FIRE-MEDIATED SUCCESSION AND REVERSION OF WOODY VEGETATION IN THE KWAZULU-NATAL DRAKENSBERG, SOUTH AFRICA

Andrew de Villiers

School of Animal, Plant and Environmental Sciences

Faculty of Science

University of the Witwatersrand

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Declaration

I declare that this dissertation is my own work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

ADV

Signature of candidate

19 October 2012.

Abstract

Long term fire exclusion has been attempted in Catchment IX (CIX) at Cathedral Peak. Baseline vegetation of CIX was sampled in 1952, with follow-up surveys in 1973, 1986 and 2010. These took place at key times in terms of changes in fire history within the catchment. Complete fire exclusion was achieved between 1973 and 1986, but eight accidental fires burnt part of CIX thereafter.

The woody component was resurveyed in 2010 after the latest of thirteen unintended fires had swept through CIX in 2007. This fire burnt about 90% of the catchment. The vegetation of the area not burnt was a distinct community and size structure indicating it had not been burnt by other accidental fires.

Partial exclusion of fire over 58 years resulted in vegetation transforming from grassland to a grassland-fynbos-scrub forest mosaic. *Erica evansii* and *Leucosidea sericea*, a reseeder and resprouter respectively, were the two dominant species in CIX. These displayed expected responses to a single fire, resulting in dominance shifting from *E. evansii* (92% mortality) to *L. sericea* (1.6% mortality). The decrease in *E. evansii* individuals resulted in a relative increase in community contribution of species not affected by fire. *Leucosidea sericea*'s post-fire dominance in burnt plots was not apparent in fire-protected areas.

A successional trend of colonisation of woody species, predominantly *E. evansii* and *L. sericea*, into grassland was observed. Despite occasional fires since 1986 vegetation did not revert to grassland. The emergent woody community was not homogenous. This was attributed to a combination of an irregular pattern of accidental burns and environmental variability within the catchment. The mosaic of distinct grassland, woodland, ecotonal and scrub forest communities are predicted to remain as such.

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To God be the glory.

"The earth is the LORD's, and everything in it, the world, and all who live in it..."

Psalm 24:1

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CHAPTER 1 :

Introduction

1.1 Fire in the natural environment

The importance of fire as a driver and regulator of vegetation types worldwide has been well documented (Gordon-Gray & Wright, 1969; Manry & Knight, 1986; Scott, 2000; Van Auken, 2000; Bond & Parr, 2010). Globally, grasslands support the most frequent fires of any vegetation type (Bond & Keeley, 2005). This inhibits tree recruitment (Trollope, 1983; Granger, 1984; Trollope & Tainton, 1986) and renders the Grassland Biome conspicuous for its near absence of tree cover (Bews, 1916; Acocks, 1953; Bayers, 1955; Everson, 1985; O' Connor & Bredenkamp, 1997; Bond & Parr, 2010; Archibald, 2010). These woody elements are generally confined to fire refugia such as riparian areas, drainage lines and rocky outcrops (Philips, 1930; Van Zinderen Bakker, 1973; Mentis & Huntley, 1982; Granger, 1984; Mucina & Rutherford, 2006).

Fire plays a key role in shaping and maintaining the Fynbos, Savanna and Grassland Biomes in South Africa (Granger, 1984; Manry & Knight, 1986; O'Connor & Bredenkamp, 1997; Titshall *et al.* 2000; Hibbard *et al.* 2003; Van Langevelde *et al.* 2003; Van Wilgen *et al.* 2004; Bond & Keeley, 2005; Bond, 2008). Changes in the fire regime within these biomes affects the ecosystems involved (Bond & Keeley, 2005; Bond & Parr, 2010).

Over the past few decades humans have become the most common source of ignition within grasslands. Manry and Knight (1986) suggest that the pre-human fire frequency in the moist grasslands of KwaZulu-Natal was between three to four years. We cannot, however, ascertain the stone- and iron-age fire regimes in these grasslands. At present fire frequency, intensity and seasonality are controlled by humans with a biennial spring burn after the first rains most commonly implemented (Morris, 1999). Both past and present fire regimes in these moist grasslands have therefore benefitted grasses at the expense of woody vegetation, as the latter require greater fire-return intervals to survive (Trollope & Tainton, 1986).

Conversely, woody colonisation is observed in the absence of fire in moist grasslands (Granger, 1976; Granger, 1984; Adcock, 1990). Over time a shift in ecosystem state occurs: from flammable fire-dependent grasslands to inflammable fire-protected woody systems (Granger, 1984; Bond & Parr, 2010; Archibald, 2010). This is as a result of changes in understory flammability and woody species composition and densities (Granger, 1976; Adcock, 1990; Scholes, 2003; Archibald, 2010). Grassland and forest vegetation types can thus be seen as alternate ecosystem states, each displaying positive feedback systems that promote favourable conditions for one at the expense of the other (Manry & Knight, 1986; Granger, 1984; Bond & Parr, 2010).

A number of questions are raised regarding the transformation of grassland to woody vegetation in the absence of fire. These include: (i) is it possible to exclude fire from moist grasslands; (ii) what is the impact of a single fire on transformed grassland-woody vegetation communities should infrequent fires be expected; (iii) what is the nature of woody elements that colonise montane moist grasslands in the absence of fire; (iv) are certain areas expected to become fire-protected over time and if so which areas; (v) are vegetation changes reversible should fire frequency increase;

(vi) how do plants with contrasting life history strategies respond to fire exclusion and accidental fires; (vii) what is the interplay between fire, altitude and other abiotic variables on transformed montane vegetation?

1.2 Catchment IX: An experimental catchment

By excluding fire from moist grasslands, one is in the position to empirically observe the resultant vegetation changes. This approach was taken in 1952 at Catchment IX (CIX) at Cathedral Peak (29°00'S; 29°15'E) in the KwaZulu-Natal Drakensberg. This first-order 77 ha experimental catchment was established in 1942 in order to examine the effect of fire exclusion on the hydrological functioning in the KwaZulu-Natal Drakensberg, with formal fire breaks completed in 1952 (De Villiers, 1970; Killick, 1963; Granger, 1976). A baseline study was carried out in 1952 by Killick (1963). Subsequent changes in the vegetation were assessed by Granger (1976) in 1973 and by Adcock (1990) in 1986. Despite efforts to maintain fire exclusion, thirteen runaway fires swept through the catchment between the time of its establishment and 2007, eight of which occurred between 1991 and 2010.

Four attributes pertaining to Catchment IX (CIX) provide this project with a unique and fortuitous opportunity to examine the effects of woody vegetation responses to infrequent fires in moist montane grasslands:

1) Three comparable vegetation surveys prior to 2010

Killick's (1963) baseline study in 1952 determined that the catchment was predominantly *Themeda triandra* grassland, with woody elements restricted to the immediate vicinity of streams. Granger (1976) and Adcock's (1990) studies noted the expected trend of woody colonisation into fire excluded areas. *Erica evansii* (Oliver, 1987; formerly *Philippia evansii* (Brown, 1905)) and *Leucosidea sericea*'s (Ecklon & Zeyher, 1836) were the two main woody colonisers in CIX. These resurveys formed the basis for examining subsequent vegetation changes within CIX by 2010.

2) Differing fire-return periods between each survey

Of particular interest were the fire-return periods of accidental fires between the resurveys. Between 1952 (Killick, 1963) and 1973 (Granger, 1976) there were five accidental fires, total fire exclusion between 1973 (Granger, 1976) and 1986 (Adcock, 1990), and eight accidental fires between 1986 (Adcock, 1990) and 2010 (this study). This sequence offered a unique opportunity to examine the vegetation changes as a result of contrasting fire-return periods within a single catchment.

3) A recent fire provided an opportunity to assess the impact of a single fire on the dominant woody species in CIX

Catchment IX provided an opportunity to understand the effect of a single fire on woody vegetation in transformed grasslands. The most recent fire took place in the winter of 2007 and left intact skeletons of the burnt woody vegetation. The impact of the 2007 fire on the population status of the dominant woody species could therefore be assessed. This would provide a basis for predicting the effects of repeated fires on woody vegetation in transformed moist grasslands.

4) Measureable abiotic environmental gradients were present within the catchment

Granger (1976), Granger and Schultze (1977), Everson (1979) and Adcock (1990) recorded a number of abiotic environmental variables that were deemed important in constraining woody vegetation within the catchment. This study was in the position to use this information to examine the influences of topography, soil type, radiation and soil moisture patterns on woody vegetation and fire pattern in CIX.

1.3 This study

The aim of the study was therefore to determine the effects of “top-down” (fire) and “bottom-up” (abiotic factors) pressures on the emergent woody vegetation which had developed as a result of 67 years of partial fire exclusion in the KwaZulu-Natal Drakensberg. The specific objectives were to examine: (a) the role of complete versus partial fire exclusion on the pattern, rate and reversibility of woody colonisation within moist grasslands; (b) the changes in the population distribution, density and structure of the two dominant woody species within CIX during periods of contrasting fire-return periods; (c) the mortality, persistence and changes in population structure of woody species in response to a single fire; (d) how the abiotic environment affects the spread of fire; and (e) how the abiotic environment affects the distribution and densities of dominant woody species within CIX. It was expected that: (1) woody colonisation into grasslands would be more favourable during periods of total fire exclusion than during periods of infrequent fires; (2a) woody vegetation would be negatively affected by a single fire; (2b) woody species would vary in their responses to fire as a result of their contrasting life history strategies; (3a) fires would have greater burn areas on xeric than on mesic sites; and (3b) the spatial extent of woody vegetation would be greater in mesic than in xeric areas.

CHAPTER 2 :

Literature review

2.1 Montane vegetation dynamics

Montane environments pose unique challenges to the vegetation that occurs on their slopes and valleys (Körner, 1999). Complex topography and steep environmental gradients within these systems result in mountains being able to support a wide range of plant species and vegetation types (Pritchard *et al.* 2009). Many plants that occur in montane environments live at their altitudinal limit and are exposed to growth limiting factors such as snow cover, soil moisture and local disturbance regimes (Körner, 2003).

2.2 Treelines

These constraints that montane regions impose on vegetation are expressed in the global phenomenon of treelines (Rochefort *et al.* 1994). Treelines, forestlines or alpine parklands are ecoclines between the upper limit of montane forests and the treeless vegetation at higher altitudes. Single stemmed woody growth is not favoured above this transition zone (Körner, 1998; Camareno & Gutierrez 2004; Wang *et al.* 2006), which can be denoted as a roughly marked line connecting the upper limits of forests occurring along similar isoclines (Byers, 2005; Jørgensen, 2009).

Körner (1998) notes five potential hypotheses that explain treelines: the stress hypothesis (e.g. damage by frost); the disturbance hypothesis (mechanical damage by e.g. wind or avalanches); the reproduction hypothesis (limitations to pollination and seed germination and establishment); the carbon balance hypothesis (insufficient balance between the uptake and loss of carbon to support minimum growth of trees) and; the growth limitation hypothesis (insufficient synthetic process rates required for minimum growth or tissue renewal).

The stress hypothesis is partly challenged by the observed global distribution of treelines. Additionally, Tranquillini (1979) noted that frost does not threaten tree survival, but rather injures trees and distorts their growth. Winter desiccation due to frozen soil, however, is known to cause treelines (Tranquillini 1982; Sakai & Larcher 1987), though this predominantly affects young trees (Marchand & Chabot 1978). The reproduction hypothesis has received strong opposition as seedlings have been observed to enter available land above the treeline (Griggs, 1946; Wardle, 1971; Ferrar *et al.* 1988). This said, a decrease in the reproductive success of trees with an increase in altitude (Wardle 1981) and an increase in competition of seedlings with sedges and grass has been observed above treelines (Franklin *et al.* 1971; Noble, 1980; Scott *et al.* 1987; Young 1993). Taking the abovementioned into account, Körner (1998) inferred that the ground cover vegetation above treelines is attributed to the stress and disturbance hypotheses, whilst the carbon balance and growth limitation hypotheses set seedling height limits. The result is that forests fail to form above treelines.

Montane moist grasslands are an anomaly to treelines in that grasses dominate below the treeline, whilst woody individuals are confined to rocky outcrops or stream edges (Phillips, 1930; Killick, 1963; West 1969; Rochefort *et al.* 1994; Bond & Van Wilgen, 1996; O' Connor & Bredenkamp, 1997; Bond & Parr, 2010). This is counter to Schimper's (1903) observations and Whittaker's (1975) temperature-precipitation predictions in that many grasslands are found in regions with sufficient mean annual precipitation (MAP) for trees to be dominant or at least be present (Acocks, 1953; Mouillot & Field, 2005; Bucini & Hanan, 2007; Bond, 2008). Once established, trees are usually more competitive than grasses (Granger, 1984). Indeed, large areas of southern African grasslands have the climate potential to form forests (Bond & Keeley, 2005; Archibald, 2010). This is not a recent phenomenon with palaeo- (Meadows & Linder, 1993; Scott, 2000) and biological (Cowling & Hilton-Taylor, 1997) evidence showing grasslands to pre-date human activity (Manry & Knight, 1986; Ellery & Mentis, 1992).

2.3 Reason for moist grasslands: Fire

A plethora of literature presents reasons for moist grasslands occurring in regions that could potentially support woody vegetation (Acocks, 1953; Killick, 1963; Nänni, 1969; Granger, 1976; Schultze & McGee, 1978; Mentis & Huntley, 1982; Tinley, 1982; Manry & Knight, 1986; Hilliard & Burtt, 1987; Adcock, 1990; O'Connor & Bredenkamp, 1997; Titshall *et al.* 2000; Bond & Keeley, 2005; Bond, 2008, Bond & Parr, 2010). The general consensus is that fire plays a critical role in shaping these communities (Bews, 1916; Granger, 1976; Trollope & Tainton, 1984; Oksanen, 1988; Adcock, 1990; Bond & Van Wilgen, 1996; Bond *et al.* 2003; Van Wilgen *et al.* 2003; Bond & Keeley, 2005; Dalle *et al.* 2006; Bond, 2008; Bond & Parr, 2010; Archibald, 2010) that are themselves constrained by the abiotic environment (Granger & Schultze, 1977; Odum, 1983; Titshall *et al.* 2000). Fire ecology is therefore critical in understanding these ecosystems (Hillard & Burtt, 1987; Bond & Keeley, 2005).

Grasslands can be categorised as either climate-climax or fire-climax grasslands (Tainton, 1999). Climate constrained grasslands occur either as a result of insufficient soil moisture, or low montane temperatures and frost that do not allow for trees to establish (Adcock, 1953; Bredenkamp *et al.* 2002). The latter has been challenged within non-montane areas (O' Connor & Bredenkamp, 1997) with evidence of certain trees tolerating frost and occurring in these regions (Ellery, 1992). Nonetheless, frost plays an important role in montane vegetation dynamics (Marchand & Chabot 1978; Tranquillini 1982; Sakai & Larcher 1987). Alternately, fire-climax grasslands (Tainton, 1981) are driven by fire's constraining influence on woody vegetation that would otherwise be the natural climax of the landscape (Killick, 1963; Granger, 1976; Adcock, 1990). Fire's role in shaping the vegetation is thus seen to increase as the system becomes more mesic (O' Connor & Bredenkamp, 1997).

Grasses are an important fuel source for fires in these systems. A dominant grass species in many moist fire climax grasslands of South Africa is *Themeda triandra*. *Themeda triandra* acts as a flammable and continuous fuel source that is cured by frost or becomes moribund over time (Killick, 1963; Granger, 1976; Knapp & Seastedt, 1986; Everson *et al.* 1988; O' Connor & Bredenkamp, 1997; Uys *et al.* 2004). Natural ignition comes in the form of lightning, of which moist grasslands have the highest densities in South Africa (up to 16 strikes per km^2 per annum) (Manry and Knight, 1986). This results in a natural fire-return period of between three and four years (Edwards, 1984, Manry & Knight, 1986). Fire is thus a natural occurrence in these moist grasslands and acts as both causative and regulatory agent within these systems (Manry & Knight, 1986; O'Connor & Bredenkamp, 1997; Scott, 2000).

2.4 Characteristics of fire

Fire requires three conditions for combustion to occur: a source of ignition, a combustible fuel source and oxygen (Fons, 1946; Drysdale, 1985; Bond & Van

Wilgen, 1996; Pyne *et al.* 1996). Once these preconditions are met in natural environments other factors (e.g. landscape, weather and fuel factors on the day of burn) influence the spread, intensity and duration of a fire within a system (Brown & Davis, 1973; Luke & McArthur, 1978; Cheney, 1981; Wright & Bailey, 1982; Trollope, 1983; Everson *et al.* 1985; Everson *et al.* 1988; Railla *et al.* 2010). These abiotic factors, along with vegetation, modify fire behaviour between and within ecosystems (Manry & Knight, 1986; Bond & Van Wilgen, 1996; Bond *et al.* 2003; Cowling *et al.* 2003). Fires within natural systems thus vary and have different effects on different vegetation types (Luke & McArthur, 1978; Trollope, 1978). Fire's dependence on climate makes it a secondary determinant of vegetation in many cases (O' Connor & Bredenkamp, 1997). Nonetheless it is a natural, ecologically significant and essential force in a variety of ecosystems, affecting plant fecundity, growth and mortality (Bond & Van Wilgen, 1996; Bond *et al.* 2003; Shakesby & Doerr, 2006).

Bond and Van Wilgen (1996) summarised fire's influence on plant populations through two reinforcing hypotheses namely: (i) the interval-dependent hypothesis, in which the interval between fires influences plant fecundity, growth and mortality; and (ii) the event-dependent hypothesis, in which seasonality, intensity, size of the burnt area and post-fire weather conditions influence the plant populations.

2.5 Moist grasslands and succession

Succession is seen to be driven by disequilibrium between the environment and the potential vegetation in the area. Moist grasslands have been seen as vegetation types in disequilibrium with their environments (Killick, 1963; Nänni, 1969; Manry & Knight, 1986; Bond & Keeley, 2005; Bond, 2008). In these fire-dependent ecosystems, extended exclusion of fire is seen as a greater disturbance than fire itself, as it inevitably changes vegetation communities.

Odum (1983) held a view in which one recognises a single theoretical climatic climax with a number of edaphic climaxes that are dependent on the variation in the substrate and individual species within the system. Support for this theory has been seen in CIX. The fire-climax *Themeda triandra* grassland (Killick, 1963) has been seen to become moribund when not burnt and reduce the survival of fire-dependent and/or light-requiring grasses and forbs, a trend observed elsewhere (Rutherford, 1978; Westfall *et al.* 1983; Knapp & Seastedt, 1986; Everson *et al.* 1988; Uys *et al.* 2004). *Pteridium aquilinum* later outcompeted the grass sward (Granger, 1976) as the former was shade-tolerant and vertically dominant over the latter. Later woody species (e.g. *Erica evansii, Leucosidea sericea, Searsia dentata, Diospyros austro-africana*) displaced *P. aquilinum* or invaded grassland directly (Granger, 1976; Adcock, 1990). These transformed communities were then colonised by forest precursor (e.g. *Rhamnus prinoides, Myrsine africana*) and forest species (e.g. *Olinia emarginata*, *Podocarpus latifolius*) once closed woody communities had established (Granger, 1976; Adcock, 1990).

2.6 *Erica evansii*

Erica evansii (Oliver, 1987; formerly *Philippia evansii* (Brown, 1905)) is an important species of the KwaZulu-Natal Subalpine Belt (Killick, 1953). *Erica evansii* has a shallow (10cm below the soil surface) adventitious root system with the majority of its roots radiating to a diameter from the plant stem greater than its branches (Everson, 1979). *Erica evansii* is a wind-dispersed reseeder (Everson, 1979), that is, a species in which adults are killed by fire but persist through extensive post-fire recruitment of seedlings from a seed bank or seeds stored in the canopy of the adult (Bond and van Wilgen, 1996; Kruger *et al.* 1997; Lloret *et al.* 2005). Granger (1976) and Adcock (1990) noted *Erica evansii* to be a key agent of woody colonisation in the absence of fire in moist grasslands.

2.7 *Leucosidea sericea*

Leucosidea sericea (Ecklon & Zeyher, 1836) is the sole species in the *Leucosidea* genus. This species is a respouter, that is, a species that uses underground carbohydrate reserves to initiate coppice growth following topkill by fire (Bell, 2001; Bellingham and Sparrow; 2000 Ojeda *et al.* 2005). This wind-dispersed evergreen tree is indigenous to Afromontane regions of southern Africa and its distribution ranges from the Eastern Cape in South Africa to Zimbabwe (Van Wyk & Van Wyk, 1997; Aremu *et al.* 2010; Boon, 2010) and is noted as an “important taxon” in the Afrotemperate Forest Biome in South Africa (Mucina & Rutherford, 2006). *Leucosidea sericea* can be found in grasslands, forests and along river banks or rocky outcrops. *Leucosidea sericea* is seen to colonise up slopes from the stream edges in a clumped pattern in the absence of fire (Granger, 1976), facilitating forest precursor and forest species (Adcock, 1990).

2.8 Moist grasslands and forests: alternate systems

The role of fire in grasslands is thus not only causative, but also regulatory (Mentis & Huntley, 1982; Manry & Knight, 1986; O’Connor & Bredenkamp, 1997; Van Wilgen *et al.* 2003). A specific fire-return period therefore determines the ratio and pattern of grasses and woody vegetation (Manry & Knight, 1986; Titshall *et al.* 2000; Van Wilgen *et al.* 2003; Bond, 2008). High fire frequencies facilitate near pure grasslands; whilst savanna-, woodland or forest-type vegetation types are facilitated by a low fire frequency (Manry & Knight, 1986). Grassland and forest vegetation may therefore be seen as alternate ecosystem states for a specific set of environmental conditions, and are controlled primarily by fire (Bond & Parr, 2010). In contrast to the self-regulating characteristics of moist grasslands, forests are themselves intolerant of fire and suppress growth of flammable herbaceous plants (Granger, 1984). These alternate ecosystem states thus display positive feedback systems that promote favourable conditions for themselves at the expense of the other (Granger, 1984; Titshall *et al.* 2000; Bond & Parr, 2010).

CHAPTER 3 :

Changes in woody vegetation between 1973, 1986 and 2010 as a result of partial fire exclusion in Catchment IX, Cathedral Peak, KwaZulu-Natal Drakensberg, South Africa

Abstract

Woody vegetation is expected to colonise moist grasslands in the absence of fire. Long term fire exclusion has been attempted in Catchment IX (CIX) at Cathedral Peak in order to study resultant vegetation changes. Baseline vegetation of CIX was sampled in 1952, with follow-up surveys in 1973, 1986 and 2010. These took place at key times in terms of changes in fire history within the catchment. Complete fire exclusion was achieved between 1973 and 1986, but eight accidental fires burnt part of CIX thereafter. Partial exclusion of fire over 58 years resulted in vegetation transforming from grassland to a grassland-fynbos-scrub forest mosaic. Fire excluding vegetation had developed on relatively fire-protected areas close to streams. Fire prone areas were dominated by *Erica evansii*, a reseeder, and *Leucosidea sericea*, a resprouter. Consequently, occasional fires did not revert vegetation to grassland. Catchment IX is therefore predicted to maintain a mosaic of distinct grassland, woodland, ecotonal and scrub forest communities in the face of infrequent accidental fires.

3.1 Introduction

Succession is driven by disequilibrium in a system, caused by the difference between the potential community and the actual community present in the system. This may be a result of a single or multiple drivers (Zerbe, 1998; Bond & Keeley, 2005). A change in a driver will increase or decrease this disequilibrium and communities will adjust accordingly.

Grasslands have been seen as vegetation types in disequilibrium with their environments (Nänni, 1969; Manry & Knight, 1986; Bond & Keeley, 2005; Bond, 2008). They are a global anomaly in terms of Whittaker's (1975) predictions of climate and biome distribution in that they are found in regions that have sufficient mean annual precipitation and temperature for trees to be dominant or at least present (Schultze & McGee, 1978; Bond & Keeley, 2005; Bond, 2008). Woody vegetation in these regions is, however, confined to rocky outcrops or streams (Philips, 1930; Van Zinderen Bakker, 1973; Granger, 1984; Bond & Parr, 2010).

The general consensus is that recurrent fire, a "top-down" selective pressure, plays a critical role (Bews, 1916; Granger, 1976; Adcock, 1990; Bond & Keeley, 2005; Dalle *et al.* 2006; Bond, 2008; Bond & Parr, 2010) in shaping grassland communities that are further constrained by climate, geology, soil depth and topography, "bottom-up" selective pressures (Granger & Schultze, 1977; Odum, 1983; Titshall *et al.* 2000). Fire's role in grasslands is both causative and regulatory (Mentis & Huntley, 1982; Manry & Knight, 1986; O'Connor & Bredenkamp, 1997; van Wilgen *et al.* 2003). It is causative in that a relatively high fire frequency eliminates woody vegetation and favours grasses (Granger, 1976; Adcock, 1990). It is regulatory in that a specific fire regime determines the ratio and pattern of grasses and woody vegetation (Manry & Knight, 1986; Titshall *et al.* 2000; Van Wilgen *et al.* 2003; Bond, 2008). Near pure grasslands are therefore expected in areas with a high fire frequency, whilst savanna, woodland or forest-type vegetation is expected in areas with a low fire frequency (Manry & Knight, 1986; Bond & Parr, 2010).

Grassland and forest vegetation may therefore be seen as alternate ecosystem states that depend primarily on fire frequency (Manry & Knight, 1986; Bond & Parr, 2010). Grasslands consist of shade intolerant species whose dead plant matter can be consumed by fire, a self-reinforcing mechanism for its maintenance (Bayer, 1955; Uys *et al.* 2004; Bond & Parr, 2010). Forests, by contrast, suppress growth of flammable herbaceous plants and are not themselves easily ignited (Granger, 1984). Each vegetation type thus displays a positive feedback system that promotes favourable conditions for itself, at the expense of the other (Granger, 1984; Titshall *et al.* 2000; Bond & Parr, 2010).

The moist grasslands of the KwaZulu-Natal Drakensberg exhibit the highest lightning strike frequency in South Africa, with up to 16 strikes per km^2 per annum (Edwards, 1984; Manry & Knight, 1986). High annual production resulting from a predictable wet summer (Everson, 1985) in combination with a dry winter in which frost kills the aboveground grass growth, has ostensibly resulted in a high frequency of burning (Granger, 1976; Bond, 2008). The resultant dry grass beds act as a fast burning fuel source which in turn stimulates new grass growth and thus continues the cycle (Knapp & Seastedt, 1986).

These grasslands that are dominated by *Themeda triandra* are therefore considered to be fire subclimax grasslands (Killick, 1963). It is no longer accepted that forest areas in valleys and on rocky outcrops are relics of a once dominant vegetation type which existed prior to human interference as Acocks (1935) postulated. It is predicted that if fire is excluded from these high rainfall grasslands, vegetation would shift toward a more woody nature, whose character (forest, closed woodland, savanna) would depend on "bottom-up" constraints (Odum, 1983; O' Connor & Bredenkamp, 1997; Bond & Keeley, 2005; Bond, 2008).

The ecology of fire is thus central to understanding past, present and future changes in moist grassland vegetation (Hillard & Burtt, 1987; Bond & Keeley, 2005). The extended exclusion of fire in this fire-dependent system is therefore seen as a greater disturbance than fire itself. By excluding fire from such a grassland one is able to empirically test the effects of fire on woody vegetation and to observe the resultant changes in vegetation.

This approach was taken within Catchment IX (CIX) at the former Cathedral Peak Forest Research Station in the KwaZulu-Natal Drakensberg (Killick, 1963) (figure 3.1). Catchment IX was setup up as a fire exclusion experiment in 1944 with formal fire breaks burnt in 1952 (Granger, 1976). A baseline vegetation survey was performed in 1952 (Killick (1963). At that time the catchment was grassland with woody elements restricted to the immediate vicinity of the streams. Resurveys were carried out in 1973 (Granger 1976), 1986 (Adcock 1990), and 2010 (this study). Predictions of these workers about expected vegetation changes following fire exclusion were not in complete accord.

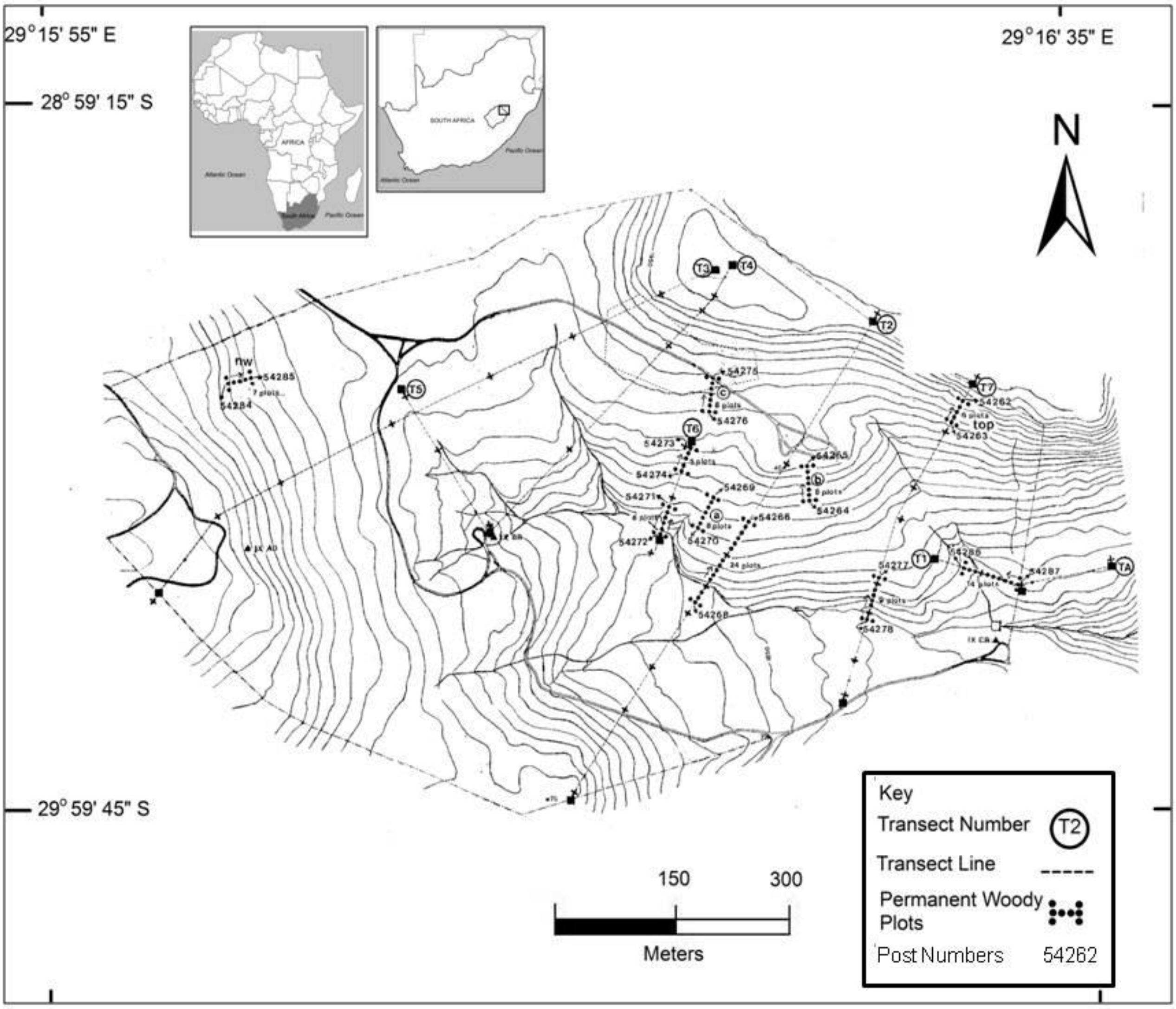

Figure 3.1: Map of CIX and the position of the permanent transects laid out by Granger in 1973 and additional woody plots laid out by Adcock in 1986 (Adcock, 1990).

Killick (1963) postulated that a fynbos vegetation type would emerge as climax. West (1951) and Acocks (1953) suggested that *Podocarpus latifolius* forest would be the climax vegetation. Granger (1976) refined these to suggest that fynbos species, are seral to forest species at a lower altitude but are climax species at higher altitude. By the time of Granger's (1976) survey in 1973, the catchment was apparently being transformed to a *Leucosidea sericea* dominated shrubland; whilst by 1986 incipient forest patches had formed (Adcock, 1990). A clearer picture could only emerge with time. Accordingly, the catchment was resurveyed in 2010, 58 years after the catchment was established as an experiment.

In spite of efforts to exclude fires, 13 fires have swept through CIX since 1952, the latest of which occurred in 2007 (figure 3.2). Five of these occurred between 1952 and 1973 (Granger, 1976), no fires occurred between 1973 and 1986 (Adcock, 1990), and eight fires occurred between 1986 and 2007. The surveys of the catchment were therefore concomitant with key changes in the fire regime.

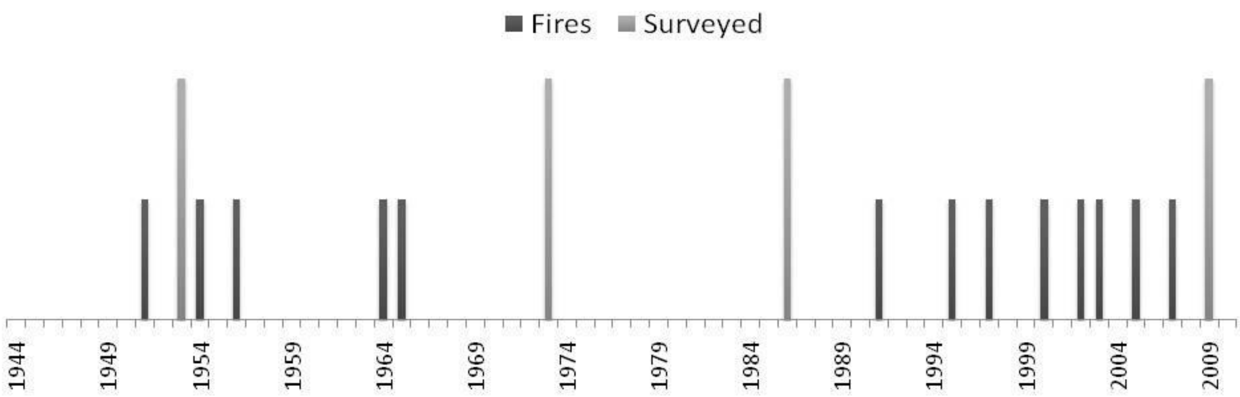

Figure 3.2: The fire and survey history of Catchment IX since 1944 (derived from Killick, 1963; Granger, 1976; Adcock, 1990; Rowe-Rowe, 1995; EKZNW records; pers obs T O' Connor). The pattern of any fire, other than the 2007 fire, is not known.

These fires apparently did not burn the entire catchment such that fire-protected communities had established by 2007 (Chapter 4). *Leucosidea sericea*, a resprouter, and *Erica evansii*, a reseeder, were the most successful woody species colonising CIX by 1973 (Granger, 1976) and 1986 (Adcock, 1990). These two species of contrasting life history strategies are therefore the main focus of this chapter.

The aim of the study was to examine the effect of attempted fire exclusion on vegetation change of this catchment, as further influenced by complete versus partial fire exclusion. Specifically, the study focuses on the pattern, rate, and reversibility of grassland transformation to woodland during periods of contrasting fire regimes based on (a) changes in woody communities and (b) changes in the population distribution, density and population structure of *L. sericea* and *E. evansii*.

3.2 Material and Methods

3.2.1 Study site

Catchment IX is situated in the Little Berg in the KwaZulu-Natal Drakensberg (29°00'S; 29°15'E) (figure 3.1). It is a 77 ha first-order catchment located between an altitude of 1810m and 1950m with an overall south east facing aspect (Granger, 1976). The geology of the area comprises Stormberg basaltic lavas of the Karoo system underlain by Karoo sandstones and shales (Van Zinderen Bakker, 1973). The main stream exiting the catchment flows from west to east, with all of its tributaries within the catchment's boundary (Granger, 1976).

Daily maxima temperatures range from between 31°C to -3°C, with January being the hottest month and June the coldest (Granger, 1976). Radiation is highest in the summer months even though the duration of radiation is highest in winter due to summer cloud cover (Granger & Schultze, 1977). CIX has a mean annual precipitation of about 1300mm and occurs in a summer rainfall area with the highest mean monthly rainfall between December and March, and the lowest between May and August (Granger, 1976). The rainfall is accompanied by occasional hail and the region experiences the highest annual frequency of lightning strikes in the country (Manry & Knight, 1986).

Catchment IX is positioned at the interface of the Northern Drakensberg Highland Grassland and uKhahlamba Basalt Grassland vegetation types, found in the afromontane ecoregion in South Africa (Mucina and Rutherford, 2006).

3.2.2 Approach

Fieldwork replicated that of Granger (1976) and Adcock (1990) (figure 3.1; table 3.1). Granger placed seven permanently located belt transects consisting of 5m x 5m contiguous plots throughout CIX, ensuring all the main vegetation types of the catchment at that time were represented along selected transects (1, 2, 6 and 7), he demarcated 64 permanent woody plots in order to assess colonisation of CIX by woody vegetation (figure 3.1). A number of these were not found by Adcock in 1986 (Adcock, 1990) whilst all were found and re-sampled in 2010 (table 3.1). Adcock placed an additional four transects of the same format as those of Granger (1976) in 1986 (figure 3.1). Only two of these were relocated in 2010 owing to dense vegetation and small (30cm) markers. A total of 96 permanent woody plots had therefore been marked within the transects during the previous two surveys, 80 of which were re-sampled in 2010 (table 3.1).

Transects were re-sampled using the transect line as the centre line (Granger, 1976; Adcock, 1990). Each live or dead woody individual within a plot was identified and measured for its height (to 0.1m), canopy area (cm^2) and stem diameter (nearest cm). Nomenclature followed Boon (2010).

Table 3.1: Permanent woody plots setup in 1973 or 1986 and relocated in 2010

Permanent woody transect	Number of plots	Number of plots relocated and re-sampled in 2010
Granger – 1973: Transect 1	14	14
Granger – 1973: Transect 2	24	24
Granger– 1973: Transect 6	11	11
Granger– 1973: Transect 7	15	15
Adcock – 1986: Transect A	8	0*
Adcock – 1986: Transect B	8	8
Adcock – 1986: Transect C	8	8
Adcock – 1986: Transect NW	8	0*
Total:	96	80

*unable to relocate

3.2.3 Statistical analyses

It was assumed that changes in woody vegetation structure and species abundances had occurred primarily in response to partial exclusion of fire. In addition, it assumed that all dead individuals sampled had died as a result of the 2007 fire, and that coppice growth was in response to this fire. Individuals of both *Erica evansii* and *Leucosidea sericea* smaller than 0.5m in height were therefore considered as either seedlings or regeneration from root stock (Granger, 1976; Adcock, 1990). Skeletons of burnt individuals were well preserved and coppice off dead stems was easily distinguishable. Small individuals without a skeleton were regarded as either seedlings or coppice growth off rootstock as these could not be distinguished because growth rates of either are not known.

Plots were categorised for soil moisture availability as dry or moist based on the proxies of distance from a stream and slope. These indirect measures further provide an indication of the exposure of a plot to fire. Categories for these variables were determined by examining their influence on the 2007 fire pattern. The following four categories were roughly distinguished: (i) 0-49m from the stream; (ii) ≥50m from the stream; (iii) slopes between 0-30°; and (iv) slopes >30°. These categories reflected that areas with potentially greater moisture occurred approximately within 50m of the stream and on slopes of less than 30°, and were thus considered to be less exposed to fire. The other categories were considered to be more likely to burn during accidental fires.

The assumption that areas greater than 50m from a stream contained no *Erica evansii* or *Leucosidea sericea* individuals in 1952 was based on Killick's (1963) description that CIX in 1952 was typical *Themeda triandra* grassland with woody individuals (bar a few *Protea* individuals on the northern ridge) confined to stream edges. Any woody individual recorded in this category by 1973 was thus as a result of woody colonisation.

Changes in the distribution and abundance of *Leucosidea sericea*, *Erica evansii* and other woody species over the period of record were assessed. Changes in distribution were assessed based on the proportion of plots occupied in each sample year and analysed using 2 x 2 contingency tables. Paired *t*-tests were used to analyse changes in mean population density and the differences in the number of seedlings and dead individuals of *E. evansii* between 1986 and 2010, using Adcocks' (1990) data. Changes in mean population height of individual species were analysed using two-tailed *t*-tests. Analyses were conducted using STATISTICA version 9.1 (StatSoft, 2010).

3.3 Results

3.3.1 Changes in the overall woody community

An overall increase in the woody vegetation of Catchment IX was observed over 58 years of partial fire exclusion. Species differed conspicuously in their success. Increases in population abundance were striking for the forest and forest-precursor species, in particular *Rhamnus prinoides* and *Searsia dentata*, found in the fire-protected areas beside the stream and at lower altitudes of CIX (figure 3.3).

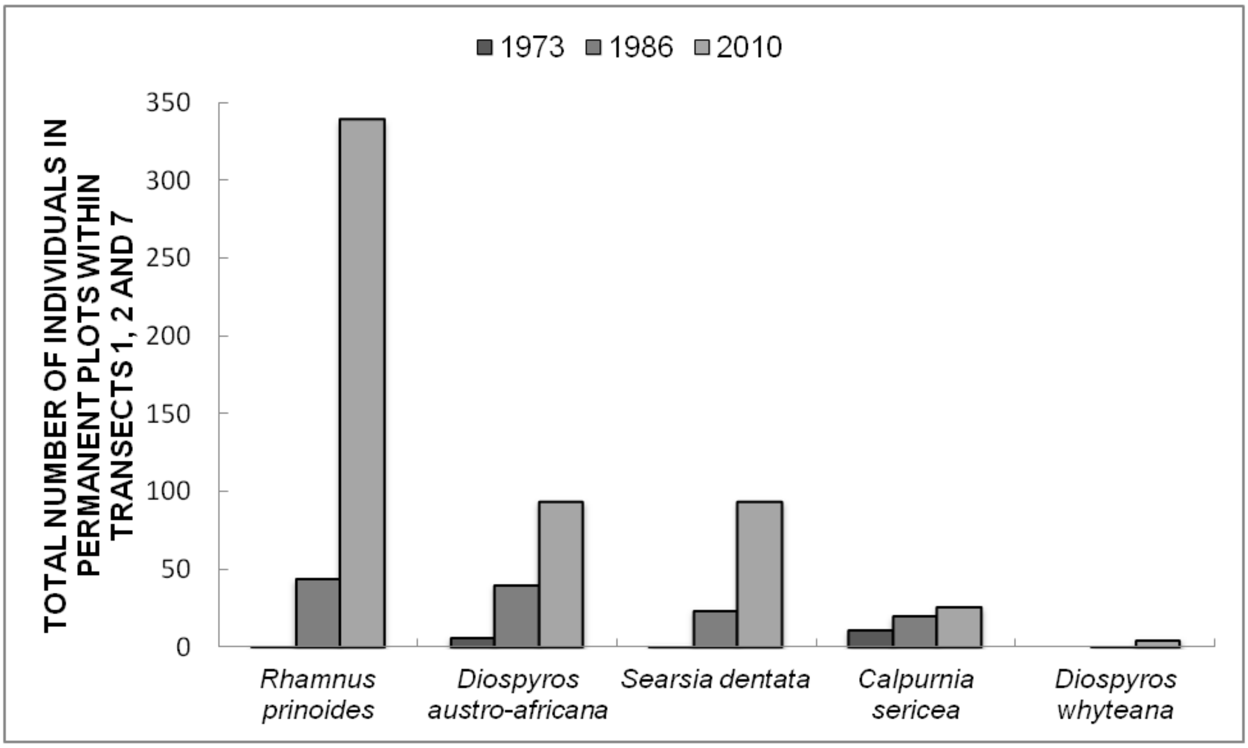

Figure 3.3: The total number of *Rhamnus prinoides*, *Diospyros austro-africana*, *Searsia dentata*, *Calpurnia sericea* and *Diospyros whyteana* individuals found in the permanent plots within transects 1, 2 and 7 following Adcock's (1990) calculations.

3.3.2 Changes in the distribution, density and mean height of the Leucosidea sericea *population during periods of contrasting fire regimes*

The spatial extent, density and mean height of *Leucosidea sericea* in CIX remained constant between 1973 and 2010 (tables 3.2, 3.5) (Statistical results are summarised in the appendices of this chapter). No overall change in density was observed for *L. sericea* as a result of an initial (1973-1986) increase negated by a subsequent decrease between 1986 and 2010 (table 3.3). Mean height displayed the opposite trend between these time frames that also resulted in no overall change between 1973 and 2010 (table 3.4).

Within relatively fire-protected areas, *L. sericea* initially increased in its spatial extent between 1952 and 1973, but then stabilised (varying by less than 14% between 1973 and 2010) (table 3.2 and 3.5). Its density in fire-protected areas increased over 34 years, following catchment establishment, but decreased after 1986. This resulted in an overall decrease in density observed between 1973 and 2010 (tables 3.3, 3.5). Mean plant height displayed a contrasting response to that of density in these areas: decreasing between 1973 and 1986 and subsequently increasing between 1986 and 2010, resulting in an overall increase observed between 1973 and 2010 (tables 3.4, 3.5).

Leucosidea sericea's response in fire-prone areas contrasted with that of fire-protected areas. Its colonisation was most pronounced during the period of total fire exclusion (1973 to 1986) when spatial extent doubled (table 3.2) and density increased 24-fold (table 3.3). This resulted in an overall increase in both spatial extent and density between 1973 and 2010, despite density decreasing as fire frequency increased (1986 to 2010). Mean plant height did not change between 1973 and 2010 (table 3.4).

Leucosidea sericea's spatial distribution increased on steep slopes (>30°) as a result of a marked increase in area occupied during the 13 years of fire exclusion (1973 to 1986) (tables 3.2, 3.5). No overall changes in *L. sericea* densities were observed on either gentle (<30°) or steep slopes (>30°) (tables 3.3, 3.5) as a result of an initial increase during the period of fire exclusion, and a subsequent decrease as fire frequency increased. Mean height displayed a contrasting pattern to that of density: decreasing between 1973 and 1986 and increasing as fire frequency increased, resulting in no overall change on either slope type (tables 3.4, 3.5).

Table 3.2: The proportion of 25m^2 plots occupied by *Leucosidea sericea* and *Erica evansii*, within fire-protected, fire-prone and slope categories, over time

Proportion of plots occupied (%)	*Leucosidea sericea*			*Erica evansii*			
	1973	1986	2010	1973	1986	2007	2010
Relatively fire-protected:	72.7	86.4	79.5	81.8	75.0	50.0	11.4
Distance from stream 0-49m	n=44	n=44	n=44	n=44	n=44	n=44	n=44
Fire-prone:	40.0	81.0	76.2	86.7	100	71.4	23.8
Distance from stream 50m+	n=15	n=21	n=21	n=15	n=21	n=21	n=21
	75.7	86.5	78.4	78.4	81.1	67.6	21.6
Slope 0-29°	n=37	n=37	n=37	n=37	n=37	n=37	n=37
	45.5	82.1	78.6	90.9	85.7	42.9	7.1
Slope 30°+	n=22	n=28	n=28	n=22	n=28	n=28	n=28
	64.4	84.6	78.5	83.1	83.1	56.9	15.4
Total	n=59	n=65	n=65	n=59	n=65	n=65	n=65

Table 3.3: The mean density per hectare of *Leucosidea sericea* and *Erica evansii*, within fire-protected, fire-prone and slope categories, over time

	Mean density (ha^{-1}) ± SE						
	Leucosidea sericea			*Erica evansii*			
	1973	1986	2010	1973	1986	2007	2010
Relatively fire-protected:	1936 ± 281	5473 ± 1039	1155 ± 193	2736 ± 509	2191 ± 367	5973 ± 1315	91 ± 45
Distance from stream 0-49m	n=44	n=44	n=44	n=44	n=44	n=44	n=44
Fire-prone:	240 ± 151	5867 ± 1953	1752 ± 398	5680 ± 1695	5581 ± 778	10686 ± 1945	362 ± 177
Distance from stream 50m+	n=15	n=21	n=21	n=15	n=21	n=21	n=21
	1730 ± 299	5470 ± 1151	1232 ± 219	2238 ± 452	3319 ± 595	8065 ± 1523	259 ± 105
Slope 0-29°	n=37	n=37	n=37	n=37	n=37	n=37	n=37
	1127 ± 361	5771 ± 1576	1500 ± 318	5582 ± 1286	3243 ± 515	6743 ± 1651	71 ± 58
Slope 30°+	n=22	n=28	n=28	n=22	n=28	n=28	n=28
	1505 ± 232	5600 ± 936	1348 ± 185	3485 ± 590	3286 ± 402	7495 ± 1116	178 ± 66
Total	n=59	n=65	n=65	n=59	n=65	n=65	n=65

Table 3.4: The mean height of *Leucosidea sericea* and *Erica evansii*, within fire-protected, fire-prone and slope categories, over time

	Mean height (m) ± SE						
	Leucosidea sericea			*Erica evansii*			
	1973	1986	2010	1973	1986	2007	2010
Relatively fire-protected:	2.35 ± 0.26	1.19 ± 0.18	3.38 ± 0.22	1.53 ± 0.08	1.48 ± 0.15	1.70 ± 0.11	2.10 ± 0.41
Distance from stream 0-49m	n=26	n=20	n=35	n=35	n=17	n=22	n=5
Fire-prone:	2.47 ± 0.26	0.81 ± 0.47	1.78 ± 0.26	1.20 ± 0.04	0.69 ± 0.04	1.39 ± 0.07	1.72 ± 0.36
Distance from stream 50m+	n=9	n=6	n=16	n=12	n=7	n=15	n=5
	2.50 ± 0.26	1.12 ± 0.20	3.19 ± 0.25	1.42 ± 0.09	1.43 ± 0.15	1.65 ± 0.10	2.21 ± 0.20
Slope 0-29°	n=22	n=17	n=29	n=29	n=15	n=25	n=8
	2.08 ± 0.24	1.06 ± 0.34	2.46 ± 0.32	1.47 ± 0.09	0.95 ± 0.22	1.40 ± 0.08	0.69 ± 0.39
Slope 30°+	n=10	n=9	n=22	n=18	n=9	n=12	n=2
	2.37 ± 0.20	1.10 ± 0.17	2.88 ± 0.20	1.44 ± 0.06	1.25 ± 0.13	1.57 ± 0.07	1.91 ± 0.27
Total	n=32	n=26	n=51	n=47	n=24	n=37	n=10

Table 3.5: A Summary of the changes in the *Leucosidea sericea* population, within fire-protected, fire-prone and slope categories, over time (→ = *P*>0.05; ↑ or ↓= *P*<0.05; ↑↑ or ↓↓= *P*<0.01; ↑↑↑ or ↓↓↓= *P*<0.001)

Leucosidea sericea	Distribution		
	1973-1986	1986-2010	1973-2010
Relatively fire-protected: Distance from stream 0-49m	→	→	→
Fire-prone: Distance from stream 50m+	↑	→	↑
Slope 0-29°	→	→	→
Slope 30°+	↑↑	→	↑
Total	↑↑	→	→
		Mean density	
Relatively fire-protected: Distance from stream 0-49m	↑↑	↓↓↓	↓↓
Fire-prone: Distance from stream 50m+	↑↑	↓	↑↑
Slope 0-29°	↑↑	↓↓↓	→
Slope 30°+	↑↑	↓↓	→
Total	↑↑↑	↓↓↓	→
		Mean plant height	
Relatively fire-protected: Distance from stream 0-49m	↓↓↓	↑↑↑	↑↑
Fire-prone: Distance from stream 50m+	↓	→	→
Slope 0-29°	↓↓↓	↑↑↑	→*
Slope 30°+	↓	↑↑	→
Total	↓↓↓	↑↑↑	→

* *P*=0.06

3.3.3 Changes in the distribution, density and mean plant height of the **Erica evansii** *population during periods of contrasting fire regimes*

Erica evansii differed from *L. sericea* in terms of changes in spatial distribution, density and mean height over time (tables 3.2, 3.3 and 3.4). Spatial distribution and density decreased (by 82% and 95%, respectively) between 1973 and 2010, mainly the result of the 2007 fire (tables 3.2, 3.3, 3.6). Initially both spatial distribution and density increased in the 21 years after catchment establishment. Thereafter spatial distribution decreased; whilst density increased as fire frequency increased, but decreased 42-fold after the 2007 fire. Mean height remained constant between 1973 and 2010.

Within relatively fire-protected areas *Erica evansii*'s spatial distribution and density decreased over time (1973 to 2010) (tables 3.2, 3.3, 3.6). Mean height remained stable over this time frame (tables 3.4, 3.6).

Erica evansii had spread into 87% of the fire-prone grassland areas by 1973 and had occupied all sample plots by 1986. Thereafter it decreased in its spatial distribution by three quarters as fire frequency increased (table 3.2). There was an overall decrease in density of *E. evansii* between 1973 and 2010 (table 3.4). Density increased between 1952 and 1973, was stable between 1973 and 1986 (when fire was completely excluded), continued to increase between 1986 and 2007, but decreased dramatically following the 2007 fire. Mean height did not change between 1973 and 2010 in these fire-prone areas: the result of an initial decrease during the period of fire exclusion (1973 to 1986) and a subsequent increase as fire frequency increased (1986 to 2010) (table 3.6).

Erica evansii's spatial distribution and density decreased on both gentle (<30°) and steep (>30°) slopes between 1973 and 2010 (tables 3.2, 3.3 3.6). In contrast, mean height increased on gentle slopes, but did not change on steeper slopes over this time frame (table 3.4).

The period of occasional fires (1986 to 2010) contrasted with the period of complete fire protection (1973 to 1986) in showing a 4-fold higher density of dead *E. evansii* individuals in 2010 as a result of the 2007 fire, but only 60% of the seedling density (figure 3.4).

Table 3.6: A Summary of the significant changes in the *Erica evansii* population, within fire-protected, fire-prone and slope categories, over time (→ = *P*>0.05; ↑ or ↓= *P*<0.05; ↑↑ or ↓↓= *P*<0.01; ↑↑↑ or ↓↓↓= *P*<0.001)

Erica evansii	Distribution		
	1973-1986	1973-2010	1986-2007
Relatively fire-protected: Distance from stream 0-49m	→	↓↓↓	↓
Fire-prone: Distance from stream 50m+	→	↓↓↓	↓↓
Slope 0-29°	→	↓↓↓	→
Slope 30°+	→	↓↓↓	↓↓↓
Total	→	↓↓↓	↓↓↓
	Mean density		
Relatively fire-protected: Distance from stream 0-49m	→	↓↓↓	↑↑
Fire-prone: Distance from stream 50m+	→	↓↓	↑
Slope 0-29°	→*	↓↓↓	↑↑↑
Slope 30°+	→	↓↓↓	↑
Total	→	↓↓↓	↑↑↑
	Mean plant height		
Relatively fire-protected: Distance from stream 0-49m	→	→	→
Fire-prone: Distance from stream 50m+	↓↓↓	→	↑↑↑
Slope 0-29°	→	↑↑	→
Slope 30°+	→**	→	→
Total	→	→	↑

* *P*=0.07; ***P*=0.05

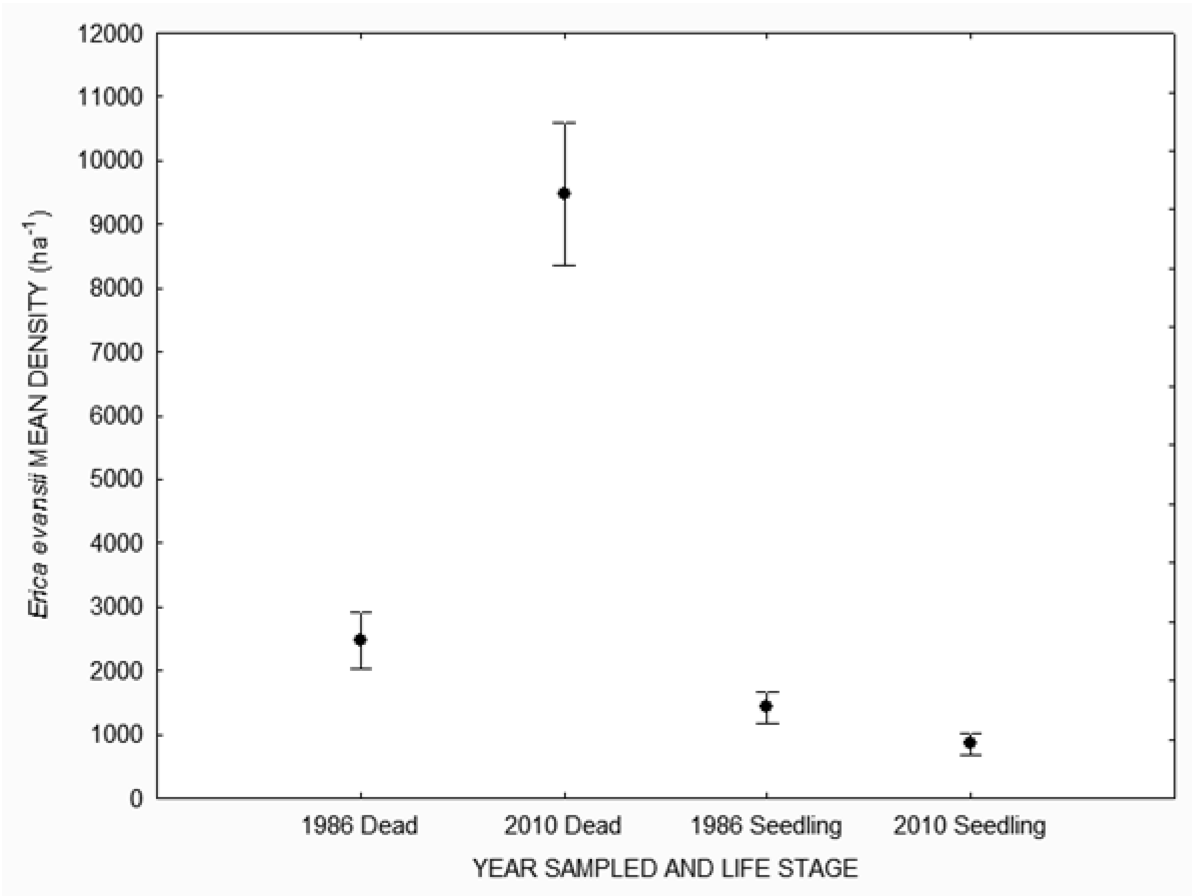

Figure 3.4: The mean density of dead individuals and seedlings of *Erica evansii* in 1986 and 2010 in the permanent woody plots. Bars denote plus/minus one standard deviation.

3.4 Discussion

3.4.1 Vegetation changes in fire-protected areas over time

Two main fire regimes developed within Catchment IX (CIX), mainly as a result of the influence of environmental gradients (Chapter 5) on the spread of accidental fires. By 2010, 10% of the catchment had not been burnt by accidental fires during the preceding 58 years because fire could not penetrate these areas (Chapter 4). A distinct vegetation woody community developed on these areas that apparently contributed to excluding fire. The remainder of the catchment had experienced an accidental fire regime (figure 3.2).

Fire-protected areas were closest to the stream (Chapter 5). These areas presumably have a high soil moisture content which is considered to have contributed to the exclusion of fire over time (Granger, 1976). Fire exclusion within this environment promoted taller woody vegetation than the surrounding communities (Chapter 4). Forest precursor and forest species established (figure 3.3) and had largely replaced the previous dominant woody species within the catchment, namely *Leucosidea sericea* and *Erica evansii.* This vegetation change had apparently altered a fire-prone vegetation type to a fire-excluding vegetation type. Forest precursor and forest species continued to show increases in distribution, abundance and plant size over time (Killick, 1963; Granger, 1973; Adcock, 1990; Chapter 4) (figure 3.3). Thus a portion of these moist grasslands were transformed to a closed woodland or precursor forest in the absence of fire. These transformed areas contained species characteristic of the Northern Afrotemperate Forest vegetation type (Mucina & Rutherford, 2006). The persistence of this forest precursor vegetation in the face of repeated accidental fires indicated that a positive feedback system had developed, wherein the newly developed vegetation type contributed toward excluding fire.

3.4.2 Vegetation changes in fire-prone areas over time

Species in fire-prone systems require life history strategies that ensure their persistence post-fire (Granger, 1976; Adcock, 1990; Bond & Van Wilgen, 1996; Bond & Midgley, 2001). The response to fire was starkly different for individual plants and for populations of *L. sericea* and *E. evansii* (Granger, 1976; Adcock, 1990; Chapter 4). The former is a resprouter that maintained much of its pre-fire population distribution (table 3.2), density (table 3.3) and structure (table 3.4); whilst the latter is a reseeder that showed near total mortality, but subsequent population recovery via seedling regeneration post-fire (Chapter 4).

Coppicing allowed *L. sericea* to maintain post-fire distribution and densities, providing it with an advantage over other woody species that relied on seedling recruitment to regain their pre-fire population status (Chapter 4). Population dynamics of *E. evansii* were in part a consequence of its ability to produce a large number of seeds, hence seedlings, that colonised post-fire environments following adult mortality (Adcock, 1990; Chapter 4) (table 3.3). A decrease in density occurred in mature stands of *E. evansii* as a result of senescence of older individuals (Adcock, 1990). Consequently, population changes in terms of spatial distribution within the catchment, density, and plant size of *L. sericea* were less dynamic than those of *E. evansii* population over time, despite the success of both species during the period of fire exclusion (tables 3.2, 3.3, 3.4). Once established, however, continued presence of *L. sericea* within the catchment, regardless of fire frequency, appears to be more secure than that of *E. evansii* (tables 3.5, 3.6) (Chapter 4).

Erica evansii's spatial extent and density was strongly influenced by fire-return period (tables 3.2, 3.3, 3.4, 3.6). Manry & Knight, (1986) suggest that a fire-return period of three to four years is sufficient for maintaining pure grassland. This begs the question: what fire-return period would allow *E. evansii* to establish and increase? The fire history of CIX suggests that a fire return period of approximately eight years is sufficient for the ongoing representation of *E. evansii* within moist grasslands of the KwaZulu-Natal Drakensberg.

Within 21 years (up to 1973), after four fires, *E. evansii* had extensively colonised the south-facing slopes of CIX, an area previously dominated by *Themeda triandra* or *Pteridium aquilinum*, to form tall (1.4m) dense stands (up to 240 individuals per hectare) where no individual had previously been recorded by Killick (1963) (Granger, 1976; Adcock, 1990). Almost all of this colonisation can be attributed to the eight year period of complete fire exclusion between 1966 and 1973 inclusive, as the 1964 and 1965 fires were judged to have burnt 100% and 70% of the catchment respectively (unpublished records). Its abundance increased further during the period of complete fire exclusion between 1973 and 1986 (Adcock 1990), and it remained the dominant woody species in CIX until prior to the 2007 fire (Chapter 4). The 1991 fire was also judged to have burnt almost the entire catchment (Rowe-Rowe, 1995), other than the 10% of fire-protected area described above. This fire history suggests that the *E. evansii* population re-established post 1991. The spatial extent of any of the six fires which occurred during the 11 year period between 1995 and 2005 inclusive is not known. The size of individual plants at the time of the 2007 fire in comparison with plant size recorded in 1986 after 21 years of complete fire exclusion (Adcock 1990) would, however, suggest that the area affected by fire in 2007 had not been burnt by the 2005 fire, and probably not by the 2002 or 2003 fires. It is therefore inferred that a fire return period of approximately eight years is sufficient for the ongoing representation of *E. evansii* within moist grasslands of the KwaZulu-Natal Drakensberg.

3.4.3 Successional pattern of change

A broad successional trend in response to partial fire exclusion has been observed in CIX. The original *Themeda triandra* grassland (Killick, 1963) became moribund when not burnt (e.g. Rutherford, 1978; Uys *et al.* 2004, Bond, 2008). This in turn reduced survival of light-requiring grasses (Westfall *et al.* 1983; Everson & Everson, 1987) and of fire-dependent forb abundances as a result presumably of self-shading. These effects were exacerbated by the expansion and competition from the shade-tolerant vertically dominant *Pteridium aquilinum* (Granger, 1976; Uys *et al*. 2004). Once a sward of *Themeda triandra* has been absent for some time it will not generally re-establish (Tainton *et al.* 1999).

Later woody species, principally *Erica evansii* and *Leucosidea sericea*, began to colonise (Granger, 1976; Adcock, 1990). Once established, forest pioneer and then forest species began to occupy the area (Adcock, 1990; Chapter 4) (figure 3.3). Future vegetation change within the catchment would appear to be closely related to the success of *L. sericea* and its facilitation of the establishment and growth of forest-related species (Adcock, 1990; Chapter 4).

Podocarpus latifolius, with a large number of associated species, is the dominant tree of established forest patches in the Drakensberg that are recorded to occur only on Cave Sandstone geology (West, 1951; Acocks, 1953; Van Zinderen Bakker, 1973). This experiment has shown that this forest type can extend onto basalt-derived soils. These forest-related species are intolerant of fire (Granger, 1984; Manry & Knight, 1986; Bond & Parr, 2010). Their expansion has apparently promoted a positive feedback that has caused a shift in ecosystem state from grassland to closed woody scrub or forest, with concomitant alteration of system structure, composition and functioning. Grassland and forest can thus be viewed as alternate ecosystem states for a specific set of environmental conditions (Bond, 2008; Bond & Parr, 2010).

Woody vegetation should continue to increase in Catchment IX if fire remains absent or infrequent. Catchment IX is not, however, predicted to transform into a homogeneous forest vegetation type in the absence of fire because environmental variation within the catchment influences both the spread of accidental fire and the dynamics and growth of the main woody species (Chapter 5).

3.5 Conclusion

As a result of 58 years of partial fire exclusion the vegetation of Catchment IX has undergone a transformation from a combination of Northern Drakensberg Highland Grassland and uKhahlamaba Basalt Grassland to Drakensberg-Amathole Afromontane Fynbos and Northern Afrotemperate Forest vegetation type (Mucina and Rutherford, 2006). These vegetation types are expressed in different areas of the catchment as a result of intrinsic environmental heterogeneity, the ability of the respouter, *L. sericea*, to maintain its population size post-fire as opposed to the reseeder, *E. evansii*, and the non-uniform fire pattern within the catchment. This study therefore underscores the value of repeated surveys over the long-term in order to understand vegetation dynamics in response to a change in the system (Sutherland, 2006).

3.6 Appendix

Table 3.7: Summary of the statistical tests for changes in the *Erica evansii* population between 1973, 1986, 2007 and 2010

Erica evansii	Distribution				
	1973-1986	1973-2007	1973-2010	1986-2007	1986-2010
Relatively fire-protected: Distance from stream 0-49m	X^2=0.60, df=1, *P*=0.44	X^2=9.91, df=1, *P*<0.01	X^2=43.89, df=1, *P*<0.001	X^2=5.87, df=1, *P*<0.05	X^2=36.31, df=1, *P*<0.001
Fire-prone: Distance from stream 50m+	X^2=2.96, df=1, *P*=0.09	X^2=1.18, df=1, *P*=0.28	X^2=13.83, df=1, *P*<0.001	X^2=7.00, df=1, *P*<0.01	X^2=25.85, df=1, *P*<0.001
Slope 0-29°	X^2=0.08, df=1, *P*=0.77	X^2=1.10, df=1, *P*=0.29	X^2=23.84, df=1, *P*<0.001	X^2=1.77, df=1, *P*=0.18	X^2=26.18, df=1, *P*<0.001
Slope 30°+	X^2=0.31, df=1, *P*=0.58	X^2=12.35, df=1, *P*<0.001	X^2=35.08, df=1, *P*<0.001	X^2=11.20, df=1, *P*<0.001	X^2=34.75, df=1, *P*<0.001
Total	X^2=0.00, df=1, *P*=0.99	X^2=9.93, df=1, *P*<0.01	X^2=56.78, df=1, *P*<0.001	X^2=10.59, df=1, *P*<0.001	X^2=59.58, df=1, *P*<0.001
	Mean density				
Relatively fire-protected: Distance from stream 0-49m	*t*=0.99, df=43, *P*=0.33	*t*=-2.43, df=43, *P*<0.05	*t*=5.19, df=43, *P*<0.001	*t*=-3.31, df=43, *P*<0.01	*t*=5.62, df=43, *P*<0.001
Fire-prone: Distance from stream 50m+	*t*=0.05, df=20, *P*=0.96	*t*=-1.94, df=34, *P*=0.06	*t*=3.12, df=14, *P*<0.01	*t*=-2.62, df=20, *P*<0.05	*t*=6.29, df=20, *P*<0.001
Slope 0-29°	*t*=-1.89, df=36, *P*=0.07	*t*=-4.29, df=36, *P*<0.001	*t*=4.97, df=36, *P*<0.001	*t*=-3.82, df=36, *P*<0.001	*t*=5.09, df=36, *P*<0.001
Slope 30°+	*t*=1.69, df=28,	*t*=-0.55, df=47,	*t*=4.28, df=21,	*t*=-2.15, df=27,	*t*=6.01, df=27,

	P=0.10	P=0.58	P<0.001	P<0.05	P<0.001
Total	t=0.28, df=104, P=0.78	t=-3.18, df=96, P<0.01	t=5.57, df=59, P<0.001	t=-4.25, df=64, P<0.001	t=7.62, df=64, P<0.001
			Mean plant height		
Relatively fire-protected: Distance from stream 0-49m	t=0.28, df=25, P=0.79	t=-1.27, df=42, P=0.21	t=-1.36, df=4, P=0.25	t=-0.93, df=5, P=0.39	t=-1.40, df=5, P=0.22
Fire-prone: Distance from stream 50m+	t=9.29, df=16, P<0.001	t=-2.42, df=22, P<0.05	t=-1.43, df=4, P=0.23	t=-9.10, df=20, P<0.001	t=-2.82, df=4, P<0.05
Slope 0-29°	t=-0.02, df=24, P=0.98	t=-1.71, df=50, P=0.09	t=-3.54, df=10, P<0.01	t=-1.24, df=26, P=0.23	t=-3.09, df=14, P<0.01
Slope 30°+	t=2.17, df=11, P=0.05	t=0.58, df=28, P=0.56	t=1.98, df=1, P=0.30	t=-1.91, df=10, P=0.09	t=0.59, df=2, P=0.62
Total	t=1.33, df=34, P=0.19	t=-1.32, df=76, P=0.19	t=-1.70, df=10, P=0.12	t=-2.13, df=37, P<0.05	t=-2.22, df=14, P<0.05

Table 3.8: Summary of the statistical tests for changes in the *Leucosidea sericea* population between 1973, 1986 and 2010

Leucosidea sericea		Distribution	
	1973-1986	1986-2010	1973-2010
Relatively fire-protected: Distance from stream 0-49m	X^2=2.51, df=1, P=0.11	X^2=0.72, df=1, P=0.40	X^2=0.56, df=1, P=0.45
Fire-prone: Distance from stream 50m+	X^2=6.36, df=1, P<0.05	X^2=0.14, df=1, P=0.71	X^2=4.82, df=1, P<0.05

Slope 0-29°	X^2=1.41, df=1, *P*=0.24	X^2=0.84, df=1, *P*=0.36	X^2=0.08, df=1, *P*=0.78
Slope 30°+	X^2=7.39, df=1, *P*<0.01	X^2=0.11, df=1, *P*=0.74	X^2=5.86, df=1, *P*<0.05
Total	X^2=6.74, df=1, *P*<0.01	X^2=0.82, df=1, *P*=0.37	X^2=3.02, df=1, *P*=0.08
		Mean density	
Relatively fire-protected: Distance from stream 0-49m	*t*=-3.38, df=43, *P*<0.01	*t*=4.38, df=43, *P*<0.001	*t*=2.72, df=43, *P*<0.01
Fire-prone: Distance from stream 50m+	*t*=-2.88, df=20, *P*<0.01	*t*=2.47, df=20, *P*<0.05	*t*=-3.67, df=23, *P*<0.01
Slope 0-29°	*t*=-3.42, df=36, *P*<0.01	*t*=3.92, df=36, *P*<0.001	*t*=1.62, df=36, *P*=0.11
Slope 30°+	*t*=-2.87, df=30, *P*<0.01	*t*=3.08, df=27, *P*<0.01	*t*=-0.78, df=45, *P*=0.44
Total	*t*=-4.25, df=72, *P*<0.001	*t*=5.00, df=64, *P*<0.001	*t*=0.53, df=113, *P*=0.60
		Mean plant height	
Relatively fire-protected: Distance from stream 0-49m	*t*=3.93, df=43, *P*<0.001	*t*=-7.66, df=53, *P*<0.001	*t*=-3.15, df=57, *P*<0.01
Fire-prone: Distance from stream 50m+	*t*=3.07, df=8, *P*<0.05	*t*=-1.80, df=8, *P*=0.11	*t*=1.87, df=15, *P*=0.08
Slope 0-29°	*t*=4.17, df=36, *P*<0.001	*t*=-6.49, df=44, *P*<0.001	*t*=-1.91, df=47, *P*=0.06
Slope 30°+	*t*=2.44, df=15, *P*<0.05	*t*=-3.01, df=22, *P*<0.01	*t*=-0.95, df=29, *P*=0.35
Total	*t*=4.85, df=56, *P*<0.001	*t*=-6.70, df=73, *P*<0.001	*t*=-1.80, df=77, *P*=0.08

*0.000001

CHAPTER 4 :

Effect of a single fire on woody vegetation in Catchment IX, Cathedral Peak, KwaZulu-Natal Drakensberg, following extended partial exclusion of fire

Abstract

Fire is a key driver in shaping and maintaining grasslands. Long-term exclusion of fire in moist grasslands has been attempted at Catchment IX (CIX) at Cathedral Peak since 1952. Vegetation was surveyed in 1952, 1973, 1986 and 2010. Woody colonisation into grasslands was the most noted change over time. The woody component was resurveyed in 2010 after the latest of 13 unintended fires had swept through CIX in 2007. This fire had an uneven burn pattern resulting in not all woody vegetation being burnt. Distinct woody communities, with varying degrees of fire tolerance, and size differences between populations in burnt and fire-protected areas alluded to the uneven burn pattern being historically recurrent. *Erica evansii*, a reseeder, and *Leucosidea sericea*, a resprouter, were the two dominant species in CIX. These displayed expected responses to fire, resulting in dominance shifting from *Erica evansii* (92% mortality) to *Leucosidea sericea* (1.6% mortality). The decrease in *E. evansii* individuals resulted in a relative increase in community contribution of species not affected by fire. The postfire dominance of *Leucosidea sericea* in burnt plots was not apparent in fire-protected areas.

4.1 Introduction

Fire occurs naturally in many terrestrial ecosystems and has shaped vegetation communities for millennia (Manry & Knight, 1986; Scott, 2000; Bond & Keeley, 2005; Bond & Parr, 2010). Plants not adapted to fire may perish during an event and in regions of high fire frequency an absence of such species can be noted (Manry & Knight, 1986).

In South Africa, fire is critical for maintaining fynbos, savanna and grassland biomes, all of which have vegetation that is adapted to the natural fire regime (Mucina & Rutherford, 2006). Consistent with the global pattern, fire frequency in South Africa is highest in the grassland biome (Manry & Knight, 1986; Mouillot & Field, 2005), especially so within the moist grasslands of the KwaZulu-Natal Drakensberg (Killick, 1963; Manry & Knight, 1986). These grasslands are of natural origin (Killick, 1963; Mucina & Rutherford, 2006), pre-dating human influence (Bond & Parr, 2010), and originally maintained by lightning fires, with a fire-return period of about three to four years (Manry & Knight, 1986). Lightning, however, has been replaced by land managers as the main ignition source in the Drakensberg for the past few decades. High and predictable fuel production resulting from high rainfall and dry winters with frost has allowed managers to implement most commonly a biennial burning regime, with burning usually taking place after the first spring rains (Morris, 1999). Frequent burning in the Drakensberg (natural or human-controlled) has maintained grassland, commonly dominated by *Themeda triandra*, with woody vegetation confined to ridges or valleys that rarely burn (Killick, 1963).

It has not always been accepted that grassland is the natural vegetation of the Drakensberg Mountains. Some early workers, recognising that fire benefits grasses at the expense of the woody vegetation (Bews, 1916; Killick, 1963), proposed that forest was the natural successional endpoint for these regions (Acocks, 1953). This theory was tested in the Cathedral Peak region of the Drakensberg by experimentally excluding fire from a complete first-order catchment known as Catchment IX (CIX) since 1952 (Killick 1963) (figure 4.1). Consequent changes in vegetation from the baseline (Killick, 1963) were assessed in 1973 (Granger, 1976) and 1986 (Adcock, 1990).

However, thirteen runaway fires swept through the catchment between the time of its establishment and 2010 (figure 3.2) of which eight occurred since 1991. None of the eight fires are known to have burnt the entire catchment. Apart from the latest fire, in 2007, the extent of each fire is not known. In spite of infrequent fires, a successional replacement of grassland by woody vegetation was observed (Granger, 1976; Adcock, 1990). The general pattern up until 1986 was for *Themeda triandra* dominated grassland to become moribund over time and to be replaced by bracken fern *Pteridium aquilinum*. In turn, pioneer woody species (e.g. *Erica evansii, Leucosidea sericea, Searsia dentata, Diospyros austro-africana*) displaced bracken fern or invaded grassland directly (Granger, 1976; Adcock, 1990). Initially, woody patches facilitate colonisation of forest precursor species (e.g. *Rhamnus prinoides, Myrsine africana*) and ultimately of forest species (e.g. *Podocarpus latifolius*).

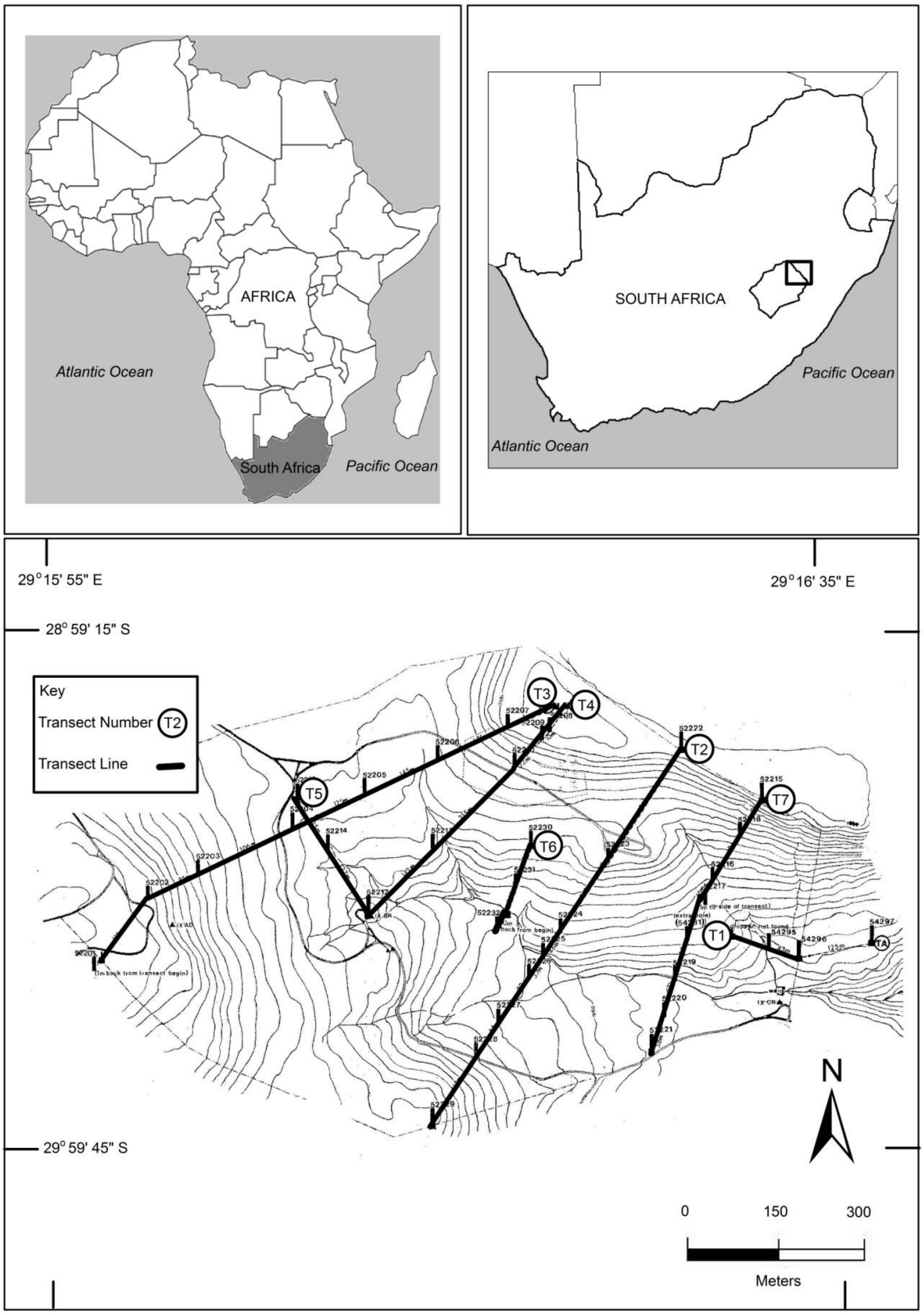

Figure 4.1: Map of CIX and the position of the permanent transects laid out by Granger in 1973 (Adcock, 1990).

These findings bring into question the frequency and severity of fire required to maintain open grassland in the Drakensberg. Conversely, there is also cause for questioning the conditions and time required for woody vegetation to become fire-protected. Most of our understanding of the impact of fire in this type of environment is derived from stand-level studies of gross compositional changes. A process-level understanding of vegetation change, however, requires an understanding of the impact of a single fire on the populations of individual species. The 2007 fire left intact standing skeletons of burnt plants. This provided an opportunity to assess the impact of a single fire on the population status and trend of the main woody species.

The two main species that had colonised into grassland of CIX were *Erica evansii* and *Leucosidea sericea* (Granger, 1976; Adcock, 1990), whose life history strategies differ. The former is a reseeder, that is, a species in which adults are killed by fire but persist through extensive post-fire recruitment of seedlings from a seed bank (Bond & Van Wilgen, 1996; Kruger *et al.* 1997; Lloret *et al.* 2005). By contrast, the latter is a respouter that uses underground carbohydrate reserves to initiate coppice growth following topkill by fire, although a small proportion may be completely killed (Bell, 2001; Bellingham & Sparrow; 2000 Ojeda *et al.* 2005). The distribution of either of these species within CIX was not homogenous. *Erica evansii* was most abundant on south-facing slopes having initially colonised with high seedling densities and then thinning into mature stands (Adcock, 1990). *Leucosidea sericea* commonly colonised from stream edges in a clumped manner to form mature stands with closed canopies (Granger, 1976; Adcock, 1990).

On account of both life history strategy and distribution throughout the landscape, it was expected that *E. evansii* should experience complete mortality if burnt, followed by seedling recruitment. By contrast, *L. sericea* should experience little mortality and most burnt individuals should coppice, although the effect of fire on seedling recruitment could not be predicted. Corresponding changes in the density and population size structure should be evident. The specific objectives of the study were to determine: (a) mortality and topkill of woody species in response to fire; (b) changes in population structure as a result of fire; and (c) consequent changes in community structure.

4.2 Material and Methods

4.2.1 Study site

Catchment IX (29°00'S; 29°15'E) is a 77 ha experimental first-order catchment that was established in 1952 in order to examine the effect of fire exclusion on hydrological functioning in the KwaZulu-Natal Drakensberg (De Villiers, 1970; Granger, 1976) (figure 4.1). CIX lies between an altitude of 1810m and 1950m (mean of 1903m) with an overall south east aspect (Granger, 1976). Geology comprises Stormberg basalts (Granger, 1976) and the main stream running out of the catchment is a fourth order stream which flows in a west-east direction. All of its surface tributaries start within the boundaries of the catchment (Granger, 1976).

Daily temperatures range from between 31°C to -3°C with January being the hottest month and June the coldest. CIX has a mean annual precipitation of 1300mm, 80% of which falls between October and March (Granger, 1976; Schultze & George, 1987). The rainfall is either orographic in nature or in the form of heavy thunderstorms which are accompanied by lightning and occasional hail (Killick, 1963; Manry & Knight, 1986).

Catchment IX is situated at the interface of the Northern Drakensberg Highland Grassland and uKhahlamba Basalt Grassland vegetation types, found in the afromontane ecoregion in the Maputaland-Pondoland-Albany biodiversity hotspot in South Africa (Mucina & Rutherford, 2006).

4.2.2 Approach

The approach followed that of Granger (1973) and Adcock (1990). Granger placed seven permanently marked transects, consisting of 5m x 5m ($25m^2$) contiguous plots, throughout CIX in 1973 in a manner that best gave representation to the vegetation types within the catchment (figure 4.1). These transects were resampled in 1986 (Adcock 1990) and in 2010 (this study).

A few of the original 1973 markers were not found in 1986 and 2010 owing to the dense nature of the vegetation in the area. The exact location of each contiguous plot sampled in 1973 was therefore not replicated in the subsequent surveys. A section of Transect 1 (5 plots) was not relocated in 1986 or 2010. The starting point of Transect 4 was not relocated by Adcock in 1986 (Adcock, 1990) but was estimated in 2010, using Granger's (1976) topographic references.

Adcock added 4 transects, each consisting of eight 5m x 5m contiguous plots (Adcock, 1990). Only two of these transects could be relocated in 2010. Despite these problems a total of 590 of the 598, $25m^2$ plots were found and sampled in 2010, covering an area of $14750m^2$.

Each transect was resampled with contiguous 5m x 5 m plots in 2010, using the transect line as the centre line, as previously done. Each live or dead woody individual inside a plot was identified (Pooley, 1993, 2003; Van Wyk & Van Wyk, 1997) and measured for its height (to 0.1m), canopy area (cm^2) and stem circumference (nearest cm). Similar dimensions for burnt and coppiced sections of coppiced individuals were measured as well. Individuals smaller than 20cm in height were not measured, following Granger (1976) and Adcock (1990). Canopy area was derived from measuring the longest canopy axis and the width perpendicular to that. Stem area of multiple stemmed individuals was derived as the sum of the areas of the individual stems. Slope, aspect, rock cover and aerial cover of *Pteridium aquilinum* were recorded for each plot, with each plot being scored as burnt or unburnt. A plot was scored as burnt if even only one individual had been burnt. A plot with no burnt individuals was considered fire-protected, whilst a plot with a mixture of burnt and unburnt individuals was considered an ecotone between vegetation dominated by woody plants versus herbaceous plants. Nomenclature followed Boon (2010).

4.2.3 Statistical analyses and assumptions

It was assumed that all dead individuals had died as a result of the 2007 fire, and that coppice growth was in response to this fire. Woody individuals that had not been burnt were readily evident as such, as was regrowth following partial or complete topkill.

A second assumption was that any burnt adult individual would retain its skeleton after the fire, with its dimensions reflecting the dimensions of a pre-fire individual. For this reason, woody species with soft stems (*Euphorbia epicyparissias*, *Rubus ludwigii, Indigofera hedyantha*, *Lotononis lotononoides*) that did not leave complete skeletons were not used in analyses of community changes.

Based on adult height, it was assumed that individuals of *Erica evansii, Leucosidea sericea, Rhamnus prinoides, Diospyros austro-africana, Buddleja salviifolia, Searsia dentata, Searsia pyroides, Olinia emarginata* and *Asparagus lavicinus* smaller than 0.5m, and individuals of *Myrsine africana*, *Searsia discolor* and *Relhania acerosa* smaller than 0.4m, were either seedlings or had regenerated from root stock. It was impossible to distinguish between the two growth forms and thus they were termed "regenerated".

Frequency tests were used to analyse survival in response to the 2007 fire. Differences in mean height or canopy area were analysed using *t*-tests, whilst differences in the distribution of these variables were analysed using a Komologorov-Smirnov two-sample test. Analyses used STATISTICA version 9.1 (StatSoft, 2010).

4.3 Results

The 2007 fire did not burn uniformly across the catchment or along individual transects (table 4.1). Overall 91.2% of the total sample burnt covering an area of 13450m^2. Less than 80% of plots along transect 1 burnt, whereas transects 3, 6 and Adcock's (1990) additional transects were completely burnt. The resulting mosaic allowed for comparison of burnt with unburnt (totalling 1300 m^2) plots.

Table 4.1: Number and percentage of plots along each transect burnt by the 2007 fire

Transect	Total	% Burnt	% Unburnt
1	15	6.7	93.3
2	147	97.3	2.7
3[1]	160	100	0
4	89	88.8	11.2
5	45	82.2	17.8
6	26	100	0
7	92	82.6	17.4
Adcock	16	100	0
TOTAL	590	91.2	8.8

[1] It was assumed that Transect 3 had burnt completely in 2007 owing to its predominantly grassland-*Pteridium aquilinum* matrix and mean height of 0.46m (SD=0.23m, n=468) for all living woody individuals sampled therein.

The fire resulted in a decrease of 36.3% in the number of woody individuals, owing mainly to the 92% mortality of the reseeder *E. evansii*. This was the most abundant species prior to the fire (table 4.2), comprising more than 50% of the woody individuals (table 4.3). Seedling regeneration of *E. evansii* by the time of study compensated for less than 3% of individuals killed by fire (table 4.2).

Table 4.2: Percentage composition of the population of each species in Catchment IX in 2010 in terms of unburnt, coppiced, regenerated or dead individuals in burnt plots, and living individuals in unburnt plots

		Percent within individual species				
Species	N	Regeneration[1] in burnt plots	Unburnt in burnt plots	Coppiced in burnt plots	Dead in burnt plots	Alive in unburnt plots
Erica evansii	5266	2.7	4.8	0.0	91.9	0.6
Leucosidea sericea	2507	6.2	29.6	52.5	1.5	10.2
Rhamnus prinoides	350	3.7	5.4	0.0	0.3	90.6
Myrsine africana	1177	8.5	21.9	0.0	0.1	69.5
Diospyros austro-africana	183	6.0	71.6	6.0	0.0	16.4
Buddleja salviifolia	127	1.6	57.5	15.0	0.0	26.0
Searsia discolor	764	18.2	70.8	0.0	2.0	9.0
Searsia dentata	50	2.0	18.0	0.0	0.0	80.0
Searsia pyroides	83	2.4	33.7	0.0	4.8	59.0
Olinia emarginata	12	0.0	0.0	0.0	0.0	100.0
Asparagus lavicinus	20	0.0	70.0	0.0	0.0	30.0
Euphorbia epicyparissias[2]	530	19.1	73.8	0.0	0.0	7.2
Rubus ludwigii[2]	2022	97.1	0.1	0.0	0.6	2.2
Indigofera sp. [2]	1535	15.6	76.0	0.0	0.3	8.1
Lotononis lotononoides[2]	314	6.4	58.0	0.0	29.3	6.4
Total Count	14983					

[1] Seedlings, or regenerated individuals from undetermined rootstock. [2] Soft stem woody species. *Rubus ludwigii* did coppice, but due the presumed destruction of potential skeletons during the fire, no distinction was made between coppice and post-fire seedlings and were thus grouped as “regeneration”.

Table 4.3: Pre- and post-fire composition of the woody community (contribution to total number of individuals), and spatial extent of each woody species, in Catchment IX

Woody species	Percent contribution			Percent of plots occupied	
Species	Pre- fire[1]	Post-fire[2]	Species	Pre- fire[1]	Post-fire[2]
Erica evansii	51.2	7.5	49.8	46.9	12.9
Leucosidea sericea	23.5	43.6	23.7	65.9	65.8
Rhamnus prinoides	3.4	6.2	3.3	6.9	6.9
Myrsine africana	10.8	20.7	11.1	10.8	10.8
Diospyros austro-africana	1.7	3.2	1.7	17.1	16.9
Buddleja salviifolia	1.2	2.2	1.2	5.9	5.9
Searsia discolor	6.2	13.2	7.2	15.8	15.6
Searsia dentata	0.5	0.9	0.5	2.7	2.7
Searsia pyroides	0.8	1.4	0.8	4.7	4.7
Olinia emarginata	0.1	0.2	0.1	0.8	0.8
Asparagus lavicinus	0.2	0.4	0.2	1.4	1.4
Relhania acerosa	0.4	0.5	0.4	1.4	1.2

[1] Pre-fire values were calculated from individuals in the "Unburnt Plots", Unburnt in Burnt Plots", "Coppiced in Burnt Plots" and "Dead in Burnt Plots" categories.
[2] Post-fire values were calculated from individuals in the "Unburnt Plots", Unburnt in Burnt Plots", "Coppiced in Burnt Plots" and "Regeneration in Burnt Plots" categories.

Table 4.4: Density of woody species in burnt and unburnt plots within Catchment IX. Categories of individuals for burnt plots were unburnt, coppiced, dead, or regenerated

	Density (ha^{-1}) ± SE				
Species	Regeneration* in burnt plots	Unburnt in burnt plots	Coppiced in burnt plots	Dead in burnt plots	Alive in unburnt plots
Erica evansii	105.6 ± 51.4	189.6 ± 40.6	0.0 ± 0.0	3597.8 ± 303.1	230.8 ± 120.3
Leucosidea sericea	116.0 ± 16.3	551.7 ± 30.8	978.4 ± 137	27.5 ± 1.5	1969.2 ± 449.3
Rhamnus prinoides	9.7 ± 3.4	14.1 ± 5.6	0.0 ± 0.0	0.7 ± 0.1	2438.5 ± 588.9
Myrsine africana	74.3 ± 23.5	191.8 ± 55.7	0.0 ± 0.0	0.7 ± 0.1	6292.3 ± 1369.1
Diospyros austro-africana	8.2 ± 3.6	97.4 ± 14.3	8.2 ± 3.6	0.0 ± 0.0	230.8 ± 59.7
Buddleja salviifolia	1.5 ± 0.9	54.3 ± 13.4	14.1 ± 8.5	0.0 ± 0.0	253.9 ± 123.6
Searsia discolor	103.3 ± 17.7	402.2 ± 68.5	0.0 ± 0.0	11.5 ± 6.0	530.8 ± 266.1
Searsia dentata	0.7 ± 0.7	6.7 ± 3.6	0.0 ± 0.0	0.0 ± 0.0	307.7 ± 115.7
Searsia pyroides	1.5 ± 0.9	20.8 ± 20.8	0.0 ± 0.0	3.0 ± 1.8	376.9 ± 135.1
Olinia emarginata	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	92.3 ± 42.0
Asparagus lavicinus	0.0 ± 0.0	10.4 ± 4.8	0.0 ± 0.0	0.0 ± 0.0	46.2 ± 27.8
Relhania acerosa	5.2 ± 3.6	14.1 ± 2.1	0.0 ± 0.0	12.6 ± 8.4	0.0 ± 0.0

***** Seedlings or regeneration from rootstock, defined by height

By contrast, the fire killed only 2.7% of the individuals of the resprouter *L. sericea*, the second-most abundant species prior to the fire, with 97.3% coppicing (tables 4.2, 4.3). Differential impact of fire among species was influenced by their spatial distribution within the catchment. *Erica evansii* was the only species to have its highest densities in areas that were burnt, whereas *L. sericea* was well represented in the burnt matrix, ecotone and fire-protected areas (table 4.4). Most of the other woody species were relatively unaffected by the fire because they were situated in closed woodland or ecotones that did not burn (tables 4.3, 4.4). The fire did not change the proportion of plots occupied by any species, with the exception of *Erica evansii,* which occurred in 34% fewer plots (table 4.3).

The differential impact of the fire on mortality of the two most abundant species resulted in a marked change in community composition (table 4.3). *Leucosidea sericea* replaced *E. evansii* as the most abundant species, with the relative contribution of most of the other species approximately doubling. Forest-precursor species such as *Myrsine africana* and *Searsia discolor* became relatively more prominent following the fire. Despite high mortality, *E. evansii* was the fourth most abundant species post the fire. Soft-stemmed woody species were also an important component of the woody community, constituting 29.4% (*n*=4401) of the total of individuals sampled (*n*=14983) (table 4.2). Their presence in fire-protected areas of the catchment indicates that they were part of the pre-fire community (table 4.4), but their lack of a skeleton despite having been exposed to fire precludes assessment of their response. Of the four soft-stemmed species listed, coppicing was only observed for *Rubus ludwigii*.

The fire altered the population size structure of both *L. sericea* and *E evansii* with plant height being reduced. Mean height of *L. sericea* and *E. evansii* was higher for dead (1.7m and 1.4m respectively) than living individuals (1.5m and 1.3m, respectively) in burnt plots (t=6.8, df=3546, P<0.05; t=3.4, df=5112, P<0.05 respectively) (table 4.5). In addition, the mean height of fire-protected *E. evansii* individuals (unburnt in burnt plots, unburnt plots) was greater than that of the burnt *E. evansii* individuals (t=18.2, df=5122, P<0.05). This was not the case with *L. sericea* (t=0.52, df=3580, P>0.1). By contrast, mean canopy cover of *Erica evansii* individuals was greater after the fire (t=4.3, df=5216, P<0.05), whereas that of *L. sericea* was less (t=-5.2, df=3397, P<0.05) (table 4.6).

Plant size influenced whether a coppicing individual of *L. sericea* had regained its pre-fire height by the time of study (figure 4.2). Plant height at the time of burning was equalled or exceeded by coppice growth for smaller individuals (<2.5m) by up to 2 m. For taller (>2.5m) individuals, coppice growth was as much as 3.6m below pre-fire height. Individuals as tall as 5.4 m had been burnt. The mean live height of coppicing *L. sericea* individuals was, however, no different to the height at time of topkill (both 1.72m) (t=-0.28, df=1314, P=0.78), indicating that the fire had offset growth in height by about two years. By contrast, mean height of coppicing *Buddleja salviifolia* (1.7 m) was greater than their height (1.4m) at time of burning (t=2.45, df=18, P<0.05). A similar influence of plant size was observed for the response of canopy cover of *L. sericea* to burning (figure 4.3). Mean canopy cover of coppiced individuals (18263cm^2) was, however, less than their mean cover at time of topkill (21080cm^2) (t=4.28, df=1314, P<0.05).

Table 4.5: Mean height and differences between unburnt, regenerated and dead individuals in burnt plots and living individuals in unburnt plots within species recorded across catchment IX

	Mean height (m) ± SE			
Species	Regeneration[1] in burnt plots	Unburnt in burnt plots	Dead in burnt plots	Alive in unburnt plots
Erica evansii	0.2 ± 0.01	1.8 ± 0.05	1.4 ± 0.01	2.0 ± 0.16
Leucosidea sericea	1.6 ± 0.02	1.4 ± 0.02	1.7 ± 0.02	2.3 ± 0.10
Rhamnus prinoides	0.3 ± 0.02	1.9 ± 0.26	1.9 ± 0.00	1.3 ± 0.08
Myrsine africana	0.3 ± 0.01	0.8 ± 0.02	1.5 ± 0.00	0.9 ± 0.02
Diospyros austro-africana	0.8 ± 0.04	1.2 ± 0.05	1.5 ± 0.24	1.3 ± 0.15
Buddleja salviifolia	1.6 ± 0.05	1.5 ± 0.05	1.4 ± 0.20	2.6 ± 0.43
Searsia discolor	0.3 ± 0.01	0.6 ± 0.01	0.5 ± 0.03	0.7 ± 0.03
Searsia dentata	0.2 ± 0.01	1.4 ± 0.25	0.0 ± 0.00	1.5 ± 0.23
Searsia pyroides	0.4 ± 0.05	1.7 ± 0.19	1.2 ± 0.27	1.6 ± 0.20
Olinia emarginata	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.9 ± 0.13
Euphorbia epicyparissias	0.3 ± 0.01	1.0 ± 0.02	0.0 ± 0.00	0.8 ± 0.06
Rubus ludwigii	0.3 ± 0.01	0.7 ± 0.01	1.0 ± 0.11	0.6 ± 0.07
Asparagus lavicinus	0.0 ± 0.00	1.2 ± 0.09	0.0± 0.00	1.7 ± 0.21
Indigofera sp.	0.3 ± 0.01	1.2 ± 0.02	2.4 ± 0.28	1.0 ± 0.04
Relhania acerosa	0.3 ± 0.01	0.5 ± 0.02	0.4 ± 0.02	0.0 ± 0.00
Lotononis lotononoides	0.4 ± 0.02	0.8 ± 0.02	0.7 ± 0.02	0.7 ± 0.05

[1] Seedlings or regeneration from rootstock, defined by height. Includes identified coppice of resprouters (i.e. *Leucosidea sericea, Diospyros austro-africana* and *Buddleja salviifolia*).

Table 4.6: Mean canopy cover of woody species for different plant states resulting from exposure to or protection from fire

	Mean canopy cover (cm^2) ± SE			
Species	Regeneration[1] in burnt plots	Unburnt in burnt plots	Dead in burnt plots	Alive in unburnt plots
Erica evansii	100 ± 0	12952 ± 591	6057 ± 139	25983 ± 5241
Leucosidea sericea	16743 ± 690	16459 ± 699	20819 ± 914	55378 ± 5380
Rhamnus prinoides	208 ± 40	31832 ± 10823	16800 ± 0	21212 ± 3199
Myrsine africana	100 ± 0	1642 ± 196	9600 ± 0	2687 ± 205
Diospyros austro-africana	9074	8965 ± 1155	17455 ± 6704	9921 ± 3643
Buddleja salviifolia	8303 ± 1506	8560 ± 1570	4668 ± 2277	56660 ± 20570
Searsia discolor	100 ± 0	700 ± 78	326 ± 116	1049 ± 208
Searsia dentata	100 ± 0	12667 ± 5142	0 ± 0	27388 ± 13592
Searsia pyroides	500 ± 400	26607 ± 8653	9425 ± 7868	10822 ± 3031
Olinia emarginata	0 ± 0	0 ± 0	0 ± 0	2050 ± 602
Euphorbia epicyparissias	99 ± 1	1958 ± 131	0 ± 0	740 ± 322
Rubus ludwigii	92 ± 1	290 ± 20	597 ± 1105	666 ± 277
Asparagus lavicinus	0 ± 0	7564 ± 2562	0 ± 0	16550 ± 6627
Indigofera sp.	100 ± 0	2662 ± 285	9017 ± 4164	1386 ± 360
Relhania acerosa	1200 ± 140	3037 ± 258	2394 ± 557	0 ± 0
Lotononis lotononoides	100 ± 0	3344 ± 280	1260 ± 150	2142 ± 728

[1]Seedlings, or regeneration from rootstock, smaller than 0.5m. Includes coppice of resprouters (i.e. *Leucosidea sericea, Diospyros austro-africana* and *Buddleja salviifolia*.

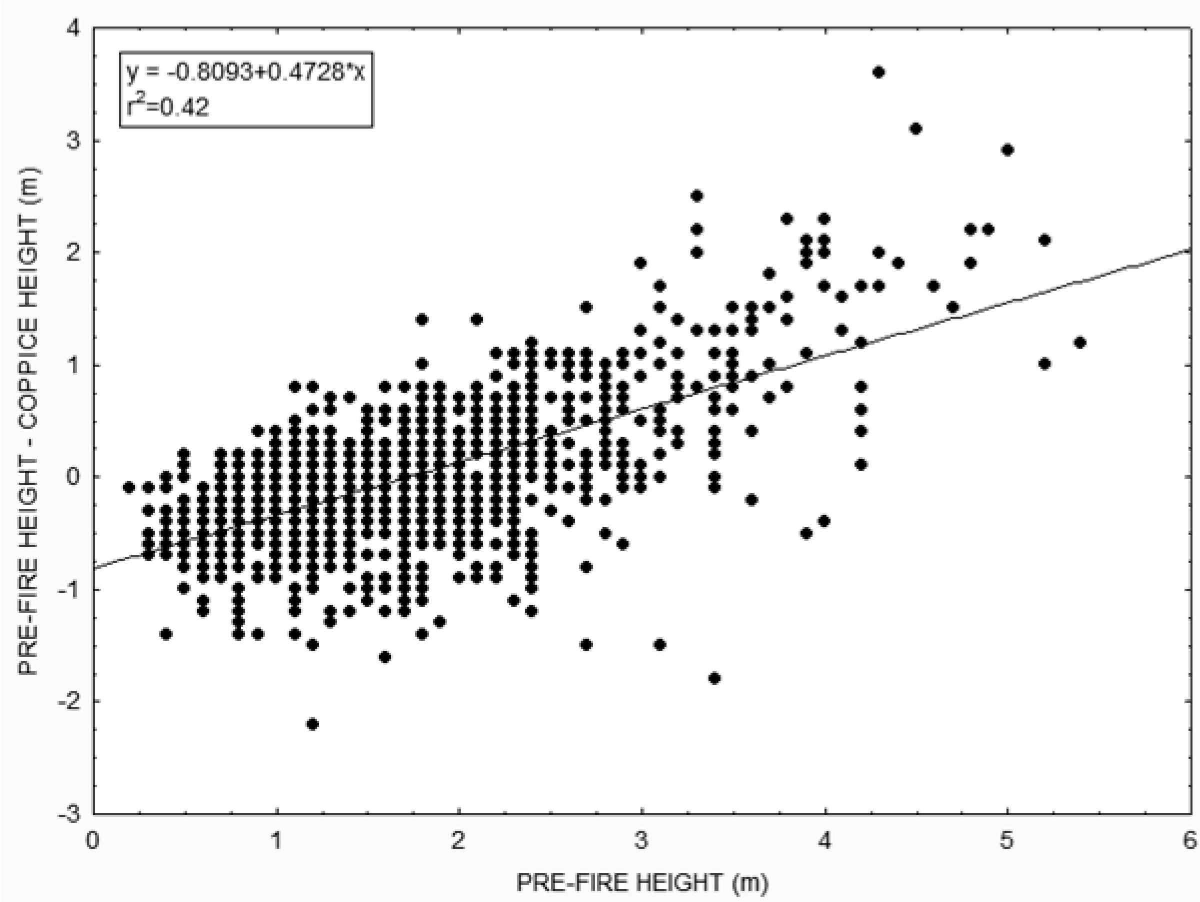

Figure 4.2: The relationship between pre-fire height and difference between pre-fire height and coppice height of *Leucosidea sericea* individuals. The pre-fire height was the measure of the tallest burnt stem on the individual.

Fire changed the height class distribution of *E. evansii*, but its influence was affected by location. This is inferred from comparison of the living with the dead population in burnt plots (P<0.05), the dead population in burnt plots with the living population in unburnt plots (P<0.05), and the living population in burnt versus unburnt plots (P<0.05) (figure 4.4). The size distribution of the bulk of the population immediately prior to the fire (i.e. dead individuals on burnt plots) was approximately bell-shaped, with only 1% of individuals recorded at less than 0.4 meters in height. By contrast, the living population on burnt plots was strongly unimodal (modal height class of 0-0.4m) with the smallest height class comprising 35.8% of the population, judged to be seedling recruits. Other than the smallest size class, the remainder of the living population on burnt plots occurred within the ecotone, and its size distribution was similar to that of the dead population.

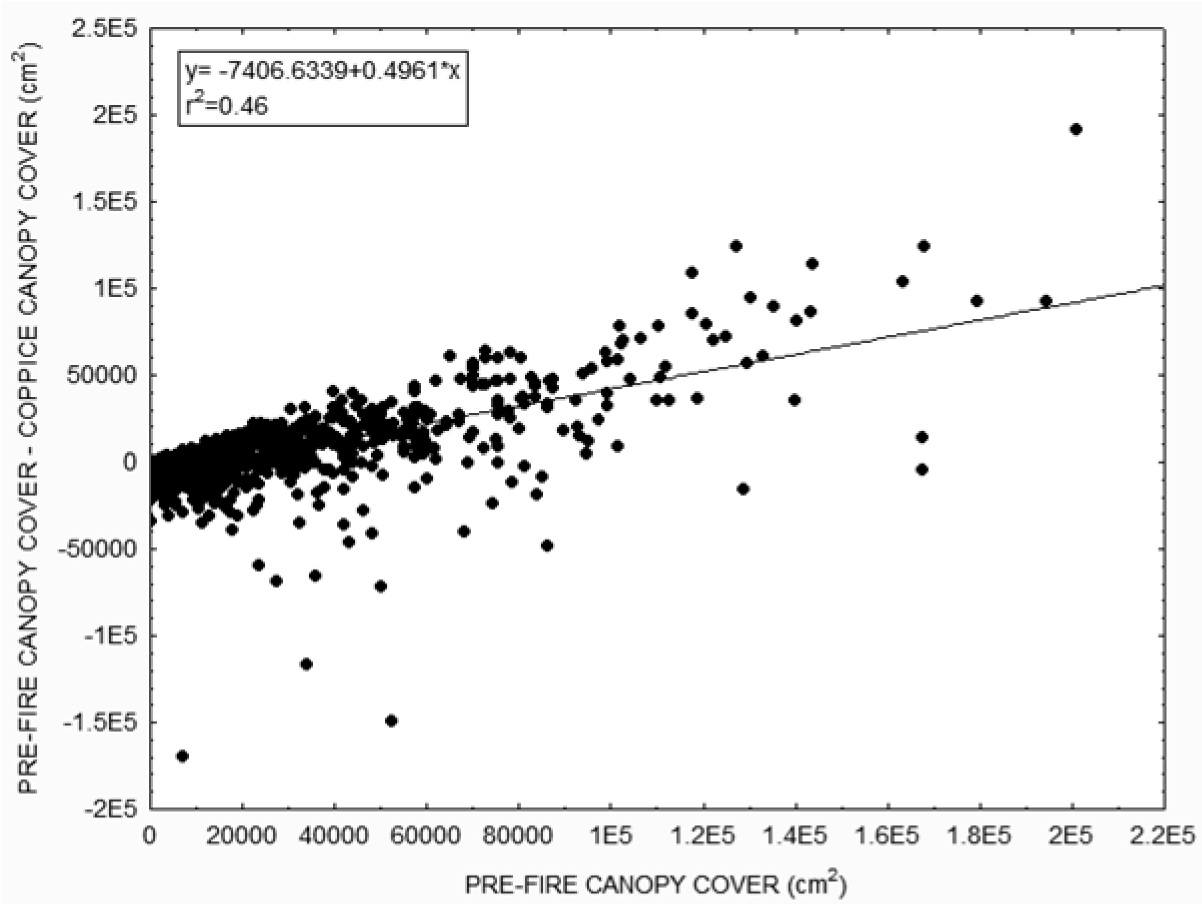

Figure 4.3: The relationship between pre-fire canopy cover and difference between pre-fire canopy cover and coppice canopy cover of *Leucosidea sericea* individuals.

Fire-protected areas (unburnt plots) were characterised by a population dominated by large individuals, with 93% of individuals being taller than 1 m, and 37% taller than 2.5m in height. These results can be attributed to presumed good growth conditions for woody individuals. For the entire *E. evansii* population within the catchment, the effect of fire in promoting seedling recruitment was apparent in the marked difference in distribution of stem diameter between dead and living individuals (P<0.05) (figure 4.5).

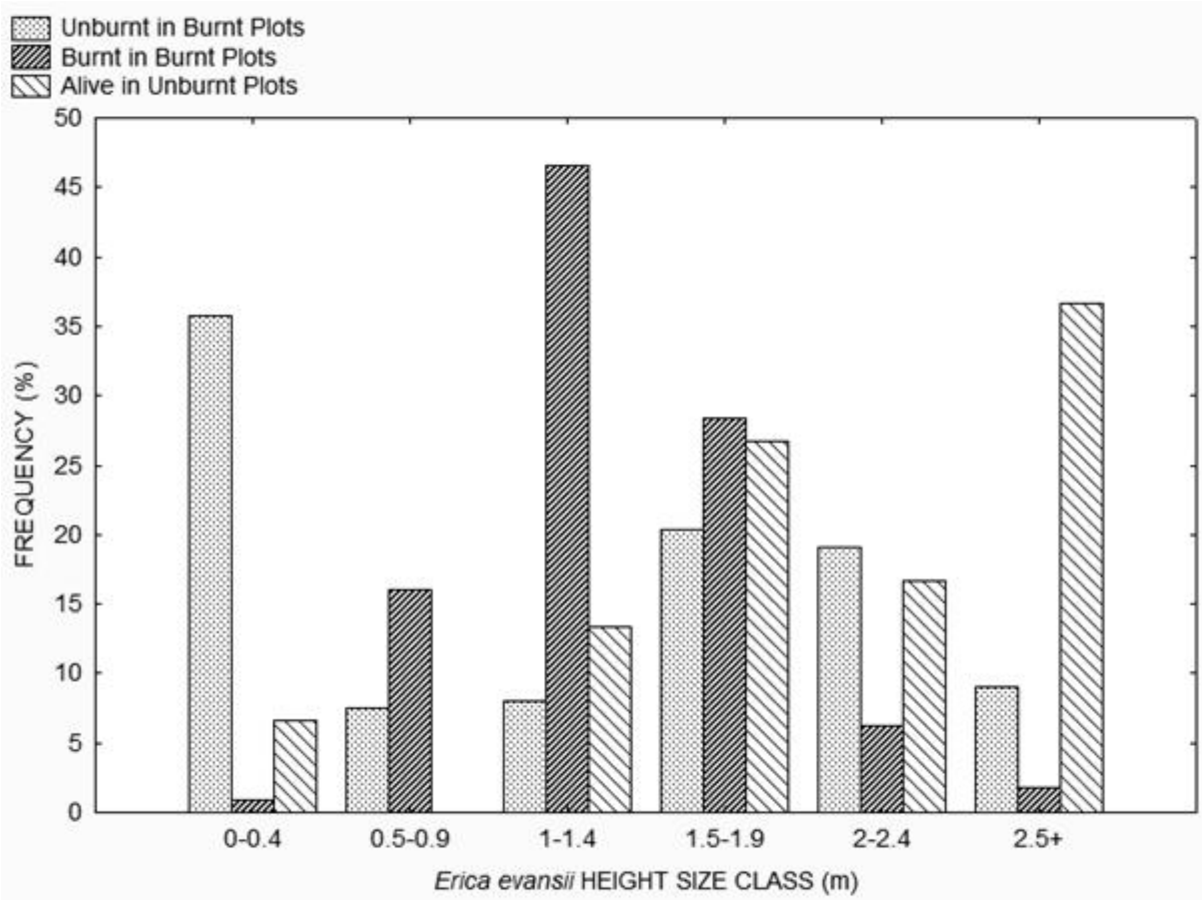

Figure 4.4: Height class distributions of *Erica evansii* within burnt and unburnt plots.

The fire had comparable effects on the height distribution of *L. sericea*, but with some notable differences that were attributed mainly to its resprouter strategy (figure 4.6). Height class frequencies were different amongst three categories: alive in burnt plots, coppice in burnt plots and those in unburnt plots (P<0.05). For coppicing individuals, distribution of coppice height differed from that of height at the time of fire (P<0.5) despite no difference in mean height. The height distribution of dead individuals (burnt plots) was similar to that of coppice individuals before they were burnt (P>0.1), indicating that all affected individuals had a similar chance of being killed by fire. Notably, mortality occurred in all height classes.

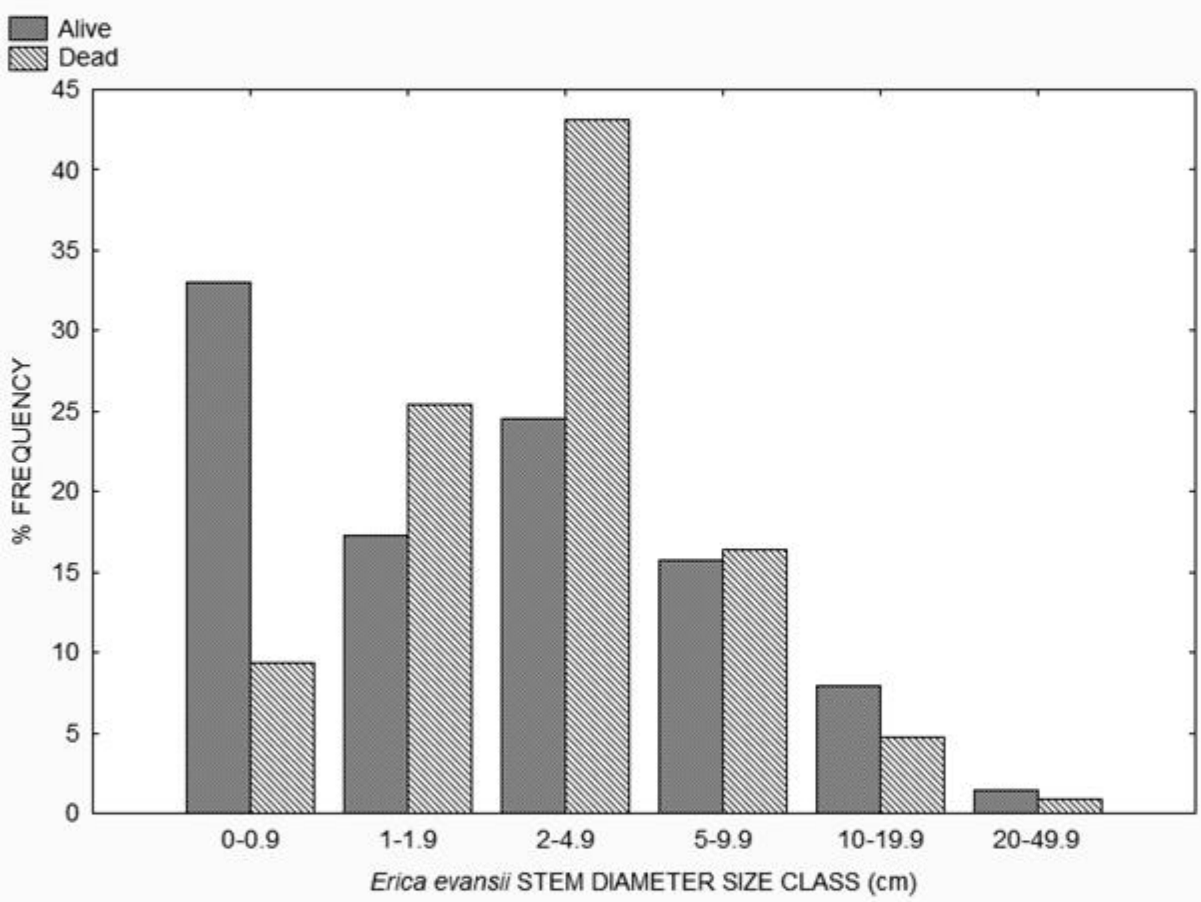

Figure 4.5: The stem size class frequency distribution for living and dead *Erica evansii* individuals.

The mean canopy cover of *E. evansii* and *L. sericea* populations was significantly greater in fire-protected than in burnt areas (t=-6.9, df=431, P<0.05; t=-14.1, df=2408, P<0.05, respectively) (table 4.6). Differences in size between the two most abundant species following the fire might influence relationships, and consequently vegetation dynamics. The *Leucosidea sericea* population was, on average, taller (table 4.5; t=6.38, df=2740, P<0.05) and individuals had larger canopies (table 4.6; t=7.28, df=1843, P<0.05) than the *E. evansii* population. In terms of spatial relations however, the two species were not well associated (X^2=394, df=1, P<0.05). The two species co-occurred on 30.1% of plots, *L. sericea* occurred alone on 35.1%, *E. evansii* on 14.1%, and both species were absent from 20.7% of plots.

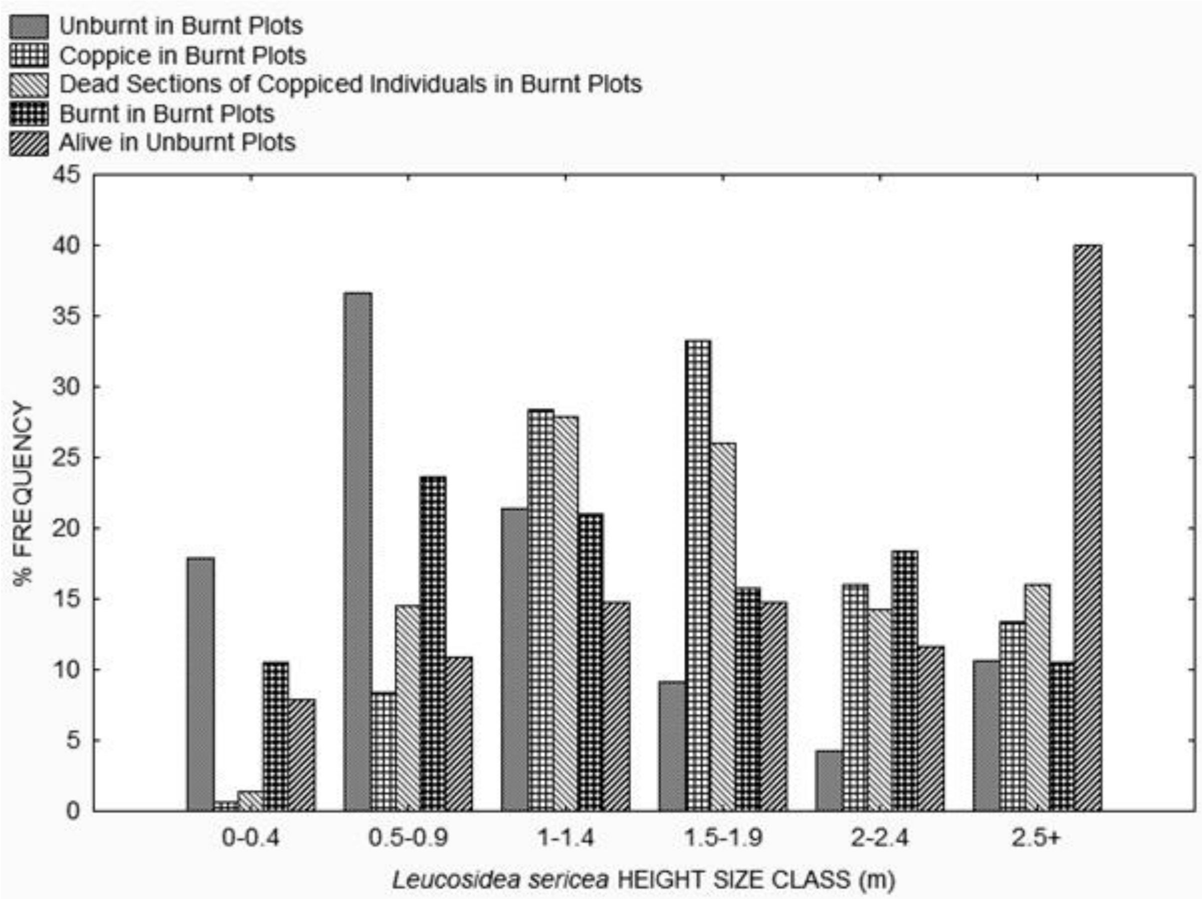

Figure 4.6: Height class distributions of *Leucosidea sericea* within burnt and unburnt plots.

4.4 Discussion

Topographic and hydrological variability within Catchment IX (CIX) resulted in an uneven, albeit extensive, burn pattern during the 2007 fire (Chapters 3, 5; table 4.1). Similarly, species distribution within the catchment was not uniform and as a result not all species were equally subjected to the fire (tables 4.2, 4.3, 4.4). Community composition was therefore different between burnt, ecotonal and fire-excluded areas.

In burnt areas, changes in the pre and post-fire community were largely explained by the contrasting responses of the two dominant species to the fire. These responses represented the two main mechanisms for coping with fire in plants (Lloret *et al.*

2005, Bond & Midgley, 2001). Both the *Erica evansii* and *Leucosidea sericea* populations had smaller individuals in the pre-fire community in burnt plots in comparison to unburnt plots (tables 4.5, 4.6), suggesting a history of higher fire frequency in the burnt matrix than in fire-protected areas. This was highlighted by the skewed height class distributions within these populations (figures 4.4, 4.6). Burnt areas were thus concluded to have been burnt more frequently than the unburnt areas with the latter consequently being considered fire-protected, supporting a distinct community that excludes fire (tables 4.2, 4.3, 4.4, 4.5) (Chapter 3).

Pre-fire dominance of *E. evansii* in the catchment, in terms of abundances and spatial distribution pre-fire, was lost as a result of its expected mortality of burnt individuals, and seedling recruitment that was unexpectedly insufficient to compensate for the loss of individuals during the fire (figures 4.4, 4.5, 4.6; tables 4.2, 4.3, 4.4). The resultant decrease in numbers therefore led to a decrease in its relative community dominance, as nearly half of CIX's pre-fire community (45.7%) was destroyed when these *E. evansii* individuals perished.

The pre-fire dominance of *E. evansii* seemed anomalous, given the above described outcome and fire history of CIX (figure 3.2). This species had, however, maintained dominance of the woody community over 55 years of partial fire exclusion (Granger, 1976; Adcock, 1990). The initial post-fire loss of dominance may thus represent observation of a short term response that may change in the long term with continued recruitment of this reseeder, dependent on fire-return period. Further decline of *E. evansii* is expected if the fire-return period experienced between 1990 and 2010 (figure 3.2) continues, as recovery of this species would appear to require a longer period.

Leucosidea sericea was the only other species in the burnt matrix with a large enough population to affect a shift in the relative dominance of other species within CIX. It responded differently to fire than *E. evansii*, coppicing and persisting with less than 3% of the population perishing. Coppice regrowth by *L. sericea* was relatively rapid (up to 1m per annum), promoting coppice to regain pre-fire size within two years (figures 4.2, 4.3). Its post-fire dominance supported both Bellingham and Sparrow's (2000) and Bond and Midgley's (2001) observations that resprouters are dominant over other woody species in a post-fire system as coppicing individuals grow more rapidly post-fire than recently germinated seedlings. This ability of *L. sericea* to regain its pre-fire structure by coppicing and retain its distribution, suggests that its population is secure. Of interest was *Buddleja salviifolia*, another resprouter in the catchment, which was able to regenerate to such an extent as to outgrow its pre-fire height.

The observed colonisation of woody individuals into the grassland of CIX over time seems to suggest a continuation of colonisation in the face of infrequent accidental fires, with *E. evansii* and *L. sericea* being the key agents of colonisation. The past pattern of colonisation had created an ecotone that was conspicuous after the 2007 fire. The area between the burnt matrix and fire-protected areas contained a distinct community (tables 4.2, 4.3). *Asparagus lavicinus, Buddleja salviifolia, Diospyros austro-africana* and *Searsia discolor* had more than half their populations occurring in this ecotone, indicating it is their key habitat. *Myrsine africana* and live *E. evansii* were also conspicuous thereby accentuating its transitional character. The ecotone is thus considered to delineate the frontline of forest colonisation into grassland and often scrubland. The shift from a fire tolerant to intolerant community was inferred due to woody colonisation over time despite infrequent fires, with fire-protected forests being the end-point of this transition.

With the exception of *E. evansii*, densities of all species were greatest in the fire-protected areas (table 4.4). In this unique community, monopodial (grow upward from a single point) fire-intolerant species were more abundant than reseeders or resprouters. Specifically *M. africana* and *Rhamnus prinoides* were more abundant than *L. sericea* in fire-protected areas. A similar pattern of replacement of resprouters by monopodial species was observed by Givinish (1984), Midgley (1996) and Kruger *et al.* (1997), ostensibly because resources were allocated to vertical growth as opposed to carbohydrate reserves and multi-stemmed resprouting. Fire-protected areas in CIX contained more than half the population of *Myrsine africana*, *Olinia emarginata, Rhamnus prinoides*, *Searsia dentata* and *Searsia pyroides*, highlighting their dependence on a fire-excluded environment for persistence.

4.5 Conclusion

The extended partial exclusion of fire and burn pattern mosaic in CIX resulted in the development of distinct woody communities within a catchment that was once considered a single grassland unit (Killick, 1963). These communities were the result of a historically irregular burn pattern. Shifts in dominance within CIX's woody community were primarily as a result of the two dominant species' contrasting responses to fire. The resprouter species maintained its pre-fire population size, with the converse observed for the reseeder species. Population decline of the latter following the fire is considered to be a consequence of its life history strategy and time since fire.

Leucosidea sericea's ability to resprout and maintain dominance in burnt and ecotonal regions does not appear to be an advantage in fire-protected areas. Here monopodial fire-intolerant species that allocated their resources to vertical growth rather than underground carbohydrate reserves, had an advantage in these communities, in which light is the main limiting factor. The aforementioned trend can thus be seen as a key factor in aiding the transition from pioneer woody species to forest pioneer and forest species within fire excluded moist grasslands of the KwaZulu-Natal Drakensberg. The historically uneven spatial distribution and frequency of fires in CIX will not allow for a consistent or complete dominance of the one life history strategy over others in time and space (Midgley, 1996; Bellingham & Sparrow, 2000; Bond & Midgley, 2001) and the continuation of distinct communities in the burnt, ecotonal and fire-protected areas seems assured.

Although insights gained from this study are history and site specific, life-history strategy offers a means of extrapolating results. Nonetheless, deeper insight into reseeder-resprouter dynamics in response to a single fire in partial fire excluded moist grasslands of the KwaZulu-Natal Drakensberg has been achieved, revealing a relatively rapid reaction to disturbance as opposed to succession (Van Hulst, 1979). The knowledge of the effect of this single fire has thus given insight into the effects of fire as a recurrent process on long-term vegetation change. Projection of future change has to become more spatially explicit with the effects of future fire being dependent on the vegetation states of the catchment.

CHAPTER 5 :

Influence of the abiotic environment on the response of woody vegetation to the partial exclusion of fire in Catchment IX, Cathedral Peak, KwaZulu-Natal Drakensberg, South Africa

Abstract

Woody vegetation communities dominate moist grasslands in the absence of fire. The abiotic environment influences woody vegetation communities both directly, through vegetation responses to abiotic gradients, and indirectly, through influencing the spread and intensity of fire. This has been observed at Catchment IX (CIX) in the KwaZulu-Natal Drakensberg in the responses in distributions and densities of the two dominant woody species, *Erica evansii* and *Leucosidea sericea*, and of fire pattern to abiotic gradients respectively. Distance from the stream, relative altitude, average annual solar radiation and soil type were identified as key explanatory variables modifying both *E. evansii* and *L. sericea* populations and fire pattern through complex interrelationships. *Erica evansii* and *L. sericea* were present in all measured environmental categories. *Erica evansii* favoured high lying areas away from the stream and did not tolerate radiation loads above 18 x 10^6 J/m^2; whilst *L. sericea* displayed a contrasting pattern. Fire had burnt greater areas on more xeric sites as was expected, with vegetation further modifying burn pattern in CIX.

5.1 Introduction

Fire requires three preconditions for combustion to occur: a combustible fuel source, oxygen and a source of ignition (Fons, 1946; Drysdale, 1985; Pyne *et al.* 1996). Once these preconditions are met in the natural environment, other factors (e.g. landscape, weather and fuel factors on the day of burn) influence the spread, intensity and duration of the fire (Brown & Davis, 1973; Luke & McArthur, 1978; Cheney, 1981; Wright & Bailey, 1982; Trollope, 1983; Everson *et al.* 1985; Everson *et al.* 1988; Railla *et al.* 2010).

The three aforementioned preconditions for fire are found in the moist grasslands of the KwaZulu-Natal Drakensberg in the form of a *Themeda triandra* dominated landscape that acts as a flammable, continuous and seasonally predictable fuel source (Killick, 1963; Granger, 1976; Bond *et al.* 2003; Uys *et al.* 2004), and the highest lightning strike rate in South Africa as ignition source (Manry & Knight, 1986). Fire is thus a natural occurrence in these moist grasslands (Manry & Knight, 1986; O'Connor & Bredenkamp, 1997).

Themeda triandra's fire-dependence results in a self-regulating system that restricts the otherwise more competitive woody vegetation to rocky outcrops or stream edges (Killick, 1963; Van Zinderen Bakker, 1973; Trollope, 1983; Granger, 1984; Archibald, 2010). Fire is therefore an important "top-down" selective pressure in shaping, maintaining and regulating these communities (Bews, 1916; O'Connor & Bredenkamp, 1997; Bond & Keeley, 2005; Dalle *et al.* 2006; Bond, 2008).

Woody vegetation is seen to colonise moist grasslands in the absence of fire (Granger, 1976; Westfall *et al.* 1983; Adcock, 1990; Titshall *et al.* 2000; Chapter 4). Once established, these woody communities can promote a positive feedback that excludes fire (Granger, 1984; Archibald, 2010; Bond & Parr, 2010; Chapter 4). A homogeneous climax woody vegetation type has been predicted to develop should fire be excluded from these systems for a sufficient amount of time, though the composition of these woody communities is widely debated (West, 1951; Acocks, 1953; Killick, 1963; Granger, 1976; Everson, 1979; Adcock, 1990).

Catchment IX (CIX), an experimental first-order fire exclusion catchment in the KwaZulu-Natal Drakensberg (figure 4.1) has provided an opportunity to investigate such predictions (Killick, 1963; Granger, 1976; Everson, 1979; Adcock, 1990). The result of 58 years of partial fire exclusion has not been a homogeneous climax woody vegetation type, but rather grassland-fynbos-scrub forest mosaic (Chapter 4). This phenomenon has been partly attributed to accidental fires that entered the catchment (figure 3.2). The influence of the abiotic environment could be seen as a ancillary reason for the lack of a homogeneous climax vegetation type within CIX.

Schelpe (1946) was the first researcher to document the effects of the abiotic environment on the woody vegetation in the Cathedral Peak area and noted that slope, aspect, and radiation were potentially factors influencing fynbos distributions. This view was supported by Granger (1976) and Granger and Schultze (1977). Furthermore, *Erica evansii* (Oliver, 1987; formerly *Philippia evansii* (Brown, 1905)) and *Leucosidea sericea* (Ecklon & Zeyher, 1836) were seen to prefer the lower winter radiation south-facing slopes and the higher radiation north-facing respectively (Granger; 1976; Everson, 1979; Everson & Breen, 1983).

Everson (1979) however contended that radiation was not the most important factor influencing *E. evansii* distributions within CIX, as *E. evansii* growth rates were seen to be higher in areas with high radiation than in areas with low radiation. He therefore concluded that other factors, most notably soil moisture, needed to be examined. Everson (1979) further noted that soil moisture changed markedly over relatively short distances within CIX, thus indicating the short comings of simple predictions regarding woody vegetation responses to the abiotic environment. Adcock (1990) also suggested that radiation was an important factor in constraining the woody community in CIX, but considered that the woody community was modified by other factors such as soil type and relative altitude. Complex interrelationships among abiotic variables are therefore expected in determining the distribution and densities of woody vegetation in CIX.

Erica evansii and *L. sericea* constituted 75% of the woody population prior to the 2007 fire in CIX and were seen as precursors to relatively fire-protected communities in CIX (Granger, 1976; Adcock, 1990; Everson, 1979; Chapter 4). It was therefore deemed prudent to examine the effects of an *a priori* selected group of environmental variables (table 5.1) that could be seen to affect soil moisture, and thus *E. evansii* and *L. sericea* populations in CIX.

Fire pattern is influenced by a combination of the abiotic environment (Luke & McArthur, 1978; Wright & Bailey, 1982; Trollope *et al.* 2003) and the woody vegetation present in a system (Bond *et al.* 2003; Bond & Parr, 2010). Chapters three and four described in part the influence of woody vegetation on fire pattern. This chapter is concerned with influence of the abiotic environment on fire pattern within CIX, and thus its indirect influence on woody vegetation.

Aspect, distance from the drainage line, relative altitude, slope, rockiness, average annual solar radiation, relative wind speed, ambient temperature, soil moisture and soil type are some of the environmental variables seen to directly or indirectly affect the continuity and/or flammability of the fuel source present in these grasslands (Granger, 1976; Granger & Schultze, 1977; Luke & McArthur, 1978; Wright & Bailey, 1982; Adcock, 1990; Trollope *et al.* 2003). An *a priori* selection of these variables (table 5.1) was examined in order to determine their influence on the extent of the most recent fire to burn in CIX. This fire occurred in 2007, burning as much as could be expected within CIX (Chapter 4) and was thus seen as a suitable indicator of what was burnable in CIX.

Table 5.1: The environmental variables considered for examining their potential effects on fire pattern and woody vegetation patterns and densities in CIX

Variable	Description and assumption	Categories used
Aspect	Aspect determines the amount of solar radiation received by a given area of land (Granger & Schultze, 1977; Everson, 1979). This in turn affects the relative humidity, soil moisture and vegetation of the area (Granger, 1976; Everson, 1979). North-facing slopes are seen to be more favourable for the ignition and fire spread than south-facing slopes. The former are seen to have a lower relative humidity with drier fuels and higher fuel temperatures as opposed to the latter.	• North-facing • South-facing
Distance from the drainage line	Soil moisture negatively affects the spread of fire (Granger & Schultze, 1977). Higher soil moisture results in higher fuel moisture content in areas of suitable growth. This in turn determines the intensity and rate of a fire's spread as it affects combustible fuel availability. Higher moisture contents require higher heat energy levels required to attain the low heat of combustion, ignite and burn the material. Regions in close proximity to drainage lines generally have deeper soils, as a result of colluvial and alluvial processes, and thus have greater storage volumes than those areas further away from drainage lines. Soils in the former areas additionally have higher moisture content than those in the latter areas as a result of the higher water table near drainage lines, receiving runoff from	• Distance from Stream 0m-49m • Distance from Stream 50m+; Relative altitude 30m+

	others regions in the catchment.	
Relative altitude	Regions at a lower relative altitude generally have higher soil moisture contents than those at a higher relative altitude as a result of surface run-off and flow through the soil through gravitational pull (Everson, 1979). Relative temperature is lower at lower altitudes, thus affecting relative humidity within a system.	• Relative altitude 0-29m • Relative altitude 30m+
Slope	Slope affects the flame angle of the fire (Luke & McArthur, 1978; Trollope *et al.* 2002). Fuels upslope are preheated from lower flame fronts, increasing the fuels' combustibility and rate of spread (Rothermel, 1985). Fires therefore burn faster with greater flame lengths up steeper slopes than more gradual slopes. Slope also affects potential soil moisture content with steeper slopes allowing for less infiltration and thus more runoff resulting in drier soils than those of more gradual slopes or flat areas. Steeper soils additionally have smaller soil storage volumes than those of the more gradual slopes as a result of colluvial and alluvial weathering.	• 0°-29° • 30°-59° • 60°-90°
Rockiness	Rockiness affects potential infiltration, runoff and vegetation cover of an area of land. Although infiltration is concentrated around the surfaces of rocks, the water storage capacity of the soil decreases along with habitat availability for plants, whilst runoff increases. Rockier areas are thus seen as potential barriers to fire spread as they negatively affect fuel continuity	• 0% • 1%-30% • 31%-60% • 61%-100%

	(Wells, 1965).	
Soil type	Soil type determines soil water storage capacity and nutrient availability for plants. The Katspruit soil form, for instance, has an Orthic topsoil with a G-horizon (signs of anaerobic reduction) below whereas the Mispah soil form is characterised by hard rock below the Orthic A-horizon (Soil Classification Working Group, 1991). The latter has limited soil moisture or subterranean space for root growth that extends below the A-horizon that would not be apparent when just taking surface rockiness cover.	• Clovelly form & series, deep phase • Clovelly form & series, shallow phase • Griffin form & series, deep phase • Griffin form & series, shallow phase • Hutton form, Farningham series • Hutton form, Farningham series, wet phase • Katspruit form & series • Mispah form & series *Based on Granger (1976)
Radiation	Incoming solar radiation affects the surface energy budget, temperatures and soil moisture (Granger & Schultze, 1977). Measures as the average annual solar radiation levels (AASRL) (Granger, 1976), this variable differs from aspect as it differs as intensity of radiation, the time of year, cloud cover and water vapour content change (Granger & Schultze, 1977). Incoming solar radiation therefore affects the soil moisture content of an area, and thus increases, or decrease, the likelihood of fires and woody vegetation in the system.	• 9 to 11.9 x 10^6 J/m^2 • 12 to 14.9 x 10^6 J/m^2 • 15 to 17.9 x 10^6 J/m^2 • 18 to 20.9 x 10^6 J/m^2 • 21 to 23.9 x 10^6 J/m^2 • 24 to 26.9 x 10^6 J/m^2 • 27 to 29.9 x 10^6 J/m^2 *Based on Granger (1976)

The aim of this chapter was thus to determine both the direct and indirect effects of the abiotic environment on woody vegetation. The direct effects would be observed in the responses in distributions and densities of *E. evansii* and *L. sericea*, whilst the indirect effects observed in fire pattern. It was hypothesised that: 1) *E. evansii* and *L. sericea* favours mesic over xeric environments and 2) that fire has a greater burn pattern in xeric than in mesic areas within moist grasslands. If, as hypothesised, fire is constrained by the abiotic environment we would have then defined where forest precursor and forest woody species will occur in CIX as these are primarily constrained by fire pattern within CIX (Granger, 1976; Chapters 3, 4).

5.2 Material and Methods

5.2.1 Study Site

Catchment IX (29°00'S; 29°15'E) is a 77 ha experimental first-order catchment that was established in 1952 in order to examine the effects of fire exclusion on hydrological functioning and vegetation in the KwaZulu-Natal Drakensberg (De Villiers, 1970; Granger, 1976) (figure 4.1). Catchment IX lies between an altitude of 1810m and 1950m (mean of 1903m) with an overall south east aspect (Granger, 1976). The north- and south-facing slopes in CIX are dissimilar with slopes on the south-facing side of CIX being steeper and rockier than those on the north-facing side (Granger, 1976) (figure 5.1). Granger (1976) considered this to be a result of the differences of incoming radiation between north- and south-facing slopes which results in differential rates of weathering.

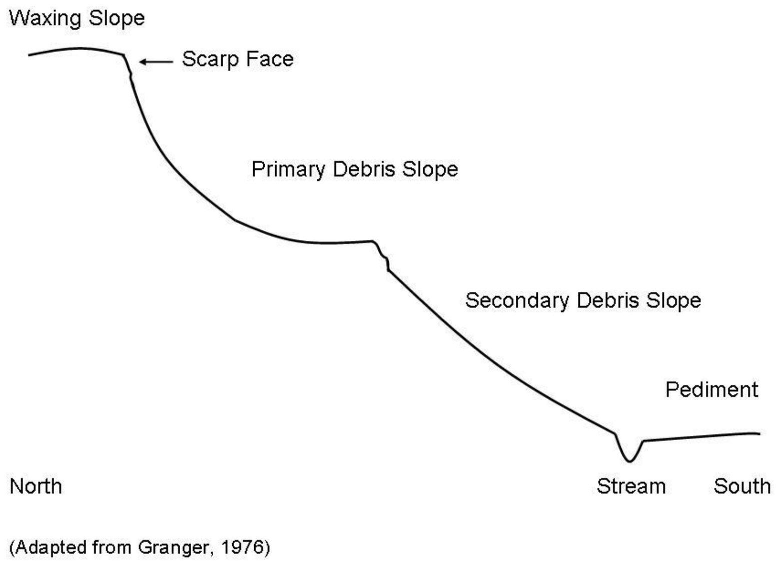

Figure 5.1: A cross section of the south-facing slope in CIX. The five slope types are illustrated.

The geology is relatively uniform, comprised of Stormberg basalts, rich in feldspars, pyroxenes, olivine, magnetite and ilmeninte (Granger, 1976). Granger (1976) noted that unlike most basalts, those of CIX displayed a texture more typical to that of dolerite. The soils are thin black clays (0cm – 46cm) with a relatively high cation exchange capacity and organic composition (27%-50%) (Killick, 1963). Clovelly, Griffin, Hutton, Katspruit and Mispah soil forms are found within the catchment (Granger, 1976; Adcock, 1990). The main stream running out of the catchment is a fourth order stream which flows in a west-east direction. All of its surface tributaries start within the boundaries of the catchment (Granger, 1976).

Daily maxima temperatures range from between 31°C and -3°C, with January being the hottest month and June the coldest (Granger, 1976). June, July and August are the only months with negative absolute minimum temperature means. Snow occasionally falls in the Little Berg during the dry winter months (Killick, 1963) with frost having been recorded in the research area from late April through to September, but is most common in June and July (Granger, 1976). In moist shaded areas frost can persist for a few weeks, thawing only for a few hours a day (Granger, 1976). Average annual solar radiation levels range between 9 and 30 x 10^6 J/m^2 (Granger, 1976; Granger & Schultze, 1977; Everson, 1979). Radiation is highest in the summer months although the duration of radiation and radiation differences within the catchment are higher in the winter months (five times higher on north-facing slopes, with south-facing shaded for 6 hours longer) due to the lack of cloud cover and the inclined angle of incoming radiation in winter respectively (Granger & Schultze, 1977; Everson, 1979).

Catchment IX occurs in a summer rainfall area and has a mean annual precipitation of 1300mm, 80% of which falls between October and March (Granger, 1976; Schultze & McGee, 1987). The rainfall is either orographic in nature or in the form of heavy thunderstorms which are accompanied by lightning and occasional hail (Killick, 1963; Manry and Knight, 1986).

Catchment IX is situated at the interface of the Northern Drakensberg Highland Grassland and uKhahlamba Basalt Grassland vegetation types, though the vegetation has changed to a Drakensberg-Amathole Afromontane Fynbos and and Northern Afrotemperate Forest vegetation type (Mucina and Rutherford, 2006) as a result of partial fire exclusion (Chapter 3).

5.2.2 Approach

The approach followed that of Granger (1973) and Adcock (1990). Granger placed seven permanently marked transects, consisting of 5m x 5m (25m^2) contiguous plots, throughout CIX in 1973 in a manner that gave best representation to the vegetation types within the catchment (figure 4.1). These transects were resampled in 1986 (Adcock 1990) and in 2010 (this study).

A few of the original 1973 markers were not found in 1986 and 2010 owing to the dense nature of the vegetation in the area. The exact location of each contiguous plot sampled in 1973 was therefore not replicated in the subsequent surveys. A section of Transect 1 (5 plots) was not relocated in 1986 or 2010. The starting point of Transect 4 was not relocated by Adcock in 1986 (Adcock, 1990) but was estimated in 2010, using Granger's (1976) topographic references.

Adcock added four transects, each consisting of eight 5m x 5m contiguous plots (Adcock, 1990). Only two of these transects could be relocated in 2010 owing to the dense nature of the vegetation. Despite these problems, 98.6% of the $25m^2$ plots were found and sampled in 2010, covering an area of $14750m^2$.

Each transect was sampled with contiguous 5m x 5 m plots in 2010, using the transect line as the centre line. Each live or dead woody individual inside a plot was identified (Pooley, 1993, 2003; Van Wyk and Van Wyk, 1997; Boon, 2010) and measured for its height (to 0.1m), canopy area (cm^2) and stem circumference (nearest cm). Slope, aspect, distance from the stream, relative altitude, basal rock cover (rockiness), average annual solar radiation levels (AASRL) and soil type were recorded for each plot, with each plot being scored as burnt or unburnt (table 5.1). A plot was scored as burnt if even only one individual had been burnt. Relative altitude was calculated by assigning a 0m value to the lowest point in the catchment.

Thresholds for plot categorisation of “distance from stream” and “relative altitude” were calculated by examining these variables’ influence on the 2007 fire pattern. These overlapped and were thus grouped into the same category. Soil type and average annual solar radiation levels were obtained from Granger’s (1976) data. The soil type and average annual solar radiation levels for Transect 1 were not available from Granger’s dataset (Adcock, 1990).

Wind was not examined as a potential factor influencing *E. evansii* and *L. sericea* distributions as turbulent mixing of the atmosphere within the catchment was seen to reduce the potential differences in water stress within CIX that would possibly be caused by wind (Everson, 1979). Additionally, Everson (1979) did not consider wind to affect the distribution of *E. evansii*, arguing that despite the prevailing wind being westerly to south-easterly, the wind-dispersed *E. evansii* was found predominantly on the south-facing slopes of CIX.

5.2.3 Analyses

The influence of the abiotic environment on the distributions of the 2007 fire, and of the two main woody species *E. evansii* and *L. sericea* was examined using logistic regression. Aspect, distance from stream, relative altitude, slope, rockiness, average annual solar radiation levels (AASRL) and soil type were selected as an *a priori* list of potential explanatory variables (table 5.1). Collinearity among this set was identified through the use of principal component analysis and correlation matrixes, resulting in a simplified list of distance from stream, relative altitude (used as substitute for rockiness), AASRL (used as substitute for both aspect and slope) and soil type. Distance from stream and relative altitude categories were transformed by dividing their number of 5m categories by 20 and 15 respectively. Differences in the number of burnt and unburnt plots or plots occupied by either *E. evansii* or *L. sericea* between abiotic categories were analysed using Chi-square analyses.

The influence of the abiotic environment on the abundances of *E. evansii* and *L. sericea* was examined with multiple regression analyses. Backward stepwise selection was used to analyse the main and interaction effects of the above mentioned simplified list of *a priori* selected explanatory variables' influence on *E. evansii* and *L. sericea* densities. Only plots with *E. evansii* or *L. sericea* present in them were used in the analysis. There was no expected direction of change and two-tailed *t*-tests were therefore used to analyse density differences between each abiotic variable category. The 2007 pre-fire *L. sericea* and *E. evansii* density data were used so as to minimise fire's confounding effect on vegetation. Analyses used STATISTICA version 9.1 (StatSoft, 2010).

Dry areas were seen as those areas on north-facing slopes that were far away from the stream (>50m), at high relative altitudes (>30m), on steep slopes (>30°), on rocky soils (>30%) or with high AASRL's (>21 x 10^6 J/m^2). Conversely, it was assumed that wet areas were those areas on south-facing slopes, close to the stream (<50m), at low relative altitudes (<30m), on flatter (<30%) slopes, with few or no rocks (<30%) or with low AASRL's (<17.9 x 10^6 J/m^2).

5.3 Results

The abiotic environment affected woody vegetation in Catchment IX (CIX) both directly and indirectly. The direct effects were that despite *Erica evansii* and *Leucosidea sericea* occupying all the measured environmental categories, these species displayed contrasting responses to environmental gradients within CIX. Distance from the stream, relative altitude, radiation and soil type were all seen to be important variables modifying *E. evansii* and *L. sericea* distributions (X^2=222.8, df=10, P<0.05; X^2=134.4, df=10, P<0.05 respectively) (table 5.2) and densities (R^2_{adj}=0.51; F=11.03, df=57, P<0.05; R^2_{adj}=0.42; F=7.99, df=57, P<0.05 respectively) (tables 5.3, 5.4) within CIX.

Distance from the stream (P<0.05), relative altitude (P<0.05) and radiation (P<0.05) proved predictors of both *E. evansii* and *L. sericea* distributions, and soil type was a predictor (P<0.05) of only *L. sericea* distribution (table 5.2). *Erica evansii* spatial distribution was more extensive on high lying areas (>30m) away from the stream (>50m) than on low lying areas close to the stream (by 5.6%; X^2=9.10, P<0.05) (table 5.5). Areas with the lowest radiation loads were completely occupied by *E. evansii*, with *E. evansii* spatial distribution decreasing by two thirds as radiation loads increased up until 18 x 10^6 J/m^2 (X^2=25.46, P<0.05) (table 5.6).

Table 5.2: Summary of logistic regression analysis for significant explanatory variables predicting the presence or absence of *Leucosidea sericea* (N=362), *Erica evansii* (N=250) and fire within 25m^2 areas within CIX

	Leucosidea sericea			*Erica evansii*		
X^2			134.36			222.79
df			10			10
% present			64.8			44.7
P			<0.05			<0.05
Predictor variable	*B*	e^B	*P*	*B*	e^B	*P*
Distance from Stream	0.21	1.23	<0.05	-0.20	0.82	<0.05
Relative Altitude	0.32	1.37	<0.05	0.70	2.01	<0.05
Radiation	0.26	1.29	<0.05	0.70	2.01	<0.05
GD	-1.90	0.15	<0.05			
GS	-2.14	0.12	<0.05			
HH	-1.66	0.19	<0.05			

	Fire		
X^2			56.90
df			10
% present			81.9
P			<0.05
Predictor variable	*B*	e^B	*P*
Distance from Stream	0.23	1.26	<0.05
Relative Altitude	0.24	1.27	<0.05

B= B-value; e^B= exponetiated B (odds ratio); GD= Griffin form & series, deep phase; GS= Griffin form & series, shallow phase; HH= Hutton form, Farningham series, wet phase.

Table 5.3: Summary of multiple regression statistics for the predictor variables to mean density of *Erica evansii* (n=250; model contained all main effects)

Predictor variable	b	SE b	*t*	*P*
H	13.39	3.00	4.47	<0.05
HH	5.56	2.01	2.77	<0.05
Relative altitude*AASRL	-34.44	9.35	-3.69	<0.05
Distance from stream*HH	-18.95	9.34	-2.03	<0.05
Radiation*HH	-19.21	6.00	-3.20	<0.05
Relative altitude*GD	25.77	8.20	3.14	<0.05
Distance from stream*Relative altitude * AASRL	59.18	25.11	2.36	<0.05
Distance from stream*Relative altitude *CS	32.18	9.64	3.34	<0.05
Distance from stream*Relative altitude *GS	-18.14	5.39	-3.37	<0.05
Distance from stream*Relative altitude *GD	22.82	7.34	3.11	<0.05
Distance from stream*Relative altitude *M	-115.15	48.39	-2.38	<0.05
Distance from stream*AASRL *CS	37.61	12.79	2.94	<0.05
Distance from stream*AASRL *GD	47.06	15.23	3.09	<0.05
Distance from stream*AASRL *H	69.48	18.53	3.75	<0.05
Distance from stream*AASRL *HH	49.74	11.88	4.19	<0.05
Distance from stream*AASRL *M	45.07	16.57	2.72	<0.05
Distance from stream*Relative altitude * AASRL *HH	-41.72	17.43	-2.39	<0.05

b= un-standardised beta coefficient; SE b= standard error, *t*= *T*-test statistic, *P*= significance value, CD= Clovelly form & series, deep phase; CS= Clovelly form & series, shallow phase; GD= Griffin form & series, deep phase; GS= Griffin form & series, shallow phase; H= Hutton form, Farningham series; HH= Hutton form, Farningham series, wet phase; M= Mispah form & series; AARSL= average annual solar radiation levels

Table 5.4: Summary of multiple regression statistics for the predictor variables to plot density of *Leucosidea sericea* (n=362; model contained all main effects)

Predictor variable	b	SE b	*t*	*P*
Relative altitude*CD	-26.20	12.51	-2.09	<0.05
Relative altitude*GD	-19.03	8.91	-2.14	<0.05
Distance from stream*AASRL*CS	-28.06	13.90	-2.02	<0.05
Distance from stream*AASRL *H	-39.68	20.14	-1.97	<0.05

b= un-standardised beta coefficient; SE b= standard error, *t*= *T*-test statistic, *P*= significance value, GD= Griffin form & series, deep phase; CD= Clovelly form & series, deep phase; CS= Clovelly form & series, shallow phase; H= Hutton form, Farningham series; AARSL= average annual solar radiation levels

Unlike *E. evansii*, *L. sericea* preferred low lying areas (<30m) close to the stream (<50m) to high lying areas (>30m) far from the stream (>30m) (occupying 26% more area; X^2=28.95, *P*<0.05) (table 5.5). Areas with the lowest and mid-range radiation loads hosted the highest (92%) and lowest (56%) distributions of *L. sericea* respectively (table 5.6). *Leucosidea sericea* preferred deep soils with good soil moisture (i.e. the Hutton (wet phase), Griffin (deep phase) and Katspruit soil forms) over shallow soils (i.e. the Mispah, Griffin (shallow phase) and Clovelly (shallow phase) soil forms), having its highest and lowest distributions on the former and latter soils respectively (table 5.7).

Distance from the stream, relative altitude, radiation and soil type were all predictors of both *E. evansii* and *L. sericea* densities (tables 5.3, 5.4). The interactions between the distance of an area away from the stream and its relative altitude or radiation load seemed to affect the soil forming processes and thus soil type. In addition, varying altitudes within CIX seemed to have a number of potential incoming radiation loads. Combinations between these interactions affected *E. evansii* and *L. sericea* densities, with *E. evansii* being more dynamic than *L. sericea* in this regard. In spite of this complexity, rudimentary trends were observed within gradients of the significant predictors of *E. evansii* and *L. sericea* densities.

Erica evansii had higher densities in high lying areas (>30m) away from the stream (>50m) than in low lying areas (<30m) close to the stream (<50m) (3701 and 2386 individuals.ha^{-1} respectively; t=-3.71, df=412, P<0.05) (table 5.5). Areas with the lowest and highest radiation loads had the highest (12831 individuals.ha^{-1}) and lowest (504 individuals.ha^{-1}) densities of *E. evansii* respectively (table 5.6). *Erica evansii* had its highest (5405 individuals.ha^{-1} and 5015 individuals.ha^{-1}) and lowest (640 individuals.ha^{-1} and 1744 individuals.ha^{-1}) densities on the Mispah and Katspruit, and Clovelly deep and shallow soil forms respectively (table 5.7).

In contrast to *E. evansii*, *L. sericea* had higher densities in low lying areas (<30m) close to the stream (<50m) than in higher lying areas (>30m) away from the stream (>50m) (2244 and 1390 individuals.ha^{-1} respectively; t=2.31, df=412, P<0.05) (table 5.5). Areas with the highest (21-26.9 x 10^6 J/m^2) and lowest (9-14.9 x 10^6 J/m^2) radiation loads had the highest densities of *L. sericea* (between 1530 and 2144 individuals.ha^{-1}), with no differences in density observed between these two categories (table 5.6). *Leucosidea sericea* had its highest (2984 mean density.ha^{-1}) and lowest (388 mean density.ha^{-1}) densities on the Hutton (wet phase) and Mispah soil forms respectively (table 5.7).

The abiotic environment directly affected fire pattern, which indirectly affected woody vegetation in CIX. The 2007 fire burnt within all categories measured (table 5.1), though the fire pattern differed along environmental gradients. Both distance from the stream (*P*<0.05) and relative altitude (*P*<0.05) were seen as important variables influencing fire pattern (X^2=56.90, df=10; *P*<0.05) (table 5.2). The 2007 fire had a greater burn pattern (by 12.0%, X^2=8.82; *P*<0.05) in the drier regions (>50m from the stream and at higher relative altitudes (>30m)) than moister regions (<50m from the stream and at lower relative altitudes) (table 5.5). Radiation and soil type were not predictors of fire pattern within CIX.

Table 5.5: The proportion of burnt plots, plots occupied by and mean densities of *Leucosidea sericea* and *Erica evansii* within distance from stream and relative altitude categories

	Burnt Plots		*Leucosidea sericea*		*Erica evansii*	
Distance from Stream	n	% Burnt	Proportion of plots occupied	Mean density (ha^{-1})	Proportion of plots occupied	Mean density (ha^{-1})
Close to stream / Lower altitudes	118	71.2	86.4	2244.1	39.8	2386.4
Far from stream / Higher altitudes	471	83.2	60.1	1390.2	45.4	3701.1

Close to stream = Distance from Stream 0-49 / Lower altitudes = Relative Altitude 0-29
Far from stream = Distance from Stream 50+ / Higher altitudes = Relative Altitude 30+

Table 5.6: The proportion of burnt plots, plots occupied by and mean densities of *Leucosidea sericea* and *Erica evansii* within average annual solar radiation level categories

	Burnt Plots		*Leucosidea sericea*		*Erica evansii*	
Radiation	n	% Burnt	Proportion of plots occupied	Mean density (ha^{-1})	Proportion of plots occupied	Mean density (ha^{-1})
9 to 11.9 x 10^6 J/m^2	13	100.0	92.3	1723.1	100.0	12830.8
12 to 14.9 x 10^6 J/m^2	78	89.7	69.2	2143.6	67.9	5492.3
15 to 17.9 x 10^6 J/m^2	87	89.7	66.7	1246.0	71.3	8620.7
18 to 20.9 x 10^6 J/m^2	164	72.6	55.5	1190.2	32.9	2707.3
21 to 23.9 x 10^6 J/m^2	194	79.9	69.1	1868.0	30.9	554.6
24 to 26.9 x 10^6 J/m^2	23	100.0	56.5	1530.4	34.8	504.3

Table 5.7: The proportion of burnt plots, plots occupied by and mean densities of *Leucosidea sericea* and *Erica evansii* within soil type categories

	Burnt Plots		*Leucosidea sericea*		*Erica evansii*	
Soil Type	n	% Burnt	Proportion of plots occupied	Mean density (ha^{-1})	Proportion of plots occupied	Mean density (ha^{-1})
Clovelly form & series, deep phase	15	93.3	60.0	1653.3	33.3	640.0
Clovelly form & series, shallow phase	86	74.4	59.3	1827.9	33.7	1744.2
Griffin form & series, deep phase	76	85.5	78.9	1573.7	50.0	4157.9
Griffin form & series, shallow phase	26	84.6	61.5	1153.8	50.0	3153.8
Hutton form, Farningham series	225	83.6	66.7	1642.7	41.8	3441.8
Hutton form, Farningham series, wet phase	50	76.0	92.0	2984.0	46.0	2872.0
Katspruit form & series	13	76.9	69.2	1076.9	53.8	5015.4
Mispah form & series	68	83.8	30.9	388.2	60.3	5405.9

5.4 Discussion

The abiotic environment affected woody vegetation distribution and abundances both directly and indirectly in CIX. Previous researchers (Schelpe 1946, Granger, 1976, Granger and Schultze, 1977, Everson, 1979; Adcock, 1990) saw *Erica evansii* and *Leucosidea sericea* populations to be influenced by one or two abiotic factors. However, this study has shown the complex nature in which combinations and gradients of four key abiotic variables (tables 5.2, 5.3, 5.4), namely distance from the stream (table 5.5), relative altitude, radiation (table 5.6) and soil type (table 5.7), interact to shape the populations of *E. evansii* and *L. sericea*. Notwithstanding the complex nature of these interactions, a number of elementary statements can be made regarding the extent to which the aforementioned four variables influence *E. evansii* and *L. sericea* distributions and densities.

Erica evansii and *L. sericea* largely preferred contrasting environmental gradients within CIX (tables 5.5, 5.6, 5.7). It was therefore inferred that these contrasting responses, along with the variable fire pattern in CIX, were typically responsible for these species not being spatially associated (Chapter 4).

Erica evansii was seen to be more sensitive to changes in the abiotic environment than was *L. sericea*, supporting Everson's (1979) observations. The unexpected trend of *E. evansii* favouring the xeric high lying areas over the mesic low lying areas in CIX (table 5.5) can potentially be explained by the presence of Mispah soils, found predominantly on the scarp slopes in CIX (Granger, 1976) (figure 5.1), that *E. evansii* favoured. These soil types could potentially retain moisture in their Orthic A-horizons as a result of their impermeable hard rock B-horizons (Soil Classification Working

Group, 1991). *Erica evansii*'s shallow (<50cm) root system (Everson, 1979) would be well suited to utilise this available soil moisture. An alternate explanation for *E. evansii* tolerating high lying areas in CIX could be the presence of fire-protected communities that colonised the mesic low lying areas in the absence of fire (Chapters 3, 4). The resultant fire protection in these communities is therefore seen to be more of a disadvantage to the fire dependent *E. evansii*'s (Everson, 1979) survival than a decrease in soil moisture.

In contrast to *E. evansii*, *L. sericea* responded to all variables measured as would be expected by woody vegetation (table 5.1). The seemingly anomalous observation of *L. sericea*'s preference of north-facing slopes to south-facing slopes, noted by Granger (1976) and Adcock (1990), can be attributed to *L. sericea*'s tolerance of relatively high AASRL's (table 5.6).

In addition to the direct effects of the abiotic environment on woody vegetation, this study has shown the extent to which distance from the stream and relative altitude have modified fire pattern (table 5.2), and in so doing indirectly affected the woody vegetation within CIX. As expected, the 2007 fire had a greater burn area on the more xeric high lying areas away from the stream than on the more mesic low lying areas closer to the stream (table 5.5). This could be attributed to a combination of the more mesic conditions and the presence of fire-protected communities that developed in these areas (Chapters 3, 4).

The anomalous observation of radiation not seen as a predictor of fire (table 5.2) seemed to be linked to the 2007 fire's complete burn pattern on areas with not only highest radiation loads, as expected, but also on areas that received the lowest radiation loads (table 5.6). The latter areas were favoured by the flammable reseeder *Erica evansii*'s (Everson, 1979; Chapter 4). The potential fuel source in these mesic areas could therefore have been modified to be more favourable for fires. If this inference holds true, the hypothesis that xeric areas burn more than mesic areas in CIX is thus modified to include the effects of woody vegetation on fire pattern, namely the fire-excluding or fire-prone nature thereof.

5.5 Conclusion

The abiotic environment influenced the woody vegetation in Catchment IX both directly, affecting *Erica evansii* and *Leucosidea sericea* distribution and densities, and indirectly, by affecting fire pattern. Woody community assemblages in CIX are therefore seen to be the product of fire (Chapters 3, 4), the presence of other woody species present within the catchment (Adcock, 1990; Chapter 4) and the abiotic environment. Simplistic assumptions are therefore not sufficient in predicting or explaining woody vegetation patterns in partial fire excluded moist grasslands. A combination of the fire history, woody community dynamics and complex multiple interrelationships between the abiotic variables involved are required in order to understand woody vegetation, and indeed fire dynamics in these systems. The fact that *E. evansii* and *L. sericea* abundances were primarily explained by complex interrelationships between explanatory variables highlights Everson's (1979) conclusion that generalised models are inadequate for understanding woody colonisation in fire excluded moist grasslands. Catchment IX provides an opportunity for future studies to further our understanding of the interconnected influences of fire, woody vegetation and the abiotic environment on one another in a partial fire excluded moist grassland. The effect of the woody vegetation on the abiotic environment is recommended as a topic for future study in CIX.

CHAPTER 6 :

Overall Conclusion

6.1 Woody vegetation changes in Catchment IX over time

The study attempted to determine the effects of fire and the abiotic environment on the woody vegetation in a partial fire excluded moist grassland catchment in the KwaZulu-Natal Drakensberg by asking several questions: (i) what is the required fire-return period for maintaining open grassland; (ii) what are the required conditions and time for woody vegetation to become fire-protected; (iii) what is the impact of a single fire on the woody vegetation of a partial fire excluded catchment; (iv) what is the effect of the established woody vegetation on the spread of fire within a partially fire excluded system; and (v) what is the effect of the abiotic environment on fire pattern and woody distribution and density within the moist grasslands of the KwaZulu-Natal Drakensberg?

Owing to four attributes unique to Catchment IX (CIX), the study was in the position to address these questions regarding the effects of woody vegetation responses to infrequent fires and total fire exclusion in moist montane grasslands. These four attributes were: (a) three comparable vegetation surveys prior to 2010 (Killick, 1963; Granger, 1976; Adcock, 1990); (b) contrasting fire-return periods between each survey; (c) the most recent fire, in 2007, left intact adult skeletons of burnt woody individuals; (d) data on the abiotic heterogeneity of CIX was readily available (Granger, 1976; Granger & Schultze, 1977; Adcock, 1990).

Firstly, the study found that a return to the purported natural fire-return period (Manry & Knight, 1986) after 20 years of total fire exclusion in moist grasslands did not revert the transformed vegetation, a grassland-woody mosaic vegetation type with clear fire-protected forested areas (Adcock, 1990), back to grassland. Consequently, the grassland ceased to maintain its character and gradually gave way to woody colonisation though colonisation rates were determined by the fire-return period, abiotic environment and species within the system. It therefore seems that provided a period of total fire exclusion has elapsed, woody colonisation can subsequently occur despite a return of fire.

Fire-protected areas formed within CIX as result of 58 years of total fire exclusion afforded in certain sections of the catchment. These communities supported a unique assemblage of forest precursor and forest species, and seemed to gradually expand into the more fire-prone regions between fire events. This expansion promoted a positive feedback that further drove a shift in ecosystem state from grassland to closed woody scrub or forest with associated changes in system structure, composition, and functioning (Granger, 1984). This supported the view that grasslands and forests can be seen as alternate ecosystem states for a specific set of environmental conditions (Bond, 2008; Bond & Parr, 2010). The future of fire-protected woody vegetation within CIX is thus seen to be relatively secure and we now have a better understanding of what the effect of the established woody vegetation is on the spread of fire within this kind of system.

Fire pattern was further constrained by the abiotic environment. Xeric sites burnt more readily than mesic sites, as indicated by distance from a stream and relative altitude. The historically uneven fire pattern thus was influenced by both the abiotic environment and the woody community present, being excluded by fire-protected vegetation.

The uneven fire pattern in CIX posed a unique challenge to those woody species subjected to fire events. The second question regarding vegetation responses to infrequent fire events was also answered as woody vegetation within these fire-prone regions of CIX responded differently to fire events owing to their life history strategies. Despite infrequent fires and subsequent high mortality rates observed post-fire, the reseeder *Erica evansii* maintained its dominance within the catchment over time. *E. evansii*'s high mortality rates post-fire resulted in a shift in community dominance to other species (e.g. *Rhamnus prinoides*, *Myrsine africana*, *Diospyros austro-africana*, *Searsia discolor*, *Buddleja salviifolia*) that were generally confined to ectonal areas or fire-protected patches of vegetation. *Erica evansii*'s dynamic nature was expressed in its ability to become the dominant species within a matter of years due to its high density seedling reseeder nature. This resulted in the paradoxical phenomenon that is so common amongst reseeders: the majority of the population was found in the burn pattern area of the catchment, attesting to the species' dependence on fire for persistence within partial fire excluded moist grasslands. This is of interest as fire is seen to been negatively impacted with an increase in woody percentage occupancy.

Erica evansii's response to fire was contrasted by the most dominant species post-2007, and only second to *E. evansii* in terms of pre-fire woody dominance, the resprouter *Leucosidea sericea*. *Leucosidea sericea*'s post-fire dominance was attributed to its ability to coppice and maintain its population distribution and densities within CIX. *Leucosidea sericea*'s post-fire dominance in the fire-prone areas of CIX was translated to the ectonal areas of CIX, though not to the fire-protected areas. Here monopodial fire-intolerant species (i.e. species that allocate their resources to vertical growth rather than underground carbohydrate reserves) dominated in these light-limited areas. *Leucosidea sericea* was therefore seen as precursor to these communities. The abovementioned responses to a single fire by *E. evansii* and *L. sericea* therefore gave a basis for predicting repeated fires, with *Leucosidea sericea* and *Erica evansii* further inferred to facilitate the colonisation of more fire-intolerant species.

Thirdly, it was found that, along with fire, the woody community within CIX was further constrained by the abiotic environment. Once again, the two dominant species *L. sericea* and *E. evansii* responded in contrasting manners to abiotic variables measured, resulting in these species not being well associated spatially within CIX. *Erica evansii* preferred areas further than 50m from drainage lines, higher relative altitudes (>30m), areas between 9 and 17.9 x 10^6 J/m^2 average annual solar radiation levels and Mispah soil forms; whilst *L. sericea* was seen to prefer being near to the drainage line (<50m), at lower relative altitudes (<30m), AASRL's at the lowest or highest categories and Hutton soil forms. Distances from drainage line, relative altitude, radiation were seen to be predictors of both *E. evansii* and *L. sericea* distributions and densities and constrained density through complex multiple second, third or fourth level interactions with one another and soil type within CIX.

6.2 What we have learnt

This study has shown that the vegetation of Catchment IX has displayed marked changes in its vegetation as a result of 58 years of partial fire exclusion, changing from a combination of Northern Drakensberg Highland Grassland and uKhahlamba Basalt Grassland to Drakensberg-Amathole Afromontane Fynbos and Northern Afrotemperate Forest vegetation type, with moribund grasses or *Pteridium aquilinum* mosaic in between. Variation in the abundances of dominant woody species was seen as the result of an uneven fire pattern and constrained by environmental variability within the catchment. As a result, distinct fire-prone, ecotonal and fire-protected woody communities developed within CIX over time.

A further understanding into the fire-proneness and effects of "top-down" and "bottom-up" selective pressures on emergent vegetation, a continuum between a fire-prone grassland and fire-protected forest vegetation, in a partial fire excluded montane catchment has thus been achieved at CIX. Woody vegetation dynamics and interactions are seen to take place within the complex milieu of abiotic (fire and environmental limitations) and biotic processes, with fire's role seen as the most important of these drivers. Woody vegetation dynamics and interactions are further constrained by the woody individual's life history strategies, life stage and physiology. Notwithstanding these complex interactions, successional concepts were useful in understanding the change in woody vegetation in CIX.

Insights gained from this study were history and site specific. However, life-history strategy, environmental variables and fire offered a means of extrapolating results. Projection of future change needs to be more spatially explicit with the effects of future fires being dependent on the vegetation states of the catchment.

This study underscores the need for repeated surveys over the long-term in order to understand woody vegetation dynamics in response to anthropogenic changes in natural systems. Catchment IX provides an opportunity for future studies to further our understanding of the interconnected influences of fire, woody vegetation and the abiotic environment on one another in a partial fire excluded moist grassland. The presence of other drivers, that would have had synergistic influences on the woody vegetation of CIX were not examined and future studies should examine these potential catalysts in transforming grasslands into woody vegetation states.

CHAPTER 7 :

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