RESPROUTING AND MULTI-STEMMING AND THE ROLE OF THE PERSISTENCE NICHE IN THE STRUCTURE AND DYNAMICS OF SUBTROPICAL COASTAL DUNE FOREST IN KWAZULU-NATAL PROVINCE, SOUTH AFRICA

EMMANUEL F. NZUNDA

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Abstract

Resprouting is an important means of plant regeneration especially under conditions that do not favour regeneration through seeding such as frequent disturbances, low productivity, unfavourable soil conditions, extreme cold and limited understorey light availability. Sprouts may be advantageous over seedlings because they have higher survival and growth rates than seedlings, since they use resources from parent plants unlike seedlings that have to acquire their own resources. Resprouting is well documented for ecosystems that experience severe disturbances that damage aboveground biomass. For example, resprouting is important for plant persistence against fire in fire-prone savannas and Mediterranean shrub-lands, and hurricanes and cyclones in tropical forests. In these ecosystems, resprouting often results in multi-stemming, because this dilutes the risk of damage among many stems, improving the chances of individual survival.

This study was conducted at coastal dune forest at Cape Vidal in north-eastern South Africa, where there is a high incidence of multi-stemmed trees due to resprouting in response to chronic disturbances of low severity. This study examines (1) the importance of resprouting to tree survival and dynamics in an environment where disturbance severity is low but pervasive, and (2) how this resprouting strategy differs from the more familiar sprouting response to severe disturbances such as fire and hurricanes.

Analysis of the relationship between multi-stemming and a number of disturbances potentially causing multi-stemming revealed that stem leaning and substrate erosion were the most important disturbances associated with multi-stemming. There were fewer multi-stemmed trees on dune slacks that had a stable substrate and were protected from sea winds than on dune crests and slopes that had unstable substrate and were exposed to sea winds.

Trees resprouted and became multi-stemmed from an early stage to increase their chances of survival against leaning caused by strong sea winds and erosion, and occasional slumping of the unstable dune sand substrate. These low severity disturbances are persistent and are referred to as chronic disturbances in this thesis. As a result of these chronic disturbances, both single and multi-stemmed trees had short stature because taller individuals that emerged above the tree canopy would be exposed to wind damage.

Under chronic disturbances plants may manifest a phylogenetically determined sprouting response. However, in this study resprouting and multi-stemming were the results of the tree-disturbance interaction and not a property of a plant or species and were not phylogenetically constrained.

Because the disturbances are predominantly of low severity, leaning trees were able to regain the vertical orientation of the growing section by turning upward (a process referred to as 'turning up' in this study) and hence survive without resprouting. Species that were prone to turning upward had a low incidence and degree of leaning of their individuals, low frequency of loss of primary stems and high abundance of individuals. Although turning up is less costly to the individual than resprouting, it could only be used by leaning trees that had small angles of inclination and were not eroded. High intensities of the latter require that individuals resprout to survive.

The form and function of resprouting varied between seedlings and juvenile and mature trees. Resprouting in seedlings resulted in a single replacement shoot, unlike sprouting in juvenile and mature trees that resulted in multi-stemmed trees. Like sprouting in juvenile and mature trees, sprouting in seedlings was not phylogenetically constrained. Resprouting in seedlings increased seedling persistence; hence species with more sprout seedlings had larger individual seedlings and seedling banks. Resprouting in seedlings increased the chances of

seedling recruitment, whereas resprouting in juvenile and mature trees increased the chances of an established plant maintaining its position in the habitat.

After disturbances of high severity, which destroy the photosynthesizing parts, plants resprout using carbohydrates stored below- or aboveground. In this study, good resprouters stored more carbohydrates both below- and aboveground than poor resprouters. The carbohydrates were mobilized for resprouting after disturbance. More carbohydrates were stored in stems than in roots because the prevailing disturbances were mostly of low severity and hence aboveground resources were readily available. Similar to storage by plants in severely disturbed habitats, carbohydrates were stored by reserve formation, which competes for carbohydrates with growth and maintenance and forms permanent storage, rather than accumulation, which temporarily stores carbohydrates in excess of demands for growth and maintenance. Stored carbohydrates are not necessary for resprouting of plants after disturbances of low severity because they can resprout using resources remobilized directly from the disturbed photosynthesizing parts. However, in this study, stored carbohydrates served as a bet-hedge against occasional severe disturbances that occurred in addition to chronic disturbances. Allocation of carbohydrates to permanent storage diverts them from growth and reproduction and hence good resprouters had lower growth rates, seed output, seed size and seedling recruitment than poor resprouters. However, the costs of these traits that resulted in low recruitment from seed by good resprouters, were compensated for by high persistence of established individuals of good resprouters through recruitment of sprout stems.

This study demonstrates that resprouting is not only advantageous in severely disturbed environments, but also in environments where disturbances are of low severity but nevertheless confer an advantage on individuals that persist. Thus in forest environments

where aboveground biomass is seldom destroyed and individuals are relatively long-lived, resprouting can confer significant fitness and selective advantage on individuals.
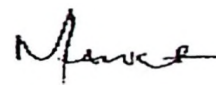
Declaration

The work described in this thesis was conducted in the Forest Biodiversity Research Unit in the School of Biological and Conservation Sciences at the University of KwaZulu-Natal, Pietermaritzburg, from April 2004 to May 2007, under the supervision of Prof. M.J. Lawes and Dr. M.E. Griffiths. The study represents original work by the author and has not been submitted in any form to another university. Where use has been made of the work of others, it is duly acknowledged.

The thesis is compiled as a collection of papers (except the Introduction – Chapter 1, and Summary – Chapter 8) and the content presented in the chapters is the same as the content either submitted to or published in a journal, hence some repetition has been inevitable.

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E.F. Nzunda

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Prof. M.J. Lawes

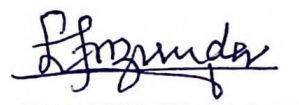Supervisor

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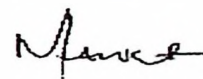
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Chapter 1

Introduction

The Cape Vidal coastal dune forest in northern KwaZulu-Natal, South Africa, has a high incidence of multi-stemmed trees. Multi-stemmed trees are a feature of disturbed or stressed environments, however there are few apparent disturbances of low severity in this coastal dune forest. Typically, in disturbed or stressed forests, trees resprout and become multi-stemmed to increase their likelihood of surviving disturbance. Multi-stemmed individuals maintain their position in the habitat and recruit vegetatively rather than from seed. Unlike seedlings, sprouts can withstand the disturbance conditions because they obtain resources from the established parent plant. This study was conducted to examine why so many trees are multi-stemmed at Cape Vidal and determine the implications of multi-stemming, and the obvious persistence and longevity this confers on individuals, to the structure and dynamics of coastal dune forests in north-eastern South Africa.

The persistence niche

The coexistence of many species of plants with similar life-forms and life history is a fundamental interest in community ecology (Loehle 2000; Silvertown 2004). A number of mechanisms have been suggested to explain coexistence. With the notable exception of neutral theory (Hubbell 2001), a common element of these mechanisms is the idea that species differentiate into niches and that there are tradeoffs for species occupying particular niches (Silvertown 2004). Thus, individual advantage in one niche is accompanied by disadvantage in an alternative niche. Two such niches, the regeneration niche and the persistence niche, are

alternative strategies that enable plant species to coexist in an ecosystem (Grubb 1977; Bond & Midgley 1995; Loehle 2000; Nanami *et al.* 2004). Unlike the regeneration niche, which relies on seeding to form a new generation of plants, the persistence niche maintains the current generation through sprouting with or without multi-stemming (Bellingham & Sparrow 2000; Bond & Midgley 2001).

Resprouting is the process whereby a plant develops secondary shoots that may either replace the primary shoot or grow alongside the primary shoot. Closely related to resprouting is clonal growth, whereby vegetative pieces of a plant detached from the parent plant develop into new plants (Greig 1993). Resprouting differs from clonal growth in that it does not entail vegetative spread beyond the parent plant, although resprouting through root suckering may achieve this (Del Tredici 2001; Bond & Midgley 2003).

Multi-stemmed growth form in woody plants may either result from an inherent tendency of individuals of a species to produce and maintain many stems, or as a response to destruction of the terminal shoot in individuals that are not inherently multi-stemmed (Brown *et al.* 1967; Chamberlin & Aarssen 1996; Vesk & Westoby 2004b). Multi-stemming in response to destruction of the terminal shoot is a result of successful establishment of more than one stem from lateral secondary shoots produced by resprouting (Ng 1999). In some cases only one lateral shoot is released or the released lateral shoots are thinned and hence the plant grows as a single stemmed individual even after destruction of the primary terminal shoot (Bond & Midgley 2001; Yamada & Suzuki 2004). Whether resprouters are multi-stemmed and short or single stemmed and tall, depends on the interactive effect of species and habitat. In contrasting habitats the same species can grow in different forms (Kruger *et al.* 1997; Bellingham & Sparrow 2000; Del Tredici 2001; Kruger & Midgley 2001). Where there is high competition for light and low frequency of disturbance, resprouters thin to single stems

whereas low competition for light and high disturbance frequency results in multi-stemmed architecture (Bellingham & Sparrow 2000). While the per stem probability of resprouting of multi-stemmed plants is the same as that of single stemmed plants (Vesk & Westoby 2004b), the whole plant probability of resprouting is higher for multi-stemmed plants than single stemmed plants (Paciorek *et al.* 2000; Vesk & Westoby 2004b).

Forms of resprouting

There are seven types of resprouting, four of which may lead to formation of secondary stems (Del Tredici 2001), namely: (1) collar sprouts from the base of the trunk (basal epicormic); (2) sprouts from specialized underground stems (lignotubers and rhizomes); (3) sprouts from roots (root suckering); and (4) opportunistic sprouts from layered branches. Three additional resprouting types may not necessarily result in formation of stems (Bellingham *et al.* 1994; Zimmerman *et al.* 1994), namely: (5) axillary sprouts (6) branch epicormic sprouts and (7) stem epicormic sprouts. The amount of plant part that is recovered increases from axillary through basal epicormic resprouting (Bellingham & Sparrow 2000). There is no qualitative difference between resprouting at the base of the plant and resprouting from branches higher in the canopy (Burrows 2002). Hence, the multi-stemmed architecture of woody plants that resprout from the base is analogous to the canopy of a monopodial tree at ground level (Hallé *et al.* 1978; Bellingham & Sparrow 2000). As such, resprouting can be viewed in a hierarchy framework along a continuum of the amount and type of plant part that is recovered (Bellingham & Sparrow 2000).

Collar sprouts are derived from meristematic tissue in the axils of the cotyledons of dicotyledonous seedlings (Del Tredici 2001). Buds develop from this tissue with a direct

connection to the vascular cylinder. In mature trees the collar develops at or just below ground level and can be visible as numerous suppressed buds protruding from the trunk. Collar sprouts and suppressed buds are ubiquitous features of angiosperm trees although they may be lost from mature trees (Del Tredici 2001). Many conifers lack cotyledonary buds and functional collars and typically do not sprout at the base (Bellingham & Sparrow 2000; Del Tredici 2001). Some fire-adapted species that lack cotyledonary buds have become sprouters secondarily by evolving the ability to sprout from axillary buds above the cotyledonary node (Keeley & Zedler 1998).

Lignotubers are swollen structures that develop from suppressed buds at the cotyledonary node of seedlings (Del Tredici 2001). The structures protrude from the stem (by several metres, in some cases) so that sprouts typically emerge some distance from the primary stem. Lignotubers are common in fire-prone environments, although they are also found in areas where fires are rare or absent (Lloret *et al.* 1999). Though still debated (Carr *et al.* 1984; James 1984; Canadell & López-Soria 1998; Bond & Midgley 2003), their main function seems to be maintenance of bud banks for continuous or disturbance-induced episodic resprouting (Mesleard & Lepart 1989; Bond & Midgley 2003). In some instances, lignotubers store large quantities of starch, which is mobilized for resprouting of stems (DeSouza *et al.* 1986; Canadell & López-Soria 1998), while in other cases lignotubers are not important for starch storage and resprouting is not dependent on mobilization of starch from lignotubers (Cruz & Moreno 2001; Wildy & Pate 2002). Rhizomes are specialized underground stems with distinct nodes and internodes, which grow out from the base of the trunk and produce aerial stems some distance away from the parent (Del Tredici 2001). Rhizomes are a feature of some drought-adapted tree and shrub species (Del Tredici 2001).

The advantage of lignotubers and rhizomes is that their sprouts can form adventitious roots because they typically emerge from below ground (Del Tredici 2001).

Root suckers are shoots that develop from meristematic tissue on roots of some plants. Although some woody plants produce root suckers spontaneously as part of normal development, in most trees root suckering is an induced response to injury such as from fire or logging (Del Tredici 2001; Bond & Midgley 2003; Rodrigues *et al.* 2004). Root suckering allows resprouting plants to propagate vegetatively, spreading from the original site of establishment (Del Tredici 2001; Bond & Midgley 2003).

Layering is another type of resprouting whereby adventitious roots are produced from lateral branches that come into contact with the soil (Del Tredici 2001; Bond & Midgley 2003). The frequency and ecological importance of layering largely depends on the branching architecture of a plant in addition to its ability to develop adventitious roots from branches (Bond & Midgley 2003; Feild *et al.* 2003).

Factors that favour resprouting over reseeding

Disturbance frequency, severity, heterogeneity and site productivity are the main factors that determine whether resprouting or reseeding is favoured in a habitat (Bellingham & Sparrow 2000; Clarke *et al.* 2005). Resprouting is favoured over reseeding at intermediate disturbance frequency. At low disturbance frequency reseeders establish and outgrow and overtop resprouters (Enright & Lamont 1992; Bond & van Wilgen 1996; Enright & Goldblum 1999; Karlsson *et al.* 2004). Resprouters predominate when disturbance frequency is high enough to prevent successful completion of the reproductive cycle of sexual maturity, seed production and seedling establishment of reseeders (Zedler *et al.* 1983; Cowling *et al.* 1990; Enright & Goldblum 1999; Clarke 2002a, b). However, reseeders predominate when disturbance

frequency is too high to allow sufficient growth of the storage organ that is needed to support resprouting (Iwasa & Kubo 1997; Bellingham & Sparrow 2000).

Disturbance severity determines the form of resprouting (Bellingham & Sparrow 2000). The only option for resprouting in response to disturbance of high severity (e.g., stem-kill fire) is basal resprouting, whereas low disturbance severity (e.g., minor herbivory and superficial wind damage) allows other forms of resprouting (Chamberlin & Aarssen 1996; Bellingham & Sparrow 2000; Del Tredici 2001). Hence, basal resprouters often dominate habitats with high disturbance severity (Bell 2001; Bond & Midgley 2001; Clarke & Knox 2002; Clarke *et al.* 2005).

Heterogeneous disturbance results in islands that are not affected by the disturbance. In these islands, reseeders flourish because they are better able to colonise these islands than resprouters. Thus, higher disturbance heterogeneity results in dominance of reseeders (Clarke 2002a, b; Clarke *et al.* 2005). Resprouters dominate productive sites provided the disturbance regime favours resprouting (i.e., high disturbance frequency and severity) (Lamont & Markey 1995; Clarke & Knox 2002; Clarke *et al.* 2005; Knox & Clarke 2005). High site productivity allows rapid development of storage that is used in resprouting, whereas low site productivity results in smaller reserves that make resprouting less competitive than reseeding (Knox & Clarke 2005). Where the disturbance regime favours reseeding (i.e., low disturbance frequency and severity), resprouters dominate sites with low productivity because reseeders overtop resprouters on highly productive sites (Midgley 1996; Kruger *et al.* 1997; Bellingham & Sparrow 2000).

The role of the persistence niche in forest structure and dynamics

Resprouters have greater longevity than nonsprouters (Bond & Midgley 2001; Lamont & Wiens 2003). This results in low rates of replacement of individuals, which in turn can lead to lower species richness (Phillips *et al.* 1994; Kruger & Midgley 2001). Furthermore, resprouters may lower species richness per unit area because one multi-stemmed resprouting individual occupies a larger area than a single stemmed nonsprouter (Ohkubo 1992; Del Tredici 2001; Kruger & Midgley 2001). Resprouters could also affect species richness by altering the rate of speciation and extinction (Kruger & Midgley 2001). Reprouters usually have fewer successful reproductive events due to later reproductive maturity, lower seed output and less vigorous seedlings compared to nonsprouters (Bond & Midgley 2003). Due to fewer reproductive events, resprouters could have fewer opportunities for fitness selection and hence have lower rates of speciation (Wells 1969). Thus, ecosystems dominated by nonsprouters tend to have high species richness (Le Maitre & Midgley 1992; Cowling *et al.* 1996; Wisheu *et al.* 2000). However, the argument for a lower rate of speciation as a result of resprouting is weak because clades do not differ markedly in species richness on the basis of their resprouting ability (Bond & Midgley 2003; Lamont & Wiens 2003). In fact, in highly disturbed systems, resprouters may contribute to higher species richness due to their wider environmental tolerance and greater persistence once mature, which decreases their rate of extinction (Bond & Midgley 2001; Lamont & Wiens 2003).

Resprouting enables forests to regenerate without depending on seedlings (Kruger *et al.* 1997). This allows species with a limited ability for recruitment by seedlings to maintain their presence in the face of factors that restrict seedling regeneration such as dense understorey vegetation (Ohkubo 1992) or after catastrophic disturbance (Bellingham *et al.* 1994; Zimmerman *et al.* 1994). In addition, because sprouts grow faster than seedlings,

resprouting reduces the time for recovery of a forest after disturbance (Bellingham & Sparrow 2000; Paciorek *et al.* 2000; Bond & Midgley 2001; Vesk & Westoby 2004a).

A forest dominated by resprouters can be shorter than that dominated by reseeders (Midgley 1996; Kruger *et al.* 1997; Bellingham & Sparrow 2000). This is because resprouters are often multi-stemmed and hence shorter than single stemmed trees due to resource and structural constraints on the growth of multiple stems (McMahon 1973; Bellingham & Sparrow 2000; Falster & Westoby 2005). However, some resprouters produce only one sprout and others thin the sprout stems to a single stem allowing them to achieve great height (Bond & Midgley 2001; Yamada & Suzuki 2004). Nevertheless, there is a limit to the maximum height that most resprouters can achieve and hence reseeder species dominate the canopy in the long-term absence of disturbance (Falster & Westoby 2005).

The mechanism underlying the influence of the persistence niche on forest structure and dynamics is allocation by resprouters of carbohydrates to storage for resprouting after disturbance (Bowen & Pate 1993; Canadell & López-Soria 1998; Bond & Midgley 2003). Allocation of carbohydrates to storage results in lower aboveground growth, delayed reproductive maturity and lower seed set in resprouters compared to closely-related nonsprouters (Vesk & Westoby 2004a; Knox & Clarke 2005; Schwilk & Ackerly 2005). Some resprouters store carbohydrates by accumulation when carbohydrates are in excess of demands for growth and maintenance and by reserve formation whereby carbohydrates have to be partitioned between storage and growth and maintenance (Chapin *et al.* 1990; Knox & Clarke 2005; Lambers *et al.* 2006). Reserve formation may be necessary where the prevailing disturbance regime results in competition between growth and storage for carbohydrates. For instance, rather than allocating all carbohydrates to growth, resprouters in environments with

chronic disturbance, of predominantly low severity with occasional severe disturbance events, may allocate a portion of the carbohydrates to reserves as a bet-hedge against the possibility of damage from disturbances of greater severity. In this case, the low severity of disturbance makes height competition important while at the same time plants must maintain the ability to resprout by forming reserves because the strong selection events also occur.

Study area

The study was conducted in the Indian Ocean coastal dune forest at Cape Vidal (28°05'32"S, 32°33'40"E) in the iSimangaliso Wetland Park in KwaZulu-Natal, South Africa (Fig. 1). The iSimangaliso Wetland Park is under the jurisdiction of the iSimangaliso Wetland Park authority and the conservation management is done by Ezemvelo KwaZulu-Natal Wildlife. The mean annual rainfall is approximately 1200 mm, spread evenly throughout the year (von Maltitz *et al.* 1996; Schulze 1997). Mean annual minimum and maximum temperatures are 17.8°C in July and 25.6°C in January respectively, with a mean annual temperature of 21.5 °C. Strong coastal winds occur in the area from August to October. Understorey available photosynthetically active radiation (PAR) varies from 1% in areas with *Isoglossa woodii* cover to 8% in areas without *I. woodii* cover (Griffiths *et al.* 2007).

Soil nutrients are low at Cape Vidal, particularly N (total N: mean ± 1 SD = 1898.6 ± 106.68 mg/kg) and P (17.3 ± 1.27 mg/kg) (Boyes 2006). Analysis of soils from different dune habitats (dune crest, landward slope, seaward slope, dune slack, and dune slack with *Acacia karroo*) revealed no significant differences in either N (ANOVA; $F_{4,70} = 0.96$, $P = 0.436$) or P ($F_{4,70} = 0.18$, $P = 0.946$).

The topography consists of a series of steep (slopes up to 55°) longitudinal sand dunes parallel to the coastline that are as high as 100 m above sea level. The seaward slope of the first dune is covered by vegetation stunted by exposure to onshore wind. On the landward side of this first dune, forest vegetation begins. The loose sand substrate, steep slopes and the action of coastal winds make trees growing at Cape Vidal highly susceptible to leaning (Nzunda *et al.* 2007b).

The Cape Vidal coastal belt dune forest forms part of a narrow strip of forest (0.1-4 km wide) extending in a contiguous belt for 240 km along the KwaZulu-Natal coast (Tinley 1985). These forests have never been commercially logged. Some dune slacks in the area are dominated by *Acacia karroo* (Fabaceae) (Weisser 1980; Tinley 1985; Boyes 2006). The most abundant tree species in the forest is *Diospyros natalensis* (Ebenaceae), followed by *Drypetes natalensis* (Putranjivaceae), *Ochna natalitia* (Ochnaceae) and *Diospyros inhacaensis* (Ebenaceae) (Nzunda *et al.* 2007b). Commonly multi-stemmed tree species include *Euclea racemosa* (Ebenaceae), *Dovyalis longispina* (Salicaceae), *Sideroxylon inerme* (Sapotaceae) and *Olea woodiana* (Oleaceae) (Nzunda *et al.* 2007a). *Mimusops caffra* (Sapotaceae) has the largest (by both girth and height) individuals in the forest. The highest tree canopies are 19.50 ± 0.40 m (mean ± SE of height of 10 tallest *M. caffra* trees encountered).

Carissa bispinosa (Apocynaceae), *Allocassine laurifolia* (Celastraceae), *Pancovia golungensis* (Sapindaceae) and *Erythroxylum emarginatum* (Erythroxylaceae) are among the species that form the shrub layer. The frequency of shrubs in the forest is low because of the effect of the herb *Isoglossa woodii* (Acanthaceae) that covers 65-95% of the forest understorey (Griffiths *et al.* 2007). Liana species found in the forest include *Rhoicissus spp.* (Vitaceae),
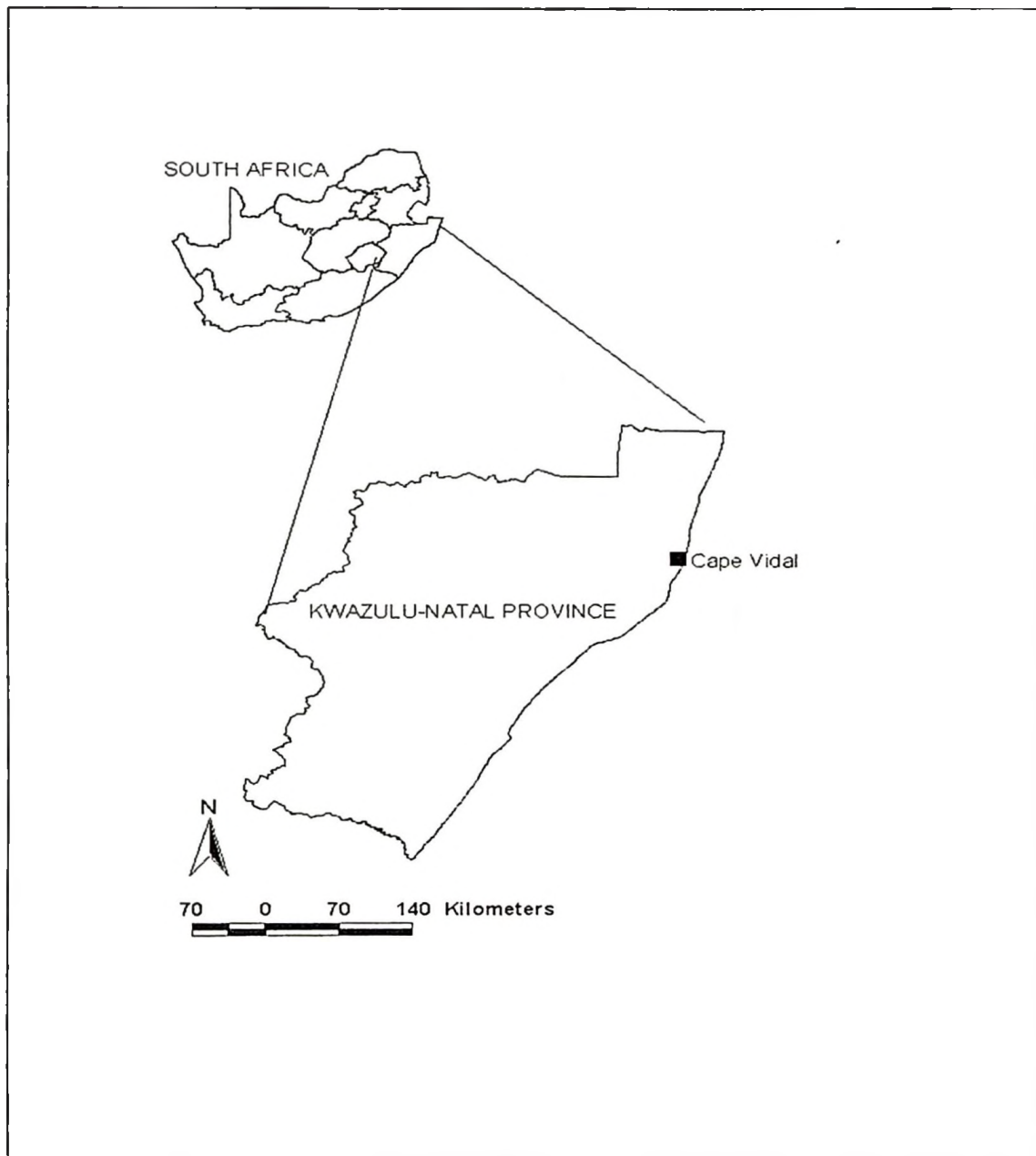
Figure 1. A map showing the location of the study area at Cape Vidal in KwaZulu-Natal province, South Africa

Scutia myrtina (Rhamnaceae), *Grewia caffra* (Tiliaceae), *G. occidentalis* (Tiliaceae) and *Acacia kraussiana* (Fabaceae).

Isoglossa woodii is a dominant species of the understorey vegetation. This Acanthaceous herb that may reach a height of 3 m, exerts a dominant influence on the forest vegetation, suppressing woody seedling recruitment (Griffiths *et al.* 2007). Its canopy may become so dense that hardly any sunlight filters through to the forest floor. The distribution and size of *I. woodii* depends on light availability in the understorey (Griffiths *et al.* 2007).

Definition and description of some terms and concepts used in the study

Disturbance severity is defined in terms of the proportion of the plant destroyed (Bellingham & Sparrow 2000; Vesk 2006) and the time taken between the occurrence of disturbance and the death of the plant or its part (Sakai *et al.* 1997; Sakai & Sakai 1998). Thus severe disturbance, such as stem-kill fire, kills the aboveground part of the plant immediately whereas low-severity disturbance, such as wind that results in stem leaning, leaves the aboveground part of the plant alive or results in death later due to unfavourable growth conditions imposed by the disturbance, for example the death of a leaning stem due to shading by neighouring tree crowns.

Chronic disturbance such as caused by a loose substrate, is a pervasive and continual disturbance. In sites with chronic disturbance not all trees may be affected by the disturbance at all times because other factors may reduce the effect of the disturbance. For instance, on loose substrate, tree roots may firm the soil and reduce the incidence of stem leaning.

Good resprouters are species with a high percentage of multi-stemmed trees in the forest. For comparison of traits that may be phylogenetically constrained such as seed size, good and poor resprouters were defined relatively within families.

Rationale and hypothesis of the study

As an alternative explanation to the regeneration niche in maintaining species diversity in ecosystems, the persistence niche currently needs more attention. The importance of the persistence niche in vegetation dynamics has often been neglected and is not fully understood (Bond & Midgley 2001). A better understanding of the persistence niche and its incorporation into vegetation models can result in more realistic inferences about plant community dynamics (Loehle 2000; Paciorek *et al.* 2000; Vesk *et al.* 2004).

So far, there is bias in the studies that have been conducted on the persistence niche. Most studies on resprouting have been conducted in habitats where disturbances are severe and episodic including fire-prone Mediterranean type shrublands and woodlands (Cruz & Moreno 2001; Clarke & Knox 2002; Wildy & Pate 2002), fire-prone chaparral (Keeley & Keeley 1977; Keeley & Zedler 1978; Thomas & Davis 1989), forest areas subjected to strong winds (Bellingham *et al.* 1994; Everham & Brokaw 1996) and forest areas subjected to slash-and-burn agriculture and logging (Kammesheidt 1998, 1999; Del Tredici 2001). Consequently, little is known about the ecology of resprouting in areas with low disturbance severity (Sakai *et al.* 1995; Yamada *et al.* 2001; Yamada & Suzuki 2004). Although some studies of resprouting in trees have been conducted, most research on resprouting in woody plants has focused on shrubby perennials, partly because it is easier to conduct experiments

using small plants (Iwasa & Kubo 1997) and partly because the role of resprouting is more

obvious in fire-prone shrublands. This study contributes to our understanding of resprouting

and multi-stemming by trees in forests affected by disturbance of low severity.

The study integratively investigated the relationship between the persistence niche and

species abundance as a function of species performance in terms of resource allocation and

water use, growth rate, leaf traits and stature, seed yield and size, seedling recruitment and

population structure (Fig. 2). The role of phylogeny, site productivity and disturbance

frequency and severity in determining the influence of the persistence niche on species

performance was analysed (Fig. 2). It was hypothesised that the persistence niche would

enable species to maintain their presence in the forest with little need for investment in
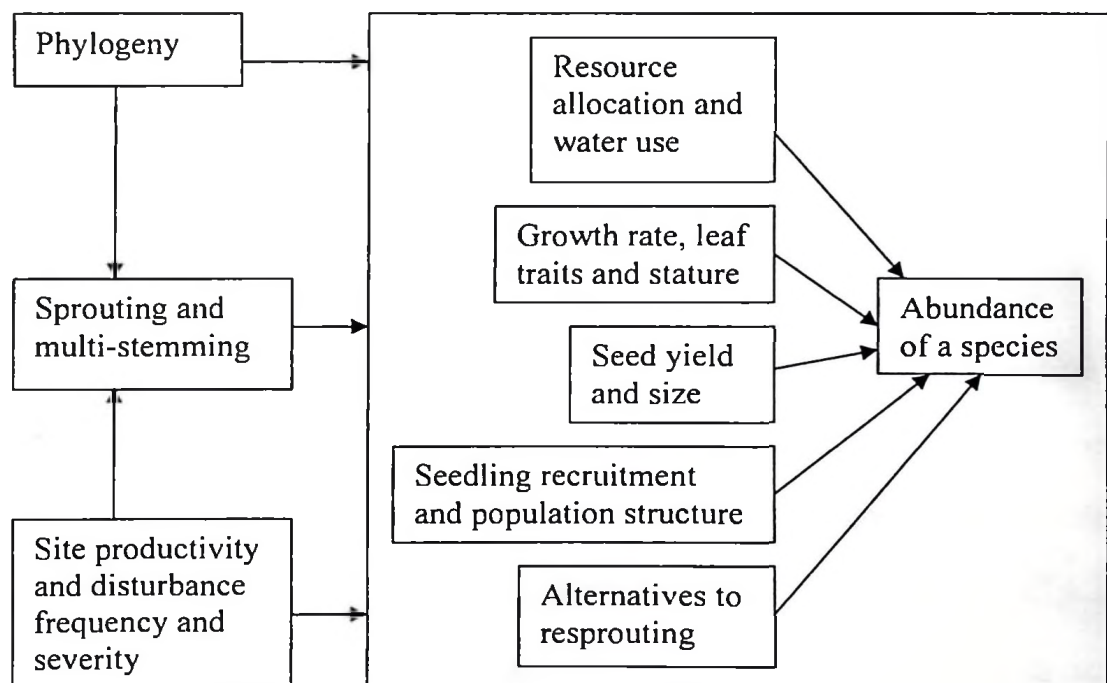
Figure 2. A conceptual framework of the study of the role of resprouting and multi-stemming

in forest structure and dynamics. Arrows point to the influenced aspects.

reproduction and other traits that facilitate effective recruitment of new individuals (Bond & Midgley 2001, 2003). Thus, persistent species should have small seed and low seed output, few seedlings and maintain few individuals for a long time mostly on sites with low productivity that are predominantly exposed to disturbance. Because of the need for storage for resprouting after disturbance, good resprouters should have higher allocation of resources to storage and thus lower growth rate than poor resprouters (Bond & Midgley 2003). Low-severity and chronic disturbance would necessitate storage by reserve formation, which directly competes for resources with growth (Chapin 1990). Good resprouters were also expected to have high sclerophyly, which is associated with low growth rate and high conservation of water (Lambers *et al.* 2006). Further, good resprouters were expected to be shorter than poor resprouters because good resprouters divide resources for growth among many stems (Kruger *et al.* 1997).

Objectives

The general objectives of the study are: (1) to examine the ecological correlates and implications for forest dynamics of resprouting and multistemming; and (2) to investigate the ecophysiological and functional morphology characteristics and costs and benefits of resprouting and multistemming. The specific aims of the study are to investigate the following:

(i)   the role of multi-stemming as a survival strategy in response to chronic disturbance of low-severity;

(ii)   the alternatives to multi-stemming that promote survival under conditions of chronic disturbance;

(iii)   the role of resprouting in seedlings;

(iv)   the relationship between resprouting and patterns of resource allocation and carbohydrate storage;

(v)   the effect of stress and disturbance on growth, leaf traits, biomass allocation, water relations and carbohydrate storage size and process in relation to resprouting ability; and

(vi)   the relationship between resprouting and multi-stemming and performance in sexual reproduction.

Outline of the thesis and questions addressed

The thesis comprises 8 chapters. Chapter 1 (this chapter) provides an introduction to the study and the theory underlying the study. The introduction includes a discussion of the persistence niche, forms of resprouting, factors that favour resprouting over reseeding and the role of the persistence niche in forest structure and dynamics. The rationale of the study, objectives and introduction to the study area are also presented in Chapter 1.

Chapter 2 addresses the following questions: Is multi-stemming a survival strategy in response to chronic disturbance? Is multi-stemming under phylogenetic control? What environmental factors are associated with multi-stemming? When do trees initiate growth of multiple stems? Do multi-stemmed trees have reduced stature?

Chapter 3 tackles the question: if multi-stemming is so important for survival at Cape Vidal, why and how do individuals of species that exhibit low frequency of multi-stemming

survive? Do species that exhibit low frequency of multi-stemmed individuals have low abundance? Are species affected by disturbance to the same extent?

Chapter 4 addresses the questions: Is the role of resprouting in seedlings the same as that in juvenile and mature trees? Do seedlings exhibit as high a frequency of multi-stemming as juvenile and mature trees? Is resprouting in seedlings phylogenetically constrained? What is the effect of resprouting on species seedling banks?

Chapter 5 asks: Do good resprouters differ from poor resprouters in allocation to root biomass and carbohydrate storage? Do plants store more reserves above or below ground? Is resprouting achieved using resources from above or below ground parts of the tree?

Questions addressed by Chapter 6 are: How do good resprouters differ from poor resprouters in terms of growth, leaf traits, biomass allocation, water relations and carbohydrate storage in response to stress and disturbance? Is carbohydrate storage achieved through reserve formation or accumulation?

Chapter 7 addresses the questions: What is the relationship between resprouting and multi-stemming and seed production and population structure? Is there a trade-off between allocation to storage and seed production? Do good and poor resprouters differ in seed size?

Chapter 8 provides a summary of the study and conclusions on the primary question of the thesis – the role of the persistence niche in forest structure and dynamics.

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Chapter 2

Multi-stemmed trees in subtropical coastal dune forest: survival strategy in response to chronic disturbance

Abstract

Questions: Is multi-stemming a survival strategy in response to chronic disturbance? Is multi-stemming under phylogenetic control? What environmental factors are associated with multi-stemming? When do trees initiate growth of multiple stems? Do multi-stemmed trees have limited stature?

Location: Subtropical Indian Ocean coastal dune forest at Cape Vidal in the Greater St. Lucia Wetland Park, northeastern South Africa.

Methods: Tree physiognomy and environmental conditions were sampled in 20 transects that were 300 m long × 5 m wide.

Results: 38.9 % of trees were multi-stemmed, with no correlation between multi-stemming and taxonomic grouping. The multi-stemming trait was most associated with stem decumbency and substrate erosion and multi-stemmed individuals were less common in protected dune slacks. Trees at Cape Vidal appear to facultatively produce multiple stems from an early stage. There was no trade-off between tree height and stem number.

Conclusions: Coastal winds and the unstable dune substrate are important environmental correlates of multi-stemming. Both short stature and the high incidence of multi-stemming are related to the tree-disturbance interaction. The taxonomically widespread phenotypic plasticity

in this trait indicates the importance of multi-stemming to tree survival even under low levels of disturbance.

Keywords: Persistence; Regeneration; Resprouting; Vegetative reproduction.

Nomenclature: Coates Palgrave (2002).

Abbreviations: AIC = Akaike's information criterion; ANCOVA = Analysis of covariance; ANOVA = Analysis of variance; CV = Coefficient of variation; DBH = Diameter at breast height; GLM = Generalised linear model; IV = Importance value; PCA = Principal components analysis.

Introduction

The importance of resprouting as a survival strategy in plants is recorded from a variety of habitats worldwide (Basnet 1993; Bellingham et al. 1994; Zimmerman et al. 1994; Lamont & Markey 1995). Most studies have focused on ecosystems subject to large-scale disturbance events such as floods, cyclonic storms, volcanoes, and fires. In response to these disturbances, many species resprout from dormant buds rather than regenerating from a seed or seedling bank, allowing the plants to recover quickly and maintain their presence in the ecosystem (Lamont & Markey 1995).

The relative importance of resprouting in plant communities depends on the frequency and severity of the disturbance regime as well as ecosystem productivity, with resprouting favoured at intermediate levels (Bellingham & Sparrow 2000; Sparrow & Bellingham 2001).

Resprouting by plants in fire-dominated systems is well documented. All shrub species in Mediterranean maquis regenerate vegetatively after fire (Verdú 2000), and in the fire-disturbed South African fynbos, just less than half the species in the characteristic fynbos families resprout (le Maitre & Midgley 1992). Resprouting is also found in habitats not associated with recurrent fires but which experience periodic loss of biomass due to disturbance. Many forest tree species resprout from damaged stems after hurricanes and volcanic eruptions, allowing trees to persist after disturbance (Basnet 1993; Bellingham et al. 1994; Boucher et al. 1994; Zimmerman et al. 1994; Tsuyuzaki & Haruki 1996).

While there is no doubt that some tree species resprout in response to disturbance, others may sprout from undamaged stems in the absence of large-scale or high-intensity disturbance, producing multi-stemmed trees. In temperate forests at the southern limits of their range in Australia, Johnston & Lacey (1983) note that several species, although exposed to minimal disturbance, sprout continuously and produce multi-stemmed trees. There is evidence that plants with vegetative reproduction are better able to persist in more competitive environments (Clarke et al. 2005) and, furthermore, that multi-stemmed trees are selected for in habitats with competition from a dense understorey layer (Veblen 1982). On the other hand, a possible consequence of multi-stemming may be a reduction in forest canopy height (Midgley 1996). Because multi-stemmed plants must share their resources among several stems, there may be fewer resources to devote to vertical growth. For example, Kruger et al. (1997) found that canopy height declined with increasing levels of multi-stemming in a number of forests in the southern Cape region of South Africa.

Few studies have explored the occurrence of multi-stemmed plants in subtropical and temperate forests. Here we evaluate the incidence of multi-stemming in Indian Ocean coastal dune forest in South Africa, and explore the possibility that it is a response to low-level

chronic disturbances. We investigate associations between multi-stemming ability and phylogeny, and examine spatial patterns in the distribution of multi-stemmed individuals relative to environmental gradients within the subtropical forest. In addition, we conduct simulations to test whether observed frequency distributions in stem sizes of multi-stemmed individuals result from random variation or are a direct response to disturbance events. Finally, we compare canopy height of tree species relative to the number of stems per individual to determine whether a potential trade-off in resource allocation exists between sprouting or multiple stems and vertical growth.

Methods

Study area

The study was conducted in the Indian Ocean coastal dune forest at Cape Vidal (28°05'32"S, 32°33'40"E) in the Greater St. Lucia Wetland Park in KwaZulu-Natal, South Africa. The mean annual rainfall is approximately 1200 mm, with average temperature ranges from 17.8°C in July to 25.6°C in January. Coastal winds occur in the area from August to October.

At Cape Vidal, longitudinal sand dunes that are parallel to the coastline extend from sea level inland achieving a height of more than 100 m. The seaward slope of the first dune is covered by vegetation stunted by exposure to onshore wind. On the landward side of this first dune, forest vegetation begins. Some of the dune valleys, or slacks, are dominated by even-aged stands of *Acacia karroo* (Tinley 1985).

Soil nutrients are low at Cape Vidal, particularly N (mean ± 1 SD = 0.2 % ± 0.07) and P (21.7 mg/L ± 12.04) (Boyes, 2006). Analysis of soils from different dune habitats (dune crest, landward slope, seaward slope, dune slack, and dune slack with *A. karroo*) found no

significant differences in either N (ANOVA; $F_{4,70} = 0.96$, $p = 0.436$) or P ($F_{4,70} = 0.18$, $p = 0.946$) (data not shown). Soil nutrients were not examined for this study.

Field survey methods

Multi-stemming in trees was examined in 20 transects that were each 300 m long × 5 m wide and divided into 10 m × 5 m quadrats. Fitted quadratic regressions showed the cumulative species curve asymptote at 15 transects ($F_{2,19} = 44.87$, $r^2 = 0.84$, $p < 0.001$). Transects were 50 m apart and oriented perpendicular to the dune crests that run parallel to the coastline.

The following were recorded for trees with diameter at breast height (DBH) ≥ 1.5 cm: (1) species; (2) number of stems per individual (shoots originating from the base of the tree and with a DBH ≥ 1.5 cm); (3) DBH for each stem; and (4) height of the largest stem. Individual trees were differentiated from one another by their physical separation on the forest floor, while the stems of multi-stemmed trees were visibly connected to one another at the base of the tree. We recorded three potential sources of competition: (5) distance to main stem of nearest neighbour; (6) absence or presence of an over-topping neighbour canopy; and (7) absence or presence of *Isoglossa woodii* (Acanthaceae) around the base of the tree. This herb dominates the understorey at Cape Vidal (Griffiths et al. 2007). Several environmental factors were also measured, including: (8) erosion level (no erosion, slight erosion, or high erosion around roots); (9) decumbency, the angle of inclination of the main stem relative to the vertical; (10) presence of stumps at the tree base indicating missing stems; (11) snapping of the main stem high in the canopy; and (12) wind- or salt-pruning of the canopy (Venter 1976). Dune habitat (dune crest, landward slope, seaward slope, dune slack, and dune slack with *A. karroo* cover) and slope angle were also recorded for each quadrat.

Importance values (*IV*) for each species were determined using the formula:

$$IV = (RD + RDo + RF) \tag{1}$$

where RD = relative density, the number of individuals of one species as a percentage of the total number of individuals of all species; RDo = relative dominance, the total basal cover (at breast height) of one species as a percentage of the total basal cover of all species; and RF = relative frequency, the frequency of a species as a percentage of the frequency of all species in the study plots (Mueller-Dombois & Ellenberg 1974).

We used two-term local quadrat-variance (TTLQV), paired-quadrat variance (PQV) and random paired-quadrat variance (RPQV) methods (Ludwig & Reynolds 1988) to examine the spatial distribution of multi-stemmed individuals along transects. Analysis of Variance (ANOVA) was used to test for patterns in multi-stemming as a function of dune habitat.

Phylogenetic analysis

The expression of multi-stemming across lineages was analysed using phylogenetic autocorrelation (PA; Luh et al. 1994). Two criteria determined significance: (1) at least one Z-value greater than 1.96 (i.e., observed PA at $p < 0.05$) and (2) a correlogram that was high at lower taxonomic ranks with a decay to negative autocorrelation at higher taxonomic ranks.

We analysed the relationship between tree height and number of stems using standardized linear independent contrasts in Mesquite (Maddison & Maddison 2005). This analysis was performed using data for the 34 most common species at Cape Vidal (i.e., all those species with greater than 10 observations each in the dataset). The phylogeny was based on a tree by Griffiths & Lawes (2006) (App. 1) and branch lengths were assigned according to Pagel's arbitrary method (Pagel 1992). The variance homogeneity of contrasts was verified by

examining the relationship between the absolute value of the standardized contrasts and the sum of the squares of branch lengths (Garland et al. 1992).

Modelling multi-stemming

We used a generalised linear model (GLM) based on a Poisson distribution with a logarithmic link function to model multi-stemming in relation to environmental conditions. Predictor variables represented factors potentially influencing multi-stemming: substrate instability (erosion status), wind damage (decumbency), and competition (canopy cover, nearest neighbour distance, and *I. woodii* cover). Decumbency was chosen to represent wind damage after principal components analysis (PCA) revealed that decumbency, pruning, snapping, and missing stems were closely correlated and that decumbency had the strongest overall influence (data not shown). Collinearity among variables was checked in SPSS (SPSS 2002).

The GLM was in the form:

$$\ln(y) = a + bx_1 + cx_2 + \ldots \tag{2}$$

where ln is the logarithm to base e, y is a count of the number of multi-stemmed individuals in a quadrat, and a, b, c, ... are estimated coefficients for the predictor variables x_1, x_2, ... All models were fitted using GenStat (GenStat Committee 2005) and included dune position as a blocking factor and transect number as an absorbing function.

Six candidate models were formulated *a priori*. Predictor variables were added one at a time into the model, starting with the variable that was expected to have the most influence based on PCA (data not shown). The most parsimonious model was selected using Akaike's Information Criterion (AIC) (McCullagh & Nelder 1989). The model with the lowest AIC value (and a difference of at least two AIC units from other models) was accepted as the best fit. In addition, we estimated the relative importance of predictor variables by summing the

Akaike weights (w_i) across all models in which the variable occurred (Burnham & Anderson 2002). The larger the w_i (range = 0 – 1), the more important a variable is relative to the others.

Stem size-frequency distribution in multi-stemmed individuals

We explored patterns in multi-stemming by analysing the size-frequency distribution of stems within individuals. To explain the timing of multi-stemming, we formulated three cases of individual size-frequency distribution, with the reasoning that if the multiple stems of an individual were: (1) of uniform size, the individual facultatively grew multiple stems from an early stage; (2) of many different sizes, then the individual resprouted regularly in response to continual disturbance; and (3) were grouped into several discrete size classes with large size differences, the individual resprouted multiple times. These scenarios assume that growth rates are relatively constant and that stem size reflects stem age. Tree rings are not a reliable means of estimating growth rate and tree age in the tropics (Ogden 1981) therefore stem size is the best available indicator of age (Niklas et al. 2003). All analyses were on a per-species basis because growth rate potential varies among species (Clark & Clark 1999).

For the 20 most important species we tested the fit to the above three cases. We first calculated the coefficient of variation (CV) of stem size for each multi-stemmed individual and the mean CV ($\overline{CV}$), for the entire population. Next, we used bootstrapping to draw for each individual tree with n_i stems, n_i stem sizes from the distribution and calculated the $\overline{CV}$ based on these randomised data. This procedure was repeated 1000 times to determine a cumulative distribution of $\overline{CV}$ for the randomisations. If the actual $\overline{CV}$ was smaller than the 5th percentile of the randomised $\overline{CV}$ distribution ($p < 0.05$), the stem size distributions within multi-stemmed individuals were uniform and we interpreted the data as tending towards case

(1). If the actual $\overline{CV}$ fell between the 5th and 95th percentile ($0.05 > p > 0.95$), the data were randomly distributed and tended towards case (2). If the actual $\overline{CV}$ was larger than the 95th percentile ($p > 0.95$), then the stems were aggregated and tended towards case (3). Because 20 species were tested, there was a high probability of accumulating experiment-wise Type I error, so a sequential Bonferroni procedure was used to determine significance (Holm 1979).

Finally, we tested whether trees grow multiple stems when they are relatively young by comparing the size-frequency distributions of the primary stem of single-stemmed and multi-stemmed trees using Kolmogorov-Smirnov tests (Massey 1951). If the shapes of the size-frequency distributions were similar and the test failed to reject the null hypothesis, there was support that multi-stemming occurs in young trees and persists throughout their lifetime.

Multi-stemming and tree height

We investigated the relationship between multi-stemming and tree height by dune habitat using ANCOVA, with number of stems per individual as a covariate. Species with fewer than 10 observations were excluded from the analysis. To ensure homogeneity of variances, we applied Taylor's power law to tree height and transformed tree height to the power 0.383.

Results

Overall, 3901 trees were sampled, belonging to 53 species. There were 195.1 ± 52.2 trees (mean $\pm$ 1 SD) and 27.2 ± 3.2 species per transect. While most of the measured trees had a single stem, 38.9% ($n = 1516$) were multi-stemmed. Of the 20 most important species, all showed some degree of multi-stemming (Table 1). Only five species in the study showed no multi-stemming: *Inhambanella henriquesii, Trichilia emetica, Kigelia africana, Balanites*

maughamii, and *Cussonia natalensis*. However, these species were extremely rare in the study area, and each had 6 or fewer occurrences in total across all 20 transects.

Table 1. The most important tree species at Cape Vidal based on surveys of 20 transects. Importance values were calculated using a formula from Mueller-Dombois & Ellenberg (1974). The multi-stemming index is the percent of total individuals of a species that had multiple stems.

Species	Importance value	Total number of individuals	Basal area (m^2/ha)	Density (individuals/ ha)	Multi-stemming index
Diospyros natalensis	31.1	733	9.8	249.7	14.5
Mimusops caffra	19.5	174	12.0	59.3	40.2
Drypetes natalensis	15.1	429	3.3	146.2	45.7
Celtis africana	14.4	209	7.2	71.2	47.4
Ochna natalitia	14.2	392	3.3	133.6	31.6
Diospyros inhacaensis	10.6	214	4.0	72.9	11.2
Strychnos gerrardii	9.5	56	6.4	19.1	64.3
Sideroxylon inerme	9.1	62	6.0	21.1	72.6
Teclea gerrardii	8.6	183	3.1	62.4	25.7
Acacia karroo	8.0	99	4.3	33.7	37.4
Euclea racemosa	6.5	156	2.0	53.2	69.9
Dovyalis longispina	5.8	122	2.1	41.6	78.7
Ziziphus mucronata	5.7	35	3.9	11.9	65.7
Eugenia woodii	5.7	140	1.7	47.7	45.7
Olea woodiana	4.4	47	2.6	16.0	59.6
Deinbollia oblongifolia	3.6	116	0.5	39.5	26.7
Gymnosporia nemorosa	3.5	84	1.1	28.6	66.7
Scolopia zeyheri	2.7	53	1.1	18.1	32.1
Tricalysia sonderiana	1.9	70	0.1	23.9	72.9
Canthium ciliatum	1.8	29	0.8	9.9	31.0

Based on quadrat-variance methods, we conclude that multi-stemmed individuals were randomly dispersed along transects because there was random fluctuation in variances (data not shown). Although there was a significant difference in the number of multi-stemmed individuals per quadrat by dune position ($F_{4, 563} = 15.20$, $p < 0.001$), this difference was driven by a significantly lower incidence of multi-stemmed individuals in the dune slacks (Fig. 1).

Phylogenetic analysis

There was no phylogenetic pattern in the expression of multi-stemming. The trait occurred in almost all tree species regardless of their taxonomic placement and multi-stemming occurred in almost all lineages. Furthermore, when analysed by phylogenetic autocorrelation, we found all Z-values to be less than 1.96 and the correlogram did not decrease to negative autocorrelation at higher taxonomic ranks (data not shown).
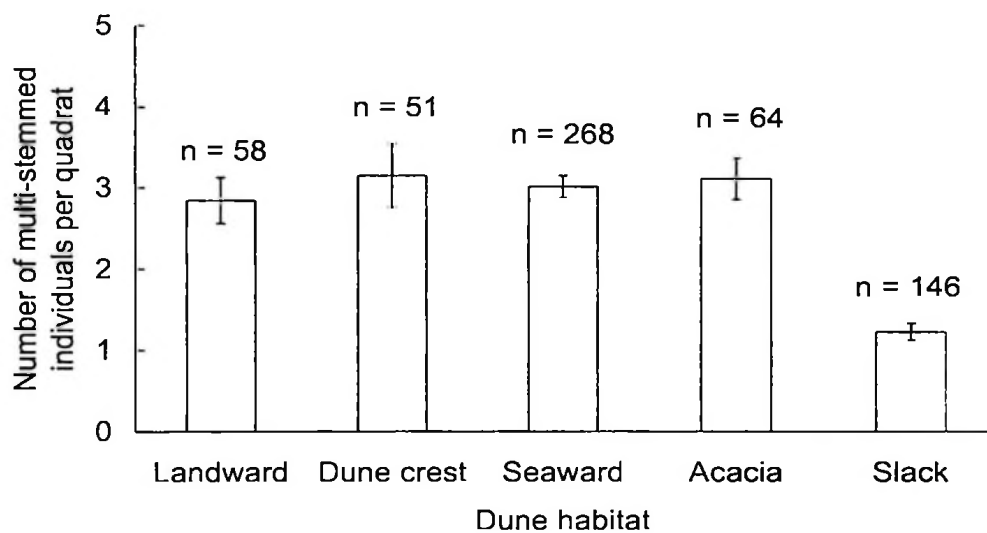
Fig. 1. A comparison of the incidence of multi-stemmed individuals by location on the dune topography. Bars represent the mean number of multi-stemmed individual per quadrat with a particular topographic position ± 1SE.

Modelling multi-stemming

The best-fit GLM included all factors (Table 2). The number of multi-stemmed individuals was positively associated with substrate instability, wind disturbance, and competition. Across all possible models, the most important variable affecting the number of multi-stemmed individuals was wind disturbance as measured by decumbency (w_i = 0.82), followed by

substrate instability as measured by erosion (w_i = 0.51), then by canopy cover from neighbouring trees (w_i = 0.15), the incidence of the herb *I. woodii* (w_i = 0.11), and the distance to the nearest neighbour (w_i = 0.08).

Table 2. Summary of six candidate models built to infer the relationship between multi-stemming and environmental conditions at Cape Vidal. All models used dune position as a blocking factor. Model 6, highlighted in bold, had the lowest Akaike's Information Criterion (AIC) value and therefore is the model best fitting the data. K = the number of parameters in the model.

Model	Model number	Residual deviance	df	K	AIC	ΔAIC
Constant (Null)	Null	1140	586	1	1142	773.3
Dune position	1	978.3	582	5	988.3	619.6
Dune position(erosion)	2	838.7	559	29	896.7	528.0
Dune position(erosion+decumbent)	3	556.4	554	34	624.4	255.7
Dune position(erosion+decumbent+canopy cover)	4	520.2	549	39	598.2	229.5
Dune position(erosion+decumbent+canopy cover+nearest neighbour distance)	5	491.4	544	44	579.4	210.7
Dune position(erosion+decumbent+canopy cover+nearest neighbour distance+*Isoglossa woodii*)	**6**	**270.7**	**345**	**49**	**368.7**	**0**

Stem size-frequency distribution in multi-stemmed individuals

Of the 20 most important species, 16 had stem distributions within individuals that were more similar in size to one another than would be expected under a random allocation of stems (App. 2). We found no difference between the size-frequency distributions of primary stems in single-stemmed and multi-stemmed trees ($D = 0.10, p = 0.997$).

Multi-stemming and tree height

We found a slight but significant positive relationship between the number of stems per individual and tree height ($F_{1, 3708} = 28.20$; height$^{0.383}$ = 2.108+0.017[no. stems]; $t_{slope} = 5.31$,

$r^2 = 0.007$, $p < 0.001$) (Fig. 2a). The relationship between height and number of stems varied among species ($F_{33,3642} = 2.08$, $p < 0.001$). This interaction comprised two groups, each with homogenous slopes: (1) the first group consisted of *Ochna natalitia, Diospyros natalensis, Celtis africana, Teclea gerrardii, Drypetes natalensis,* and *Eugenia woodii* and demonstrated a slight negative relationship between individual height and number of stems (height$^{0.383}$ = 2.11 - 0.013[no. stems]; $t_{slope} = -2.09$, $p = 0.036$); (2) in the remaining 28 species overall individual height increased with the number of stems per individual (height$^{0.383}$ = 2.16 + 0.04[no. stems]; $t_{slope} = 5.53$, $p < 0.001$). Phylogenetically independent contrasts suggested no trade-off between tree height and number of stems per individual (Fig. 2b).

Controlling for stem diameter (i.e., potential tree age) there was no effect of number of stems per individual on tree height ($F_{1, 1941} = 0.05$; height = 10.29 -0.007[no. stems]; $t_{slope} = -0.23$, $r^2 < 0.001$, $p = 0.82$). When examined by dune position, the slopes of the respective ANCOVA interactions were the same. However, tree height in sheltered dune slacks (10.96 ± 0.15 m) was significantly greater than on dune crests (9.95 ± 0.22 m) and the wind-swept seaward slopes (10.03 ± 0.09 m), but not in *A. karroo*-dominated dune slacks (10.46 ± 0.31 m) or on the sheltered landward facing dune slopes (10.47 ± 0.22 m; $F_{4, 1933} = 7.19$, $p < 0.001$).

Discussion

Multi-stemming by forest trees is more important than general accounts would suggest (Grubb 1996). Most plant species have the capacity to reproduce vegetatively, but the expression of sprouting is often subject to control by environmental (Bond & Midgley 2001) or ontogenetic (Vesk 2006) factors. The coastal dune forest at Cape Vidal offers an excellent opportunity to study this phenomenon, as a substantial proportion of the trees (38.9 %) are multi-stemmed.

We found no phylogenetic constraints on multi-stemming, indicating that the incidence of multi-stemming is under environmental control.
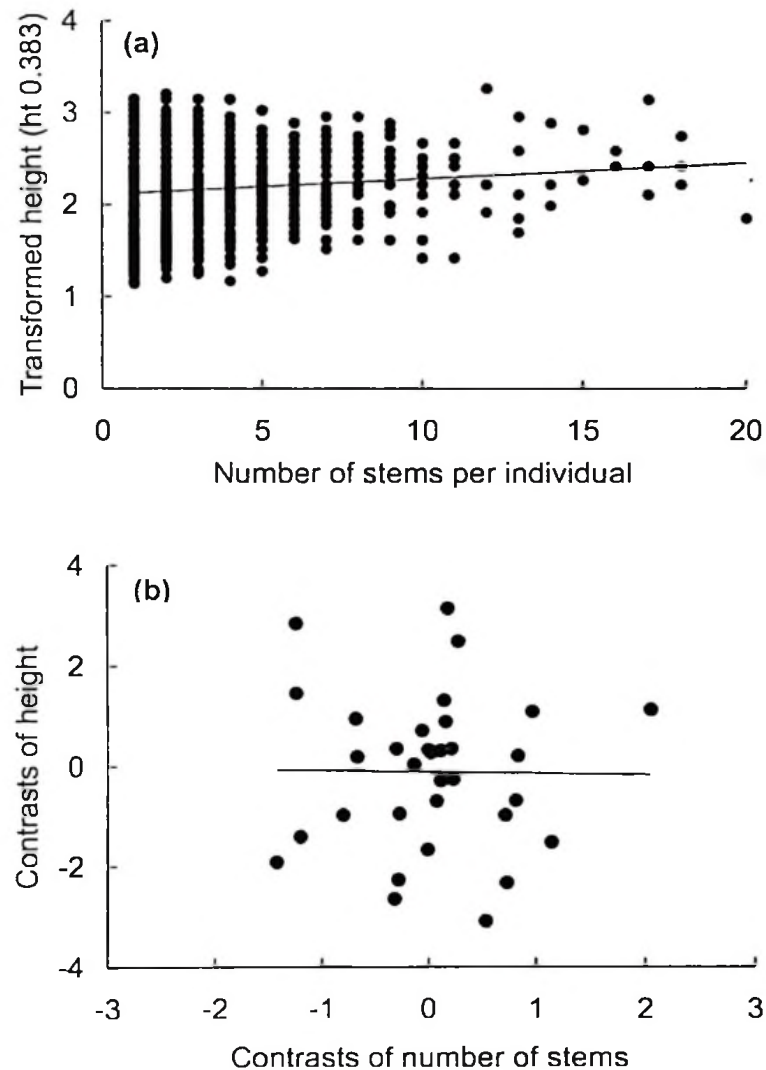
Fig. 2. a. Relationship between tree height and the number of stems per individual. **b.** Influence of phylogeny on the relationship between height and number of stems.

Individuals at Cape Vidal persist by sprouting from the base of both previously damaged and apparently undamaged stems under low-level, chronic disturbance, consistent with other studies (Johnston & Lacey 1983; Bellingham et al. 1994). Our analysis of stem sizes within multi-stemmed individuals demonstrates that trees at Cape Vidal grow multiple

stems from an early stage. This is further supported by the comparison of size-frequency distributions of primary stems in single-stemmed and multi-stemmed trees, which indicated that multi-stemming is initiated in young trees in this tree community. In combination, these results suggest that there is an advantage for trees of facultatively growing multiple stems.

Multi-stemmed trees are better able to persist through disturbances such as wind (Tanner & Bellingham 2006). The forest at Cape Vidal is subject to north-easterly winds that blow almost constantly from August to October. This imposes a strong selection pressure for individuals and species that grow multiple stems (Sakai & Sakai 1998). The sand dunes at Cape Vidal provide an unstable substrate for forest. Substrate instability is known to promote multi-stemmed growth forms because individuals that become eroded or decumbent can persist through resprouting (Ohkubo 1992; Yamada & Suzuki 2004). Thus, wind and unstable sandy substrate confer a competitive advantage on multi-stemmed individuals on steep and seaward-facing dune slopes. This is also indicated by the lower incidence of multi-stemmed individuals in the dune slacks at Cape Vidal, which are protected from wind and have a stable substrate.

Site productivity and climate also impose a selection pressure on multi-stemming and resprouting (Midgley 1996; Bellingham & Sparrow 2000). The sandy soils at Cape Vidal are highly susceptible to leaching (Boyes 2004), which would favour multi-stemmed trees that are better able to cope with a nutrient-poor environment (Bellingham & Sparrow 2000). In terms of carbon gain, multi-stemmed plants have a competitive advantage over neighbouring single-stemmed plants in unproductive or disturbed sites where there is little risk that they will be overtopped (Givnish 1984; Midgley 1996; Bond & Midgley 2001).

Apart from facilitating persistence, resprouting is predicted to have other life history consequences (Bond & Midgley 2003). One cost of producing multiple stems may be that tree

height is compromised (Midgley 1996). In South Africa, Kruger et al. (1997) note that short forests tend to be dominated by multi-stemmed trees, while tall forests are dominated by single-stemmed trees. The forest at Cape Vidal, with its high proportion of multi-stemmed individuals, is three times shorter than the forests dominated by single-stemmed trees described in Kruger et al. (1997). Such a trend could be a consequence of maintaining multiple stems, which diverts resources from vertical growth. However, we found no evidence of a trade-off between tree height and number of stems, indicating that tree height is constrained regardless of whether or not a tree is multi-stemmed. Trees that over-top the canopy would be susceptible to wind damage, whereas shorter trees would have less wind-induced mortality (Tanner & Bellingham 2006). Therefore, it is likely that both the short stature and the high incidence of multi-stemming are caused by wind disturbance and substrate instability at Cape Vidal.

We conclude that multi-stemming is a survival strategy in response to chronic disturbance in the form of wind and substrate instability, as well as pervasive environmental stress in the form of low soil nutrient availability. The taxonomically widespread multi-stemming response indicates the importance of this trait for tree survival and fitness even under low levels of continuous disturbance. In contrast, in fire-prone ecosystems resprouting and multi-stemming are favoured by intermediate levels of disturbance (Bellingham & Sparrow 2000; Sparrow & Bellingham 2001). The advantage gained from multi-stemming is that a tree maintains its presence in a forest through the persistence niche (Bond & Midgley 2001). This would hold the greatest benefit in an environment that experiences long-term chronic disturbance or environmental stress. Thus, multi-stemming appears to be related to the plant-disturbance interaction rather than being a property of a plant or species.

Acknowledgements

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Appendices
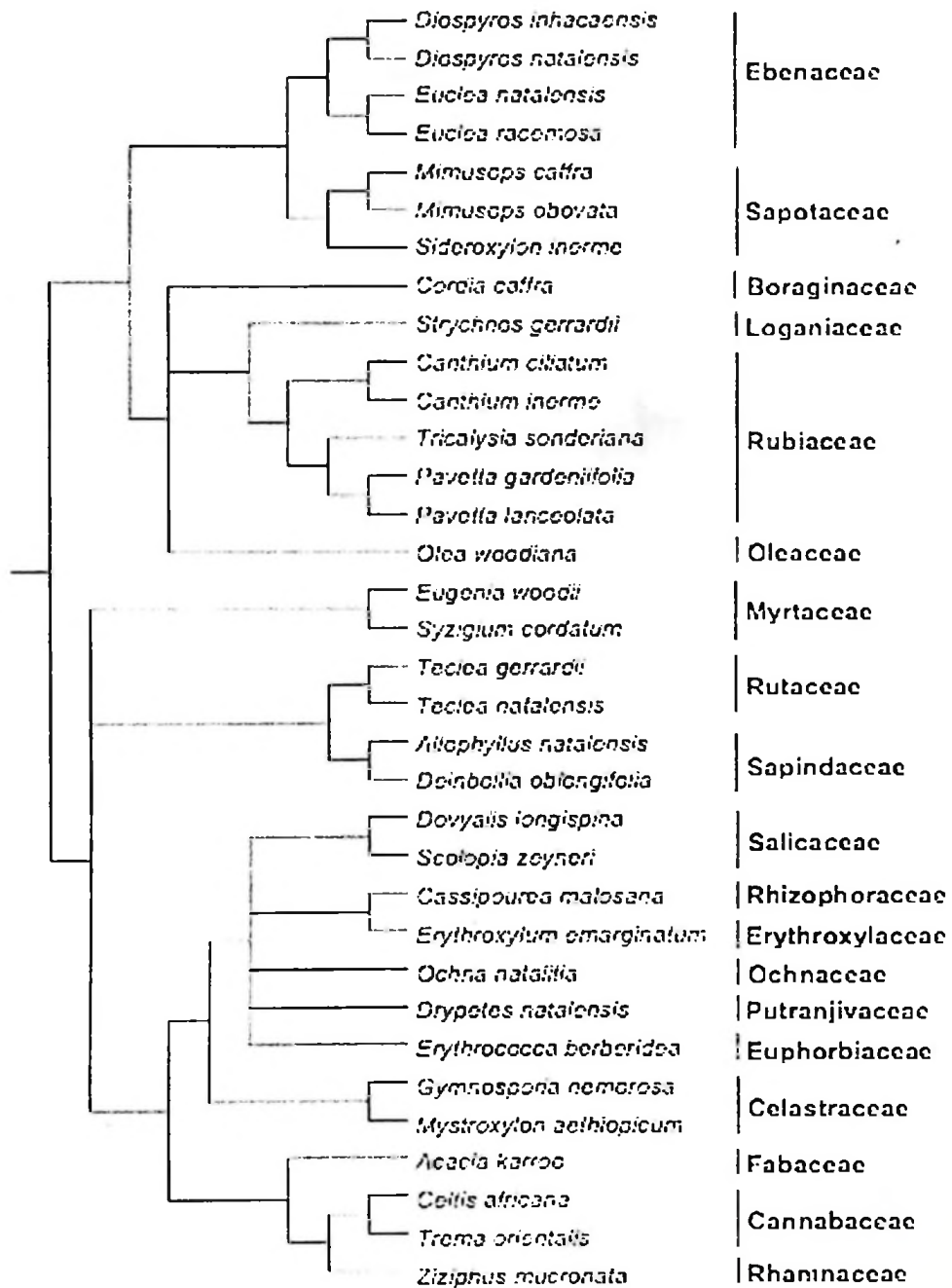
Appendix 1. A hypothesis of the phylogenetic relationships between tree species in coastal dune forests at Cape Vidal constructed as described in Griffiths and Lawes (2006).

Appendix 2. Results from randomisation tests examining the stem size-frequency distributions within multi-stemmed tree individuals at Cape Vidal, where p-values indicate the probability that stem size-frequency distributions are random. Significance (*) was determined according to adjusted alpha levels based on a sequential Bonferroni procedure.

Species	p	Significance
Acacia karroo	0.003	*
Canthium ciliatum	0.025	
Celtis africana	< 0.001	*
Deinbolia oblongifolia	< 0.001	*
Diosoyros natalensis	< 0.001	*
Diospyros inhacaensis	0.075	
Dovyalis longispina	0.035	
Drypetes natalensis	< 0.001	*
Euclea racemosa	< 0.001	*
Eugenia woodii	< 0.001	*
Gymnosporia nemorosa	< 0.001	*
Mimusops caffra	< 0.001	*
Ochna natalitia	< 0.001	*
Olea woodiana	0.029	
Scolopia zeyheri	0.004	*
Sideroxylon inerme	< 0.001	*
Strychnos gerrardii	< 0.001	*
Teclea gerardii	< 0.001	*
Tricalysia sonderiana	< 0.001	*
Ziziphus mucronata	0.005	*

Chapter 3

Resprouting versus turning up of leaning trees in a subtropical coastal dune forest in South Africa

Abstract: To survive, leaning trees on steep slopes with loose substrate can either resprout or turn upward to regain the normal vertical orientation of the growing tip. Data from 19 tree species were collected from 20 transects in coastal dune forest. Resprouting was negatively correlated with turning up and species abundance, and positively correlated with leaning and a dead primary stem. In contrast, turning up was associated with low probabilities of leaning and higher species abundance but not with a dead primary stem. Slightly inclined trees turned upwards more than severely inclined ones, which mostly resprouted. Leaning trees without exposed roots turned upwards, while severe erosion caused leaning and resprouting. Consistent with the latter, leaning trees in stable dune slacks frequently turned upwards, whereas leaning trees on narrow dune crests and steep landward slopes seldom did so. Small trees were more likely to turn upwards than big trees. Because of potentially greater costs to the individual of sprouting, stem reorientation precedes the resprouting response across the disturbance gradient. Consequently, species prone to stem reorientation and less likely to resprout, are dominant during late-succession. This study emphasizes the advantage under low levels of disturbance of turning up as an alternative strategy to repsrouting for leaning trees.

Key words: disturbance response, erosion, sprouting, stem persistence, survival, tree size, tree abundance

INTRODUCTION

Plant strategies in response to disturbance play a key role in maintaining plant diversity, species coexistence and succession (Loehle 2000). The resprouting strategy, which defines the persistence niche (Bond & Midgley 2001), is receiving increasing interest due to its role in plant dynamics (Kruger *et al.* 1997, Loehle 2000, Nanami *et al.* 2004, Vesk & Westoby 2004a). Plants affected by severe disturbances, such as crown fire, where a large proportion of the above-ground structure is immediately destroyed, must resprout or die (Bond & Midgley 2001, Vesk & Westoby 2004b). Trees that lean because of wind damage, unstable substrate, or erosion may also need to resprout because of the displacement of the growing tip from the vertical (del Tredici 2001, Sakai *et al.* 1995, Yamada & Suzuki 2004, Yamada *et al.* 2001). However, leaning trees can restore a vertical growth form (Mattheck 1995) because the above-ground biomass of the affected tree is not immediately destroyed (Sakai & Sakai 1998, Sakai *et al.* 1997). We refer to the process by which a tree turns its growing tip upward to restore vertical orientation as 'turning up'. Turning up is a geotropic and phototropic response that occurs by active formation of reaction wood (Mattheck 1995, Zimmermann *et al.* 1971).

We examine the relationships between resprouting and turning up of leaning trees and some of their functional correlates. There is a high prevalence of leaning trees in the study area that have either resprouted or undergone turning up. Species abundance appeared to vary with the prevalence of leaning, resprouting and turning up. We investigated the variation in leaning, sprouting, turning up and the abundance of tree species to determine functional differences among species. Four predictions of the hypothesis that resprouting and turning up of the main stem represent alternative plant strategies that enhance individual survival were tested. First, we predicted a negative relationship between the incidence of resprouting and

turning up of the main stem. Second, because a leaning primary stem most likely dies after resprouting, leaving sprout stems in its place (Sakai & Sakai 1998, Yamada & Suzuki 2004), resprouting species should be less likely to undergo turning up and be more likely to lose their primary stem. Third, resprouting ability is associated with a tendency for stems to lean (Sakai *et al.* 1997, Yamada & Suzuki 2004). Hence, species that resprout and seldom undergo turning up should also be more likely to lean. Lastly, sprouting may not be favoured where there is strong competition for canopy space and reseeders overtop resprouters (Bellingham & Sparrow 2000, Bond & Midgley 2003, Midgley 1996). By putting resources into growth of many stems, resprouters trade off increased survival or persistence for lower reproduction and thus produce fewer recruits than reseeders (Bond & Midgley 2001, 2003). Hence, we predicted that species that resprout but seldom undergo turning up of leaning stems should be less abundant than species that can regain vertical orientation. A resprouting but leaning stem gives up canopy space whereas a reoriented stem that turns upward can reclaim canopy space.

Two further questions were addressed by the study: one on the influence of stem size on death of primary stems, and another on the relationship of the likelihood of stem turning up with degree of leaning, slope incline, tree size, dune topography and exposure of roots by soil erosion.

STUDY SITE

The study was conducted in an Indian Ocean coastal dune forest at Cape Vidal (28°05'32"S, 32°33'40"E). Cape Vidal is part of the Greater St. Lucia Wetland Park, which is under the jurisdiction of Ezemvelo KwaZulu-Natal Wildlife. The mean annual rainfall is approximately 1200 mm, spread evenly throughout the year (range = 80–90 mm mo^{-1}) (Tinley 1985).

Average minimum and maximum temperature is 17.8°C in July and 25.6°C in January, respectively. The soil is loose unconsolidated sand with limited organic matter. The topography consists of a series of steep (slopes up to 55°) longitudinal sand dunes whose crests are parallel to the coastline. The loose sand substrate, steep slopes, and the action of wind make trees growing in this area particularly susceptible to a leaning growth form.

The dune forest at Cape Vidal forms part of a narrow strip of forest (0.1-4 km wide) extending in a contiguous belt for 240 km along the KwaZulu-Natal coast (Tinley 1985). The forest does not have any history of commercial logging activities. The climax tree community is dominated by *Diospyros natalensis, Mimusops caffra, Drypetes natalensis* and *Ochna natalitia* (Venter 1976). Some dune slacks, or valleys in between the dunes, are dominated by natural stands of *Acacia karroo* that established following human disturbance 50 y ago.

METHODS

Trees were sampled along 20 transects measuring 5 × 300 m that were established perpendicular to the coastline at intervals of about 50 m. Transects crosscut the longitudinal dunes that run parallel to the coastline in this region. The starting point of each transect was typically the crest/valley of the second longitudinal dune from the shoreline (50 m from the forest edge). Diameter at breast height, resprouting, whether the primary stem was dead or alive, inclination of stems from the vertical, the turning up of stems, and dune slope were recorded for every tree with a girth at breast height (gbh) of >5 cm. Inclination and slope were measured using a clinometer. Only resprouts taller than 1.3 m and with a gbh >5 cm were included in the sample. In most cases, sprouting trees had one big leaning stem with several progressively smaller and increasingly vertical stems attached to this stem on its upper side at

or close to ground level (Figure 1a). As in other studies on resprouting of leaning trees, leaning stems sprouted before the death of the primary stem (Sakai & Sakai 1998, Sakai *et al.* 1997, Yamada & Suzuki 2004).

Figure 1. Resprouting and turning up of leaning trees. A resprouting and leaning *Sideroxylon inerme* tree with multiple resprouted stems varying in size and degree of leaning (a), and a *Diospyros natalensis* with turning up, resulting in a leaning stem base and upright stem (b).

Dead but leaning primary tree stems were at different stages of decomposition. Trees that had undergone turning up were identified from their bow-shaped stem and their inclined base (Figure 1b). For most leaning trees, turning up resulted in the crown occupying the same crown position it would have had had the stem been straight; i.e. directly above the tree bole. For a few trees that had very large angles of inclination, turning up did not recover the crown position but nevertheless restored the vertical orientation of the growing tip.

Stem inclination was categorized into two classes: leaning trees with an inclination >10° from the vertical, and non-leaning trees with an inclination ≤10° from the vertical (Yamada & Suzuki 2004). Probably because not enough time had elapsed between their leaning and the time of the survey, some leaning trees had neither resprouted nor turned upward to regain vertical orientation. These were recorded as no response trees. Some trees sprouted due to factors other than leaning (Nzunda *et al.* 2007).

The probabilities of turning up, resprouting and of having a dead primary stem were calculated as a proportion of leaning individuals of a species. The probability of leaning for a species was calculated as the ratio of the number of leaning trees to the total number of trees of the species in the sample. The total number of individuals of a species in the sample was used as a measure of abundance of the species in the forest. The logit transformation was applied to the probabilities of turning up and of a tree having a dead primary stem. A value of one was added to the probabilities of turning up before logit-transformation because two cases of the variable had a value of zero. Species stem counts were log-transformed. Linear regression was used to analyse the relationship between leaning, turning up, resprouting, dead primary stem and the abundance of individuals in the forest. Although phylogenetic influence affects any interspecific analysis, meaningful interspecific analysis can be performed without phylogenetic analysis, in this case because the species are examined as independent entities (Westoby *et al.* 1995).

To analyse the effect of degree of leaning, tree size, slope, dune position and root exposure by erosion on the incidence of vertical reorientation among trees we used logistic regression (binomial response variable and logit link function). Model selection was achieved by using Akaike's Information Criterion (AIC) (Burnham & Anderson 2001). The model with the lowest AIC was taken as the best fit to the data. Where models differed by less than 2 AIC

units they were regarded as equivalent and the model with the fewest parameters was chosen. In addition, we calculated the Akaike weight, w_i, for each model (Burnham & Anderson 2001), which provides an approximate probability that a given model is in fact the best of the candidate set.

Only species that had at least 50 individuals in the sample were used in the analyses (Table 1). Nomenclature follows Coates Palgrave (2002).

RESULTS

Leaning, resprouting, turning up, death of the primary stem and abundance of species

There was a significant negative relationship between the probability of turning up and the probability of resprouting (Figure 2a; $r^2 = 0.40$, P =0.004, n = 19). The likelihood of resprouting was positively correlated to the probability of a dead primary stem (Figure 2b; $r^2 = 0.56$, P = 0.000, n = 19). Most dead primary stems had a small diameter (Table 2), indicating that they were mainly lost during the establishment phase. The relationship between the probability of a stem turning upward and the probability of a dead primary stem was not significant ($r^2 = 0.18$, P = 0.078, n = 19). The probability of leaning was negatively correlated with the probability of a stem turning upward (Figure 2c; $r^2 = 0.44$, P = 0.002, n = 19) and positively correlated with the probability of resprouting (Figure 2d; $r^2 = 0.55$, P < 0.001, n = 19). There was a significant positive relationship between species abundance and their probability of turning up (Figure 2e; $r^2 = 0.23$, P = 0.040, n = 19) and a negative relationship between species abundance and their probability of resprouting (Figure 2f; $r^2 = 0.25$, P = 0.029, n = 19).

Table 1. Sample sizes of tree species in relation to leaning, resprouting, turning up of the stem and whether the primary stem is dead or not.

Species	Family	Resprouting without leaning	Leaning trees					Total number of trees
			Resprouting	Turning up	No response	Total	Dead primary stem	
Diospyros natalensis	Ebenaceae	25	81	137	194	412	14	733
Drypetes natalensis	Putranjivaceae	35	161	43	88	292	53	429
Ochna natalitia	Ochnaceae	45	79	59	98	236	25	392
Diospyros inhacaensis	Ebenaceae	7	17	29	30	76	6	214
Celtis africana	Celtidaceae	44	55	11	40	106	6	209
Teclea gerrardii	Rutaceae	8	39	28	59	126	4	183
Mimusops caffra	Sapotaceae	9	61	24	30	115	17	174
Euclea racemosa	Ebenaceae	4	105	10	21	136	42	156
Eugenia woodii	Myrtaceae	8	56	6	33	95	9	140
Dovyalis longispina	Salicaceae	7	89	12	2	103	24	122
Deinbollia oblongifolia	Sapindaceae	5	26	9	39	74	6	116
Acacia karroo	Fabaceae	1	26	0	35	61	6	99
Gymnosporia nemorosa	Celastraceae	4	52	0	15	67	20	84
Tricalysia sonderiana	Rubiaceae	3	48	4	8	60	7	70
Pavetta gardeniifolia	Rubiaceae	2	8	7	29	44	2	63
Sideroxylon inerme	Sapotaceae	3	42	3	7	52	9	62
Erythroxylum emarginatum	Erythroxylaceae	5	34	1	11	46	5	59
Strychnos gerrardii	Loganiaceae	3	33	5	2	40	6	56
Scolopia zeyheri	Salicaceae	1	16	10	4	30	4	53
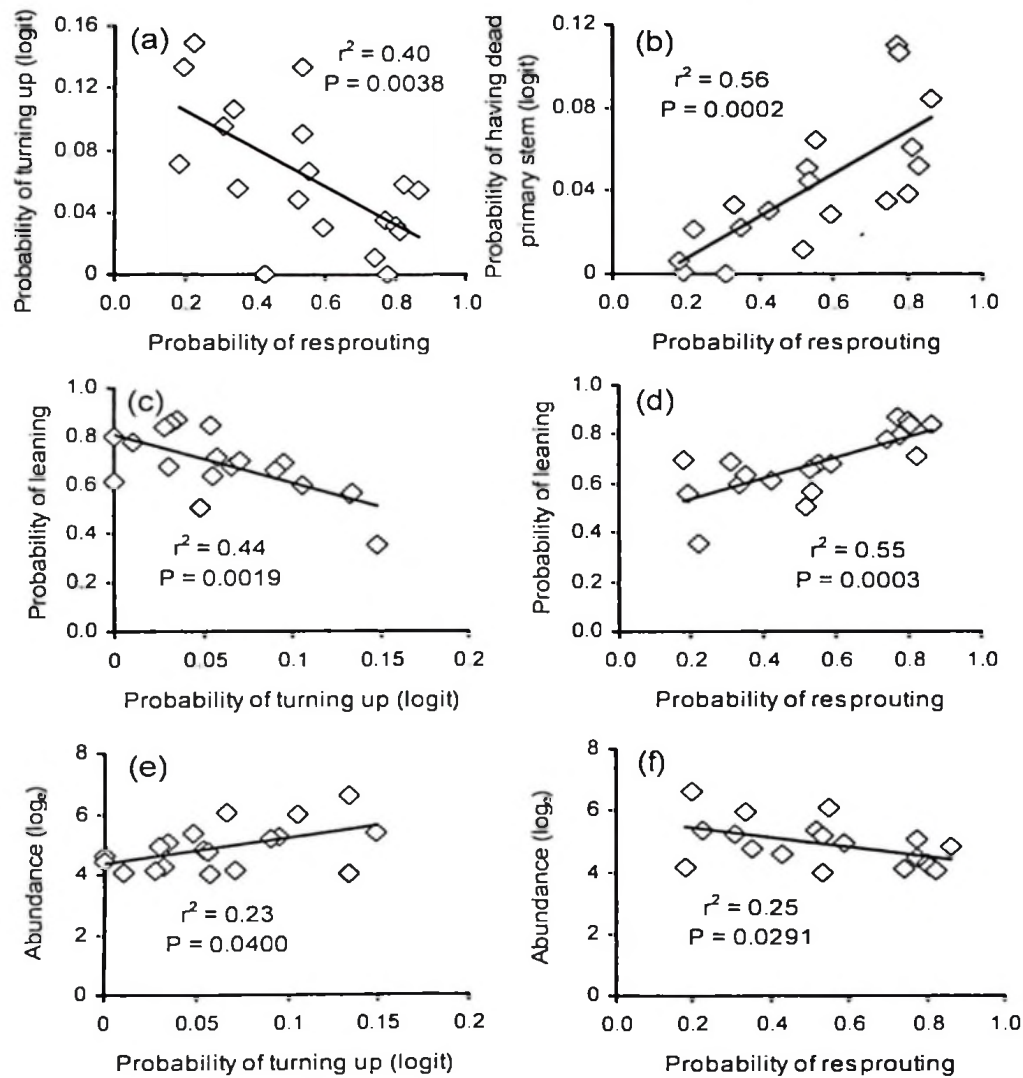
Figure 2. Relationships between probability of resprouting and probability of turning up and their correlates. The probability of turning up decreased with increasing probability of resprouting (a). Probability of having dead primary stem increased with increasing probability of sprouting (b). Probability of leaning decreased with increasing probability of turning up (c). Probability of leaning increased with increasing probability of resprouting (d). Abundance increased with probability of turning up (e). Abundance decreased with increasing probability of resprouting (f).

Table 2. Frequency distribution of diameters of dead leaning stems.

Species	Diameter class (cm)					
	<10	10-19	20-29	30-39	40-49	≥50
Diospyros natalensis	7	6	1			
Drypetes natalensis	24	20	5	3	1	
Ochna natalitia	15	7	3			
Diospyros inhacaensis	5	1				
Celtis africana	4	1		1		
Teclea gerrardii	1	2	1			
Mimusops caffra	6	4	3	1	2	1
Euclea racemosa	12	22	6	2		
Eugenia woodii	6	2	1			
Dovyalis longispina	9	9	5	1		
Deinbollia oblongifolia	4	2				
Acacia karroo	4	2				
Gymnosporia nemorosa	12	7	1			
Tricalysia sonderiana	4	3				
Pavetta gardeniifolia	2					
Sideroxylon inerme	6	3				
Erythroxylum emarginatum	5					
Strychnos gerrardii		2	3	1		
Scolopia zeyheri	4					

Influence of tree and site factors on response of leaning trees

The best-fit logistic regression model (w_i = 0.73, AIC = 1458) included the factors erosion intensity, dune position and the angle of leaning (Table 3). Slope steepness did not enter the best-fit model. Turning up of the stem was more likely for small deviations from the vertical than for large angles of inclination of a stem from the vertical. Small trees were on average 10% more likely to reorient vertically than big trees. Small trees growing on forested dune slacks (not dominated by *A. karroo* trees) and seaward-facing dune slopes were the most likely (52.3 and 62.5% likelihood, respectively), and small trees on dune crests and the landward-facing slopes the least likely (9.8% and 31.3% likelihood, respectively) to undergo turning up. *Acacia karroo* trees that dominated previously disturbed dune slacks were least likely to turn upwards (Figure 3). Trees with roots exposed by erosion were 22% less likely on average to reorient vertically than trees without exposed roots.

Table 3. Parameter estimates for the logistic regression of turning up of stems on site and tree factors and variables. The model was an excellent fit to the data ($\chi^2 = 19.3$, P<0.001).

Parameter	Estimate	SE	t	P
Constant	-0.218	0.256	-0.85	0.394
Erosion	-0.902	0.259	-3.49	<0.001
Landward slope	-0.322	0.324	-0.99	0.320
Seaward slope	0.557	0.235	2.37	0.018
Dune slack without *Acacia karroo*	0.891	0.264	3.38	<0.001
Dune slack dominated by *Acacia karroo*	-1.758	0.479	-3.67	<0.001
Big tree size	-0.329	0.129	-2.54	0.011
Inclination	-0.025	0.004	-6.56	<0.001
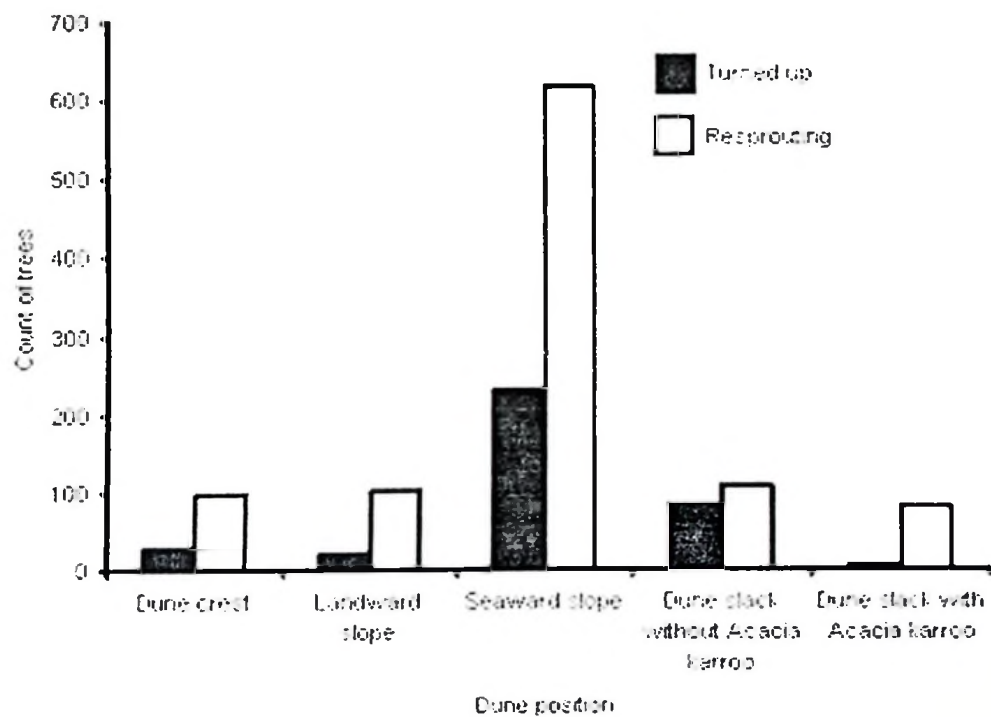
Figure 3. Frequency distribution of resprouting and turning up of stems of leaning trees by dune position.

DISCUSSION

The negative relationship between the likelihood of turning up of a stem and the likelihood of resprouting supports the hypothesis that resprouting and the ability to reorient vertically are alternative strategies for enhancing individual survival. As found in other studies, a high likelihood of resprouting was associated with a high likelihood of losing the primary stem (Yamada & Suzuki 2004), causing high stem turnover for the individual but nevertheless ensuring individual persistence in the long term (Bond & Midgley 2001).

The negative relationship between the prevalence of resprouting and species abundance and the positive relationship between the prevalence of turning up of stems and species abundance may be explained by the costs and benefits of the two alternative responses to leaning. Costs of sprouting include allocation of resources to storage (Bell 2001, Chidumayo 1992, McPherson & Williams 1998) and buds (Bellingham & Sparrow 2000, Kruger *et al.* 1997, Midgley 1996, Vesk & Westoby 2004c), which result in restricted growth rate and seedling recruitment due to low seed set. If resource remobilisation is used (Sakai & Sakai 1998, Sakai *et al.* 1997), the structural part and the non-structural portion that are not remobilized represent a wasted investment. Other costs include delayed reproductive maturity because sprouts take time to replace the primary stem and sprout mortality due to shading (Borchert 1976, del Tredici 2001, Fontanier & Jonkers 1976, Ohkubo *et al.* 1996, Paciorek *et al.* 2000). These costs are important because the abundance of individuals in a population is exponentially related to the number of surviving individuals, number of recruits and delay to reproduction (Crawley 1986). Consequently, fewer individuals are expected of species that typically resprout (those that rely on vegetative reproduction) compared with those species

that are typically seeders (Bond & Midgley 2001). This prediction is supported by our findings.

In addition, successful sprouting causes multi-stemming in individuals, which diverts resources from vertical growth and limits tree height (Chamberlin & Aarssen 1996, Kruger *et al.* 1997, Midgley 1996). Resprouting and multi-stemmed plants would have a competitive advantage over neighbouring single-stemmed plants, but only in unproductive or disturbed sites where chances are low that seedlings will survive, or where there is little risk that multi-stemmed trees will be overtopped by single-stemmed seeders (Bond & Midgley 2001, Grime 1977, Midgley 1996). Thus, depending on the severity of disturbance and considering the costs and benefits of resprouting and turning up, it would be advantageous for an individual to reorient its stem if it can and only resprout if it cannot.

The ability of stems to turn upwards may depend upon other traits that enhance persistence, such as higher wood density, shade tolerance, defence against herbivory and greater size (Claussen & Maycock 1995, Loehle 2000). These traits result in low growth rate (Falster & Westoby 2005, Loehle 1988, 2000) and poor competitive ability in the early successional stages of a forest (Falster & Westoby 2005). The forest in this study was predominantly at a late-successional stage. In addition to the latter, the prevalence of turning up of stems among the studies species indicates that although disturbance is an important driver of forest physiognomy it is likely of constant but relatively low intensity.

Several factors may explain the relationship between the probability of leaning, resprouting and turning up of stems. Buttressed roots prevent leaning (Crook *et al.* 1997) and resultant sprouting (Yamada & Suzuki 2004). A poorly developed taproot and extensive lateral roots that are adapted to extract nutrients from shallow steep sites may result in higher susceptibility to leaning (Sakai *et al.* 1997). However, lateral roots may be adapted for

mechanical support and hence prevent leaning (Crook *et al.* 1997). A strong root system would also provide a leaning stem with better mechanical support for turning up. In our study, turning up of stems was mostly associated with disturbances that caused small angles of deviation of the main stem from the vertical. Highly eroded root systems that caused leaning of the main stem were more likely to result in resprouting than in turning up of the main stem. Leaning has been considered a passive result of disturbance in this study although it is possible for trees to actively use leaning to their adaptive advantage (Ishii & Higashi 1997).

Smaller trees were more likely to turn up than bigger trees probably because bigger trees had no clear leader to respond due to decreasing apical dominance with tree growth (Ng 1999). To enhance survival, disturbed trees have the option to reorient their main stem rather than resprouting. Disturbance severity should determine the sprouting (Bellingham & Sparrow 2000) and stem reorientation response. The costs of resprouting can be considerable where, as found in our study, resprouting often is associated with lost investment due to the death of the primary stem (Sakai & Sakai 1998, Sakai *et al.* 1997, Yamada & Suzuki 2004). A stem that is too disturbed to survive ensures survival of the individual by resprouting. Thus, it follows that where a stem is not severely disturbed (by leaning and/or root exposure) equal survivorship can be achieved by avoiding costly resprouting and turning upward. We predict that turning up of stems should play an important role in other ecosystems that are affected by disturbance factors that make trees lean (Sakai & Sakai 1998, Yamada & Suzuki 2004, Yamada *et al.* 2001).

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Chapter 4

Resprouting enhances seedling persistence in a subtropical coastal dune forest

Abstract

In theory, resprouting enables species with low reproductive output (i.e., few seedlings) to persist. The advantage conferred by seedling sprouts on tree species persistence was evaluated in a subtropical coastal dune forest in South Africa. Species with a higher frequency of seedling sprouts demonstrated greater persistence as evidenced by a larger proportion of seedlings > 1 year old and a larger seedling bank than species with few seedling sprouts. Resprouted seedlings had a larger basal diameter than true seedlings. Although resprouting resulted in the maintenance of multiple stems in some seedlings, the proportion of multi-stemmed seedlings was low. Multi-stemming was not a favoured form of seedling growth except in one species that occupied relatively open sites. Despite the apparent difference among species in resprouting ability, we found that seedling resprouting was not phylogenetically constrained. These results demonstrate that seedling sprouts form an important component of seedling banks in coastal dune forest.

Key words: multi-stemming, persistence niche, regeneration, seedling bank

Introduction

Seedling resprouting is the production of a new shoot following damage to the original shoot arising from seed (Del Tredici, 2001). The new shoot may be produced by the seed that produced the original shoot (Harms & Dalling, 1997) or by the stump of an established seedling (Powell & Tryon, 1979; Hara, 1987). Here we examine resprouting by established seedlings. Seedlings that have resprouted are referred to as seedling sprouts whereas those that have not resprouted are called true seedlings (Powell & Tryon, 1979; Hara, 1987). The ability of seedlings to produce serial sprouts that enhance individual persistence on the forest floor is important for the survival and regeneration of many tree species (Bond & Midgley, 2001). Seedling resprouting and resultant persistence contribute to the formation and maintenance of seedling banks (Grime, 1979). Seedling banks are particularly important for regeneration of tropical forest trees because most species have poor seed dormancy and do not maintain seed banks (Fenner & Thompson, 2005).

Seedling sprouts usually have larger and older rootstocks than true seedlings of the same shoot size (Hara, 1987). The larger rootstock enables these seedlings to resprout recurrently and hence achieve greater longevity than true seedlings (Hara, 1987). The longer lifespan of seedling sprouts ensures the persistence of the seedling bank so that seedlings can take advantage of appropriate growing conditions when they occur (Hara, 1987). When an opportunity for growth arises, for instance by understorey gap formation, seedling sprouts grow faster than true seedlings (Hara, 1987). Hence, understanding the composition and structure of seedling banks and the ecological importance of true seedlings versus seedling sprouts provides a better understanding of the regeneration dynamics of forest tree species.

Some seedlings exhibit a multi-stemmed growth form either because of sprouting (Hara, 1987) or as a normal growth habit of the species (Vesk & Westoby 2004). One advantage of maintaining multiple shoots is that the plant covers a larger area, hence captures more resources, and thus has an increased competitive ability (Chamberlin & Aarssen, 1996; Bellingham & Sparrow, 2000). On the other hand, multi-stemming can restrict the overall height of a plant due to resources being divided among many stems and there is mechanical limitation caused by non-vertical stem orientation (Chamberlin & Aarssen, 1996; Kruger, Midgley & Cowling, 1997). Therefore, multi-stemming in seedlings is only advantageous under conditions of limited resources where multi-stemmed individuals are not likely to be rapidly over-topped by competing single-stemmed species (Bellingham & Sparrow, 2000). In the coastal dune forests of KwaZulu-Natal studied here, a high proportion of adult individuals from most tree species are multi-stemmed and we conclude that multi-stemming is an emergent property of the tree-disturbance interaction and not a species trait (Nzunda, Griffiths & Lawes, 2007a).

The objectives of this study were to: (i) determine and compare the frequency, density, and abundance of true seedlings and seedling sprouts of different tree species of different ages; (ii) examine the effect of resprouting on seedling persistence; (iii) compare the frequency of multi-stemmed seedlings with multi-stemming in adult trees across the species and (iv) test whether seedling resprouting is phylogenetically constrained.

Materials and methods

Study area

The study was conducted in subtropical Indian Ocean coastal dune forest at Cape Vidal (28°05'32"S, 32°33'40"E). Cape Vidal is part of the Greater St. Lucia Wetland Park, a world heritage site under the jurisdiction of Ezemvelo KwaZulu-Natal Wildlife. The mean annual rainfall is approximately 1200 mm, spread evenly throughout the year (range 80 mm – 90 mm per month) (Schulze 1997). Average minimum and maximum temperature is 17.8°C in July and 25.6°C in January respectively (mean annual temperature is 21.5 °C). The topography consists of steep and high (up to 146 m a.s.l.) longitudinal sand dunes that are parallel to the coastline.

The Cape Vidal dune forest forms part of a narrow strip of Indian Ocean coastal forest (0.1-4 km wide) extending as a contiguous belt for 240 km along the KwaZulu-Natal coast (Tinley, 1985). The tree community is dominated by *Diospyros natalensis, Mimusops caffra, Drypetes natalensis* and *Ochna natalitia* (Moll, 1972; Venter, 1976). *Carissa bispinosa, Allocassine laurifolia, Pancovia golungensis* and *Erythroxylum emarginatum* are among the species that form the shrub layer. The frequency of shrubs in the forest is low due to the effect of *I. woodii*, which is a dominant and suppressive herb covering 65-90% of the forest understorey (Griffiths, Lawes & Tsvuura, 2007). This acanthaceous species may grow to 3 m tall and its canopy can become so dense that less than 1% of available sunlight filters through to the forest floor where other smaller plants and tree seedlings grow (Griffiths *et al.*, 2007). *I. woodii* is monocarpic, with synchronous dieback after flowering over large areas of the forest.

Because of its dominance, *I. woodii* affects tree regeneration dynamics at Cape Vidal (Griffiths *et al.,* 2007).

Moll (1972) described the soil for this forest type as unstructured brown sand with a limited amount of humus. The mean moisture content of the topsoil at field capacity is 12.7% of the dry mass, while the permanent wilting point is 10.8% of the dry mass. Hence, there is very low moisture available for plant growth. Wilting of seedlings and herbs is detectable even after short dry spells and seedlings may resprout to recover from wilting. The pH of the forest topsoil ranges from 6.7 to 7.4 and the organic matter content varies from 4.6 to 6.2 per cent of the dry mass of the soil.

Herbivores including hippopotamus (*Hippopotamus amphibious*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalophus natalensis*) and bush pig (*Potamochoerus porcus*) browse on forest floor vegetation including seedlings (Boyes, 2006), making resprouting particularly important for long-term seedling survival (Harms & Dalling, 1997).

Sampling, measurement and data analysis

Tree seedlings were sampled in seventy-two 2 × 2 m randomly distributed quadrats. All tree seedlings in the quadrats were uprooted and brought to the laboratory for identification, classification, and measurement. Seedlings were classified by their year of germination (i.e., the current year or the previous years), and as true seedlings or seedling sprouts. Seedling sprouts were identified by the scar left by the replaced shoot (Fig. 1). The number of times a seedling had resprouted was determined by counting scars left by the replaced shoots. For all

seedlings, basal diameter was measured at ground level. Regression analysis and analysis of variance were used to test the effect of resprouting, age (current year or previous years), and species on variation of basal diameter.
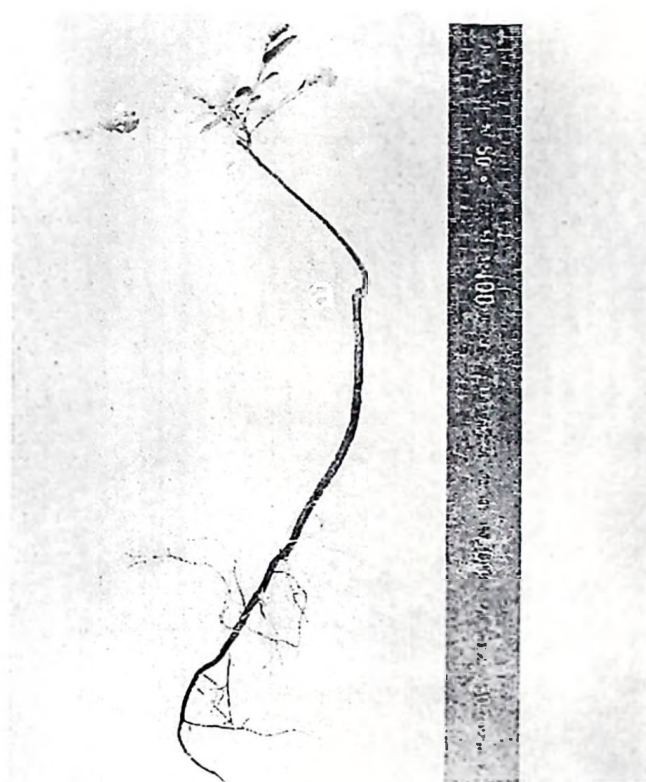
Fig 1 A *Clausena anisata* seedling sprout showing two scars left by replaced terminal shoots (a and b). The two scars show that the seedling resprouted twice

Data on multi-stemming of trees with circumference at breast height (cbh) > 5 cm were obtained from a transect survey conducted to determine multi-stemming characteristics in the study forest; using 20 transects measuring 300 m × 5 m (Nzunda *et al.*, 2007a). Nomenclature follows Coates Palgrave (2002).

To test whether seedling resprouting was phylogenetically constrained, phylogenetic autocorrelation (PA; Luh, Gittleman & Kot, 1994) was used. Two criteria determined significance: (i) at least one Z(r)-value greater than 1.96 (i.e., observed PA at $p < 0.05$) and (ii) a correlogram that was high at lower taxonomic ranks with a decay to negative autocorrelation at higher taxonomic ranks.

Results

Size, frequency, density and abundance of seedlings

The size, frequency, density and abundance of seedlings varied among species (Table 1). The mean basal diameter ranged from 0.5±0.3 mm for *Celtis africana* to 3.1±1.7 mm for *Drypetes natalensis*. This size range is consistent with that reported in a study on seedling resprouting by Hara (1987). *Diospyros natalensis* had the highest frequency of occurrence (occurring in 69 quadrats out of 72), seedling density (ten seedlings per quadrat), and abundance. Most of the remaining species had a density of < 1 seedling per quadrat, except *Teclea gerrardii, M. caffra* and *Clausena anisata* (Table 1). *T. gerrardii* and *M. caffra* seedlings occurred in more than half the sampled quadrats. *C. anisata* had higher seedling density than *M. caffra* although the latter occurred in more quadrats than the former and were more uniformly distributed than *C. anisata* seedlings. Among species that occurred in more than 20 quadrats, *Diospyros natalensis, M. caffra, Celtis africana* and *Allophylus natalensis* had more new (current year) seedlings than seedlings from previous years, whereas the reverse was true for *T. gerrardii, Pavetta gardeniifolia, Diospyros inhacaensis, Ochna natalitia, C. anisata* and *Drypetes natalensis*. Species with more new seedlings were also more likely to have more seedlings

from previous years than those species with fewer new seedlings ($R^2 = 0.42$, $F_{1,8} = 5.83$, $P = 0.042$).

Table 1 Size, frequency, density and abundance of seedlings based on 72 randomly located 2 × 2 m quadrats. Numbers in brackets are % of total.

Species	Basal diameter, mm (mean±SD)	Quadrat frequency	Seedling density per 4 m² (mean±SD)	Current year seedlings	Previous years seedlings
Diospyros natalensis	1.2±0.7	69	9.99±8.20	424 (59.0)	295 (41.0)
Teclea gerrardii	1.8±0.7	63	6.65±8.74	112 (23.4)	367 (76.6)
Mimusops caffra	1.0±0.1	40	1.76±2.36	122 (96.1)	5 (3.9)
Pavetta gardeniifolia	2.7±2.1	30	0.63±0.90	14 (31.1)	31 (68.9)
Celtis africana	0.5±0.3	25	0.72±1.57	41 (78.8)	11 (21.2)
Diospyros inhacaensis	1.7±0.6	24	0.58±1.29	7 (16.7)	35 (83.3)
Ochna natalitia	1.4±0.6	24	0.51±0.90	7 (18.9)	30 (81.1)
Clausena anisata	1.6±1.2	23	2.11±5.36	44 (28.9)	108 (71.1)
Drypetes natalensis	3.1±1.7	22	0.60±1.16	6 (14.0)	37 (86.0)
Allophylus natalensis	0.8±0.5	21	0.97±3.02	57 (81.4)	13 (18.6)
Euclea racemosa	0.9±0.4	16	0.26±0.56	7 (36.8)	12 (63.2)
Strychnos gerrardii	2.3±0.5	12	0.56±1.64	3 (7.5)	37 (92.5)
Dovyalis longispina	1.7±2.3	9	0.18±0.59	4 (30.8)	9 (69.2)
Acacia karroo	1.2±0.5	7	0.11±0.36	5 (62.5)	3 (37.2)
Canthium ciliatum	0.7±0.2	5	0.10±0.38	6 (85.7)	1 (14.3)
Sideroxylon inerme	1.4±0.5	4	0.10±0.42	1 (14.3)	6 (85.7)
Erythroxylum emarginatum	2.7±1.0	3	0.06±0.29	0 (0.0)	4 (100.0)
Gymnosporia nemorosa	0.7±0.0	3	0.71±5.66	51 (100.0)	0 (0.0)
Cordia caffra	1.7±1.4	2	0.07±0.42	3 (60.0)	2 (40.0)
Mystroxylon aethipicum	1.5±0.9	2	0.04±0.26	2	1
Syzygium cordatum	1.2±0.8	2	0.04±0.26	2	1
Ziziphus mucronata	1.8±1.1	2	0.03±0.17	2	0
Clerodendrum glabrum	1.1	1	-	1	0
Erythrococca berberidea	1.0	1	-	1	0
Eugenia woodii	0.7	1	-	1	0
Scolopia zeyheri	1.3	1	-	0	1
Tricalysia sonderiana	3.0	1	-	0	1

Resprouting and seedling persistence

Ochna natalitia had the highest proportion (37.8%) of seedlings that had resprouted once whereas *P. gardeniifolia* had the highest proportion (51.1%) of seedlings that had resprouted more than once (Table 2). Some seedlings had resprouted as many as six times. Of the species occurring in more than 20 quadrats, seedlings of *M. caffra* and *C. africana* did not resprout more than once. The proportion of current year seedlings that had resprouted was generally

low and restricted to a single resprouting event. The mean frequency of resprouting of a seedling was positively correlated with the proportion of older (previous years) seedlings in a species' seedling bank ($R^2 = 0.61$, $F_{1,8} = 12.69$, $P = 0.007$) and suggests that serial resprouting enhanced seedling persistence.

Further evidence of the effect of resprouting on seedling persistence was provided by comparing the basal diameter of seedling sprouts and true seedlings. Individual seedlings that had sprouted more frequently had larger basal diameters (Fig. 2). Sprouted seedlings had significantly larger basal diameters than true seedlings and this difference increased with the age of the seedling ($F_{1,1862} = 7.44$, $P = 0.006$; Fig. 3) and this trend was consistent across species ($F_{18,1862} = 10.09$, $P < 0.0001$).

Multi-stemmed seedlings

Most species had a low proportion of multi-stemmed seedlings (Table 2), which suggests that multi-stemming is not a favoured strategy for seedling growth. An exception was *P. gardeniifolia* in which 24.4% of seedlings were multi-stemmed. In contrast, adults of *P. gardeniifolia* in this forest were mainly single stemmed and 14.1% of trees with cbh > 5 cm were multi-stemmed (Table 2). For other species, the frequency of multi-stemmed trees with cbh > 5 cm was much higher than for their seedlings (Table 2).

Phylogenetic influence

There was no phylogenetic pattern in the expression of resprouting. The trait occurred in tree species regardless of their taxonomic placement. Furthermore, when analysed by phylogenetic autocorrelation, we found all Z-values to be less than 1.96 and the correlogram did not decrease to negative autocorrelation at higher taxonomic ranks (data not shown).

Table 2 Seedling resprouting and multi-stemming for species with quadrat frequency > 20. Numbers of individuals for seedlings are shown in Table 1. Figures in brackets are number of individuals used in the calculation of percentage

Species	All seedlings			Current year seedlings		Previous years seedlings		% Multi-stemmed	
	% Sprouted once	% Sprouted more than once	Maximum number of times sprouted	% Sprouted once	% Sprouted twice	% Sprouted once	% Sprouted more than once	All seedlings	Trees with cbh > 5 cm
Diospyros natalensis	15.4	10.4	5	1.7	0	35.3	25.4	0.8	14.5(733)
Teclea gerrardii	14.6	4.6	4	2.7	0	18.3	6.0	1.5	25.7(183)
Mimusops caffra	1.6	0	1	0.8	0	20.0	0	0	40.2(174)
Pavetta gardeniifolia	11.1	51.1	6	0	0	16.1	74.2	24.4	14.1(71)
Celtis africana	7.7	0	1	0	0	36.4	0	1.9	47.4(209)
Diospyros inhacaensis	16.7	28.6	3	0	0	20.0	34.3	0	11.2(214)
Ochna natalitia	37.8	13.5	3	14.3	14.3	43.3	13.3	0	31.6(392)
Clausena anisata	21.1	17.1	5	9.1	0	25.9	24.1	2.0	33.3(9)
Drypetes natalensis	30.2	30.2	4	16.7	0	32.4	35.1	2.3	45.7(429)
Allophylus natalensis	20.0	5.7	2	14.0	1.8	46.2	23.1	0	71.0(31)
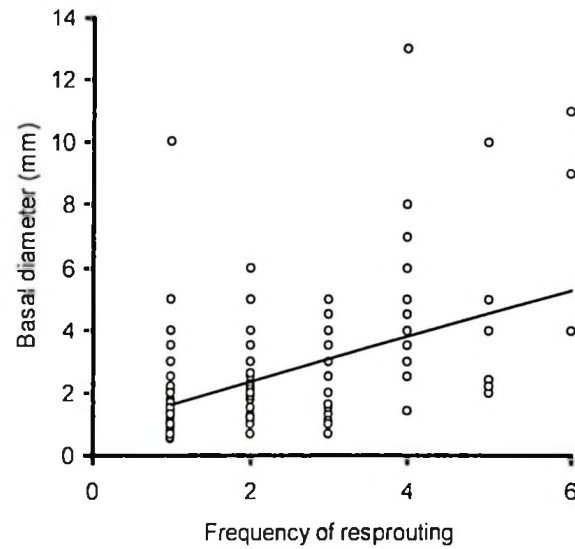
Fig 2 Basal diameter of seedling sprouts increased significantly with the frequency of resprouting of a seedling ($\ln y = 0.19 + 0.26x$, $R^2 = 0.28$, $F_{1,499} = 197.55$, $P < 0.001$)
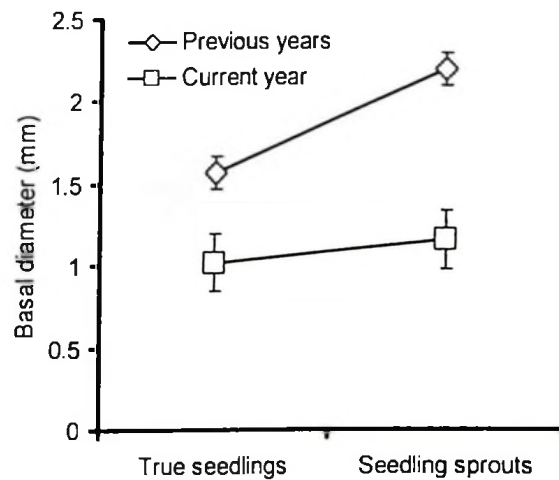
Fig 3 Seedling sprouts had larger basal diameters than true seedlings and this difference increased with the age of the seedling ($F_{1,1862} = 7.44$, $P = 0.006$). Bars show standard error about the mean

Discussion

Assuming basal diameter is proportional to seedling age, resprouting appears to enable seedling sprouts to survive longer than true seedlings, as true seedlings were restricted to smaller basal diameter sizes. For the growing conditions at the study site, the likelihood of a seedling attaining relatively large size without resprouting is low. The fact that the proportion of seedling sprouts among the older seedlings was higher than that among the current year's seedlings supports this observation.

A higher percentage of *Diospyros natalensis* seedlings resprouted more than once as compared with *C. africana* (Table 2). *Diospyros natalensis* seedlings may need to persist more through resprouting than seedlings of *C. africana* because the former is a shade-tolerant species whose seedlings grow under the canopy, whereas the latter is a light-demanding species with seedlings that grow in open sites. Seedlings of shade-tolerant species have evolved means to survive damage because they are more likely to suffer damage under the canopy than seedlings of light-demanding species that grow in the open (Putz & Brokaw, 1989).

The high frequency of resprouting and multi-stemming for *P. gardeniifolia* seedlings may play an important role in maintaining populations of this species. *P. gardeniifolia* is a small tree that occupies relatively open sites in the forest. Sprouting and multi-stemming enable seedlings of *P. gardeniifolia* to survive under the canopy of trees and understorey cover of the herb *I. woodii*. When disturbance occurs these seedlings occupy the gaps in the understorey cover. High levels of seedling multi-stemming in addition to sprouting has been reported for *Fraxinus lanuginosa* and several *Acer* species that occur in canopy gaps of beech-dominated forests in Japan (Hara, 1987). Seedling sprouts of these species have to wait for

appropriate growth conditions to reach the adult stage under closed forest canopy. As there are low levels of seedling multi-stemming for dominant canopy tree species at Cape Vidal and elsewhere (Hara, 1987), multi-stemming may be a strategy for seedlings of trees occupying canopy or understorey gaps. These multi-stemmed species only have an advantage in situations where resources are limited and the gaps cannot be easily occupied by fast growing reseeders that would over-top and out-compete resprouters (Bellingham & Sparrow, 2000; Bond & Midgley, 2001).

Resprouting in seedlings was not phylogenetically constrained. This is similar to the condition of multi-stemming in adult trees, which was also not phylogenetically constrained (Nzunda *et al.*, 2007a). The lack of phylogenetic control on resprouting of seedlings and multi-stemming of adult trees indicates that the two processes are under environmental control. However, resprouting in seedlings did not result in seedling multi-stemming to the same level as was observed for trees with cbh > 5 cm. This suggests that the two traits potentially serve subtly different functions.

Generally, seedlings resprout to survive herbivory and other disturbances that have a clipping effect (Vesk, 2006), whereas resprouting and multi-stemming for adult trees in systems with unstable substrate acts mainly as insurance against leaning and erosion (Sakai & Sakai, 1998; Nzunda *et al.* 2007a, b).

Seedling resprouting serves to enhance the survival of the seedling so that it can capture the regeneration niche opportunities in a forest, whereas resprouting (and multi-stemming) of adult trees ensures the persistence of already established individuals (i.e., maintenance of the persistence niche). Hence, seedling resprouting increases the survival of newly-established individuals giving them a competitive edge over other species vying for access to space on the forest floor. On the other hand, resprouting in adult trees increases the

likelihood that an already established individual will maintain its position, usually in the face of disturbance effects and other environmental stressors (Bond & Midgley, 2001; Nzunda *et al.*, 2007a). Although its ecological significance is great, seedling resprouting is less conspicuous than resprouting by mature trees (del Tredici, 2001).

Acknowledgements

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Chapter 5

Sprouting by remobilisation of above-ground resources ensures persistence after disturbance of coastal dune forest trees

Summary

1. Resprouting in woody plants is a trait that facilitates persistence in disturbance-prone environments. Patterns of allocation of resources for resprouting may depend on the severity of disturbance to which the plants are adapted. Fire-adapted plants allocate more resources to below-ground structures for resprouting after destruction of above-ground structures. However, plants that resprout in response to disturbances where above-ground structures survive, may remobilise above-ground resources for resprouting.

2. In coastal sand dunes, stem leaning and partial uprooting of trees result in high frequency of resprouting (38.9% of individuals; 90.6% of species). We tested whether 'good' and 'poor' resprouters differed in allocation to root biomass and root carbohydrate reserves. Species were assigned to categories of resprouting ability based on the frequency of multi-stemmed individuals in the local population. To control for phylogenetic effects we contrasted poor and good resprouter species pairs from three families.

3. We tested whether plants stored more reserves in roots or stems and whether above-ground resources were remobilised for resprouting. The latter was measured from the

number and dry mass of sprouts produced by trees cut to stump heights of 10 cm and 150 cm above ground level.

4. Good resprouters had larger seedling root:shoot ratios and higher stem and root carbohydrate concentrations than poor resprouters. Both good and poor resprouters maintained higher carbohydrate concentrations in stems than in roots.

5. For both good and poor resprouters, 150-cm stumps produced more sprouts than 10-cm stumps. At each stump height, good resprouters produced more sprouts than poor resprouters.

6. Resource allocation in coastal dune trees appears to be a bet-hedging strategy. After low-severity disturbances, resprouting occurs by remobilization of above-ground resources. Below-ground resources may be more costly to remobilise but may allow recovery from occasional more severe disturbances.

Key-words: biomass allocation, carbohydrate reserves, disturbance severity, sprouting ability, root:shoot ratio

Introduction

Resprouting is a trait that facilitates persistence in disturbance-prone environments. Resprouting ability and the relative dominance of resprouters depends in large part on the severity of disturbance to the above-ground biomass and whether resources in below and remaining above-ground structures can be mobilised (Knox & Clarke 2005). In fire-prone ecosystems, resprouters allocate more resources to root than shoot biomass and store larger carbohydrate reserves for resprouting after fire than do reseeders (Bowen & Pate 1993; Knox

& Clarke 2005). Where fire consumes most of the aboveground biomass, the carbohydrates necessary for resprouting are often stored in specialised underground structures such as lignotubers and rhizomes (Carr, Jahnke & Carr 1984; James 1984; Desouza, Silka & Davis 1986; Bellingham & Sparrow 2000; Bond & Midgley 2001; Vesk & Westoby 2004).

However, resprouting is not restricted to fire-prone systems (Sparrow & Bellingham 2001; Nzunda, Griffiths & Lawes 2007a, b). Plants may persist by resprouting when only part of the above-ground biomass is damaged by disturbances such as hurricanes and volcanic eruptions (Basnet 1993; Bellingham, Tanner & Healey 1994; Boucher *et al.* 1994; Zimmerman *et al.* 1994; Tsuyuzaki & Haruki 1996). In addition, plants may resprout in response to disturbances that do not damage above-ground biomass, such as low-level winds and substrate instability that cause stem leaning or partial uprooting (Sakai, Ohsawa & Ohsawa 1995; Del Tredici 2001; Yamada, Kumagawa & Suzuki 2001; Yamada & Suzuki 2004; Nzunda *et al.* 2007a, b). Here we examine resprouting response and the allocation of resources to resprouting among trees in a subtropical dune forest, where disturbance does not destroy the above-ground biomass.

The pattern of allocation of resources to resprouting in fire-adapted plants is expected to differ from the pattern in habitats where fire is not an important disturbance (Bond & Midgley 1995; Bellingham & Sparrow 2000). For instance, *Euptelea polyandra*, a tree species that resprouts readily on steep hillslopes in Japanese old-growth temperate forests, lacks the allocation and reserve formation strategies exhibited by fire-prone resprouters (Sakai, Sakai & Akiyama 1997). Sakai *et al.* (1997) hypothesised that *E. polyandra* resprouted using resources remobilised from above-ground parts after leaning or partial uprooting. Hence *E. polyandra* does not need larger root and stem reserves of carbohydrates than the poor resprouters with which it co-exists (Sakai *et al.* 1997; Sakai & Sakai 1998).

Most studies on storage of reserves for resprouting have analysed root reserves only, rather than both root and shoot reserves (Knox & Clarke 2005; Schwilk & Ackerly 2005). These studies have largely been conducted in fire-prone systems where carbohydrate reserves are typically stored in the roots. The few studies that have analysed reserves in both roots and shoots suggest that the reserves in different plant parts could play different roles in determining the resprouting ability of a species depending on the disturbance severity to which resprouting is adapted (Bell, Pate & Dixon 1996; Sakai *et al.* 1997). Where disturbance is for the most part at a low level, occasional severe selection may maintain both above- and belowground reserves to allow maximum flexibility of sprouting response to disturbance.

We explored biomass and carbohydrate reserve allocation patterns for poor and good resprouters in a coastal dune forest, where trees mainly resprout in response to chronic low-severity disturbances that cause leaning and partial uprooting (Nzunda *et al.* 2007a, b). We examined whether good and poor resprouters differed in their seedling root:shoot ratios, and stem and root carbohydrate concentrations. We also conducted an experiment where we cut trees creating stumps in two height classes to determine the effect of the remobilization of above-ground resources on number and biomass of sprouts produced.

We predicted that:

1. If resprouting can be achieved through resource remobilisation from above-ground structures, then good resprouters will not differ from poor resprouters in their root biomass allocation or carbohydrate reserves.

2. If trees subjected to low-severity disturbances resprout primarily by remobilising above-ground resources, taller stumps will produce more sprouts than shorter ones (Sakai & Sakai 1998).

Materials and Methods

STUDY AREA

The study was conducted in subtropical Indian Ocean coastal dune forest at Cape Vidal, South Africa (28°05'32"S, 32°33'40"E). Cape Vidal is part of the Greater St. Lucia Wetland Park. The mean annual rainfall is *c.* 900 mm, spread evenly throughout the year (range 80 mm – 90 mm per month) (Schulze 1997). Mean annual minimum and maximum temperatures are 17.8°C in July and 25.6°C in January respectively, with a mean annual temperature of 21.5 °C. The topography consists of steep (slopes up to 55°) longitudinal sand dunes that are orientated parallel to the coastline. The loose sand substrate, steep slopes, and seasonal winds create a low-level but chronic disturbance regime that make trees susceptible to leaning and partial uprooting (Nzunda *et al.* 2007a, b)

The dune forest at Cape Vidal forms part of a narrow strip of forest (0.1-4 km wide) extending in a contiguous belt for 240 km along the KwaZulu-Natal coast (Tinley 1985). Important tree species in decreasing order include *Diospyros natalensis* (Ebenaceae), *Mimusops caffra* (Sapotaceae), *Drypetes natalensis* (Putranjivaceae), *Celtis africana* (Celtidaceae) and *Ochna natalitia* (Ochnaceae) (Nzunda *et al.* 2007a). The incidence of resprouting, which results in multi-stemmed individuals, is high in this forest, with 38.9% of trees being multi-stemmed (Nzunda *et al.* 2007a). Of 53 species recorded, 48 exhibited multi-stemming (90.6%). Because of the high incidence of resprouting in this forest and variation in resprouting ability among species, this is a good site for examining resource allocation in resprouters.

METHODS

Because most species are capable of both vegetative (resprouting) and sexual reproduction, species were designated as either poor or good resprouters based on their relative frequency of multi-stemmed individuals in the forest (Kruger, Midgley & Cowling 1997; Holness 1998; Nzunda *et al.* 2007a). Poor resprouters in our study differ from non-resprouters in fire-prone ecosystems in that they are not obligate reseeders. The categories of sprouting were matched in three species pairs from three families to control for the effect of phylogeny on resource allocation characteristics (Table 1).

Table 1. Species used in the study. Nomenclature follows Coates Palgrave (2002). Frequency of multi-stemmed individuals from Holness (1998) and Nzunda *et al.* (2007a).

Species	Family	Frequency (%) of multi-stemmed individuals	Resprouting ability
Diospyros natalensis	Ebenaceae	14.5	Poor
Teclea gerrardii	Rutaceae	25.7	Poor
Scolopia zeyheri	Salicaceae	32.1	Poor
Euclea racemosa	Ebenaceae	69.9	Good
Clausena anisata	Rutaceae	33.3	Good
Dovyalis longispina	Salicaceae	78.7	Good

Ten seedlings per species were excavated to their full rooting depth. Seedlings were 10 – 20 cm in height. The seedlings were divided into roots, stems and leaves and oven dried at 70°C for 96 h. Dry mass of the root and shoot portions was determined to 0.001g. Subsamples of root and stem were ground for determination of total non-structural carbohydrate (TNC) concentrations. TNC was not determined for leaves because the levels in leaves fluctuate daily in response to photosynthetic activity and export of starch out of the leaves (Graham *et al.* 2003; Myers & Kitajima 2007).

TNC was measured as the sum of starch and three sugars: fructose, glucose and sucrose (Sakai *et al.* 1997). Starch is the main food and reserve compound in woody plants, while fructose, glucose and sucrose are the most essential assimilation products (Zimmermann & Brown 1971; Sakai *et al.* 1997). Concentrations of fructose, glucose and sucrose were determined using gas chromatography (Varian 3800 Chromatograph, Walnut Creek, CA) based on standard procedures (Sweeley *et al.* 1963; Grob 2001). The concentration of starch was determined as glucose equivalents in the residues of the ethanol extracts (Rose *et al.* 1991; Sakai *et al.* 1997). Starch was extracted and hydrolysed to glucose by perchloric acid (Rose *et al.* 1991). After neutralisation by ammonia solution, the extract was subjected to gas chromatography to determine the glucose concentration.

We then tested the effect of stump height on the number and dry mass of sprouts produced. For each of the six species, 10 trees were cut to a stump height of 10 cm above the ground (hereafter referred to as short stumps) and 10 trees to a stump height of 150 cm (referred to as tall stumps). The 120 trees used in this experiment ranged from 2.5 to 11.1 cm diameter at breast height (d.b.h). Only single-stemmed individuals were used. The number of stumps that resprouted and the number and dry mass of sprouts per stump were determined after one year of growth. Stumps were caged to prevent herbivory by large browsers.

Root:shoot ratio (a measure of relative biomass allocation to roots) and TNC data were analysed using a split-plot design in analysis of variance after ln-transformation. To avoid the risk of incurring Type I errors, multivariate analysis of covariance (MANCOVA) was used to analyse the effect of resprouting, stump height and their interaction on number and dry mass of sprouts per stump simultaneously with stump d.b.h as a covariate. These data were blocked by family. Stump d.b.h was included as a covariate because resprouting ability may depend on tree size (Bellingham *et al.* 1994; Iwasa & Kubo 1997; Yamada & Suzuki 2004). Both number

and dry mass of sprouts were ln-transformed. All data transformations were based on examination of the distribution of model residuals (Kéry & Hatfield 2003). Data were analysed using GENSTAT 9.1. (Lawes Agricultural Trust 2006).

Results

Root:shoot ratios varied according to resprouting category ($F_{1,56}$ = 36.97, P < 0.001). Controlling for the effect of family, seedlings of good resprouters had higher root:shoot ratios than poor resprouters (Fig. 1).
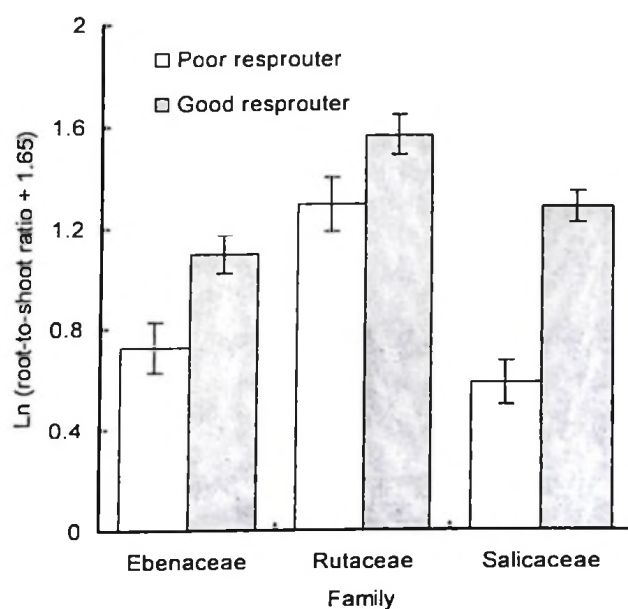
Fig. 1. Mean ± SE of seedling ln root:shoot ratio for pairs of poor and good resprouters within families.

Table 2. Split-plot analysis of variance (ANOVA) for the effect of resprouting (poor or good resprouter) and plant part (root or stem), and their interaction on the concentration of total non-structural carbohydrates. Family (Ebenaceae, Rutaceae or Salicaceae) was used as a blocking factor in the ANOVA. TNC data were ln-transformed.

Source of variation	df	MS	F	P
Family	2	3.46	3.29	
Family.Sprouting				
Sprouting	1	9.81	9.34	0.092
Residual	2	1.05		
Family.Sprouting.Part				
Part	1	6.62	32.21	<0.001
Sprouting × Part	1	0.91	4.44	0.037
Residual	112	0.21		
Overall residual	119			

TNC concentration in seedlings was significantly influenced by resprouting ability and plant part (Table 2). Good resprouters had higher TNC concentrations than poor and stems had higher TNC concentrations than roots (Fig. 2). Good resprouters had higher TNC concentrations in their stems than poor resprouters. For good resprouters, stems had higher TNC concentration than roots whereas there was no difference in TNC concentration between stems and roots for poor resprouters (Fig. 2).

The proportion of stumps that resprouted was greater for good than poor resprouters and for taller than shorter stumps (Fig. 3a). Stumps produced sprouts just below the cut end regardless of stump height. Controlling for the effect of stump d.b.h, there was a significant difference in the number and the dry mass of sprouts produced between resprouting categories
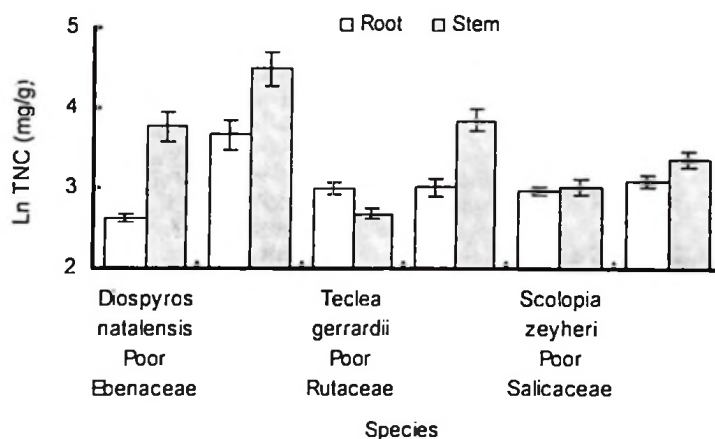
Fig. 2. Mean ± SE of ln total non-structural carbohydrate (TNC) concentration in seedling stems and roots for pairs of poor and good resprouters within families.

and stump heights, but no interaction between resprouting category and stump height (Table 3). Good resprouters mostly produced more sprouts than poor resprouters, while tall stumps generally produced more sprouts than did short stumps (Fig. 3b). For good resprouters, tall stumps produced a significantly greater dry mass of sprouts than any other combinations of sprouting category and short stump height (Fig. 3c). For the mass of sprouts, there was no significant interaction between resprouting category and stump height (Table 3).

Discussion

The pattern of larger seedling root:shoot ratios and root TNC concentration for good resprouters compared with poor resprouters is similar to the pattern of differences in root:shoot ratios and root carbohydrate concentration in fire - prone shrublands between
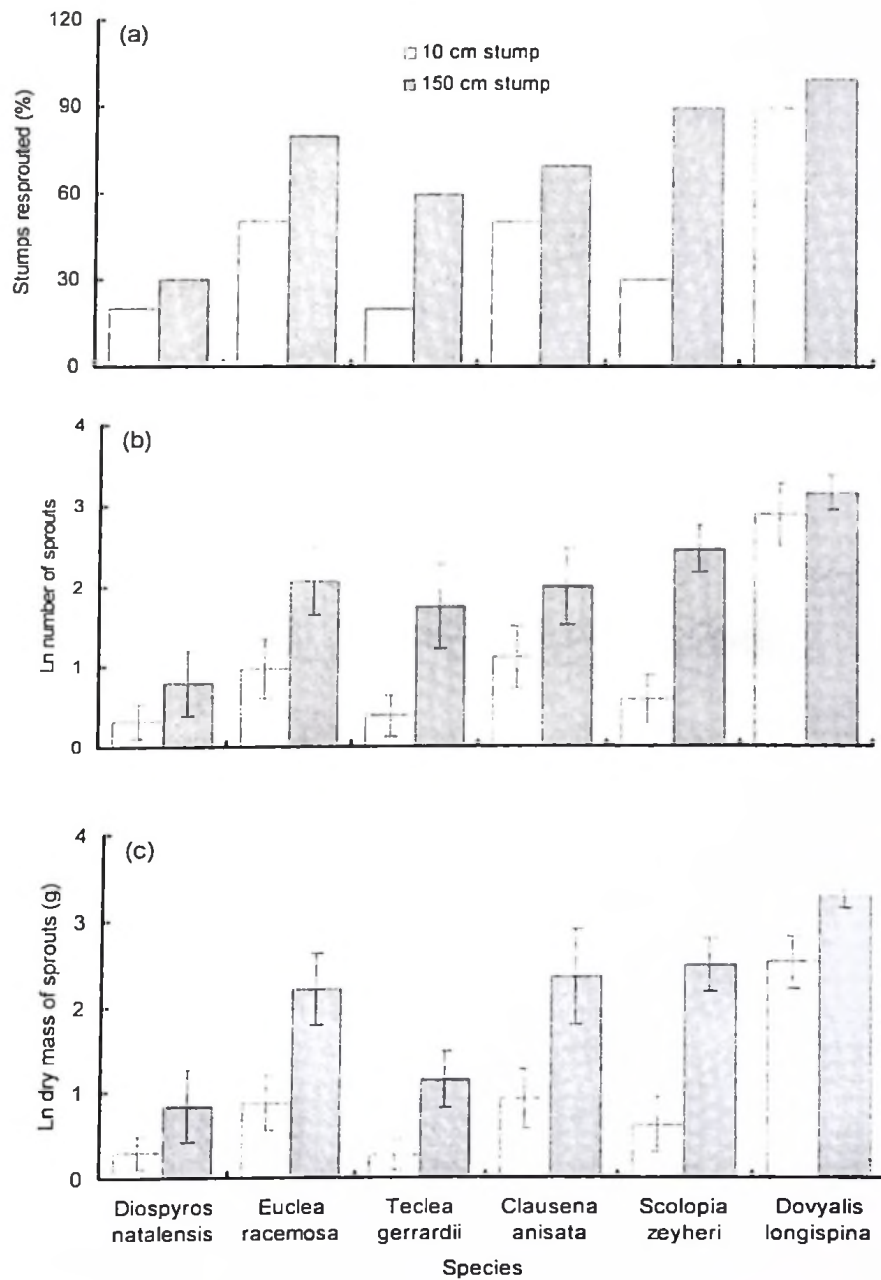
Fig. 3. Influence of stump height on resprouting ability of species pairs of poor and good resprouters within families (see Figure 2 for sprouting and family categories). Percent of stumps that resprouted (a); mean ± SE of ln number of sprouts per stump (b) and; mean ± SE of ln dry mass of sprouts (c).

Table 3. Multivariate analysis of covariance (MANCOVA) for the effect of resprouting (poor or good resprouter), stump height (short = 10 cm or tall = 150 cm) and their interaction on the number and dry mass of sprouts per stump. Data were blocked by family (Ebenaceae, Rutaceae or Salicaceae) and diameter at breast height (dbh) of stumps was included as a covariate. Number and dry mass of sprouts per stump were ln-transformed.

Dependent variable	Source of variation	d.f.	m.s.	F	P
Number of sprouts	Family				
	Covariate (dbh)	1	11.21	0.50	0.609
	Residual	1	22.51	16.14	
	Family units				
	Resprouting (R)	1	29.58	21.21	<0.001
	Stump height (H)	1	28.59	20.50	<0.001
	R × H	1	1.76	1.26	0.264
	Covariate (dbh)	1	0.003	0.00	0.961
	Residual	113	1.39		
Dry mass of sprouts	Family				
	Covariate (dbh)	1	8.53	0.32	0.671
	Residual	1	26.30	21.72	
	Family units				
	Resprouting (R)	1	39.04	32.24	<0.001
	Stump height (H)	1	36.14	29.84	<0.001
	R × H	1	0.04	0.03	0.857
	Covariate (dbh)	1	0.39	0.32	0.572
	Residual	113	1.21		

resprouters and reseeders, respectively (Bowen & Pate 1993; Bell & Ojeda 1999; Verdaguer & Ojeda 2002; Knox & Clarke 2005). However, good resprouters in this study differ from resprouters in fire-prone habitats because they maintain higher concentrations of TNC in their stems than in their roots (Bell *et al.* 1996). Although in fire-prone systems there is a strong selective advantage to storing reserves below-ground than above-ground (Bond & Midgley

2001), higher TNC concentration in stems than in roots is favoured in good resprouters in this study, because they can usually remobilise above-ground reserves for resprouting after disturbance. Disturbances at our study site tend to cause leaning (Nzunda *et al.* 2007a, b). Leaning may break roots on the side opposing the lean, resulting in loss of TNC stored in the disconnected roots. Having higher TNC concentration in the stem could bet-hedge against this possibility.

Another factor that might favour higher concentration of TNC in stems than in roots in sand dune forests is that leaning trees may use an alternative to resprouting that involves regaining of the vertical orientation of the growing tip of the leaning stem; a process we refer to as 'turning up' (Nzunda *et al.* 2007b). When the growing tip of a leaning stem regains its vertical orientation, the tree's survival is ensured and the TNC in the stem is not wasted. However, because turning up occurs by formation of reaction wood that requires more resources than formation of normal wood, extra TNC has to be used (Zimmermann & Brown 1971; Mattheck 1995; Jiang *et al.* 2006). During turning up it might be easier to redistribute TNC within the stem than to translocate it from roots, providing another explanation for higher TNC concentration in stems than in roots in these subtropical forests.

In spite of similarity in the severity of disturbance that causes resprouting, good resprouters in our study generally differed in root:shoot ratios, carbohydrate storage, and stump resprouting response, from *E. polyandra* studied in Japan by Sakai and colleagues (Sakai *et al.* 1995; Sakai *et al.* 1997; Sakai & Sakai 1998). In our study, good resprouters had larger root:shoot ratios, root and stem TNC concentration and number and dry mass of sprouts produced by stumps than poor resprouters. In contrast, *E. polyandra* did not differ from a poor resprouter in root:shoot ratio, root and stem TNC concentration and number of sprouts; and had lower dry mass of sprouts produced by stumps. In fact, *E. polyandra* produced

surprisingly few sprouts of low dry mass even from tall (150 cm) stumps, unlike good resprouters in our study. Sakai & Sakai (1998) suggested that much larger trunk volume or additional above-ground structures such as foliage and branches were necessary for resprouting in *E. polyandra*. Moreover, resprouting in *E. polyandra* may be achieved using resources remobilised directly from the disturbed photosynthesising parts rather than using stored resources because the species maintains very low levels of reserves in both roots and shoots (Sakai *et al.* 1997; Sakai & Sakai 1998).

Because *E. polyandra* resprouted abundantly in response to natural stem leaning and partial uprooting and resprouted only slightly after cutting, Sakai & Sakai (1998) concluded that resprouting in *E. polyandra* was uniquely adapted to disturbances that cause stem leaning and partial uprooting. In that case, resprouting is achieved using resources drawn from the disturbed, but, live shoot, unlike in cutting where most of the shoot is removed. Similarly, good resprouters in our study might be expected to have a poor resprouting response to cutting. However, a vigorous resprouting response to cutting by good resprouters in our study suggested that although resprouting and multi-stemming are strongly associated with stem leaning and partial uprooting at Cape Vidal (Nzunda *et al.* 2007a, b), resprouting ability is not uniquely adapted to disturbances that cause stem leaning and partial uprooting. Trees in our study area persist by resprouting in response to other disturbances as well, and depending on the severity of the disturbance, are clearly capable of using either or both below- and above-ground resources to resprout. This versatility of resource deployment for resprouting may be advantageous in the coastal dune forests where low-intensity background levels of chronic disturbance (e.g., wind; Nzunda *et al.* 2007a) are occasionally punctuated by high-intensity disturbances (e.g., dune slump).

Resource allocation in coastal dune trees appears to be a bet-hedging strategy. After low-severity disturbances, resprouting occurs by remobilization of above-ground resources. Below-ground resources may be more costly to remobilise but may allow recovery from occasional more severe disturbances. This study emphasises the adaptive advantage of sprouting through remobilisation of above-ground resources and the importance of the persistence niche (Bond & Midgley 2001) in this habitat.

Acknowledgments

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Chapter 6

Trade-offs between aboveground growth, allocation to root biomass and total non-structural carbohydrates (TNC) storage in resprouting trees of coastal forest

Nzunda, E.F., Griffiths, M.E. & Lawes, M.J. submitted to *Functional Ecology*

Summary

1. Many plants persist by resprouting after disturbance. However, the costs of resprouting are traded off against growth and reproduction. Resources (particularly total non-structural carbohydrates - TNC) that would otherwise be allocated to growth or reproduction are stored or mobilised to support the sprouting habit.

2. Furthermore, TNC may either be stored by accumulation when its availability exceeds the requirements for growth or by reserve formation when storage is achieved at the expense of growth. Resource allocation and the mechanism of storage may differ between good and poor resprouters in response to nutrient availability and disturbance. Reserve formation represents 'true storage' and good resprouters may reserve resources to tide them over periods of disturbance and stress.

3. We test whether good and poor resprouters in a coastal forest, under chronic disturbance of low severity, differ in growth rates, biomass allocation, leaf traits, water relations and storage of root TNC. Seedlings from confamilial pairs of tree species representing poor and good resprouters were subjected to nitrogen addition, water stress and clipping (simulating herbivory) treatments under greenhouse conditions over 21 months.

4. Poor resprouters had greater height growth rate, larger specific leaf area, lower root mass ratio and lower root TNC than good resprouters. These differences between poor and good resprouters were maintained irrespective of the levels of nitrogen, water and clipping treatment. Good resprouters did not increase TNC concentration under nutrient stress, indicating that reserve formation rather than accumulation of TNC is the mechanism of storage.

5. Good resprouters have to store TNC by reserve formation as a bet-hedging strategy against strong selection events that occur in addition to chronic stresses. Bet-hedging against damage is important for persistence of individuals as shown by the high incidence of multi-stemmed trees in dune forest.

Keywords: aboveground competition, carbohydrate storage, disturbance regime, plant strategies, resource allocation, sprouting ability

Introduction

Disturbance and site productivity exert selective pressure on resprouting and reseeding as alternative strategies for survival of woody plants (Bellingham & Sparrow 2000; Bond & Midgley 2001; Knox & Clarke 2005). Consequently, resprouters differ from obligate seeders in allocation of resources to growth, reproduction and storage. Obligate seeders maximize their fitness by growing fast so as to be reproductively mature before the next disturbance (Bond & Midgley 2003; Knox & Clarke 2005; Schwilk & Ackerly 2005) and attain greater height, which confers a competitive advantage over sprouters where disturbance is infrequent and of low severity (Midgley 1996; Falster & Westoby 2005; Vesk 2006). Rapid stem growth

is achieved by minimising allocation of resources to root biomass and carbohydrate storage (Bond & Midgley 2003; Knox & Clarke 2005; Schwilk & Ackerly 2005). Because allocation of resources to root biomass and carbohydrate storage enhances resprouting ability (Bowen & Pate 1993; Canadell & López-Soria 1998) and hence chances of surviving disturbance, obligate seeders have a poor capacity to resprout and are often killed by disturbance. However, when disturbance destroys an obligate seeder, and provided disturbance intervals are long enough for growth of new individuals from seed, seeding can ensure population maintenance. In contrast, resprouters maximize their long-run fitness by allocating resources to structures that increase their chance of surviving the next disturbance. Hence, resprouters often have higher root-to-shoot ratios and carbohydrate reserves than their closely related obligate seeders (Bowen & Pate 1993; Bell & Ojeda 1999; Verdaguer & Ojeda 2002). When disturbance destroys aboveground biomass, resprouters use belowground resources to produce new aboveground biomass. This ability of resprouters is traded off against growth and seed output (Bond & Midgley 2003; Knox & Clarke 2005; Schwilk & Ackerly 2005).

Resprouting is most common in fire-prone Mediterranean shrublands and tropical savannas (Midgley 1996; Bond & Midgley 2003). In these habitats, the interplay of allocation pattern, productivity, disturbance severity and frequency may favour the resprouting strategy over the reseeding strategy (Bellingham & Sparrow 2000; Luoga, Witkowski & Balkwill 2004; Clarke *et al.* 2005; Knox & Clarke 2005). For example, in fire-prone Australian shrublands, allocation of resources to root biomass and carbohydrate storage enable resprouters to dominate fertile sites (Knox & Clarke 2005). Resprouting has also been recorded in forests in association with catastrophic disturbance such as hurricane or cyclone damage (Bellingham, Tanner & Healey 1994; Boucher *et al.* 1994; Zimmerman *et al.* 1994;

Tsuyuzaki & Haruki 1996), or low-severity disturbance and low productivity (Sakai, Ohsawa & Ohsawa 1995; Kruger, Midgley & Cowling 1997; Nzunda, Griffiths & Lawes 2007a, b).

Few studies of resource allocation in resprouters and obligate seeders have been based on manipulative experiments and all are from fire-prone habitats dominated by shrubs (Knox & Clarke 2005; Schwilk & Ackerly 2005). However, there are some similarities between resource allocation pattern in resprouters from habitats that are fire-prone and those that are not (Sakai, Sakai & Akiyama 1997; Sakai & Sakai 1998; Nzunda, Griffiths & Lawes 2008). More data are needed on the relationship between resource allocation and resprouting ability for species from habitats that are not fire-prone to assess the generality of the resource allocation patterns for resprouting. This study provides such information for coastal dune forest that is not fire-prone but experiences low-severity chronic disturbance due to coastal winds and substrate instability, which result in a high incidence of multi-stemmed trees (Nzunda *et al.* 2007a).

Resources may either be stored by accumulation or reserve formation (Chapin, Schulze & Mooney 1990; Lambers, Chapin & Pons 2006). Accumulation is the storage of compounds that do not directly promote growth and occurs when resource supply and acquisition exceeds demands for growth and maintenance (Lambers, Pons & Chapin 1998). In contrast, reserve formation is the regulated synthesis of storage compounds and is achieved at a cost to growth, maintenance and reproduction (Chapin *et al.* 1990). An increase in the proportion of photosynthate allocated to storage as non-structural carbohydrates (TNC) in stressed environments compared with optimum environments represents accumulation. In contrast, reserve formation is indicated by a lack of difference in allocation to storage between stressed and non-stressed plants (Wyka 2000; Knox & Clarke 2005). Reserve formation represents true storage whereas accumulation is a result of fluctuations in external conditions (Chapin *et al.*

1990). When external conditions are optimal for growth, the accumulated TNC is used for growth (Wyka 2000). Reserve formation is selected in plants that need storage for a specific purpose such as resprouting after disturbance, although reserve formation and accumulation are not mutually exclusive (Wyka 2000). In fire-prone Australian shrublands, resprouters form storage by both accumulation and reserve formation depending on nutrient availability (Knox & Clarke 2005). However, it is not known whether reprouters in other systems that are not fire-prone, form storage by accumulation or reserve formation or both processes.

Apart from allocating resources according to a predetermined pattern depending on whether a plant is growing under stressed or optimal conditions, a plant may also change its allocation pattern in direct response to immediate disturbance. One disturbance that often affects resource allocation by plants is herbivory. Herbivory promotes sprouting through the growth of secondary shoots that are otherwise suppressed by the primary shoot (Chamberlin & Aarssen 1996; Del Tredici 2001; Karlsson *et al.* 2004). In this way herbivory favours growth and performance of multi-stemmed resprouters (Chamberlin & Aarssen 1996; Karlsson *et al.* 2004). However, experimental evidence for the effect of herbivory on sprout growth, biomass allocation and TNC storage is lacking.

The aims of this study are to test: (1) whether poor and good resprouters differ in their growth rates, biomass allocation, leaf characteristics, water relations and TNC storage in response to stress and disturbance; and (2) whether root TNC storage occurs as a result of accumulation and/or reserve formation. We predict that: (1) poor resprouters will have higher growth rates and lower allocation to root biomass and root TNC than good resprouters; (2) clipping will result in higher growth rates in good resprouters than in poor resprouters; and (3) good resprouters will store TNC by reserve formation because these reserves promote the resprouting response to unpredictable disturbance, whereas poor resprouters accumulate TNC

under nutrient stress because they need it for high growth rate when nutrient availability returns to optimal.

Materials and Methods

STUDY AREA

The tree species used in this study are from Indian Ocean coastal dune forest at Cape Vidal (28°05'32"S, 32°33'40"E). The mean annual rainfall is approximately 1200 mm, spread evenly throughout the year (range 80 mm – 90 mm per month) (Schulze 1997). Average minimum and maximum temperature is 17.8°C in July and 25.6°C in January respectively. The soil is loose unconsolidated sand with limited organic matter and low nutrient levels (Boyes 2006). The topography consists of steep (slope up to 55°) sand dunes. The loose sand substrate, steep slope and the action of wind present low-intensity chronic disturbance that result in tree decumbency and partial uprooting. Trees resprout and become multi-stemmed in response to these disturbances (Nzunda *et al.* 2007a, b).

SPECIES SELECTION AND ESTABLISHMENT

Because most species are capable of both vegetative and sexual reproduction (resprouting and seeding, respectively), species were designated as either poor or good resprouters based on their relative frequency of multi-stemmed individuals in the forest (Kruger *et al.* 1997; Holness 1998; Nzunda *et al.* 2007a). Poor resprouters in this study differ from non-resprouters in fire-prone ecosystems because the poor resprouters are not obligate reseeders. Poor and good resprouters from three species pairs from three families were contrasted to control for the

effect of phylogeny on resource allocation characteristics (Table 1). Newly germinated seedlings were collected from the forest and planted into 110 mm diameter by 500 mm deep pots (volume 4.75 ℓ). All seedlings were watered to field capacity twice a week for 4 weeks before introducing water, nutrient and clipping treatments. The treatments were applied for 21 months from May 2005 to February 2007.

Table 1. Species used in the study. Nomenclature follows Coates Palgrave (2002).

Species	Family	Frequency (%) of multi-stemmed individuals	Resprouting ability
Diospyros natalensis	Ebenaceae	14.5	Poor
Teclea gerrardii	Rutaceae	25.7	Poor
Scolopia zeyheri	Salicaceae	32.1	Poor
Euclea racemosa	Ebenaceae	69.9	Good
Clausena anisata	Rutaceae	33.3	Good
Dovyalis longispina	Salicaceae	78.7	Good

EXPERIMENTAL DESIGN AND RESPONSE VARIABLES

The water, nutrient and clipping treatments each had two levels. A fully crossed $2 \times 2 \times 2$ design was used to evaluate the effect of the treatments. The two levels of nutrients were addition of 20 g m^{-2} Limestone Ammonium Nitrate (LAN) or no addition of LAN to the sand growing medium. LAN is a granulated 28% nitrogen fertilizer. The fertilizer was applied 4 weeks after seedlings were planted in the pots and again after 56 weeks (John & Turkington 1997; Turkington *et al.* 2002). For the two soil moisture treatments, pots were watered to field capacity twice a week or watered to field capacity once after three weeks (when the soil water potential approached −1.5 Mpa). The moisture content of the soil was determined using the pressure-plate technique (Kutílek & Nielsen 1994). A known weight of water was added to the pots, so that the weight of pots could be used to determine when soil approached −1.5 MPa. For the clipping treatment the terminal bud was removed 4 weeks after seedlings were planted

in the pots and some plants were not clipped. Six replicates were used for each level of each treatment resulting in an experiment with 8 treatment combinations × 6 species × 6 replicates.

Stem height, leaf area (Li-Cor 3100 Area Meter, Lincoln – USA), leaf number, water potential and stomatal conductance were measured for each plant during the last month of the experiment (84th–88th week). Stomatal conductance (LI-1600 Steady State Porometer, Lincoln - USA) was measured during a water-stress phase in mid-morning (09.00 – 11.00 h). Water potential was measured using a Scholander bomb (Scholander *et al.* 1965). During the 88th week, plants were harvested, divided into roots, stems and leaves and dried at 70°C for 96 h. Relative growth rate (RGR_h = [log h_1–log h_0]/t_1–t_0 where h = height, t = time, 0 = start and 1 = end of experiment), specific leaf area (SLA = leaf area/leaf dry mass), leaf area ratio (LAR = leaf area/total plant dry mass), stem mass ratio (SMR = stem dry mass/total plant dry mass), leaf mass ratio (LMR = leaf dry mass/total plant dry mass) and root mass ratio (RMR = root dry mass/total plant dry mass) were derived from primary measurements.

Subsamples of root and stem were ground for determination of total TNC concentration. TNC was not determined for leaves because TNC levels in leaves fluctuate daily in response to photosynthetic activity and export of starch out of the leaves (Graham *et al.* 2003; Myers & Kitajima 2007). TNC was measured as the sum of starch and three sugars: fructose, glucose and sucrose (Sakai *et al.* 1997). Starch is the main food and reserve compound in woody plants while fructose, glucose and sucrose are the most essential assimilation products (Zimmermann & Brown 1971; Sakai *et al.* 1997). Concentrations of fructose, glucose and sucrose were determined using gas chromatography (Varian 3800 Chromatograph, USA) based on standard procedures (Sweeley *et al.* 1963; Grob 2001). The concentration of starch was determined as glucose equivalents in the residues of the ethanol extracts (Rose *et al.* 1991; Sakai *et al.* 1997). Starch was extracted and hydrolysed to glucose

by perchloric acid (Rose *et al.* 1991). After neutralization by ammonia solution, the extract was subjected to gas chromatography for determination of the concentration of glucose.

STATISTICAL ANALYSIS

Differences between resprouting categories and the effect of the treatments on the response variables were tested using randomized complete block ANOVA in GenStat Release 9.1 (Lawes Agricultural Trust 2006), where family was the random blocking factor and resprouting ability, nitrogen addition, water and clipping were fixed factors. Because some variables were correlated with each other a subset of the suite of response variables was selected using principal components analysis in PC-ORD Version 4.34 (McCune & Mefford 1999). Five response variables were selected out of 15 variables for use in the analyses: RGR_h, which represented aboveground growth; RMR, which represented root biomass allocation; SLA, which represented leaf traits; water potential, which represented water relations and root TNC concentration, which represented carbohydrate storage.

Results

Poor resprouters had higher RGR_h than good resprouters with the addition of nitrogen resulting in higher RGR_h in both resprouting categories (Table 2; Fig. 1). Water and clipping treatments had no effect on RGR_h (Table 2). The difference in RGR_h between good and poor resprouters was maintained across nutrient, water and clipping treatment levels as indicated by the lack of interaction of these factors with resprouting category.

Good resprouters had higher RMR than poor resprouters (Table 2; Fig. 2). Addition of nitrogen decreased RMR for both poor and good resprouters, whereas water and clipping
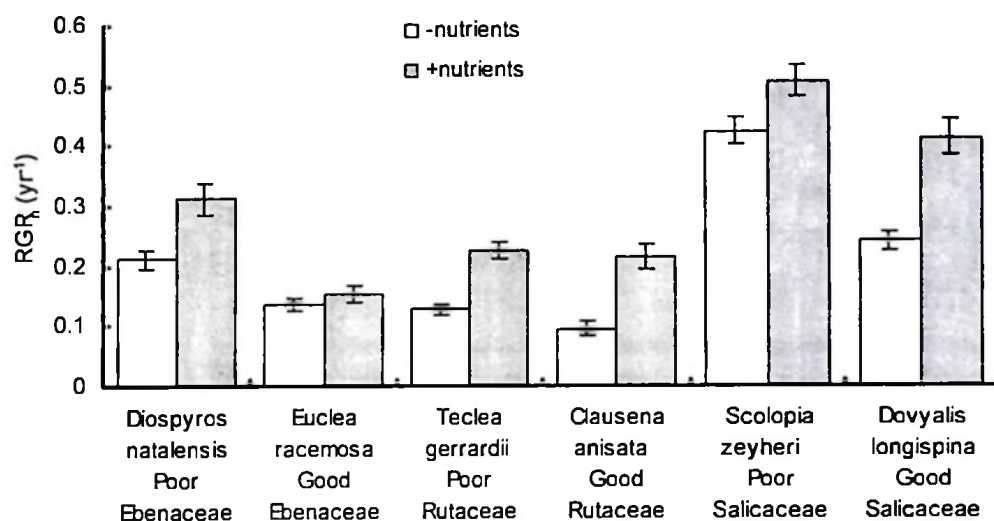
treatments had no effect on RMR (Table 2; Fig. 2). The difference in RMR between good and poor resprouters was not affected by nutrient, water and clipping treatments.

Good resprouters had consistently lower SLA than poor resprouters across all levels of nutrient, water and clipping treatments as indicated by the lack of interaction between resprouting category and nutrient, water and clipping treatments (Table 2; Fig. 3). Water stress increased SLA whereas nitrogen addition, clipping and all the interactions had no effect on SLA (Table 2).

Table 2. Randomized complete block ANOVA for relative growth rate, root mass ratio, specific leaf area, water potential and root total non-structural carbohydrates (starch + sucrose + glucose + fructose) with resprouting, nutrients, water and clipping as fixed factors and family as a random blocking factor. Bold type indicates significant effect at $P < 0.05$.

Source of variation	d.f.	RGR$_h$ F	RGR$_h$ P	RMR F	RMR P	SLA F	SLA P	Water potential F	Water potential P	Root TNC F	Root TNC P
Family stratum	2	157.45		48.92		49.88		1.48		26.15	
Family units stratum											
Resprouting (R)	1	64.76	**<0.001**	118.54	**<0.001**	40.14	**<0.001**	0.19	0.663	95.64	**<0.001**
Nutrients (N)	1	73.66	**<0.001**	29.84	**<0.001**	2.88	0.091	4.71	**0.031**	<0.01	0.969
Water (W)	1	1.00	0.318	2.48	0.116	4.51	**0.035**	124.22	**<0.001**	0.29	0.594
Clipping (C)	1	2.98	0.086	3.45	0.064	<0.01	0.967	0.79	0.374	0.23	0.631
R × N	1	0.18	0.675	0.02	0.891	0.01	0.936	2.38	0.124	<0.01	0.983
R × W	1	0.63	0.430	0.03	0.862	0.58	0.445	0.08	0.784	0.39	0.531
N × W	1	1.21	0.271	0.10	0.756	0.06	0.801	0.35	0.553	0.05	0.826
R × C	1	0.06	0.808	<0.01	0.99	0.03	0.860	2.59	0.109	0.02	0.891
N × C	1	1.32	0.252	0.11	0.743	1.24	0.267	0.17	0.677	1.19	0.277
W × C	1	0.01	0.920	0.10	0.748	0.65	0.421	3.51	0.062	0.67	0.414
R × N × W	1	1.21	0.273	2.26	0.134	0.13	0.716	2.53	0.113	<0.01	0.966
R × N × C	1	3.19	0.075	1.24	0.266	0.41	0.523	8.56	**0.004**	1.36	0.245
R × W × C	1	<0.01	0.989	0.62	0.433	2.07	0.152	0.03	0.871	0.27	0.603
N × W × C	1	0.06	0.813	0.38	0.540	1.04	0.309	9.51	**0.002**	0.15	0.698
R × N × W × C	1	0.03	0.868	2.54	0.112	<0.01	0.991	2.16	0.143	0.04	0.846
Residual	268										

Fig. 1. Mean ± SE of relative growth rate for pairs of poor and good resprouters within families with and without nitrogen addition.
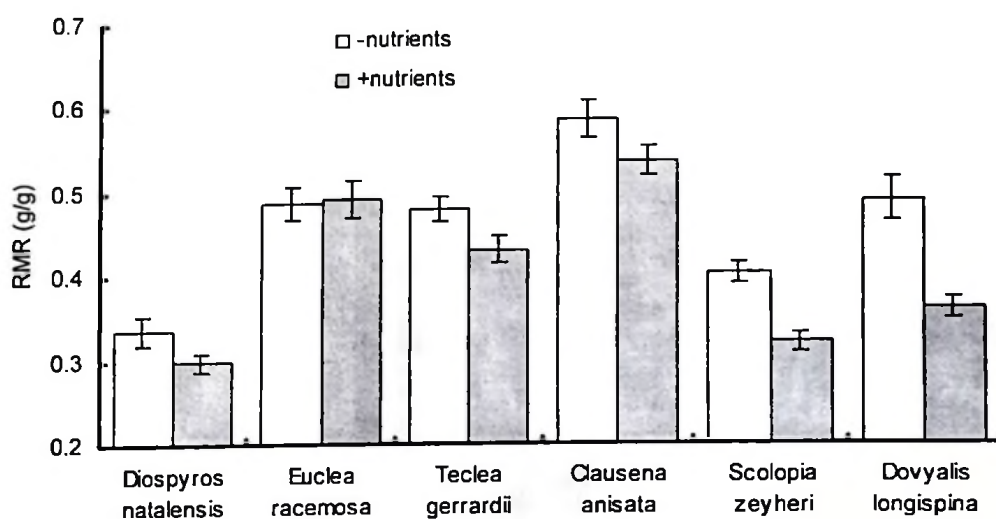

Fig. 2. Mean ± SE of root mass ratio for pairs of poor and good resprouters within families with and without nitrogen addition (see Figure 1 for family and sprouting categories).
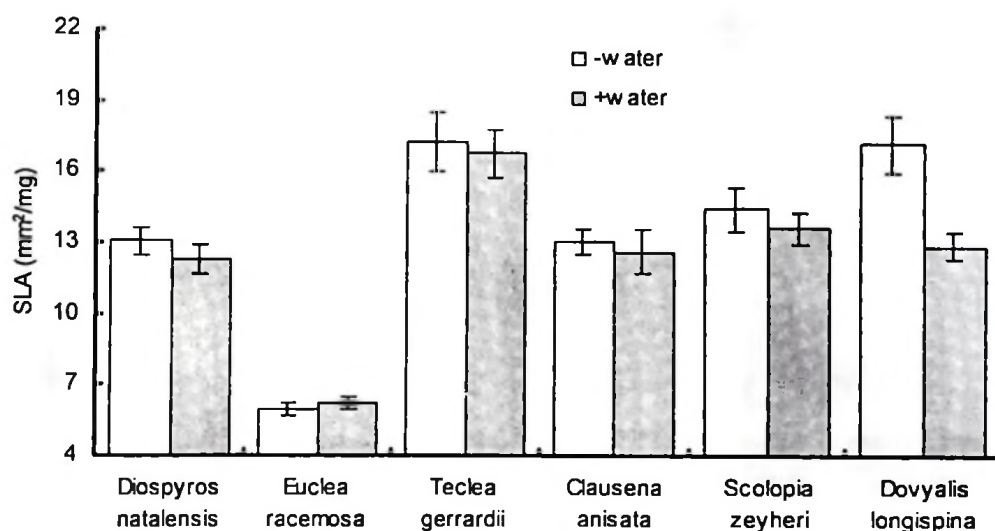
Fig. 3. Mean ± SE of specific leaf area for pairs of poor and good resprouters within families with and without water addition (see Figure 1 for family and sprouting categories).

The difference in water potential between good and poor resprouters varied according to nutrient and clipping treatments (Table 2). For clipped seedlings, nitrogen addition decreased the water potential of poor resprouters whereas it had no effect on water potential of good resprouters. For unclipped seedlings there was no effect of nitrogen addition on water potential for both poor and good resprouters.

Good resprouters had higher root TNC concentration than poor resprouters across all treatment levels of nutrients, water and clipping (Table 2; Fig. 4). Nitrogen addition and water stress had no effect on root TNC concentration. Thus the TNC storage capacity of the studied species was by reserve formation rather than by accumulation.
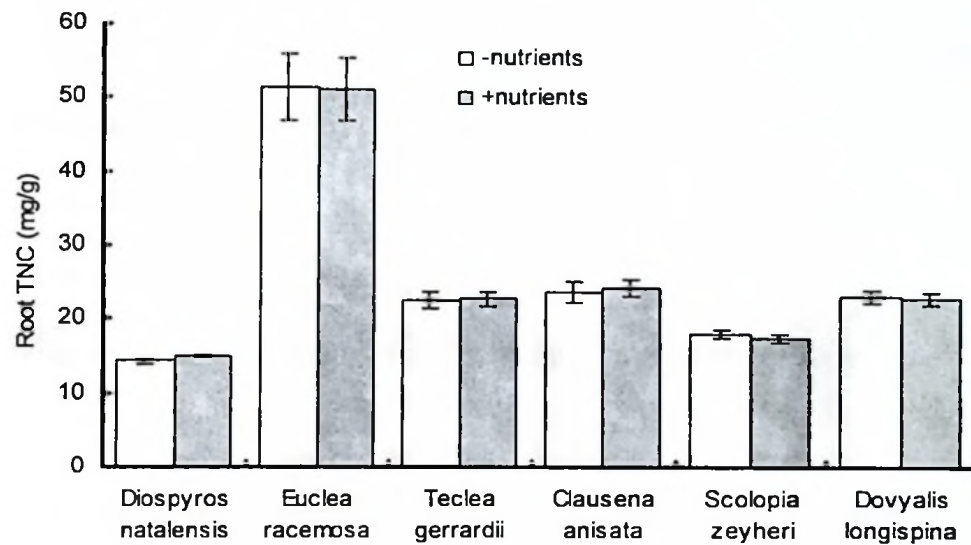
Fig. 4. Mean ± SE of root non-structural carbohydrate concentration for pairs of poor and good resprouters within families with and without nitrogen addition (see Figure 1 for family and sprouting categories).

Discussion

Higher allocation to root biomass and root TNC storage for good resprouters than poor resprouters in this study is similar to experimental results from fire-prone environments (Knox & Clarke 2005; Schwilk & Ackerly 2005). However, the higher height growth for poor resprouters than good resprouters is contrary to the results from fire-prone environments, where there was no difference in growth between resprouters and obligate seeders (Knox & Clarke 2005; Schwilk & Ackerly 2005). Nevertheless, obligate seeders from fire-prone environments achieved earlier reproductive maturity than resprouters. Fast growth may be competitively advantageous in environments where there is a higher risk of being overtopped by neighbours due to low disturbance frequency and severity (Midgley 1996; Bellingham & Sparrow 2000). The tree species in this study are from forest with chronic disturbance of low-severity, unlike the shrub species from fire-prone environments studied by Knox & Clarke

(2005) and Schwilk & Ackerly (2005). Because the disturbances in dune forest are of low severity, there is a possibility of being overtopped by neighbours and poor resprouters gain a competitive advantage by growing fast. However, because the disturbance is chronic there is also the possibility that growth will be interrupted by disturbance and hence good resprouters gain a competitive advantage by allocating resources to root biomass and TNC storage, which increases resprouting ability (Nzunda *et al.* 2008) and the capacity to persist in disturbed environments.

Poor resprouters have less need to resprout because they are more likely to use 'turning up', an alternative to resprouting that enables leaning trees to regain the vertical orientation of the growing section (Nzunda *et al.* 2007b). The low severity of the disturbance favours poor resprouters (Nzunda *et al.* 2007b) whereas the chronic nature of the disturbances favours good resprouters (Nzunda *et al.* 2007a), resulting in coexistence. In contrast, in fire-prone shrubland there is less danger of being overtopped by neighbours but a higher risk of severe disturbance before reproductive maturity. Unlike savanna trees that can avoid fire damage by growing fast and attaining a threshold escape height (Trollope 1984; Higgins, Bond & Trollope 2000; Archibald & Bond 2003; Wilson & Witkowski 2003), shrubs cannot avoid fire damage through fast growth because of their limited potential height (Vesk 2006). Resprouter shrubs can survive both short and long fire intervals whereas obligate seeders are vulnerable to short fire intervals and hence they need to reproduce before the next fire (Malanson 1985; Cowling, Lamont & Enright 1990; Enright & Goldblum 1999). Hence shrub obligate seeders increase their fitness by earlier reproductive maturity than resprouters, rather than by higher height growth rate (Knox & Clarke 2005; Schwilk & Ackerly 2005).

Nutrient stress did not result in higher TNC concentrations and thus the TNC storage capacity of the studied species was by reserve formation rather than by accumulation. Low-

severity and chronic disturbance in the study area necessitates TNC storage by reserve formation. Good resprouters must reserve a portion of their carbohydrates as a bet-hedge against possible damage that results in resprouting and multi-stemming (Nzunda *et al.* 2007a). Carbohydrate reserve formation is achieved at the expense of growth and hence good resprouters have lower growth rate than poor resprouters (Chapin *et al.* 1990; Bond & Midgley 2003).

By having lower SLA than poor resprouters, good resprouters were more sclerophyllous than poor resprouters. One good resprouter, *Euclea racemosa*, had a thick cuticle and stiff leaf structure. This feature is often used to qualitatively assign sclerophylly (Read & Sanson 2003). Higher sclerophylly for good resprouters than poor resprouters in coastal dune forests is advantageous against desiccating coastal winds. The pattern of lower SLA for poor resprouters reported here is contrary to that observed in Mediterranean shrublands and Californian chaparral where resprouters have higher SLA than obligate seeders (Ackerly 2003; Paula & Pausas 2006). High SLA leads to excessive water loss. Higher water loss by resprouters than obligate seeders in Mediterranean shrublands is countered by resprouters having deeper roots than obligate seeders (Keeley 1986; Bell 2001; Silva, Rego & Martins-Loução 2002; Ackerly 2003; Paula & Pausas 2006). In contrast, in forests a good resprouting ability is associated with shallow roots (Sakai *et al.* 1997) and hence lower SLA for good resprouters prevents excessive water loss.

In summary, plant growth form and disturbance regime determine the nature of competition between plants with varying resprouting ability (Bellingham & Sparrow 2000). In fire-prone shrublands, shrubs cannot avoid damage imposed by fire due to their low height. Shrub resprouters allocate resources to root biomass and root TNC storage so that they can restore aboveground structures after disturbance. Due to severe disturbance in shrublands,

aboveground competition is less important than the risk of damage before reproduction. Hence shrub obligate seeders allocate resources in such a way as to achieve early reproductive maturity rather than allocating resources to fast height growth. In dune forest, low severity of disturbance favours fast growth of poor resprouters whereas good resprouters maintain the capacity to resprout under conditions of chronic disturbance by building TNC reserves at the expense of rapid height growth. Because disturbance is chronic, partitioning of TNC between growth and reserve formation by good resprouters serves as a bet-hedge against occasional severe disturbance events. Bet-hedging against disturbance is necessary for trees in dune forest because it is important for persistence of individuals as shown by the high incidence of multi-stemmed trees in the forest (Nzunda *et al.* 2007a).

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Chapter 7

Are the costs of resprouting by subtropical coastal dune forest trees traded off against
growth and reproduction?

Nzunda, E.F., Griffiths, M.E. & Lawes, M.J. submitted to *Journal of Vegetation Science*

Abstract

Questions: Is resprouting ability in coastal forest trees traded off against seed output, seed size, seedling abundance and recruitment by seedlings? Is seedling abundance of good resprouters higher in understorey gaps than at sites with understorey vegetation cover? Do good resprouters recruit more sprout stems than poor resprouters? Do good resprouters occur at sites with more disturbance than poor resprouters?

Location: Subtropical Indian Ocean coastal dune forest at Cape Vidal in the iSimangaliso Wetland Park, north-eastern South Africa.

Methods: Species were designated as good and poor resprouters based on their frequency of multi-stemmed individuals at Cape Vidal. Seed number and mass produced by good and poor resprouters were determined. Seed size, seedling abundance, diameter size class frequency distribution and resprouting ratio (total number of sprout stems of a species/total number of individuals of a species) of good and poor resprouters were compared. The relationship between the occurrence of good resprouters and understorey gaps and topography was analysed.

Results: Good resprouters produced less seed and had a lower seed mass per individual than poor resprouters. Good resprouters also had lower seedling abundance and fewer individuals in small diameter size classes than large diameter size classes. Seedling abundance for good

resprouters was not influenced by understorey gaps. Good resprouters recruited more stems by resprouting than did poor resprouters. Good resprouters tended to occur on dune crests and seaward slopes that are more exposed to sea winds.

Conclusions: Good resprouters trade off recruitment of new individuals for traits, such as multi-stemming, that increase the persistence of established ones. Persistence of established individuals is important where a chronic disturbance regime reduces individual survival and thereby the opportunities for reproduction. Through persistence, good resprouters improve their fitness in the long-run. Thus, good resprouters at Cape Vidal were most common on dune crests and seaward slopes that were exposed to strong sea winds.

Keywords: Disturbance; Persistence; Regeneration; Reproduction; Size distribution; Resprouting.

Nomenclature: Coates Palgrave (2002)

Abbreviations: dbh = diameter at breast height; ANOVA = Analysis of variance; MANOVA = Multivariate analysis of variance; SDI = Size distribution index.

Introduction

Resprouting can be an important means of regeneration for forest tree species, especially under conditions that do not favour regeneration through seeding (Kruger et al. 1997). These conditions may include low productivity (Bellingham & Sparrow 2000), unfavourable soil (Verwijst 1988), extreme cold (Pigott 1993) and limited light availability particularly where there is dense understorey vegetation (Koop 1987; Ohkubo 1992; Griffiths et al. 2007). Unlike

seedlings that have to acquire their own resources for survival, sprouts can develop using resources from parent plants and hence can thrive under stressful conditions that may be too harsh for seedlings (Ohkubo et al. 1996; Nanami et al. 2004).

Resprouting ability tends to be negatively associated with reproductive performance for several reasons. Firstly, allocation to storage and the production and maintenance of buds that are necessary for resprouting diverts resources from sexual reproduction (Keeley & Zedler 1978; Vesk & Westoby 2004). This results in lower seed production in resprouters than in nonsprouters (Keeley 1986; Enright & Goldblum 1999; Verdu 2000; Bond & Midgley 2001). Secondly, resprouters generally have longer life spans than nonsprouters (Bond & van Wilgen 1996; Lamont & Wiens 2003) and may accumulate a genetic load of detrimental alleles resulting from somatic mutations (Wiens et al. 1987; Lamont & Wiens 2003). This might result in lower seed set in resprouters than in nonsprouters (Bond & Midgley 2003; Lamont & Wiens 2003). The long life span of resprouters may also result in recruitment limitation caused by a need for outbreeding and greater dispersal distance (Carpenter & Recher 1979; Keeley 1986; Lamont & Wiens 2003). Thirdly, nonsprouters experience more reproductive cycles than sprouters, consequently nonsprouters can be subjected to different selection pressures than resprouters, that may be more frequent and intense than those experienced by resprouters (Wells 1969; Clark 1991). As a result, seedlings of nonsprouters may have greater vitality than seedlings of resprouters (Bond & Midgley 2003). Hence seedling growth and survival is usually greater in nonsprouters than resprouters (Thomas & Davis 1989; Pate et al. 1990; Bell 2001; Falster & Westoby 2005).

The expected negative relationship between resprouting ability and reproductive performance is based on research from fire-prone environments (Moreno & Oechel 1992; Groom et al. 2001). However, there is support for this relationship from forests where fire is

rare (Bellingham et al. 1994; Kruger et al. 1997; Nanami et al. 2004). In forests, higher resprouting ability has been shown to be associated with low numbers of seedlings (Bellingham et al. 1994; Kruger et al. 1997), flat size class distributions and clumped spatial dispersion that suggest temporally and spatially restricted recruitment by seedlings (Nanami et al. 2004).

This study examines the relationship between resprouting ability and reproductive performance of tree species in a coastal dune forest in KwaZulu-Natal in South Africa. The forest has a high incidence of resprouting that results in multi-stemming (Nzunda et al. 2007a). Trees resprout in response to chronic disturbances of low-severity such as winds and an unstable sand substrate. Species with good resprouting ability were expected to have low seed output and a population structure reflecting restricted recruitment by seedlings with their individuals occurring mainly on disturbed sites.

Methods

Seed production

Ten species representing five good and poor resprouters respectively, were used in measurement of fruit production (Table 1). For each stem, the smallest branch size that could appropriately be used as the unit for counting fruit was determined. All the branches of that size on the stem were counted. The diameter of the butt end of the branches was approximately 1 cm. A random sample of five branches was carefully severed and the total number of fruits on each branch determined. The number of fruits produced by a stem was estimated by multiplying the average number of fruits per branch by the total number of

branches per stem. Fruit per unit canopy volume was estimated by dividing the total number

of fruits per stem by the volume of the canopy. The canopy was assumed to have the shape of

Table 1. Species used in measurement of seed production

Species	Family	Resprouting category	Number of trees assessed
Celtis africana	Celtidaceae	Poor	20
Diospyros natalensis	Ebenaceae	Poor	17
Euclea natalensis	Ebenaceae	Poor	20
Euclea racemosa	Ebenaceae	Good	20
Olea woodiana	Oleaceae	Good	20
Pavetta gardeniifolia	Rubiaceae	Poor	21
Sideroxylon inerme	Sapotaceae	Good	20
Teclea gerrardii	Rutaceae	Poor	20
Tricalysia sonderiana	Rubiaceae	Good	20
Ziziphus mucronata	Rhamnaceae	Good	20

a hemisphere. Variables used were the distance from the outer surface of the canopy foliage to

the inner surface of the canopy foliage (foliage depth) and the average of two perpendicular

diameters of the canopy. By subtracting foliage depth from average canopy diameter, the

diameter of the inner vacant part of the canopy was obtained. The formula used for calculation

of the volume of the hemisphere was: $V = (2/3)\pi R^3$, where V is volume and R is radius. The

canopy volume involved in fruit production was calculated as the difference between the

volume of the outer hemisphere and the inner hemisphere of the canopy. For multi-stemmed

trees, the total number of fruits produced was obtained by summing the number of fruits

produced by each stem. Since some good resprouters did not produce fruit in some years, fruit

production was standardized to production per annum. A sample of fruits was taken to the

laboratory for determination of number of seed per fruit and seed dry mass.

After seed extraction, the seeds were oven-dried at 70°C for 96 hours. MANOVA was

used to compare seed production between good and poor resprouters with number and mass of

seed per canopy volume as dependent variables, resprouting category as a fixed factor and

family as a random factor. Seed dry mass was compared using ANOVA with resprouting category as a fixed factor and family as a random factor using three confamilial pairs.

Seedling abundance

Seedling abundance was evaluated by ANOVA using data from 72 randomly located 2 × 2 m quadrats (Nzunda et al. 2008a), with resprouting category as a fixed factor and family as a random factor. In this forest, tree regeneration is influenced by a monocarpic understorey herb *Isoglossa woodii*, which experiences population-wide synchronous die-back on a 4-7 year cycle (van Steenis 1978; Griffiths et al. 2007). Sites without *I. woodii* cover have higher seedling abundance than sites with *I. woodii* cover (Griffiths et al. 2007). The influence of *I. woodii* gaps on abundance of seedlings of good resprouters was examined using 30 paired plots at sites covered by *I. woodii* and from *I. woodii* gaps respectively using ANOVA.

Population structure and resprouting

A full description of the sampling methods used in analysis of diameter size-class distribution, relationship between resprouting category and site factors and dependence on resprouting for regeneration is given in Nzunda et al. (2007a). Diameter size-class distribution of main stems was evaluated using a size distribution index (SDI) that is the coefficient of skewness of the diameter at breast height (dbh) distribution around the midpoint of the dbh range (Nanami et al. 2004). The following formula was used:

$$SDI = \frac{1}{N} \sum_{i=1}^{N} (x_i - 0.5)^3$$

where N is the total number of individuals of a species in the sample, x_i is the standardised dbh of the main stem of the ith individual calculated as: $x_i = d_i/D$, where d_i is the dbh of the ith individual and D is the maximum dbh of the species in the sample. x_i ranges from 0 to 1. For a species with many small individuals the SDI is negative and relatively small whereas for a species with few small individuals the SDI is positive and relatively large. The SDI of good and poor resprouters was compared using analysis of variance (ANOVA). Species were designated as good or poor resprouters based on the frequency of multi-stemmed individuals from Nzunda et al. (2007a).

Because resprouting and multi-stemming are influenced by site factors at Cape Vidal (Nzunda et al. 2007a, b), it was expected that the occurrence of good resprouters would also be influenced by site factors. Thus the relationship between resprouting category and dune position, leaning of trees, erosion and slope was analysed using logistic regression.

To assess the degree of dependence on sprouts for regeneration, a resprouting ratio was calculated as the ratio of the total number of sprout stems to the total number of main stems of a species (Nanami et al. 2004). The largest stem of an individual was defined as the main stem and the other stems attached to it at or below ground level were defined as sprout stems. Two resprouting ratios were calculated: one for main stems with dbh > 5 cm and the other for main stems with dbh < 5 cm. The resprouting ratios for good and poor resprouters were compared using multivariate analysis of variance (MANOVA). To ensure homoscedasticity, inverse hyperbolic sine transformation was applied to the resprouting ratios.

Results

Poor resprouters produced more than twice the amount of seed in terms of both number (mean $\pm$ SE = 1742 $\pm$ 318 vs. 776 $\pm$ 279 m^{-3}) and mass of seed per unit canopy volume (mean $\pm$ SE =

221.02 ± 45.44 g m^{-3} vs 80.86 ± 22.12 g m^{-3}) in relation to that produced by good resprouters

(Wilk's λ = 0.92, $F_{2,289}$ = 8.05, p < 0.001). Poor resprouters also invested more resources in

individual seed as shown by higher individual seed mass for poor resprouters than good

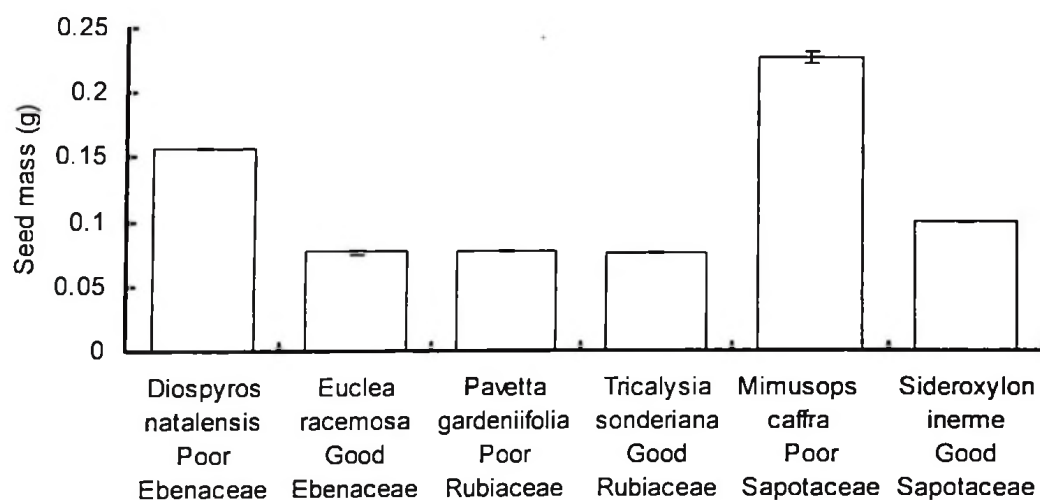resprouters ($F_{1,596}$ = 578.47, p < 0.001; Fig. 1).

Fig. 1. Mean ± SE seed mass (g) for pairs of poor and good resprouters within families.

Good resprouters had fewer seedlings than poor resprouters ($F_{1,142}$ = 88.34, p < 0.001;

Table 2). The abundance of seedlings of good resprouters was not influenced by *I. woodii* gaps

($F_{1,58}$ = 0.37, p = 0.545). Most of good resprouters had dbh size-class frequency distributions

indicative of restricted recruitment from seed because they had fewer individuals in small

diameter size classes than large diameter size classes or equal number of individuals in small

and big diameter size classes (Fig. 2) and had significantly higher SDI than poor resprouters

(mean ± SE = -0.012 ± 0.006 vs. -0.031 ± 0.004; $F_{1,18}$ = 7.45, p = 0.014). For example, *Olea*

woodiana had progressively fewer individuals in the smaller size-classes (Figure 2). Good

resprouters mostly occurred on dune crests and seaward slopes that are exposed to sea winds

and were consequently more likely to have leaning stems (Table 3).

Table 2. Number of seedlings per 2 × 2 m quadrat. $n = 72$.

Species	Family	Resprouting category	Mean	SE
Diospyros natalensis	Ebenaceae	Poor	9.99	0.97
Euclea racemosa	Ebenaceae	Good	0.26	0.07
Teclea gerrardii	Rutaceae	Poor	6.65	1.03
Clausena anisata	Rutaceae	Good	2.11	0.63
Mimusops caffra	Sapotaceae	Poor	1.76	0.28
Sideroxylon inerme	Sapotaceae	Good	0.10	0.05
Pavetta gardeniifolia	Rubiaceae	Poor	0.63	0.11
Tricalysia sonderiana	Rubiaceae	Good	0.01	0.01
Scolopia zeyheri	Salicaceae	Poor	0.01	0.01
Dovyalis longispina	Salicaceae	Good	0.18	0.07

The resprouting ratio was significantly different for the two resprouting categories particularly for main stems with dbh > 5 cm (Wilk's $\lambda = 43$, $F_{2,17} = 11.50$, $p < 0.001$) for which the resprouting ratio was significantly higher for good resprouters than poor resprouters ($F_{1,18} = 1.74$, $p < 0.001$; Fig. 3a). For main stems with dbh < 5 cm, the difference in the resprouting ratio for good and poor resprouters was non-significant ($F_{1,18} = 1.56$, $p = 0.090$; Fig. 3b). For all species, there was a steep decline in number of sprout stems from dbh class 0-5 cm to dbh class 6-10 cm unlike the more gradual decline in number of sprout stems between larger dbh classes (Fig. 2). This shows that the proportion of sprouts that suffer mortality in growing from dbh class 0-5 cm to dbh class 6-10 cm is higher than that between other dbh classes.

Discussion

Good resprouters had fewer seedlings and more restricted recruitment of seedlings than poor resprouters. Seedling recruitment may be influenced by seed production and gap formation which increases light availability (Hara 1987). However, seedling abundance of good
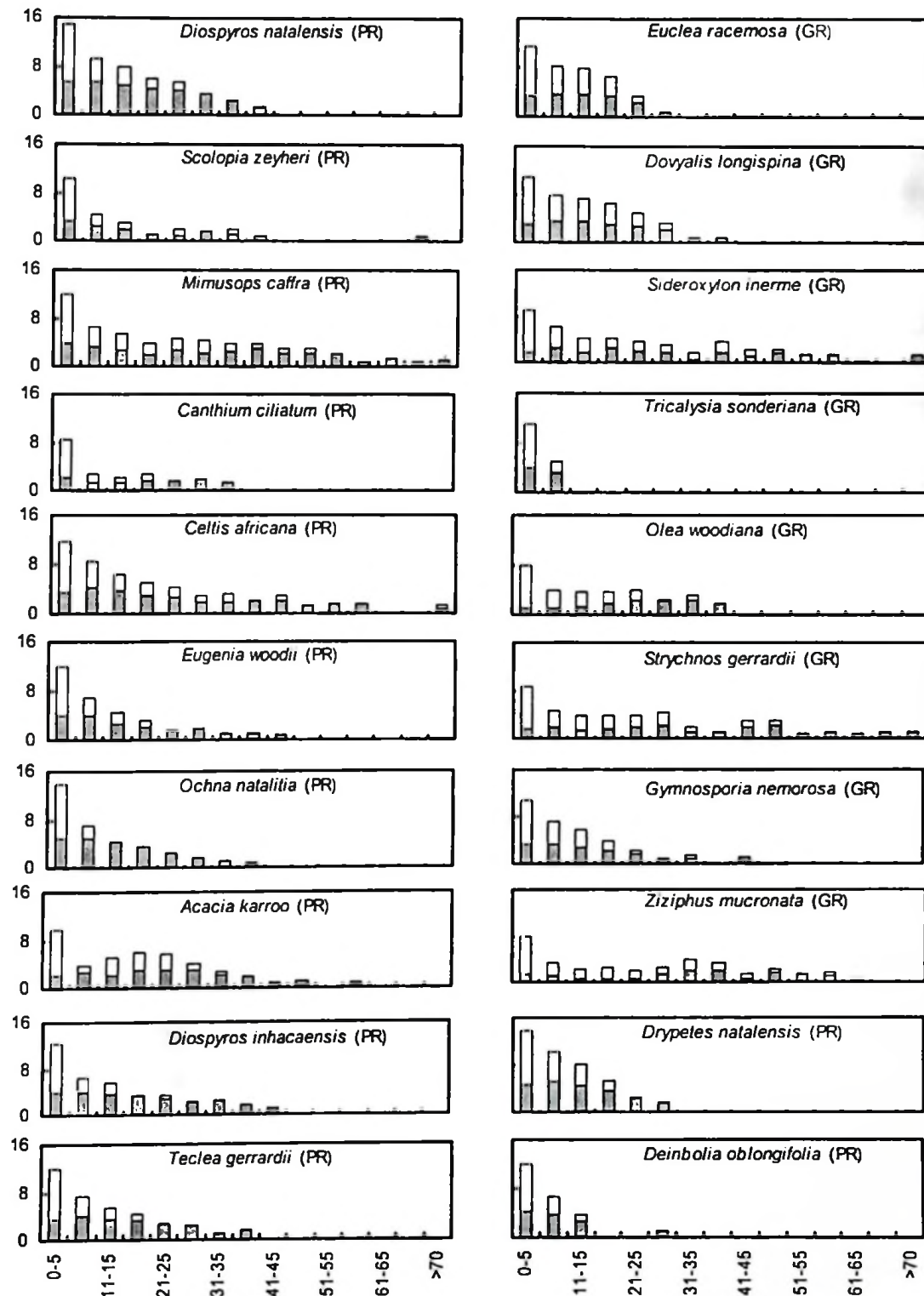
Fig. 2. Diameter size class distribution of top 20 tree species (according to importance value index rating from Nzunda et al. 2007a). Main stems are represented by filled bars and sprout stems by open bars. The y axis represents ln(stems 3 ha^{-1}) and the x axis the diameter size classes. GR = good resprouter, PR = poor resprouter.

Table 3. Parameter estimates for the logistic regression of occurrence of good resprouters on site and tree factors and variables.

Parameter	Estimate	SE	Wald	df	p
Intercept	-3.384	0.314	116.156	1	<0.001
Inclination	0.020	0.002	116.914	1	<0.001
Slope	0.009	0.005	3.198	1	0.074
Dune crest	1.668	0.290	32.988	1	<0.001
Landward slope	0.754	0.305	6.126	1	0.013
Seaward slope	1.019	0.280	13.206	1	<0.001
Dune slack without *Acacia karroo*	0.577	0.295	3.831	1	0.050
Erosion	0.158	0.155	1.040	1	0.308

resprouters was not influenced by *I. woodii* gaps. Hence the low recruitment of poor resprouters from seedlings is due to their low seed production and subsequent performance of seed, seedlings, saplings and later stages, and not due to other factors such as light and space availability.

Higher allocation of resources to root biomass and storage by good resprouters than poor resprouters (Nzunda et al. 2008b) results in lower investment in seed by good resprouters than poor resprouters (Bond & Midgley 2003). Thus good resprouters produced smaller quantities of seed that were also smaller in size than those produced by poor resprouters. Larger seeds of poor resprouters may have higher probability of emergence from deeper in the soil and greater first year seedling survival than smaller seeds of good resprouters (Brown et al. 2003). Also, larger reserves of resources in bigger seeds allow seedlings to resprout recurrently in response to damage in their early stage of development before exhaustion of the cotyledonary reserves and hence increase their tolerance against damage (Harms & Dalling 1997). Hence the larger seed size of poor resprouters may contribute to their higher seedling abundance.
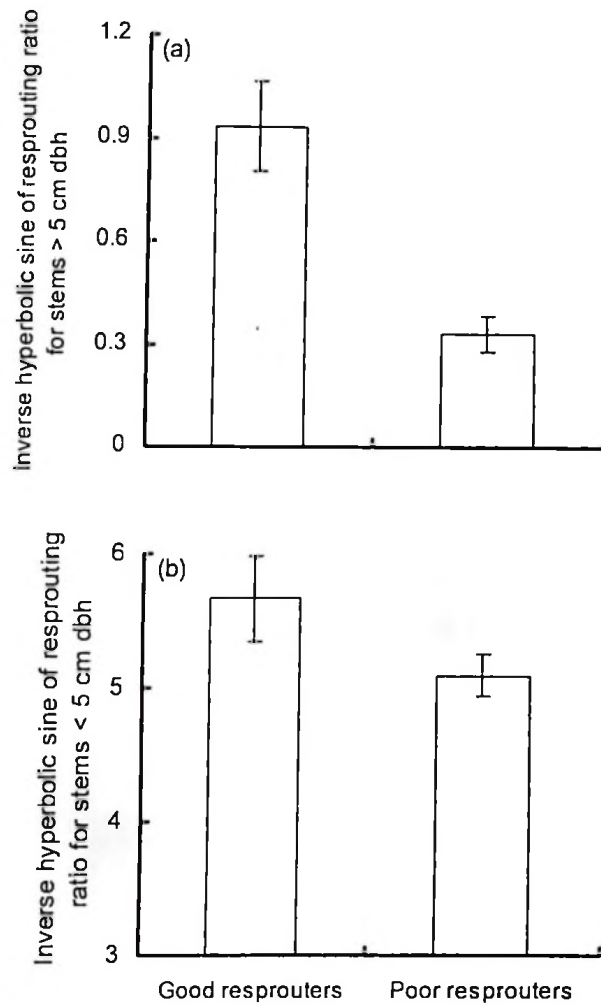
Fig. 3. Mean ± SE of inverse hyperbolic sine of resprouting ratio for (a) stems with dbh > 5

cm and (b) stems with dbh < 5 cm for good and poor resprouters.

Recruitment of new individuals from seedlings is restricted for good resprouters

because they occupy dune crests and seaward slopes that are exposed to sea winds and favour

resprouting rather than reseeding (Nzunda et al. 2007a, b). Good resprouters also suffer more

from leaning than poor resprouters (Nzunda et al. 2007b). Leaning hinders recruitment of new

individuals of a species unless the leaning individuals recover from the damage (Yamada &

Suzuki 2004). In response to leaning, good resprouters mostly resprout and lose the primary stem whereas poor resprouters mostly regain the vertical orientation of the primary stem and hence avoid resprouting (Nzunda et al. 2007b). In these circumstances, the sprout shoots of a good resprouter may have delayed reproductive maturity in comparison to the surviving primary stem of a poor resprouter (Borchert 1976; Fontanier & Jonkers 1976). Sprouting may also fail due to shading (Ohkubo et al. 1996; Paciorek et al. 2000) or severe disturbances that destroy the root system (Tremblay et al. 2002) resulting in loss of an established individual. Delayed reproductive maturity and loss of established individuals result in lower abundance of a species and lower likelihood of recruiting new individuals (Crawley 1986; Tremblay et al. 2002; Nzunda et al. 2007b). However, loss of an established good resprouter may be infrequent due to investment in root biomass and storage that enhance the ability of good resprouters to persist, rarity of severe disturbances and canopy openness that allows light to sprouts at Cape Vidal (Griffiths et al. 2007; Nzunda et al. 2008b).

Although maximum tree height at Cape Vidal does not differ between good and poor resprouters and is instead influenced by dune position that determines exposure to sea winds (Nzunda et al. 2007a), higher growth rate of poor resprouters than good resprouters may be advantageous in competition for space during tree development or architectural adjustment in response to canopy openings (Kruger et al. 1997; Falster & Westoby 2005). Due to lower growth rate, good resprouters tend to be restricted to sites with more disturbance than those occupied by poor resprouters at Cape Vidal as well as elsewhere (Kruger et al. 1997; Bellingham & Sparrow 2000; Nanami et al. 2004), because at less disturbed sites good resprouters are quickly over-topped by poor resprouters.

The limited recruitment of seedlings by good resprouters was compensated for by higher recruitment of stems from resprouting as shown by higher resprouting ratios for good

resprouters than poor resprouters. Commensurate with these findings, species with restricted seedling recruitment usually acquire more stems from sprouting (Yamamoto et al. 1995; Kruger et al. 1997; Nanami et al. 2004). Production of more sprout stems demands more buds which are costly to produce, maintain and protect, and hence good resprouters have fewer resources for height growth and sexual reproduction (Kruger et al. 1997; Del Tredici 2001; Vesk & Westoby 2004).

In conclusion, this study provides an example of the trade off between recruitment of new individuals and persistence of established ones (Bond & Midgley 2001; 2003). Good resprouters trade off recruitment of new individuals for persistence of established ones. Persistence is achieved by allocating more resources to root biomass and carbohydrate storage (Bowen & Pate 1993; Canadell & López-Soria 1998) and production and maintenance of multiple stems, which in turn result in lower growth rate and fewer resources for sexual reproduction (Kruger et al. 1997; Bond & Midgley 2003). Thus, good resprouters are typically multi-stemmed and maintain few individuals over a long time with low individual turnover, whereas poor resprouters are mostly single stemmed and maintain many individuals with high individual turnover (Lamont & Wiens 2003). Through persistence, good resprouters improve their fitness in the long-run. Thus, good resprouters at Cape Vidal were most common on dune crests and seaward slopes that were exposed to strong sea winds (Nzunda et al. 2007a).

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Chapter 8

Summary and conclusions

Resprouting and multi-stemming are well known for habitats that experience severe disturbances. For instance, resprouting and multi-stemming are important for individual persistence against fire in the Cape fynbos (Le Maitre 1992; Le Maitre & Midgley 1992; Bond & Midgley 2001) and savanna (Boaler & Sciwale 1996; Frost 1996; Luoga et al. 2004) ecosystems, and hurricanes and cyclones for tropical forests (Bellingham et al. 1994; Zimmerman et al. 1994). These plant attributes have not been closely investigated in habitats that experience disturbances of low severity and chronic stresses such as wind, loose substrate and low site productivity. However, some of these habitats, for example subtropical forest and thicket, show high incidence of resprouting and multi-stemming (Kruger et al. 1997; Kruger & Midgley 2001). This study examined species responses and the advantages to individuals of resprouting under a chronic disturbance regime of low severity in an environment with low soil productivity at Cape Vidal in KwaZulu-Natal, South Africa. This study investigated the following:

(i)   the role of multi-stemming as a survival strategy in response to chronic disturbance of low-severity;

(ii)   the alternatives to multi-stemming that promote survival under conditions of chronic disturbance;

(iii)   the role of resprouting in seedlings;

(iv)   the relationship between resprouting and patterns of resource allocation and carbohydrate storage;

(v)   the effect of stress and disturbance on growth, leaf traits, biomass allocation, water relations and carbohydrate storage size and process in relation to resprouting ability; and

(vi)   the relationship between resprouting and multi-stemming and sexual reproduction performance.

Multi-stemming is a survival strategy in response to chronic disturbance

As a first step to understanding the significance of resprouting and multi-stemming at Cape Vidal, the incidence of multi-stemmed trees was quantified. A high incidence of multi-stemming was found and 38.9% of individuals were multi-stemmed and all of the 20 most important species showed some degree of multi-stemming. Only five species (9.4% of 53 species) that had fewer than six occurrences in the whole sample did not show multi-stemming. A high incidence of multi-stemming indicates that resprouting and the persistence that it confers on individuals are important for survival of individuals under disturbance and stress (Kruger et al. 1997; Bellingham & Sparrow 2000; Bond & Midgley 2001).

To reveal the disturbance and stress factors that are responsible for the high incidence of multi-stemming, the relationship between multi-stemming and dune position, erosion, decumbency, canopy cover, nearest neighbour distance and *Isoglossa woodii* cover was investigated. Decumbency was measured as an indicator of disturbance by wind, erosion as an indicator of substrate instability and canopy cover, the incidence of *I. woodii* and nearest neighbour distance as indicators of competition. Multi-stemming was most strongly associated with decumbency followed by erosion, showing that wind disturbance and substrate instability are the most important factors influencing multi-stemming at Cape Vidal. Strong coastal

winds that occur in the area from August to October and a steep and loose substrate present disturbances to trees that are of low severity but nevertheless a chronic stress. Multi-stemmed trees are better able to persist through disturbances such as wind (Tanner & Bellingham 2006) and erosion (Sakai et al. 1995) because they dilute the risk of individual mortality among many stems. Multi-stemmed trees are also better competitors than single stemmed trees at Cape Vidal where soils are nutrient poor (Boyes 2006). Multi-stemmed trees have a competitive advantage over single-stemmed trees in unproductive or disturbed sites where there is little risk of being overtopped by faster growing but nutrient demanding species (Givnish 1984; Midgley 1996; Bellingham & Sparrow 2000).

Dune slacks with protection from wind and higher substrate stability had fewer multi-stemmed trees. Protection from disturbance offers safe sites for establishment of new individuals from seed and results in a prevalence of poor resprouters (Clarke 2002a, b; Clarke et al. 2005), hence the lower incidence of multi-stemmed trees in the protected dune slacks.

At Cape Vidal, multi-stemmed trees were not shorter than single-stemmed trees unlike in other habitats (Kruger et al. 1997). Trees on protected and stable dune slacks were taller than trees on dune crests and slopes that have unstable substrate and expose trees to sea winds. Trees that overtop the canopy would be susceptible to wind damage, whereas shorter trees would have less wind-induced mortality (Tanner & Bellingham 2006). Therefore, both the short stature and multi-stemming are the result of the plant-disturbance interaction and not a characteristic of a plant or species.

Phylogeny does not constrain resprouting

The possibility that resprouting is phylogenetically constrained was tested. No phylogenetic pattern in the expression of resprouting was found. Almost all species and lineages were found to be multi-stemmed. Generally, resprouting appears to be a labile trait that is not under phylogenetic control (Bond & Midgley 2003). A regional study also found resprouting to be independent of phylogeny (Clarke et al. 2005) as did a global meta-analysis of data from diverse vegetation communities with plants resprouting in response to various disturbance types (Vesk & Westoby 2004b). The prevalence of resprouting is influenced by disturbance and productivity more than phylogenetic history (Bellingham & Sparrow 2000; Clarke et al. 2005).

Resprouting varies with ontogeny

At Cape Vidal, trees resprout and become multi-stemmed at an early stage. In habitats with loose substrate, resprouting may be important during juvenile stages when the tree is still not properly anchored (Yamada & Suzuki 2004). Most angiosperm trees resprout as seedlings and saplings and lose the ability to resprout as adults (Del Tredici 2001; Yamada et al. 2001; Yamada & Suzuki 2004; Vesk 2006). Trees lose their resprouting ability as they grow older due to lack of resting buds, inability of sprouts to emerge through thick bark or inhibition of sprout growth due to high concentrations of compounds for resistance against wood-rotting organisms (Putz & Brokaw 1989).

Resprouting in seedlings differs from resprouting in juvenile and adult trees in terms of incidence of resprouting and form and function of resprouting (Vesk 2006). As found at Cape

Vidal, resprouting in seedlings usually serves to maintain a single shoot while vying for appropriate conditions for growth such as gap formation (Hara 1987). In contrast, in juvenile and adult trees, resprouting may result in multi-stemming (Ohkubo 1992; Del Tredici 2001). Resprouting in seedlings may be considered a part of the regeneration niche because it increases the chances of seedling recruitment, whereas resprouting in juvenile and adult trees may be considered a part of the persistence niche because it increases the chances of an established plant maintaining its position in the habitat (Bond & Midgley 2001, 2003).

Resprouting is not the only strategy in response to disturbance

After leaning due to disturbance, trees may regain the vertical orientation of the growing section (Mattheck 1995; Jiang et al. 2006), a process referred to as 'turning up' in this study (Nzunda et al. 2007). By using turning up, leaning trees may avoid losing the leaning primary stem unlike resprouting that may result in the loss of the primary stem. Loss of the primary stem results in delayed reproductive maturity which negatively influences species abundance (Crawley 1986). Hence, species that were more likely to undergo turning up were more abundant than species that were more likely to resprout after leaning. However, turning up could only be used by trees whose angle of decumbancy was small and were not eroded, which had to resprout to survive. Hence turning up can be used only where disturbances are of low severity.

Alternatives to resprouting are not restricted to habitats where leaning is the main effect of disturbance. For example in fire-prone systems, woody plants may avoid resprouting by growing fast and attaining large size and escaping the flame zone (Vesk 2006). The more commonly considered alternative to resprouting is reseeding whereby plants produce prolific

seed and recruit from seed after disturbance (Bellingham *et al.* 1994; Bond & Midgley 1995; Bellingham & Sparrow 2000; Bond & Midgley 2003; Miura & Yamamoto 2003). However, reseeding differs from all the other alternatives to resprouting because it results in a new generation of plants. Turning up and growing fast and large are similar to resprouting in terms of prolonging the life of the same individual.

Resource allocation to storage enhances resprouting ability

Resprouting in response to severe disturbances such as fire that consume all the aboveground biomass, depends on resources stored in belowground structures (Bellingham & Sparrow 2000; Bond & Midgley 2001; Vesk & Westoby 2004b). Trees that resprout in response to disturbances that allow survival of aboveground parts, such as leaning due to wind disturbance and erosion due to substrate instability, may not need belowground storage because they can remobilise resources from aboveground biomass (Sakai et al. 1997; Sakai & Sakai 1998). At Cape Vidal, good resprouters stored more resources below- and aboveground than do poor resprouters. However, since resprouting at Cape Vidal is mostly a response to leaning and erosion that do not destroy the aboveground parts, remobilisation of aboveground resources is favoured. In addition, the chronic disturbances of low-severity are occasionally punctuated by high-severity disturbances (e.g., dune slump). Thus good resprouters have more stored resources than poor resprouters below- and aboveground as a bet-hedging strategy that enables them to resprout using below- and aboveground resources depending on disturbance severity and type.

Carbohydrates may be stored by accumulation when they are in excess of demands for growth and maintenance and by reserve formation where they are partitioned between storage and growth and maintenance (Chapin *et al.* 1990; Knox & Clarke 2005; Lambers *et al.* 2006). Good resprouters at Cape Vidal store resources by reserve formation because the prevailing disturbance regime results in competition between growth and storage for carbohydrates. Low disturbance severity makes aboveground competition important and hence good resprouters have to allocate to height growth while the possibility of occasional severe disturbance necessitates reserve formation as a bet-hedge against future damage.

The costs of resprouting are traded off against growth and reprodution

Resprouting ability tends to be negatively associated with growth and reproductive performance due to allocation to storage and production and maintenance of buds that are necessary for resprouting (Keeley & Zedler 1978; Vesk & Westoby 2004a). At Cape Vidal, good resprouters had lower growth rates and produced fewer seeds of lower individual seed mass than poor resprouters. Good resprouters also produced seed only in some years whereas poor resprouters produced seed every year. As a result, good resprouters had lower seedling abundance and restricted recruitment of seedlings into juvenile and adult trees.

However, as is the case elsewhere, the lower recruitment of new individuals by good resprouters at Cape Vidal was compensated for by having higher persistence through recruitment of more sprout stems than poor resprouters (Kruger et al. 1997; Bellingham & Sparrow 2000; Bond & Midgley 2001; Nanami et al. 2004). Thus, good resprouters trade off recruitment of new individuals for persistence of established ones. Persistence of established

individuals is important where a chronic disturbance regime reduces individual survival and thereby the opportunities for reproduction. Through persistence, good resprouters improve their fitness in the long-run. Thus, good resprouters at Cape Vidal were most common on dune crests and seaward slopes that were exposed to strong sea winds.

Conclusions

- Resprouting and multi-stemming are survival strategies for chronic disturbance of predominantly low severity with occasional severe disturbance events at Cape Vidal. Trees resprout and become multi-stemmed to increase their chances of survival in response to leaning caused by strong sea winds and erosion and dune slump due to unstable substrate.

- The expression of multi-stemming is the result of the tree-disturbance interaction and not a property of a plant or species and is not constrained by phylogeny.

- Trees resprout and become multi-stemmed from an early stage. However, resprouting in seedlings mainly results in a single replacement shoot. Resprouting in seedlings is a part of the regeneration niche because it increases the chances of seedling recruitment whereas resprouting in juvenile and adult trees is a part of the persistence niche because it increases the chances of an established plant maintaining its position in the habitat.

- Chronic disturbance results in short tree stature regardless of multi-stemming because taller individuals would be exposed to wind damage and are disadvantaged.

- Because disturbance is of predominantly low severity, leaning trees can regain the vertical orientation of the growing section and hence survive without resprouting.

However, this can only happen when the angle of inclination of decumbency is small and when leaning is not accompanied by erosion.

- Good resprouters store carbohydrates below- and aboveground to increase their resprouting ability. Where low severity disturbances are not punctuated by high severity disturbances, belowground storage of carbohydrates is not required because plants can remobilise aboveground resources for resprouting. However, the occasional disturbances of high severity necessitate storage of carbohydrates belowground.

- Low severity disturbances make aboveground competition important and hence plants have to allocate carbohydrates to growth, while the possibility of high severity disturbances makes carbohydrate storage imperative. Hence carbohydrates are stored by reserve formation, which develops storage in competition with growth.

- Allocation of resources to storage diverts resources from reproduction. Hence, good resprouters produce less seed of smaller size. Lower investment in seed by good resprouters results in lower recruitment of seedlings and new individuals from seedlings. Hence, good resprouters had a low abundance of individuals, mainly comprising large trees with few small trees.

- The lower recruitment of new individuals by good resprouters was compensated for by higher recruitment of sprout stems that confer persistence of established individuals. Hence, good resprouters traded off recruitment of new individuals for persistence of established ones. In the long-run, persistence enhances fitness. Hence, good resprouters were most common on dune crests and seaward slopes that were exposed to sea winds.

Future directions in research on the persistence niche

A number of research issues that are related to the persistence niche in environments with chronic disturbance of low severity are still unexplored, including time to maturity, wood properties, defence against herbivory, longevity, mechanical resistance and seedling survival. In fire-prone environments, obligate seeders mature earlier than resprouters (Knox & Clarke 2005; Schwilk & Ackerly 2005). Because of the cost of resprouting in terms of allocation to storage found in this study (Nzunda et al. 2008a), poor resprouters in environments with chronic disturbance may also mature earlier than good resprouters.

Wood properties and defence mechanisms that enhance longevity may be necessary for poor resprouters if they attain larger size than good resprouters through living longer, but may not be necessary if they have short lifespan but attain large size by growing fast (Loehle 1988; 2000). Although good resprouters may live longer than poor resprouters, they may not necessarily need wood properties and defence that enhance longevity because the persistence of the individual is achieved through replacement of old stems by new ones (Ohkubo 1992; Karlsson et al. 2004).

Good resprouters are more likely to lean than poor resprouters (Sakai et al. 1997; Nzunda et al. 2007). Research into the relationship between resprouting ability and rooting characteristics and mechanical properties of stems (Mattheck 1995; Crook et al. 1997) may reveal whether the higher likelihood of leaning of good resprouters is only a function of more exposure to disturbance (Chapter 7) or is due to lower mechanical resistance of good resprouters than poor resprouters.

Apart from higher seedling growth rate for poor resprouters than good resprouters (Chapter 6), resprouting ability has also been associated with lower seedling survival (Bond & Midgley 2003). Experiments are needed to examine the relationship between resprouting ability of adult trees and seedling survival and confirm whether species with higher seedling resprouting ability have higher seedling survival as suggested by the results of this study (Nzunda et al. 2008b).

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