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Highlights

South African Journal of Botany xxx (2012) xxx–xxx

Do freeze events create a demographic bottleneck for *Colophospermum mopane*?

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► Level of freeze-damage was measured on *Colophospermum mopane* along a gentle slope. ► Compared the amount of freeze-damage between low and high elevation individuals. ► Identified a potential 'freeze-trap' with the severest damage occurring at ±2 m. ► Recovery of damaged trees was compared to undamaged trees after a growing season. ► Topkill was identified as a driver of height differences along the slope.

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Do freeze events create a demographic bottleneck for *Colophospermum mopane*?

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Abstract

Frost disturbance is often mentioned in southern African savanna literature, but it is seldom discussed or investigated further. However, it can represent an above-ground disturbance as effective as fire or browsing, depending on the resistance capacity of the effected plants. A severely freeze-damaged stand of *Colophospermum mopane* along a slope in the Venetia Limpopo Nature Reserve provided an opportunity to investigate the nature of freeze-damage impacts on *C. mopane*. Is this disturbance a possible demographic limitation of *C. mopane* preventing its southwards spread? Freeze-damage of individual trees was assessed according to tree height and landscape position — with lower elevations representing the most severe freeze zones and higher elevations representing the least severe. Lower elevation trees were relatively small (2.24 m) and coppicing, whilst higher elevation trees were taller (3.65 m) with no coppice present. No freeze-damage was observed on tree canopies above 4 m in height. Trees < 4 m in height that had experienced 100% freeze-damage, failed to regrow to their original heights of the previous season. This is a possible driver of the pre-freeze height differences seen across the slope; with trees at low elevations having to recover from freeze events and subsequent topkill more frequently, resulting in a net decrease in tree height for that growing season. It appears that *C. mopane* has limited resistance to freeze events, and this may be linked to the absence of this species at colder latitudes in the Southern Hemisphere.

Keywords: *Colophospermum mopane*; Freeze-damage; Frost; Recovery growth; Savanna; Topkill

1. Introduction

Frost events in general, and more specifically severe freeze events, are disturbances within savanna systems that are often overlooked when compared with other more prevalent disturbances such as fire or herbivory (Holdo, 2005, 2007). However, they are major environmental stressors responsible for agricultural losses and limiting the distribution of numerous wild and crop plant species (Holdo, 2005; Pearce, 2001). To date, very little research on freeze events within savanna systems has been conducted and questions such as 'How a freeze event affects savanna vegetation?' and 'What impacts this disturbance has in savannas?' are yet to be answered in detail. If these questions can be solved, freeze impacts could be incorporated into vegetation models, further improving the accuracy of the predictions these models are able to make and assisting ecologists in predicting future distribution shifts of species under climate change conditions.

There is growing consensus, both from climate modelling and empirical datasets, of significant changes in the temperature environments which plants are experiencing (Ausperger, 2009; Inouye, 2000; Woldendorp et al., 2008). The general pattern is an increase in temperature, which may result in a reduction of the number of extreme freeze events per year, thus allowing for freeze-intolerant species to expand their ranges (Rigby and Porporato, 2008). On the other hand, given that weather events are also becoming more variable (Ausperger,

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2009), we may see an increase in the frequency of this disturbance. There may be areas which will remain cold enough, especially over the late winter into spring periods, for freeze events to take place, exposing new growth to increased risks of damage (Inouye, 2000; Agrawal et al., 2004). If a freeze event is a noteworthy driver of savanna species distributions, even small changes in the occurrence of this disturbance might have large impacts on vegetation structure throughout southern African savannas and global savannas in general.

Frost and freeze events can vary in impact depending on the ability of plants to withstand exposure to cold temperatures. Frost forms as a layer of ice on the surface of the earth when the air temperature drops below 0 °C and the dew point is situated close to the surface of the earth (Pearce, 2001). Water outside of the plant turns solid at these low temperatures and this not only causes the plant to experience water stress, but also can lead to severe damage or death of plant tissues (Pearce, 2001; Snyder and Paulo de Melo-Abreu, 2005). Freeze-damage caused through the formation of ice crystals inside the cell structures will usually result in a higher proportion of tissue mortality owing to the increased severity of this type of disturbance (Pearce, 2001; Snyder and Paulo de Melo-Abreu, 2005). The degree of damage experienced by the affected plant is influenced by the duration of exposure to freezing temperatures and the rates of freezing and thawing (Holdo, 2007; Robotham et al., 1978; Rushworth, 1975). After freeze-damage, leaves will turn brown (occasionally black) and both the leaves and branches become brittle (Ausperger, 2009). Frosts can be classified as white/mild frosts which describe the formation of ice crystals on plant tissue when the saturated air temperature is reduced below freezing temperatures (Rosenburg, 1974). The more severely damaging black frosts, which we have termed as freeze events, are the result of plant material freezing under low air moisture content conditions such that ice crystals do not form on the surface of the plant, but within its tissues, usually resulting in fatal freeze-damage (Rosenburg, 1974; Snyder and Paulo de Melo-Abreu, 2005).

Freeze events are difficult to predict, especially in areas which are not normally associated with frequent frost occurrences, such as South African lowveld savannas (Schulze, 2007; Fig. 1A). Freeze-damage can have devastating consequences for vegetation in these areas, where the life history strategies and phenology are not adapted to regular freeze disturbances occurring (Ausperger, 2009; Brando and Durigan, 2004; Holdo, 2005, 2007; Inouye, 2000). Plants have evolved different tolerance and avoidance strategies to assist them in overcoming the impacts of freeze events (Agrawal et al., 2004). Some strategies include the incorporation of anti-freeze proteins into plant tissues, which help to lower the freezing point of that material, but this strategy seems largely absent in southern African savanna species (Griffin and Antikienen, 1996). In southern Africa, the majority of species tolerate frost conditions by being deciduous and shedding leaves prior to temperatures becoming cold enough for freeze events to occur (Rutherford et al., 2006). However, certain savanna species, such as *Colophospermum mopane* (Kirk ex. Benth) Léonhard, retain their leaves late into the winter, potentially exposing them to an increased risk of freeze-damage (Mojeremane and Lumbile, 2005; Van Wyk and Van Wyk, 2000). The distribution of *C. mopane* suggests that it grows successfully in areas which are warm and seldom affected by freeze events, with a prevalent southern distribution limit (~31°23′ 12″ E, 24°2[illegible]3[illegible]S) (Henning and White, 1974; Fig. 1B). Other drivers of this distribution include low rainfall (< 800 mm per year) and the presence of alkaline, clayey soils (Brailey, 2009; Mapaure, 1994; Poilecot and Gaidet, 2010; Scholes et al., 2002). Recent findings by SAEON indicate that minimum temperatures during the coldest month of the year appear to be another important factor limiting the southern spread of *C. mopane* (Stevens et al., unpublished). Within a landscape (from the top of the slope to the bottom) and across regions, *C. mopane* appears to withdraw from the community when minimum winter temperatures reach below 4.5 °C (Stevens et al., unpublished). Thus, if freeze-damage is a potential distribution controller of *C. mopane*, we would expect to see a negative impact on the growth after exposure to a severe freeze event. There are various possible mechanistic explanations for this pattern, including slower growth rates over the winter period (Holdo, 2007) and reduced competitive ability (MacGregor and O'Connor, 2002). However, it is also possible that susceptibility to severe freeze events might be a limiting factor keeping *C. mopane* from spreading into regions with cold winter temperatures.

By investigating how a freeze event can reduce *C. mopane* fitness, we hoped to determine whether freeze-damage is a legitimate explanation for the unique distribution of this species (Fig. 1B). Studying the demographic impacts of a severely freeze-damaged population of *C. mopane* in the Venetia Limpopo Nature Reserve (VLNR) will enable us to answer some of the previously mentioned questions. We tested how elevation could affect the amount of damage experienced by trees, as well as how vertical height differences could change freeze-damage impacts. The implications of the freeze-damage were investigated through an analysis of the recovery of the damaged trees, compared to the growth of the undamaged trees after one growing season.

2. Materials and methods

2.1. Study species

Colophospermum mopane is a medium to large tree often found in mono-dominant stands or dense clusters in alluvium and other poorly drained soils (Mapaure, 1994; Van Wyk and Van Wyk, 2000). They are typically found in areas of low altitude (400–700 m.a.s.l.) and low rainfall (200–800 mm/year) (Mapaure, 1994). Leaves are butterfly shaped and remain on the tree up to the dry-season (Mojeremane and Lumbile, 2005). Fruits mature between May and October (Mapaure, 1994). It is an economically important species and is used for timber, firewood and poles, whilst also playing host to one of the main protein sources in the area, *Imbrasia belina* (Westwood, 1849), commonly known as the mopane worm (Mojeremane and Lumbile, 2005). *C. mopane* also provides several ecosystem services which help to maintain the environments in which they occur, such as nutrient cycling (Mojeremane and Lumbile, 2005). Conversely, the mono-dominant stands formed by *C. mopane* (Mapaure, 1994; Timberlake, 1995) result in decreases in woody species diversity and grass biomass (Henning and White, 1974). Mopane savanna supports lower densities of herbivores and is

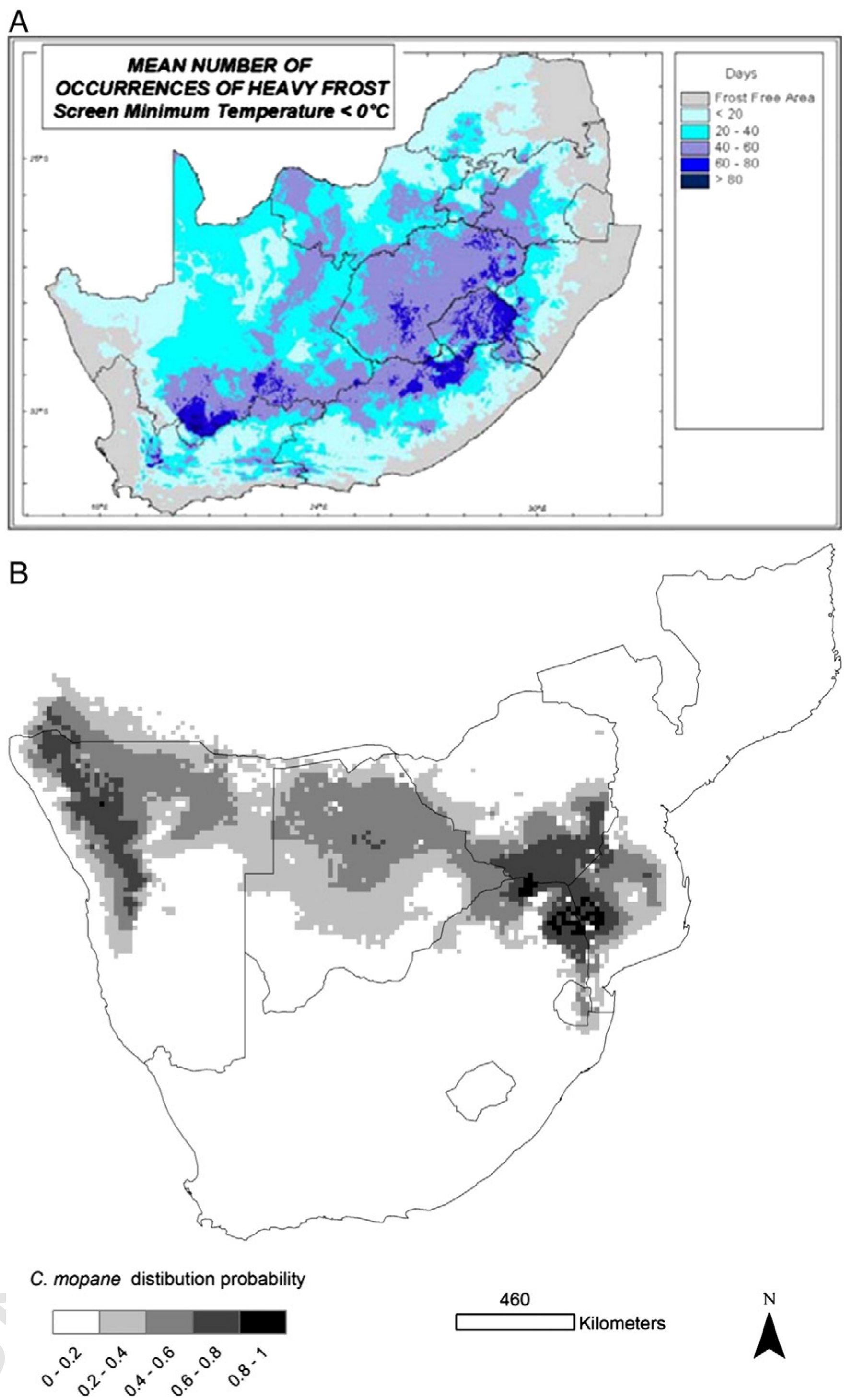

Fig. 1. (A) Map indicating the mean number of radiation frost occurrences in South Africa per year (Schulze, 2007). (B) The probability of distribution for *Colophospermum mopane* mapped in southern Africa (SANBI, 2011).

less productive for cattle grazing, thus the distribution of this savanna sub-type is important as it affects the types of livelihoods which can be supported (Dovie et al., 2006).

The areas in which *C. mopane* are distributed are perceived to be areas with a low annual freeze occurrence (Rutherford et al., 2006; Schulze, 2007; Smit and Rethman, 2000). Current predictions for changes in *C. mopane* distributions state that the species will disperse to the south and west of its current distribution (Rutherford et al., 1999). This prediction however is currently under re-assessment by Stevens et al. (unpublished).

2.2. Study site

A freeze event occurs when a large-scale cool air mass moves over an area causing a rapid decrease in temperatures and wide spread freeze-damage to vegetation found in those areas (South African Weather Service, 2010, 2011). The cold-front system responsible for the freeze-damage which occurred in the Venetia Limpopo Nature Reserve (VLNR) between the 15th and 17th June 2010 was followed by a ridging high pressure cell that brought sub-polar air over most of the South African interior, causing widespread frost/freeze-damage all over South Africa (South African Weather Service, 2011).

Topographical features on the earth's surface, such as mountains or valleys, influence the movement of air across a landscape (Ahrens, 2007; Hough, 1945; Vergeiner and Dreiseitl, 1987). The general trend for temperatures within the troposphere on a calm day with no wind is an average decrease of 6.5 °C for every 1000 m increase in altitude (Ahrens, 2007). However, at night, cool, dense air will sink to the lowest area in a landscape causing a temperature inversion to occur. Frost can often occur in these low areas and vegetation that is established there is at risk of damage (Ahrens, 2007; Cox, 1910). Thus vegetation which is established slightly higher up the valley slope has less chance of being affected.

This study was conducted on a gentle slope in the VLNR, Limpopo Province South Africa (22.26723°S 29.33057°E). The site falls within the Musina Mopane Bushveld type close to the southern distribution limit of *C. mopane* (Rutherford et al., 2006; SANBI, 2011). The study area is dominated by *C. mopane* with scattered patches of *Acacia* savanna (Rutherford et al., 2006). The species associated with the *Acacia* savanna have distributions that extend further south than *C. mopane*, which may suggest these species are less susceptible to freeze-damage. The reserve is approximately 30 km south of the Limpopo River and is characterised by wet, hot summers and dry, mild winters (MacGregor and O'Connor, 2002; Rutherford et al., 2006). The mean annual rainfall is only 339 mm and the mean monthly maximum and minimum temperatures for both October and April are 30 °C and 15 °C (South African Weather Service, Musina Station 1961–1990). The mean number of frost days per year is recorded as 1 day (Rutherford et al., 2006). The average minimum temperatures through June, July and August are well above 0 °C; however, the lowest recorded figures for this period are below freezing and would almost certainly result in frost/freeze events occurring (South African Weather Service, 2011).

The slope is classified as gentle with an elevation range between 554 and 572 m.a.s.l. and a 0.66° angle of inclination and a west–south–west aspect. Deep red, sandy loam is the dominant underlying soil type in VLNR and soils across the reserve consist of an average of 20% clay and 19% silt (Botha, 1994).

C. mopane is known to display shifts in demographics along a slope as the soil characteristics change, with smaller individuals being associated with lower slope areas (Brailey, 2009; Poilecot and Gaidet, 2010; Scholes et al., 2002). Hence, soil pits were dug at the top and bottom of the VLNR slope to assess whether there were any detectable changes in texture and depth that may have influenced the *C. mopane* demographics along the slope. Using the MacVicar et al. (1977) binomial soil classification system, the minor changes found in soil depths are thought to have less influence on the overall demographics of this population, when compared to the investigated freeze-damage impacts.

2.3. Experimental design and protocol

2.3.1. Temperature assessment

The post-hoc nature of this study did not allow for temperature sampling to occur during the freeze event of 2010; however, by sampling the 2011 temperatures we hoped to gain an understanding of the average winter temperatures across the site. Temperature sensors (iButtons: Dallas Semiconductor Maxim, DS1922L/T, United States of America (CA)) were placed along the length of the slope both inside and outside of *C. mopane* canopies. Temperatures were measured inside the canopies at 0.5 m and 1.5 m (16 iButtons), and outside the canopies at half-meter intervals from ground level up to 5 m (22 iButtons). iButtons were setup to record the temperature every 2 h from April to July 2011.

2.3.2. Freeze-damage assessment

Three transects were established running perpendicular to the slope to sample the highest area of freeze-damage, the central zone and lowest area of freeze-damage along the slope in October 2010. A GPS (Garmin *GPS 296*) was used to predetermine the locations of 22 sites that were sampled using the point-centre quarter method (PCQ) (Cottam and Curtis, 1956). The two closest individuals to the centre point within each quarter were sampled, resulting in a total of 176 trees being measured and compared. Each individual's height, stem diameter (20 cm above the ground surface) and number of stems were measured, followed by an investigation into any freeze-damage found on the tree. Freeze-damage was estimated as a proportion of the whole canopy, and as a proportion for each half-meter height interval within the canopy. This indicated whether uniform damage throughout the canopy had occurred or not. The maximum height of freeze-damage was also recorded to indicate whether any of the upper canopies had escaped damage. Freeze-damaged branches were tagged and measured to identify any growth ~~on~~ the following year.

2.3.3. Growth and recovery assessment

We returned to the sites after one growing season (April 2011), re-measured the heights and stem diameters of the same individuals, as well as the extent of the canopy growth on each individual. Tree recovery after freeze-damage was estimated based on the percentage of leaf fullness on the canopy. Where branches remained without leaves or had broken after freeze-damage, it was assumed that recovery had not taken place. The maximum height of regrowth was measured to indicate any loss of height after the freeze-event. Any coppice regrowth present was recorded. Tagged branches were re-measured to see whether any growth had taken place after one growing season.

2.3.3.1. Soil structure assessment. Soil texture and depth were sampled by digging a one meter depth soil pit at upper and lower slope positions. Samples from the surface layer, as well as 20 cm and 60 cm deep were collected. Soil texture was established using the "finger test" in the field. The soil profile (soil depth, colour and structure) was assessed using the MacVicar et al.'s (1977) binomial soil classification.

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2.3.3.2. Data analyses. All analyses were conducted using the R Statistics package (v2.12.2).

2.3.3.3. Temperature assessment. Temperature data was analysed between 1st May and 31st July 2011. The total number of days with a minimum temperature of ≤ 0 °C was totalled for soil temperatures, 0.5 m, 1.5 m and 4 m, to identify if vertical height was influencing the micro-scale temperatures at low and high elevations. This serves as an indication of the possible number of frost events that may occur during winter at the VLNR. The mean minimum and maximum temperatures for each slope position and height were calculated both inside and outside of the canopy.

2.3.4. Freeze-damage analyses

A generalised logistic model between total canopy damage and elevation was used to determine whether elevation could be used as a proxy for freeze severity along the slope. Two thresholds were identified from the severity data, the first being the high severity threshold where ≥ 80% of a canopy was likely to be damaged and then the low severity threshold where ≤ 20% damage occurred. Hence, the slope was divided into three zones: high, intermediate and low severities. The mean damage per half meter height division across the slope was averaged to estimate the generalised pattern of damage experienced by the trees in the freeze event. The height division damage estimates were also compared using predictive logistic regression models to identify the changing patterns along the slope, using elevation as the predictor variable. The influence of tree height on freeze-damage was calculated by dividing trees into two groups (low and high elevation) and the proportion of damage was compared across tree heights using logistic regressions. An ANCOVA was used to identify the combined effect of both elevation and vertical height on potential freeze-damage incurred. The percentage of branches which did not recover from freeze-damage was calculated.

2.3.4.1. Growth and recovery analyses. The net growth estimates were calculated as the difference between the whole canopy freeze-damage and recovery estimates, where a negative value indicated that loss of canopy had occurred. The division recovery estimates were compared using predictive logistic regression models, where elevation was the predictor variable. Topkill which had taken place due to the freeze-damage was calculated based on the difference between initial tree height at the time of the freeze-event and the maximum height of regrowth after one growing season. The overall canopy recovery relative to elevation was tested using Spearman's Rank Correlation and a regression analysis to determine the nature and significance of the relationship between these two variables.

2.3.5. Demographics analyses

The population demographics of the *C. mopane* on the slope were calculated based on the sampled heights of individuals between low and high elevations. The proportion of coppicing individuals in the highest severity zone was also calculated.

3. Results

3.1. Temperature data

As expected, we recorded lower average temperatures at lowest elevations, as well as an increase in the number of days with a recorded minimum temperature of ≤ 0 °C. No evidence of a freeze event occurring during the 2011 winter period was found; however, sub-zero temperatures were recorded throughout that period. The temperature sensors, which were buried below the ground surface at the lowest elevation, recorded no sub-zero temperatures, with an average of 12.5 °C at 5 cm and 7.5 °C at 2 cm below the surface. At 0.5 m height the number of ≤ 0 °C days at the low elevation was 35 relative to 11 at the highest elevation. At 1.5 m the low elevation had 21 days vs. 17 days at the high elevation and at 4 m the low and high elevation had 3 and 4 days respectively.

Inner canopy temperature averages were at least 3 °C higher than the corresponding sensors placed outside of the canopy. At 0.5 m, the difference between low and high elevation inner canopy temperatures was only 1 °C, whilst the outer canopy difference was 2.4 °C between elevations. The low elevation average minimum temperatures were lower than the high elevation temperatures for all heights inside and outside of the canopies, with the exception of the four-meter sensors outside the canopies where the low elevation average temperature was 0.5 °C warmer than the high elevation temperature.

3.2. Freeze-damage results

Of the total 176 *C. mopane* individuals sampled, 78.4% showed signs of freeze-damage. Elevation was used as a proxy for freeze severity, with the lowest elevation representing the most severe freeze conditions (logistic regression: residual deviance = 52.82, d.f. = 174, $p < 0.001$). A high severity zone was assigned to any trees located below 564 m.a.s.l. in elevation, whilst the low severity zone was assigned to trees located above this threshold, where total canopy damage remained < 20%.

The predicted mean freeze severity estimates were calculated using logistic regressions for the level of damage occurring at the 564 m.a.s.l. threshold (Fig. 2). No freeze-damage was recorded above 4 m anywhere on the slope. The corresponding photograph indicates the severely damaged section of canopy between 1.5 m and 2.5 m (Fig. 2).

To test for the influence of vertical height on the percentage of damage incurred by the trees, high and low elevation trees were separated and tested for the percentage of total damage measured on each canopy (Fig. 3). High elevation trees had little damage and thus displayed no detectable pattern (Fig. 3A). At low elevations, trees that were < 2 m experienced close to 100% freeze-damage, whilst trees that were > 4 m did not experience more than 75% total freeze-damage (logistic regression: residual deviance = 56.26, d.f. = 166, $p < 0.001$) (Fig. 3B). The 4 m freeze-damage cut-off explains the increased proportion of undamaged canopies on trees taller than 4 m. Thus in the high severity zone, tree height has an effect on the extent of damage experienced.

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A combined effect of elevation and tree height on the level of damage experienced by the trees was confirmed, which may explain the damage patterns observed along the slope (ANCOVA: $R^2 = 0.72$, d.f. = 170, $p < 0.001$).

Freeze-damaged branches were tagged in October 2010 and re-measured after one growing season; however, 96% were recorded as dead in April 2011. This clearly indicates the severity of damage caused by the freeze event and is one of the reasons for decreased fitness in freeze-affected individuals through the loss of canopy after a freeze event.

3.3. Response to freeze-damage

After one growing season, recovery assessments of both the freeze-damaged and non-freeze-damaged *C. mopane* were conducted using estimates of canopy leaf fullness. The leaf fullness is estimated as the proportion of leaf production on the branches available within a canopy. An increase in tree recovery was observed with an increase in elevation (decrease in freeze severity) ($r_{Spearman} = 0.72$; $R^2 = 0.48$, d.f. = 160, $p < 0.001$). On average, trees lost between 35 and 60% of their canopies after exposure to severe freeze conditions (<564 m.a.s.l.). There was an 80% or higher recovery above the 564 m.a.s.l. threshold.

The difference between overall freeze-damage and recovery was calculated to show the net growth (recovery) of the trees across the freeze severity (elevation) gradient. Almost all individuals found in the lowest elevations (<558.75 m.a.s.l.) experienced an overall loss of canopy cover (20–90%) and subsequently a decrease in maximum canopy height. The only individual that experienced a positive canopy gain (5%) in the lowest elevations was a 5 m individual whose upper proportion of canopy had escaped freeze-damage and continued to grow over the next season. This could indicate the potential for a freeze trap which could make it difficult for individuals < 4 m at low elevations to gain substantial height over subsequent years. Above the low-severity threshold (>564 m.a.s.l.) trees were able to recover with positive net growth and no overall canopy losses. The net growth in the intermediate zone (558.75–564 m.a.s.l.) was highly variable (−70 to +90%) and this may be related to a further influence of tree height in improving an individual's chances of less damage and more recovery.

Canopy division estimates of recovery were measured on each tree. As seen with the freeze-damage estimates, recovery at low elevations decreased from the base of the tree upwards to a threshold between 1.5 m and 2.5 m and then increased again up the canopy until it reached full recovery at 4 m, above which there was no freeze-damage recorded. At 564 m.a.s.l. mean recovery was worst between 2 and 3 m in height with only 50% of the canopy growing back.

The remaining topkill seen on the trees after one growing season was measured as the difference between a tree's total height prior to the freeze event and its current height of living material after one growing season (Fig. 4). Low elevation trees indicated a higher proportion of topkill (0.79) than intermediate (0.68) or higher elevation trees (0.16); however, trees above 4 m did not experience topkill after the freeze event at any of the elevations (Fig. 4). This loss of height is most likely the responsible driver for the differences in tree heights observed across the slope.

3.3.1. Demographic impacts

If this type of freeze event is a frequent occurrence in the VLNR, it could explain the clear difference in heights of *C. mopane* across the slope ($t = -7.6265$, d.f. = 174, $p < 0.001$) (Fig. 5). At low elevations, trees of 2 m height had the highest frequency which corresponds to the vertical freeze-damage structure's most severe height, whilst the high elevation trees had the highest frequency of 4 m trees (Fig. 5).

Freeze-damaged and non-freeze-damaged trees were assessed for evidence of coppice growth in April 2011. Of the 52 trees measured with ≥ 80% canopy damage, 40% produced coppice regrowth in the following growing season. All coppicing individuals were <3 m. The intermediate and high elevation

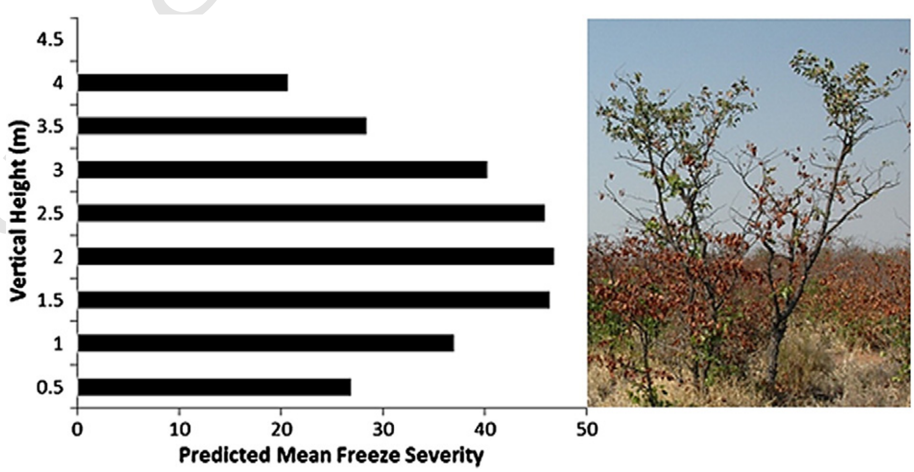

Fig. 2. A unique vertical freeze-damage pattern was detected using the half-meter divisions of canopy damage, where the most severe damage occurred between 1.5 and 2.5 m. The calculated means for freeze-damage at each height indicate the shifts in damage percentage with increased vertical height above the ground. The photograph of severely freeze-damaged *Colophospermum mopane* displays the increase in freeze-damage at the centre height intervals, with less damage at the top and bottom of the tree.

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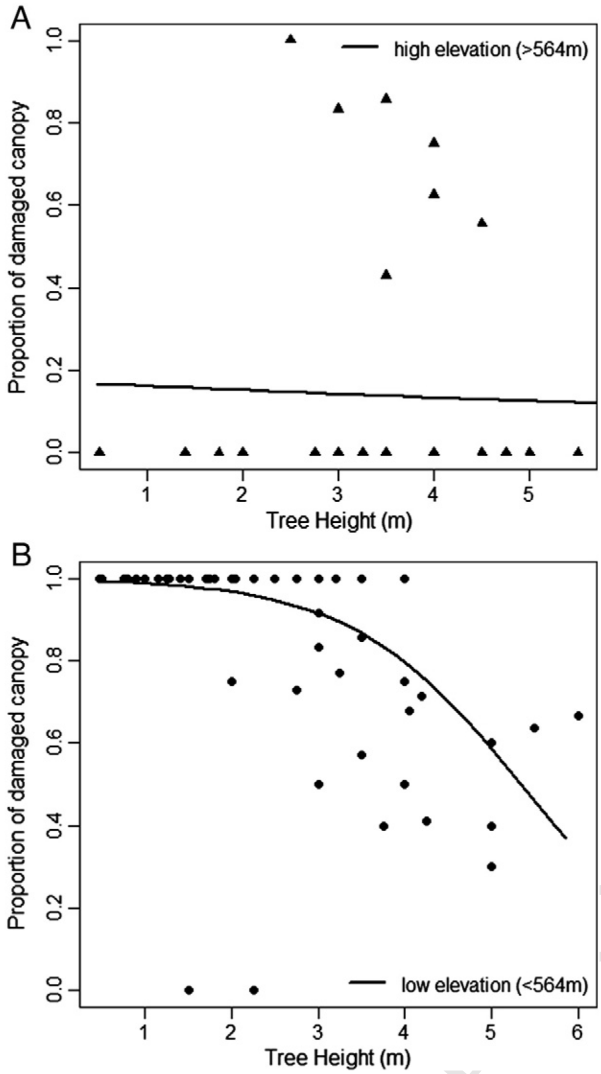

Fig. 3. The proportion of damaged canopy remaining in October 2010 relative to total tree height. Trees were categorised based on the freeze severity gradient. (A) Trees above the low-severity threshold (high elevation) displayed no significant trend. (B) Smaller trees found in the high-severity zone (low elevation) displayed more total canopy damage. A logistic regression curve for each category is indicated by the solid black line.

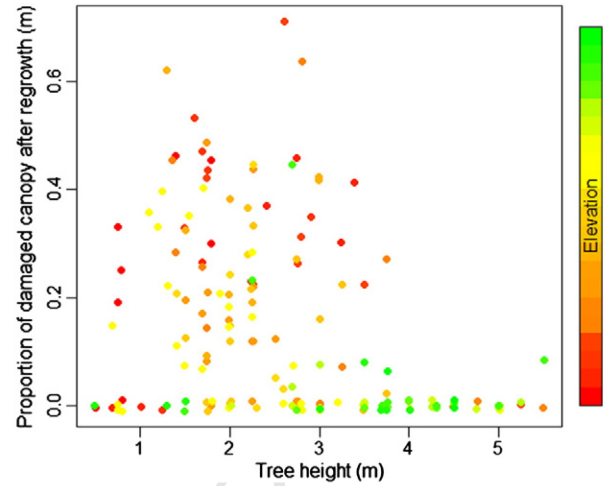

Fig. 4. Proportion of damaged canopy remaining after one growing season across all elevations relative to the maximum tree height measured. This indicates what topkill has taken place after the freeze event and one growing season. Red indicates low elevations (high freeze severity) whilst green indicates high elevations (low freeze severity). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

individuals did not develop coppice growth as a result of freeze-damage impacts.

4. Discussion

It is clear that freeze-damage can cause structural damage to *C. mopane*, which has long-term effects on height structure and reduces overall fitness. We showed that both elevation and vertical height have an influence on the nature of freeze-damage experienced by an individual tree; where low elevation trees will experience the most severe damage from the lowest temperatures. This concurs with Haiden and Whiteman's (2005) suggestion that a slight increase in elevation on the leeward side of the slope can provide protection to patches of vegetation from this type of disturbance. Tree canopies can create a slight increase in micro-temperatures within their canopies relative to outside their canopies, potentially helping to protect the central stems. On a typical winters' evening this may offer protection from frost to leaves near the centre of the tree; however, it appears that in the case of a severe freeze event, the majority of the canopy is likely to be damaged. Only areas of the canopy that are above the 4 m threshold were able to escape damage. This 4 m height threshold may be the sign of a potential 'freeze trap' on the VLNR slope, trapping trees below the 4 m threshold through topkill after freeze events. The unique pattern uncovered by the height division damage estimates indicated that the most severe damage is occurring between the heights of 1.5 m and 2.5 m. The high percentage of freeze-damaged branches that did not regrow is a clear indication of the permanent effects this type of disturbance can have on a tree and evidence for topkill as the driver of the height differences seen along the slope is strong. The long-term demographic effects of such a freeze event can be seen through the height distributions of this population with smaller, coppicing individuals at low elevations and taller individuals at high elevations.

Both the severity and frequency of the disturbance, as well as the productivity of the area in which the disturbance occurs influence resprouting as a life-history strategy (Bellingham and Sparrow, 2000). Trees in areas where productivity is low as a result of low rainfall and/or poor soil nutrient content, such as the VLNR, will tend to use resprouting as a life-history strategy rather than increasing the seedling recruitment in that area (Bellingham and Sparrow, 2000). The noteworthy resprouting ability of most savanna trees, including *C. mopane*, must be acknowledged at this point (Bellingham and Sparrow, 2000; Bond and Midgley, 2001). It is seldom found that whole-tree mortality occurs after exposure to a freeze event. Stem mortality appears to occur more frequently as a result of these disturbances (Rutherford, 1981; Trollope, 1984). After stem mortality occurs, trees will often resprout from above or below ground organs

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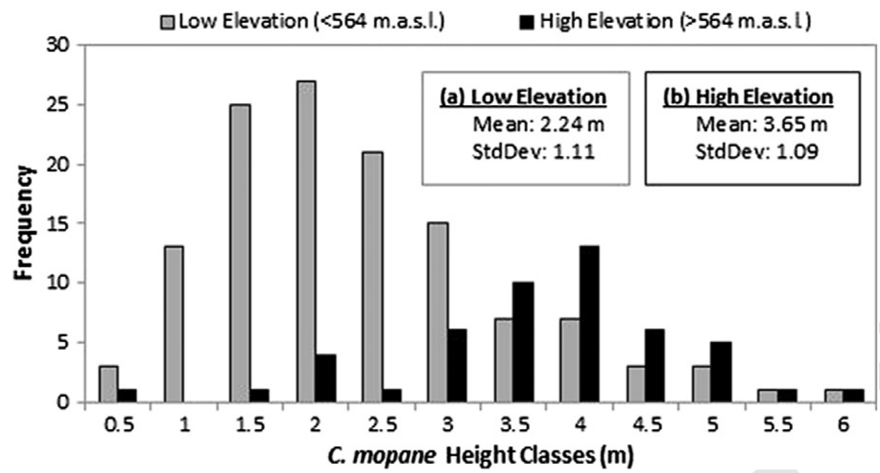

Fig. 5. Size class distributions of *Colophospermum mopane* trees situated (a) at moderate to high severity (<564 m.a.s.l.) and (b) at low severity (>564 m.a.s.l.). Corresponding means and standard deviations are shown.

where resources have been stored depending on the type of damage experienced (Rushworth, 1975; Rutherford, 1981). *C. mopane* has a shallow root system with a large root biomass which enables them to store resources during times of stress, such as droughts and during fires or freeze events (MacGregor and O'Connor, 2002; Smit and Rethman, 2000). Stable temperatures underground may assist in maintaining and protecting the trees' root biomass during cold surface conditions in winter, providing the tree with usable reserves in the following growing season. The root biomass is large in comparison to the leaf biomass of a *C. mopane* canopy (Smit and Rethman, 2000). Using the resources stored in this large root biomass to resprout when conditions become favourable again in the growing season, enables *C. mopane* to continue to grow even with a total loss of canopy through disturbances such as fire or freeze events. Recovery growth, however, may not be to the same level as previous seasons depending on the severity of freeze-damage experienced.

The impacts on net recovery of this freeze-damaged population show clearly that severely damaged trees will lose overall height and canopy size after a freeze event. This can have negative effects on their overall productivity as loss of canopy leads to less reproductive output and *C. mopane* trees will only begin to produce seeds after approximately five years or after they have reached a height of over 2 m (Timberlake, 1999). The VLNR freeze trap therefore has the potential to slow the reproductive rates of this *C. mopane* population by maintaining low elevation trees below the reproductive height. Further work into assessing the differences in seed set along the slope would help us in determining how much of an influence this disturbance has on reproduction in this population.

4.1. Why are C. mopane so susceptible to freeze events?

Deciduous plants in temperate forests confront a trade-off between leafing out early so as to maximise the utilization of available resources over the growing season, or delaying the timing of their leaf out to decrease the risk of encountering late frosts and potentially fatal freeze-damage (Ausperger, 2009). Sakai and Larcher (1987) found that species with early leaf emergence stood the greatest risk of frost-damage, but the probability of this risk tended to decrease as the individuals aged and the tissues developed a lower sensitivity to frost-damage over time. *C. mopane* is a deciduous species which can retain its leaves late into the winter months (Mojeremane and Lumbile, 2005; Timberlake, 1999). As a result of this late retention, sap flow within the stems continues and places the trees at risk of freeze-damage (Henning and White, 1974). The southern African winter in the savanna biome is noted for its low moisture and rainfall, hence the increased likelihood of freeze-damage occurring within the plant tissues should temperatures become cold enough (Rosenburg, 1974; Rutherford et al., 2006; Snyder and Paulo de Melo-Abreu, 2005). The areas in which *C. mopane* are distributed are considered to be warm, arid areas where frost occurrence is low or non-existent (Rutherford et al., 2006). Thus, the occurrence of a severe freeze event in these areas has the potential to cause extensive damage, which was observed over the VLNR winter.

The majority of previous studies conducted on the impacts of frost on different types of vegetation appear to centre on Northern Hemisphere species found in the deciduous and coniferous forest belts (Agrawal et al., 2004; Ausperger, 2009; Sklenář et al., 2010). However, some studies have been done on Brazillian cerrados (Snyder and Paulo de Melo-Abreu, 2005), Australian *Eucalyptus* spp. (Thomson et al., 2001; Woldendorp et al., 2008) and southern African savanna species such as *Dichrostachys cinerea*, *Acacia nilotica*, *A. robusta*, *A. gerrardii* (Smit, 1990), *Baikiaea plurijuga* (Harms), *Burkea africana* (Hook.) and *Combretum* spp. (Loefl.) (Holdo, 2005, 2007). The southern African species are all savanna based trees which were negatively affected by frost events (Holdo, 2005, 2007). As seen with *C. mopane*, total tree mortality was rare in these species after the freeze event; however, stem mortality occurred frequently (Holdo, 2005). Topkill was also recorded in these species, and has the potential to decrease overall fitness of all of the affected species (Holdo, 2005, 2007).

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4.2. Are freeze events an important determinant of the C. mopane distribution?

Given the negative effects that this freeze event has had on the *C. mopane* in the VLNR, it is plausible to assign some of this species' distribution limitations to freeze effects. *C. mopane* is unlikely to establish in areas with a high probability of freeze events occurring; however, the effects of other influential factors such as soil type, precipitation and other disturbances must also be acknowledged. If a repeat study on the impacts of a second freeze event in the VLNR could be investigated we may begin to see the compound long-term effects that freeze-damage is having on this population. Another area that needs to be investigated is the effect of freeze events on the recruitment of *C. mopane* seedlings. If a better understanding of this impact could be established, further work into the overall impact of freeze disturbances on the long-term population dynamics could be conducted.

The ability of *C. mopane* to persist in an area after harsh disturbances such as a severe freeze event suggests that this species will be able to expand its range under climate change conditions. However, this expansion will likely be slow and reduced fitness caused through freeze-damage may allow for other fast-growing species to establish before *C. mopane* can dominate an area.

4.3. How do freeze events compare to other savanna disturbances?

There is a need to acknowledge the importance of freeze events as important disturbances in southern African savannas, as well as to compare this disturbance with other savanna disturbances, such as fire. Like fire and unlike herbivory, freeze events are not continuous — occurring as sporadic incidents, which are separated by long periods where the trees are not exposed to freeze-damage. Freeze events are also unselective and do not target specific individuals or species — although as shown, certain parts of the landscape are more prone to severe freeze effects than others. There also appears to be a 'freeze trap' similar to the 'fire trap' and 'browse trap' in which sapling trees growing into the mature canopy are more frequently, and more severely exposed to freeze-damage. The data indicate that this 'freeze trap' is most severe between 1.5 and 2.5 m — which is very different from fire and herbivory, which act most severely on the very small tree saplings (Bond and Midgley, 2001; Trollope, 1984). However, the data show that small saplings were still severely damaged by the freeze event. Trees which were able to grow above the freeze threshold were able to avoid total freeze-damage similar to those which outgrow the 'fire trap' (Trollope, 1984).

After freeze-damage has occurred, it will dry out vegetative material which contributes to the available fuel load for potential fires (Holdo, 2007). This dried out vegetation increases the heights of available flammable material, allowing understory fires to spread into the canopies, causing widespread damage (Calvert, 1986). Disturbance combinations can thus have compounded effects on savanna vegetation and cause increased damage to larger areas of savanna because of this (Holdo, 2005, 2007). If modellers can account for the effects of these disturbances in isolation, as well as combined, there is likely to be an improvement in the accuracy of the predictions which they are producing. There is a need for a regional definition of a potential 'freeze trap' to understand the influence of different landscape positions, aspects and gradients on the impacts of freeze events on impacted vegetation. This information could then be applied across agricultural practices to potentially develop crop saving technology and assist in the global food security problem facing the world in the future.

5. Uncited reference

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R Development Core Team, 2010

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