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The ecology of sprouting in South African forests, savannas and fynbos

By

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Thesis submitted for the degree of Doctor of Philosophy in the Department of Botany at the University of Cape Town

September 2005

Statement:

The conception, planning, execution and writing of this study were entirely my own except in the specific instance mentioned below.

Chapter 1 and 2 are adapted from published papers, which were co-authored with my supervisor, Jeremy Midgley, and Richard Cowling. Their contributions were mainly through discussions and suggestions on how to improve the manuscripts. Jeremy Midgley 's ideas were particularly important in Chapter 3 and 6, while William Bond provided useful discussion on Chapter 4 and key insight into the concepts in Chapter 5. Jeremy Midgley helped to improve existing manuscripts through discussion and suggestion.

Appendix A is a paper written Jeremy Midgley, with myself as a co-author. We worked on the idea together and the paper contains some of my data and observations.

Acknowledgements

I have thoroughly enjoyed working with Jeremy Midgley, my supervisor, and am extremely grateful to him for his constant support, unending patience and our thoroughly inspiring interactions, both scientifically and other. Under his easy-going, but sharply incisive supervision I have significantly developed my interests in functional and evolutionary ecology. Apart from deriving great pleasure from working with him, I learnt about so much more than just ecology, but most importantly, about a sense of humour. My thanks too, to William Bond for his guidance and the interest he took in my work, and the insight he provided on my subject matter.

I am also thankful to the many people that I interacted with during my work. My thanks to Richard Cowling, Jan Vlok, Allan Ellis, Sally Archibald, Peter Carrick, Phillip Desmet, Nick Helme, Donovan Kirkwood and Ronnie Brereton-Stiles for the many valuable conversations and interesting perspectives on my work. Others who have helped with my fieldwork include Xolani, John, Halzka and Navashni, from the Earthwatch programme, Alexandra Kruger, Anne Kraemer, Nick Helme, Danjelle and Amy Midgley.

At UCT, my thanks to Sandy Smuts and the technical staff, Gonzalo, Des and Robert, for putting up with all of the logistical nightmares incurred during the project. Without their support, I would not have managed to do half the work I set out to do. In Knysna, I am grateful to Armin Seydack and Johan Huysamen for their logistical support and useful comments on my research.

Many thanks to the Zululand people: Dave Balfour, for allowing us to work in Hluhluwe Imfolozi Game Reserve, for the many pleasant hours spent in the field, and for his vast scientific input. Abednigo Mkwanasi, provided me with invaluable guidance and inspiration in the field, without whom much of our work would not have been possible. My thanks also to Bekhi Mnguni, Sicelo Nkosi, Dennis Nhleko, Owen Howison, Ruth Howison and Sue van Rensburg for their invaluable assistance in the field and helping making life interesting and bearable on the many hot days.

My thanks, also, to the conservation agencies for allowing me access to areas under their jurisdiction (Ezemvelo Kwa-Zulu Parks Board, Department of Water Affairs and Forestry and the Cape Nature Conservation Board).

I am grateful for financial support from the National Research Foundation, Jeff Morris and Pretoria Software Solutions, the Institute for Plant conservation and Fred Kruger consulting.

My thanks, lastly, to my parents and those close to me. Fred Kruger who set me on this path, by providing me with the many opportunities to fossick about in the field with him, and especially the numerous conversations about the project and so much more. Glaudin Kruger, for the moral support and unending patience. Alex, Oliver and Lizzie, thanks for all your never-ending support and sense of humour with this behemoth that is a PhD.

Finally, this thesis is dedicated to my grandfather, Cecil Kruger, who taught me so very much: about compassion, integrity and especially a love for this country.

Plate1. i. Tall Afromontane forests (c. 20 – 30m) near Knysna, southern Cape Province. **ii.** Grootbos forest, a shorter canopied coastal forest (c. 5 – 10m) near Stanford, western Cape Province. **iii.** *Olea capensis* subs *macrocarpa,* a single-stemmed species that dominates the taller Afromontane forests, Knysna, southern Cape Province. **iv.** The multistemmed architecture of *Sideroxylon inerme*, a dominant canopy species in Grootbos forest, Stanford, western Cape Province (all photos: L. Kruger).

ABSTRACT

Sprouting has only recently received attention as a key life history strategy, especially in less disturbance prone environments. The aims of this thesis were to explore the ecological role of sprouting in selected South African biomes. In particular, to explore the biogeographic, community and individual level consequences of adopting sprouting as a life history strategy. The thesis is broadly divided into 4 sections. The first three dealing with the ecology of sprouting in forests, fynbos and savannas respectively; and the fourth undertakes to determine whether sprouting is considered in plant ecological strategy schemes.

Chapter 1 and 2 deals with the role of sprouting in forests in relation to reseeding as key regeneration strategies in southern Cape forests. Sprouting has been largely been ignored as a regeneration strategy in favour of reseeding in southern African forests. I found that tall forests are dominated by reseeding species, while sprouting species dominate shorter canopied forests. The relative dominance of sprouters has an effect on forest canopy species richness: as sprouter abundance increases, with decreasing canopy height, canopy species richness decreases. Sprouters are able to retain their *in situ* position in the forests for longer periods of time than do reseeders, which reduces individual and species turnover, and hence canopy species richness.

In Chapter 3 and 4, I explore Proteaceae Life History strategies in relation to fire. Sprouting ability and bark thickness are used as key traits in defining Proteaceae life history strategies. Five functional groups are described and are broadly divided into two categories resisters and non-resisters. Resisters include thick barked fire resisting and epicormic sprouting species and non resisters basal sprouting and thin barked non-resistant species. Sprouting strategy and bark thickness were also found to influence plant architecture and hence individual and stand flammability. Non-resisting species tend to display a more ramified architecture, resulting in a more flammable state.

Conversely, thick barked species tend to display a less ramified and therefore more fire resistance architecture.

In Chapter 5 I explore how changes in disturbance regime affect *Acacia* life history strategies in Hluhluwe-Umfolozi Park, KwaZulu Natal, South Africa. Four functional groups are defined based on sprouting ability, bark thickness, seed mass, plant height and wood density. The functional groups are seen to reflect local disturbance regimes: *Acacia* species found in mesic, frequently burnt portions of the park sprout strongly as adults and/or are fire resistant, but are poorly defended against herbivory. Conversely, species found in more xeric portions, where fire frequency is lower, and herbivore densities higher, are fire-sensitive, well defended against herbivory and sprout weakly as adults.

Chapter 6 addresses whether plant ecological strategy schemes take sprouting into account as a key life history strategy. Westoby's LHS scheme, which comprises specific leaf area (SLA), plant height and seed mass, is of the more practicable existing plant ecological strategy schemes. I show that the LHS scheme does not consistently identify sprouting across genera or families. In general, basal sprouters tended to be shorter than congeneric reseeders, but there were no consistent patterns for SLA or seed mass. The results suggest that sprouting ability is mostly orthogonal to other life history traits and should be therefore considered as a separate attribute.

A published paper, which is ancillary to the main themes of the thesis, has been included as an appendix.

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INTRODUCTION

The ability to sprout is widespread in woody taxa, and virtually all angiosperm, and some gymnosperm plants are able to do so (Del Tredici, 2001, Bond & Midgley, 2003; Vesk & Westoby, 2004a). Typically, sprouting is only seen as an expedient manner in which plants recover their lost above-ground biomass after severe disturbance i.e. sprouting is only seen as an effective way for plants to recover. Certainly this may hold for some cases, but most often it is not as simple as this and sprouting may come in many guises. Sprouting ability varies between species, in type (Del Tredici, 2001), with plant age or life history phases (Peterson & Carson, 1996; Del Tredici, 2001; Bond & Midgley, 2003) and with disturbance severity (Bellingham & Sparrow, 2000, Pausas, 2001).

However, sprouting is important in ecosystems not prone to large scale disturbances that are traditionally not seen as disturbance driven. For example, Pauw *et al.* (2004) explored regeneration and sprouting dynamics of seedlings under closed canopy forests in Costa Rica and found that sprouting ability was critical in the survival of seedlings that are prone to damage from litterfall (Clark *et al.* (1991). Furthermore, Kruger *et al.* (1997) found sprouting to play an important role in forest dynamics in southern Cape forest, an ecosystem also not prone to large disturbance events. Also, rather than just sprouting in response to damage, plants may also respond to changes in light regime (e.g. Miura & Yamamoto, 2003).

Defining sprouting

Del Tredici (2001) succinctly defines sprouting as the production of secondary trunks as an induced response to injury or a dramatic change in surrounding environmental conditions. The development of form in trees is controlled by growth regulators that emanate from the distal tip of a shoot, through apical control. Some trees will produce secondary trunks naturally, but the vast majority will only do so when apical control is removed by an extrinsic factor (Del Tredici, 2001) i.e. by disturbance events such as fire, wind-throw or herbivory. Sprouting differs from clonal growth in that it does not imply the potential for vegetative spread (Del Tredici, 2001). Many more species are sprouters than clonal, although virtually all clonal species are sprouters (Bond & Midgley, 2001).

Del Tredici (2001) describes four basic types of sprouting: sprouts from specialised underground stems (e.g. lignotubers and rhizomes), sprouts from roots (root suckering), collar sprouts from the base of the trunk ("basal epicormic"), and opportunistic sprouts from layered branches. While sprouting from the base, from underground storage organs and aerial parts (branch epicormic) is often seen as a response to disturbance, root suckering and opportunistic sprouting from branches can often be regarded as a mode of regeneration (Bond & Midgley, 2003). Root suckering shrubs can produce sprouts spontaneously, but it is usually an induced response to either injury or changes in the environment. For example, *Dichrostachys cinerea*, a short multi-stemmed savanna shrub, can produce root suckers in response to changes in light regimes close to their roots (G. Hempson, unpubl. data).

Variation in sprouting

Sprouting ability varies with age (or size) of the plant and type and severity of injury as a consequence of disturbance (Bellingham & Sparrow, 2000, Del Tredici, 2001; Bond & Midgley, 2003). Most if not all woody plants can sprout as juveniles, but may lose this ability with age, especially gymnosperms (Del Tredici, 2001; Bond & Midgley, 2003). In fire prone shrublands, where often all the above-ground biomass is removed, sprouting ability (as adults) is often expressed as a binary state i.e. seeding vs sprouting (Keeley & Zedler, 1977, Bell *et al.*, 1984; Keeley, 1986; le Maitre & Midgley, 1992). However, once you move from these systems, the classification becomes more complex because of the variation in sprouting responses (see Bellingham & Sparrow, 2000), as a consequence of a broader range in disturbance regimes (Bond & Midgley, 2003; Vesk & Westoby, 2004). This then results in a continuum of responses (Vesk & Westoby, 2004).

While sprouting as a seedling or sapling is ubiquitous and important (Bond & van Wilgen, 1996; Higgins *et al.* 2000; Del Tredici, 2001; Pauw *et al.* 2004), the consensus is that it is best ot use adult behaviour as the best functional descriptor of sprouting ability (Bond & Midgley, 2003). Nonetheless, It is important to bear in mind the importance of sprouts in regeneration dynamics.

Terminology

The literature is fraught with confusion around the terms used to describe sprouting including, amongst others, reiteration, coppicing, resprouting and sprouting. These terms are often used interchangeably to mean the same thing i.e. producing shoots in response to disturbance or damage. Furthermore, terms like resprouting suggest producing these shoots only in response to disturbance, when plants may sprout in response to changes in the light regime or stress. Thus, for the sake of brevity and to avoid the associated semantic pitfalls I use the term sprouter. I mean it to include sprouting from underground organs, root suckering, collar sprouting, stem and branch epicormic sprouting and opportunistic" sprouting i.e. where plants sprout in response to changes in light regime rather than physical disturbance.

Sprouting and plant functional type schemes

Ecologists have long tried to classify of plants according to life history traits e.g. life forms (Raunkiaer, 1937), plant vital attributes, (Noble & Slatyer, 1980), strategies (e.g. Grime, 1979) and functional types (McIntyre *et al.* 1999) to name but a few. The primary aim of these schemes is to find functional descriptions of vegetation based on plant attributes that show a common response to the environment (Rusch *et al.* 2003). More specifically, these aims include: a) to understand important opportunities and selective forces that shape the ecologies of plants; b) to describe plant componentry of ecosystems in terms of a limited number of ecological component types (Westoby, 1998) e.g. Noble and Slatyer's (1980) "vital attributes", where species are categorised according to which of their life-history phases are present at different years after disturbance; and to determine species response rules in order to predict how species will respond to perturbation e.g. disturbance (fire, herbivory) and/or changing environments (e.g. Pausas, 1999). If these are consistent, then plant life history classifications can be used for predictions between regions and at global scales (Rusch *et al.* 2003).

Since sprouting is a key life history strategy trait, it is critical to see how it is incorporated into such schemes. While the field has advanced substantially, and the understanding of plant functional types is becoming more sophisticated, until recently, the inclusion of sprouting has been fairly limited in the mainstream literature. Sprouting has received attention in literature pertaining to fire-prone Mediterranean literature (Keeley, 1978; Le Maitre & Midgley, 1992; Zedler, 1995) it has only recently received broader attention (Loehle, 2000; Cornelissen *et al.* 2003).

Aims and rationale of this study

Sprouting is well reported in disturbance prone environments e.g. fire-prone Mediterranean-type ecosystems such as the kwongan (Specht, 1979; Hansen *et al.*, 1991), chaparral (Wells, 1969; Keeley & Zedler, 1978), fynbos (Kruger, 1979; le Maitre & Midgley, 1992) and hurricane (Bellingham *et al.*, 1994; Zimmerman *et al.*, 1994) or landslide (Sakai & Sakai, 1998) affected forests. Despite this, only relatively recently has the ecology of sprouting been considered in mainstream literature (Keeley & Zedler, 1998; Bellingham & Sparrow, 2000; Del Tredici, 2001; Midgley & Bond, 2001, 2003), and certainly little attention has focussed on less disturbance-prone environments such as old growth temperate forests.

For example, most work in forest regeneration in gaps in South Africa has concentrated on recruitment via seedlings. Gap theory suggests that the larger the gap the greater the importance of seedling establishment relative to ingrowth and understorey recruitment (Whitmore, 1982; Merrens & Peart, 1992). Cooper-Ellis *et al.* (1999) assessed regeneration after simulating hurricane damage in hardwood forests in Massachusetts, and found that sprouting and releafing of damaged trees accounted for far more stand basal diameter than recruitment, even after 6 years. Sprouting behaviour is an ecologically important trait for understanding vegetation dynamics but is still poorly described in many biomes (Bond & Midgley, 2003), and it is this that is the central focus of this study.

The aims of this thesis were to 1) explore the ecological role of sprouting as a life history strategy in three South African biomes; 2) assess the consequences of adopting a sprouting life history strategy at the individual, community and biogeographic levels; and 3) assess how sprouting correlates with other life history strategy characteristics.

Context for the study and thesis layout

Part 1: Forests

This study was conducted in Afromontane and Coastal forests of the southern Cape, which comprise by far the largest continuous patches of South African temperate forests (Midgley *et al.,* 1997). The forests of South Africa, although they cover a maximum area of only c. 0.5% of the total land area (less than 5000km^2), are considered to be the richest temperate forests per unit area in the world (Silander, 2001). Forests, for the purpose of this study, are defined as closed-canopied plant communities comprising mainly woody plants more than 5m tall (Midgley *et al.,* 1997). Forest distribution is generally determined by climate at a landscape scale (MAR of 650mm – 1800mm +). At a local scale, forests are restricted to mesic, fire-protected microsites (Midgley et al., 1997).

Forest species are generally fire retardant (van Wilgen *et al.*, 1990) and the forests of South Africa are generally not disturbance prone (Geldenhuys & Maliepaard, 1983), although invasion of surrounding vegetation is prevented by fire (Cowling *et al.*, 1997b). Thus, as previously mentioned, the majority of research into forest dynamics has focussed on gaps (Midgley et al. 1995a) and on shade-tolerance versus shade intolerance (Midgley et al., 1991, 1995b). Consequently, little has been done in these forests on the role of sprouting, as it is generally only seen to be response to severe disturbance (but see Kruger *et al.,* 1997). Chapter 1 firstly describes the trade-offs associated with sprouting and secondly, the role of sprouting as a key regeneration strategy in forests. Chapter 2 assesses the implications of sprouting for forest canopy tree species richness.

Part 2: Fynbos

The fynbos biome, much celebrated for its impressive floral diversity (8500 species in only 71 337 km^2), is found in the extreme south-western and southern parts of southern Africa (Cowling *et al.*, 1997a). It is found in winter rainfall areas and confined to ancient, sandy, infertile soils (Kruger, 1978). The vegetation is evergreen, fire-prone vegetation and is characteristically fine-leaved (hence the vernacular term meaning fine-leafed) (Cowling & Holmes, 1992; Cowling *et al.*, 1997a). The structure of fynbos vegetation is typified by the occurrence of restiods (evergreen graminoids), a high cover of ericoids (especially Ericaceae) and the overstorey proteoid shrubs (Kruger, 1979; Cowling & Holmes, 1992). Fynbos, described as a heathland (Specht, 1979), is similar in structure and function to kwongan of the of the mediterranean-climate region of south-western Australia (Cowling *et al.*, 1997a).

Fire plays an important role in fynbos ecology and has been a significant selective force in the evolution of plants' reproductive ecology (le Maitre & Midgley, 1992) e.g. serotiny, myrmecochory, heat-stimulated germination of seeds and in particular sprouting (Cowling, 1987; Le Maitre & Midgley, 1992; Bond & van Wilgen, 1996). Although the role of sprouting is well reported (le Maitre & Midgley, 1992), in chapter 3 and 4 I explore the importance of the ecological role of sprouting in relation to other fire life-history traits.

Part 3: Savannas

The savannas of South Africa are typical of savannas around the world in that they are characterised by a two-layered above-ground structure: a tree layer with a discontinuous crown cover 2-10m tall overlies a grassy layer 0.5–2m tall (Scholes, 1997). A key feature to these is a climate with a hot wet season and a warm dry season for the rest of the year (Nix, 1983). The strongly seasonal water availability leads to the accumulation of fine, dry, easily ignited fuels (Scholes, 1997), resulting in fire prone vegetation, which may experience fire return periods of between annual and 30 years (Bond & van Wilgen, 1996). Furthermore, Africa is home to some of the last remaining megaherbivores (species exceeding 1000kg) e.g. African elephant, black and white rhinos and hippopotamus, and other large grazers such as buffalo, which exert significant influence on savanna ecology through their feeding behaviour (Owen-Smith, 1988). Thus savanna trees are significantly exposed to both fire and mammalian related disturbance.

Research into the role of sprouting in savannas has focussed largely on juveniles (Bond & van Wilgen, 1996; Gignoux *et al.*, 1997; Higgins *et al.*, 2000). Sprouting as juveniles i.e. surviving the fire and herbivory trap (Bond & van Wilgen, 1996), has been implicated a being a critical for continued grass-tree coexistence in savannas (Higgins, et al., 2000), although little empirical work has been done. Also, sprouting ability as adults and where this might be important, has been largely overlooked. Chapter 5 assesses the sprouting ability of *Acacia* species as both adults and juveniles, and deals with the ecological role of sprouting relative to other life history strategy characteristics, and whether species can be grouped into functional types according to these disturbance-related life history traits.

Part 4: Plant ecological strategy schemes

Plant ecological strategy schemes (PESS) are useful in understanding important selective forces that shape plant strategies, describing vegetation according to plant life history strategy types and they are useful in determining how species respond to perturbation (Westoby, 1998). Given the importance of sprouting as a key life history trait, in Chapter 6 I assess whether general models of life history strategies are address sprouting adequately.

It should be noted that each chapter is written as a stand-alone paper, and each chapter has a more specific introduction to the relevant literature.

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1. Resprouters vs. reseeders in South African forest trees; a model based on forest canopy height[*]

ABSTRACT

This study assesses the importance of sprouting in South African forests. I expected tree species that regenerate primarily by sprouting to produce fewer seedlings than co-occurring species that regenerate mainly from seedlings, because of the trade-off between allocating resources either to ensuring vegetative reproduction (e.g. protective bark/latent buds) or to sexual reproduction (e.g. seeds). Furthermore, sprouting species, because of their generally multi-stemmed nature, should be at a relative disadvantage, and therefore, relatively infrequent, in tall forests. This is because a resprouting individual allocates resources to a number of basal branches/stems and buds rather than maximizing vertical extension of a single leader, as is the case in a seeder. Also, many tall stems arising from the same multi-stemmed base, as is the case in resprouters, will be relatively poorly supported in comparison to the single stem of a reseeder. To test these two ideas I surveyed a number of plots in a range of South African forests and thicket communities. I noted the numbers of seedlings and resprouts for each species and determined a mean for each site. Short forests and thickets were dominated by multi-stemmed species and there was an almost total absence of seedlings. In contrast, tall forests were dominated by single-stemmed reseeding species and were accompanied by seedlings.

INTRODUCTION

Forest trees may respond to damage or senescence either by producing new individuals (seedlings) or by resprouting from dormant buds below or above ground. Some species are also able to resprout from dormant buds continuously, rather than only resprouting after stress. While the role of

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[*] Adapted from Kruger *et al.* (1997)

sprouting is now widely acknowledged in tropical forests (Kauffman, 1991; Dalling *et al.* 1997, Kennard *et al.*, 2002; Pauw *et al.* 2004), some temperate forests (Bellingham *et al.*, 1996) and especially in forests susceptible to large scale disturbances (Bellingham *et al.*, 1994; Zimmerman *et al.* 1994, Miura & Yamamoto, 2003; Nanami *et al.*, 2004). However, little work has been done on the role of sprouting in temperate forests in South Africa. These forests, compared to many tropical forests, are less prone to stand replacing disturbance events (Midgley *et al.*, 1997), and here so the role of sprouting as a regeneration strategy has been largely overlooked.

Because sprouting species in South African systems often tend to be multi-stemmed (Midgley, 1996), their relative frequency will influence the architecture of the forest. In the pioneering work of Hallé *et al.*, (1978) on forest architecture, the term ‘reiteration’ was used to describe the process of architectural adjustment (‘branching’) during maturation from sapling to tree stage. In most cases reiteration corresponds with resprouting (e.g. from dormant buds after damage), although in some cases it refers to architectural modification which occur when a tree experiences supra-optimal conditions (e.g. a gap). They indicate that reiteration is a possibility for many architectural models, i.e. most trees. Hallé *et al.* (1978) also noted that the height at which trees first branch in a particular forest reflects post-disturbance processes at a site. Hallé *et al.* (1978) termed the line through a forest joining these points the ‘morphological inversion surface’.

Now that attention has been focused on resprouting and its architectural consequences, it remains to be seen just how important seedling regeneration is in comparison to persistence by resprouts, in relation to a range of forest types. In this chapter I propose a simple model of forest regeneration dynamics that incorporates both the reseeding and resprouting modes of regeneration. From first principles I make some predictions and then test these predictions in a range of forests in South Africa.

Predictions regarding seeders vs. resprouters

Although correlations between tree growth habit and environment exist (e.g. Horn 1971), the role of resprouting has not been sufficiently studied. I will first develop the argument that resprouters should be rare in tall forest and secondly that resprouters will only rarely produce seedlings.

In tall forests where the ability to grow tall is critical for potential canopy species, a resprouter is likely to be at a disadvantage for both resource allocations and structural reasons. Sprouters divert resources to developing, maintaining and protecting a bud-bank (see Vesk & Westoby, 2004a, for review) and allocating carbon to starch or other underground reserves (Pate *et al.* 1990; Bell *et al.*, 1996; Bell & Ojeda, 1999) instead of devoting it to vertical growth. There is, however, some debate about the cost of buds: Vesk & Westoby (2004a) argue that the buds themselves may not be energetically expensive, but rather it is the protection and supply of these that would be costly.

Furthermore, because sprouting species are often multi-stemmed in our systems, they also share their resources amongst several stems. Reseeding species, in contrast, can divert resources to maximizing rates of vertical extension of a single stem. Based on this resource allocation argument I suggest that reseeding species will be able to grow taller and/or faster than resprouters. Again, because of their multi-stemmed nature, each stem of a resprouter will be poorly structurally supported than will the single stem of a reseeder. This too will disadvantage resprouters in tall forests. The first prediction then is that sprouting species and multi-stemmedness should be more common in short forests than tall forests.

Resprouters should produce fewer viable seeds and seedlings than reseeders First, this is because parent resprouters must devote resources to maintaining and protecting latent buds. Second, this is because seedlings of resprouters will be less competitive because they too must allocate resources to developing and protecting buds rather than growing tall. These differences between resprouters and reseeders are well known for shrublands (e.g.

Hansen *et al.* 1991) but have not been well studied in forests. Reseeders thus have more resources to allocate to sexual reproduction and also their seedlings grow relatively rapidly because they too do not have to develop, maintain and protect a bud-bank. The second prediction is that seedlings of reseeding species will be more common than seedlings of co-occurring resprouting species.

To date there are only limited data to evaluate the above predictions in the context of forests. Midgley & Cowling (1993) noted that many species of the spinescent sub-tropical thickets of South Africa, a short (1.5 - 5m) type of closed canopy forest, are resprouters. Bellingham *et al.* (1994) noted that species that sprout strongly in a Jamaican forest typically produced few germinants. Evidence from South African thickets (Midgley & Cowling 1993) and in fire-prone shrublands (le Maitre & Midgley 1992), indicates that resprouters usually produce fewer seedlings than reseeders. Finally, Midgley (1996) noted that in a wide range of genera, the reseeders tended to be taller than the resprouters.

METHODS

Study sites

I sampled a range of forest and thickets along the southeastern coast of South Africa (Fig. 1). The strong environmental gradients in the region allowed us to sample a range of physiognomic and phytochorological types in a fairly small area (Cowling 1984). All sites sampled supported closed-canopy woody communities that remain relatively undisturbed by humans or large stand-replacing events like fire or hurricane-strength winds. Communities ranged from low (c. 2m) thickets of subtropical affinity to tall (c. 30m) Afromontane forests (Table 1; see Midgley *et al.* 1997 for further description). Variation in height of forest canopy is a consequence of site productivity (i.e. rainfall), slope, aspect and stress e.g. drought stress on deep sands and wind shear in less sheltered sites. Occasionally forest fringes may burn, but the forests are generally considered fire retardant (van Wilgen *et al.*, 1990).

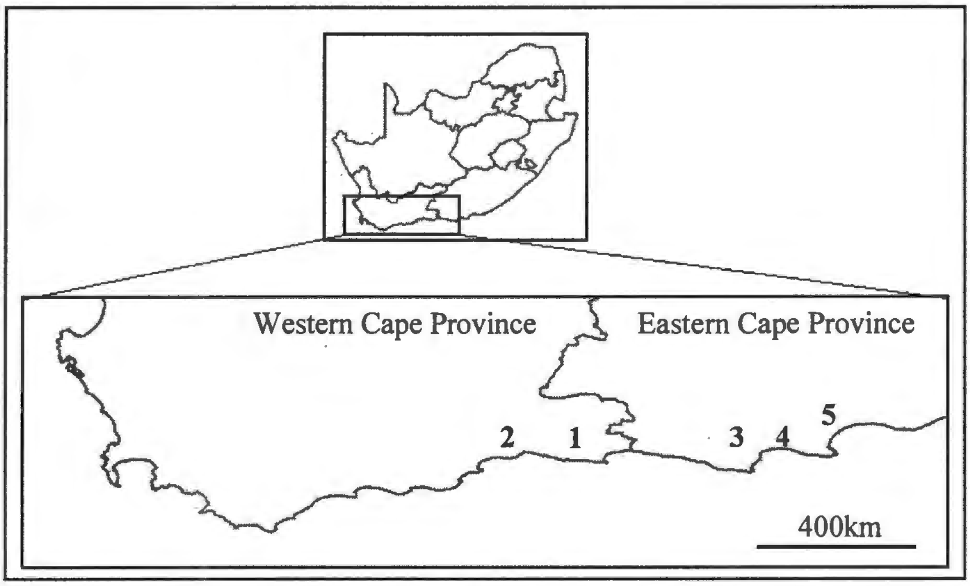

Figure 1. Map of the study sites. Area 1 includes Lilyvlei, Gouna, Diepwalle and Groenvlei. Area 2 includes Ebb & Flow, Beervlei and Holiday Inn. Area 3 includes Seal Point, St. Francis, Brandewynkop, van Stadens, Maitland and Nature Reserve. Area 4 includes the Gamtoos Valley and are 5 includes the Spring Nature Reserve.

Between two and seven plots of variable size (see below) were randomly located at each site. Sampling intensity within sites depended on the physiognomic variation encountered there. Because sites were long undisturbed by humans or stand replacing disturbance events, the physiognomic patterns reported are not the ontogenetic patterns of forest development directly after disturbance.

Sampling methods

Essentially, I was interesting in determining (1) how each canopy species was regenerating in terms of a ratio between the numbers of sprouts and seedlings it produced, (2) how this varied between forests and (3) how this influenced the incidence of multi-stemmedness in various forests.

There are difficulties in allocating species to the category of seeder or sprouter because this dichotomy is, in reality, a continuum. My field studies indicated that almost all trees are able to sprout to a lesser or greater degree.

Some sprouters may start off as being multi-stemmed but shed stems until they appear to be single stemmed. Furthermore, some weak resprouters may also produce seedlings. Thus, a seedling index (S.I), which takes into account the ratio of seedlings to sprouts, was used. Branching index (B.I.) reflects the degree to which trees in a forest are multi-stemmed. These two indices are further described below. A "regenerating individual" (R.I.) was defined as any stem between 10 and 50cm tall, regardless of whether it was a seedling (genet) or sprout (ramet). All regenerating individuals that were not obviously attached to parent plants were excavated, to determine whether they were seedlings or sprouts from a runner. Seedlings had no side connections with other individuals.

Obviously sprouting species are those individuals that only regenerate by the production of new stems into the canopy from underground organs (such as ligno-tubers) or even from lateral runners. Obviously seeding species are species which are always clean-boled, they never reiterate from buds or below ground level and generally they produce an abundance of seedlings.

A seeding index and branching index were then calculated on a per forest basis. S.I was computed as the number of seedlings/number of R.I. for each species. This was converted to a mean S.I. for each forest where S.I. (forest) = mean S.I. (species). A high S.I. value indicates a forest where most species produce more seedlings than sprouts.

The branching index was computed as the mean height of first branching/plant height for each species. The B.I. for each forest was computed as the mean B.I. for all species in that forest. Only individuals reaching the canopy were included in the analysis. A forest with a high B.I. is a forest largely composed of single-stemmed seeders, which branch near the canopy. Simple regression analyses were used to determine whether significant relationships existed between S.I., B.I. and canopy height.

Table 1. Details of the dominant species at each study site and rainfall (estimated from rainfall maps of Government printer)

Forest	**Rainfall (mm)**	**Dominant species**
Diepwalle	1200	*Olea capensis ssp. macrocarpa, Podocarpus latifolius*
Gouna	1000	*Pterocelastrus tricuspidatus, Faurea macnaughtonii*
Lilyvlei	900	*Olea capensis ssp. macrocarpa, Podocarpus latifolius*
Beervlei	1100	*Olea capensis ssp. macrocarpa, Podocarpus latifolius*
Ebb & Flow	700	*Podocarpus falcatus, Platylophus trifoliatus*
Holiday Inn	700	*Chrysanthemoides monilifera, Olea europea*
Groenvlei: Short	800	*Sideroxylon inerme, Maytenus heterophylla*
Groenvlei: Tall	800	*Celtis africana, Zanthoxylon capensis*
Seal Point	700	*Dovyalis rotundifolia, Schotia afra*
St Francis	800	*Pterocelastrus tricuspidatus, Olea exasperata*
Gamtoos: Medium	600	*Euphorbia triangularis, Aloe pluridens*
Gamtoos: Short	500	*Sideroxylon inerme, Euclea undulata*
Gamtoos: Tall	700	*Schotia latifolia, Calpumia aurea*
Springs	400	*Ptaeroxylon obliquum, Portulacaria afra*
Paradys	500	*Pterocelastrus tricuspidatus, Olinia ventosa*
Brandewynkop	800	*Pterocelastrus tricuspidatus, Zanthoxylon capensis*
van Stadens	800	*Vepris undulate, Eugenia zeyherii*

To obtain the above data the following arbitrary working definition was made: connected stems within a radius of 1/10 height of a main canopy constitute the same 'individual'. This definition was needed because some resprouters are particularly extensive and it is almost possible to determine where an individual begins or ends.

Plot size

Given the large range of canopy height of forests sampled, the plot size was scaled to the canopy height of a particular forest. This facilitates the sampling of similar numbers of individuals or stems. Not only is a scaled plot size sensitive to the size of the individuals involved but it is also sensitive to forest processes, such as rates of gap formation and relative gap dimensions. For example, it is the ratio of gap diameter to canopy height, rather than gap diameter alone, which is important in determining prevailing disturbance regimes (e.g. Midgley *et al.*, 1995a). The length of each side of the square plots used in this study was therefore scaled to be equal to the forest canopy height. For example, in a forest with a canopy height of 20m, the sizes of the plots laid out were 20m by 20m.

Plot data

Data were collected on actual or potential canopy species only (i.e. avoiding herbaceous, climbing and understorey species.) From each plot and for each species separately, the following data were collected: numbers of regenerating individuals (see R.I. above) and numbers of branches and stems for each individual already in the canopy. To determine the degree of multi-stemmedness, only those stems originating at or below ground level and that had already reached a canopy were counted. Unlike stems, branches originate at a point above ground level. The height of first branching was also noted by measuring the height of the point of intersection of the lowest two branches or stems (both of which needed to reach into the canopy before qualifying as a stem or branch).

RESULTS

There was a significant positive relationship between mean canopy height (log m) and the seeding index (S.I.) (Fig, 2) and between canopy height (log m) and branching index (B.I.) (Fig. 3). Thus reseeding species that branch near the canopy dominate taller forests. Mean number of stems per individual was negatively related to mean canopy height (log m) (Fig. 4). Again, single-stemmed species dominate the taller forests.

Table 2. Physiognomic and reproductive attributes of Cape forests.

Forest	Mean canopy height (m)	Mean first branch height (m)	Mean no. stems	Total no. plots	Total no. seedlings	Mean seedling density (m^{-2})	Total seeders (total spp.)
Gouna	29	22	1	3	296	0.16	17 (17)
Lilyvlei	29	17.5	1.1	2	561	0.45	11 (12)
Diepwalle	28	14	1.2	3	403	0.21	9 (14)
Beervlei	23	10.5	1.3	2	359	0.28	7 (14)
Van Stadens	15	6.5	1.7	3	157	0.23	8 (20)
Ebb & Flow	13	6.25	1.5	3	180	0.26	7 (12)
Nature Reserve	11	3.65	2.4	3	135	0.2	6 (20)
Brandewynkop	8.5	2,25	2.6	3	95	0.32	6 (10)
Groen: Med.	7.5	3	1.5	2	71	0.35	5 (7)
Maitland	6	0.16	4.6	2	3	0.01	2 (10)
Gamtoos: Tall	5.5	0.75	3.6	2	16	0.08	2 (12)
Groen: Short	5	0.75	3.8	3	140	0.46	5 (11)
Seal Point	4.5	0.5	4.3	3	50	0.16	2 (9)
Paradys	3.5	0.8	2.8	3	23	0.03	4 (15)
Gamtoos: Med.	3	1.5	3.1	7	11	0.06	1 (7)
Springs	2	0	8.1	6	0	0	0 (16)
Holiday Inn	1.5	0	3.1	5	0	0	0 (8)
Gamtoos: Short	1.5	0.25	5.1	5	6	0.3	3 (15)
St. Francis	1.25	0	5.8	5	0	0	0 (10)

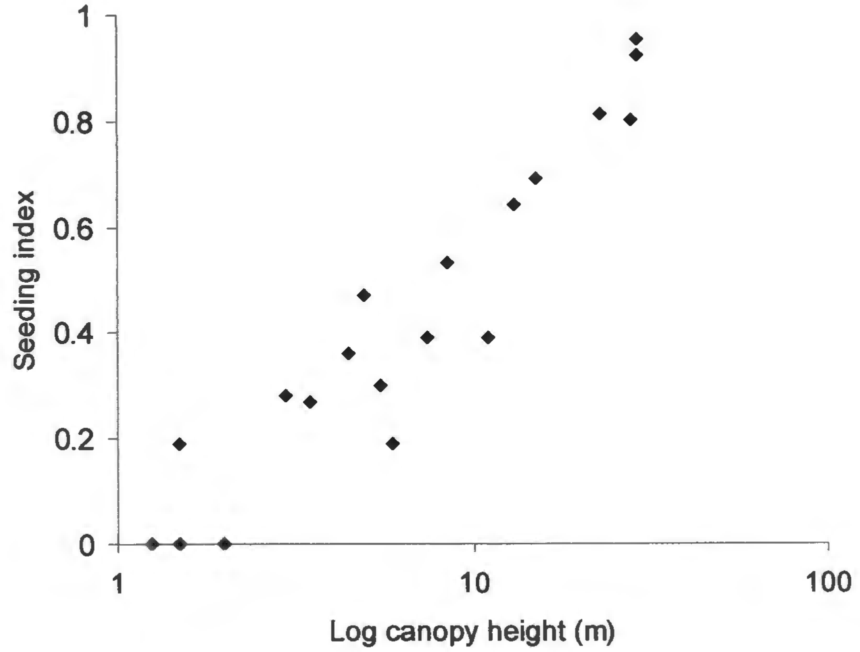

Figure 2. The relationship between seeding index and canopy height in some South African forests ($r^2 = 0.89$; $P<0.005$, $n = 19$).

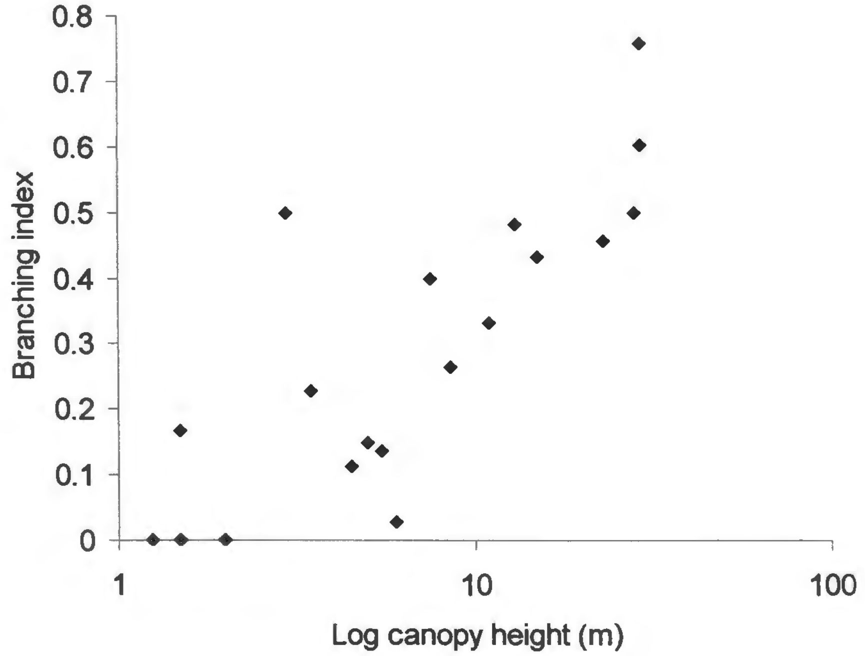

Figure 3. The relationship between branching index and canopy height in some South African forests ($r^2=0.65$; $P<0.01$, $n = 19$).

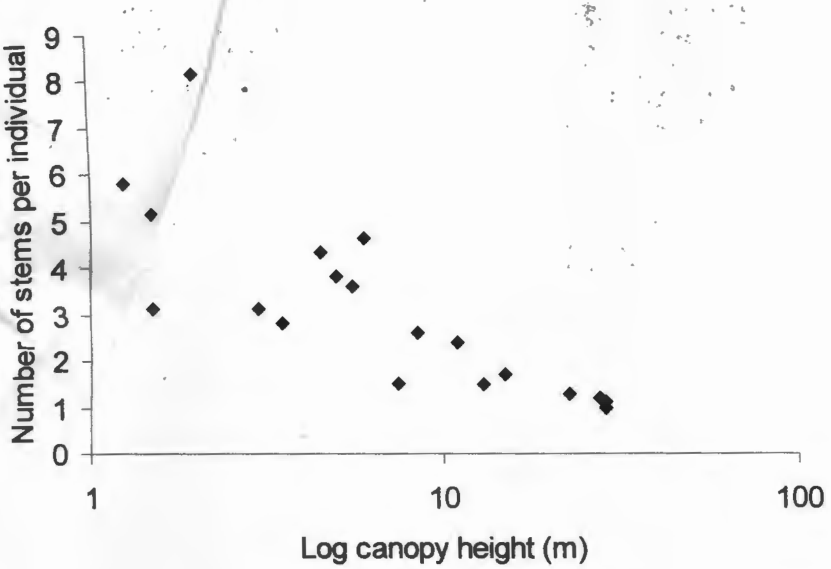

Figure 4. The relationship between number of stems per individual and canopy height in some South African forests (r^2=0.63; P<0.01, n = 19).

DISCUSSION

The results are consistent with the predictions stated that tall forests would be dominated by seeding species and short forests dominated by sprouters (Fig. 2). Thus, regeneration mode and the associated tree architecture vary with the height of the forest canopy. The B.I. is analogous to the morphological inversion surface of Hallé *et al.* (1978). The indications are that in mature forest it is not a fixed proportion, say 40% of the height of a forest, but is relatively lower in short forests (see Fig. 3).

Some species occurred in a range of forests and displayed a plasticity of reproductive and growth characteristics depending on local conditions. *Sideroxylon inerme* (Sapotaceae) occurred as a multi-stemmed resprouter with no seedlings in short forests but in taller forests it tended to be single stemmed and produced seedlings. *Pterocelastrus tricuspidatus* (Celastraceae) is primarily sprouts in the short dune forests near Wilderness, while in the Knysna forests at Lilyvlei it apparently relies mostly on seedlings as a means of regeneration. Further research is necessary to ascertain whether these differences are phenotypic (e.g. lack of apical dominance in short forest individuals permits continued multi-stemmedness) or genotypic (e.g. an evolved resprouting response in forests historically kept short by factors such as aridity).

No matter what the underlying cause is of the above empirical relations, I believe this model is important and also useful to forest conservation and management. First, it is relatively simple to use and suggests a non-floristic assembly rule based on forest physiognomy. Sprouting species dominate short forest and seeders dominate tall forests. This study is, however, restricted to South African temperate forests, and the predictions are probably limited to fine-grained forests (Midgley *et al.*, 1991; 1995a) i.e. systems that are driven by endogenous growth and recruitment processes in which resource supply proves the ultimate driver for forest ecology so that trees mostly die competing for these resources (Phillips *et al.*, 2004). Nonetheless, these patterns are worth exploring in other systems.

Second, it may help to provide a framework for predicting and interpreting forest dynamics, such as indicating those forests where gaps will frequently be colonized by resprouts as opposed to saplings. Also, conservation efforts may need to be focused on tall forests where relatively more species appear to regenerate by seedling recruitment. It is here that changes, such as patterns of herbivory, disturbance and predation, may most influence future composition. For example, Midgley *et al.* (1995b) expressed concern at the apparent absence of regeneration of some trees in southern African forests. They speculated that there might be some recent changes in disturbance regimes in these areas. However, in retrospect, it is clear that some of the species with apparently low levels of seedling regeneration are actually resprouters. These species may this persist by resprouting and a relative absence of seedlings may not be cause for concern.

Finally, I concur with Zimmerman *et al.* (1994); Bellingham & Sparrow (2000); Bond & Midgley (2003) and Vesk & Westoby (2004b) that the ability to resprout is an important life-history attribute, particularly in less disturbance prone environments. The relative importance of sprouting vs. reseeding for forest trees needs more attention, particularly in less disturbance prone as South African temperate forests. Forest ecologists have collected considerable data on other aspects of tree reproductive biology, such as seed banks, dispersal and seedling gap requirements, but very little information is available on the importance of resprouting. This bias towards recruitment of genets rather than persistence of ramets is reflected in some studies on reproductive traits of forest trees (e.g. Ibarra-Manriquez & Oyama 1992) which have not even taken into account whether a tree sprouts or not. Bond (1994) suggested that the possibility of cascading extinctions in plants, owing to extinction of mutualists, will only occur in those species that are seed limited (i.e. the non-sprouters). In the short term, conservation efforts should be concentrated on those species which cannot sprout and those forests that are dominated by reseeding species. I predict that these will be the taller forests.

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2. The influence of sprouting forest canopy species on richness in southern Cape forests, South Africa*

ABSTRACT

In this study I test the hypothesis that forests dominated by sprouting species will support fewer species due to the reduction in individual turnover and hence forest dynamism. I investigated the relationship between species richness and numbers and types of individuals and species present in forests with different physiognomies, in the southern Cape Province, South Africa. To control for the effect of scale, data were collected from three different "plot" types: 400m^2, canopy scaled (plot length is directly proportional to canopy height) and per 100 individuals closest to a point. Canopy species richness was inversely proportional to the abundance of sprouting species. The strength of the relationship between the abundance of sprouting species and canopy species richness increased progressively from the 400m^2 plots to the canopy scaled plots and finally to the plots of 100 individuals. Sprouting species abundance decreased, whilst canopy species richness increased, with increasing canopy height. Sprouting species are able to retain their in situ position in the forests for longer periods of time than do reseeding species. This reduces individual and species turnover, thus reducing species richness in sprouter dominated forests.

INTRODUCTION

Many factors have been shown to influence species richness e.g. environmental factors (soil nutrient-status, productivity), top-down controls (Terborg, 1992), disturbance history (Connell, 1978) and speciation/extinction scenarios (Cowling *et al.* 1997), but the possibility that sprouting may be among them has been given little consideration. Recent ideas concerning plant richness may be further

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* Adapted from Kruger & Midgley (2001)

influenced by considering the ability of some plants to sprout and how this would influence forest dynamics and consequently species richness. Firstly, forests with high dynamism (mortality and growth of new individuals) have higher richness than less dynamic systems (Phillips *et al.* 1994). Based on this correlation, I predict that forests dominated by sprouters should have low richness because sprouting plants have low dynamism (especially mortality).

Secondly, recent debate has surrounded the role of numbers of individuals in determining species richness (Oksanen, 1996, 1997; Schiel *et al*, 1999, Henry *et al.* 1999). Oksanen in his "no-interaction model" proposes that a fixed plot size does not allow for the change in size of plants or numbers of individuals with different plant physiognomies. For example, in short vegetation a fixed plot size would possibly sample more individuals than the same plot size would in tall vegetation (i.e. high biomass). Henry *et al.* (1999) support Oksanen's argument to a degree, but argue that factors affecting stand density, such as fertility, are the prime determinants of local species richness. In essence, they suggest that if number of individuals sampled remained constant, then species richness should not differ. However, numbers of individuals depends not only on size of plot and the plants concerned, but also on the presence of sprouters. For example, a single sprouter or clonal plant could occupy an entire plot and thus reduce local diversity at the plot level, but not necessarily at the level of a fixed number of individuals.

The study concerns forest species richness at the plot level and the effect that the abundance of sprouting species has on diversity patterns. The importance of sprouting as a means of regeneration after disturbance or as a form of persistence is now well established in forest ecosystems (Bellingham *et al.*, 1994; Zimmermann *et al.*, 1994; Sakai *et al.*, 1995, 1997; Kruger *et al*, 1997; Bellingham & Sparrow, 2000; Bond & Midgley, 2001). What is not known is how forests with different abundances of sprouters differ in richness (Bond & Midgley 2001). In the previous chapter, I noted that the percentage of sprouting species in Cape forests was negatively correlated with canopy height (Kruger *et al.*, 1997). In essence, taller forests were dominated by species that reproduced by seedlings, whereas shorter forests were dominated by species that are able to sprout and in those forests the occurrence of seedlings was rare.

METHODS

Study sites

The study was conducted in a range of forests throughout the western, southern and eastern Cape Province, South Africa (Figure 1). The 19 study sites, all supporting closed-canopied woody communities, ranged from low (approx. 3.5m) subtropical coastal thickets to tall (approx. 30m) close-canopied Afromontane forests. Sampling was restricted to essentially closed-canopy parts of these forests.

Sampling methods

Plot size and number

Three different sizes of plots were sampled in each of the forests, namely fixed 400m^2 square plots, canopy scaled plots (the length of the square plots was equal to the height of the canopy) and plots of 100 individuals (closest to a point). The different plot sizes were used to control for the effect of scale on diversity (see Oksanen, 1996), thus plots scaled to the height of the canopy are sensitive to the size of the trees. Three replicates of each plot type were randomly located throughout each forest.

Sampling was restricted to only those woody species that potentially form part of the canopy. Thus herbaceous, climbing and understorey plants were excluded. For each species, the following data were collected: number of stems per individual, diameter at breast height (DBH) (of each of the stems), height and primary regeneration mode (seedlings and sprouts).

Given that some plants can root sucker, it is potentially difficult to determine where one individual starts or ends and thus what constitutes an individual. There were relatively few root-suckering species in our study area and for them we formulated a number of rules for sampling.

Preliminary excavations were made to determine whether individuals were connected underground, thereafter for suckering species all potentially connected stems falling within a radius of 1/10 of the height of the main stem were considered to be from the same individual. Stems were only counted as "stems" if they originated close to the base (<10 cm) and they reached the canopy i.e. small branches and "agony shoots" (sprouts that stressed plants produced that were unlikely to reach the canopy) were ignored.

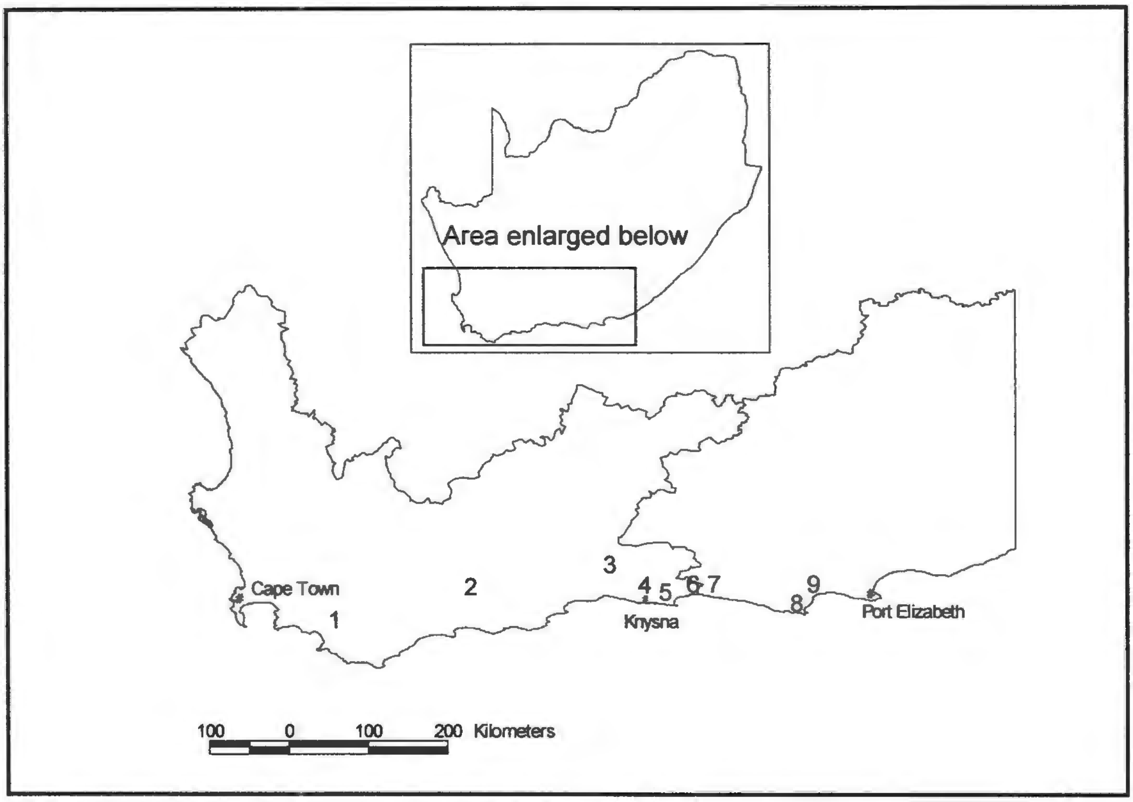

Figure 1. Map of study sites within the eastern and western regions of the Cape Province, South Africa.

1: Stanford forests: Grootbos, Kleinbos, Steynsbos and Platbos (4); 2: Grootvadersbos forests: Boosmansbos, Grootvadersbos, tall (2); 3: Biervlei forest (1); 4: Knysna forests: Diepwalle medium moist, Diepwalle moist, Ysternek (3); 5: Harkerville forests: Harkerville medium moist, Harkerville dry (2); 6: Crags forest (1); 7: Natures Valley Forests: Rugbos, Natures Valley medium, Natures Valley short (2); 8: St Francis Forests: short thicket forest, Brandewynkop forest (2); 9: Paradysstrand thicket forest (1);

Figure in brackets is the number of forests per labelled site

Sprouting versus reseeding is not a binary attribute, but is a continuum with weak sprouters being intermediate. To deal with this a regeneration mode was determined for each species by taking into account the degree of multistemmedness as well as the incidence of seedlings

The seeding index (SI) is the ratio between ramets (sprouts [re]) and genets (seedlings [se] up to 50cm tall) relative to total numbers of regeneration individuals per species i.e. SI = Se / (Se + Re) (see Kruger *et al*, 1997 for more details). Multistemmedness was calculated as the mean number of stems per individual per species. Species were then divided into three classes and assigned a regeneration index according to their predominant mode of regeneration.

The regeneration index (RI) was assigned according to the following rules:

Obligate sprouting species (RI of 1):
Species with low SI (0 to ≤ 0.25 i.e. a high proportion of sprouts to seedlings) and high degree of multistemmedness (> 2.5 mean stems per individual).

Reseeding species (RI of 0):
Species that rely predominantly on seedlings i.e. high SI (≥ 0.75) and low multistemmedness (1 to ≤ 1.5 stems per individual)

Facultative seeding/sprouting species (RI of 0.5):
Species with intermediate SI (0.25 to < 0.75) and intermediate degree of multistemmedness (> 1.5); species with high SI (≥ 0.75) and high degree of multistemmedness (> 2.5 stems per individual)

For example, *Olea capensis* subsp. *macrocarpa* (C.H. Wr.) a species that relies primarily on seedlings and is predominantly single stemmed, was assigned a RI value of 0. *Sideroxylon inerme* L., on the other hand, rarely produces seedlings and is generally multistemmed, and was therefore assigned a RI value of 1. *Pterocelastrus tricuspidatus* (Lam.) Sond. relies on both seedlings and sprouts and the degree of multi-stemmedness varies and it was therefore classified as a facultative seeder-sprouter.

Regeneration mode was reassessed for each species in every forest, since it is often not a fixed characteristic. For instance, *Pterocelastrus tricuspidatus* (Lam.) Sond. is largely a reseeding species in taller forests and a basal sprouter in the more disturbed canopied forests. Likewise, *Eucalyptus leucoxylon* (F.Muell) is a monopodial, reseeding tree of up to 30m on relatively fertile soils at 1000 mm annual rainfall, but becomes a short multistemmed mallee form on infertile soils at 400 mm rainfall (Specht, 1972).

Forest species richness was compared to the degree of multi-stemmedness (calculated as an average for the forest based on per species means), the abundance of sprouters and height of the canopy. The relative abundance of sprouters in a forest was calculated by determining the total basal area of each species and by multiplying it by the regeneration index (RI). Thereafter abundances were converted to percentages data and then arcsine converted to normalise the data for statistical analysis. Results were similar for analyses of data from all three scales; for brevity I have mainly reported results from plots involving 100 individuals.

RESULTS

Canopy tree species richness decreased with increasing abundance of sprouting species in all three plot types sampled (Fig 2 A,B & C). Tree canopy richness was lowest in the $400m^2$ plots, marginally greater in the canopy scaled plots (which varied from 16 m^2 to 784 m^2) and greatest in the 100 individual plots (Table 1). Not only did richness decrease with increasing abundance of sprouting species but also as these increased as a proportion of the species present in a forest (Fig. 3).

There was a significant negative relationship between the height of forest canopy and the abundance of sprouting species (Fig. 4). Thus, short forests support an abundance of multi-stemmed species, while taller forests were dominated by single stemmed individuals (Fig. 5). Furthermore, the taller canopied forests were more species-rich than the shorter forests (Fig. 6). These findings were supported by multiple regression analysis, with height and sprouting species abundance (percentage data arcsine transformed) as independent variables, and species richness as the dependant variable (Multiple $r = 0.974$, $r^2 = 0.94$, $B_{(height)} = 0.46$, $B_{(sprouting)} = -0.53$, $P < 0.01$. Data from 100 individual plots used in the analysis). Thus, as canopy height increases, sprouting species abundance decreases and canopy tree species richness increases.

Table 1. General data from study sites indicating site name, forest type, location, forest canopy height (Ht) and species richness (as calculated by the three different plot types: 400 m^2 square plots, canopy scaled plots (C.S.) and plots of 100 individuals). Canopy scaled plot sizes were calculated by using the height of the canopy as the length of square plots.

Forest	Forest type	Ht	Location	Species richness		
				400 m^2	C. S.	100 ind.
Diepwalle M	M Afro	28	33 56 19 S 23 08 02 E	11.7	12.7	17.3
Diepwalle MM	MM Afro	28	33 57 00 S 23 09 50 E	11.3	15.3	17.3
Beervlei	MM Afro	27	33 55 50 S 21 43 31 E	16	17	17
Hakeville, MM	MM Afro	27	33 04 05 S 23 13 46 E	15.7	19	17
Rugbos	M Afro	26	33 57 S 23 39 24 E	14.7	16.7	17.3
Grootvadersbos	M Afro	26	33 57 12 S 20 49 07 E	13.3	15.7	17
Ysternek	W Afro	20	33 54 41 S 23 10 49 E	8.3	12	12
Hakeville Dry	D Afro	20	33 04 29 S 23 14 25 E	14	14	14.7
Crags	D Afro	20	33 57 25 S 23 26 48 E	16.3	16.3	16.6
Natures medium	M Afro	17	33 58 28 S 23 34 21 E	14.3	14	15.7
Boosmansbos	D Afro	14	33 57 06 S 20 49 07 E	12.7	10.7	12.3
Van Stadens	D Afro – Alexandria	14	33 54 48 S 29 11 32 E	9	11	13
Platbos	D Afro	9	34 34 05 S 19 10 38 E	10	9	13
Brandewynkop	Sub. Dune Forest	8.2	24 03 56 E 34 07 17 S	4	4	4.3
Natures short	D Afro	7	33 59 23 S 23 32 46 E	8.3	6	8.3
Grootbos	A - TP Th	5	34 33 51 S 19 09 45 E	4.7	3.3	6
Paradys	Th	4	34 05 35 S 24 55 21 E	8	4	4.7
Kleinbos	A - TP Th	4	34 34 25 S 19 09 37 E	4	3.3	5
Steynsbos	A – TP Th	4	34 31 48 S 19 09 32 E	5	3.3	8
Seal Point short	Dune Thicket	4	34 10 30 S 24 48 48 E	5	3.3	5.3

D Afro: Dry Afromontane forest, *MM Afro*: Medium Moist Afromontane forest, *M Afro*: Moist Afromontane forest; *W Afro*: Wet Afromontane forest; *A - TP*: Afromontane - Tongoland-Pondoland subtropical thicket; *Th*-thicket; *Dune Thicket*: subtropical Dune Thicket; *Sub. Dune Forest*: Subtropical Dune Forest; *D Afro – Alexandria*: Mixed Dry Afromontane - Alexandria Forests.

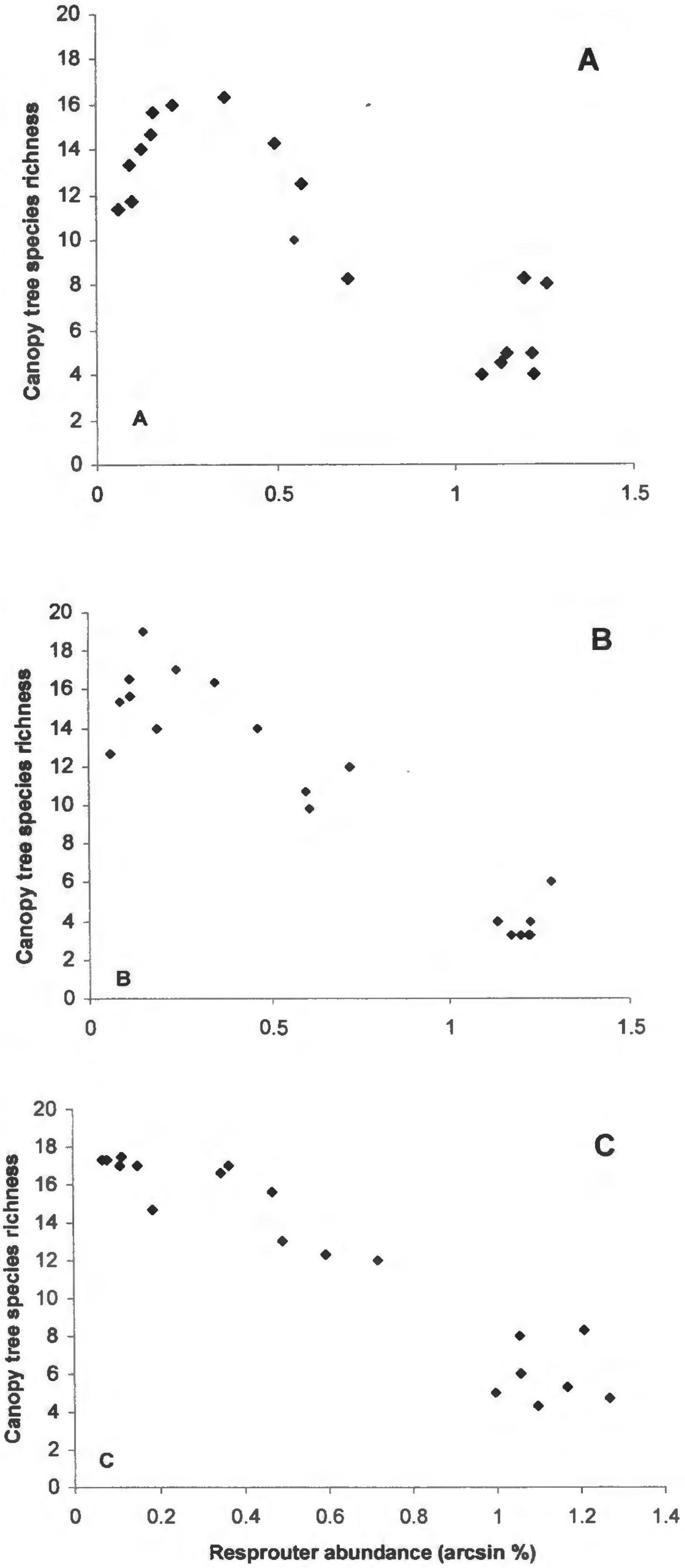

Figure 2. The relationship between mean sprouter abundance and mean canopy tree species richness, south-eastern Cape, South Africa. A) 400 m^2 plot data (r^2=0.76, p< 0.05), B) Canopy scaled plots (r^2=0.89, p< 0.05) and C) 100 individual plots (r^2=0.91, p< 0.05) all n = 19.

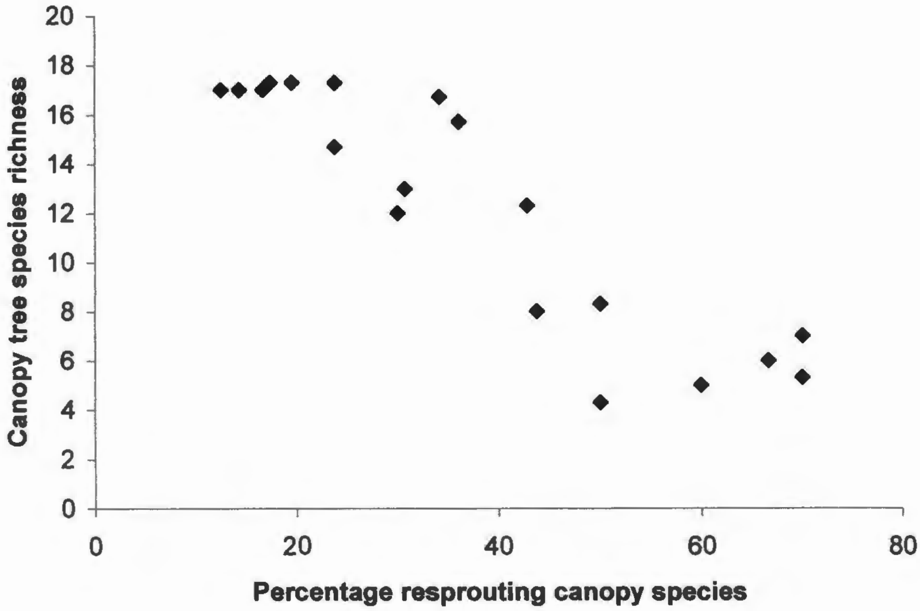

Figure 3. The relationship between mean percentage sprouting species and mean canopy tree richness. Data used in regression analysis, derived from 100 individual plots, were arcsin transformed to normalise the data ($r^2=0.81$, $p< 0.05$; n = 19).

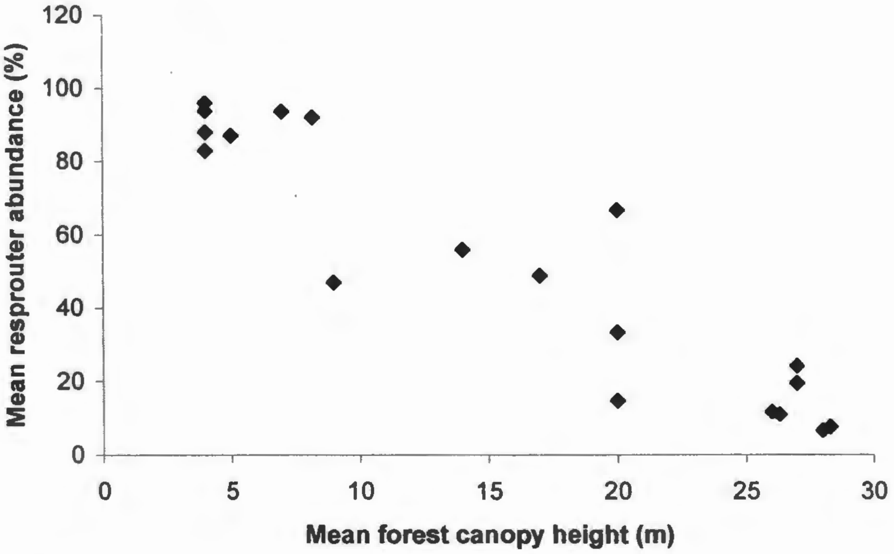

Figure 4. The relationship between mean forest canopy height and mean sprouter abundance. Data from the 100 individual plots were used for this analysis ($r^2=0.86$, $p< 0.05$; n = 19).

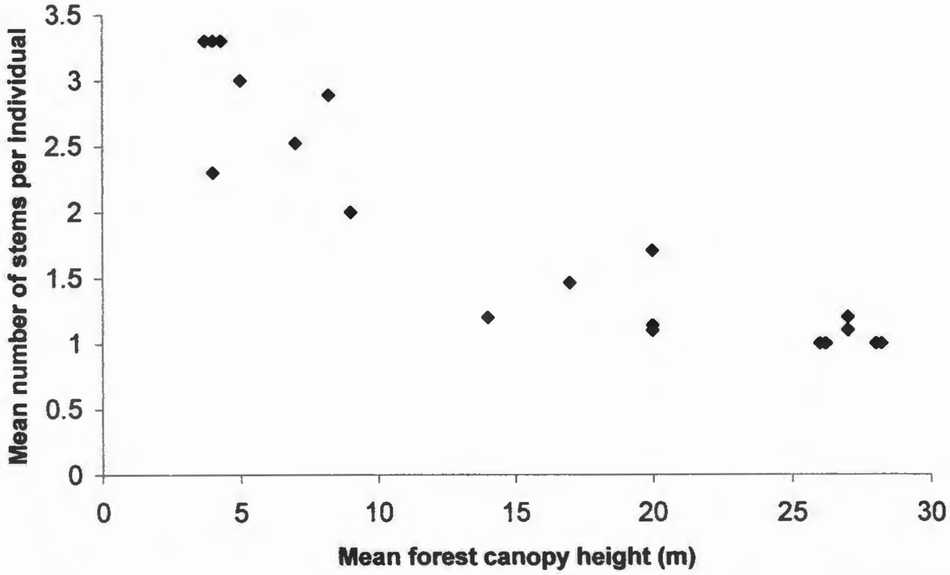

Figure 5. Relationship between canopy height and multi-stemmedness (mean number of stems per individual) (r^2=0.86, $p< 0.05$; n = 19). Data from 100 individual plots were used for the analysis.

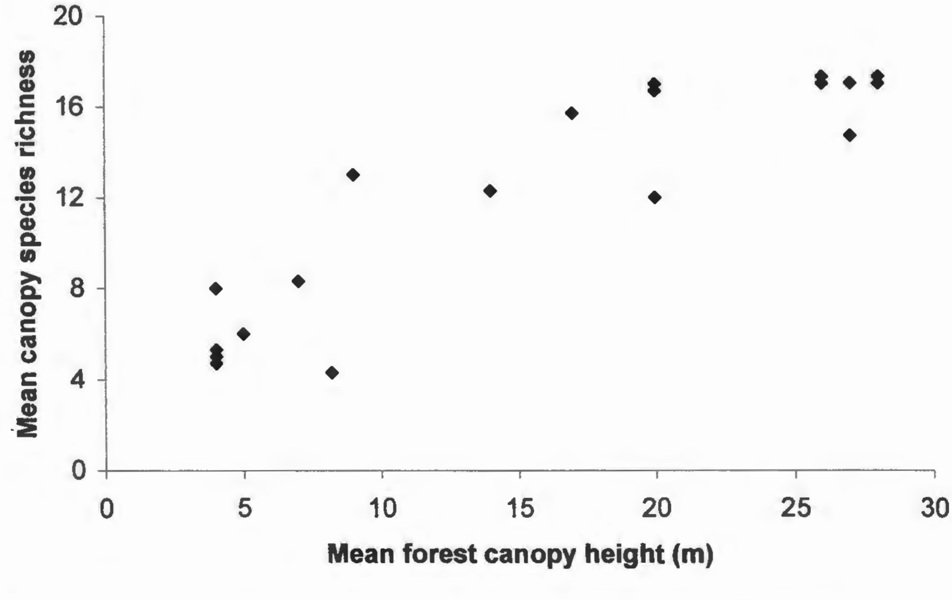

Figure 6. Relationship between species richness and forest height (r^2=0.83, $p< 0.05$, n = 19). Data from the 100 individual plots were used for this analysis.

DISCUSSION

That the presence of spouting species appears to depress local species richness and at all scales (Fig.2), suggests that richness in these forests is not an artefact of plot size. What is remarkable is that the pattern is consistent across the scale range of plot measured i.e. that plots scaled to canopy height can be used as effectively as plots based on measuring 100 individuals. This would suggest that scaling plots to canopy height is an appropriate and perhaps more efficient way of analysing forest dynamics. Furthermore, Phillips *et al.* (1994) in their world-wide analysis of tropical forest richness and dynamics, kept numbers of individuals sampled at a constant 500, yet species richness varied amongst forests. This is further evidence that variation in richness in forests is not an artefact of plot size and thus a rejection of the Oksanen hypothesis.

Sprouting is an efficient mechanism by which plants regain or retain aboveground biomass after disturbance, thereby maximising temporal occupancy of a site. Sprouters can potentially persist indefinitely *in situ*. High abundance of sprouting species may thus result in a slower turnover of species as a consequence of reduced mortality i.e. a less dynamic forest (*sensu* Phillips *et al.* 1994) relative to non-sprouter dominated forests. This argument is consistent with the low richness, at all scales, of Cape forests dominated by sprouting species. The dynamism argument of forest diversity (Phillips *et al.*, 1995) has been criticised for, amongst other reasons, that forests with a more rapid dynamic are merely speeded up version of slower forests (Sheil, 1995, 1996). Under these conditions, “faster” dynamics should increase any progression to competitive exclusion. Therefore more productive sites with higher dynamism shouldn't necessarily support more species. While this debate still continues (e.g. Condit, 1997; Phillips & Sheil, 1997; Lewis *et al.*, 2004), I feel that the concept remains relevant particularly when considering systems dominated by sprouting species i.e. sprouting would still have impact on dynamism by reducing individual mortality and therefore in this case, result in a true reduction forest turnover and therefore dynamism.

This pattern of canopy species richness decreasing with increased sprouting species abundance and decreasing canopy height is of potential interest to management authorities. The taller forests dominated by reseeding species would seem to be richer in canopy tree species and, therefore, according to biodiversity driven conservation priorities, would necessitate greater conservation efforts. Furthermore, since these taller forests are dominated by reseeding species, which are probably less resilient to large-scale disturbance, this would reinforce the need for greater levels of management.

I suggest that the abundance of respouting species needs to be incorporated into models of forest species richness. Cape shrublands are well-known for high species richness (Cowling *et al.* 1997) and a high proportion of non-sprouting shrub species (Le Maitre & Midgley 1992). Does this pattern of higher richness in non-sprouting communities apply in other, especially forest, systems?

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3. Proteaceae life history strategies in relation to fire: bark thickness and sprouting ability as key defining traits.

ABSTRACT

Plants in fire-prone ecosystems can survive fires by 1) resisting fire though thick bark, 2) recover through sprouting or 3) perish and reproduce through seed production. Nineteen Proteaceae species were classified into functional groups according to their bark thickness attributes, their mean adult size and sprouting ability in order to describe life history strategies in relation to fire. Thick bark (and hence resistance) can be achieved in several ways: having inherently thick bark, acquiring it quickly or by growing large. Sprouting strategies included epicormic sprouting from aerial parts and basal sprouting from rootstocks. Five functional groups were determined. Resisters comprised thick-barked epicormic sprouters, thick barked reseeding species and thin barked species that acquire resistance by growing large. Non-resisters include thin-barked basal sprouters and thin barked seeders that perish and recruit after fires. I predict that species with greatest resistance to fire i.e. thick bark, are to be found in areas characterised by either high frequency and/or low intensity fires. Conversely, non-resistant thin-barked species are found in areas of high fire intensity.

INTRODUCTION:

Fire is recognised as an important process in ecosystem functioning in biomes throughout the world, even in those not considered fire prone (Gignoux *et al.*, 1997). Plants can survive fires by developing resistance, lose their aboveground biomass and sprout basally, or perish and recruit through seedlings (le Maitre & Midgley, 1992; van Wilgen & Forsyth, 1992). In woody plants, survival depends both on the extent to which the live crown is scorched and the survival of stem and root tissue.

In characterising tree resistance to fire, a number of bark characteristics have been studied: bark thickness (Pinard & Huffmann, 1997, Uhl & Kaufmann, 1990), bark specific gravity, moisture content and physical structure (texture, anatomy, fissuring and scaling) (Pinard & Huffmann, 1997). Thermal diffusivity has been reported as nearly constant over a wide range of density, moisture content and temperatures (Uhl & Kaufmann, 1990). Small differences in bark thickness produce large differences in fire resistance, since duration of a heat pulse is proportional to the square of the bark thickness (Hare, 1965; Ryan & Reinhardt, 1988). Pinard & Huffmann (1997) found that species with thicker bark take longer to reach peak cambial temperature and had lower peak temperatures than thin barked species. Thus bark thickness is the key defence against fire damage.

There are three ways in which plants can develop thick bark. Firstly, plants can achieve resistance through early commitment of resources to thick bark (Pinard & Huffmann, 1997; Masaka *et al.*, 2000). Secondly, plants can acquire thick bark by continuous, high allocation of resources to bark i.e. acquire thickness rapidly, despite initial thinness. Lastly, thick bark can be achieved through simply growing large i.e. continuous development of bark thickness with increased stem diameter (Gignoux *et al.,* 1997).

An understanding of ontogenetic changes in allocation to bark thickness can provide insight into allocational patterns and hence plant strategies, as well as the ambient disturbance regime. Jackson *et al.* (1999) modelled the relative advantages of negative (early defensive investment) versus positive (delayed defensive allocation) allometry in bark thickness in *Quercus* and *Pinus* species. Species displaying positive allometry are characterised by a convex (logarithmic) shaped relationship between stem diameter and bark thickness, and those displaying negative allometry, a more concave (exponential) curve. They found that negative bark allometry and thick sapling bark were associated with habitats characterised by frequent low intensity burns, where the ability to resist fire early in their lifespan is key to survival. Thus the timing of allocation to defences i.e. the allometry of constitutive defences, would have significant bearing on species' strategies.

Presumably the development of bark thickness as a defence would come at an allocation cost to plants (Loehle, 1988, Bond & Midgley, 1995). Therefore, there should be a range of trade-offs between allocation to growth, defence and reproduction, resulting in a variety of plant life history strategies. Bark thickness thus might provide key information about plant life histories (see also Cornelissen *et al.*, 2003) and in particular their regeneration strategies.

Fynbos, in common with other heathlands worldwide, is subject to recurrent fires (Kruger, 1979). However, despite the important role that fire plays in Fynbos ecology (Kruger, 1977, Cowling, 1987a, 1987b), little is known about variation in bark thickness in Fynbos species, other than a brief description in Kruger (1979). For example, it has been suggested that species such as *Leucospermum conocapodendron* subs *conocarpodendron* and *Leucadendron argenteum* have thick bark (Rourke, 1972; Kruger, 1979; Bond & Midgley, 1995). However, these are thick-stemmed species and it is possible that their thick bark is merely an allometric consequence of greater girth. Fynbos is a worthwhile system for exploring the importance of bark thickness because plants adopt a range of strategies from those that lose above–ground biomass through to those that survive.

Bark thickness alone, however, is not enough to separate species into fire response strategies because sprouting is another key strategy employed by fynbos plants, and it may or may not be related to bark thickness. Sprouting strategies include above-ground sprouting i.e. from aerial parts of the plant from epicormic buds or below-ground sprouting, including from lignotubers, burls and corms, or simply from the base of the stem (Manders & Cunliff, 1987; le Maitre & Midgley, 1992; van Wilgen & Forsyth, 1992, Schutte *et al.*, 1995, Bond & van Wilgen, 1996; Strasser *et al.*, 1996).

Within the context of Proteaceae, I ask the following questions:

1. How do species differ in acquiring thick bark (e.g. constitutively or allometrically)?
2. How does bark thickness correlate with other fire survival strategies such as sprouting?

METHODS

Study site

Fynbos communities: Cape Peninsula

The study sites were located in mountain and sand-plain fynbos communities throughout the Cape peninsula, western Cape Province, South Africa (Figure 1). The climate is typically Mediterranean-type (winter rainfall and summer drought), and the soils nutrient poor. The fynbos biome is dominated by members of the Proteaceae, Restionaceae, Ericaceae and Asteraceae. Here I chose to conduct our study on a range of 17 species (of 6 genera) within the Proteaceae which display a variety of fire life histories.

Savanna communities: eastern Cape Province:

I further included *Protea caffra* and *P. roupelliae* subsp. *roupelliae* found largely in the moist savannas of the eastern Cape Province. Plants were sampled from sites at Mkambati and Sethlabathebe, in the eastern Cape Province, South Africa (Figure 1). These species experience frequent surface fires that seldom reach the canopy.

Sampling was restricted to locations of similar slope and aspect at each of the study sites (except the savanna proteas). Where possible, sites were selected to include as many species as possible in order to minimise local edaphic and climatic effects. The selected species were chosen so as to cover a range of regeneration strategies, including basal sprouting, aerial (epicormic) sprouting and reseeding. I sampled from communities that were between 8 and 25yrs old, (the average inter-fire period in fynbos communities) to ensure that I assessed populations that would be considered of average age. Sampling younger stands would result in an underestimating of the adult size, whilst sampling older, moribund stands would overestimate this value. When sampling the larger proteas e.g. *P. nitida*, *Ls. conocarpodendron* and *M. fimbriifolius*, co-occuring, smaller proteoid shrubs were used as an indication of stand age, as thicker barked species can resist fire and not all individuals would be a good indication of post fire age.

General Bark characteristics

Bark Thickness - All the species investigated in the study are members of the Proteaceae and have superficially similar external bark i.e. all were smooth barked (pers. obs.). As a result only bark thickness was investigated as a measure of the ability of a species to survive fire. Bark thickness and stem diameter were measured, at various (random) points along the length of 40 randomly selected individuals. Effort was made to ensure that measurements were taken along the entire stem to assess ontogenetic variation of bark thickness relative to stem diameter.

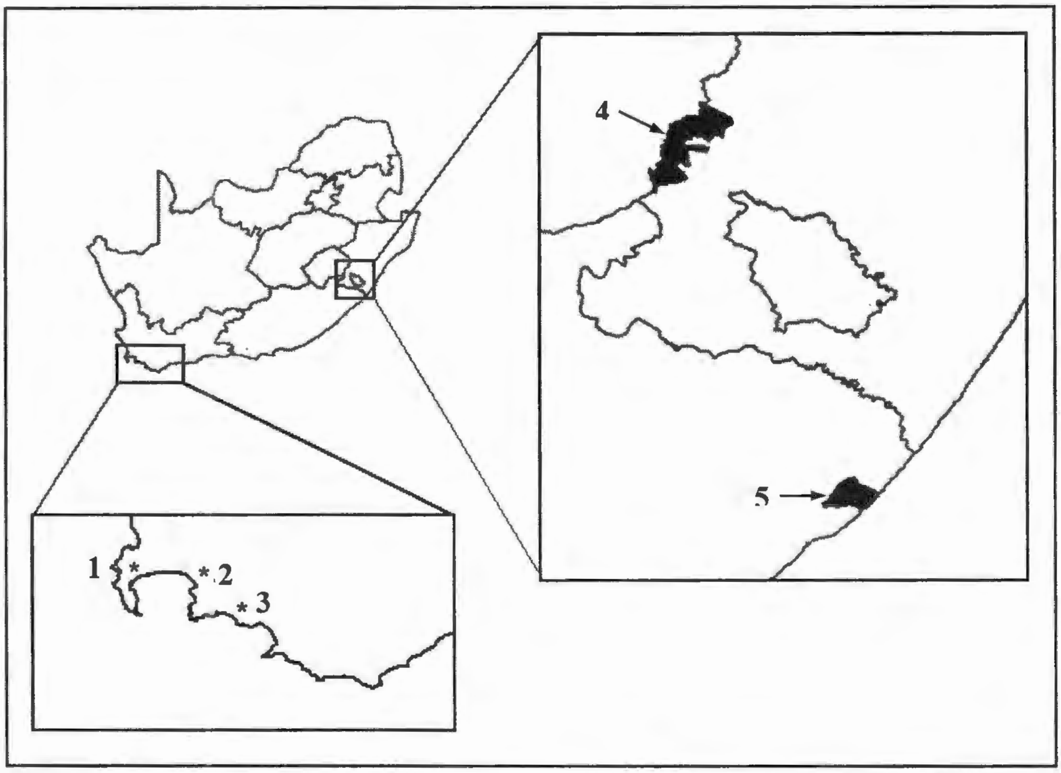

Figure 1. Map of South Africa, showing location of study sites in the western and eastern Cape Province, South Africa. Fynbos Proteaceae were sampled on the Cape Peninsula (1), Grabouw (2), and Betty's Bay (3), and savanna Proteaceae in Sehlabathebe Nature Reserve (4) and Mkambati Nature Reserve (5).

Bark thickness were measured by removing the bark (cambium included) and measuring at the thickest point. Samples were measured in the field to avoid variation in measurements due to water loss. Measurements were taken on dry days to avoid the confounding effects of rain on bark thickness. Individuals of both sexes of dioecious *Leucadendron argenteum, L. laureolum* and *L. xanthoconus* were sampled and compared to control for the effects of gender. Bark thickness was regressed against stem diameter. Regression of untransformed data provides an indication of allocational patterns of each species i.e. determines whether species display negative or positive allometry i.e. early or late allocation to defences (Jackson *et al*., 1999). The log-log transformed regression curves were used to determine species differences because 15 of 19 log-log analyses produced more significant relationships than the untransformed data. The slope of the log-log relationship between stem diameter and bark thickness provides an indication of the rate at which species acquire bark with increasing stem diameter. The predicted y intercept is an indication of the initial commitment of resources to bark.

Thin versus thick barked reseeding species: the role of growth rate trade-offs

Because bark thickness should come at an allocational cost to plants, those species with thicker bark may grow in height more slowly (Loehle, 1988). One consequence of early allocation to bark might be a reduction in growth rates and despite the accumulation of bark: the stem might not be thick enough and perish in the fire. Would "resisters" have a) stems as thick; and b) thicker bark than co-occuring, even aged non-resisters i.e. do thick barked species allocate resources to accumulating thick bark at a rate that could compensate for their potentially slower growth? Members of Fynbos Proteaceae lay down distinctive annual nodes, and can be aged reasonably accurately by counting these. Bark thickness and stem diameter measurements, at 3-year intervals, were compared for two co-occurring non-sprouting species: *Leucospermum conocarpodendron* (inherently "thick" bark) and *Protea lepidocarpodendron* ("thin" bark). Measurements of stem diameter and bark thickness were compared for stems of equal age.

Characterising life history strategies

Sprouting ability – The sprouting ability of Proteaceae species were documented by the Protea Atlas Project (Rebelo, 1996) and these data were extracted for the study species.

Bark thickness- Because bark thickness can be achieve in a number of different ways, a single bark thickness value is perhaps not as valuable as the slope and y-intercept of log-log relationships were used as indicators of rate of bark accumulation and initial allocation to bark respectively. .

Mean adult stem diameter - Since some plants are able to attain thick bark by growing large, I measured mean adult stem diameter. Diameter (measured at 10cm above the ground) was measured of at least 30 randomly selected adult individuals from 3 populations. An individual was deemed adult if the branches reached the (overstorey) canopy.

Data Analysis

Student's t-test (Zar, 1984) was used to test whether there was an intraspecific difference in slopes of the regression lines of male and female individuals of *Leucadendron* species. Microsoft Excel and Statistica packages were used for the analysis of the bark thickness data.

Defining functional groups: Multivariate analyses.

The statistical package PRIMER (Clarke & Warwick, 1994) was used to perform non-metric multi-dimensional scaling (MDS) ordination to develop graphic representations of the proteoid species' function groups. All data were equally weighted but $\sqrt{\sqrt{}}$ transformed to ensure that larger trait values (e.g. adult size) are not over-emphasised by the analysis. MDS was considered to be the best analysis to use, as it makes no assumptions about the data distributions (especially regarding linearity and normality) and is therefore more widely applicable. The MDS algorithm is an iterative process, whereby the placement of samples on the ordination is progressively refined, in order to satisfy the original similarity/dissimilarity matrix. The principle of the MDS ordination is to minimise the "stress" or distortion between calculated dissimilarity rankings and the final ordination.

Stress increases with decreasing dimensionality, and can be interpreted as follows:

Stress < 0.05	indicates an excellent representation of the data
0.05 < Stress < 0.1	indicates a good ordination
0.1 < Stress < 0.2	Indicates a potentially useful 2-dimensional plot
0.2 < Stress < 0.3	The points are close to an arbitrary placement

RESULTS

Bark thickness variation

Rate of accumulation: All 19 species displayed a strong, significant relationship between bark thickness and stem diameter (Fig 2). The slope of the regression relationship between stem diameter and bark thickness, which indicates rate of bark thickness accumulation, ranged from 0.583 (*Leucadendron laureolum*) to 0.915 (*Protea nitida*).

Minimum bark thickness: These values varied from 0.75mm for *Serruria glomerata* to 2.3mm for *Protea caffra* (Table 1). Some species, such as *Leucadendron argenteum*, despite initial thinness (low minimum thickness) and low slope value, can eventually acquire thick bark by adult plants growing large. No significant difference in (log - log) regression slope or intercept was found between sexes for the three *Leucadendron* species sampled (Table 2), therefore only the female plants were used for further comparisons.

Table 1. Summary of primary post fire regeneration strategy, bark thickness characteristics and mean diameter of 19 selected Proteacea species. Data on bark thickness characteristics include log-log regression relationship between stem diameter and bark thickness, the predicted bark thickness at 10mm, 25mm, 50mm and 100mm stem diameter (derived from the log-log relationship).

Species	**Regeneration Mode**	**Stem dia. vs bark th. Transformed data**			**Predicted bark thickness**				**Mean Diameter (mm)**
		Slope	Intercept	r^2	10mm	25mm	50mm	100mm	(mean, SEM)
Ld. laureolum	Seeder	0.583	-0.61	0.91	0.95	1.00	1.05		52.1 (3.34)
Ld. xanthoconus	Seeder	0.732	-0.78	0.92	0.89	1.74			38.8 (2.23)
H. drupaceae	Seeder	0.660	-0.79	0.94	0.74	1.39	2.22		47.9 (3.09)
P. lepidocarpo.	Seeder	0.611	-0.41	0.93	1.59	2.78	4.24		72.3 (3.30)
S. glomerata	Seeder	0.967	-1.00	0.88	0.75				16.2 (1.09)
P. coronata	Seeder	0.680	-0.62	0.91	1.15	2.17	3.46		73.5 (3.86)
P. repens	Seeder	0.646	-0.59	0.91	1.11	2.01	3.15		69.6 (4.39)
A. umbellata	Seeder	0.838	-0.913	0.95	0.84	1.81			25.6 (1.79)
Ld. salignum	Basal Sprouter	0.435	-1.01	0.83	1.57				23.7 (2.19)
M. cucullatus	Basal Sprouter	0.809	-0.81	0.84	1.00	2.11			25.5 (1.84)
A. pallasia	Basal Sprouter	0.942	-1.00	0.91	0.86	2.06			27.8 (1.60)
Ls. cuneiforme	Basal Sprouter	0.86	-0.69	0.87	1.48	3.24	5.89		76.6 (3.61)
P. cynaroides	Basal/Epi sprouter	0.819	-0.51	0.82	2.03	4.30			29.9 (2.49)
Ld. argenteum	Seeder	0.969	-1.01	0.96	0.91	2.21	4.37	8.56	298.6 (23.12)
P. roupelliae	Seeder	0.604	-0.49	0.93	1.31	2.29	3.48	5.28	150.3 (12.79)
M. fimbriifolius	Seeder	0.799	-0.51	0.97	1.97	4.10	7.14	12.42	203.9 (13.38)
Ls. conocarpo.	Seeder	0.887	-0.59	0.95	1.98	4.46	8.24	15.24	226.1 (15.37)
P. nitida	Epi sprouter	0.915	-0.60	0.94	2.07	4.80	9.02	17.02	251.3 (14.42)
P. caffra	Epi sprouter	0.59	-0.23	0.91	2.30	3.97	5.99	9.04	210.9 (13.73)

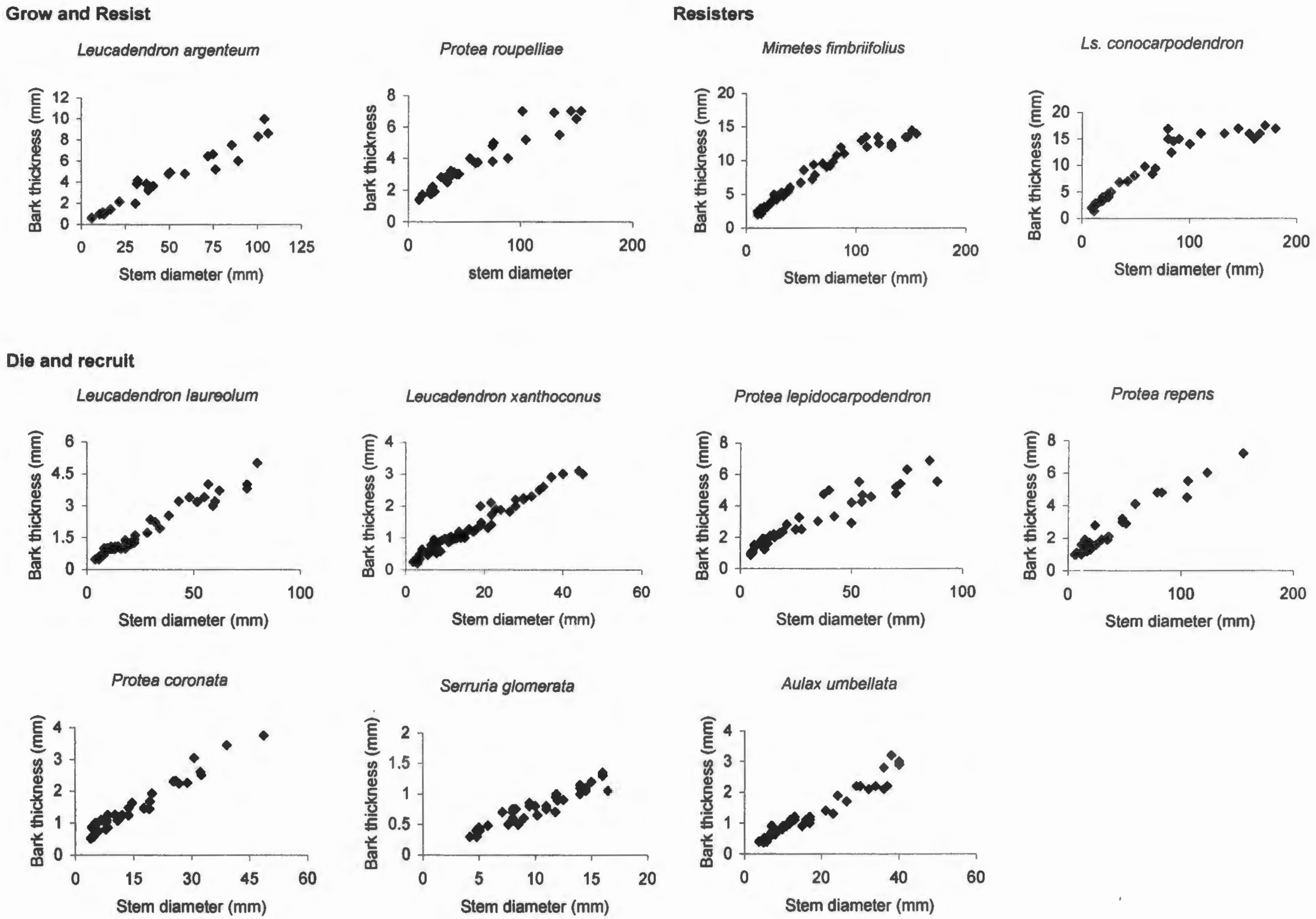

Figure 2. Relationship between stem diameter and bark thickness of 19 Proteaceae species.

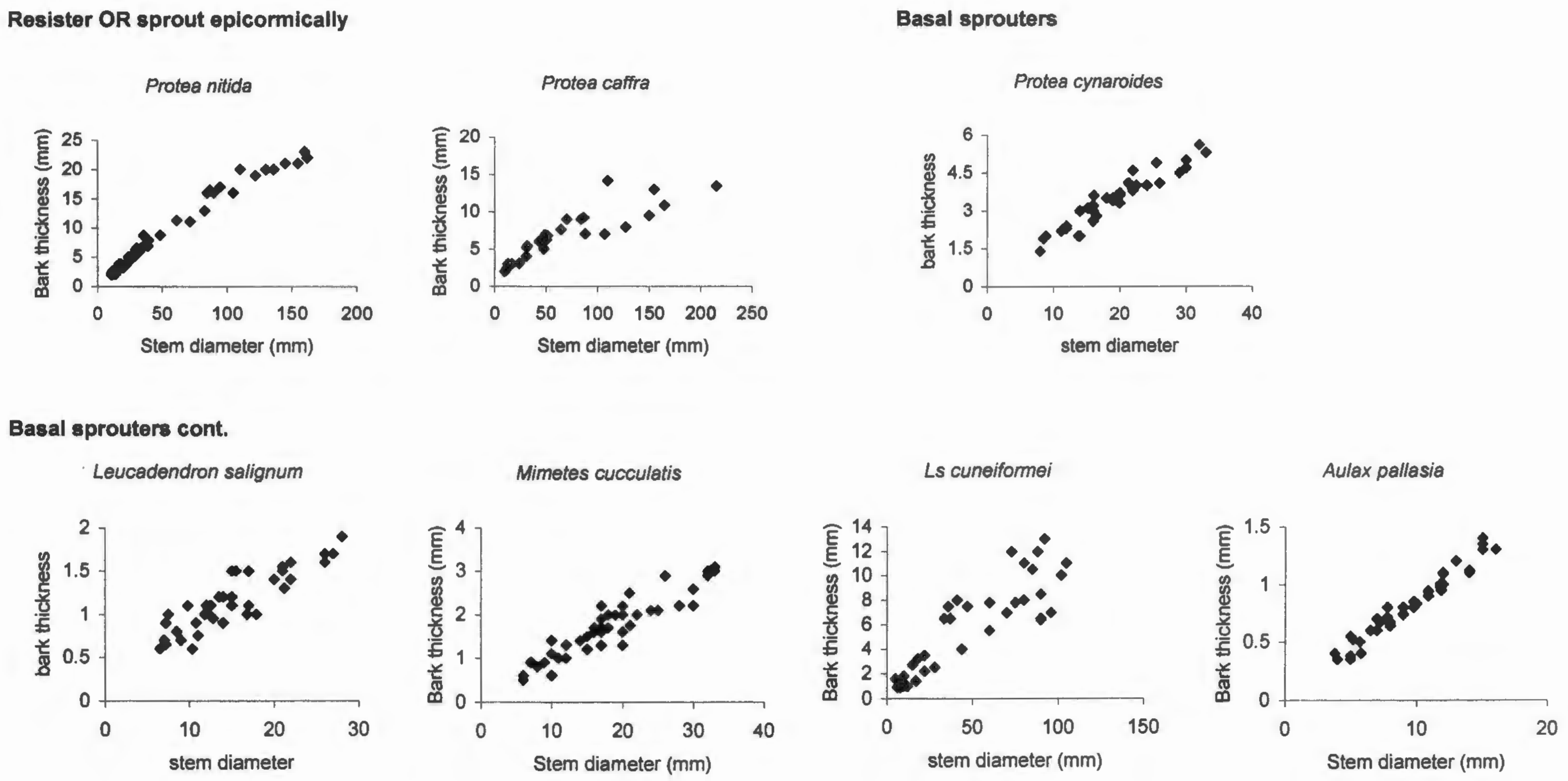

Figure 2 cont. Relationship between bark thickness and stem diameter of 19 species of Proteaceae. Species include: *Leucadendron argenteum* ($y = 0.098x^{0.97}$, $r^2 = 0.96$), *Protea roupelliae* ($y = 0.32x^{0.61}$, $r^2 = 0.95$), *Mimetes fimbriifolius* ($y = 0.385x^{0.73}$, $r^2 = 0.97$), *Leucospermum conocarpodedron* ($y = 0.33x^{0.802}$, $r^2 = 0.95$), *P. repens* ($y = 0.43x + 0.809$, $r^2 = 0.95$), *Ld. laureolum* ($y = 0.05x + 0.35$, $r^2 = 0.96$), *Ld xantheconus* ($y = 0.068x + 0.186$, $r^2 = 0.96$), *P. lepidocarpodendron* ($y = 0.063x + 1.03$, $r^2 = 0.89$), *P. coronata* ($y = 0.071x + 0.413$, $r^2 = 0.95$), *Serruria glomerata* ($y = 0.073x + 0.04$, $r^2 = 0.90$), *Aulax umbellata* ($y = 0.065x + 0.17$, $r^2 = 0.94$), *P. nitida* ($0.28x^{0.88}$, $r^2 = 0.97$), *P. caffra* ($y = 0.59x^{0.59}$, $r^2 = 0.91$), *P. cynaroides* ($y = 0.152x + 0.503$, $r^2 = 0.90$), *M. cucculatus* ($y = 0.08x + 0.203$, $r^2 = 0.86$), *Ls. cuneiforme* ($y = 0.204x^{0.86}$, $r^2 = 0.87$), *Ld salignum* ($y = 0.05x + 0.404$, $r^2 = 0.77$) and *A. pallasia* ($y = 0.083x + 0.034$, $r^2 = 0.95$). All relationships are significant to at least $p < 0.01$)

Table 2. Relationship between stem diameter and bark thickness for the range of species sampled. (Difference in slope and intercept were statistically assessed using Student's t test.)

		Slope	Intercept	R^2	Students T test	
					Diff. in slope	Diff. in intercept
Ld. argenteum	male	0.081	0.279	0.941	*	*
	female	0.093	0.103	0.966		
Ld. laureolum	male	0.043	0.519	0.89	*	*
	female	0.054	0.314	0.926		
Ld. xanthoconus	male	0.068	0.186	0.896	*	*
	female	0.077	0.104	0.896		

(* indicates that there was no significant difference)

T-test significance levels: * not significant, ** significant, *** highly significant.

Twelve of the 19 species studied displayed a linear relationship between stem diameter and bark thickness i.e. the plants allocated a constant amount of resources to protection throughout their life-span. *Protea caffra*, *P. roupelliae* , *P. lepidocarpodendron, Leucadendron argenteum, Mimetes fimbriifolius, Leucospermum conocarpodendron* subsp. *conocarpodendron* and *Ls. cuneiforme* species displayed negative allometry i.e. early allocation to protection (Figure 2).

Thick-barked vs. thin barked reseeding species

When comparing stem diameter and bark thickness for equivalent ages, the stem diameter did not differ significantly, but the bark thickness differed significantly (Table 3). Thus the bark of *Ls. conocarpodendron* was significantly greater than equal aged individuals of *P. lepidocarpodendron* of like diameters. Therefore, despite the costs of producing additional bark, resisters have branches as thick as non-resisters.

Table 3. Comparative stem diameter and bark thickness for equivalent ages of *Leucospermum conocarpodendron* and *Protea lepidocarpodendron*, two co-occurring reseeding proteoid shrubs (SEM values in parentheses).

Age/years		3	6	9	12	15
Stem diameter (mm)	*Ls. cono.*	11.81 (0.48)	17.48 (0.87)	25.52 (0.98)	38.82 (1.95)	56.42 (2.11)
	P. lepido.	9.67 (0.47)	16.09 (0.93)	23.71 (1.46)	35.16 (1.77)	53.09 (4.31)
	T Test	** $p < 0.01$	* $p = 0.337$	* $p = 0.364$	* $p = 0.225$	* $p = 0.27$
Bark thickness (mm)	*Ls. cono.*	2.33 (0.07)	3.21 (0.14)	4.45 (0.15)	6.52 (0.30)	9.24 (0.33)
	P. lepido.	1.62 (0.03)	2.02 (0.06)	2.49 (0.09)	3.20 (0.11)	4.31 (0.27)
	T Test	*** $p < 0.0001$	*** $p < 0.0001$	*** $p < 0.0001$	*** $p < 0.0001$	*** $p < 0.0001$

Life history strategy guilds

Five broad categories of response strategies are defined including A: Seeding resisters; B: Grow large and resist; C: Die and recruit; D: Basal sprouters; E: Resist or sprout epicormically (Table 4, graphically illustrated in Fig. 2).

Table 4. Six primary life history strategies of over storey Proteoid species.

Primary Reproductive Mode	Bark Thickness	Max. growth	Description	Example
Seeders	Thick bark	Large	*1. Resisters* Plants have high intrinsic fire resistance (on account of thick bark). Display negative allometry of constitutive defence i.e. early allocation of resources to defence.	*Ls. conocarpodendron,* *M. fimbriifolius.*
	Thin bark	Small	*2. Die and recruit from seed* Plants are characterised by inherently thin bark (low fire resistance).	*P. lepidocarpodendron,* *P. coronata,* *Ld. xanthoconus,* *Se. glomerata.*
		Large	*3. Grow large and resist* Plants have inherently thin bark, but resistance is developed through fast and continuous growth. May display negative allometry.	*Ld. argenteum,* *P. roupelliae.*
Sprouters	Thick bark	Large	*4. Resist OR sprout epicormically* Plants have inherently thick bark, can sprout from both aerial parts and rootstock. May display negative allometry.	*P. nitida,* *P. caffra.*
	Thin/thick bark	Small	*5. Basal sprouters* Plants have inherently thin bark, die in most fires and sprout from the base.	*Ld. salignum,* *M. cucculatus,* *A. pallasia. P. cynaroides.*

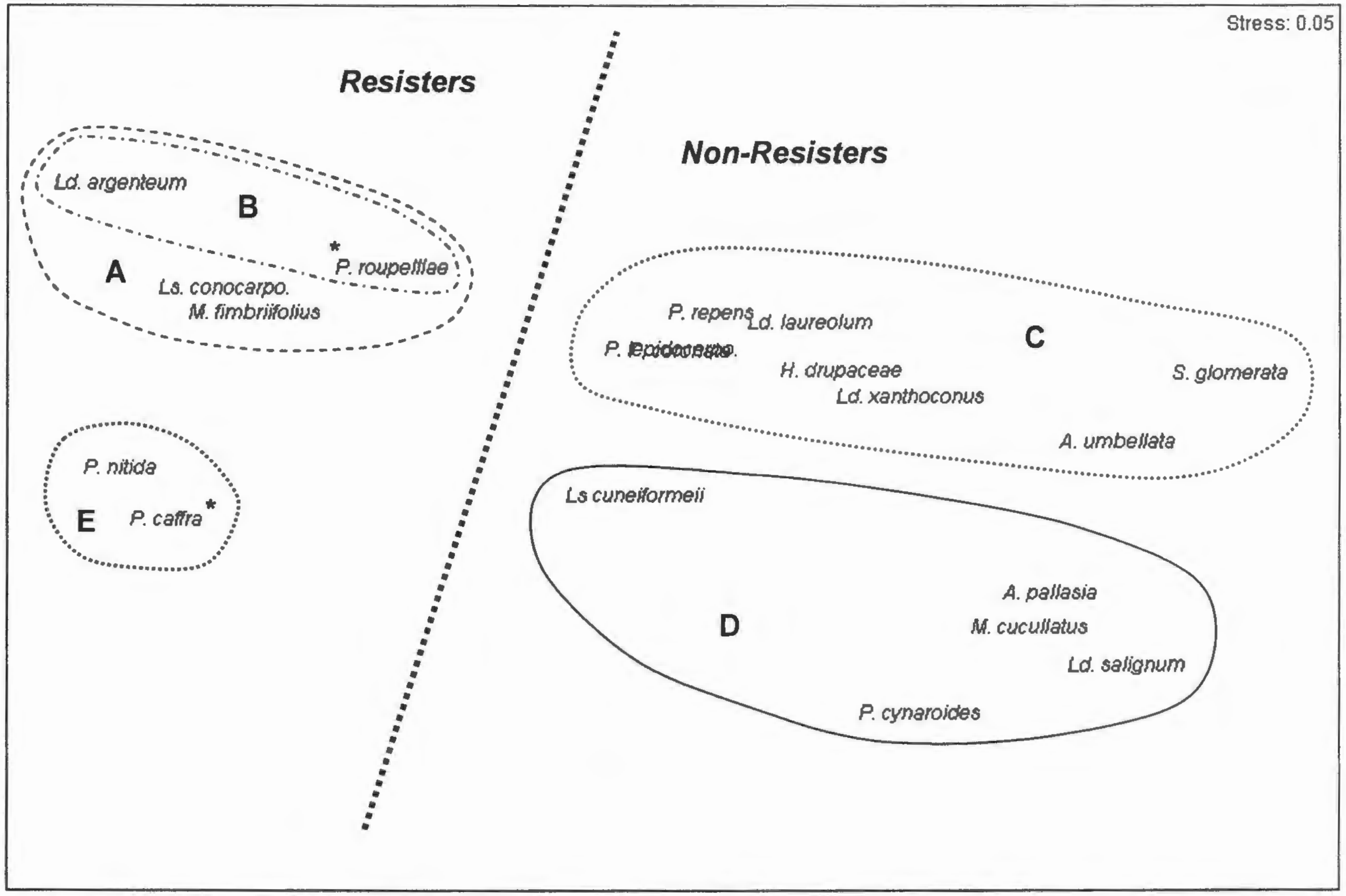

Figure 2 . MDS plot of 19 Fynbos proteoid species based on √√ transformed data and Euclidean distances (stress = 0.05). A: Seeding resisters; B: Grow and resist; C: Die and recruit; D: Basal sprouters; E: Resist or sprout epicormically. * = denotes non Fynbos species.

DISCUSSION

How do Proteaceae species attain thick bark?

This study, in agreement with Gignoux *et al.* (1997) and Jackson *et al.* (1999), suggests that acquiring fire resistance through developing thick bark is complex issue. The data suggests that Proteaceae species can attain thick bark in one of four ways. Firstly, by possessing initially thick bark i.e. large minimum bark thickness (intercept) e.g. *Protea caffra*. Secondly. through rapid accumulation of bark thickness i.e. high slope value e.g. *P. cynaroides*, *Leucospermum conocarpodendron* and *Mimetes fimbriifolius.* Thirdly through a combination of both a high inherent bark thickness and a high rate of accumulation of bark e.g. *P. nitida* and lastly, by growing large, and thus developing thick bark by virtue of thicker girth despite low intercept and slope (*Leucadendron argenteum* and *Protea roupelliae*) (Figure 5). The remaining 13 species were found to have relatively thinner bark once they reach their mean adult size and are known to perish in fires.

The comparison of stem diameter and bark thickness of *Ls. conocarpodendron* and *P. lepidocarpodendron* yields an interesting result. *Ls. conocarpodendron* achieves thick bark by a greater initial stem diameter to bark thickness ratio (i.e. has thicker bark initially) and it accumulates bark more rapidly, but not at the cost of growth (using stem diameter as an indicator of growth). Thus, individuals of similar post-fire age would differ significantly in bark thickness, but not in stem diameter, and resisters achieve can achieve thicker bark despite allocational costs of thick bark.

Predicted life history strategies

A number of life history strategy schemes exist that explicitly attempt to categorise species according to their response to disturbance e.g. Pausas (1999), Pausas & Lavorel (2003), Pausas *et al.* (2004), and this is not the first study to suggest the inclusion of bark thickness as a key tolerance trait e.g. Gignoux *et al.* (1997); Lavorel & Garnier (2002); Cornelissen *et al.* (2003). However, in this chapter I have attempted to combine both plant resistance traits with fire response strategies i.e. how plant might respond to the loss of canopy. The results suggest that when combining bark thickness attributes, mean size and sprouting ability, proteoid species can be separated into five functional groups of life history strategies in response to fire (Table 4). These groups can essentially be grouped into two categories, namely fire resisters (groups A, B and E) and non-resisters (groups C and D). Resisters include thick barked reseeding species, thin-barked reseeding species that acquire resistance through growing large ("allometric" means) and thick-barked epicormic sprouters. Non-resisters are those that will lose their aboveground biomass in the event of a fire, whereupon they either sprout strongly from underground organs or perish and recruit after fire. Therefore plants are likely to either allocate their resources to bark thickness and resist fires, and achieve this through a variety of means or not allocate resources to resistance and but concentrate on strong post-fire recovery (Zedler, 1995). For example, all the basal sprouters, which generally remain fairly small in comparison with the fire-resisting species (Table 1), have thin bark, suggesting that there is no evolutionary pressure to acquire thick bark when it is likely that all the above-ground biomass will be lost in a fire (Zedler, 1995).

Although I have grouped species by their strategies, they are by no means restricted to these. For example, some species that generally don't get large under normal fire regimes (8 – 16 years) such as *P. lepidocarpodendron*, may under exceptional circumstances, when fire is excluded, grow very large and thereby develop fire resistance.

Furthermore, this classification of Proteaceae functional types in relation to fire is not exhaustive. I have concentrated on over-storey species, but other members of the Proteaceae can resist fire through a prostrate mat-like growth form (W. Bond, pers. comm.). These "ground" species e.g. *Diastella divaricata*, *Leucospermum prostratum* and *Protea scolopendriifolia* adopt a low, spreading architecture. They resist cool fires, despite their thin bark, by virtue of their architecture that keeps the fuel-load low, thereby reducing the risk of fire.

Where do these functional types occur in the landscape?

Fire regimes have significant influence on the distribution of species in a landscape (e.g. Zedler, 1995; Keeley & Zedler, 1998; Asselin *et al.,* 2003). The nutrient-poor status of the soils and summer droughts of the fynbos, result in strong selection for the retention of leaves and branches and consequently the fuel load can be high. Fire intensity is considered high relative to other fire prone ecosystems (Bond & van Wilgen, 1996), although lower than Californian chapparal (Kruger, 1979, Bond & van Wilgen, 1996). Fires tend to reach the crown and remove most aboveground biomass, resulting in high intensity stand replacing burns. There is however, significant variation in fire intensities, ranging from 500 to 30 000kWm^{-1} (Bond & van Wilgen, 1996). It is this variation that presumably allows for the existence of the range in strategies. Fire intensity is highest in dense stands of even aged proteoid shrubs, or in areas of high productivity. Conversely, fire intensity is lower in unproductive sites, or in areas where frequent fires have reduced inter-fire biomass (Yeaton & Bond, 1991).

Bond and van Wilgen (1996) remarked that one of the ironies of fire ecology was that plants with thin bark and canopies consumed by fires often dominate fire-prone ecosystems. I expect the thin barked species to dominate in areas of high fire intensity, as the intensities are too great for the thick barked species to survive (Bond & van Wilgen, 1996). These non-resister species have additional traits that ensure survival after intense burns. The sprouting species e.g. *Ld salignum, M. cucculatus* and *A. pallasia* are able to so by regenerating strongly from large underground rootstocks and some may also display relatively strong serotiny, i.e. storage of seeds in fire-proof cones within the canopy. The reseeding species e.g. *P. lepidocarpodendron, M. hirtus, Ld. xanthoconus,* and

A. cancellata have life histories closely associated with fire e.g. strong serotiny or fire-enhanced seed germination (Pierce & Cowling, 1991).

Fire resisting species would be restricted to areas of lower fire intensities i.e. in unproductive sites or frequently burnt sites where understorey biomass is kept low by fire but the overstorey remains unaffected by mild fires. The thin barked species, however, would still perish in these burns. *Protea caffra* and *P. roupelliae* occur in savannas where the fire frequency is high but the intensity low (Booysen & Tainton, 1984; Bond & van Wilgen, 1996). *P. nitida, Ls. conocarpodendron, M. fimbriifolius* and *Ld. argenteum* are found in fynbos sites analogous to savannas, where the fire intensity is generally lower and/or of higher frequency (see Yeaton & Bond, 1991; Bond & van Wilgen, 1996). Fire-resisting species tend to display negative allometry i.e. early allocation to defences (*sensu* Jackson *et al.*, 1999), thereby ensuring fire resistance as early as possible.

In contrast to studies performed in savannas (Gignoux *et al.,* 1997) and forests (Uhl & Kaufmann, 1990; Pinard & Huffman, 1997; Hegde *et al.*, 1998), where species with thick bark were found in sites of highest fire intensity, I expect the opposite in the Fynbos. Keeley and Zedler (1998) found similar patterns in *Pinus* species distribution. Thick barked, weakly serotinous species e.g. *Pinus palustris* and *P. ponderosa* occur in areas of low productivity and low fire frequency, characterised by frequent cool understorey. In contrast thin barked, but strongly serotinous species e.g. *P. attenuata* and *P. serotina,* were abundant in areas of high intensity burns (areas of high productivity resulting in stand replacing crown fires). Similarly, Jackson *et al.* (1999) found fire-resilient *Pinus* and *Quercus* species, which displayed negative allometry (early allocation to defences), occurred in habitats characterised by frequent low-intensity burns.

CONCLUSION

Fire resistance at an individual level depends on a number of traits rather than a single characteristic (see also Gignoux *et al.*, 1997). I would suggest that when assessing resistance to fire, a single measure of bark thickness of an adult may not always be enough (e.g. Cornelissen *et al.,* 2003) but that both the slope and the intercept may be a more comprehensive measure. Furthermore, I have demonstrated that a few easy to measure characteristics, bark thickness, sprouting ability and plant size, can be useful in categorising species into life history strategy guilds. Data on vital attributes and life history strategies of this nature can be used to predict presence or absence of species given different frequency and intensity of disturbance (van Wilgen & Forsyth, 1992).

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4. Bark thickness and resprouting strategy affects plant architecture and flammability of Fynbos Proteaceae.

ABSTRACT

Plant architecture is important for, amongst others, reproductive output and vegetation flammability. In this chapter I explore the influence bark thickness characteristics and resprouting strategy have on architecture, and hence individual and stand flammability characteristics of fynbos Proteaceae. Thick barked species and epicormic resprouters tended to have less ramified architecture, and are generally found in sparse and uneven-aged, and therefore comprise less flammable stands. In contrast, thin barked and basal resprouting species were found to have highly ramified architecture. Furthermore, thin barked species are found in dense, even-aged, and hence more flammable stands. Because flowering in these species is often terminal, a more ramified architecture would improve reproductive potential. This, in conjunction with simultaneous release of seeds after being burnt, would result in dense, even aged stands. Thick barked species, displaying less ramified architecture (and possibly lower reproductive potential) and the ability to resist fires, results in staggered cohorts and sparse populations. The data therefore suggests that bark thickness would influence both individual and stand flammability.

INTRODUCTION

An understanding of architecture in plants is important for a number of reasons. Firstly, architectural design of trees is critical for optimising foliage arrangement as adaptive responses for light interception and in response to availability of water and therefore unravelling competitive interactions in forest gaps (Horn, 1971, Hallé *et al.* 1978). The relationship between reproductive output and architecture is also important in determining reproductive output (Bond, 1991; Bond & Maze, 1999): the greater the ramification, at least for fynbos proteaceae that flower terminally, the greater the floral display, and hence the greater the chance of pollination success and seed set in females, and greater pollinator visitation in male *Leucadendron xanthoconus*.

In fire prone ecosystems, architecture also is key to understanding flammability (Mutch, 1970; Bond & Midgley, 1995; Bond & van Wilgen, 1996; Keeley & Zedler, 1998, Schwilk & Ackerly, 2001, Schwilk, 2003). The shape, size and arrangement of plant parts have a major influence on flammability. Surface area to volume ratio determines both the rate of moisture loss, as well as the fuel to air ratio (Bond & van Wilgen, 1996). Plant architectural traits that increase flammability include high stem surface area to volume ratio (i.e. fine foliage), thin branches; and denser branching) and branching patterns that carry fire from the ground to the canopy (Rundel, 1981; Papio & Trabaud, 1990; Keeley, 1995; Keeley & Zedler, 1998; Cornelissen *et al.*; 2003, Cruz *et al.*; 2003, Schwilk 2003).

In the previous chapter, the importance of bark thickness, plant height and resprouting ability were explored to gain insight into life history strategies of Proteaceae in relation to fire. In this chapter I examine the relationship between acquiring resistance to fire through bark thickness, resprouting strategy and plant architecture, and the implications that this would have for their life history strategies.

Bark thickness and plant architecture

Corner's (1949) rules state that 1) the stouter the stem the bigger the appendages and 2) the stouter the stem, the lower the ramification. I suggest that bark thickness will influence stem thickness and hence the architecture of the plant. If a plant develops thick bark in response fire, this will be in addition to a minimum vasculature to supply and support the foliage and other appendages. Therefore, thicker barked species should display a thicker minimum stem thickness. Thus, according to Corner's rules, thick barked species should have a less ramified architecture and the plant would possibly be less fire prone (Bond & Midgley, 1995; Keeley & Zedler, 1998).

Bark thickness and stand characteristics

Individual architecture is not the only important characteristic when considering vegetation flammability. Stand characteristics such as even-agedness (or even-sized) and stand density affect flammability (Keeley & Zedler, 1998). However, linking the evolution of individual traits to stand level characteristics is risky due to group selectionist arguments. Nonetheless, I argue that some individual characteristics might have implications for stand characteristics, and in so doing influence stand level flammability.

The development of thick bark in part involves early allocation to defences (Jackson *et al.*, 1999; Chapter 3). Loehle (1988) found that early allocation influences other key life history traits, and predicts that allocation to defences would result in delayed allocation to reproduction i.e. late maturation, and in the long run, enhanced longevity. Thus thick barked species ("resisters") should display delayed reproduction while I expect the opposite for thin barked species ("non-resisters").

Furthermore, many Proteaceae overstorey species produce terminal inflorescences (see Bond, 1991; Bond & Maze, 1999), so a more ramified architecture could potentially contribute to an in increase reproductive output. However, although this stands to reason, it is debatable, as the link between flowering output and fecundity is not clear. However, Bond *et al.* (1995) found in fynbos proteoid species that flower terminally, reproductive output is closely linked to the number of tips and that population fluctuations are prone to chaos. In sparse stands, *P. neriifolia* displayed more ramified architecture and high reproductive output. Conversely, in dense stands where intraspecific competition reduced the ramification of the architecture and consequently the number of branch tips, the post fire populations crashed as a consequence of reduced reproductive output.

Lastly, in most fynbos plants regeneration is cued by fire (Cowling, 1987; le Maitre & Midgley, 1992). Thus the characteristics of non-resisters i.e. early, increased reproduction and simultaneous release after fires could result in very dense, even-aged populations in the post-fire environment, thereby influencing stand flammability.

Additionally, sprouting may also influence plant architecture (Midgley, 1996; Kruger *et al.* 1997; Bellingham & Sparrow, 2000). In less disturbed environments, sprouting plants generally replace above-gound biomass through branch and stem epicormic resprouting (Bellingham & Sparrow, 2000; Chapter 3). Conversely, in more disturbed environments, where the loss of above-ground biomass is more severe, sprouting plants tend to sprout basally. Basal resprouting generally results in a more multistemmed architecture (Midgley, 1996; Kruger *et al*, 1997) and hence a more ramified architecture, and potentially more flammable state.

The aim of this study is to investigate how bark thickness and resprouting influence individual architectural characteristics, stand characteristics and hence vegetation flammability.

METHODS

Study sites:

The study sites were located in mountain and sand-plain fynbos communities in the Cape Peninsula, Betty's Bay and Grabouw districts in the western Cape Province, South Africa (Figure 1, Chapter 3). The climate is typically Mediterranean-type (winter rainfall and summer drought), and the soils, nutrient poor. It is fire-prone vegetation that burns every 5 – 25 years (Kruger, 1979). The fynbos biome is dominated by members of the Proteaceae, Restionaceae, Ericaceae and Asteraceae.

The study focussed on Proteoid overstorey shrubs that dominate many mountain and lowland fynbos communities (Rebelo, 1996). These included *Leucospermum conocarpodendron, Ls. cuneiforme, Leucadendron xanthoconus, Ld. laureolum, Ld.salignum, Ld. meridianum, L. argenteum, Protea nitida, P. lepidocarpodendron, P. repens, P.cynaroides, Serruria glomerata , Mimetes fimbriifolius, M. cucculatis, M. hirtus, Aulax pallasia* and *A. umbellata*. Proteaceae overstorey shrubs are broad-leafed sclerophyllous shrubs, which mostly bear terminal inflorescences on perennially leafy shoots (Yeaton & Bond, 1991; Bond & Midgley, 1995; Bond & Maze, 1999). Study species were selected on the basis that they flowered terminally. Species often did not all occur sympatrically, so it was necessary to sample from a range of different sites in the western Cape (see Fig 1, Chapter 3). A number of different populations of each of the species were sampled to ensure that as much variation within a species was accounted for.

Sampling methods

Corner's Rules and bark thickness.

To investigate how bark might influence appendage size and architecture owing to Corner's rules, I assessed the relationship between bark thickness and leaf area (as an indication of appendage size). Bark thickness, stem diameter and corresponding leaf area were measured at the first fully expanded, hardened leaf from each of the 17 species. This point was chosen as an indication of the minimum stem diameter able to support a fully developed leaf. At least 30 measurements were taken from different, randomly selected individuals from at least 3 different populations. Bark thickness was sampled by removing the bark, with the cambium included, and measured in the field. Five measurements were taken for each sample and the averaged. Leaf area (including petiole) was calculated using a Licor leaf area meter (LI-3100C Area Meter) (in accordance with Cornelissen *et al.* (2003)). Total stem diameter; bark thickness and stem vasculature (total stem minus bark) at the minimum stem thickness were compared to leaf size (leaf area), to determine which explained the most variation in appendage size. Data were pooled across the populations and sites sampled.

The influence of bark thickness on minimum stem diameter was assessed by comparing bark thickness to the above-mentioned minimum branch diameter. In order to standardise the measurement across species, I chose to compare bark thickness at 20mm of stem diameter. Given the variation of bark thickness with size (Chapter 3) the regression relationship between bark thickness and stem diameter was used to calculate the predicted bark thickness at 20mm of stem. To obtain the regression relationship, at least 30 bark thickness and stem diameter measurements were taken randomly along the full length of a stem (1 measurement per individual). Individuals were selected randomly from 3 to 5 different populations and sampling of damaged or stunted plants was avoided. Data were pooled across the populations and sites sampled.

The influence of bark thickness on architecture:

Data of number of branches per node and total number of branch tips per terminal 20mm of stem were counted to obtain an indication of the ramification of plant's architecture. To test the relationship between bark thickness and architecture these were compared with predicted bark thickness measures at 20mm of stem diameter. Also, since proteoid overstorey shrubs generally bear their inflorescences terminally on the branches, or are at least associated with terminal branches, the number of terminal branches is a measure of reproductive potential.

Stand characteristics

In order to control for factors that may influence stand characteristics e.g. rainfall, soil type and slope, I chose sites on the Cape Peninsula that supported the highest diversity of sympatric proteoid overstorey species. Three thick barked species *Ls. conocarpodendron, P. nitida* and *M. fimbriifolius* and 4 thin barked species *Ld. xantheconus, Ld. salignum, Ld. laureolum* and *P. lepidocarpodendron* were found within a 10km radius and were therefore chosen to be assessed. Five populations of each species were sampled from 6 sites on the southern Cape Peninsula. I avoided sampling populations on very rocky sites or steep slopes. Only populations of between ca. 7 and ca. 20 years old were sampled. Stands were aged by counting the number of annual nodes of overstory proteoid shrubs, a method which is considered to be reasonably reliable and accurate (Tony Rebelo, personal communication). However, in the case of some of the thick barked species, where generation may overlap, other proteoid shrubs were used to age the stands.

Stand level flammability is influenced by both uniformity of the size of plant in the population and stand density (Keeley & Zedler, 1998). Stand densities were calculated for 5 different populations using 10m by 10m plots. Other Proteaceae species encountered in the plots were included in the calculation of stand density, as they would form part of the fuel load. The heights of 30 randomly selected individuals per population were measured within five populations to obtain a size class distribution.

Age of first flowering

The age at which plants first start flowering would also contribute to the density of a stand i.e. the earlier a plant begins to flower, the greater the accumulation of seeds (either in the canopy in the case of serotinous species or in the soil). Data on age of first flowering were collected by visiting burnt sites of varying post fire age, and aging the plants that had flowered for the first time.

Sprouting ability.

Data on sprouting ability of the various study species were obtained from Rebelo (1995) and Chapter 3.

RESULTS

Bark thickness and Corners Rules.

Leaf size (leaf area) generally increased with stem diameter, stem vasculature and bark thickness (Fig.1 A, B, C), although stem vasculature explained more of the variation in leaf size. Furthermore, there is a strong positive relationship between predicted bark thickness and minimum stem diameter (Fig. 2) i.e. thick barked species have thicker minimum stem diameters.

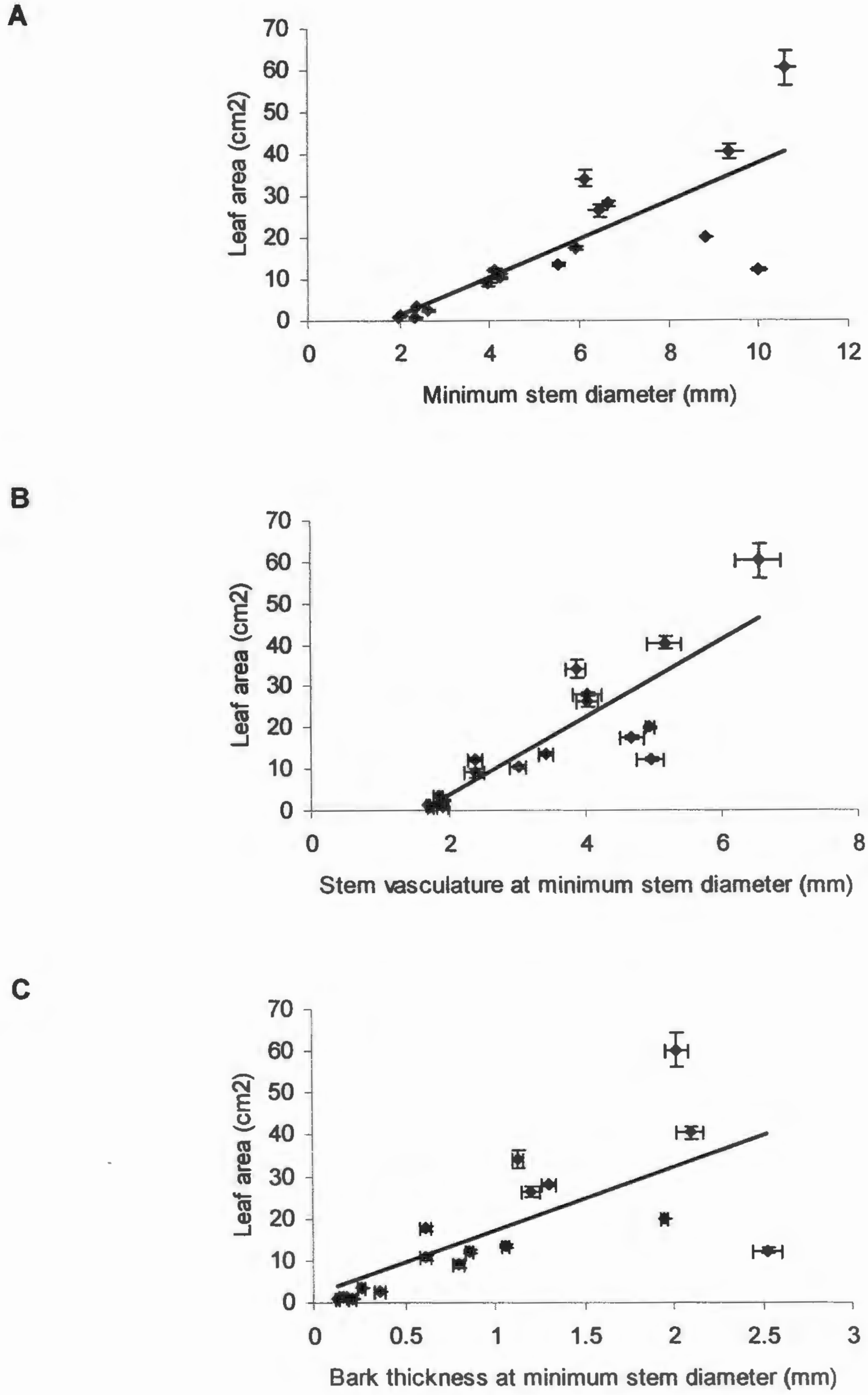


Figure 1. The relationship between A: stem diameter ($y = 4.53x-7.56$, $r^2 = 0.65$, $p<0.02$, $n = 17$); B: stem vasculature ($y = 9.39x-14.99$, $r^2 = 0.74$, $p < 0.01$, $n = 17$) and C: bark thickness and leaf area ($y = 15.17x-1.79$, $r^2 = 0.48$, $p < 0.05$, $n = 17$).

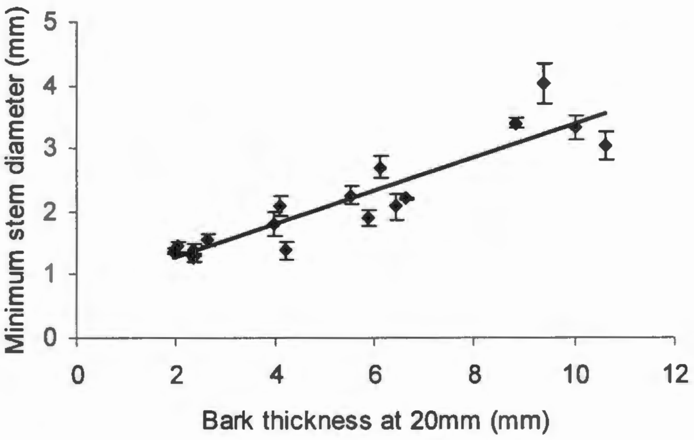


Figure 2. Relationship between bark thickness at 20mm and minimum stem diameter ($y = 0.26x + 0.75$, $r^2 = 0.83$, $P < 0.001$, $n = 17$). Minimum stem diameter increased with increasing bark thickness.

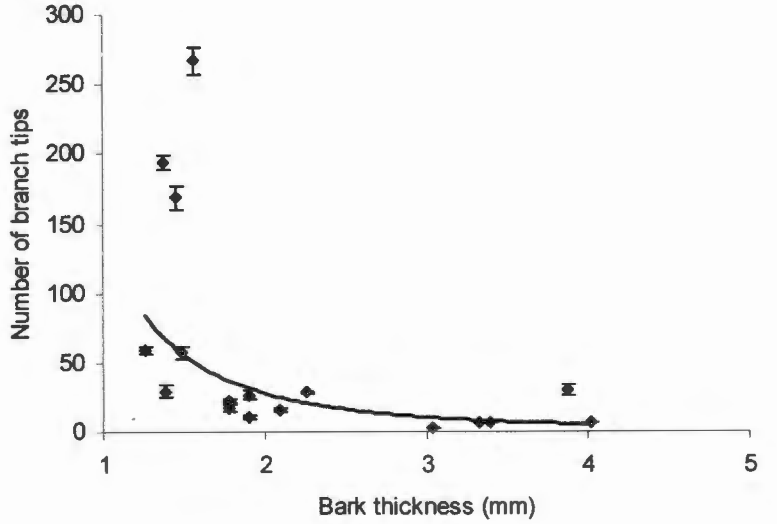
Bark thickness and architectural characteristics.

There was a strong negative relationship between bark thickness and the number of branches per 20mm of terminal branches (Fig. 3A). Similarly, when comparing bark thickness and branching indices, I found that as bark thickness increased, the number of branches per node decreased significantly (Fig. 3B).

Stand characteristics.

The thin barked species or non-resisters, *Ld xantheconus, Ld. salignum, Ld. laureolum* and *P. lepidocarpodendron*, were found to grow in even aged stands and greater densities. The species with thicker bark were found in uneven aged stands (Fig. 4) and low densities (Fig. 5, Table 1). Resisters also flower later than thin barked species (Figure 5B, Table 2).

A



B

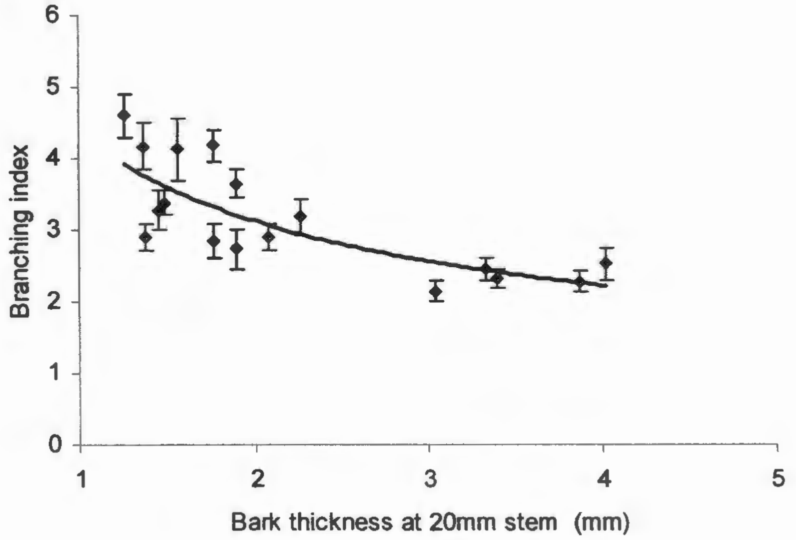
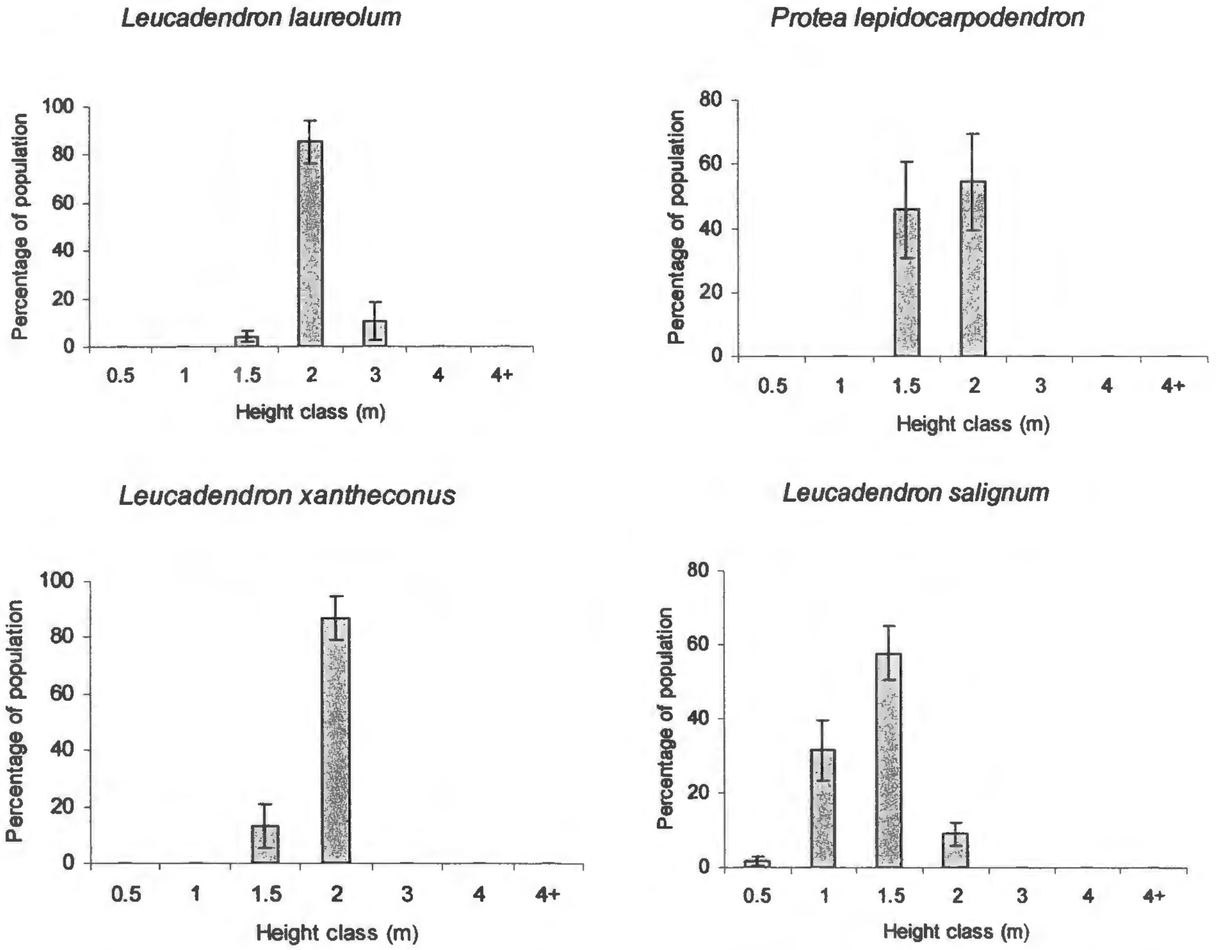


Figure 3. Relationship between bark thickness and number of branches per 20mm ($y = 144.5x^{-2.4}$, $r^2 = 0.51$, $p < 0.002$, $n = 17$) (A) and number of branches per node ($y = 4.4x^{-0.49}$, $r^2 = 0.65$, $p < 0.001$, $n = 17$) (B).

Non-resisters: thin barked species


Leucadendron laureolum

Protea lepidocarpodendron

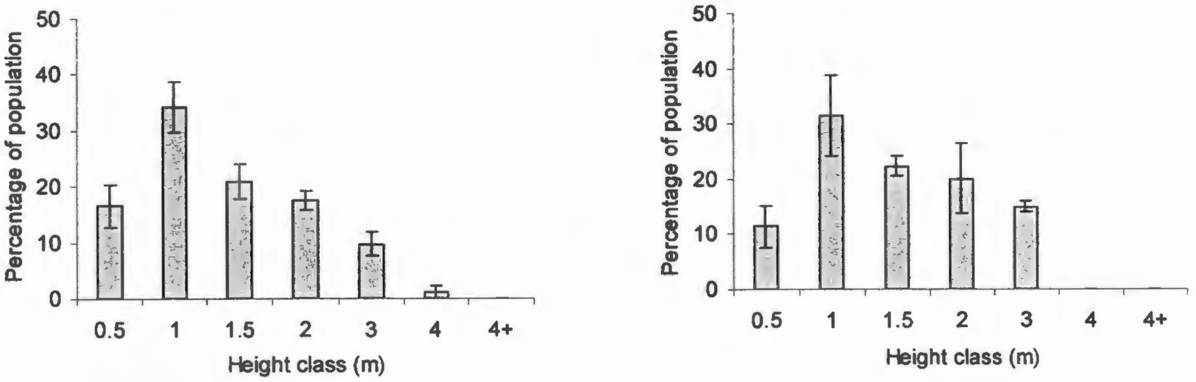
Leucadendron xantheconus

Leucadendron salignum

Figure 4. Mean size class distribution of selected thin barked proteoid species, western Cape Province, South Africa. Size class distributions of the two groups were significantly different (all $Chi^2 > 16.81$, $p < 0.01$; Mann Whitney U on Chi^2 values of thin versus thick barked species: $z = -2.449$, $p < 0.02$). Error bars show ±1 SE.

Resisters: thick barked species

Leucospermum conocarpodendron *Mimetes fimbriifolius*



Protea nitida

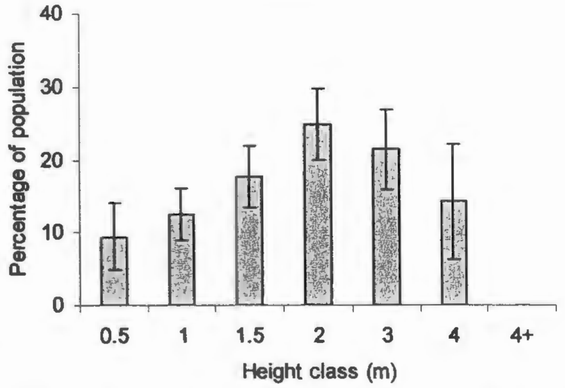


Figure 4. cont. Mean size class distribution of selected thin barked proteoid species, western Cape Province, South Africa. Size class distributions of the two groups were significantly different (all $Chi^2 > 16.81$, $p < 0.01$; Mann Whitney U on Chi^2 values of thin versus thick barked species: $z = -2.449$, $p < 0.02$). Error bars show ±1 SE.

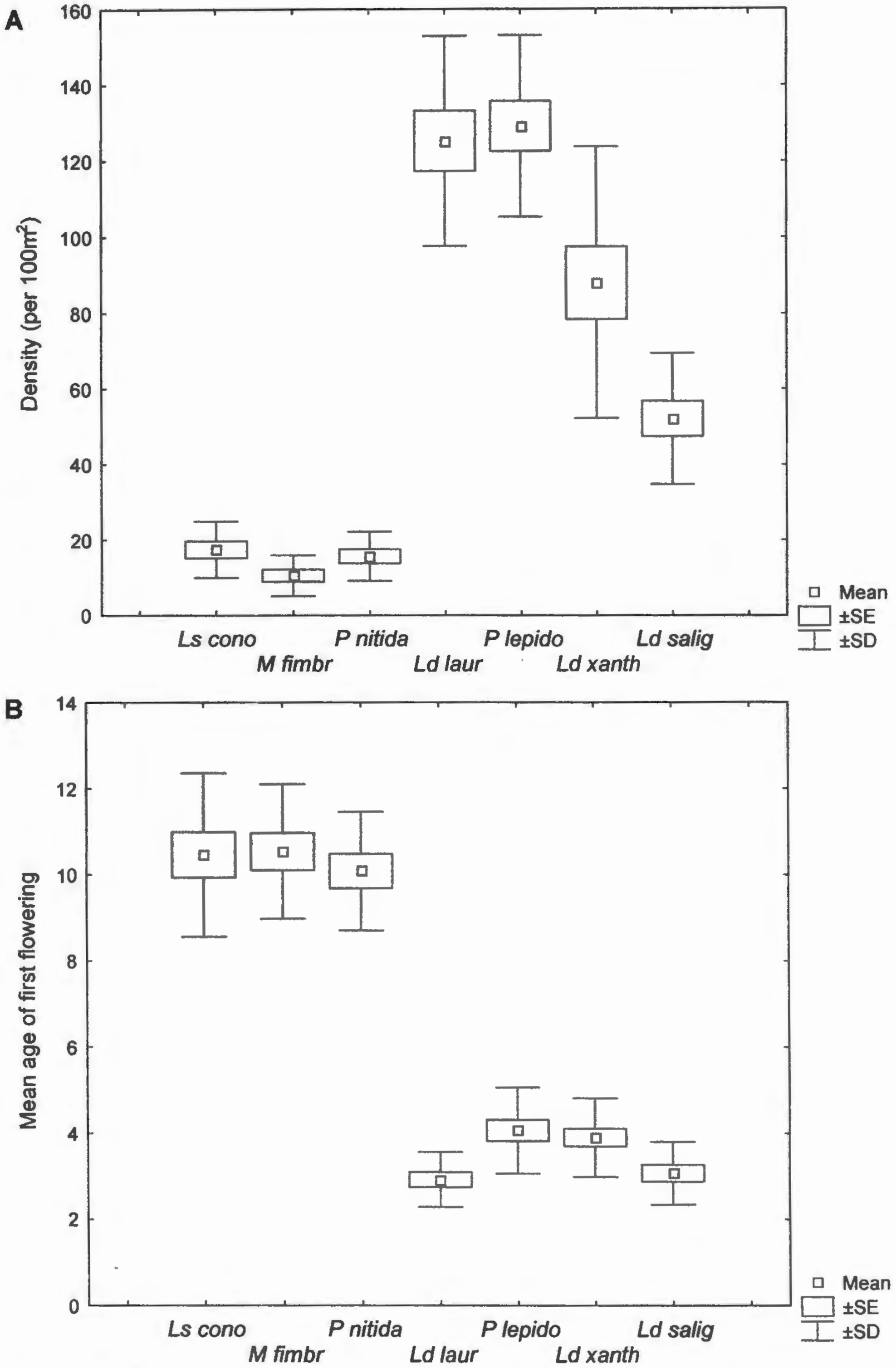


Figure 5 Mean stand density (A) and mean age of first flowering (B) of 7 fynbos proteaceae in the western Cape, South Africa. Stand density of thick barked species were significantly lower than thin barked species ($H_{(6,\,87)} = 73.16$, $p<0.001$). Thick barked species flowered significantly later than thin barked species ($H_{(6,\,101)}=78.31$, $p<0.001$).

Table 1. Mean stand density of 7 fynbos barked proteoid species. Rows joined by the same letter do not differ significantly from one another at the 95% confidence level when comparing using a multiple comparisons of mean ranks of the Kruskal-Wallice Anova (SE values in parentheses).

Species					**Mean stand density** Indiv/100m^2
Resisters					
Leucospermum conocarpodendron	A				17.5 (2.24)
Mimetes fimbriifolius	A				10.5 (5.4)
Protea nitida	A				15.6 (2.05)
Non-resisters					
Leucadendron laureolum				D	125.8 (8.72)
Protea lepidocarpodendron				D	129.2 (7.21)
Leucadendron xanthoconus			C		88 (10.8)
Leucadendron salignum		B			51.36 (4.79)

Table 2. Mean age of first flowering of 7 fynbos barked proteoid species. Rows joined by the same letter do not differ significantly from one another at the 95% confidence level when comparing using a Multiple comparisons of mean ranks of the Kruskal-Wallice Anova (SE values in parentheses).

Species			**Mean age of first flowering (SEM)**
Resisters			
Leucospermum conocarpodendron	B		9.9 (0.44)
Mimetes fimbriifolius	B		10 (0.41)
Protea nitida	B		10.1 (0.42)
Non-resisters			
Leucadendron laureolum		C	2.9 (0.21)
Protea lepidocarpodendron		C	4.1 (0.30)
Leucadendron xanthoconus		C	3.9 (0.28)
Leucadendron salignum		C	3.07 (0.19)

DISCUSSION

In fynbos Proteaceae, bark thickness, appendage size (leaf size) and plant architecture are correlated traits (Fig 1 A,B,C, Fig. 2). Although stem vasculature, rather than bark thickness, explains more of the variation in leaf size (Fig.1B) (see also Waring *et al.*, 1982), bark thickness and appendage size are correlated traits (Fig 1C). Furthermore, bark thickness certainly influences minimum stem diameter (Fig. 2). The data are consistent with the prediction that bark thickness would influence plant architecture, and is correlated with appendage size. However, the precise mechanism of how bark may influence appendage size, unfortunately remains unclear. It may be that if selective pressures drive a plant toward developing thick bark, it increases the minimum thickness of the stem. It follows then, according to Corner's Rules that as a consequence of thick bark the plants architecture will be less ramified. Thin barked species tend to have smaller leaves and a far more ramified branched architecture i.e. smaller leaves (Fig. 1C) and many more branch tips (Fig. 3). Conversely, the thicker barked species tend to support larger appendages (although the size range is greater) and a far less branched architecture. The difference in architectural traits would have important implications for flammability (Rundel, 1981; Papio & Trabaud, 1990; Keeley & Zedler, 1998; Schwilk, 2003), reproductive output (Bond & Maze, 1999) and susceptibility to senescence and hence longevity (Midgley & Kruger, 2000)

Bark thickness, resprouting, architecture and life history strategies

Thick barked species: resisters

Reduced flammability: To complement their inherent fire resistance acquired through developing thick bark, *Ls. conocarpodendron, M. fimbriifolius* and *P. nitida* also display an architecture that is ideally suited to reducing flammability. The thicker branches and reduced degree of branching and larger leaves, result in a reduction in branch surface area to volume ratio and hence flammability (Bond & van Wilgen, 1996). Thus, not only will thick bark enhance fire survival by protecting cambium and bud banks, but will result in a more fire retardant life form, thereby further increase its "resistance" to fire.

Many proteoid shrubs bear inflorescences terminally on the branches, or at least are associated with terminal branches (Bond, 1991), so the number of terminal branches is an indication of reproductive potential (e.g. Bond *et. al.,* 1995). Thick barked species generally have fewer branch tips relative to thin barked species (Fig. 3), and, in addition to this, their delayed reproduction (Table 1) would result in relatively lower overall reproductive output. Furthermore, trade-offs associated with the production of thick bark in *Ls. conocarpodendron* resulted in a competitive disadvantage (slower growing seedlings, later reproduction) when compared to thin barked co-occurring species (Yeaton & Bond, 1991). This could then potentially reduce the stand density further.

Coupled with this are the high survival rates of the larger individuals, due to either their thick bark and/or recovery through epicormic resprouting and resulting uneven aged population. The net result is a low density, multi-cohort community (Fig. 4) which, in turn, reduces stand flammability (Bond & van Wilgen, 1996; Keeley & Zedler, 1998). Indeed, Yeaton and Bond (1991) found that 56% percent of *Ls. conocarpodendron*, a thick barked species, found in the open survived a cool fire compared to 21% found in closed communities.

Therefore, not only does thicker bark confer individual fire resistance by better protecting the cambium of the plants, but also results in a far less ramified architecture, further enhancing its ability to avoid burning. Furthermore, individual resistance and potentially lower reproductive output would result in sparse, uneven-aged stands further reducing flammability at the stand level.

Reduced senescence: A less ramified architecture could also be considered a predisposition to reducing vulnerability to mechanical failure. Midgley & Kruger (2000) found that senescence in fire adapted Proteaceae was strongly linked to architecture (see Appendix 1). They found that less ramified species (including *Ls. Conocarpodendron, P. nitida* and *M. fimbriifolius*), with a lower canopy spread to stem diameter ratio were less prone to structural collapse than highly ramified species. This corroborates Loehle's (1988) suggestions that delayed reproduction, and early allocation of resources to defences, enhances longevity.

Resistance strategy. Therefore, plants that are adapted to survive low to medium intensity burns, by accumulating thick bark, are also predisposed to being less flammable and also possibly increased life spans due to reduced risk of senescence (Midgley & Kruger, 2000). Thus their traits lead to delayed allocation to reproduction, slower reproductive output, high resistance to fires and longer life spans, and enhanced persistence in the landscape relative to other Proteaceae in the Fynbos. These species probably only survive mild fires that do not reach the canopy, and would be restricted to sites characterised by low intensity burns (Chapter 3). Ryan & Reinhardt (1988) and Keeley & Zedler (1998) found similar patterns for North American conifers, where thick barked species could resist cool ground fires, but perished if the fires reach the crowns.

Thin barked species: non-resisters

In contrast to the thick barked species, species such as *Ld. xanthoconus, P. lepidocarpodendron* and *Ld. laureolum* initially allocate less of their resources to protection (thin bark) and more to early reproduction (Fig 5B, Table 2). The increased allocation of resources to early and prolific branching (Fig. 3) promotes rapid initial canopy branching, greater floral display and potentially increased fecundity but also increases the risk of the spread of crown fires.

Higher flammability: I suggest that the species with thinner bark, smaller leaves, greater branching index and hence more ramified architecture, tend be more flammable (Cornelissen *et al.,* 2003, Schwilk, 2003). Furthermore, these species also tend to grow in dense, even-aged stands (Fig 4, 5A, Table 1). The uniformity of the stand results in positive feedback, in turn increasing the probability of a crown fire spreading (Keeley & Zedler, 1998). Thus, both on an individual and population level, these species display characteristics that suggest that they are predisposed to burning.

Additionally, sprouting will influence plant architecture. Those thin barked species that resprout after fire do so from the base (Chapter 3). Hallé *et al.* (1978) have shown that the typical multistemmed architecture of basal resprouters is analogous to the canopy of a monopodial tree i.e. a canopy at ground level. Compared to monopodial trees and epicormic resprouters, basal resprouters would therefore tend to have a more flammable architecture.

Early senescence: Given their highly ramified architecture and increased reproductive output, thin barked species (including *P. repens, P. lepidocarpodendron, Ld. laureolum* and *Ld. xanthoconus*) are more vulnerable to senescence due to mechanical failure (Midgley & Kruger, 2000) but also, mortality due to increasing costs of large floral displays (Bond & Maze, 1999). Bond & Maze (1999) found that the probability of survival decreased with increasing reproductive output (measured as the number of terminal branches) in *Leucadendron xanthoconus* i.e. the greater the floral display, the greater the probability of death.

Thin barked species, given their bark, architectural and stand characteristics, rather than being fire avoiders, tend to burn more easily (Bond & Midgley, 1995; Bond & van Wilgen, 1996; Keeley & Zedler, 1998). Furthermore, many of these species are well adapted to recovering after fire e.g. resprouts strongly from rootstock, serotiny (le Maitre & Midgley, 1992) and seed germination cued by fire (Pierce & Cowling, 1991).

Comparing Life History Strategies

Although the patterns are relatively clear and the explanation of the strategies are reasonably straightforward (Table 3 summarises the key characteristics of resisters versus non-resisters), the mechanism of co-existence remains untested. Based on field observations e.g. skeletons of thick barked species in the middle of the dense stand of thin barked species, it would seem that once the non-resisting species establish in high densities around the thick barked species, the intensity of the next burn would be too great for resisters to survive. Conversely, if the thick barked species, which often grow far larger than the non-resisters, can overtop the other species and suppress the understorey growth, the rate of accumulation of fuel in the understorey may be reduced, ensuring their continued survival. This, however, is speculation and would need to be tested in the field.

Table 3. Summary characteristics of thin and thick barked species

	Thick barked species: Resisters	**Thin barked species: Non-resisters**
Species	*Ls. conocarpodendron, M. fimbriifolius, P. nitida*	*Ld. xanthoconus, Ld. laureolum, P. lepidocarpodendron* and *Ld. salignum.*
Reproduction	Delayed flowering (9 – 12 years) and lower reproductive output Epicormic resprouting	Early flowering (2 – 5years) and high reproductive output Some may be basal resprouters
Architecture	Simple architecture, few branches per node.	Complex, highly ramified architecture.
Stand characteristics	Broad range in size class distributions; Low stand density.	Dense, even aged stands.
Longevity	Delayed senescence	Higher susceptibility to senescence

Resisters and Non-resisters; support for Mutch's Hypothesis?

Mutch (1970) argued that fire–prone vegetation might have evolved characteristics that increase flammability and therefore contribute to the perpetuation of fire dependant communities. However, his ideas were criticised as the flammability traits might be purely coincidental i.e. selective pressures such as herbivory, nutrient retention or drought tolerance might be more plausible determinants of "flammability" traits (see Bond & Midgley, 1995).

However, Bond & Midgley (1995) suggest that flammability could evolve if it were linked to traits that would improve recruitment in the post-fire environments. Flammable species or "torches" would have to burn intensely enough to burn themselves and their non-flammable neighbours ("damps") and then recruit more successfully into the post fire environment. Non-resprouting torches dominate in the post fire environments because of their higher fecundity, which is related to early and prolific branching (Grime, 1979; Tilman, 1988). Resprouting "torches", they suggest would dominate the post-fire environment, because they could resprout strongly after intense fires i.e. basal resprouters can recover better than epicormic resprouters or reseeding species.

Although I haven't tested the mechanism of coexistence, there seems to be some overlap between the resister and non-resister strategies and that of Bond & Midgley's (1995) "damps" and "torches". The thin barked non-resisters would seem to have architecture and stand characteristics pre-adapted to be more flammable, and life history strategies designed to recover strongly after fires (basal resprouting or early flowering, high reproductive output and fire-cued seed germination). Resisters, or "damps" are designed to resist fires and persist in the landscape. However, Zedler (1995) raises the problem that they were unable to show that fire selection is a necessary element in the explanation of specific traits e.g. fine branches make bushes burn better but they can also be explained as the only efficient canopy structure for a small leafed plant in a drought-prone environment. In this study I demonstrate a potential mechanism of how individual flammability traits and subsequently stand flammability may be influenced by bark thickness, a trait that is strongly linked to fire resistance (although not exclusively so, see Cornelissen *et. al.* 2003 for review).

Furthermore, the study also provides some evidence for the link between individual and stand (population) level traits, thus providing some support for the ideas of Mutch (1970). It highlights the importance of bark thickness and resprouting as key characteristics in determining individual and vegetation flammability.

Based on these findings, I predict that thin barked *Banksia* and *Hakea* species should share the characteristic of the non-resister fynbos Proteaceae species (highly ramified architecture, even-aged dense stands and early reproduction). The reverse should be seen for thick barked species.

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5. Acacia life history strategy variation along a disturbance gradient in a South African savanna.

ABSTRACT

In this chapter I assessed the effect that disturbance regimes may have on shaping *Acacia* life history strategies and consequently plant distribution patterns in Hluhluwe Imfolozi Park, South Africa. Key life history traits of *Acacia* species (seed size, height, sprouting ability, bark thickness and wood density) were assessed in order to group them into functional types. Seed size was positively correlated with plant height, while multistemmedness and bark thickness were negatively correlated with plant height. Bark thickness increased with increasing multistemmedness. I described four functional groups of species: xeric reseeding species, mesic seeders, mesic resprouters and riverine species. The mesic species were found to be fire resistant, but poorly defended against herbivores, and xeric species vulnerable to fire, but well defended. The single riverine species was both poorly defended against fire and herbivory, but escaped both by growing tall. All species could resprout as juveniles, but adult sprouting was most important in mesic savannas where the probability of losing above-ground biomass in fire was greater. Thus the differing selective pressures in mesic versus xeric savannas result in a switch in acacia life history strategies. Disturbance regime can therefore have significant influence on species distribution in savannas.

INTRODUCTION

One of the central aims of evolutionary ecology is to determine how natural selection jointly moulds life histories and limits the distribution of organisms. In chapter three I explored the life history strategy variation in Proteaceae, found predominantly in the fynbos. In savannas, however, the selective pressures are significantly different in that fires are more frequent, less intense and herbivory plays a significant role. Disturbance regimes differ significantly from each other in type, intensity and frequency, and consequently, exert different selective pressures on both individuals and communities. One can therefore expect a range in life forms/life history strategies of plants growing in savannas, both between (Gignoux *et al.*, 1997) and within species (Archibald & Bond, 2003).

Savanna disturbance regimes: Fires and Herbivory

Fires are an essential feature in the regeneration and modification of savanna vegetation communities (Bond & van Wilgen, 1996). Fires in South African savannas occur with frequencies ranging from annual to 1 in 30 years depending on rainfall and grazing pressure (Bond & van Wilgen, 1996), while intensity can vary from < 100 to > 5000 $kW.m^{-1}$. In savannas the dominant fuel is derived from the bunch grass layer (Trollope, 1984a), and surface fires are most common. However, should substantial fuel build up, crown fires may occur, albeit rarely. Fires are therefore more likely to affect shorter species or regenerating individuals, and kill the shoots of juvenile acacias and short individuals, a process called "top-kill" (Trollope, 1984a). Thus regenerating individuals (ramets or genets) have to be able to survive the "fire-trap" (Higgins *et al.*, 2000) in order to successfully recruit into the canopy.

Similarly, mammalian browsing can have an equally significant impact upon savanna trees (Pellew, 1983, Bond & Loffell, 2001). As is the case with fires, savanna trees have to run the gauntlet of a zone of herbivory, as most herbivory (other than giraffe and elephant feeding) takes place less than 3m from the ground (Owen-Smith & Danckwerts, 1997; Bond & Loffell, 2001). Stem, rather than leaf, removal is more important in limiting juvenile escape. Also, browsers such as black rhino and kudu are capable of browsing relatively large shoots (Owen-Smith & Danckwerts, 1997). Thus browsing is also an important factor limiting recruitment into adult size classes (Pellew, 1983; Owen-Smith & Danckwerts, 1997) and is not considered in Higgins *et al.* (2000).

Mesic versus Xeric savannas: Fire versus herbivore driven systems

The occurrence of fire is determined by the availability of dry season grass fuel (Bond, 1997), and production of fuel is linearly dependant on moisture availability (Scholes & Walker, 1993; O'Connor & Bredenkamp, 1997). Mesic savannas, characterised by higher productivity, tend to support more frequent, intense burns when compared to xeric savannas (Scholes, 1997; Higgins *et al.* 2000), Balfour & Howison (2001) clearly showed the a decrease in fire frequency between mesic and arid savannas in Hluhluwe Imfolozi Park (HIP).

In xeric savannas fire frequencies are lower because grass production is variable and fuel loads often too sparse to support fires (Scholes, 1997; Balfour & Howison, 2001), one might expect herbivores to have an increased influence on plant life history strategies as a disturbance agent. Indeed, Scholes (1997) suggests that large mammals consume greater proportions of biomass in xeric savannas compared to mesic savannas (10 -50% versus 5 – 10%). This pattern is further enhanced in areas of greater soil fertility, where herbivore densities can be up to 2 – 3 times greater than nutrient poor sites (Owen-Smith & Danckwerts, 1997) and arid savannas tend to be more nutrient rich (Scholes, 1997). Thus in mesic savannas, fire alone can control plant densities, whereas in xeric savannas, herbivores arguably play an increased role (Scholes, 1997; Bond *et al.* 2001, Archibald & Bond, 2003).

Plant response: Resist or regenerate?

Generally, if plants do not escape disturbance by growing in protected areas, they can either resist disturbance (develop protection e.g. thick bark or spines) or lose their aboveground biomass and regenerate vegetatively or sexually.

Resistance to disturbance

Fire

Individual persistence through a fire is determined by the degree to which living buds are laid down and protected from heat. The effects of fire depend both on the extent to which the live crown is scorched and the subsequent survival of stems and protection of stems and root cambial tissue (Bond, 1997). Bark thickness is a key trait determining stem and bud survival and thus a plant's resistance to fire (Pinard & Huffman, 1997, Uhl & Kaufmann, 1990). Thick bark can be achieved though growing larger, by having inherently thick bark or by acquiring bark rapidly (Gignoux *et al.*, 1997; Chapter 3). Furthermore, depending on the local disturbance regime, plants may allocate their resources to defences i.e. bark early or later in their lifespan (negative versus positive allometry) (Jackson *et al.*, 1999). For example, Jackson *et al.* (1999) found that negative bark allometry and thick sapling bark of *Quercus* and *Pinus* species were associated with habitats characterised by frequent low intensity burns, where the ability to resist fire early is key to survival.

Herbivory

Savanna trees have developed a range of defences against mammalian herbivory both chemical (Owen-Smith & Danckwerts, 1997) and mechanical defences (Gowda, 1996; Midgley *et al.*, 2001). An important chemical factor discriminating palatable from unpalatable woody plants is condensed tannin content in leaves relative to protein levels (Cooper & Owen-Smith, 1985). On the other hand, thorns and spines do not prevent browsing because ungulates have counter adaptations to cope with these structures, but rather they restrict bite size and rate, thereby reducing leaf loss to herbivores (Cooper & Owen-smith, 1986). Also, architectural characteristics such as wide canopies and highly branched shoots can further protect plants from herbivores (Brown, 1960; Milton, 1991). A highly branched architecture may work in conjunction with spines to form a cage-like structure, thus protecting the internal parts of the plant (Archibald & Bond, 2003).

Regeneration: Sprouting or sexual reproduction

Despite a growing realisation of the importance of sprouting in savanna systems, especially as juveniles (Gignoux *et al.*, 1997; Hodgkinson, 1998; Higgins *et al.*, 2000; Bond & Midgley, 2003), little empirical knowledge is available on species' sprouting ability. In most studies of the demography of savanna trees, little or no mention has been made of sprouting as a key regeneration strategy (Midgley & Bond, 2001). Juvenile tree species in savannas resprout vigorously after injury from burning or herbivory (Bond, 1997). Recruitment into mature size classes depends on rare opportunities when a tree gains sufficient height between fires to escape the top kill i.e. escapes the "fire trap" (Higgins *et al.*, 2000). In mesic savannas, fires may be so frequent that individuals remain in this short sprouting "Gulliver" state for lengthy periods of time (Maze, 2003).

Alternatively, plants perish in the fire and reproduce sexually. Little is known about the regeneration niches of savannas tree species (Higgins *et al.*, 2000), but what is clear is that seedling establishment, rather than seed output, seed predation or germination rates, represent the most significant recruitment bottleneck for Acacias (Prins & van der Jeugd 1993, Midgley & Bond, 2001). Seedling establishment is reportedly governed physiologically by moisture availability (Midgley & Bond, 2001), and of course browsing and fire (Bond, 1997, Owen-Smith & Danckwerts, 1997; Augustine & McNaughton, 2004).

In this chapter I aim to explore how the difference in disturbance regimes between mesic and xeric savannas would influence tree life history strategies. I have adopted the approach of Keeley & Zedler (1998). They grouped *Pinus* species into functional groups according to selected life history traits, and then attempted to explain these in terms of different disturbance regimes. This study was based on the following questions:

1. Do species life history traits e.g. sprouting ability, bark thickness, seed size and plant height, group together and thus can species be grouped into functional groups based on these traits?
2. Do the *Acacia* life history traits change in relation to varying disturbance regimes?

METHODS

Study site

The study was conducted in Hluhluwe Imfolozi Park (HIP), in the northern Kwa-Zulu Natal province, South Africa (28°00' – 28°26' S, 31°43' – 32°09' E). This park is a reserve system of around 90 000 Ha comprising Hluhluwe Game Reserve, Imfolozi Game Reserve and an intervening corridor of land. The park has varied topography and its altitude ranges from 40m above sea level in the lowlands of the south and western portions to c. 750m a.s.l. in the higher elevations of north and east. Mean annual rainfall ranges from c. 600 in the lowlands to c. 1000mm pa. at higher elevations (Balfour & Howison, 2001).

The vegetation of HIP comprises three broad types: grassland and forested hilltops, riverine forests and acacia-dominated savannas (Whateley & Porter, 1983) with strong Tongoland-Pondoland affinities (Downing & Gibbs-Russel, 1981). The dominant grass species, and therefore the majority of the fuel load, is *Themeda triandra* Forsk. (Balfour & Howison, 2001). I conducted my research in the Hluhluwe, a more mesic region of the park, and Imfolozi a more xeric region of the park (Balfour & Howison, 2001).

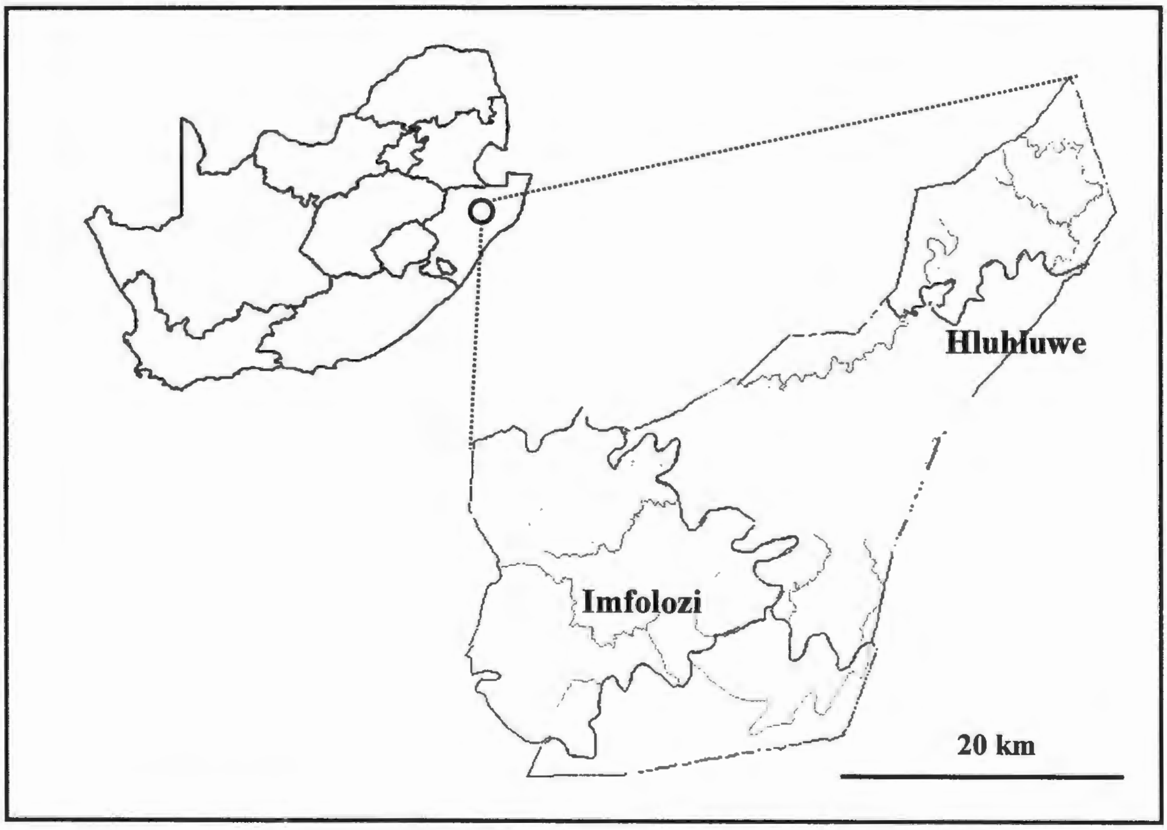

Figure 1. Map of Hluhluwe Imfolozi Park, Kwa-Zulu Natal Province, South Africa.

Hluhluwe vs. Imfolozi: Mesic versus Xeric savannas

Fire regime:

There is considerable spatial diversity in the fire regime, much of which is related to changes in topography, and its effect on rainfall and fuel production (Balfour & Howison, 2001). Hluhluwe generally lies at a higher altitude, receives more rain and is characterised by a more varied topography. The area experiences a frequent mean fire return period of once in every 2.9 years (median 1.3yrs)

(Balfour & Howison, 2001). Imfolozi, on the other hand, with more xeric conditions, rainfall of c. 625mm.a^{-1} (Downing & Gibbs-Russel, 1981), has a mean fire return period of 3.8 years (median of 1.8 yrs) (Balfour & Howison, 2001). HIP experiences long-term wet/dry phases of between four and ten years. During the dry periods the difference between Hluhluwe and Imfolozi fire return periods is further accentuated (Balfour & Howison, 2001).

Herbivore densities

Data from the Ezemvelo KZN Park Earthwatch Institute 2002 game census suggest that herbivore densities are higher in Imfolozi (Table 1). Imfolozi supports 33% greater browser and 32 % greater grazers densities (kg.km^{-2}) than Hluhluwe. Hluhluwe does, however, support greater densities of giraffe, nyala and buffalo.

Table 1. Browser and grazer densities (kg/km^2)of Hluhluwe and Imfolozi Game Reserves.

		Hluhluwe	**Imfolozi**
		Imfolozi	**Imfolozi**
Browsers	Black rhino (*Diceros bicornis*)	348	572
	Giraffe (*Giraffa camelopardalis*)	1521	929
	Impala (*Aepyceros melampus*)*	835	2517
	Kudu (*Tragelaphus imberbis*)	286	558
	Nyala (*Tragelaphus angasi*)	1156	949
	Total	4146	5524
Grazers	White rhino (*Ceratotherium simum*)	3310	5615
	Warthog (*Phacochoerus aethiopicus*)*	240	477
	Wildebeest (*Connochaetes taurinus*)	827	1641
	Buffalo (*Syncerus caffer*)	3008	2441
	Zebra (*Equus burchelli*)	1548	1638
	Total	8933	11811

Data from Earthwatch Institute 2002 census. Density values were calculated using male mean weight; Body weight data from Owen-Smith (1988).
* denotes a mixed diet of grass and browse.

Grazers and fire regime

Higher grazing pressure could result in less fuel and thus contribute to a decrease in potential for fires (Owen-Smith & Danckwerts, 1997; Higgins *et al.*, 2000). Archibald (2003) found a strong interaction between grazers, grass biomass and fire regime in HIP.

Areas dominated by tall bunch grassland may be reduced to a shorter state by intense grazing pressure. In time, heavy grazing can favour herbivore-resistant yet less flammable stoloniferous grasses, further decreasing fire intensities and frequency (Trollope, 1984b; Bond *et al.,* 2001). Therefore a negative feedback develops between grazing, standing biomass and consequently fire regime. Archibald (2003) found greater densities of grazing lawns in Imfolozi, where the grazer numbers are higher, thus further reducing the potential for fires. Therefore, in xeric savannas where productivity is lower and fires more infrequent than mesic savannas, the greater herbivore densities may further reduce fire frequency.

Study species

I used *Acacia* species as they are of the most specious woody genera in the HIP, and vary substantially in life forms between species (Midgley & Bond, 2001) and within species (Archibald & Bond, 2003), making it the ideal genus to study variation in savanna life forms. Furthermore, by studying a single genus, some of the pitfalls associated with phylogenetic constraints could be avoided.

Acacia karroo, *A. gerrardii* var *gerrardii, A. nilotica* var *kraussiana*, *A. davyi*, *A. caffra*, *A. burkeii* and *A. robusta*, were sampled from populations in Hluhluwe, while *A. grandicornuta*, *A. nigrescens*, *A. tortilis* and *A. luederitzii* var *luederitzii* were sampled from Imfolozi. It should be noted that *A. gerrardii, A. nilotica* and *A. burkeii* are also found in Imfolozi, but I chose to sample the Hluhluwe populations. *A. senegal* and *A. borlei* also occur in the reserve but in very low densities and consequently was omitted from the study.

Sampling Methods

Ten individuals (5 juveniles: 2.5 to 8cm diameter at breast height (DBH); and 5 adults: > 15cm DBH) of each of the 11 chosen species were randomly sampled. I avoided sampling any damaged or stunted individuals.

Bark thickness

At least 50 bark and stem measurements were taken from randomly selected individuals (including the 5 adult trees selected for the sprouting experiment). Bark thickness (cambium included) and stem diameter were measured at least five randomly selected points along the length of the stem. Samples were measured in the field to avoid variation in measurements due to water loss.

Research conducted on bark thickness in savannas (Jackson *et al.*, 1999) and fynbos Proteaceae (Chapter 3) suggests that allocation to bark is not always constant, and may well vary with size/age. Comparing bark thickness and stem diameter as plants get bigger allows for an assessment of ontogenetic variation in allocation i.e. negative versus positive allometry (Jackson *et al.*, 1999).

For general comparisons between species, the predicted bark thickness at 100mm of stem diameter was calculated using the regression relationships between stem diameter and bark thickness. One hundred millimetres was used as the standard measure because this is the point where the all the species' regression curves have flattened off (see Appendix 1).

Sprouting response to experimental cutting

The same ten individuals of each of the 11 species were cut down 30cm above the ground to simulate sprouting after either intense burns or heavy browsing (e.g. elephant breaking). To protect the resprouts from subsequent herbivore damage, the portion of tree removed was used to cover the cut stems. Experimental sites were revisited a year later, and the number of and vigour (length) of each live resprout was measured for each individual to provide insight into sprouting ability and sprouting strategy.

Plant defences against herbivory

Owen-Smith & Cooper (1987) found that acacias were generally palatable relative to other deciduous and evergreen species, so for this study I focussed primarily on structural defence characteristics. Data from Midgley *et al.* (2001)

Table 2. Summary of traits measured on each tree and method employed

Trait	Units	Rationale	Method of data collection
Height	m	Height is key in determining whether plants escape both the fire-trap (Bond & van Wilgen, 1996) and herbivory (Midgley *et al.*, 2001, Young *et al.*, 2003). Size can also determine fire resistance (Gignoux *et al.*, 1997) i.e. taller trees can acquire thick bark allometrically by growing taller.	Measured as height of the top of the canopy. Data were supplemented by information collected from 350 ¼ Ha plots.
Seed size	mg	Seed size is a crude measure for both reproduction allocation and potential establishment success (Westoby, 1996). It provides an indication of the reliance on seeds for regeneration.	Dry seed mass was calculated for 15 mature, alive seeds collected from each individual. Seeds were stripped of dispersal structures (such as wings, arils and elaiosomes) and were oven dried for until constant mass at 80° C for 24 hours and weighed.
Wood density	g/cm^3	Wood density is a useful indicator of both structural integrity and defence against pathogens and fire (Loehle, 1988).	Wood samples were collected from each species and wood density was calculated. Samples were dried at 80° C for 24 hours and weighed. The samples were then covered in Vaseline and immersed in a measuring cylinder to calculate volume.
Multistemmedness	Number	Multistemmedness is considered a useful surrogate measure of sprouting ability (Midgley, 1996, Kruger *et al.*, 1997).	Multistemmedness was calculated as the numbers of stems per individual originating from below the ground.
Bark thickness	% of stem diameter	Bark thickness is key in determining a plant's resistance to fire (Gignoux *et al.*, 1997, Pinard & Huffman, 1997, Chapter 3).	The stem thickness vs. bark thickness regression analyses were used to determine the predicted bark at 100mm of stem. Bark thickness values were represented as a % of stem diameter to standardise the measurement across a range of stem diameters.

were used to assess the degree to which the various acacia species are defended against herbivory. The index (comprising measurements of thorn length and density as well as shoot length) is a composite measure of the degree to which plants defended against herbivory.

Defining functional groups

Table 2 details the traits measured and methods employed to quantify the variation in *Acacia* species functional types. Bark thickness, plant height, seed mass and multistemmedness data from the five adult individuals of each of the 11 species were used in the multivariate analyses. Stem density data were not included as the MDS analysis as they did not contribute significantly to the ordination. Since I ordinated 5 individuals of each species and not the mean values for each species, I used a bark thickness at a standard stem diameter rather than using average slope and intercept values of the regression relationship between bark thickness and stem diameter (as suggested in chapter 3).

Data analyses

General

Statistical analyses were conducted using MICROSOFT EXCEL and STATISTICA software packages, although linear regression analyses were performed using the RMA software package (http://www.bio.sdsu.edu/pub/andy/rma.html). RMA or Reduced Major Axis Regression (Type II regression) reduces the error associated with the fitting of regression slopes as it makes use of perpendicular least squares as opposed to vertical least squares (type 1 regression, Sokal and Rohlf, 1981). Since I was interested in comparing slopes and intercepts in this study, it is important to use Type II regression analyses.

Multivariate analyses: assessing functional groups.

The statistical package PRIMER was used to perform a sequence of multivariate statistical routines on the date (Clarke & Warwick, 1994). Non-metric multi-dimensional scaling (MDS) ordination was used to develop graphic representations of the *Acacia* species' function groups. All data were equally weighted but √√ transformed to ensure that larger trait values (e.g. plant height vs seed mass) are not over-emphasised by the analysis.

RESULTS

Bark thickness

The thickness of bark increased with stem diameter for all the species (Appendix 1). Furthermore, all species displayed negative allometry i.e. early allocation to defences, as indicated by the convex curves of the regression analysis (Appendix 1). Thus juveniles tend to have proportionally thicker bark than adults. *A. karroo*, *A. nilotica* and *A. burkeii* have inherently thick bark (high intercept (c) value). Others, such as *A. caffra*, *A. gerrardii* and *A. davyi* develop thick bark by having inherently thick bark to begin with as well as through rapid accumulation (steep regression slope) (Table 3).

Sprouting in response to experimental cutting

For the majority (9 of 10) of species, 100% of the experimentally cut stems of juveniles resprouted. The exception was *A. nigrescens*, of which only 60% of the juveniles individuals resprouted. Adults displayed greater variation in sprouting ability than juveniles. Of the Hluhluwe species, only two species, *A. caffra* and *A. davyi,* resprouted strongly (100%) as adults. This is reflected in their high degree of multistemmedness as adults. In contrast, *A. nilotica* and *A. gerrardii* did not resprout at all as adults, while *A. burkeii* and *A. karroo* sprouted relatively strongly (60 – 80%). The adults of Imfolozi species sprouted relatively weakly (40 – 50% sprouting) (Table 3).

Both adults and juveniles of the mesic savanna species produced fewer sprouts on average than Imfolozi species (Mann-Whitney U, $p = 0.024$, Fig. 2) although the difference was not statistically different in adults (Mann-Whitney U: $p = 0.063$, Fig. 2). Mesic savanna species produced more vigorous (longer) sprouts than xeric savanna species, although the difference between juvenile sprout lengths was not statistically significant (Juveniles: Mann-Whitney U, $p = 0.0727$; Adults: Mann-Whitney U: $p = 0.015$, Fig. 3).

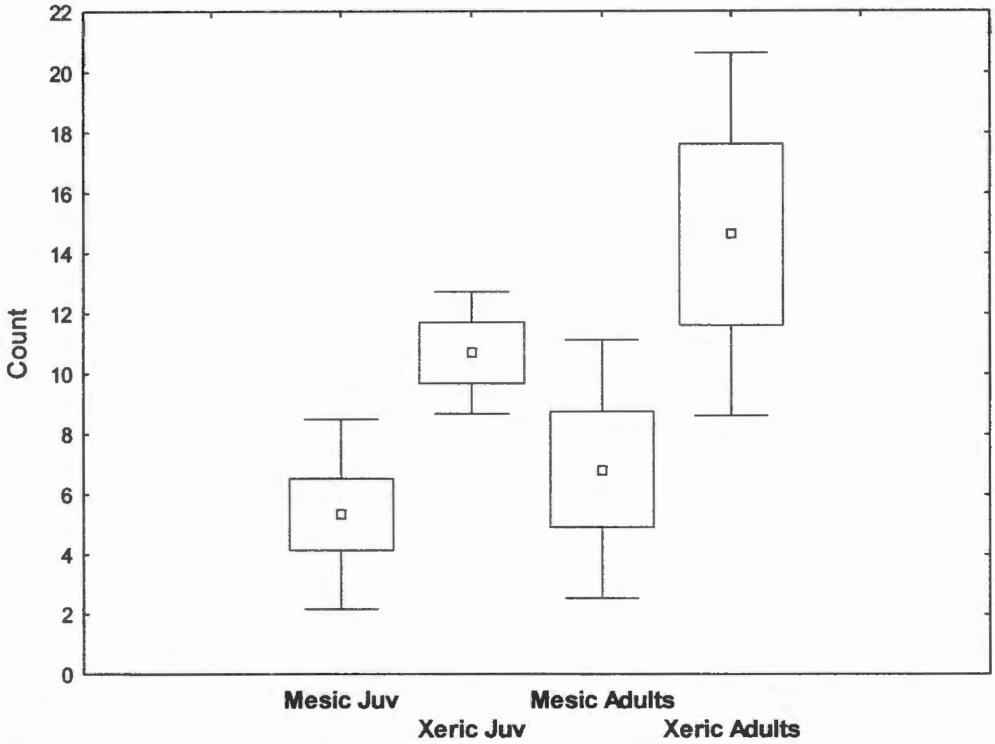

Figure 2. Mean number of sprouts per individual. Box-whisker plots indicate mean, SE and SD.

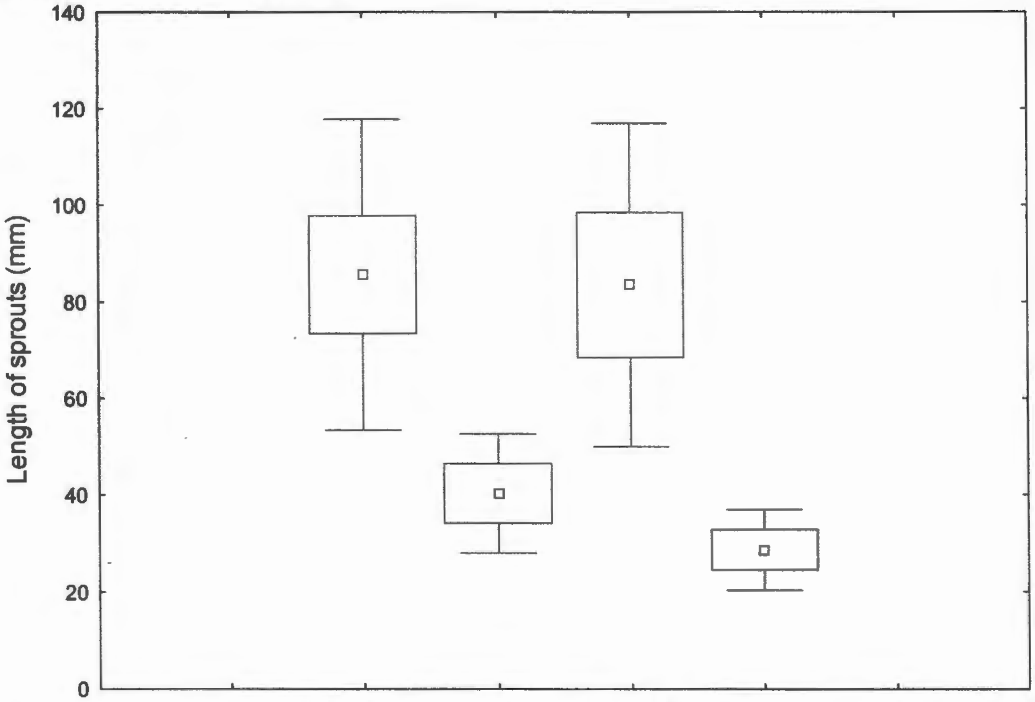

Figure 3. Mean length of sprouts of juveniles and adults, mesic versus xeric savannas. Box-whisker plots indicate mean, SE and SD.

Plant mechanical defences

Although not statistically different, the mean spinescence index values of the xeric savanna species was greater than the mesic savanna species (Xeric: mean = 8.74, SE = 7.09 vs Mesic: mean = 0.701, SE = 0.64; $z = -1.55$, $p = 0.121$), suggesting that xeric savanna species tend to be better defended than the mesic savanna species (Fig. 4).

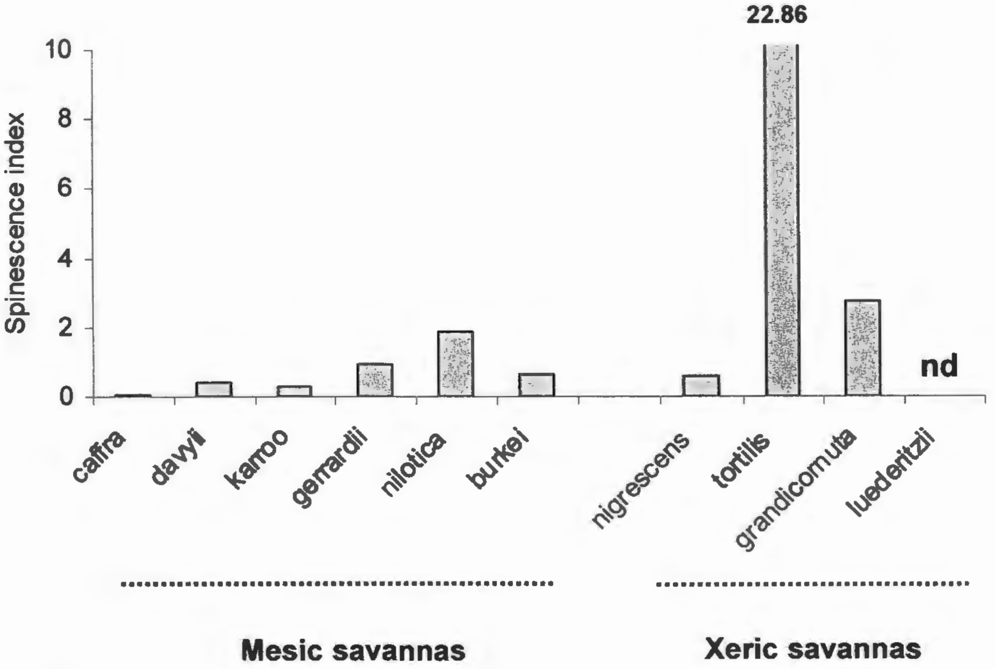

Fig 4. Spinescence indices for Hluhluwe-Imfolozi Park *Acacia* species (after Midgley *et al.*, 2001). No data available for *A. luederitzii.*

Functional groups

When comparing mean trait values across species (Table 3) the following are the only significant regression relationships: Number of stems per individual versus plant height, seed size versus plant height and seed weight versus plant height. Plant height decreased with increasing bark thickness and number of stems per individual, while plant height increased with increasing seed size (Fig. 5 A-C). Wood density did not correlate with any of the other traits measured.

Table 3. Life history traits measured for each of 11 Acacia species in HIP: including seed mass, wood density, height, predicted bark thickness at 100mm of stem, the log-log regression equations and sprouting after experimental cutting (percentage of individuals sprouting, mean count of sprouts and vigour i.e. mean length of sprouts, SEM in parentheses).
* denotes significance at $p < 0.005$ level

Species	Seed mass (mg)	Wood density ($g.cm^3$)	Height (m)	No. stems	Bark (mm)	Stem vs Bark (logged data)			Sprouting					
									Juvenile			Adult		
						slope	intercept	r^2	%spr	mean count	mean length	% spr	mean count	mean length
Mesic savannas														
Seeders														
A. burkeii	0.126 (0.01)	0.84 (0.04)	10.04 (0.37)	1.02 (0.01)	10.34	0.67	-0.32	0.924 *	100	9.2 (1.11)	24.64 (3.86)	60	6.3 (2.23)	47.04 (8.89)
A. karroo	0.043 (0.002)	0.84 (0.038)	5.27 (0.44)	1.19 (0.02)	9.82	0.69	-0.36	0.913 *	89	2.2 (0.35)	88.70 (8.05)	80	4 (0.73)	46.56 (1.39)
A. nilotica	0.095 (0.002)	0.93 (0.034)	4.65 (0.38)	1.03 (0.01)	10.44	0.67	-0.32	0.89 *	100	1.4 (0.55)	92.00 (9.33)	0	0	0
A. gerrardii	0.085 (0.002)	0.87 (0.023)	5.38 (0.06)	1.06 (0.01)	10.97	0.86	-0.68	0.905 *	100	3.5 (1.18)	64.06 (2.11)	0	0	0
Sprouters														
A. caffra	0.089 (0.001)	1.01 (0.034)	3.57 (0.15)	2.19 (0.01)	12.37	0.93	-0.722	0.967 *	100	5.5 (0.81)	110.48 (5.72)	100	4.25 (0.56)	108.75 (8.59)
A. davyi	0.032 (0.001)	0.86 (0.023)	2.53 (0.202)	4.47 (0.45)	15.90	0.94	-0.67	0.945 *	100	6.4 (1.83)	119.61 (11.81)	100	5.25 (1.48)	105.64 (4.71)
Riverine habitats														
A. robusta	0.168 (0.006)	0.78 (0.034)	12.44 (0.14)	1.03 (0.01)	7.55	0.70	-0.53	0.944 *	100	9.2 (1.56)	99.88 (7.86)	75	13.3 (1.81)	109.31 (4.89)

Table 3. cont.

Species	Seed mass (mg)	Wood density (g.cm^3)	Height (m)	No. stems	Bark (mm)	Stem vs Bark (logged data)			Sprouting					
									Juvenile			Adult		
						slope	intercept	r^2	%spr	mean count	mean length	% spr	mean count	mean length
Xeric savannas														
Seeders														
A. grandicornuta	0.113 (0.004)	0.97 (0.07)	7.43 (0.079)	1.18 (0.02)	7.23	0.67	-0.48	0.933 *	100	10.2 (2.16)	38.84 (4.71)	40	17 (3.02)	30.94 (6.46)
A. nigrescens	0.158 (0.005)	1.07 (0.103)	10.36 (0.103)	1.05 (0.01)	8.88	0.78	-0.99	0.956 *	66	13.3 (2.26)	26.85 (1.99)	50	22 (4.42)	25.56 (0.55)
A. tortilis	0.045 (0.009)	0.93 (0.91)	4.74 (0.91)	1.11 (0.02)	8.24	0.78	-0.64	0.947 *	100	11.0 (2.19)	56.75 (11.35)	40	10.5 (2.75)	19.28 (6.14)
A. luederitzii	0.038 (0.002)	1.03 (0.023)	3.89 (0.023)	1.52 (0.13)	7.61	0.83	-0.84	0.946 *	100	8.4 (1.98)	38.73 (6.50)	40	9 (2.35)	38.89 (5.72)

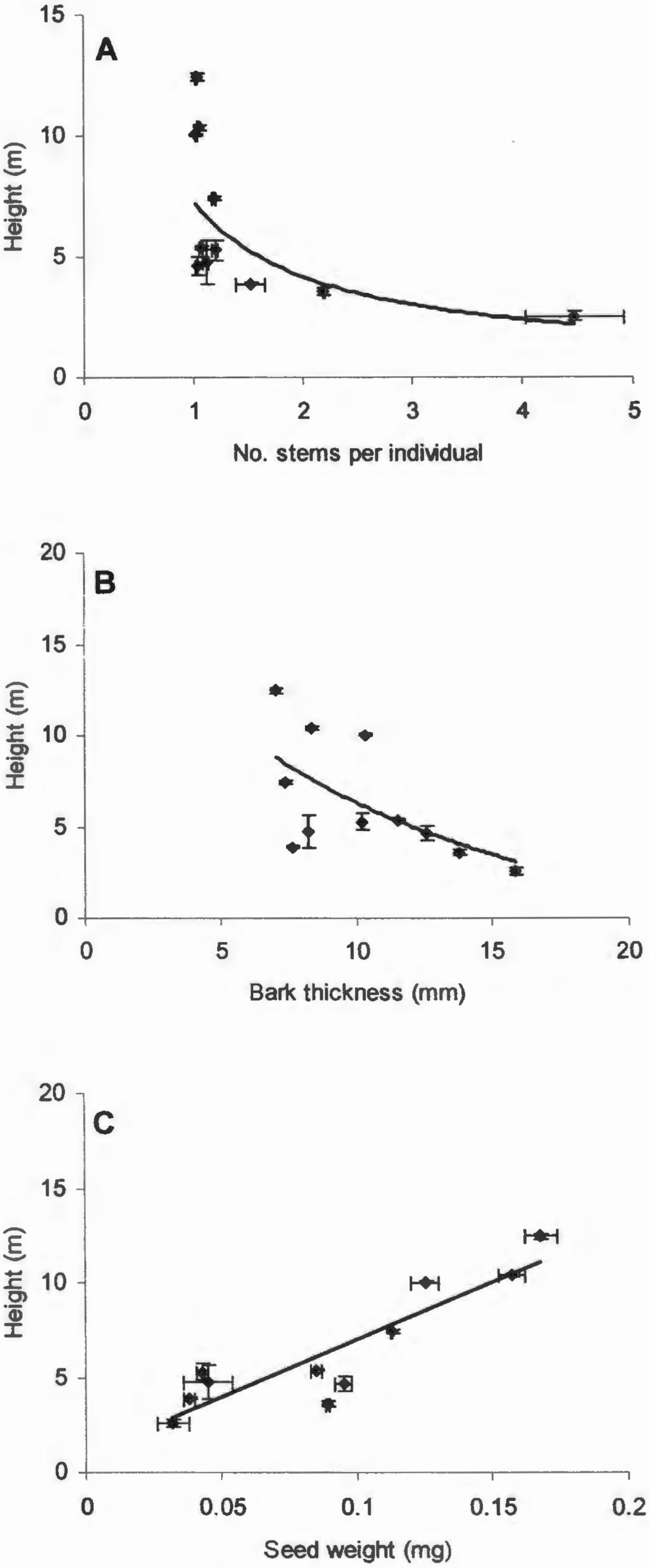

Figure 5. Relationship between A) height and numbers of stems per individuals (multistemmedness) ($r^2 = 0.55$, $P < 0.01$, $y = 7.28x^{-0.80}$), B) plant height and bark thickness ($r^2 = 0.45$, $p < 0.05$, $y = -6.99\ln x+22.4$, C) height and seed weight ($r^2 = 0.79$, $p < 0.005$, $y = 60.2x + 0.96$) for 11 species of Acacia in Hluhluwe-Imfolozi, KwaZulu Natal province, South Africa.

The MDS ($\sqrt{\sqrt{}}$ transformed data, Euclidean distances) clearly distinguishes between xeric and mesic savanna species; and within the mesic group, between seeders and basal resprouters (stress = 0.06 indicating a strong, significant ordination) (Fig. 6). I further separated out *A. robusta* as a riverine species, as they are found in both mesic and xeric savannas. These characteristics of the four groups are described in Table 5.

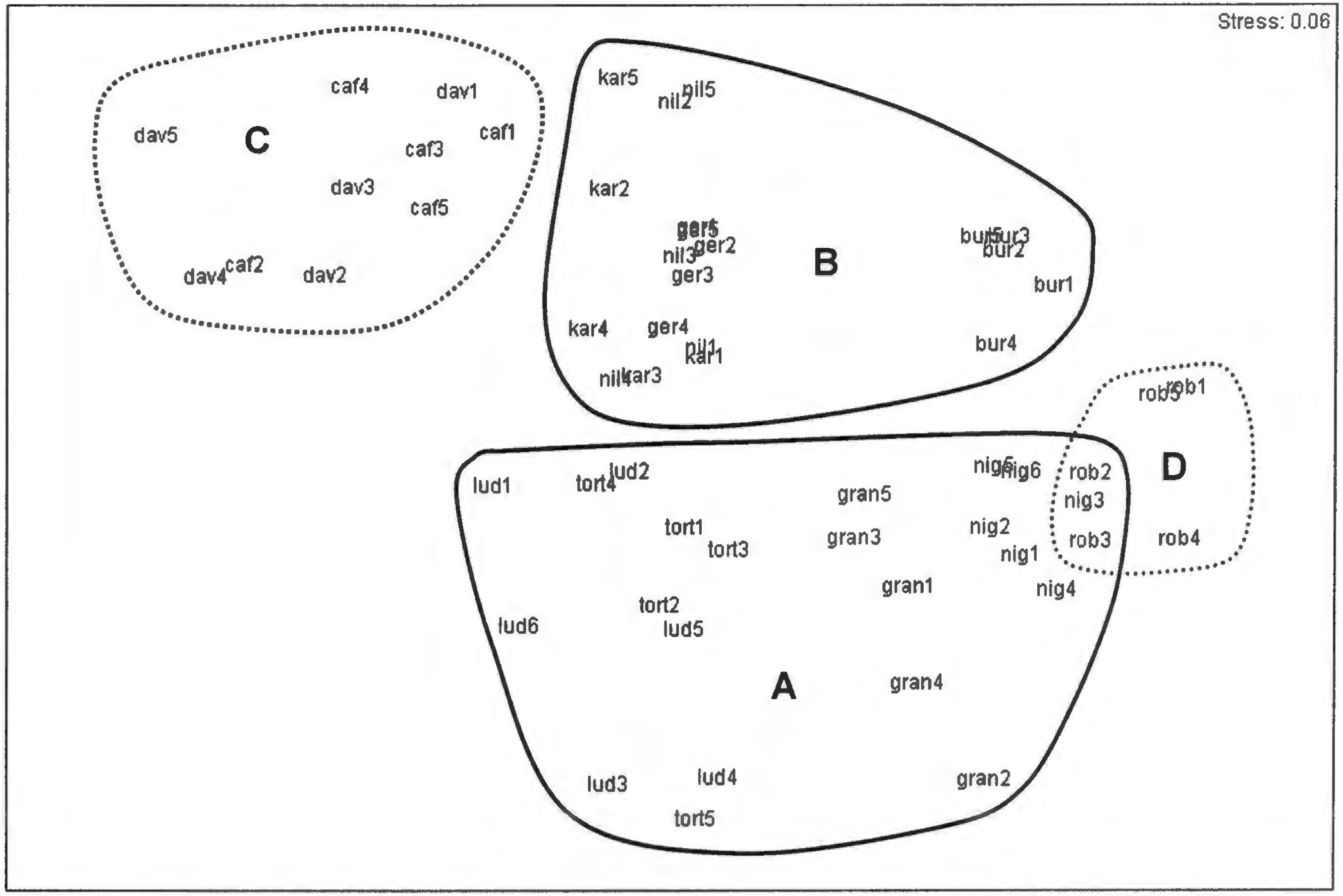

Figure 6. Hluhluwe-Imfolozi Acacias. MDS ordination of the 11 species of *Acacia* based on √√-transformed data and Euclidean distances (Stress = 0.06). A: Imfolozi reseeding species; B: Hluhluwe reseeding species; C: Hluhluwe sprouting species; D: Reseeding riverine species.

Table 4. Four primary groups of Acacia functional types.

Group	Description
Xeric savanna species	
Group A: **Reseeding species**	These species are characterised by being generally single stemmed, thin bark and have medium to large seeds. *A. luederitzii, A. tortilis, A. grandicornuta, A nigrescens* As both juveniles and adults, these species' resprouts tend to form a cage like architecture (many short sprouts, and in conjunction with their spines, form imposing defences).
Mesic savanna species	
Group B: **Reseeding species**	Single stemmed, medium to large seeds with thick bark. They can all resprout as juveniles. The adults that do resprout (*A. karroo* and *A. burkeii*), do so relatively strongly (60 – 80%). *Acacia karroo, A. gerrardii, and A nilotica, Acacia burkeii*
Group C: **Basal sprouting**	Short, multistemmed individuals with small seeds and are well defended against fire. They resprout strongly as both juveniles and adults. *A. caffra* and *A. davyi*
Group D: **Riverine Species**	Tall, single stemmed, with large seeds and thin bark. *A. robusta* Although *A. robusta* has been grouped with the Imfolozi species, it can be separated out as a functional group as it is a riverine species, found in both predominantly in Hluhluwe Game Reserve, but also in Imfolozi Game Reserve.

Group B, C and D are all relatively poorly defended, except for *A. nilotica* (Fig. 4). When sprouting, these species allocate their resources to fewer, but more vigorous resprouts, thus favouring elongation growth (Table 3.).

DISCUSSION

The results suggest that *Acacia* species can be grouped according to their disturbance life history traits. Furthermore, the distributions of these functional groups correlate with local disturbance regimes. The functional groups, based on the MDS ordination (Fig. 6) are graphically depicted in the context of both disturbance regimes and species characteristics in Figure 7, and are fully discussed below.

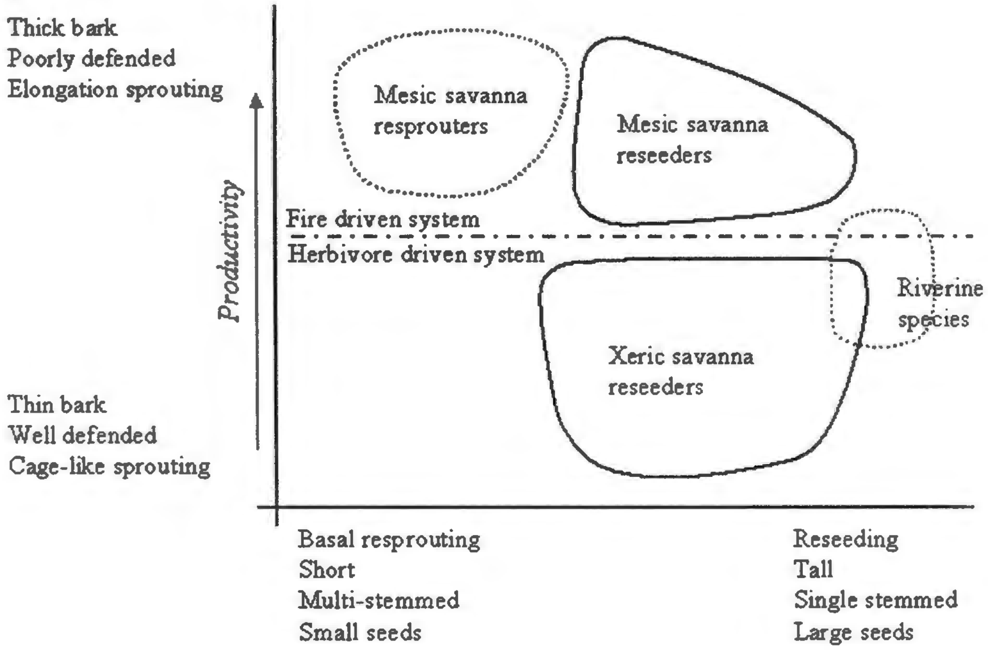

Figure 7. Stylised model of *Acacia* species functional groups in HIP. Grouping based on MDS of character traits (Figure 6).

Imfolozi species: Browsing-related functional groups (Group A)

The species found in the more xeric savannas of Imfolozi, *Acacia luederitzii, A. tortilis, A. grandicornuta* and *A. nigrescens*, displayed characteristics associated with heavy browsing pressure rather than frequent, intense fires. They are sensitive to fire as indicated by their relatively thin bark as juveniles and don't resprout strongly (basally) as adults (Table 3). They display life forms seemingly better adapted to coping with herbivore pressure than *Acacias* found in mesic areas. They are generally well defended, as indicated by their high spinescence indices e.g. *A. tortilis* and *A. grandicornuta* (Fig. 4) and the resprouts display a cage-like sprouting structure. This is an effective architectural defence against herbivory in that, working in conjunction with spines, the inner parts of the plant are well defended (Brown, 1960).

The defence of juvenile individuals would be particularly important, as they would come under the greatest selective pressures from browsing (Bond & van Wilgen, 1996, Midgley *et al.*, 2001). Brooks & Owen-Smith (1994) tested this notion, and found that juvenile *A. tortilis* stems bear longer thorns in higher densities than adults i.e. juveniles are better defended than adults for this species.

Although I didn't assess adult architecture, *A. luederitzii*, which is the shortest of the Imfolozi species (mean height: 3.89m) and therefore remains in the zone of highest herbivory, has a highly branched architecture even as an adult (per obs.). *A tortilis*, bears impressive spinescent defences, and has often been recorded as being highly resistant to herbivory (du Toit *et al.* 1990; Bond & Loffell, 2001). The remaining species, especially *A. nigrescens,* would make up for their relative lack of spinescence (Fig. 4) by growing tall and escaping the majority of browsing impact (Midgley *et al.*, 2001). Furthermore, du Toit *et al.* (1990) found that *A. nigrescens* can more than adequately compensate for loss of foliage through browsing by strong shoot regrowth i.e. by sprouting epicormically. Epicormic sprouting or sprouting from aerial portions of the plant (Bellingham & Sparrow, 2000) has been found to be an effective strategy in areas characterised by lower fire intensities in the fynbos (Chapter 3), in contrast to basal sprouting, which is rather an adaptation to intense disturbance.

Hluhluwe species: Fire-related functional groups

Reseeders (Group B)

As a group these species (*A. karroo, A. nilotica, A. burkeii* and *A. gerrardii*) would seem to have a life history strategy adapted to cope with intense and/or frequent fires rather than herbivory. In general these species are fire survivors (thicker bark as juveniles) but are generally poorly defended against herbivores (Fig. 4).

When sprouting after loss of above-ground stems, both adults and juveniles of these species produce a few, but vigorous resprouts. Rapid height gain would be selected for as it increases the chances of pushing the new shoots above the firetrap and recruiting into the canopy (Archibald, 2003). Also, when modelling tree-grass coexistence for mesic savannas, Higgins *et al.* (2000) found that sprouting of at least 0.6m per annum was required for continued tree persistence. I found that the shoots were on average this length or longer, (Table 3), suggesting that these species are adapted to a fire-prone existence. However, the elongated nature of the resprouts, in conjunction with poor mechanical defences (Fig. 4), would render them vulnerable to browsing.

Also, these species have larger seeds than the Hluhluwe sprouting species (Fig. 5c). Larger seeds are reported to have an advantage in the regeneration niche, in that seed size is a good indicator of cotyledon-stage seedlings ability to survive various hazards (Westoby *et al.*, 1996) i.e. it confers an advantage in seedling establishment, a critical stage of acacia demography (Midgley & Bond, 2001). Furthermore, seedling size may also be an indication of species' ability to cope with disturbance once established (Harms & Dalling, 1997). They found that seedlings of woody dicotyledenous species in Barro Colorado Island displayed a greater sprouting success following clipping.

Basal resprouters (Group C)

Given the short adult height of *A. caffra* and *A. davyi* (mean of c. 3.5 and c. 2.5m) in Hluhluwe, these species remain within the firetrap for the duration of their lifespan, and thus require strong ability to persist. These species could be considered the best fire-survivors as they are well protected from fires by their thick bark and can resprout vigorously, both as juveniles and adults if they should lose their aboveground biomass (Table 3). Sprouting after damage requires a substantial pre-fire allocation to stored reserves (Hodgkinson, 1988). This prior allocation of resources to ensure fire survival is a major cost, which may result in a trade-off between storage versus growth and reproduction (Bond & van Wilgen, 1996).

Together with their weak spinescence (Fig. 4) and the elongated nature of their resprouts, these species would be particularly poorly defended against herbivory. As adults these two species have been found to be particularly susceptible to browsing by giraffes (Bond & Loffell, 2001). According to these authors, in areas of high giraffe densities, these species tend to go extinct; whilst in areas with steeper terrain and inaccessible to giraffes, both species survive.

Riverine species (Group D)

Acacia robusta is tall, single-stemmed and bears large seeds. However, it is both fire-sensitive and vulnerable to herbivory. Generally found in fire retardant riverine forests communities (Whateley & Porter, 1983), *A. robusta* escapes being burnt, and avoids herbivory through rapid height growth (Table 3) and by becoming tall.

Some argue that seed and seedling ecology is less important in savanna dynamics than tree persistence once they have established (Higgins *et al.*, 2000, Midgley & Bond, 2001). However, in the light-limited, tall riverine forests perhaps seeds and seedling ecology is of more importance. These riverine forests are analogous to the taller southern Cape forests of South Africa, where reseeding is a key strategy when competition for light is critical (Kruger *et al.*, 1997). An increased allocation to larger seeds would be would confer greater advantage in the regeneration niche in this environment (Westoby *et al.* 1996), which is critical in taller forests (Kruger *et al.*, 1997). Furthermore, in an environment such as forests, where light is the most limiting resource, the ability to grow tall is vital in order to outgrow competitors and to access light. Obligate, basal sprouting species would be at a competitive disadvantage in their limited reproductive output (Bond & Midgley, 2003), and limited height growth (Midgley, 1996).

A robusta juveniles nonetheless resprouts strongly when damaged (Table 3). However, here the extension growth of the resprouts could be an adaptation to getting to the light rather than escaping flame height. In the light-limited environment of the riverine forests, elongation growth as sprouts is critical in getting to the canopy, so as to over-top neighbours and access the light.

Are traits plastic?

Some of these attributes may be genotypically plastic, as is the case with *A. karroo* (Archibald & Bond, 2003). The authors found that *A. karroo* adopted a well-defended, broad-canopied, multistemmed form in xeric savannas (high browsing pressures, high light conditions) and a tall, thin, unbranched form in forests (lower browsing pressures, low-light environments). Furthermore, *A. caffra* is a short multistemmed individual in HIP, but can occur as a tall, single stemmed plant (pers. obs.) in Ithala game reserve, an upland savanna, that has experienced little historical browsing and few fires (Bond & Loffell, 2001). Thus some species may be genotypically plastic enough to switch strategies with changing disturbance regimes.

The importance of sprouting

Age/size strongly influences sprouting ability. All juveniles can resprout, and seen in the context that fire and herbivore related disturbance are most intense in the first 2-3m above ground, thus it is not surprising. However, it would seem that adult basal sprouting after disturbance is more important in mesic savannas, as I found only Hluhluwe species *A. caffra* and *A davyi,* to resprout strongly basally. Thus strong sprouting as adults plays a more significant role in mesic savannas, where the probability of losing all of the above-ground biomass to fire is greater.

Fire resistance

These results demonstrate that, similar to members of the Proteaceae (Chapter 3), acacias can acquire resistance to fires through a number of traits: intrinsic resistance (naturally thick bark) or rapid acquisition of bark. Furthermore, ontogenetic changes in defence allocation are another piece of evidence for understanding woody plant fire resistance strategies (Jackson *et al.*, 1999). All the species studied in HIP, displayed negative allometry i.e. early allocation to defences. In the context of frequent surface fire in savannas, the development of fire resistance as early as possible would essential for continued survival. It should be noted that most adults can eventually acquire thick bark and hence fire resistance through allometric means (Gignoux *et al.*, 1997) i.e. bark thickens with increasing thickness of the stem.

Conclusions

Traditionally, soils and rainfall have always been cited as the primary factors influencing plant distribution patterns in savannas (Scholes & Walker, 1993; Scholes, 1997). The results of this study show that disturbance regimes can also play a role major role in predicting plant distribution, in conjunction with soils and climate requirements.

Life forms could thus be used as useful predictors of primary processes sculpting plant life history strategies and communities (see also Bond & Archibald, 2003). I predict that, in the herbivore-dense, dry savannas of east Africa, that acacias such as *A. drepanolobium,* would have a life history adapted to herbivory i.e. well defended against herbivory, a cage-like architecture but strongly fire sensitive. Conversely, species in the mesic savanna such as *A. sieberiana,* will have thick bark and poor anti-herbovore defences.

This study also highlights the importance of sprouting both juveniles and adults acacias in savannas, and in which environments these are important (see also Everham & Brokaw, 1996; Hodgkinson, 1998; Bellingham & Sparrow, 2000). In particular, it shows the importance of basal sprouting as adults in mesic savannas.

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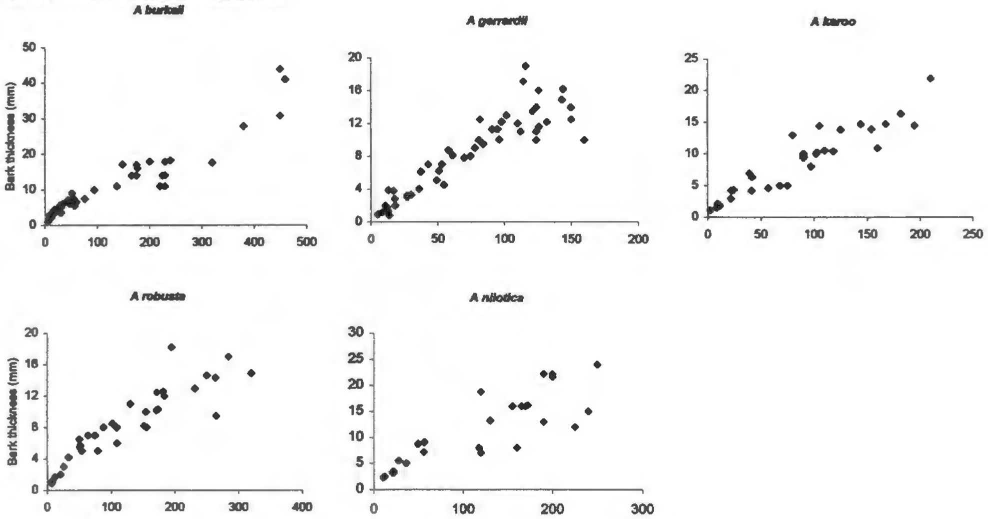
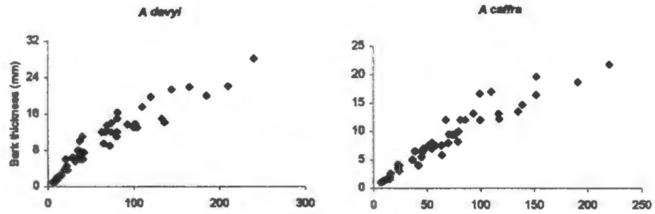
Appendix 1

MESIC SAVANNAS Reseeders

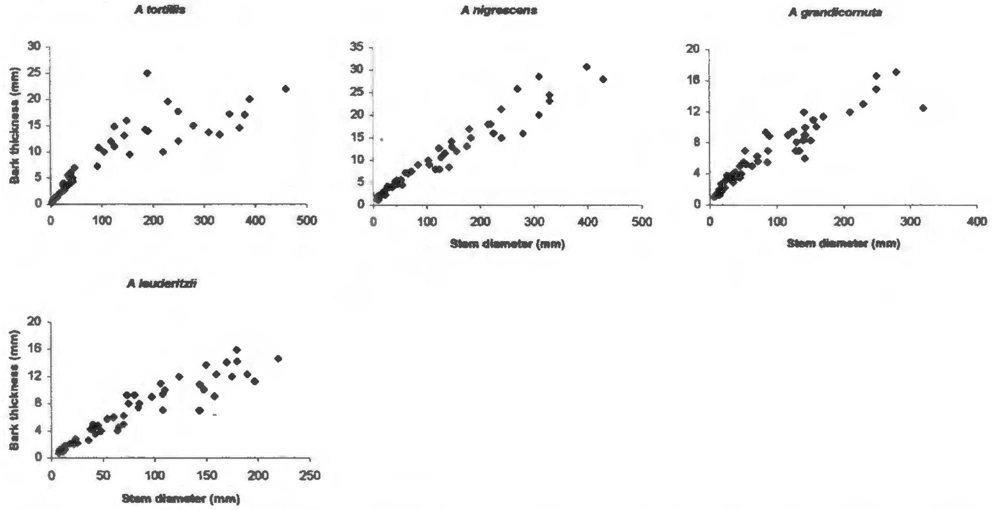


Resprouters



XERIC SAVANNAS

Reseeders



Appendix 1: Regression relationships between stem diameter and bark thickness for 11 Acacia species in Hluhluwe-Imfolozi. *Acacia burkeii* : $y = 0.485x^{0.66}$, $r^2 = 0.95$; *A. gerrardii*: $y = 0.21x^{0.86}$, $r^2 = 0.91$; *A. karroo:* $y = 0.43x^{0.69}$ $r^2 = 0.92$; *A. robusta:* $y = 0.295x^{0.704}$, $r^2 = 0.94$; *A nilotica:* $y = 0.47x^{0.673}$, $r^2 = 0.89$; *A. davyi*: $y = 0.221x^{0.92}$, $r^2 = 0.9445$; *A. caffra:* $y = 0.169x^{0.93}$, $r^2 = 0.967$; *A. tortillis:* $y = 0.23x^{0.78}$, $r^2 = 0.95$; *A. nigrescens*: $y = 0.28x^{0.76}$, $r^2 = 0.97$;

6. Does Westoby's LHS ecological strategy scheme take sprouting into account as a key life history strategy?

ABSTRACT

Plant ecological strategy schemes (PESS) are useful in a) understanding important selective forces that shape plant strategies b) describe vegetation according to plant life history strategy types, in so doing, retaining important ecological information and c) they are useful in determining how species respond to perturbation. Westoby's Leaf-Height-Seed (LHS) scheme is one of the easier schemes to apply as he provides conceptually simple, clear methodology. The aim of this study was to determine whether the LHS scheme incorporates sprouting as a key life history trait by default. The LHS axes are specific leaf area (SLA), height of plant's canopy at maturity and seed mass. The strategy of a species is described by its position in the volume formed by the three axes. I tested the LHS scheme on *Acacia* species and 5 genera within Fynbos Proteaceae. The LHS scheme did not consistently separate sprouters from seeders at the level of genus or family. Although sprouters were found to be shorter than reseeders, no consistent conclusions could be drawn about sprouter seed mass and SLA. Given the importance of sprouting as a regeneration strategy and mode of persistence, I propose the inclusion of sprouting as another axis to be considered in plant ecological strategy schemes.

INTRODUCTION

There are three principal aims to using ecological strategy schemes (Westoby, 1998). The first is to understand the important opportunities and selective forces that shape the ecologies of plants. One such example would be Tilman's model of plant succession (Tilman, 1988, 1994). Plant succession and hence community structure is determined by plants ability to cope with resource or light stress and disturbance. In assessing competition for resources, he predicts the traits of species expected along fertility and disturbance gradients, and also the relationships between plant traits and succession. Grime's (1974, 1979) C-S-R scheme, another example, invoked the process of disturbance, stress and competition as opposing forces selecting for contrasting syndromes of characteristics. He proposes three types of life history strategies: Ruderals (dominate in sites characterised by high disturbance), Competitors (tall plants with high growth rates) and Stress tolerators. The R dimension expresses plants' response to disturbance, while the S-C dimension expresses capacity to take advantage of favourable growth conditions. Both schemes predict life history types, depending on the prevailing conditions (nutrient stress, elevated levels of competition). More recent models that predict plant response to disturbance in particular, include Loehle (2000), Lavorel & Garnier (2002), Cornelissen *et al.* (2003) and Pausas & Lavorel (2003).

A second aim is to describe plant componentry of ecosystems in terms of a limited number of ecological component types (Westoby, 1998) e.g. Noble and Slatyer's (1980) "vital attributes", where species are categorised according to which of their life-history phases are present at different years after disturbance. Using models for vegetation description are useful in that there is no loss of key ecological information, and these easy to measure characteristics reduce vegetation description to easily manageable parts (e.g. Kruger *et al.*, 1997). The third aim of ecological strategy schemes is to determine species response rules in order to predict how species will respond to perturbation e.g. disturbance (fire, herbivory) and/or changing environments (e.g. Pausas, 1999).

A real stumbling block to the world wide acceptance of ecological strategy schemes is that either they are conceptually difficult to grasp, or are difficult to implement because their trait measurements are based on abstract concepts (Westoby, 1998; Loehle, 2000) e.g. how does one measure competition or stress? Recently Westoby (1998) proposed the Leaf-Height-Seed (LHS) scheme. Of the plant ecological strategy models available, the LHS model would seem to be the easiest to apply as the author has set up clear, easy to implement methodology/protocols. Conceptually, the LHS scheme broadly overlaps with Grime's CSR scheme, and comprises three axes: specific leaf area (SLA), height of plant at maturity and seed mass. The author argues that these axes are not chosen only as conveniently measurable indicators, but rather as fundamental trade-offs controlling plant strategies.

SLA (light capturing area deployed per dry mass allocated) is inversely related to leaf life span and positively to mass-based net photosynthetic capacity and mass based leaf nitrogen (Reich *et al.*, 1992, 1998). It explains most of the variation in potential relative growth rate (potRGR) (Loehle, 1988, Reich *et al.*, 1992), an indicator of responsiveness to favourable conditions. High SLA species have strategies associated with rapid production of new leaves during early life, faster turnover of plant parts and higher relative growth rates. Thus, SLA corresponds with the C-S axis of the CSR scheme: the adaptation to opportunities of rapid growth versus continuing enforcement of slow growth (competitors to slow growth) (Westoby, 1998).

Seed mass variation expresses a species' chance of successfully dispersing a seed into an establishment opportunity and is also a good indicator of cotyledon-stage seedling's ability to survive various hazards (Westoby, 1998). Height and seed mass reflect separate aspects of coping with disturbance (Westoby, 1998), correlating with Grime's R-axis.

Ecological strategy schemes and Sprouting

Most ecological strategy schemes, however, make limited mention of sprouting as a key component of life history strategies, despite the recent attention it has received in the literature. Loehle (2000) is of the first general models to give prominence to sprouting. le Maitre & Midgley (1992), Keeley & Zedler (1998), Bellingham & Sparrow (2000), Bond & Midgley (2001 & 2003) and Vesk & Westoby (2004) amongst others, have highlighted the importance of sprouting as a key life history strategy in disturbance prone environments. Sprouting is ubiquitous in woody dicotyledenous plants in all environments and clearly has not evolved only as a response to disturbance (le Maitre & Midgley, 1992). For example, Kruger *et al.* (1997) have identified sprouting as being an important regeneration strategy even in less disturbance prone environments such as coastal forests in South Africa. Such is the importance of sprouting that it is now considered being a life history strategy rather than simply a trait, with distinct trade-offs between persistence, growth and recruitment (Pate *et al.*, 1990; le Maitre & Midgley, 1992, Bond & Midgley, 2003). It is therefore vital that, in all biomes, sprouting is considered in any ecological strategy scheme.

LHS and sprouting

LHS doesn't attempt to account for sprouting specifically. However, trade-offs associated with sprouting may influence the LHS traits, such that a characteristic or unique combination of may result. To be able to sprout, a plant needs surviving meristems and stored reserves to support regrowth. Allocation to these would result in a trade-off against growth and reproduction (Bond & Midgley, 2001, Vesk & Westoby, 2004b), and these trade-offs may affect the three traits measured in the LHS scheme.

In many cases basal sprouting leads to a multistemmed architecture, and a consequent reduction in height (Midgley, 1996, Kruger *et al.*, 1997). Midgley (1996) found that nonsprouters are typically single stemmed and taller that co-occurring congeneric sprouters. Furthermore, increased allocation to maintenance and defences may also result in reduced allocation to reproduction (Loehle, 1988). One consequence of this trade-off might be the reduction in seed size. I found that sprouting *Acacia* in South African savannas tended to have smaller seeds (Chapter 5), although little other evidence is available to support this assertion.

Lastly, one could expect a trade-off between storage and growth rates (Bond & Midgley, 2003), and consequently sprouters may have a lower SLA. Sprouting shrubs in Australian and South African fire-prone ecosystems (Kwongan and

Fynbos) tend to allocate more of their carbon to starch or other reserves and not to their shoots (Pate *et al.*, 1990, Bell & Ojeda, 1999). Consequently, sprouters have a far higher root to shoot ratio and slower growth rates than reseeders, as seedlings. Furthermore, studies of the Australian *Bossiaea* (Hansen *et al.*, 1991) have shown that seedlings of reseeders generally grow significantly faster than those of sprouting species.

I predict, therefore, that sprouters will be shorter, have smaller seeds and lower SLA than reseeders, and in this way Westoby's LHS could distinguish sprouters from seeders. The central question of this study is whether the protocol proposed by Westoby's LHS scheme could identify sprouters as a distinct life history strategy.

METHODS

Study species

Both the fire prone Fynbos and Savanna biomes in South Africa provide the ideal opportunity to test the LHS model of plant life history strategies, as the relative importance of sprouting has been well documented (Kruger, 1979; le Maitre & Midgley, 1992; Bond & van Wilgen, 1996; Midgley & Bond, 2001; Maze, 2003). Acacias are important overstorey components of natural areas in subtropical savannas in southern Africa, and display a range in life history strategies (Midgley & Bond, 2001; Archibald & Bond, 2003, Chapter 5). Acacias were sampled from populations found in Hluhluwe-Imfolozi Park (HIP), KwaZulu Natal, South Africa (see Figure 1, Chapter 5 for map of study site). In savannas, most woody plants can sprout, at least as juveniles (Trollope, 1984), although, in this case, I was particularly interested in adult sprouting.

Many Fynbos overstorey species sprout strongly in response to fire, either basally or epicormically (le Maitre & Midgley, 1992). Proteaceae genera were sampled from the Cape Peninsula, Grabouw and Hermanus districts of the western and southern Cape Province, South Africa (see Figure 1, Chapter 3 for map of location). I selected species pairs (or more) from 5 genera of Proteaceae, but compared only within genera to avoid some of the difficulties associated with phylogenetic constraints.

Sampling methods

LHS traits

Following the protocol laid out in Westoby (1998), data on seed size, plant height and SLA were collected. Dry mass was calculated for at least ten mature seeds collected from each of 10 individuals. Seeds were stripped of dispersal structures (such as wings, arils and elaiosomes) and were oven dried until constant mass at 80° C.

Ten young, mature leaves (fully expanded and hardened) were sampled from 10 individuals. Undamaged leaves were taken from fully light exposed positions on the plants. Leaves were weighed after drying to constant mass at 80°C, and area was measured using Licor leaf area meter. *Acacias* have compound leaves and consequently SLA is hard to measure in this fashion. Percentage nitrogen content was measured for these and converted to SLA using regression equations from Reich *et al.* (1998). Height at maturity, taken as the height of the uppermost foliage, was measured of 40 adult individuals. All axes were log scaled and the strategy of any one species was characterised in the scheme by a position in the 3-D volume (Westoby, 1998).

Sprouting ability

Many broad-leafed species can sprout as juveniles (Trollope, 1984, Loehle, 2000), which could be considered part of a plant's recruitment strategy (Bond & Midgley, 2001). I therefore used adult response to severe disturbance as an indication of sprouting ability, based on the suggestions in Bond & Midgley (2001). Furthermore, Vesk & Westoby (2004a) suggest that sprouting should be viewed in the light of the type of disturbance. In the case of stand replacing disturbance, a binary situation exists, whereas if disturbance is less severe, then a continuum of strategies exist. Although a continuum of sprouting ability may exist, I have considered plant strategies in the face of the more severe disturbances. Thus for simplicity's sake, a binary classification into sprouter/seeders was used and all sprouting strategies: basal, crown and epicormic, were categorised as such. Data on sprouting ability for Proteaceae were derived from Rebelo (1995) and *Acacias* from Archibald & Bond (2003), Maze (2003) and Chapter 5.

RESULTS

Sprouting *Acacia* species tended to be shorter in stature and have smaller seeds, although there was no discernable difference in SLA between seeders and sprouters (Figure 1 & 2). The proteoid sprouters, *Aulax pallasia, Leucadendron salignum, Mimetes cucculatus, Protea cynaroides* and *P. nitida* have a lower SLA when compared to congeneric reseeding species. Consistent with the findings for *Acacia* species, the reseeding proteoids tended to be shorter than the congeneric species. However, sprouting *Leucadendron, Leucospermum* and *Protea* species tended to have larger seeds. No obvious difference in seed size was found between reseeding and sprouting *Aulax* and *Mimetes* species (Figure 2 A – E).

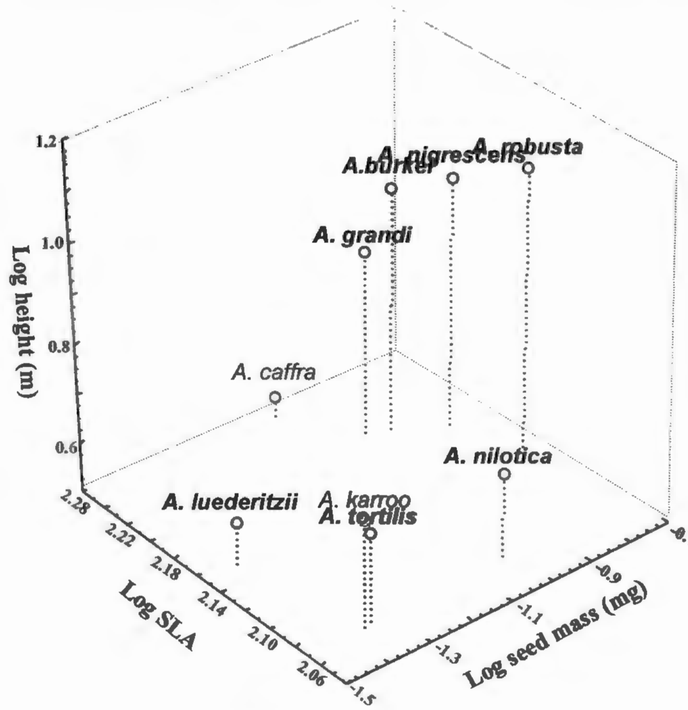


Figure 1. SLA, plant height and seed size of 9 species of *Acacia species* from Hluhluwe-Imfolozi Park, KwaZulu Natal. Axes are log scaled. Reseeding species are denoted by bold text

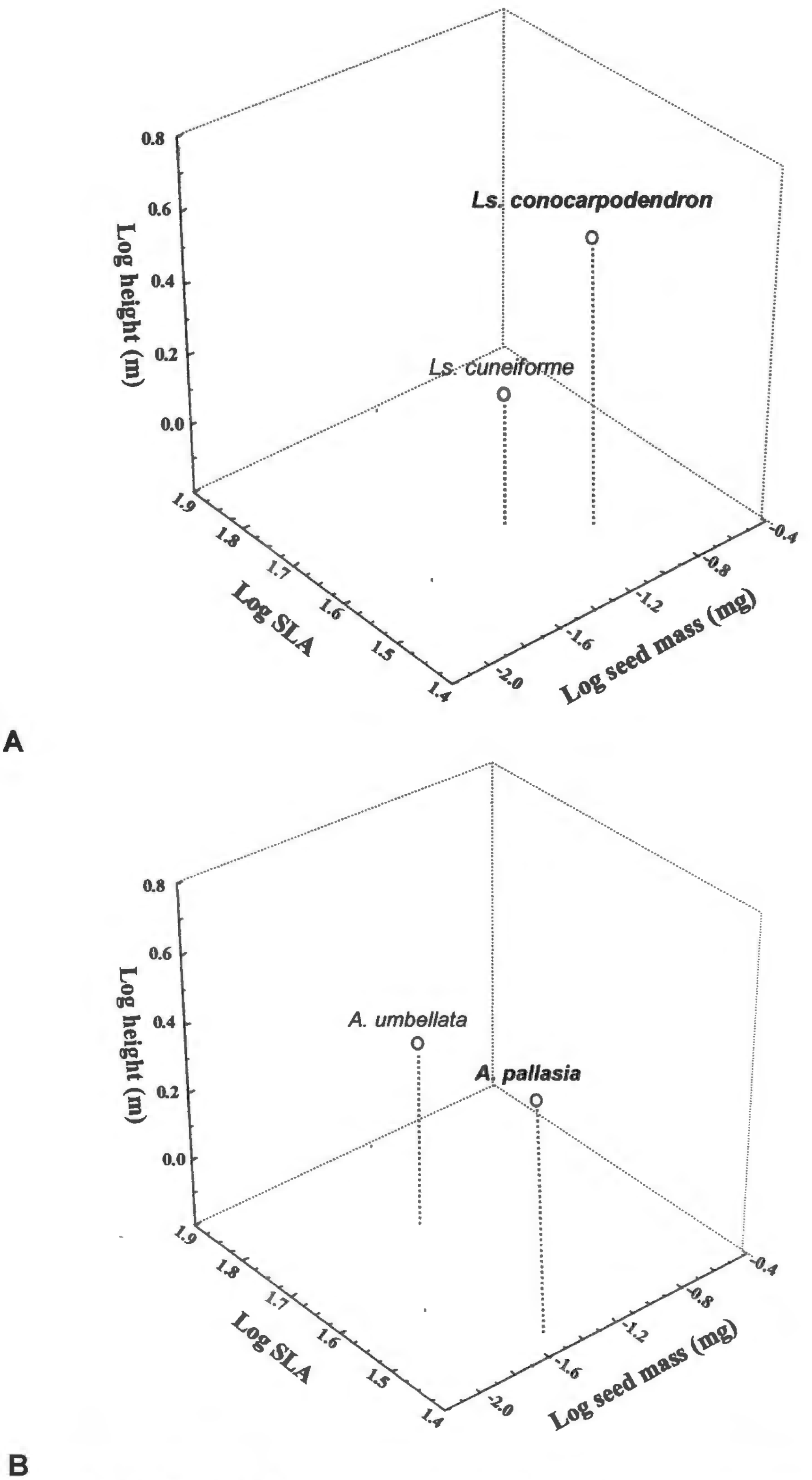


Figure 2 A - B. SLA, plant height and seed size of *Leucospermum* and *Aulax* species from western Cape Province, South Africa. Axes are log scaled. Reseeding species are denoted by bold text.

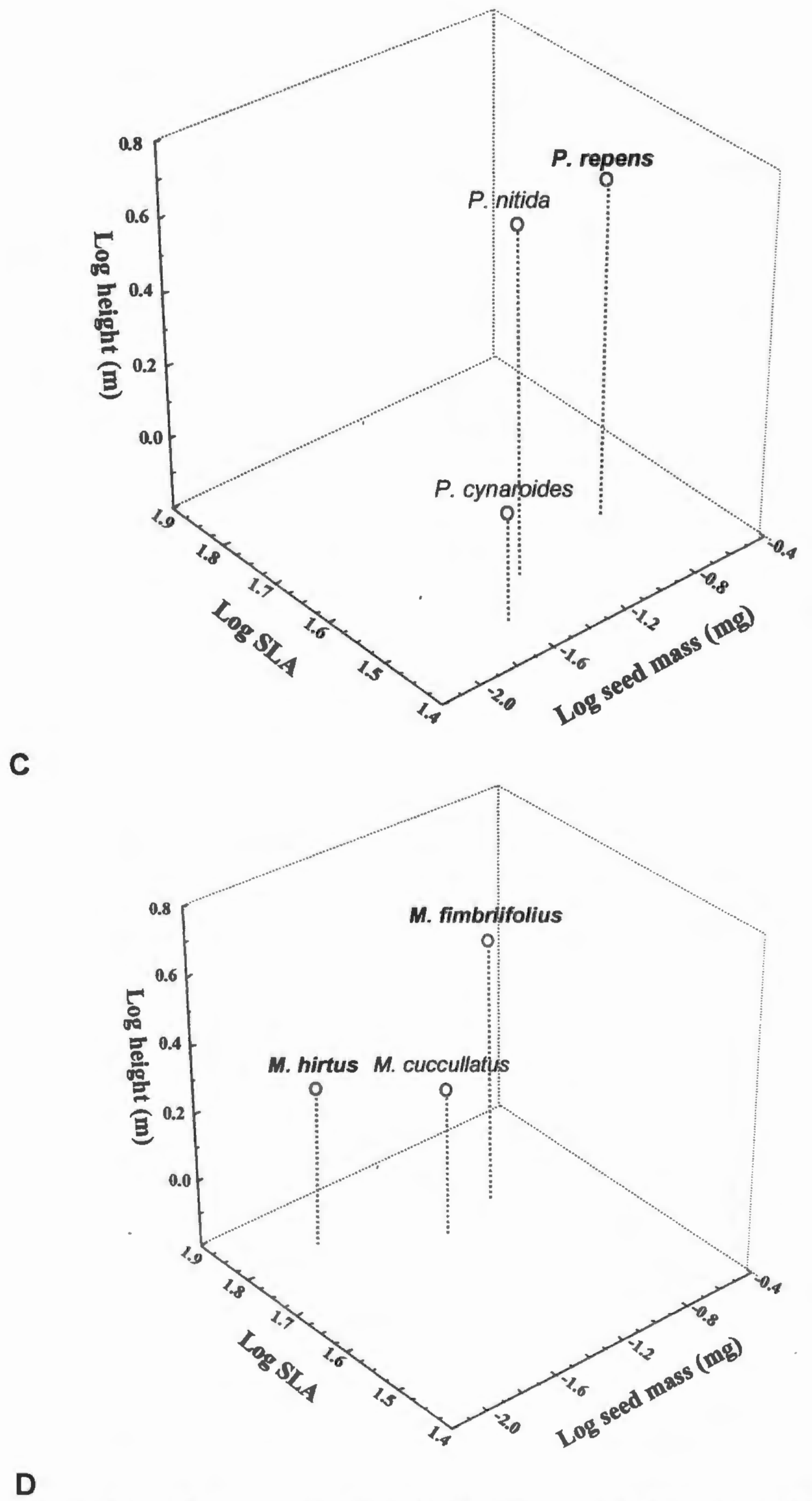
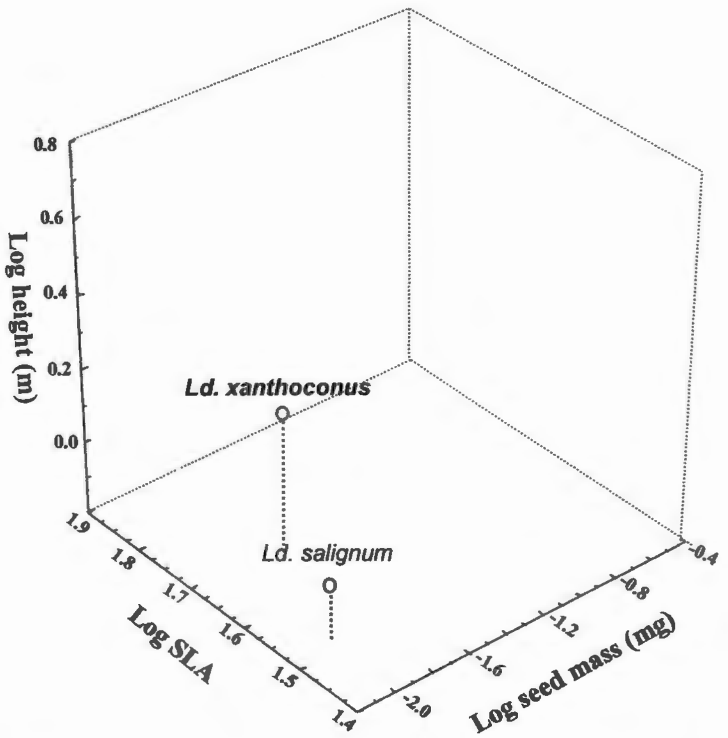


Figure 2 C - D. SLA, plant height and seed size of *Protea* and *Mimetes* species from the western Cape Province, South Africa. Axes are log scaled. Sprouting species are denoted by bold text.



E

Figure 2 E. SLA, plant height and seed size *Leucadendron* species from the western Cape Province, South Africa. Axes are log scaled. Sprouting species are denoted by bold text.

DISCUSSION

The results suggest that the LHS scheme does not separate seeders from sprouters because they are not consistently separated from each other across genera or families. Of the three traits included in the LHS scheme, only height provided a consistent indicator of (basal) sprouters in that most were shorter than congeneric seeders. SLA and seed size proved to be highly variable, and therefore no predictions regarding sprouters could be made from those results. This suggests that sprouting trait is orthogonal to seed and leaf attributes. These results echo that of Lavergne *et al.* (2003), the first to test the L-H-S scheme, who found it limiting when considering plant reproductive traits. They found that female fertility and pollen/ovule ratios discriminated better endemic and widespread species that seed mass alone.

Sprouting is important for two reasons. It is both a key recruitment strategy (Kruger *et al.*, 1997, Bellingham & Sparrow, 2000; Loehle, 2000; Bond & Midgley, 2003, Vesk & Westoby, 2004a) and an important mode of persistence (le Maitre & Midgley, 1992, Bond & Midgley, 2001, 2003). The LHS scheme, by emphasising seed size (mass), and hence that sexual reproduction is the most important trait in determining regeneration success, overlooks sprouting as a key life history strategy.

Other well-documented ecological strategy schemes also make no mention of sprouting. Tilman (1988,1994) invokes competition for resources as being the most important factor driving succession, and mentions that disturbance may "reset" the system. However, his strategy scheme makes little allowance for disturbance prone environments where the system is reset so frequently that intervals are too short for regeneration to occur via seeds, or for competition to play a significant role. For example, Bond (1991).predicts that fires every 5 – 15 years will prevent significant canopy interactions in many Fynbos Proteaceae before significant shading by competitors takes place.

Grime's CSR strategy scheme (Grime, 1974, 1979) also does not take sprouting into account. His model predicts that ruderals, that dominate highly disturbed environments, would depend on high (sexual) reproductive output to survive, yet he makes no mention of sprouting as either a recruitment option (sprouting as a juvenile) or to ensure persistence as an adult.

Loehle (2000) includes sprouting in his model of tree coexistence in forests, and is one of the first general models to give prominence to sprouting. He suggests that species coexistence in forests could be predicted from the distribution of tree species in trait space under a given disturbance regime. Four independent dimensions were used to place species in strategy space: shade tolerance: adult tree size, seed dispersal distance and, importantly, root or stump sprouting ability. However, the modelling of sprouting behaviour is limited, in that it is seen only in context of recapturing space after disturbance, whereas a far greater range in life history strategies exist (Bellingham & Sparrow, 2000, Del Tredici, 2001; Bond & Midgley, 2003, Vesk & Westoby 2004a, 2004b). For example *Sideroxylon inerme* (Sapotaceae), a southern African forest sprouting species, can invade space around it, through opportunistic sprouting in response to increased light levels e.g. into a forest gap ("opportunistic branching" Hallé *et al.*, 1978), in so doing not only replacing itself, but capturing further space in the regeneration niche (Kruger *et al.*, 1997)).

Westoby *et al.* (2002) suggest that an important aim of plant ecology is to identify leading dimensions of ecological variation in among species in order to understand the basis of them. They proposed the inclusion of a leaf-size – twig size spectrum as an additional dimension when assessing plant life history strategies. Given the importance of sprouting as a key life history strategy, I suggest the addition of a further axis, which explicitly includes sprouting.

It is, however, problematic incorporating sprouting into plant strategy schemes because of the difficulty in categorising responses (Bond & Midgley, 2001, Del Tredici, 2001). The division between reseeding and sprouting is by no means binary and sprouting varies among species, life history stages (Del Tredici, 2001; Vesk & Westoby, 2004b) and among disturbances of different frequency (Bellingham & Sparrow, 2000; Bond & Midgley, 2003).

Unfortunately, given the current lack of information on most systems (Bond & Midgley, 2001) no unifying model of sprouting exists. The work of Zedler (1995), Bellingham & Sparrow (2000) and Bond & Midgley (2001) have provided a theoretical framework within which the importance of sprouting is defined and, along with the descriptions in Del Tredici (2001), could be used as guiding principles for the framework of the seeding - sprouting dimension. However, the practical guidelines are more problematic, although Cornelissen *et al.* (2003) provides very good methodological procedures.

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Appendix 6.1

Table 1. Seed size, mean adult plant height and specific leaf area of dominant overstorey species in Hluhluwe-Imfolozi and western Cape Province.

		Seed size (g)		Height (m)		SLA ($cm^2.g^{-1}$)	
		Mean	(SEM)	Mean	(SEM)	Mean	(SEM)
	Acacia						
Sprouter	*Acacia karroo*	0.04	(0.002)	5.27	(0.44)	122.53	(3.07)
	A. caffra	0.09	(0.001)	3.57	(0.15)	186.03	(5.73)
Seeder	*A. nilotica*	0.10	(0.003)	4.65	(0.38)	123.51	(3.36)
	A. luederitzii	0.04	(0.002)	3.89	(0.03)	149.43	(3.50)
	A. tortilis	0.05	(0.009)	4.74	(0.91)	123.51	(3.80)
	A. robusta	0.17	(0.006)	12.44	(0.14)	141.76	(6.22)
	A. nigrescens	0.16	(0.005)	10.36	(0.103)	159.62	(6.32)
	A. burkei	0.13	(0.005)	10.04	(0.37)	166.04	(5.44)
	A. grandicornuta	0.11	(0.004)	7.43	(0.07)	168.38	(5.64)
	Proteaceae						
Sprouter	*Aulax pallasia*	0.03	(0.007)	2.6	(0.25)	28.77	(0.06)
Seeder	*A. umbellata*	0.03	(0.001)	2.2	(0.32)	52.88	(1.09)
Sprouter	*Leucadendron salignum*	0.01	(0.0004)	0.8	(0.37)	33.00	(1.54)
Seeder	*Ld. xanthoconus*	0.02	(0.004)	1.45	(0.45)	48.45	(1.79)
Sprouter	*Leucospermum cuneiforme*	0.05	(0.004)	1.5	(0.68)	39.32	(1.08)
Seeder	*Ls. conocarpodendron*	0.10	(0.003)	4	(0.13)	34.29	(0.48)
Sprouter	*Mimetes cucculatus*	0.04	(0.01)	1.5	(0.05)	53.34	(1.68)
Seeder	*M. fimbriifolius*	0.08	(0.004)	3.5	(0.88)	55.44	(0.66)
	M. hirtus	0.02	(0.0014)	1.75	(0.52)	64.30	(1.48)
Sprouter	*Protea cynaroides*	0.02	(0.001)	1.5	(0.08)	29.70	(1.00)
	P. nitida	0.04	(0.001)	5	(0.14)	34.05	(1.37)
Seeder	*P. repens*	0.16	(0.038)	4.5	(0.09)	36.85	(0.60)

SUMMARY

The aims of this thesis were firstly, to explore the ecological role of sprouting as a life history strategy in three South African biomes: southern Cape forests, fynbos and savanna. Secondly, I set out to assess the implications of adopting a sprouting life history strategy at the individual, community and biogeographic levels. Lastly, I aimed to assess how sprouting correlates with other life history strategy characteristics.

1. Importance of sprouting in forests, fynbos and savannas

The importance of sprouting as a reproductive strategy was assessed in Cape forests. While taller forests were dominated by reseeding species, sprouting was found to be an important mode of reproduction and persistence in shorter canopied forests.

Sprouting was seen to be a key life history trait in fynbos and savannas. Basal sprouting (either from the stem or root stock) is one of the key life history traits in areas experiencing high intensity burns in both fynbos and savannas. Conversely, epicormic sprouting is key strategy in areas of low intensity burns, where less of the plant's canopy is lost to fire.

2. Influence of sprouting at individual, community and biogeographic levels

This study suggests that at the level of the individual, sprouting has important implications for reproductive strategies and plant architecture. Although sprouting in response to severe disturbance is well known, this study suggests that sprouting is a key reproductive strategy in less disturbance prone environments such as forests.

Furthermore, sprouting was found to have an influence on plant architectural characteristics. In the fynbos, basal sprouting or sprouting from rootstock results in a multistemmed architecture, and therefore a more flammable structure, which has further implications for plants life history strategy (see below). A multistemmed architecture would affect the height to which a plant can grow, and

hence affect competitive ability in taller, light-limited forests where the ability to grow tall is critical.

In savannas, sprouting strategy differs with changing disturbance regimes. In mesic, fire driven savannas, where the ability to grow above the fire-trap is critical, plants tend to produce few, elongate sprouts. In contrast, in arid savannas where herbivory exerts greater selective pressure on woody plants, it was found that plant sprouts form a cage-like, better-protected architecture.

At the community level, sprouting may influence species richness. Due to greater persistence ability of sprouters that dominate shorter forests, individual and species turnover is reduced. Consequently, shorter canopied forests tend to support lower canopy tree species richness.

Sprouting may also have implications for biogeographic patterns. This study suggests that sprouting ability may influence species distribution in the landscape, with changing disturbance regimes. The ability to sprout may also influence species distribution by affecting competitive ability e.g. sprouters outcompeting seeders in shorter canopied forests and vice versa.

3. Correlated traits

Of the life history traits explored in this study, only plant height correlates strongly with (basal) sprouting. Otherwise, no other traits e.g. seed mass, bark thickness and SLA, consistently correlate with sprouting ability. Therefore sprouting ability would seem to be orthogonal to most other life-history traits and should be considered as an independent life history characteristic.

Sprouting ability and bark thickness are key attributes in defining life history strategies in relation to fire. The link between individual flammability and stand level flammability characteristics were explored. It was found that thick barked fire-resistant species have a less ramified architecture, thereby further enhancing their individual resistance to fire. However, potential reproductive output is reduced, as flowering in many Proteaceae is associated with terminal tips. Therefore, thick barked species tend to be found in sparse, multi-cohorted populations, which in turn, reduce stand-level flammability. Conversely, thin barked species display a highly ramified architecture, which is enhanced by basal sprouting, which leads to an increase in individual flammability. The simultaneous loss of aboveground biomass and increased reproductive potential, result in dense, even-aged community, and a consequently a more flammable stand. Thus individual traits such as thin bark and basal sprouting have implications for individual flammability characteristics, which in turn, may also influence stand level flammability.

Journal of Mediterranean Ecology 1: 181-185, 2000

Senescence in fire-adapted Cape Proteaceae

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Keywords: Death, growth-rates, life-history.

Abstract

We studied plant senescence in relation to maximum size, growth rates and branching patterns. Some species of the fire-adapted Cape Proteaceae live for only a few years reaching less than a metre in height before they die. Others may reach over 10 metres in height in the absence of fire. Since most species generally regenerate after fire from seed, they are thus of similar age in any particular area. This provides opportunities for comparative studies of life-history components such as growth-rate and longevity.

Neither wood density nor growth rates was correlated with maximum lifetime size. Canopy spread:basal diameter was negatively correlated with maximum lifetime size. A high canopy spread:basal diameter was associated with more prolific branching. We suggest that senescence is determined by mechanical failure, which in turn is dictated by factors such as the degree of branching and leaf size.

Introduction

Why and how plants senesce is controversial from both a proximate (physiological) and ultimate (evolutionary) perspective; it is a 'particularly knotty' problem (Willson 1983). Senescence and senility refer to the processes of ageing which lead to death, for example due to expression of inherited late-acting deleterious mutations or due to the ontogenetic accumulation of somatic mutations. Crawley (1997) indicated, in a recent text-book on "Plant Ecology", that plant senescence is a mystery, succinctly noting that "all the leaves on an ancient oak tree in summertime are just a few months old". Unlike most animals, most plants (and even most plant cells) can give rise to new vigorous structures indefinitely (i.e they are totipotent). The above young leaves on the ancient oak, are analogous to seedling leaves. Thus the concept of "antagonistic pleiotropy" does not seem appropriate to plants (Crawley, 1997). In animals, traits favouring early reproduction result in early senescence because natural selection is weak after the onset of reproduction and thus does not eliminate late acting deleterious genes. This does not apply in plants and nor does the concept of "accumulating mutations" (Crawley, 1977), because plants do not appear to suffer physiological decline with age. Monocarpic senescence (=semelparity e.g. the above annuals and bamboos) too is controversial on both counts because death is not associated with excessively depleted vegetative reserves due to the single bout of reproduction, nor to any other good physiological explanation nor to "death genes" (Wilson, 1997). Recently, Keeley & Bond (1999) argued that bamboo senescence is due to a "bamboo-fire cycle" and not due to mast-fruiting.

Two other possible reasons for increasing probability of plant death with time, relate to the increasing burden of respiration with size, and the increasing chance of structural failure with size . Strictly speaking, death in these instances is not due to intrinsic physiological decline (i.e. ageing). Loehle (1988) suggested that in order to defend themselves against biotic (e.g. herbivores) or abiotic (e.g. wind) forces, large plants need to produce decay resistant wood. Crawley (1997) suggested, without any back-up data, that "in the case of trees, senescence might be nothing more than the collapse of woody support structures". Collapse can occur because plant height or canopy volume become excessive in relation to the stem diameter (Niklas, 1994).

The Cape Proteaceae mostly regenerate from seed after fires and although they are woody plants they have fixed lifespans spanning the range of approximately 5-50 years. Within an area, individuals of different species are thus of the same age and this provides opportunities for simultaneously exploring differences in growth rates, architecture, maximum size and longevity. Some species senesce before they reach 1 m in height (i.e. five-ten years after a fire) whereas others grow tall (>5-15 m) and they require the prolonged (30 years plus) absence of fire before they senesce.

We ask: what differences are there between species that die early versus those that die late in terms of a) wood density, b) growth rate, c) architecture (height to basal stem diameter or canopy volume to basal diameter ratio). Wood density and branching patterns could be related to a mechanical cause for death if they are positively related to maximum size. High growth rates, if negatively related to maximum size, suggest a trade-off consequence for early death.

Table 1. Wood density and maximum lifetime height of selected species of Proteaceae from Cape Peninsula. The value in brackets represents maximum size reached on the Cape Peninsula.

Species	**wood density (gr/cm^2; s.d.)**	**max. height (m)**
Tall long-lived species		
Leucadendron argenteum	0.64 (0.3)	10
Leucospermum conocarpodendron	0.71 (0.1)	5
Mimetes fimbriifolius	0.63 (0.1)	4 (5)
Protea nitida	0.82 (0.1)	(5)-10
Intermediate species		
Protea repens	0.78 (0.1)	1-(4)
Protea lepidocarpodendron	0.82 (0.4)	3-(4)
Leucadendron laureolum	0.67 (0.1)	2
Leucadendron coniferum	0.74 (0.2)	2
Leucadendron xanthoconus	0.68 (0.7)	2
Short species		
Serruria villosa	0.74 (0.1)	0.3
Serruria glomerata	0.78 (0.2)	0.4

Methods

Of the roughly 330 species of Cape Proteaceae, fewer than 5% grow taller than 5m and, because many of these taller species have restricted distributions, it is difficult to find sites where potentially tall and long-lived species co-occur with short-lived species. The tallest member of the genera *Mimetes* (*M. fimbriifolius*), *Leucospermum* (*L. conocarpodendron*) and *Leucadendron* (*L. argenteum*) are largely restricted to the Cape Peninsula. *P. nitida*, the tallest SW Cape *Protea,* also occurs on the Peninsula. Nevertheless it was only possible to find 6 sites on the Cape Peninsula (sites 1-4 in Cape of Good Hope Nature Reserve; sites 5,6 in the NW Peninsula) that had a range of different small and large species. Our approach was to compare the species within a site and between sites in terms of various attributes such as wood density and branching patterns.

Wood density was taken as a measure of structural support and decay resistance, two highly correlated features in angiosperms (Loehle, 1988). Five samples of wood density from mature individuals were taken by cutting the plant down at the base for the shorter species and by removing large basal branches for the taller species. Wood was dried in an oven at 40°C for 48 hrs before being weighed and its volume then determined by displacement.

Data on growth rates and architecture were obtained from 10 co-occurring individuals of each species per site. So as to be able to include live samples from the short-lived species, sites were selected on the basis of being 3-5 years post-fire age. This had the added advantage of minimising impacts of competition on growth and architecture. Diameter was measured at the base. Canopy radius was taken as the mean of the maximum canopy diameter and diameter at right angles to maximum. Typically Cape protoeids are sympodial; new branches are initiated near the apex of previous years branches, often just below a terminal inflorescence. The degree of branching was determined by counting the number of branches arising from the tallest of the previous years branches. Species with small leaves produce many branches of small diameter whereas species with large leaves produce fewer and thicker branches (Bond & Midgley, 1988).

The role of relative growth rates was determined by comparing mean basal diameter and mean height with maximum lifetime size. At four sites (2,4,5,6) the species with greatest height also had the greatest diameter, making it clear that this species had the greatest growth rate. However, at two sites (1,3), the species (*P. lepidocarpodendron, L. xanthoconus*) with largest mean height was not the species with largest mean diameter (*L. conocarpodendron* in both cases). To resolve this conflict we sampled above-ground biomass and basal diameter of 25 co-occurring randomly selected individuals each of *P. lepidocarpodendron* and *L. conocarpodendron*. These two were chosen to represent the short stature/broad basal diameter versus tall/thin alternatives. Regression analysis was used to correlate biomass (dried in oven at 40°C for 48 hrs) and diameter for each species.

Table 2. Attributes of Cape Proteaceae co-occurring at 6 sites on Cape Peninsula. (P= *Protea*, Ls=*Leucospermum*, S=*Serruria*, M=*Mimetes*, L=*Leucadendron*).

Species	**ht (cm)**	**diameter (cm)**	**height/d**	**Spread/d**	**branches**
Site 1 (Klaasjagersberg)					
P. repens	67.2 (15.4)	0.87 (0.2)	78.3 (16.0)	26.5 (10.6)	1.3 (0.3)
Ls. conocarpodendron	37.0 (10.8)	2.72 (0.9)	13.6 (12.1)	8.34 (14.2)	1.1 (0.5)
P. lepidocarpodendron	91.0 (0.2)	1.22 (0.6)	74.6 (16.4)	23.9 (7.6)	1.2 (0.2)
L. laureolum	59.5 (14.9)	1.05 (0.4)	60.2 (16.4)	31.5 (7.5)	2.1 (0.3)
Site 2 (Platboom)					
M. fimbriifolius	52.6 (7.9)	4.37 (0.9)	12.36 (2.5)	9.8 (2.1)	1.4 (0.6)
S. villosus	46.6 (4.7)	1.57 (0.3)	30.58 (6.2)	30.9 (3.1)	2.7 (0.9)
Site 3 (Smitswinkel Bay)					
Ls. conocarpodendron	62.2 (10.0)	4.6 (1.1)	13.7 (2.3)	9.5 (2.3)	1.5 (0.9)
L. xanthoconus	67.6 (9.4)	2.4 (0.8)	29.8 (7.5)	27.4 (3.9)	3.0 (0.7)
Site 4 (Circle Drive)					
L. laureolum	68.5 (12.5)	1.5(0.3)	46.6(7.6)	24.2(4.6)	1.5(0.3)
S. glomerata	48.6 (6.4)	1.3 (0.2)	37.4(7.8)	37.6 (4.8)	3.1(0.4)
Site 5 (Blinkwater Ravine)					
P. lepidocarpodendron	108 (16.6)	3.2(0.8)	35.5(8.9)	55.5 (5.5)	2.2(0.2)
P. nitida	75.0 (23.1)	2.9(0.1)	27.6(8.4)	29.3 (6.1)	1.1(0.3)
Site 6 (Lions Head)					
L. argenteum	86.2(19.5)	2.1(0.7)	44.2(9.7)	19.4(5.3)	1.9(0.8)
L. coniferum	59.7(22.2)	0.7(0.4)	91.1(25.0)	30.8(8.3)	2.8(1.1)

Two types of analyses were attempted. Firstly, simple correlation analyses were performed between maximum lifetime size and various variables, such as wood density, using the total data set. Secondly, a within-site comparison between maximum lifetime size and various variables was performed. The second analysis was necessary to take into account between site variation (such as soil depth, aspect and rainfall) and because certain plant attributes (such as diameter at the base, branching patterns) were not comparable because sites were not the same post-fire age.

Results

Correlations

The correlation between wood density and maximum lifetime size was negative and weak ($r= -0.32$, $n=11$ throughout, n.s.) as was the correlation between maximum height and height:basal diameter ($r=-0.13$, n.s.). The correlation between maximum lifetime height and canopy spread:basal diameter was also negative, but significant ($r=-0.62$, $p< 0.05$).

Basal diameter was strongly correlated with biomass for both *P. lepidocarpodendron* ($n=25$, $r=0.85$, $p<0.01$;dry mass(g)=-16.6 + 6.6 (diameter in mm) and *L. conocarpodendron* ($n=25$, $r=0.90$; $p< 0.01$; dry mass (g)=-81.0+8.1 (diameter in mm). Given this relationship and the diameters measured at the two sites (1 & 3) where tallest species did not also have the largest diameter, it is clear that *L. conocarpodendron* (the species with largest diameter) had the largest biomass.

Within-site comparisons

At all 6 sites, the species with the lowest canopy spread:stem diameter was the species that achieved the greatest maximum lifetime height. This ratio is determined by the degree of branching because at all sites the species with the greatest number of branches had the greatest canopy spread:stem diameter. Species that produced many stems per year thus produce a relatively large canopy volume for a given stem diameter. Height: stem diameter was almost as well correlated with maximum lifetime size in that at 5 out of 6 sites, the species with the lowest ratio achieved the greatest lifetime size.

Based on basal diameter as the measure of growth rates, at all 6 sites the species with the greatest mean diameter was the species with the maximum lifetime size.

Discussion

The negative correlation between canopy spread and basal diameter suggests senescence occurs due to structural failure probably due to prolific branching. Three further lines of evidence suggest death is not due to physiological decay in Cape Proteaceae (i.e. the process of "ageing"). Firstly, as part of the large cut-flower industry, many members of the Proteaceae are propagated vegetatively by cuttings from mature individuals, themselves once cuttings. This is especially common in the more showy male plants in the dioecious genus *Leucadendron*, to avoid the horticultural problem of raising the less attractive females as seedlings. Successful repeated propagation by cuttings implies no physiological ageing process. Secondly, we have observed that leaves are still present on dead individuals of *P. lepidocarpodendron* in an overmature stand in the Camps Bay area. We interpret this as evidence that death is not due to slow decline, during which leaves would be shed, but is due to individuals suddenly breaking apart, possibly during high winds. Dead old individuals are typically split at the base, probably due to the above unsafe diameter/spread or diameter/height relationships. Finally, resprouting species amongst the Proteaceae have low fire mortality and are thus extremely long-lived. They have the capacity to continually produce new vigorous stems from underground organs. This too indicates that great age *per se* is not correlated with physiological decline and senescence.

Early senescence in Cape Proteaceae does not correlate with fast growth (mean basal diameter)(*contra* Loehle, 1988). Loehle (1988) noted that longevity was negatively correlated with age to reproduction (as is probably the case in this study although there are no specific data on age to maturity), however his reasons for this pattern (advantages for wind dispersal with delayed reproduction) are unlikely to be general explanations. Some tall (*M. fimbriifolius* and *L. conocarpodendron*) and some short species *(S. villosus* and *S. glomerata*) of the Cape Proteaceae are ant-dispersed, for which increased height of seed release has no known advantage. Plant height is often used as a surrogate to reflect growth rates, whereas we suggest basal diameter is a better predictor of rates of biomass accumulation. For example, Yeaton & Bond (1991) suggested that *L. conocarpodendron* was slow growing compared to *P. lepidocarpodendron*. They based this on differences in height not biomass. This point illustrates the important consequences of different allocation patterns, such as to height growth in relation to short-term competition for light or to or to basal growth in relation to long-term persistence at a site, for maximum size and longevity.

Presently there is renewed interest in plant allometry (e.g. Ackerly & Donoghue, 1998)) and Corner's two rules of plant architecture. Midgley & Bond (1989) previously suggested the following new corollary to the two Corner's Rules. Since the sizes of plant appendages (leaves and flowers) are correlated to stem diameter (rule 1), leaves and flowers should be correlated to each other (if they are borne on same shoot at same time). On the basis of this study of maximum plant height, a further corollary can be suggested. Branch frequency is related to branch diameter (rule 2), and branch frequency is related to plant height (this study). Since appendage size (leaves, flowers) is related to branch diameter and frequency (rule 1), appendage size should also be positively correlated with plant size (within an architectural type and within general habitat/disturbance regime). Ackerly & Donoghue (1998) did not report on the correlation between plant height and leaf size in *Acer*, although they noted relatively close placing of these characters in ordination space. In the analysis of *Pinus* by McCune (1988) there is a correlation of 0.45 between leaf length and maximum tree height. This is surprising, given the variation in habitats and disturbance regimes inhabited by pines.

Our hypothesis that maximum plant size and longevity in Cape Proteaceae is determined by architectural patterns can be tested in several ways. The prostrate/creeping Proteaceae species should be longer-lived than predicted from their branching patterns because their canopies are not subjected to the same mechanical forces as are erect plants. Branching patterns can be very different in the different genders of the dioecious Cape Proteaceae genus *Leucadendron* (Bond & Midgley, 1988). We predict that males should be shorter or shorter-lived in dimorphic *Leucadendron* species, because these males branch more intensely. The second corollary relating appendage size and plant height can be tested in other genera, especially those in which species with similar architecture and that coexist. We predict that in Australian Proteaceae from fireprone environments, such as *Banksia*, the taller species will have relatively large leaves.

Finally, members of the Australian Proteaceae genus *Hakea*, that have invaded the Cape grow more rapidly (height and biomass) than co-occurring indigenous Proteaceae (J. Midgley pers. data). This indicates no negative correlation between maximum size and growth rates. Some are also capable of growing far taller than local Proteaceae. We predict that they achieve a large size because of their relatively sparse branching patterns and their low canopy volume:stem diameter means they are less prone to mechanical failure. Keeley (2000) has suggested that, in chaparral, senescence is a myth. Further work is needed to determine why it should occur in the Cape and not California.

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