MULTI-STEMMED TREES IN SUBTROPICAL COASTAL DUNE FOREST: SURVIVAL STRATEGY IN RESPONSE TO CHRONIC DISTURBANCE

M. E. Griffiths, E. F. Nzunda and M. J. Lawes
Forest Biodiversity Research Unit, School of Biological and Conservation Sciences
University of KwaZulu-Natal, Pietermaritzburg

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Abstract

While much attention has been focused on resprouting by plants after large-scale disturbances, the ecological significance of sprouting from the base of undamaged stems in the absence of such disturbances has been overlooked. In adverse or unpredictable habitats multi-stemming facilitates the persistence of a tree through vegetative growth. This study investigated the incidence and conditions under which multi-stemming develops in Indian Ocean coastal belt forest at Cape Vidal. Overall, 38.9% of the trees sampled in transects were multi-stemmed. Using phylogenetic autocorrelation, we found no relationship between the ability to multi-stem and taxonomic grouping. Generalized linear models showed that multi-stemming was associated with wind disturbance, substrate instability, and competition. We also used a bootstrapping technique to investigate the stem size-frequency distributions of multi-stemmed individuals and found that stem sizes were more similar to each other than expected under random allocation of stems. This suggests that resprouting occurs once in response to a single disturbance event or that individual trees facultatively produce multiple stems from an early stage. Finally, although the forest at Cape Vidal is shorter than South African forests dominated by single-stemmed trees, we found no evidence of a trade-off between tree height and number of stems. This demonstrates that short stature is not a result of multi-stemming, but rather that both the short stature and the high incidence of multi-stemming are a response.

1. Introduction

Resprouting of plants is recorded in habitats worldwide. Most studies have focused on ecosystems subject to large-scale disturbance events such as floods, cyclonic storms, volcanoes, and fires. Following disturbance, many species resprout from dormant buds rather than regenerating from seed, allowing plants to recover quickly and maintain their presence in the ecosystem. Bond and Midgley (2001) argue that the importance of resprouting by established plants has been overlooked in plant demography and refer to resprouters as filling the “persistence niche.”

Some tree species also sprout in the absence of large-scale disturbance, producing multi-stemmed trees (Johnston & Lacey, 1983; Midgley & Cowling, 1993). There is very little large-scale disturbance in South African coastal dune forests but multi-stemmed trees are quite common. In this study we investigate the prevalence of multi-stemming in coastal dune forest and whether this trait is under phylogenetic control. We examine spatial patterns in the distribution of multi-stemmed individuals relative to environmental gradients within the forest. In addition, we conduct simulations to test for patterns in the stem sizes of multi-stemmed plants and identify the age at which multi-stemming is initiated. We also use generalised linear modelling to determine what environmental factors cause multi-stemmed trees to form. Finally, we compare canopy height of tree species relative to the number of stems per individual to determine whether a trade-off in resource allocation exists between growing multiple stems and vertical growth.

2. Methods

The study was conducted in the coastal dune forest at Cape Vidal (28°05'32"S, 32°33'40"E) in the Greater St Lucia Wetland Park, KwaZulu-Natal. Multi-stemming was examined for trees in twenty transects that were 300 m long × 5 m wide and divided into quadrats 10 m × 5 m in size. Transects were located approximately 50 m apart and oriented perpendicular to the longitudinal dune crests that run north-south, parallel to the coastline. For all trees with diameter at breast height (DBH) ≥ 1.5 cm we measured the number of stems, diameter at breast height for each stem, height, indications of disturbance or damage to the trees, and environmental conditions.

Character tracing and phylogenetic autocorrelation were used to assess the influence of taxonomy on expression of multi-stemming. Spatial patterns in multi-stemming were assessed with quadrat-variance analyses. Using bootstrapping we examined the stem size distributions of multi-stemmed individuals. The environmental correlates of multi-stemming were explored with generalised linear models. The possible trade-off between tree height and multi-stemming was also examined using linear regression.

3. Results

In total, 53 species were identified in this study. While most trees had a single stem, 38.9% were multi-stemmed. Of the 10 most important species at Cape Vidal, 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.

There was little phylogenetic pattern in the expression of multi-stemming. We found that multi-stemming occurred in almost all tree species regardless of their taxonomic placement and multi-stemming occurred in almost all phylogenetic lineages (Figure 1). Furthermore, a phylogenetic autocorrelation test confirmed that sprouting is not a phylogenetically controlled trait (data not shown).

We found that multi-stemmed individuals were randomly dispersed along transects (data not shown), implying both habitat-wide disturbance and contingent response by trees to disturbance. Although there was a significant difference in the number of multi-stemmed individuals per quadrat by dune position ($P < 0.001$), this difference was due to a significantly lower incidence of multi-stemmed individuals in the dune slacks only, compared to the other four topographic positions (Figure 2). In general, multi-stemmed individuals were randomly dispersed among all dune habitats that were subject to wind and substrate disturbance. The lower incidence of multi-stemming in dune slacks is likely a consequence of the stability of the substrate and the greater shelter from wind afforded to trees in these dune valleys.

Within multi-stemmed individual stems were significantly uniformly sized (data not shown). This suggests that the stems are all approximately the same age and initiated at the same time. We also did a comparison of size-frequency distributions of primary stems in single-stemmed and multi-stemmed trees (Figure 3). A Kolmogorov-Smirnov test found no difference between the distributions ($P = 0.997$), and we therefore conclude that multi-stemming is initiated in young trees in this tree community. Thus, it appears that in most species, trees facultatively grow multiple stems from an early stage in response to constant but low levels of disturbance.

Since local environmental conditions were thought to be important for the development of multi-stemming, the spatial pattern of multi-stemming was investigated on the assumption that multi-stemming incidence would reflect variation in local environmental conditions. The best-fit GLM showed that the most important variable affecting the numbers of multi-stemmed individuals was wind disturbance, followed by substrate instability, then by canopy and understorey competition.

A study by Kruger *et al.* (1997) found a significant positive relationship between forest canopy height and branching index, and a significant negative relationship between canopy height and the mean number of stems per individual ($P < 0.001$). Their data show that taller forests are dominated by species that branch near the canopy and have single stems. In contrast, forests with a greater frequency of multi-stemmed individuals tend to be shorter. The data from Cape Vidal are consistent with the findings of Kruger *et al.* (1997) (Figure 4).

Although the Cape Vidal forest is shorter than South African forests dominated by single-stemmed trees, a regression analysis suggested no trade-off between tree height and number of stems per individual (Figure 5; $P = 0.75$). The general trend suggests that investing in vegetative reproduction does not necessarily limit tree stature at this field site. Rather, both sprouting and tree height appear to be controlled by wind and substrate linked disturbances in dune forest habitats.

4. Discussion

Regeneration of forest trees by sprouting is more important than general accounts would suggest. A substantial proportion of the trees in the coastal dune forest at Cape Vidal were multi-stemmed. There were no phylogenetic constraints on multi-stemming and the spatial distribution of multi-stemming appears to be under environmental control.

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 can persist through resprouting (Ohkubo, 1992; Sakai *et al.*, 1997; Yamada & Suzuki, 2004). The Cape Vidal forest is also subjected to wind disturbance, an environmental factor that can select for individuals and species that grow multiple stems (De Steven, 1989; Sakai & Sakai, 1998; Vesk & Westoby, 2004). In addition, the sandy soils at Cape Vidal are highly susceptible to leaching and are nutrient poor, which would favour less competitive species that are better able to cope with a stressful environment. Thus, we suggest that winds, the unstable sandy substrate and low levels of nutrients, combine to confer a competitive advantage on, and the persistence of, multi-stemmed individuals on steep and seaward facing dune slopes.

Apart from facilitating the persistence of the plant, resprouting is predicted to have other life history consequences (le Maitre & Midgley, 1992; Bond & Midgley, 2003). Multi-stemmed trees may have limited vertical growth due to an allocation of resources to storage for resprouting (Midgley, 1996). The forest at Cape Vidal, with its high proportion of multi-stemmed individuals, is considerably shorter than the forests dominated by single-stemmed trees described in Kruger *et al.* (1997). However, we found no evidence of a trade-off between tree height and number of stems. Tree height at Cape Vidal appears to be constrained regardless of whether or not a tree is multi-stemmed. We argue that both the short stature and the high incidence of multi-stemming are a response to the chronic wind disturbance and substrate instability at Cape Vidal.

5. Conclusions

Multi-stemmed trees are a common feature of the Indian Ocean coastal dune forest. At Cape Vidal, multi-stemming appears to be a survival strategy in response to chronic disturbance. The advantage gained from sprouting is that a tree is able to persist through vegetative regeneration. This would hold the greatest advantage for a tree when it is in an environment that experiences long-term chronic disturbance or environmental stress. However, a potential cost of producing multiple stems may be that fewer resources are available for sexual reproduction (*sensu* Kruger *et al.*, 1997; Bond & Midgley, 2003). Another possible consequence of multi-stemming that has received little attention is that individual persistence through resprouting may reduce species turnover and community diversity in the long-term (Bond & Midgley, 2003). These points are the focus of continuing studies in the coastal dune forests at Cape Vidal.

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Addendum

Table 1. Top ten most important species at Cape Vidal and the percent of individuals that were multi-stemmed

Species	% Multi-stemmed
Diospyros natalensis	14.5
Mimusops caffra	40.2
Drypetes natalensis	45.7
Celtis africana	47.4
Ochna natalitia	31.6
Diospyros inhacaensis	11.2
Strychnos gerrardii	64.3
Sideroxylon inerme	72.6
Teclea gerrardii	25.7
Acacia karroo	37.4

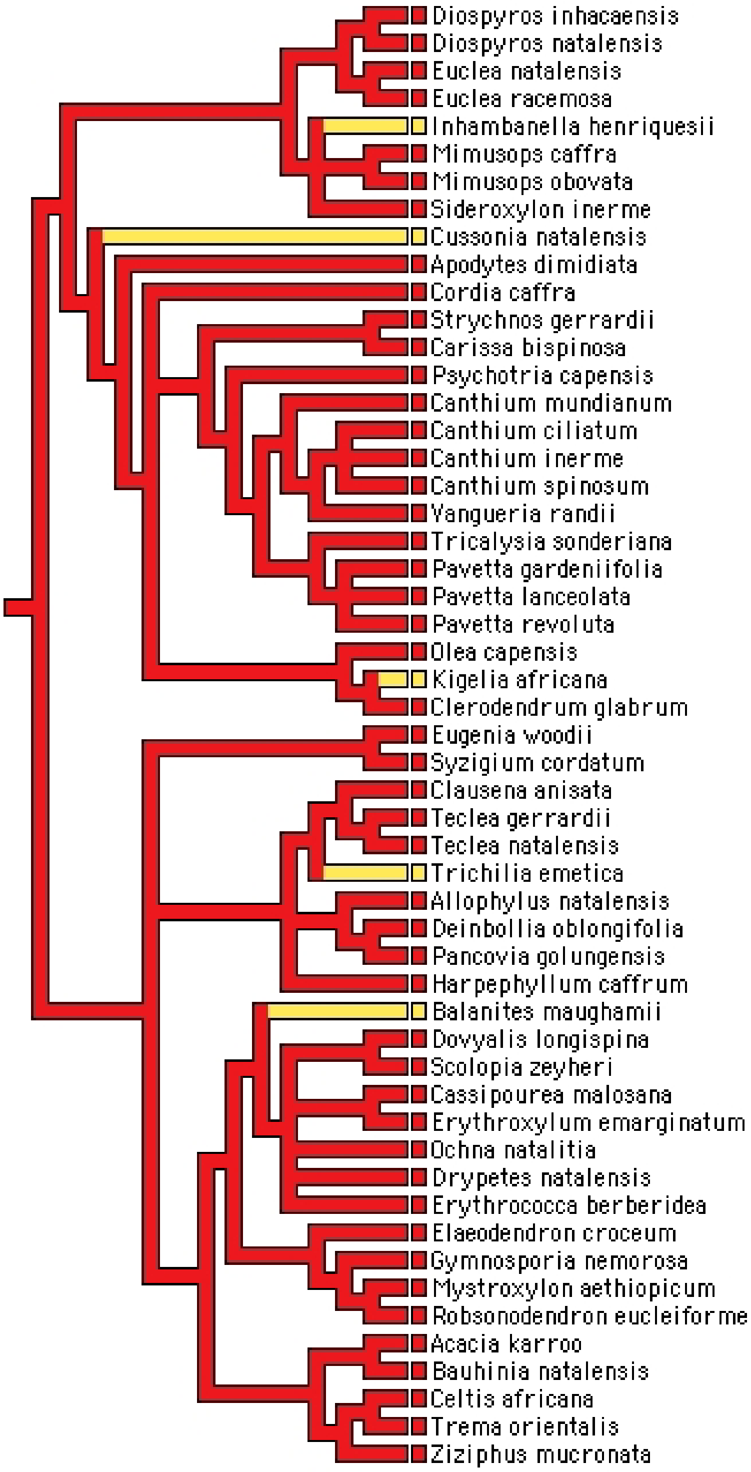

Figure 1. **A hypothesis of the phylogenetic relationships between species at Cape Vidal. Species with multi-stemming are indicated in dark and single-stemmed species are indicated by the light coloured lines.**

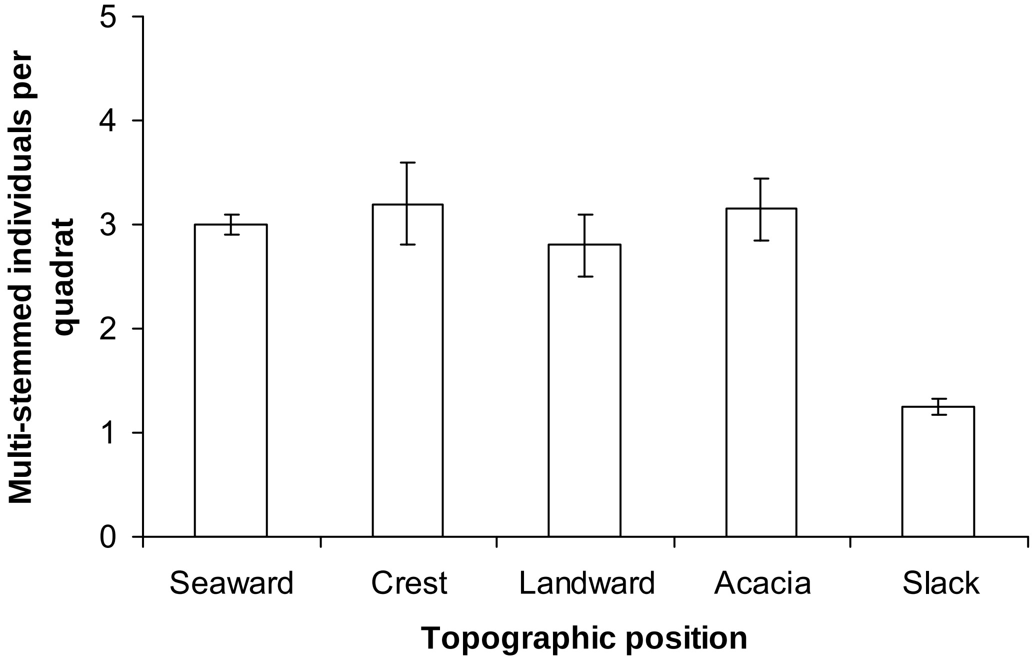

Figure 2. **A comparison of the incidence of multi-stemmed individuals by location on the dune topography.**

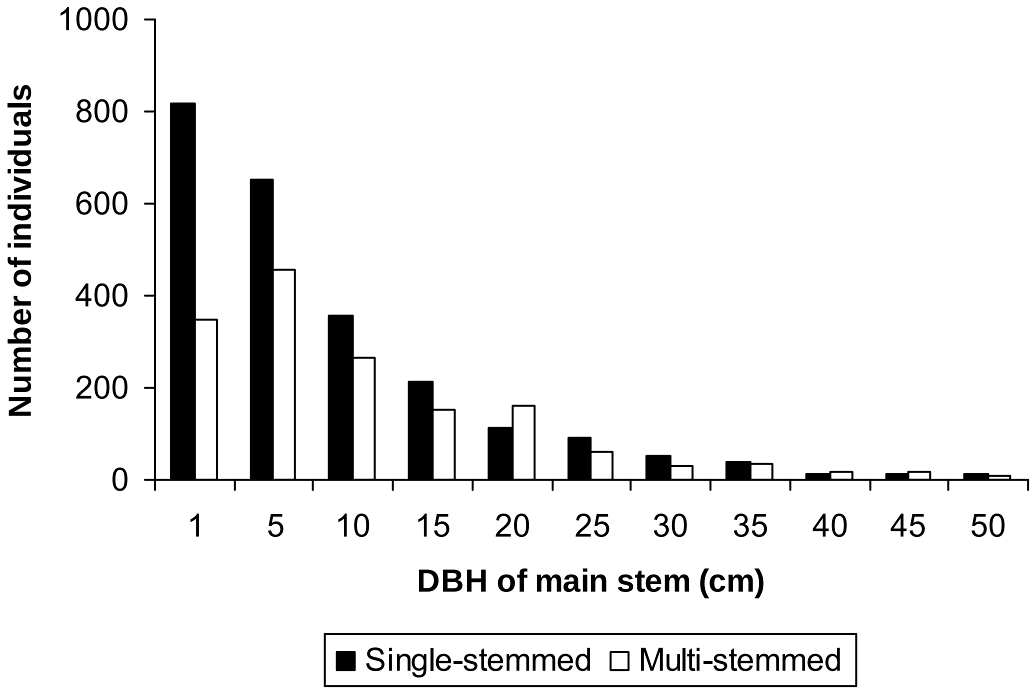

Figure 3. **Size class frequency distribution of single-stemmed and multi-stemmed trees at Cape Vidal.**

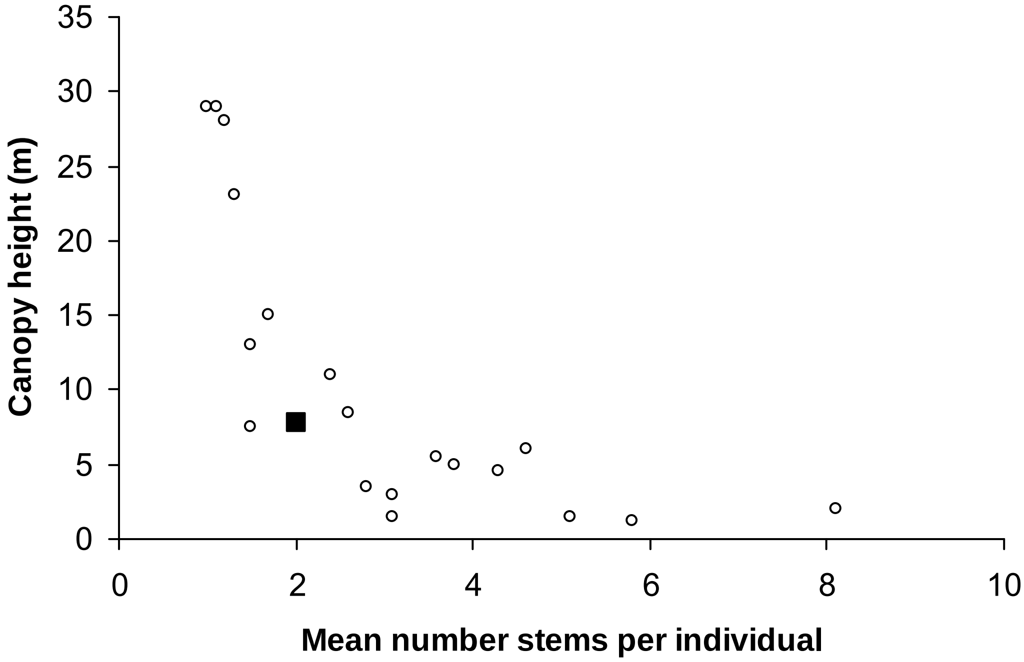

Figure 4. **Relationship between canopy height and mean number of stems per individual for southeastern Cape forests (from Kruger *et al.*, 1997) including a data point for Cape Vidal (shown as black square).**

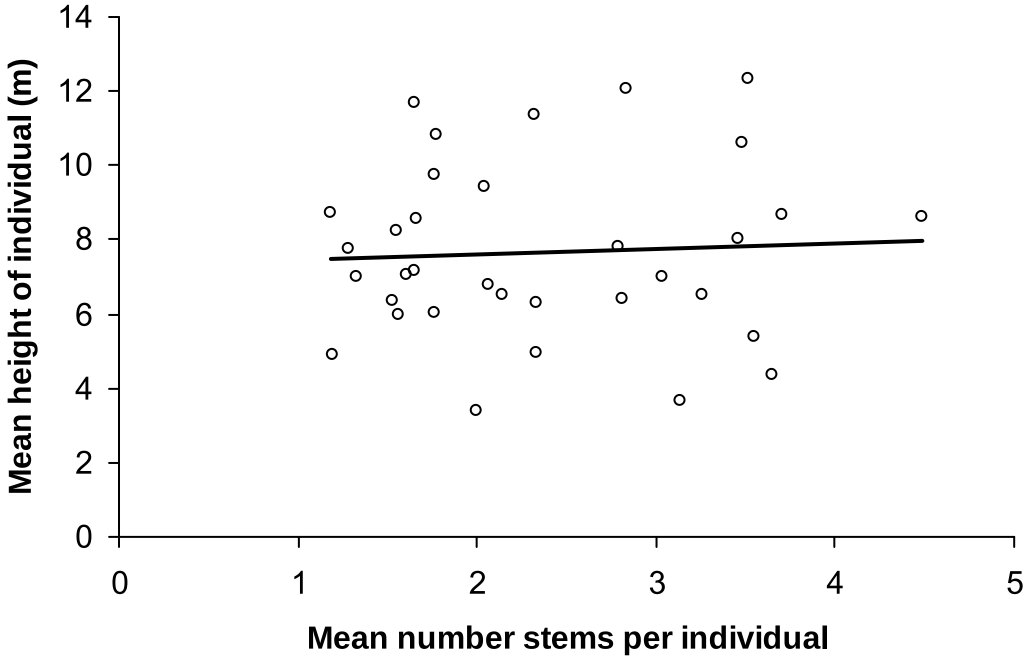

Figure 5. **Relationship between the number of stems produced per individual and the height of each individual at Cape Vidal.**