Van Wilgen et al., 2008; Van Wilgen, 2009; Parr et al., 2012). In contrast, higher mean fire return intervals due to human-caused fires lead to reduced woody and grass cover in mesic and xeric savannas respectively (Bond et al., 2003; Van Wilgen, 2009; Parr et al., 2012). Herbivory also plays an important role in maintaining the ratio of grass to woody plants typical of savannas (Scholes and Archer, 1997; Van Langevelde et al., 2003; Wakeling and Bond, 2007). In particular, grazers are most important in xeric savannas while browsers are more important in mesic savannas (Scholes and Archer, 1997; Van Langevelde et al., 2003; Wakeling and Bond, 2007).

Apart from the direct effect on grass to tree ratios, herbivores indirectly affect savanna ecosystems by their physical activities. In the context of human land use effects, livestock can have major negative effects on plant communities through high levels of grazing, trampling, and compaction (Scholes and Archer, 1997; Van Langevelde et al., 2003). Overgrazing, especially in environments with clay soils, can lead to soil degradation, soil compaction (reducing water infiltration and thus water availability), higher surface run-off (that can wash away important water soluble nutrients needed by plants, e.g. nitrate) and crust formation. All of these can reduce the ability of grasses and trees to grow (Kelly and Walker, 1976; Rietkerk et al., 1997, 2000; Van Langevelde et al., 2003; Savadogo et al., 2007).

Savanna ecosystems in South Africa are under increasing pressure to support livestock production (Scholes, 1997; Wakeling and Bond, 2007; Van Wilgen, 2009). Overstocking is common and fire suppression is often practiced to protect the animals (Van Langevelde et al., 2003; Van Wilgen, 2009). Overgrazing and fire suppression in savanna ecosystems not only leads to a loss of grass cover and erosion (Scholes, 1997; Bond et al., 2003; Van Langevelde et al., 2003), but also encroachment by woody pioneer species (Roques et al., 2001; Wakeling and Bond, 2007).

In South Africa, *Dichrostachys cinerea* Wight and Arn., a native woody plant, is a common encroacher in response to overgrazing (Hoffman et al., 1999; Roques et al., 2001; Wakeling and Bond, 2007; Orwa et al., 2009). Herbivores feed on the seed capsules of the plant and play a major role in its dispersal, while locally the plant can spread as a clone through lateral roots (Hoffman et al., 1999; Wakeling and Bond, 2007). This allows *D. cinerea* to establish very quickly in a poorly managed system such as one with high levels of grazing, a high percentage bare soil and reduced fires. Once established, it becomes very difficult to control (Wakeling and Bond, 2007).

The overall objective of this study was to elucidate the factors leading to the massive rapid die-offs of *E. ingens* in South Africa. We revisited sites previously studied by Van der Linde et al. (2012) and included a number of new sites to increase sampling frequency and geographic

distribution. The specific objectives were to 1) re-examine the role that climate plays in current patterns of *E. ingens* die-off and 2) investigate whether tree mortality could also be associated with factors related to landscape degradation.

2. Materials and methods

2.1. Study sites

Study sites included five previously sampled by Van der Linde et al. (2012) in 2010, as well as five new sites. Of the previously sampled sites, three were located in the Limpopo Province [Euphorbia Drive (coordinates: 24°10′14.02″S 29°3′4.86″E, elevation: 1180 m), Last Post (23°17′21.39″S 29°55′27.93″E, 940 m) and Capricorn (23°21′50.67″S 29°44′40.27″E, 1110 m)], and two in the North West Province [Enzelsberg (25°22′58.05"S 26°16′4.21"E, 1170 m) and Wolfaan (25°42′59.27"S 27°42′9.24"E, 1236 m)] of South Africa. Of the new sites, two were located in the province of KwaZulu Natal [Eshowe (28°48′42.64″S 31°30′30.10″E, 450 m) and Ulundi (28°26′8.47″S 31°18′25.70″E, 735 m)], two in Limpopo [Bela-Bela (24°51′48.30″S 28°20′5.90″E, 1200 m) and Modimolle (24°44′53.75″S 28°21′55.43″E, 1216 m)] and one in Mpumalanga [Lydenburg (24°55′53.87"S 30°19′7.09″E, 1155 m)] (Fig. 1). The sites were chosen from accessible E. ingens populations, where we had permission to conduct field studies, from each province in South Africa where this tree occurs.

2.2. Assessment of E. ingens mortality, degree of die-off, and the relationship of mortality and symptoms to climate and landscape variables

At each site, eight 100 m \times 50 m transects were established. Measurements were conducted in November 2014, coinciding with the timeframes used for previous sampling in 2010 and 2012. Within each transect, symptoms associated with die-off (gray discoloration and rotting associated with *Megasis* sp., hereafter referred to as moth damage) were scored for each living tree within each transect (mature and juveniles). Dead trees were also counted and percentage mortality was calculated relative to total trees in each transect. The age class of trees was not evaluated in this study as it was previously shown that both young and old trees are equally affected and that mortality is not related to age (Van der Linde et al., 2012).

Gray discoloration and moth damage were scored, independently of one another, based on a ranking system of zero to four [1: (1–25% succulent branches gray discolored and rotten from moth damage), 2: (26–50%), 3: (51–75%), 4: (76–100%)]. Gray discoloration and moth damage have different patterns of disease progress on *E. ingens* trees, hence they were scored using different systems. Gray discoloration starts at the bottom end of the tree just above the trunk and gradually moves upwards to the crown while moth damage generally affects the succulent branches more or less randomly (Figs. 2 and 3). Not all sites were monitored for the same period of time, therefore, percentage mortality and estimations of disease severity were compared using data from a four-year period for Enzelsberg, Wolfaan, Euphorbia Drive, Capricorn and Last Post (2010–2014) and a two-year period for Bela-Bela, Modimolle, Lydenburg, Ulundi and Eshowe (2012–2014).

To score environmental variables (proxies) associated with savanna degradation, a linear 100 m belt transect was established within each of the 100 m \times 50 m transects at each site. Quadrants (1 \times 1 m) were located every 2 m within each transect (50 quadrants \times 8 transects per site = 400 quadrants per site). Within each quadrant, the percentage area covered by living plants and bare soil was estimated. Coverage of dung and dead wood within each quadrant was estimated using a ranking system of low (wood or dung clumps did not occur or only occurred in one quarter of the quadrant), medium (wood or dung clumps occurred in half of the quadrant area) and high (wood or dung clumps occurred in three quarters of the quadrant area). This classification was used rather than percentage cover because these variables

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