



Impact of a severe frost event in 2014 on woody vegetation within the Nama-Karoo and semi-arid savanna biomes of South Africa



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ABSTRACT

The plains of the Nama-Karoo biome in southern Africa are characterised by a mixture of dwarf shrubs and grasses with near absence of shrubs and trees that are conspicuous in the adjacent savanna biome and on hills. We investigated the impact of a severe frost event in 2014 on the abundance and composition of woody vegetation in relation to local topography at three widely separated locations. Long-term weather records of 44, 53, and 83 years confirmed that the 2014 event was the 16th, 6th, and 12th percentile of cold years across three locations. An event of similar severity had not occurred for >7 years at the Nama-Karoo locations but had at the savanna location. Woody vegetation lost 60–100% of canopy volume at the base of a slope but no loss had occurred at elevations of 30–100 m above this. Regrowth volume after one season was linearly related to volume lost to frost although most plants had not recovered pre-frost volume. All dominant woody species experienced substantial topkill. Microphyllous species appeared particularly sensitive to frost. Results suggest frost contributes to maintaining the treeless character of the Nama-Karoo biome and to containing bush encroachment along drainage lines within the savanna biome.

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1. Introduction

Representation of different growth forms within vegetation types or biomes in southern Africa is strongly influenced by climatic and edaphic factors in combination with disturbance regime (Mucina and Rutherford, 2006). Within South Africa, distribution of the nine main biomes is determined principally by temperature and the amount and seasonality of rainfall. Biomes differ in their dominant growth forms. The common denominator for the three biomes of interest in this study is woody plants: grasslands in effect lack woody plants; savannas consist mainly of a mixture of trees and grasses; and a mix of dwarf shrubs and grasses comprise the Nama-Karoo biome from which trees are absent (Mucina and Rutherford, 2006). Any change in the representation or relative proportion of the main growth forms has the potential to alter considerably the character and functioning of a biome. Invasion of grassland or Nama-Karoo by woody plants would transform them to savanna, whereas an increase in woody plants in semi-arid savanna, termed bush encroachment

(O'Connor et al., 2014), may render them thicker.

The local distribution of a growth form may be influenced by topography. The Nama-Karoo biome, occurring on an interior plateau covering 23% of South Africa and receiving 70 mm–500 mm of precipitation per annum, contains large plains which support a mix of dwarf shrubs and grasses with large shrubs and trees absent (Palmer and Hoffman, 1997) attributed to frost (Mucina and Rutherford, 2006). Hills arising steeply from the plains show an abrupt transition to open woody vegetation of shrubs. Fire is discounted because it is a rare event in the Nama-Karoo (du Toit and O'Connor, 2014) owing to insufficient fuel (grass) (Rahlao et al., 2009), but edaphic factors may be involved (Cowling et al., 1998). In correspondence with frost as an explanation, shrubs of the Subtropical Thicket in South Africa are unable to encroach into Nama-Karoo biome because they cannot endure frost (Duker et al., 2015a). Within semi-arid savannas, woody plants are usually abundant along drainage lines owing to greater availability of water (Mucina and Rutherford, 2006). However, in one example of a woody species toward the limit of its geographical distribution, abundance was least at the lowest elevations within an undulating landscape, for which frost was proposed as a possible cause (Stevens et al., 2014).

Ability to predict variation in abundance of growth forms across

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space or over time requires identification of specific climatic or edaphic variables, or disturbance agents, which affect the vegetation of interest. Disturbance agents widely recognised to influence the abundance of woody vegetation include fire (Bond, 1997), grazing and browsing (O'Connor et al., 2014). Frost may also influence the distribution and abundance of woody plants across southern Africa. It has been identified as a key climatic determinant for the boundary between Nama-Karoo and Albany Thicket biomes (Duker et al., 2015a, 2015b), and between the savanna and grassland biomes in KwaZulu-Natal (Jewitt et al., 2015) through its effect of slowing growth rate of woody plants thereby maintaining them at a height susceptible to fire (Wakeling et al., 2012). Frost in combination with fire and elephants is an important determinant of the structure and composition of the woody vegetation of some southern African savannas (Childes and Walker, 1987; Smit, 1990; Holdo, 2006, 2007). Our general aim was to investigate an additional case study concerning the impact of frost on woody vegetation in southern Africa.

Frost is a common occurrence throughout southern Africa (Schulze, 1997) occurring when air temperature drops below zero and water freezes (Pearce, 2001; Garcia et al., 2010). Ideal conditions for frost occurrence are clear, cloudless nights when air movements are stagnant allowing cold air to pool within topographic depressions such as valleys (Cox, 1910; Garcia et al., 2010). Thus at a local landscape level, a frost event temporarily reverses the general inverse relation between altitude and air temperature (Bannister, 2007) such that high points may remain frost-free. Frost may not always be restricted to topographic depressions but may occur at higher elevation on a local slope when it forms at lower ambient temperatures in association with a light wind, a condition known as wind-frost (Garcia et al., 2010). Frost incurs damage to plants through freezing of external water and internal plant water that can cause water and structural stress to the plant and potentially damage plant tissues (Andrews, 1996; Agrawal et al., 2004). If the air is dry then black frost can form, during which cell water and internal plasma freezes (Savage, 2012). Pronounced diurnal fluctuations in temperature may result in severe frost damage because plant tissues absorb energy and thaw at different rates that may manifest as scabby bark and cracks, as well as leaves turning black and brown (Hiratsuka and Zalasky, 1993; Bannister and Lord, 2006). The net effect is loss of above-ground biomass through topkill (Holdo, 2006; Whitecross et al., 2012).

The annual frost regime of a location can be described by the average number of frost days per year and the minimum temperature experienced (Garcia et al., 2010; Savage, 2012; Jewitt et al., 2015). However, individual locations across southern Africa display marked inter-annual variation in frost incidence and severity, with a coefficient of variation for number of frost days per annum of 49% for the Northern Cape and 89% for the Eastern Cape (Schulze, 1997). Study does not seem to have been undertaken for the question of whether frost impact on vegetation is primarily the result of a cumulative effect of many individual events or of the single most severe event. However, minimum temperature under experimental conditions consistently results in the highest mortality of woody plant parts or plants (Sakai and Wardle, 1978; Read and Hill, 1989; Sklenář et al., 2012). We therefore assess frost impact in terms of the minimum temperature attained during a season. In correspondence, conspicuous frost impact on woody vegetation has been observed following a particularly severe event (Whitecross et al., 2012).

Some general predictions have emerged about frost impact on a woody community, which would usually consist of a mix of species each of whose populations could contain individuals ranging in plant size from seedlings through to adult plants. Species are not expected to be uniformly distributed along local elevational

gradients that are confounded with edaphic gradients along which growth opportunity varies. Plant size of a species could also vary along a gradient affecting growth rate. A species which is restricted to lower-lying areas within which frosting occurs is therefore potentially more susceptible to impact unless it is well adapted. Species within a community usually differ markedly in terms of the minimum temperature that can be tolerated by individual shoots (Sakai and Wardle, 1978; Read and Hill, 1989; Sklenář et al., 2012). Criteria by which to anticipate differences among species in susceptibility to frost impact have not yet emerged, although understanding is growing of frost impact on leaf phenology and shoot damage (Cannell and Smith, 1986; Augspurger, 2009; Morin and Chuine, 2014), frost hardiness (Sakai, 1966; Bannister and Lord, 2006), and genetic influence on frost tolerance (Agrawal et al., 2004). On account of frost occurring above-ground only, as opposed to prolonged seasonal freezing of soil in some cold climates, frost-impacted plants usually experience topkill but not complete mortality (Whitecross et al., 2012). African woody plants are usually adapted to loss of crown material to disturbance agents such as fire and herbivory by resprouting from the root crown, but neither impact nor response is uniform across plant species (Smit, 1990; Whitecross et al., 2012; Duker et al., 2015a). Plants of different height are not equally exposed to a frost event because the most extreme minimum temperatures occur close to the ground (Lines et al., 2012). Consequently, a short plant may have proportionately more of itself exposed, compounded by a greater surface-to-volume ratio depending on crown geometry, than a large plant during a frost event. Investigation of differences in frost impact among species or plant sizes therefore first requires demonstration that their distribution along an elevational gradient is comparable.

Study of frost impact is deserving of closer attention because climate change might result in changes in the frequency and intensity of extreme frost events (IPCC, 2014). Indeed, changes in ambient air temperature as a result of climate shifts may already be affecting vegetation (Rigby and Porporato, 2008; Augspurger, 2009). Anticipation of the consequences for the distribution and abundance of vegetation across landscapes, even across biomes, demands an improved understanding of frost impact on susceptible growth forms. A reduction in freeze events is expected by some (Rigby and Porporato, 2008) that might provide some woody species an opportunity to expand their ranges. In southern Africa, woody plants may encroach and transform both grassland and Nama-Karoo, and bush encroachment of savanna may be accelerated. Increasing variability of weather patterns may, however, constrain woody vegetation through the impact of more extreme, even if infrequent, frost events, or through freeze events occurring during the early growth season (Augspurger, 2009) that could damage new growth of woody plants (Inouye, 2000; Agrawal et al., 2004).

This study was prompted by a severe frost event which was widespread over parts of South Africa during the 2014 winter. The event was not anticipated so its impact was studied after the event. The aim of the study was to evaluate the extent to which a single severe frost event might influence the landscape-level distribution of woody plants in environments in which it was both a dominant (savanna) and at topographic boundaries between treeless and woody vegetation types. A first objective was to confirm that the 2014 frost event was a relatively severe event at a time-scale relevant to the growth rate of woody plants. A second objective was to examine whether frost occurrence on woody vegetation showed an inverse relation to local elevation, as expected, being most pronounced in the valleys and less severe or absent on local high ground. An associated objective was to assess whether infrequent severe frost could account for relatively discrete boundaries between vegetation types patterned in relation to local topography.

Finally, the expectation that species would differ in terms of ability to recover from frost impact, and that small individuals would experience proportionately greater impact, was examined to the extent afforded by vegetation composition and structure. As a prerequisite, distribution of species and plant sizes along elevational gradients were examined. Implications of the findings are discussed in the context of climate change.

2. Materials and methods

2.1. Study sites

The 2014 frost event was widespread; accordingly geographically well dispersed locations were selected in a region where the Nama-Karoo biome interfaces along its eastern boundary with the grassland biome and along its northeastern boundary with the savanna biome (Fig. 1). Available resources precluded more locations. Two locations (one site each) were in the Nama-Karoo biome and one location (two sites in separate valleys at Schmidtsdrift) was in the savanna biome. Details of each location are summarised in Table 1. For the Nama-Karoo locations, a gentle valley floor displayed a marked transition to a relatively steep hill slope (42% at Middelburg; 22% at Hofmeyr). The savanna sites were characterised by a relatively gradual slope (6% at Schmidtsdrift) rising from a narrow valley floor.

2.2. Weather data

In order to assess the severity of the 2014 frost event we obtained minimum daily temperature data from the South African Weather Service for three locations closest to our study sites (Fig. 1). Data for Kimberley are considered to reflect Schmidtsdrift, those for Cradock and Queenstown reflect Middelburg and Hofmeyr, respectively. Data for a year were included if the data for the winter period (June–August) were complete. Consequently, the

sets were 83 years for Kimberley (1932–2014), 44 years for Cradock (1959–1973, 1985–2014), and 53 years for Queenstown (1959–2014). A day was classified to have experienced frost when the daily minimum temperature, measured in a Stevenson screen at 1.2 m above ground, was below zero degrees. The lowest minimum temperature and the number of frost days per annum were extracted. These two variables were correlated (Pearson's coefficient) for Kimberley ($r = 0.707$; d.f. = 83; $P < 0.0001$), Cradock ($r = 0.766$; d.f. = 44; $P < 0.0001$) and Queenstown ($r = 0.409$; d.f. = 53; $P < 0.002$), thus only the first is discussed further. The severity of the 2014 frost event at each location was described by determining the percentage of years for which as cold or colder minimum temperatures had been recorded and the period of time since comparable cold temperatures had been recorded. The latter indicates relatively benign conditions for woody vegetation. Formal analysis of temporal trends of temperature was not undertaken on account of missing data.

2.3. Measurement of trees at field sites

At each site, frost impact was assessed along a number of transects covering the elevational change from a valley floor toward a high point. Six transects were used at Middelburg and four at each of the other sites. Each transect consisted of 5–7 non-contiguous 10 by 10 m plots. Altitude of each plot was determined using a GPS. All woody trees and large shrubs were measured in each plot. Frost damage was determined based on the tree skeleton remaining. Recent frost damage can be distinguished from drought and age die-back by the occurrence of fine twigs on the tree. The following was recorded for each plant separately for pre-frost damage and post-frost damage: species identity, stem circumference at 20 cm or below the first branch, height of canopy base, height of canopy top, largest diameter of tree-canopy and diameter perpendicular to this, shape of tree-canopy pre- and post-frost damage (scored to the closest matching volume-shape e.g., conical, ellipsoid, or

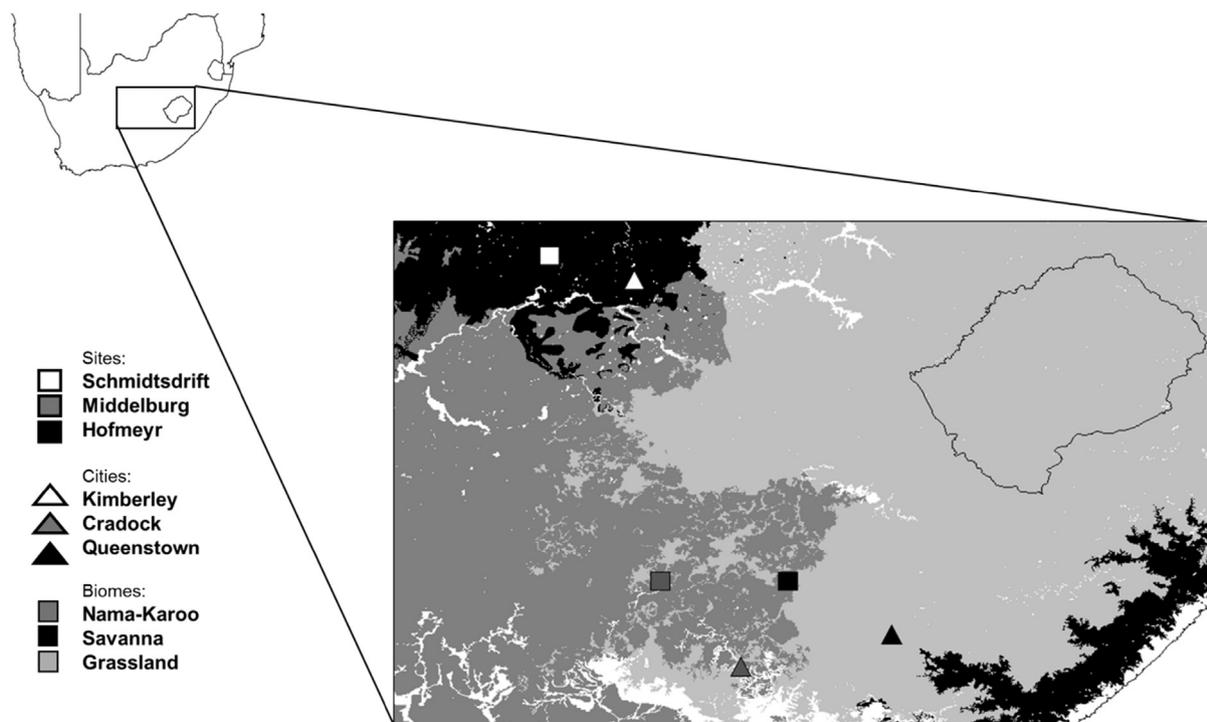


Fig. 1. Location of field sites in relation to the major biomes of South Africa. The three cities are the closest weather stations to our field sites from which weather data were obtained.

Table 1

Description of each study site including, location, altitude, vegetation type, land use, mean annual precipitation (MAP), mean annual temperature (MAT) and mean number of frost days (MFD) (Information on vegetation type and climate from Mucina and Rutherford (2006)).

Site	Co-ordinates	Altitude (m)	Vegetation type	Land use	MAP (mm)	MAT (°C)	MFD
Middelburg	S 31.43246 E 24.98281	1120–1680	Besemkaree Koppies shrubland (Gh 4)	Sheep grazing trials	234	15.1	43
Hofmeyr	S 31.43022 E 26.03278	1000–1700	Besemkaree Koppies shrubland (Gh 4) and Eastern Upper Karoo (NKu 4)	Sheep and goat farm	220	14.7	52
Schmidtsdrift	S 28.59621 E 24.07372	1000–1350	Schmidtsdrift thornveld (SVk 6) and Kimberley Thornveld (SVk 4)	Communal area grazed by sheep and goats	350	17.2	32

cylindrical). Severity of frost damage was defined as follows: none for less than 10% loss; moderate for 11–89% loss; severe for 90–99% loss with resprouting, and complete mortality for 100% without resprouting.

2.4. Analysis

Measures were required of the proportional volume of individual plants, and the proportional volume of all plants on a plot, that had been lost to frost impact. For each plant, canopy volume of live material and canopy volume killed by frost were calculated separately, each according to the procedure of Smit (2014). The two values were summed to provide a measure per plant of total plant volume prior to frost impact, from which the proportion of each individual lost to frost impact was calculated. This proportion is an underestimate because it ignores both regrowth following frost impact and growth of non-frosted portions, but this bias was considered preferable to making assumptions about dieback or growth rate. The proportion of a plot lost to frost was calculated by summing respective volumes of all the individuals in a plot.

A first expectation was that frost impact would be greatest in the valleys where pooling of cold air occurred and decrease going up the adjacent slope. Accordingly, a regression relation was sought between the proportion of tree volume lost to frost per unit ground area and elevation above the valley floor. Linear and negative exponential regressions were found to be adequate for describing the data sets at hand.

A second expectation was that small plants would be more severely impacted than large plants. If frost impact is strongly related to elevation as expected, then the extent to which distribution of plant size of a species is confounded with local elevation first needs to be determined. Accordingly, the relation between pre-frosting plant size (log-transformed canopy volume) and elevation was examined for each of the main species at each site using linear regression. For species for which distribution of plant size over elevation was acceptable, the influence of plant size on regrowth ability was examined through comparing volume of live regrowth against the volume lost to frost for individual plants which had been severely frosted (>90% volume lost) using linear regression. For each site, differences among species in the proportion of individuals showing frost impact were determined by first classifying each individual as 'unaffected' or 'affected' then testing differences between each pair of species using χ^2 tests (Yate's correction for continuity) with $\alpha = 0.02$ in order to accommodate increased experiment-wise error rate. Only species with sufficient sample size to meet an expected value of 5 per dieback category were included.

3. Results

3.1. Weather data

All three sites experienced freezing conditions for every year of record but the severity of freezing varied considerably over time

(Fig. 2). Minimum temperature was usually recorded during July at the peak of winter. The minimum temperatures recorded during the winter of 2014 were -7.4 , -5.0 and -6.8 °C for Kimberley, Cradock and Queenstown, respectively, approximately 2 °C colder than their respective long-term means. Minimum temperatures as cold or colder had been recorded for 12.2%, 16.3%, and 5.8% of years, respectively (Fig. 2). Thus 2014 was one of the colder but not the most severe winter on record. However, its importance for frost impact on plants is underscored by consideration of the temporal pattern of minimum temperatures over time. At Cradock, 2014 was the coldest winter since 1985 (2003 record missing), some 22% colder than the second coldest year of 1996 for this period. By contrast, 50% of the years between 1960 and 1973 were colder than 2014. At Queenstown, temperatures as cold or colder had been experienced seven years or so previously (1997, 1996) and 20 years before then (1977). At Kimberley, 2014 was preceded by the colder years of 2010 (coldest year on record together with 1955) and 2012, so frost impact recorded at Schmidtsdrift may have been a consequence of several frost events; the recent regrowth we recorded indicated 2014. A particularly cold spell had occurred from 1989 to 1994, with five of these six years as cold as or colder than 2014, as well as 35 years previously during 1955 and 1954. Thus at all sites, Cradock and Queenstown more so than Kimberley, 2014 was a relatively cold year that had been preceded by an extended period during which conditions were more benign for woody vegetation.

3.2. Effect of elevation

Frost damage in relation to elevation was successfully described by a negative exponential relation for all sites (Fig. 3). Frost impact was most severe at the base of slopes, up to a maximum of 60–100% loss of above-ground plant volume across sites, but declined with elevation up the slope such that no impact was recorded within an elevational increase of 30–100 m (Fig. 3). Thus this frost event had been effective in temporarily markedly reducing woody vegetation at the base of hills.

3.3. Relation between elevation and plant size of dominant species

The relation between initial plant size and local elevation was not consistent among sites or species. There was no relation between plant size and local elevation ($P > 0.05$), and all plant sizes were represented across the entire elevation gradient for *Acacia karroo* at Hofmeyr, *Searsia burchellii* and *Diospyros lycioides* at Middelburg, and *Acacia mellifera* at Schmidtsdrift 2. Other species showed weak relations: individual plants of *Acacia mellifera* and *Acacia tortilis* were on average smaller going upslope at Schmidtsdrift 1, similarly for *Searsia erosa* at Middelburg, whereas individual plants of *Acacia tortilis* were on average larger going upslope at Schmidtsdrift 2 (Fig. 4). To a limited extent, therefore, large rather than small plants were impacted at Schmidtsdrift 1 and Middelburg, and the converse at Schmidtsdrift 2, but the range of plant size observed at all elevations we contend vindicates examination of the influence of plant size on frost impact.

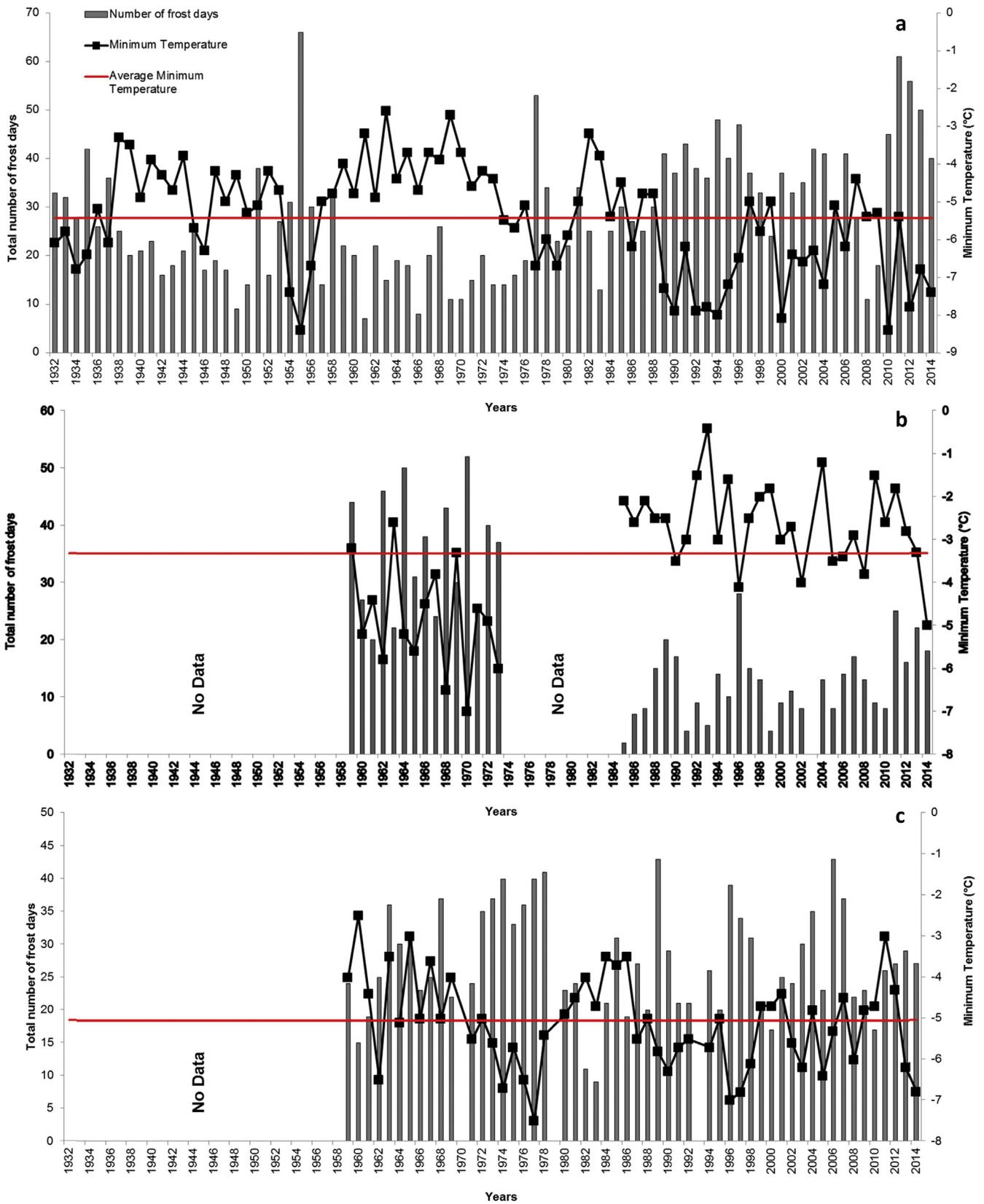


Fig. 2. Coldest temperature experienced per year (line graph) and the total number of frost days (histogram) for a) Kimberley, b) Cradock and c) Queenstown (see Fig. 1 for location). The red line is the multi-year average for the length of record available. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

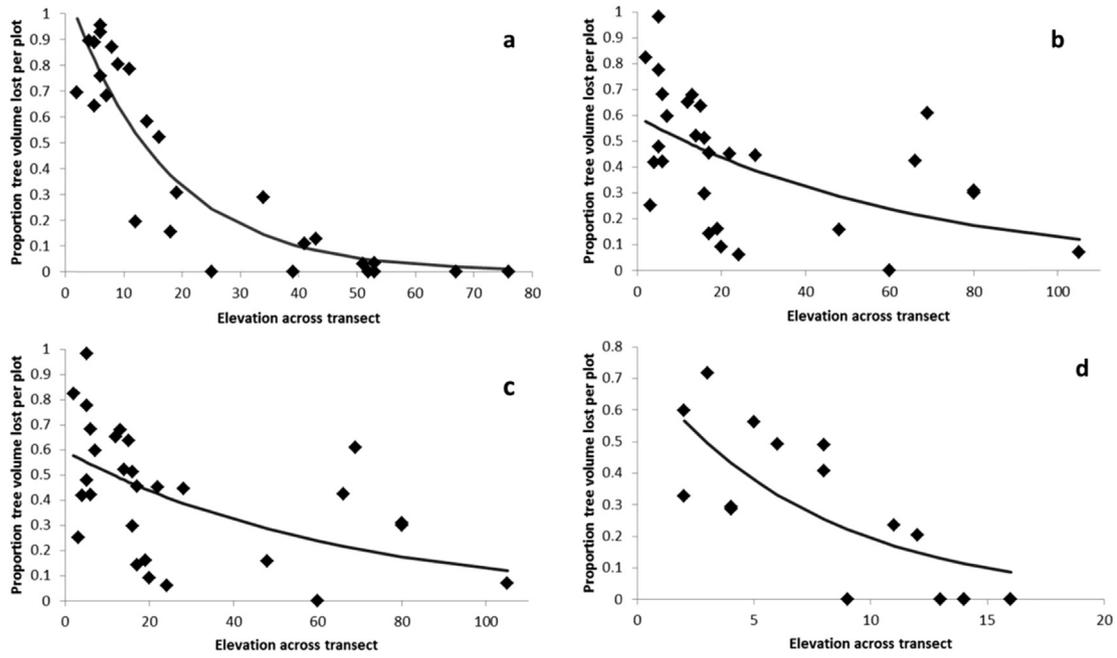


Fig. 3. Proportion of tree-volume lost to frost per plot (y) in relation to elevation (x , starting altitude scaled to zero in order to allow comparison across sites) described by a negative exponential function for **a)** Hofmeyr ($y = 1.1044e^{-0.0602x}$; $F = 165.98$, $P < 0.001$), **b)** Middelburg ($y = 0.5931e^{-0.0152x}$; $F = 56.68$, $P < 0.001$), **c)** Schmidtsdrift 1 ($y = 0.8768e^{-0.0521x}$; $F = 15.98$, $P < 0.001$) and, **d)** Schmidtsdrift 2 ($y = 0.7402e^{-0.1339x}$; $F = 33.78$, $P < 0.001$).

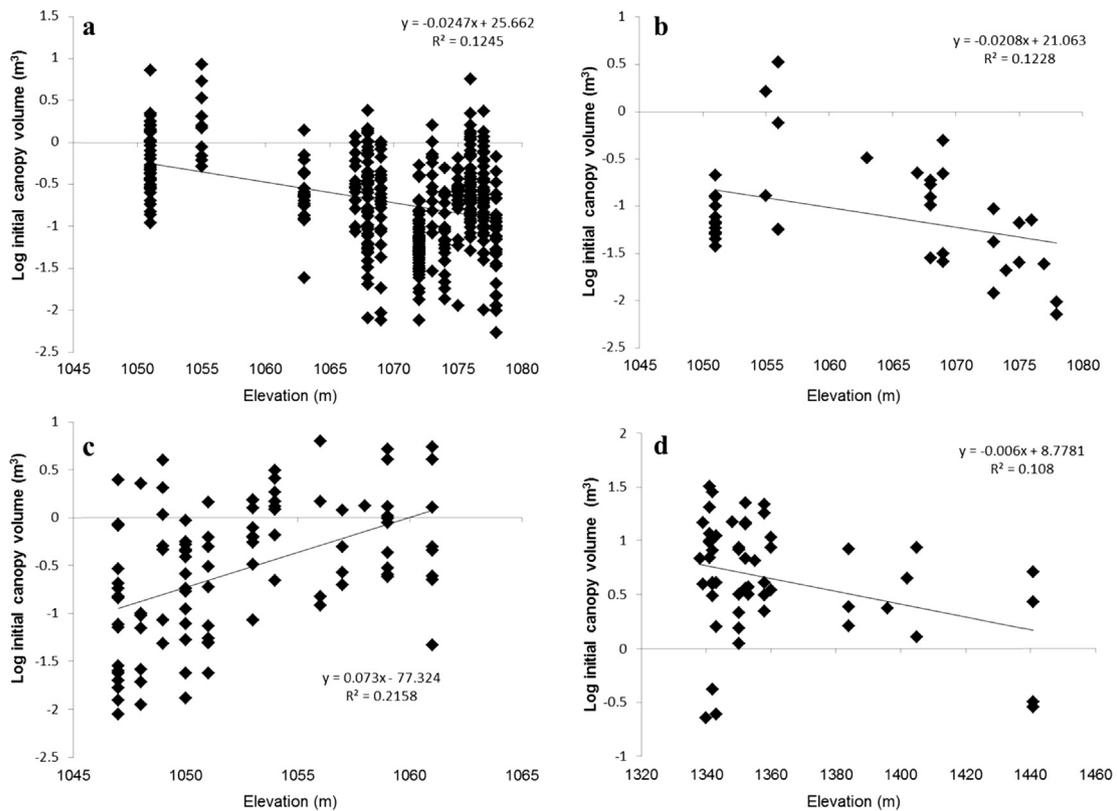


Fig. 4. Initial plant size in relation to elevation for **a)** *Acacia mellifera* at Schmidtsdrift 1, **b)** *Acacia tortilis* at Schmidtsdrift 1, **c)** *Acacia tortilis* at Schmidtsdrift 2 and, **d)** *Searsia erosa* at Middelburg.

3.4. Regrowth

For all the main species at all sites, most severely frosted plants had not regained their pre-frost volume after one season of

regrowth (Fig. 5). The relative difference increased with plant size. For a small proportion of individuals, mostly small ones, regrowth exceeded volume-lost-to-frost. For these species, regrowth volume was linearly related to volume-lost-to-frost ($P < 0.05$) for four

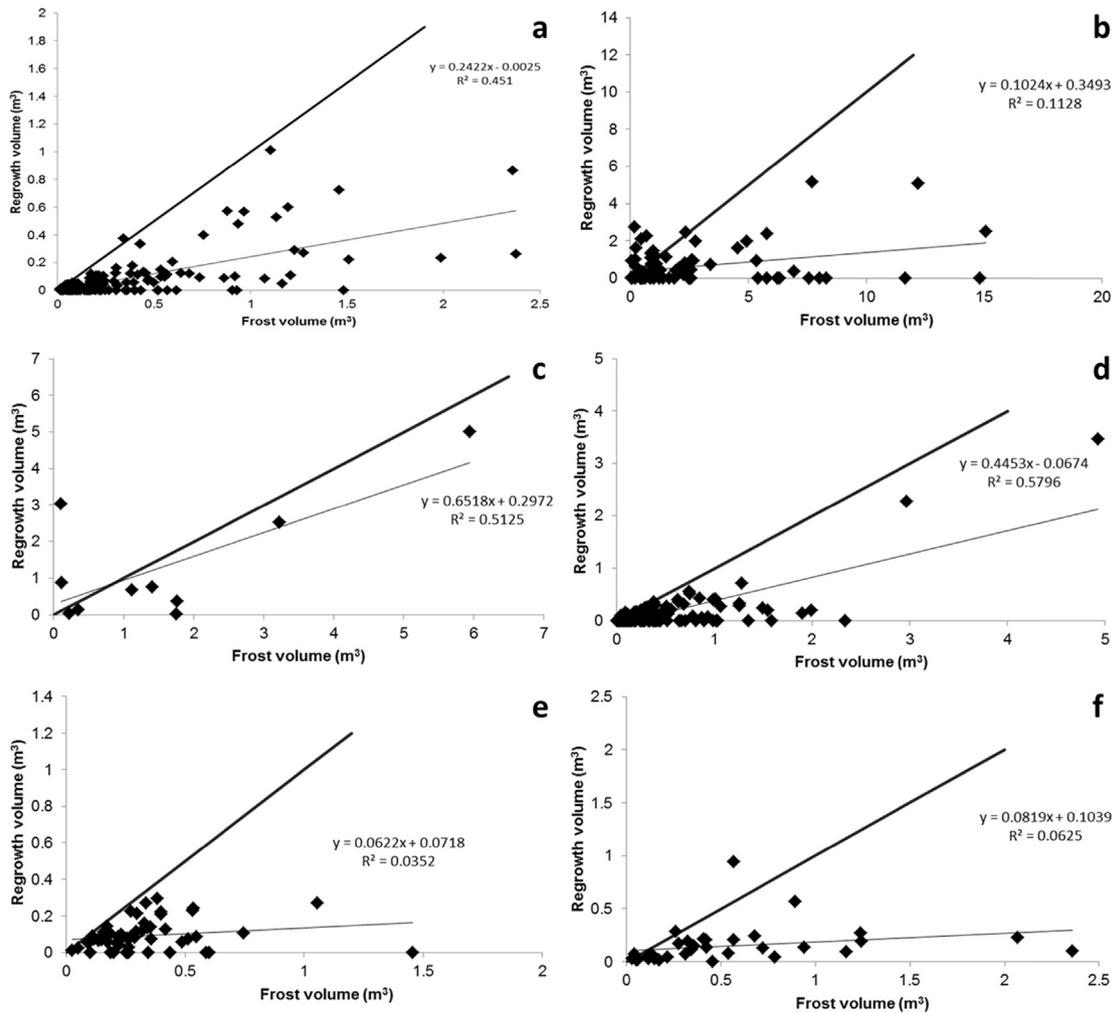


Fig. 5. Volume regrowth of severely frosted (>90% loss of volume) individuals in relation to volume-lost-to-frost for **a)** *Acacia karroo* at Hofmeyr, **b)** *Searsia burchellii* at Middelburg **c)** *Diospyros lycioides* at Middelburg **d)** *Acacia mellifera* at Schmidtsdrift 1 **e)** *Acacia mellifera* at Schmidtsdrift 2 and **f)** *Acacia tortilis* at Schmidtsdrift 2. The grey line represents replacement of volume lost; points above the black line indicate a plant growing larger than the volume-lost-to-frost.

species (Fig. 5a–d) but not ($P > 0.05$) for two species (Fig. 5e and f).

3.5. Frost impact

The extent of frost impact experienced by individual species at each of four sites is summarised in Table 2. At Hofmeyr, *Diospyros austro-africana*, *Diospyros lycioides* and *Lycium* sp. were largely unaffected whereas *Searsia burchellii*, *Searsia erosa* and the dominant *Acacia karroo* (78.1% of individuals) were impacted to a different degree. Similarly at Middelburg, these two *Diospyros* species and *Gymnosporia capitata* were relatively unaffected whereas the two *Searsia* species, *Lycium* sp. and *Tarchonanthus camphoratus* were impacted to a different degree. At both Schmidtsdrift sites, the two dominant *Acacia* species were relatively heavily impacted by frost whereas *Boscia albitrunca*, *Cisampelos capensis* and *T. camphoratus* were effectively unaffected. Dominant species, *Acacia* species at Hofmeyr and Schmidtsdrift and *Searsia* species at Middelburg, were the most heavily impacted. Complete mortality of up to 8% of a population was evident for *A. karroo*, two *Searsia* species, and *Acacia mellifera* at one Schmidtsdrift site, whereas nearly half of the small population of *Lycium* at Middelburg succumbed. Thus at each site, dominant woody species had experienced substantial top-kill or even

complete mortality as a result of frost, and frost had impacted species to a different degree.

4. Discussion

4.1. Key patterns of frost impact

Our study sought to investigate the impact of a single, severe frost event on woody vegetation in a semi-arid region covering a large geographic area in southern Africa (Figs. 1 and 2). Three well-distributed study locations suggest findings are broadly representative of this area and not simply an indication of local landscape-level responses. An expectation was for topographic influence on frost severity and frequency that would manifest in terms of impact on vegetation; specifically, diminution of impact from a valley going upslope (Garcia et al., 2010; Jewitt et al., 2015). This expectation was strongly evident at all three locations (four sites) (Fig. 3). All sites had a well-defined valley although valley and slope profile differed from a relatively gentle V-shaped slope at Schmidtsdrift to moderately steep slopes arising sharply from a relatively flat valley floor at Middelburg and Hofmeyr. Woody plants lost between 60 and 100% of their volume at the foot of a slope but no loss was evident at an elevation of only 30–100 m above the valley floor

Table 2

Extent of frost dieback as number of individuals per species population at each site: U = unaffected (<10%); M = moderate (11–89%), S = severe (90–99%), CM = complete mortality (100%), and TN = Total number of individuals sampled. Subscripts denote differences across species ($\alpha = 0.02$) within a site.

Species	Hofmeyr					Schmidtsdrift 1					Schmidtsdrift 2					Middelburg					
	U	M	S	CM	TN	U	M	S	CM	TN	U	M	S	CM	TN	U	M	S	CM	TN	
<i>Acacia karroo</i>	_b 48.6	42.0	4.4	5.0	383	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Acacia mellifera</i>	–	–	–	–	–	_b 59.8	28.7	7.4	4.1	418	_b 45.0	49.2	5.8	–	189	–	–	–	–	–	–
<i>Acacia tortilis</i>	–	–	–	–	–	_b 71.8	25.6	2.6	–	39	_b 50.7	43.8	5.5	–	73	–	–	–	–	–	–
<i>Boscia albitrunca</i>	–	–	–	–	–	100.0	–	–	–	7	_a 100.0	–	–	–	11	–	–	–	–	–	–
<i>Cissampelos capensis</i>	100.0	–	–	–	1	_a 100.0	–	–	–	53	–	–	–	–	–	75.0	25.0	–	–	–	4
<i>Cussonia paniculata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	100.0	0.0	–	–	–	2
<i>Diospyros austro-africana</i>	_a 97.0	3.0	–	–	33	–	–	–	–	–	–	–	–	–	–	_a 87.5	12.5	–	–	–	8
<i>Diospyros lycioides</i>	_a 100.0	–	–	–	13	–	–	–	–	–	–	–	–	–	–	_a 82.9	14.5	2.6	–	–	76
<i>Ehretia rigida</i>	–	–	–	–	–	100.0	–	–	–	1	100.0	–	–	–	4	–	–	–	–	–	–
<i>Euclea undulata</i>	100.0	–	–	–	1	–	–	–	–	–	–	–	–	–	–	100.0	–	–	–	–	1
<i>Gymnosporia capitata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	_a 92.9	7.1	–	–	–	14
<i>Lycium</i> sp.	_a 93.3	6.7	–	–	15	–	–	–	–	–	–	–	–	–	–	_b 10.0	45.0	5.0	40.0	–	20
<i>Rhamnus prunioides</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	100.0	–	–	–	–	2
<i>Searsia burchellii</i>	_c 70.3	18.9	2.7	8.1	37	–	–	–	–	–	–	–	–	–	–	_c 43.2	40.7	10.5	5.6	–	162
<i>Searsia erosa</i>	_d 15.4	76.9	–	7.7	13	–	–	–	–	–	–	–	–	–	–	_c 31.5	64.8	1.9	1.9	–	54
<i>Tarchonanthus camphoratus</i>	–	–	–	–	–	100.0	–	–	–	3	_b 92.9	7.1	–	–	14	_b 26.1	73.9	–	–	–	23
<i>Ziziphus mucronata</i>	–	–	–	–	–	100.0	–	–	–	1	28.6	42.9	28.6	–	7	–	–	–	–	–	–
TN	275	180	18	23	496	343	130	32	17	522	152	129	17	0	298	186	141	21	18	–	366

(Fig. 3). This response is consistent with pooling of cold air within a valley (Savage, 2012). Improved understanding of frost impact therefore depends in part on improved prediction of height distribution of minimum temperature in response to topographic influences on air pooling and flow (e.g., Savage, 2012) in relation to the severity of an event.

Severity of frost impact depended further on initial plant size (Fig. 5) and species identity. Greater vulnerability of small rather than tall plants within the frost impact zone indicates that a pronounced temperature gradient extended vertically from the ground surface upward during a frost event, but this is not commonly measured. Comment on the impact of a frost event on plant size awaits an improved understanding of the relation between vertical height and frost severity in response to topographically mediated pooling patterns. This study (Table 2) reinforced the widespread general observation that plant species comprising plant communities periodically exposed to frost differ markedly in frost-tolerance and in their ability to withstand freeze events (Sakai, 1966; Smit, 1990; Bannister and Lord, 2006). Examples of species which were barely affected included *Boscia albitrunca*, *Cissampelos capensis* and *Diospyros lycioides*; species severely affected were the microphyllous species *Acacia karroo* and *Acacia mellifera* and *Searsia* species. Smit (1990) also recorded some microphyllous *Acacia* species being particularly susceptible. Although this study has provided additional empirical evidence of which species are more impacted by a frost event of a certain severity than others, a future research direction would be to develop a predictive ability of frost tolerance of woody species in the biomes of interest based on species distribution, plant traits and attributes.

A consequence of size-related impacts of a frost event would be a change in the relative size structure of a population that could result in altered competitive relations, growth opportunities, hence population dynamics (Boyden et al., 2009). A further consequence of repeated frosts on a vulnerable species would be development of a pattern of increasing plant size from the valley floor extending upslope. Such a frost-induced pattern has been suggested for *Colophospermum mopane* in a southern African savanna (Stevens et al., 2014). There is little support that a similar pattern pertains for the locations in this study. Only *Acacia tortilis* at Schmidtsdrift 2 was consistent with this pattern (Fig. 4c), three other species showed the converse pattern (Fig. 4a, b, d) and two species showed no

relation between plant height and local elevation (Fig. 4e and f). This frost event therefore increased size inequality of the *Acacia tortilis* population at Schmidtsdrift 2 because tall individuals upslope largely escaped frost impact whereas small individuals were reduced in size. Overall, repeated frost impact would therefore not seem to be an important factor shaping the size structure of these populations, perhaps attributable to the apparent general infrequency of severe frosts preceding the 2014 event (Fig. 2).

Effect of a severe frost event on the population dynamics of a species would depend in large part on the level of complete mortality experienced and on the extent of top-kill of surviving plants. Complete mortality was recorded for only seven of 32 species-by-site combinations at three of four sites (Table 2). Complete mortality of less than 5% of the population for the dominant species *Acacia karroo* at Hofmeyr and *Acacia mellifera* at Schmidtsdrift 1 compares closely with 4% complete mortality recorded for a severe frost event in another South African savanna (Smit, 1990); that of 8% for *Searsia* species at Hofmeyr is conspicuously higher than previously recorded figures. Complete mortality is not generally expected for African savanna woody species whose individuals are usually well adapted to loss of above-ground biomass (Bond, 1997; Holdo, 2006). Fire is another disturbance agent which impacts in a manner similar to frost, for *A. karroo* resulting in a comparable level of complete mortality and size-dependent topkill (Trollope, 1980). Future endeavours therefore might address the impacts of different disturbance agents within the context of a general model for the regrowth of woody savanna plants subjected to repeated loss of above-ground biomass. Repeated annual die-back would result in a population comprised principally of small individuals, which is expected to render a population more vulnerable to decline (Feeley et al., 2011; Monleon and Lintz, 2015). Recovery of size by an impacted woody individual is therefore essential for its survival, which depends on reserves available for regrowth and an active bud bank (Teague and Walker, 1988), but these factors are not known for most of these species. In this study, almost all individuals did not regain their pre-frost size within a season (Fig. 5), the relative difference between pre- and post-frost size increasing with plant size. However, for a small proportion of small individuals their regrowth volume exceeded their volume lost to frost, emphasising that even small woody plants have adequate reserves for initiating regrowth.

4.2. Effect on biome organisation

This study has shown that a single severe frost event can temporarily contain the growth of woody vegetation. Frost has been an annual event for all study locations varying over years in severity, but the temperatures recorded during the 2014 frost event were as much as 2 °C lower than the average minimum across the eastern Karoo (Fig. 2). The long-term impact of frost on woody vegetation would therefore depend mainly on the frequency with which comparably severe frost events occur and the growth rates of woody plants and populations during intervening relatively benign periods. All three locations were characterised by pronounced variability in minimum temperature over years including extended periods of benign temperatures that would promote woody growth. For Middelburg, the 1930s, 1940s, and 1950s were particularly cold with nine of 16 years from 1943 to 1958 experiencing temperatures between –10 °C and –12 °C whereas only three in 55 years between 1959 and 2013 years experienced temperatures this low (du Toit and O'Connor, 2016). (Unfortunately the weather station was stolen shortly before the 2014 event.) By contrast, the intensity of severe frost events has intensified at Kimberley over the past three compared with the previous six decades (Fig. 2a). Rates of woody growth await investigation for assessment of the significance of frost impact.

South African biomes are recognised based on their dominant plant growth forms, and the distribution of biomes is related to broad-scale climate variables, mainly temperature and rainfall amount and seasonality (Mucina and Rutherford, 2006). The Nama-Karoo biome is characterised by a dominance of dwarf shrubs, a low biomass of grass, and a near absence of trees; the savanna biome by a mixture of trees and grass with a sparse representation of dwarf shrubs; and the grassland biome by dominance of perennial grasses. A differential effect of an agent on these components would influence biome organisation. This study has identified that frost may act as an important constraint on the abundance of woody vegetation under certain conditions, a plant growth form whose absence in part defines the Nama-Karoo and grassland biomes. Whether frost is important for maintaining the vegetation character of these biomes depends on other agents which might exercise such an effect. An obvious alternate agent that might contain woody plants is fire, fuel for which is provided by grasses in fire-prone grassland and savanna (Bond, 1997). By contrast, the Nama-Karoo usually supports a low biomass of grass fuel, hence fires are infrequent (Bond, 1997). Following an uncommon sequence of years whose rainfall pattern promoted the accumulation of grass fuel (du Toit and O'Connor, 2014), a number of isolated fires have recently occurred in parts of the Nama-Karoo that have resulted in a change from shrub- to grass-dominated vegetation (du Toit et al., 2015b; du Toit et al., 2015a). Frequent fire may therefore be effective in excluding karroid dwarf shrubs from grassland and savanna but infrequent fire is an inadequate explanation for the treeless condition of the Nama-Karoo. This study also provided further evidence that frost may contain bush encroachment by *Acacia* species (O'Connor et al., 2014) along drainage lines in savanna as reported also for *Colophospermum mopane* savanna (Stevens et al., 2014).

Biome boundaries may not necessarily be maintained by the same variables distinguishing biomes, and may be influenced by local factors such as edaphic conditions and disturbance (Moncrieff et al., 2015). Our results suggest some role for frost determining the boundary between the Nama-Karoo and savanna biomes. The two Nama-Karoo locations encompassed a boundary between two vegetation types which represent different biomes, specifically Nama-Karoo (Eastern Upper Karoo vegetation type) and a savanna-type with woody plants (Besemkaree Koppies Shrubland

vegetation type) (Table 2). These two vegetation types interface at the base of hills where the effects of frost were most apparent (Fig. 3), suggesting for this landscape scale that frost is important in the exclusion of woody plants from Nama-Karoo vegetation although the transition was confounded with a change in soil type. This evidence of frost maintaining a local biome boundary is not a sufficient basis for inferring that frost is overall a determinant of the boundary between the Nama-Karoo and savanna biomes, but evidence for the role of frost as a determinant of a biome boundary has recently been presented for the boundary between Albany Sub-tropical Thicket and the Nama-Karoo (Duker et al., 2015a, 2015b) and between the savanna and grassland biomes in KwaZulu-Natal, South Africa (Jewitt et al., 2015). Its broader role warrants further investigation.

In conclusion, our results suggest that frost may be an under-appreciated agent responsible for maintaining the vegetation character of the Nama-Karoo biome and its boundary with the savanna and grassland biomes. Its role in maintaining local or even larger biome boundaries would depend on the frequency of frost events of a particular severity, an influence whose expression depends on landscape topography. Some empirical analyses have suggested amelioration of frost impact over parts of southern Africa including the Nama-Karoo since about the 1960s (Mackellar et al., 2014; New et al., 2006), but a trend of amelioration is not consistent with a near century-long record for our Middelburg study site (du Toit and O'Connor, 2016) or for the climate stations used in this study (Fig. 2). Plants respond to the temperature regime of the location in which they grow, which begs for an increased density of temperature monitoring across the study area than currently exists (Fig. 1). Furthermore, we studied only a single, severe event. If the role of frost is to be better understood, then long-term observation of woody communities across topographic gradients at selected locations needs to be developed.

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