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Post-fire resprouting of *Colophospermum mopane* saplings in a southern African savanna

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Fire is a common feature of tropical savannas and it has an important role in the ecology and evolution of the flora. Many woody species in tropical savannas are well adapted to fire and have a vigorous resprouting ability that enables them to survive recurring fire (Frost & Robertson 1987, Hoffmann & Solbrig 2003, Meyer *et al.* 2005). Studies on the interaction between fire and woody plants in Mediterranean-climate regions have considerably increased our understanding of the subject but relationships between plant attributes (stem diameter and height) and post-fire resprouting ability of southern African savanna woody species are poorly understood. Resprouting is a widespread mechanism by which many plants regenerate after partial or total defoliation (Bellingham & Sparrow 2000, Bond & Midgley 2001).

Resprouting ability depends upon the anatomy of the plants (Verdaguer & Ojeda 2002), pre-disturbance size (Bowen & Pate 1993, Canadell & López-Soria 1998), disturbance intensity (Goto 2004, Vesk & Westoby 2004a, b), disturbance frequency (Morrison & Renwick 2000), soil fertility and water availability (Cruz *et al.* 2002, 2003). It has been hypothesized that resprouting ability in woody plants after defoliation increases with an individual's pre-disturbance size because larger individuals accumulate more reserves in below-ground organs and/or have more active underground buds (Ickes *et al.* 2003, Konstantinidis *et al.* 2005, Miura & Yamamoto 2003). In this regard, large individuals are expected to cause greater resprout density and growth than smaller individuals after fire (Meyer *et al.* 2005, Vesk & Westoby 2004a).

This study investigated post-fire resprouting ability of *Colophospermum mopane* (Benth.) J. Léonard (Leguminosae–Caesalpinioideae) saplings in relation to pre-fire plant size of burned individuals. *Colophospermum mopane* commonly known as mopane is a tree or shrub that occurs in southern and central Africa between latitudes 9°S and 25°S (Mapaure 1994). It provides fuelwood and building material for millions of rural people throughout its range, as well as browse for livestock and wildlife (Timberlake 1995). The study addressed two questions: (1) what are the post-fire resprouting patterns exhibited by *C. mopane* saplings? and (2) what factors influence such patterns? We tested the hypothesis that larger woody resprouters produce more resprouts and resprouts of larger height and diameter sizes than smaller resprouters after defoliation of above-ground organs by fire.

The study site is on City of Gweru open space lands, located 7 km south of Gweru (19°27′S, 29°51′E, 1400 m asl) on the highveld of Zimbabwe. The site receives annual rainfall of about 325–930 mm. Three climatic seasons are experienced at the site: a hot wet period from November to April, a cool dry period from May to July and a hot dry period from August to October. Mean monthly temperatures range from 14.6 °C in July to 22.3 °C in October. The site is characterized by shallow sandy loam soils derived from granite.

In August 2001 illegal fires burned much of the open grassland areas and part way into some patches of mopane. Flame heights were low, with plant matter above 2 m high not ignited, though severely scorched. Due to characteristics of the fire, mopane saplings at the site were heat-killed but not consumed by fire. In December 2001 (4 mo after fire), heat-killed mopane saplings on the study site were inspected for resprouting. Five randomly located plots of 100 × 100 m were marked in burnt patches of *Colophospermum mopane*-dominated vegetation. Since pre-fire stems were not consumed by fire, resprouted saplings could be categorized according to pre-fire basal diameter sizes (measured at 30 cm above ground) into

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Table 1. Repeated-measures ANOVA results of the effects of year, sapling size and their interaction on post-fire resprout number (RN), resprout maximum diameter (RMD) and resprout maximum height (RMH).

	RN		RMD		RMH	
Effect	F	P	F	P	F	P
Year	10.8	< 0.001	424	< 0.001	3.50	0.033
Sapling size	0.37	0.691	238	< 0.001	0.75	0.476
Year × Sapling size	2.93	0.06	14.4	< 0.001	0.99	0.417

small (2 –< 2.5 cm), medium (2.5 –< 4 cm) and large (4 –< 6 cm). Five resprouted saplings from each size category were randomly selected so that there were 15 saplings in each plot. Each sapling was marked with a numbered aluminium tag (2 × 4 cm) attached by copper wire to base of the largest pre-fire stem for future identification.

In December 2001 (the fire year 2001, hereafter Y0), the numbers of pre-fire stems per sapling were counted. Diameter and height of the largest and tallest pre-fire stems were measured respectively. In August of 2002 (Y1), 2003 (Y2) and 2004 (Y3), the numbers of resprouts (resprout number, RN), were counted, diameter of the largest resprout (resprout maximum diameter, RMD, cm) and height of the tallest resprout (resprout maximum height, RMH, cm) were measured. Resprouts identified in year Y1 were repeatedly measured until year Y3. For each sapling, the stem of the largest resprout was marked at 30 cm above ground level with a strip of white paint to ensure that subsequent measurements would be exactly at the same place.

Repeated-measures ANOVA was carried out using the General Linear Model command in SPSS version 10 to test the effects of pre-fire sapling size, time (year) since burning and their interaction on post-fire RN, RMD and RMH. 'Year' was specified as a within-subjects factor, 'sapling size' as between-subjects factor and RN, RMD and RMH as measures. Differences between means were tested using Tukey HSD *post-hoc* test with a level of significance of $P < 0.05$.

In each of the four years (including Y0), all sapling sizes had similar RN (Figure 1a, Table 1). Over the period Y0 to Y1, RN increased significantly by 32, 29 and 32% on small, medium and large saplings respectively (Figure 1a). No new resprouts were observed after year Y1. A significant decrease in RN was observed over the period Y1 to Y3 regardless of sapling size (non-significant year × sapling size interaction, Table 1). The number of resprouts decreased by 4.4, 3.9 and 3.4% on small, medium and large saplings respectively, over the period Y1 to Y3 (Figure 1a).

The diameters of resprouts increased significantly ($P < 0.05$) with increasing sapling size (Table 1, Figure 1b). Resprouts reached a diameter of 0.9 cm in small saplings, 2.3 cm in medium and 2.8 cm in large saplings 3 y after fire. In year Y3 (3 y after fire), RMD in all sapling sizes was still significantly ($P < 0.05$) lower than in year Y0. Diameters of resprouts on small, medium and large saplings were only 59, 28 and 38% of the diameters of pre-fire stems respectively (Figure 1b).

Although RMH was significantly higher ($P < 0.05$) in large saplings than in small and medium saplings in Y0, it was constant in all sapling sizes in each of the three post-fire years (Figure 1c, Table 1). Resprouts reached a height of 139.5 cm in small saplings, 137.8 cm in medium and 140.5 cm in large saplings 3 y after fire (Figure 1c). Resprouts in small, medium and large saplings were 17, 30 and 41% shorter respectively than their pre-fire height 3 y after fire.

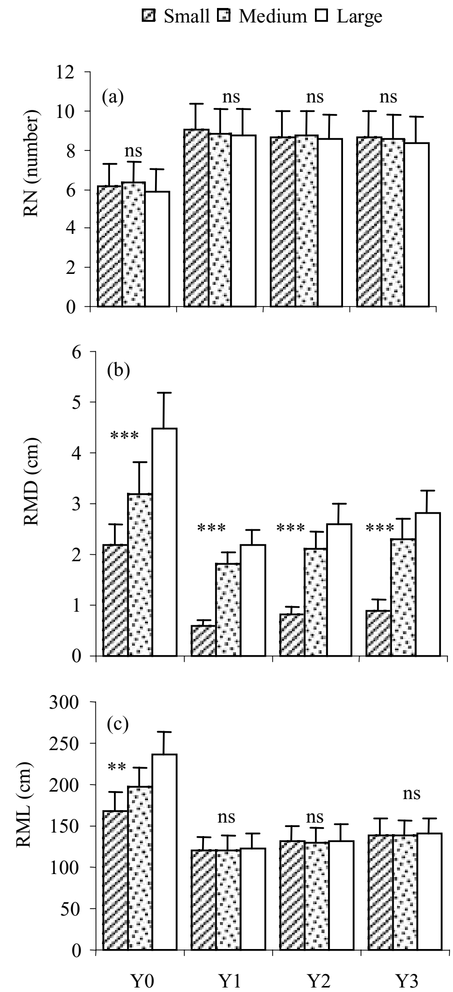

Figure 1. Post-fire resprouting patterns in small (basal diameter: 2 –< 2.5 cm), medium (2.5 –< 4 cm) and large (4 –< 6 cm) saplings of *Colophospermum mopane*; (a) resprout number (RN); (b) resprout maximum diameter (RMD); and (c) resprout maximum height (RMH). Resprout number, RMD and RMH of heat-killed saplings were measured 4 mo after fire and annually in the month of August for resprouts for a further 3 y. Y0 refers to the year prior to fire and Y1, Y2 and Y3 to first, second and third years after fire respectively. Values shown are means (± SE) and differences among sapling sizes for each period are indicated as: (n.s.) $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2. Diameter and height growth of resprouts after fire in small (basal diameter: 2 –< 2.5 cm), medium (2.5 –< 4 cm) and large (4 –< 6 cm) saplings of *Colophospermum mopane*.

	Sapling size			
	Small	Medium	Large	
RMD growth (cm y^{-1})				
Y0-Y1	0.68 ± 0.12^a	1.86 ± 0.24^b	2.28 ± 0.28^c	***
Y1-Y2	0.23 ± 0.04^a	0.32 ± 0.03^b	0.45 ± 0.07^c	**
Y2-Y3	0.14 ± 0.02^a	0.21 ± 0.04^b	0.29 ± 0.03^c	**
RMH growth (cm y^{-1})				
Y0-Y1	121 ± 15.5^a	120 ± 15.1^a	122 ± 16.7^a	n.s.
Y1-Y2	10.2 ± 2.3^a	9.98 ± 1.9^a	10.4 ± 2.5^a	n.s.
Y2-Y3	7.89 ± 1.4^a	8.20 ± 1.6^a	8.40 ± 2.1^a	n.s.

(n.s.) $P > 0.05$; (**) $P < 0.01$; (***) $P < 0.001$. Different superscript letters (a, b and c) in the same row indicate significant differences between means (Tukey's HSD, $P < 0.05$).

Resprouts in all sapling sizes grew most rapidly in the first year after fire (Table 2). However, both diameter and height growth slowed considerably after this initial growth spurt. Resprouts of large saplings grew in diameter faster than resprouts of small and medium saplings during the 3-y growth period. No significant difference ($P > 0.05$) in height growth was observed between all sapling sizes (Table 2).

The diameters of resprouts increased significantly ($P < 0.05$) with increasing pre-fire sapling size while RN and RMH were constant. This result suggests that mopane achieves greater site occupancy in a fire-prone habitat by maximizing RMD whilst maintaining RN. Alternatively, the resprouting strategy of maintaining a constant RN could be an artefact of the relatively cool-burning fire in 2001 at our study site (Bellingham & Sparrow 2000). Resprouting may be controlled by pre-fire plant size and resource reserves in two ways: (1) number of dormant buds surviving and then induced; and (2) growth rate per induced bud. Different species may allocate resources proportionately to number of induced buds and resprout growth rates in different ways. Although we have no information about the relationship between resource reserves in mopane plants and resprout production, a lack of correlation has been reported in other species (Cruz *et al.* 2002, 2003; Sparks & Oechel 1993).

Large mopane saplings did not produce resprouts of larger height sizes than smaller saplings. Although a number of studies have found a positive relationship between plant size and resprout height, the contradiction reported in this study may be attributed to differences in life history traits among species. At sapling stage, mopane appears to invest more biomass towards diameter growth than height growth. Trees in fire-prone savannas need to build a permanent long-lived, fire-tolerant trunk in order to become part of the mature canopy (Hoffmann & Solbrig 2003). While this growth habit has an advantage in fire-prone savannas, it may be costly in less fire-prone forest environments. For example, where light is the most limiting resource, it is advantageous for species to invest more in height growth than in diameter growth so as to over-top neighbours and access light (Sterck & Bongers 2001). The primary trait preventing fire damage in many savanna woody plants is the ability to develop a thick bark that insulates the cambium from high fire temperatures (Gignoux *et al.* 1997). While height is also effective in preventing top-kill, the low stature of mopane in fire-frequented habitats precludes the possibility that the species has evolved height as an adaptive response to fire.

There was a significant increase in RN per *C. mopane* sapling after fire. As RN increases, more resources are allocated towards the development of these resprouts and buds rather than maximizing height growth. Most saplings had one large resprout surrounded by resprouts of smaller diameter sizes, suggesting that more resources are allocated to the former than to the latter. Regardless of sapling size, RN decreased significantly over the period Y1 to Y3. This decline indicates gradual self-thinning of the resprouts at a rate which, if projected over *c.* 10–15 y would probably return RN to pre-fire year levels.

Mopane resprouts showed high rates of height growth immediately after fire. The presence of resource reserves in below-ground organs allowed top-killed mopane saplings to present an immediate reaction after defoliation by fire and to grow at a high rate (viz. Bowen & Pate 1993, Canadell & López-Soria 1998). Although mopane resprouts showed high rates of height growth immediately after fire, fast growth rates were not sustained over time. Rapid height gain during the first year after fire increases the chances of resprouts getting above flame height. In southern African savannas, individuals below 3 m tall have a high probability of top-kill, whereas individuals above this height usually suffer negligible shoot damage (Trollope 1984).

The slow growth rate observed after first year of resprout growth implies that top-killed mopane saplings may require many years to regain their pre-fire size. During this period of regrowth, saplings remain highly vulnerable to damaging agents including browsing animals and additional fires. Shoot dieback during the dry season may also limit sapling height growth. In fire-frequented communities, recruitment of saplings into mature size classes depends on rare opportunities when an individual gains sufficient height between fires to escape top-kill (Higgins *et al.* 2000). Apart from growing above flame height, stems should reach a certain diameter size that is less affected by fire. In southern African savannas where *C. mopane* grows, fires can be so frequent that saplings have to resprout for decades before they manage to emerge above the lethal fire zone (Higgins *et al.* 2000).

Although mopane saplings have ability to resprout after disturbance, fire may convert mopane of high stature into scrub mopane. Resprouts may lose the ability to move into the next size category, even if a fire-free period occurs due to an inability to allocate resources effectively because of competition between buds and shoots (Fensham & Bowman 1992). Investment in height growth for multi-stemmed saplings may be costly for both resource allocation and structural reasons. Single-stemmed saplings can divert resources to maximizing rates of vertical extension. Tall multi-stemmed saplings will be relatively poorly supported in comparison to single-stemmed saplings of the same height (Midgley 1996). Multi-stemmed mopane saplings generally have narrower stems than single-stemmed saplings.

We have shown that mopane's resprouting strategy is to maintain RN (and RMH) and maximize RMD. The choice to maximize RMD vs. RN and RMH may be a life history strategy of building a permanent long-lived, fire-tolerant stem in order to become part of the mature canopy. Further studies are required to investigate factors that may limit resprouting success following defoliation. Unravelling these factors is important in order to have a clear understanding of the mechanisms that control resprouting in African savanna fire-persisters.

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