

How do fires kill plants? The hydraulic death hypothesis and Cape Proteaceae “fire-resisters”

J.J. Midgley*, L.M. Kruger, R. Skelton

Botany Department, University of Cape Town, Private Bag Rondebosch 7701 South Africa

Received 4 May 2010; received in revised form 1 October 2010; accepted 1 October 2010

Abstract

The actual mechanism which causes plant death after having been burned has been poorly studied. One possibility is that fire causes direct, or indirect, fatal damage to plant hydraulic systems. If true, this suggests that burned plants ultimately die of drought. This hypothesis was tested on the post-fire response of a “fire-resister” species of the Cape Proteaceae, as well as by analysing its morphology. Fire-resisters are plants which are incapable of resprouting, but nevertheless survive some fires. Mortality of the studied fire-resister appears to be compatible with a hydraulic death hypothesis because i) most post-fire mortality occurred within days, ii) it occurred from the base-upwards and iii) correlated negatively with stem diameter rather than plant height. Higher levels of survival of the fire-resister is probably due to absolutely thicker bark than co-occurring re-seeder species of the same age. Since this bark has not evolved to protect buds, it has probably evolved to protect stem hydraulic systems.

© 2010 SAAB. Published by Elsevier B.V. All rights reserved.

Keywords: Fire ecology; Proteaceae; Top-kill; Fire death; Hydraulics

1. Introduction

Fires typically only burn or incinerate the leaves and terminal parts of stems of live plants, yet all above ground parts of some plants may die after fire. Here we ask if post-fire death is caused by damage to the xylem (hydraulic death), or to the phloem (stem-girdling death) or the cambium and buds (meristematic death)? Surprisingly there has not been much research into how fires actually cause plant death (Midgley et al., 2010). Instead post-fire mortality has traditionally been considered to be caused by death of buds in the canopy and/or in the cambium (e.g. Bond and van Wilgen, 1996). Cambium necrosis, a consequence of a reasonable period of heating to 60 °C, can now be modelled in relation to fire and stem properties (Michaletz and Johnson, 2007).

However, it is not clear whether cambium death is the primary cause of plant death. Other plant tissues may be more sensitive to heating. Ducrey et al. (1996) simulated fire impacts by applying electrically heated pads to varying proportions of

the circumference of *Pinus halepensis* stems. They took various eco-physiological measurements over a period of time from after the fire until plant death. Their aim was to determine which of these eco-physiological measurements, best predicted eventual stem death. Electrical resistance of the cambium (an indication of tissue vigour) was unaffected after heating and only declined just before these trees died. This suggests that cambium is not the most sensitive tissue to fire damage. All the trees that later died after heating, suffered significant water stress (such as lower and declining sap flux density) immediately post-fire. This led Ducrey et al. (1996) to speculate that plant death could come from a range of causes including heat induced cavitation of xylem and increased rates of air seepage through heat damaged bark. Balfour and Midgley (2006) showed experimentally that top-kill (death of the canopy and above-ground stems) is not caused by excessive fire damage to the canopy, but rather that it is rapidly manifest after heat is applied to the stem. Xylem occlusion was visible in cross-sections of heated stems.

To further understand whether hydraulic failure could cause stem and canopy death, we studied the evolutionary ecology and fire response of a member of the guild of *fire-resisters* in the

* Corresponding author. Tel.: +27 21 6505868; fax: +27 21 6504041.

E-mail address: Jeremy.Midgley@uct.ac.za (J.J. Midgley).

Cape fynbos. In the Cape Proteaceae most species die after suffering top-kill in fires (Le Maitre and Midgley, 1992). A minority of species is able to produce new growth after fires, from buds on buried lignotubers at the base of top-killed stems (i.e. they are basal reporters). An even smaller minority of species (stem reporters) is able to subsequently report from epicormic stem buds (mainly just *Protean nitida*). Amongst the reseeders are a small group of *fire-resisters*. In these species, some individuals in a population do not die despite their canopies being burned. It is not known how they survive fires, although it is clear that they cannot resprout from buds on the stem or lignotuber. Nevertheless, unlike all other reseeders, a proportion of a population of the *fire-resisters* is able to survive some fires. This is demonstrated by *fire-resisters* typically having mixed size-class distributions (Midgley et al. 1998). As far as is known, *fire-resisters* are rare in other parts of the world. *Fire-resisters* are useful for understanding the ecological and evolutionary aspects of surviving fire because they can survive fire but cannot resprout.

Clues to the causes of fire-induced mortality can be obtained from measurements of the rapidity of death of reseeders and resisters after fire. This is rarely measured. Post-fire death of stems due to cambium/meristematic death should take a considerable period of time, of the order of months to seasons to years. This is because cambium death would prevent subsequent meristematic differentiation of new xylem and phloem tissues. The lack of this new tissue would take a prolonged period to kill a plant. Phloem death effectively ring-barks or girdles a stem and this too should have a delayed impact on mortality. This is because ring-barking would prevent the downward supply of photosynthates to roots. Once roots had used up stored reserves, they would eventually die of starvation. After root death, leaves would then die of drought due to lack of hydraulic supply. In contrast to the above two slow-acting aspects, direct damage to plant hydraulics would have a relatively rapid impact on canopy death due to dehydration. Thus the rapidity of plant post-fire mortality is informative as to the process causing the mortality.

A second perspective on the hydraulic death hypothesis is whether plants die from the bottom-up or top-down. If survival of *fire-resisters* is dependent on apical meristems surviving, then we would expect plants to die from the top down. In other words if the apical meristems survive a fire, the plant will survive. Alternately, if damage to plant hydraulics is important, we would expect the plant to die from the bottom-up. This is because fires in short vegetation are most intense relatively close to the ground as opposed to in the canopy and beyond (Trollope, 1984). For example, sustained high temperatures occur at 0.6 m in savanna fires compared to temperatures at 0.01 m and 1.6 m (Miranda et al., 1993). If apices survive a fire but later die, hydraulic failure lower down on a stem where fire intensity is highest, may have caused this surviving apex to eventually die of dehydration.

Thirdly, from an evolutionary perspective, we asked, what attributes have *fire-resisters* evolved to resist the impacts of fire? In particular do they have relatively fast height growth that may allow them to escape canopy damage in fires or do they

have thick bark which may protect the stem? Many studies have shown that post-fire survival is correlated with relative bark thickness (e.g. Hoffmann et al., 2009). Relative bark thickness is the ratio of bark to stem. It is not known whether relatively thick bark is to protect epicormic buds or stem hydraulics or both. Fire resisters do not have epicormic buds, therefore the presence of thick bark in these species could suggest the thick bark evolved to protect the stem hydraulics. Rourke (1972) suggested the *fire-resister* *Leucospermum conocarpodendron* has relatively thick bark, but he provided no comparative information on bark thickness in relation to stem diameter. *L. conocarpodendron* individuals that survive several fires are able to grow fairly tall (5 m) and it is possible that the acquisition of thick bark is merely a consequence of their large diameter. Also, the critical question is whether fire resisters have absolutely thicker bark not relatively thicker bark; in other words whether *fire-resisters* have thicker bark than reseeders of the same post-fire age. There has been almost no comparative work on the morphology of the guild of *fire-resisters* in Cape fynbos. Unfortunately, there are only about 5 species of *fire-resisters* in Cape Proteaceae and this limits statistical comparisons with re-seeders. The most prominent fire-survivors are *Mimetes fimbriifolius*, *Leucadendron argenteum*, and *L. conocarpodendron*, with only the latter species being relatively widespread.

2. Materials and methods

2.1. Plants and study site

This study focussed on *L. conocarpodendron* a species which occurs on Cape Peninsula as well as on adjacent SW Cape mountains (Rourke, 1972) and is able to grow 3–5 m tall. Other co-occurring Proteaceae, such as *Leucadendron argenteum*, *Leucadendron lauroleum* and *Protea repens* were included in this study to a lesser degree. The study area was located on the northern slopes of Table Mountain below Devils Peak that experienced an arson fire during the late afternoon and evening of March 17th 2009. Because the fire burned at night time, it was not very intense and did not consume all the leaves of the proteoid shrubs (see Fig. 1). Field work began 10 days later on March 27th and continued up until April 2nd 2009. Re-measuring took place three months later (25th July).

2.2. Field observations

- i) To demonstrate the rapidity of impact of the fire on the timing of plant mortality (sudden or slow), we marked 30 live plants and 30 dead *L. conocarpodendron* plants, 10 days after the fire. Dead plants were defined as those that had no live leaves after the fire, whereas live plants were those that had live leaves on at least some apices after the fire (see Fig. 1). The aim here was to determine whether plants which have no live leaves after the fire (i.e. appear to be dead), do not later recover and produce new leaves. All of the above plants experienced some degree of heat or burning during the fire as was evidenced

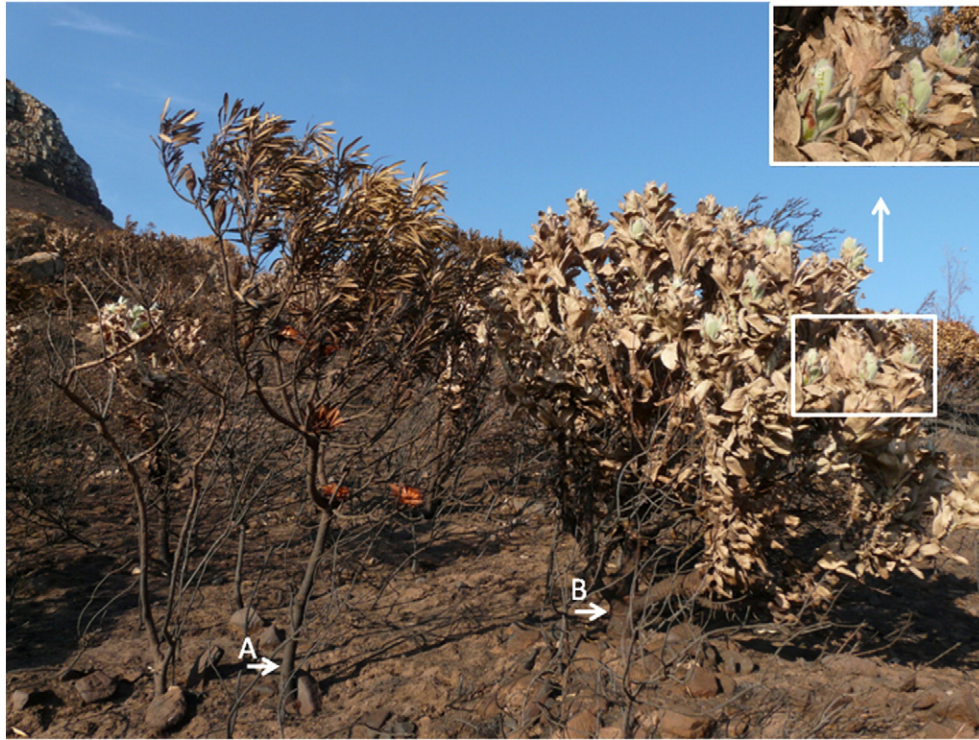


Fig. 1. *Protea repens* (A) a relatively tall but thin-stemmed reseeded co-occurring with *L. conocarpodendron* (B) a relatively short but thick-stemmed *fire-resister*. Inset indicates apices of B which survived the fire.

by a predominance of dead leaves on all plants (see Fig. 1). The marked plants were revisited 3 months after the fire to determine whether they were alive. At this time we also surveyed mortality of *L. conocarpodendron* by walking two randomly selected transects through the population. Eighty-two plants were measured for height, diameter and survival. Some of the plants initially with live leaves later died, but none of the plants labelled dead after the fire later produced any new leaves, confirming that they had died soon after the fire. This suggests that categorising plants as dead by the absence of live leaves after the fire is reasonable. We also followed the above approach on 10 live and 10 dead plants of the co-occurring reseeded *L. lauroleum*.

- ii) To demonstrate the rate of branch death that would occur as a consequence of fire-induced phloem and cambium death, we ring-barked a live terminal branch on each of 20 individuals which survived the fire. We removed a complete cylinder of bark and cambium that was 5 cm long, 20 cm from the apex. We inspected these stems 3 months later.
- iii) To demonstrate whether stem death occurs towards the apex or near the base, we cut branches every 10 cm for 30 cm from the apex towards the base and determined whether the stem was alive at the point of cutting. We defined live as the presence of a clearly visible green photosynthetic layer immediately below the bark surface and a light pink coloured xylem. Dead was defined as the presence of brown flaking bark and brown xylem. These

differences were readily apparent. Microscopic investigation, such as in Balfour and Midgley (2006), was not practical given the 1–3 cm thickness of woody stems we needed to cut. We used 10 live and 10 dead branches of *L. conocarpodendron*, 10 live branches of *L. lauroleum* (reseeded) and 15 live branches of *Leucadendron argenteum* (resister).

- iv) To demonstrate likely mechanisms of fire resistance in *L. conocarpodendron*, we compared it with co-occurring reseeded Proteaceae, for plant height and stem diameter at 20 cm above ground level for 30 pairs of plants of the same age and which were growing close enough together (base < 1 m apart) to have experienced similar fire intensity. We based the pairs on *L. conocarpodendron* individuals which survived the fire. By checking with node counts we could be sure we were comparing reseeded and *fire-resister* plants of the same post-fire age.

For comparisons of relative bark thickness between *fire-resisters* and reseeders, we measured bark thickness in relation to stem diameter in a number of individuals for seven Proteaceae species occurring on Table Mountain (see Table 3) with a minimum of 30 measurements per species. We chose unburned plants to reduce the impact of fire on bark thickness for thinner branches. To determine relative bark thickness, we correlated bark thickness (log mm) with stem diameter (log cm) and used the resulting equations to determine bark thickness at three standardised stem thicknesses (1, 2 and 5 cm).

2.3. Glasshouse observations

- v) To determine the rates of impact of ring-barking on whole plant mortality, we ring-barked 5 individuals of the reseeded *Protea repens* saplings (0.5 m tall, 1 cm basal diameter) growing in bags in a greenhouse. We removed a 5 cm cylinder of bark, 5 cm from the base of these saplings. This avoided the need to potentially kill plants in the field.

3. Results

Fire impacts are rapid (<10 days) because 76% of the mortality expressed at 3 months was expressed soon after the fire (Table 2). All of the *L. laureolum* plants alive after the fire, subsequently died. Thus mortality rates were 100% for burned reseeders (*L. laureolum* and *P. repens*), whereas survival for *L. conocarpodendron* was 37.8%, or 38.8% if the two tall individuals (Fig. 2) which were survivors from a previous fire, were included.

None of the branches we ring-barked died, except for those on 3 (out of 20) plants in which the whole plant subsequently died during the 3 month post-fire period. It took two months for ring-barked saplings to all die.

When we sectioned stems we found lower stem mortality for the apical section than the basal sections (Table 1), despite bark thickness being greater lower down on stems. Dead branches tended to have more dead sections of stem than branches which survived the fire. For example 8 out of 10 surviving *L. conocarpodendron* branches had live stems at 30 cm from the apex, whereas only 3 of the 10 dead stems had live stems at 30 cm (Table 1). Across all three species, branches with live apices after the fire had 29 out of 35 apical sections of stem alive

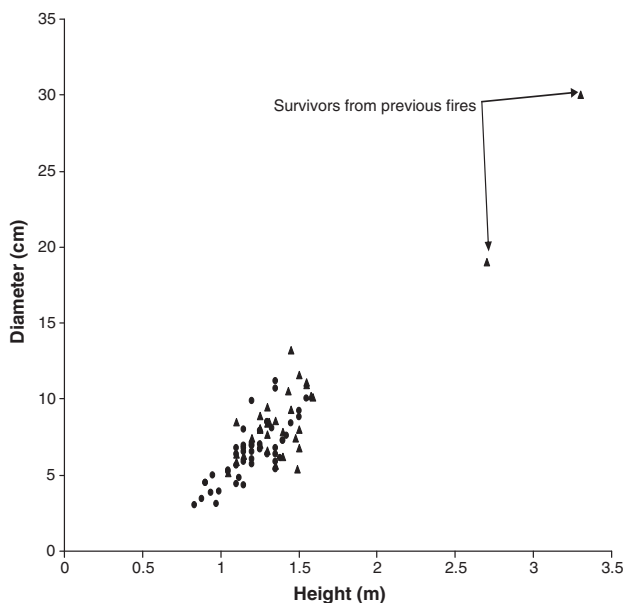


Fig. 2. Height versus stem diameter allometry of the fire-resister *L. conocarpodendron*. Triangles indicate fire survivors, including two large individuals that survived a previous fire. Rectangles indicate individuals which died in the fire.

Table 1

Assessment of branch post-fire survival in 10 cm lengths along a 30 cm terminal branch from the apex downwards. Alive branches had some surviving leaves, whereas dead branches had no live leaves 10 days after the fire.

	Apical 10 cm	Middle 10 cm	Basal 10 cm
<i>L. conocarpodendron</i> (n = 10)			
Alive branch	10	8	8
Dead branch	3	1	2
<i>L. laureolum</i> (n = 10)			
Alive branch	6	5	2
<i>L. argenteum</i> (n = 15)			
Alive branch	13	6	3

(83%), whereas only 13 out of 35 (37%) of basal sections were alive.

L. conocarpodendron has slower height growth than co-occurring reseeded Proteaceae (Table 2), but it nevertheless has relatively faster stem diameter growth (Table 2; see also Fig. 1). In all cases, *fire-resisters* such as *L. conocarpodendron* have a higher slope in stem diameter versus bark thickness regressions (Table 3). Therefore by 5 cm in stem thickness, *fire-resisters* always have relatively thicker bark than reseeders. The relative bark thickness of *L. conocarpodendron* is similar to that of the epicormic sprouter *P. nitida* (Table 3).

4. Discussion

4.1. Causes of terminal branch death

The dominant impact of the fire was rapid (plant death within 10 days), whereas the impact of ring-barking (simulated cambium and phloem death) was prolonged. No ring-barked branches died and the totally ring-barked *Protea repens* saplings took seven weeks to all die. This suggests that cambium and phloem death cannot explain the rapidity of stem death after fire.

Some individuals of *L. conocarpodendron* and *L. laureolum* were still alive 10 days after the fire but subsequently died. This death was clearly not due to fire induced mortality of meristems but could be due to progressive dehydration caused by damage of plant hydraulics. Stem damage appeared to be greater lower down the stem, in other words plants die from the bottom-up. In some cases live apices were surviving off a terminal section of stem water because the stem was clearly dead lower down on

Table 2

Mean plant height and diameter of similar aged co-occurring Proteaceae reseeders (*L. laureolum* and *P. repens*) and *fire-resister* (*L. conocarpodendron*) in relation to fire survival. Initial survival was determined 10 days after the fire and final survival, 3 months after the fire.

	Ht (m)(s.d.)		Diam (cm)(s.d.)		Survival %
	Initial	(Final)	Initial	(Final)	
<i>L. conocarpodendron</i>	1.38 (0.23)	9.86 (3.20)	100	(76)	
Reseeders	1.69 (0.24)	7.22 (2.43)	13	(0)	

Table 3

Slope and intercept of the correlation (log–log), between bark thickness (mm) and stem diameter (cm), as well as estimated bark thickness (mm) at 1, 2 and 5 cm stem diameter, for several Cape Proteaceae occurring on Table Mountain.

	Slope	Intercept	r ²	1 cm	2 cm	5 cm
Reseeders						
<i>Protea repens</i>	0.646	−0.59	0.91	1.11	2.01	3.15
<i>L. lauroleum</i>	0.583	−0.61	0.91	0.95	1.00	1.00
<i>Protea lepidocarpodendron</i>	0.611	−0.41	0.93	1.59	2.78	4.24
<i>Protea coronata</i>	0.680	−0.62	0.91	1.15	2.17	3.46
Resisters						
<i>Leucadendron argenteum</i>	0.969	−1.01	0.96	0.91	2.21	4.37
<i>L. conocarpodendron</i>	0.887	−0.59	0.95	1.98	4.46	8.24
<i>M. fimbriifolius</i>	0.799	−0.51	0.97	1.97	4.10	7.14
Epicormic resprouter						
<i>Protea nitida</i>	0.915	−0.60	0.94	2.07	4.80	9.02

the same branch. This indicates that apex branch survival is more likely than is hydraulic survival of lower branches, i.e. plant hydraulics is more sensitive to fire damage than are plant apices.

4.2. Height, diameter and bark thickness impacts on fire survival

Amongst species, stem diameter is a better predictor of post-fire survival than is plant height because despite being shortest, *L. conocarpodendron* survived fire best (Table 2). In terms of height growth *L. conocarpodendron* is a relatively slow-growing species (Midgley and Kruger, 2000).

Even within species, stem diameter is a better predictor than is plant height. The mean height of *L. conocarpodendron* individuals which survived the fire (1.34 m) was only 12% greater than that of individuals which died (1.20 m), whereas mean stem cross-sectional area of survivors (mean diameter of 8.45 cm) was 53% greater than of those that died (mean diameter of 6.82 cm). This analysis ignored the two largest individuals (see Fig. 2). Also, 19 of the 31 survivors had greater stem thickness than predicted for their height (Fig. 2).

It is not stem thickness, nor relative bark thickness which allows individuals to resist fire, it is their absolute bark thickness. *L. conocarpodendron* has greater absolute bark thickness than reseeders of similar age because it has both greater relative bark thickness and faster stem diameter growth rates (Tables 2 and 3). Most *fire-resisters* tend to have relatively thick bark and therefore at all stem thicknesses they have thicker bark. *L. argenteum*, also a *fire-resister*, is an exception in that it does not have thick bark below 3 cm stem diameter (Table 3). However, it would nevertheless have absolutely thick bark because it grows very rapidly (Midgley and Kruger, 2000). In *fire-resisters* the insulation provided by thick bark is not to protect buds because they have no latent buds (aside from buds in axils of live leaves). The development of a thick bark will not protect exposed apical meristems because these apical stems are not thick (<1 cm stem thickness and <2 mm bark thickness). The thickest bark will occur at the base of the plant where branches join into a single-stem. This is where fire

intensity is highest (Trollope, 1984) and therefore where the main stem and therefore the individual plant, is most prone to hydraulic damage. Epicormic resprouters need thick bark to protect both the buds and the hydraulics. The epicormic resprouter *P. nitida* has relatively thick bark, but not thicker than *L. conocarpodendron*. Data on stem diameter growth rates of *P. nitida* are needed to determine which species has the thickest absolute bark (i.e. the fastest bark thickness growth rates).

4.3. Causes of mortality

Our data suggests that plants ultimately die in fires due to dehydration. To resist hydraulic damage non-sprouters have evolved thick bark. Two synergistic mechanisms could explain mortality patterns based on hydraulic damage during fire. Firstly, a run-away hydraulic damage process could be caused by the plume of hot dry air produced by the fire, suddenly penetrating the plant canopy and rapidly increasing leaf moisture deficits. This stress would then be transferred to the hydraulic system, because the passage of the heat plume (a few seconds) is far faster than the reaction time of stomata. Secondly, the heat of the fire could directly damage the plant hydraulics by causing cavitation in the xylem. However, since some apices of both reseeders and *fire-resisters* survived the fire but later succumbed, it therefore appears that having a live apex does not guarantee that cavitated xylem can be repaired or refilled even under a negative water potential.

At our study site several 15–20 m tall *Pinus pinea* individuals that co-occurred with *L. conocarpodendron*, died in the fire. The canopy of these dead individuals was some 15+ m taller than the *L. conocarpodendron* individuals which, paradoxically, survived the fire. The death of these tall individuals cannot be explained in terms of an “escape height” paradigm where tall canopies avoid damage to apical buds. We suggest that the heat-plume effectively removed more water from the pine canopy than the hydraulic system could supply and this coupled with direct heat damage to the stem, fatally damaged the hydraulic system, which then resulted in death.

The hydraulic death hypothesis can be used to make testable predictions. For example, it predicts that the moisture status of plants will influence post-fire mortality. Thus a fire which occurs when plants are moisture stressed will be more damaging than when plants are less moisture stressed. This is because the greater the water tension in the xylem, the more likely it will cavitate upon heating by fire. Similarly, deciduous trees will suffer relatively more fire damage when they are leafed-out in summer, than when leafless in winter, because the latter case they will not suffer heat plume impacts on leaves.

References

- Balfour, D., Midgley, J.J., 2006. Fire induced stem death in an African acacia is not caused by canopy scorching. *Austral Ecology* 31, 892–896.
- Bond, W.J., Van Wilgen, B.W., 1996. *Fire and plants*. Chapman Hall, p. 263.

- Ducrey, M., Duhoux, F., Huc, R., Rigolot, E., 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to base of trunk. *Canadian Journal of Forest Research* 26, 1366–1374.
- Hoffmann, W.A., Adasme, R., Haridasan, M.T., De Carvalho, M., Geiger, E.L., Pereira, M.A.B., Gotsch, S.G., Franco, A.C., 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* 90, 1326–1337.
- Le Maitre, D., Midgley, J.J., 1992. Plant reproductive ecology. In: Cowling, R. (Ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity*. Oxford University Press, pp. 135–174.
- Michaletz, S.T., Johnson, E.A., 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22, 500–515.
- Midgley, J.J., Kruger, L.M., 2000. Senescence in Cape Proteaceae. *Journal of Mediterranean Ecology* 1, 181–185.
- Midgley, J.J., Enright, N.J., Cowling, R.M., 1998. Demography and co-existence of two ecologically equivalent Proteaceae. *Australian Journal of Botany* 46, 501–505.
- Midgley, J.J., Lawes, M.J., Chamaille-Jammes, S., 2010. Turner review: savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* 58, 1–11.
- Miranda, A.C., Miranda, H.S., Dias, I.F.O., De Sousa Dias, B.F., 1993. Soil and air temperatures during prescribed cerrado fires in Central Brazil. *Journal of Tropical Ecology* 9, 313–320.
- Rourke, J.P., 1972. Taxonomic studies on *Leucospermum* R.Br. *South African Journal of Botany* 50, 171–236.
- Trollope, W.S.W., 1984. Fire behaviour. In: Booyesen, P.de.V., Tainton, N.M. (Eds.), *Ecological effects of fire in South African Ecosystems*. Springer Verlag, Berlin.