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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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A B S T R A C T

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.

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 thicket.

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.