# Predicting the post-fire responses of two forest tree precursors after an autumn fire in mountain fynbos.

Fire in a *Cunonia capensis* stand.

A Botany honours project by **Marc Caplan**

Supervisor: **Prof W.J.Bond**

University of Cape Town 1993

## Abstract

This study investigated whether post-fire survival of two fynbos forest precursors *Rapanea melanophloeos* (L). Mez and *Kiggelaria africana* L. were dependent on plant size or fire intensity. Two possible mechanisms of size dependent survival were investigated; 1) is fire survival the (ability to resprout) related to concentrations of root stored nonstructural carbohydrates (TNC) or 2) the protection afforded to epicormic buds through the thermal properties associated with bark thickness.

Different sized saplings (4-40mm in basal diameter) of both species were planted before a controlled burn in autumn. TNC analysis was performed on a sub-sample of 5 plants from each size class prior to the burn. After the burn discriminant analysis were used to compare which pre- and post-fire variables are the most precise predictors of sprouting. Cambium death was found to be an accurate post fire predictor of mortality of both *K.africana* and *R.melanophloeos* saplings. Stem height and basal diameter were good predictors of post-fire mortality of *R.melanophloeos*. Fire survival of *K.africana* was independent of size, whereas *R.melanophloeos* showed a size dependent mortality, and trees with a basal diameter greater than 14mm having a 0.78 probability of surviving the fire and a 0.67 probability of resprouting. Size dependent fire survival was not related to root TNC concentrations but to the survival of meristematic initials. These findings suggest that current fire management practices which favour cool burns, promote the expansion of forest patches into fynbos.

## Introduction

The mountains of the southwestern Cape which receive more than 650 mm rainfall per annum support two very distinct vegetation systems, fynbos and afromontane forests (McKenzie et al. 1977). Forests occupy sheltered habitats such as stream banks, rocky outcrops and gorges and appear as islands in a sea of fynbos. Studies by Manders (1990) and van Daalen (1981) suggest that forest distribution could be more extensive if it were not for frequent fires in adjacent fynbos shrublands. Fynbos usually burns at intervals of 10 to 60 years, with fire intensity being related to the accumulation of biomass during time intervals between fires and season of burn (Van Wilgen 1982). Forests seldom burn as the litter layer is normally moist and the canopy has a high water content (Granger 1984; Van Wilgen et al. 1990). However, forests may burn under very dry conditions caused by bergwinds (air descending from the central plateau) (Geldenhuys 1987). Forest trees survive fire by sprouting new shoots, in some cases up to a year following fire (Martiens Pers comm).

Forest pioneers establish in fynbos between fires and are limited by seed dispersal and the differential abilities of seedlings to survive in the open (Manders and Richardson 1992). Pioneer seedlings have to grow large enough between fires, to be capable of resprouting before the next fire. If growth is too slow seedlings will be killed and fynbos will dominate the post fire environment. Plant survival may depend only on size and not on fire intensity, or may be dependent on fire intensity only (Manders et al.1992).

The biology of fire survival is generally very poorly understood, with few general rules to guide fire management strategies (Reinhardt and Ryan 1989; Bond unpublished). Predicting the loss of forest saplings due to fire is an important tool for managers of mountain catchments (Van Wilgen 1990). Forests patches may prevent erosion of streams but large forest patches may reduce run-off. Hence experimental studies are needed to help predict conditions necessary for forest colonization, including the minimum size's at which forest trees can survive fire after a given fire intensity.

Fire intensity varies with season of burn, and is a major factor determining species survival (Trollope 1984). In the fynbos the most damaging fires occur at the end of the dry summer (February-March). High intensity summer fires every 15-25 years favour the cyclic development of a serotinous proteiod overstorey at the expense of resprouting forest species. If fynbos is not burnt for over 45 years the development of forest species may preclude fire (Manders et al. 1992). The longer the interval between fires, the greater the probability of recruitment into fynbos by forest precursors, which leads to processes of forest nucleation and subsequent habitat ~~amelioration~~ Transformation (Manders and Richardson 1992). Forest nucleation facilitates the following habitat amelioration, reduced light intensities in the understorey, which promotes seedling establishment (Manders 1990), a greater abundance of perches for birds which disperse forest seeds, the buffering of seedlings from wind, increased soil available water (Manders and Richardson 1992) and the exclusion of flammable fynbos species (Van Wilgen et al. 1990).

## Research Approach

Plants are able to resprout after fire if they posses heat resistant epicormic buds on lignotubers, root crowns and stems (Pate et al.1991), and if they have immediate access to an energy source to initiate new shoot and root material (Bowden 1991). If the fire is very intense it may kill the growth points preventing regrowth. It is assumed that if the epicormic buds are not damaged, regrowth is dependent on the levels of root stored carbon, provided that all the photosynthetic apparatus is incinerated.

These are therefore two possible mechanisms which may explain size dependent fire survival.

Firstly, large plants should have sufficient root stored total nonstructural carbohydrate reserves to produce new shoots (Mallanson and Trabaud 1988) and secondly, age related thickening of the bark may reduce damage to the cambium (Ryan and Steele 1989). Whether these mechanisms underlay forest pioneer fire survival was addressed in this study. The findings would improve our predictive understanding of fire survival. Specific objectives were to test whether, (a) fire survival is size dependent, (b) whether such a dependency is due trends in nonstructural carbohydrate accumulation in the roots, or (c) due to damage of meristematic tissue.

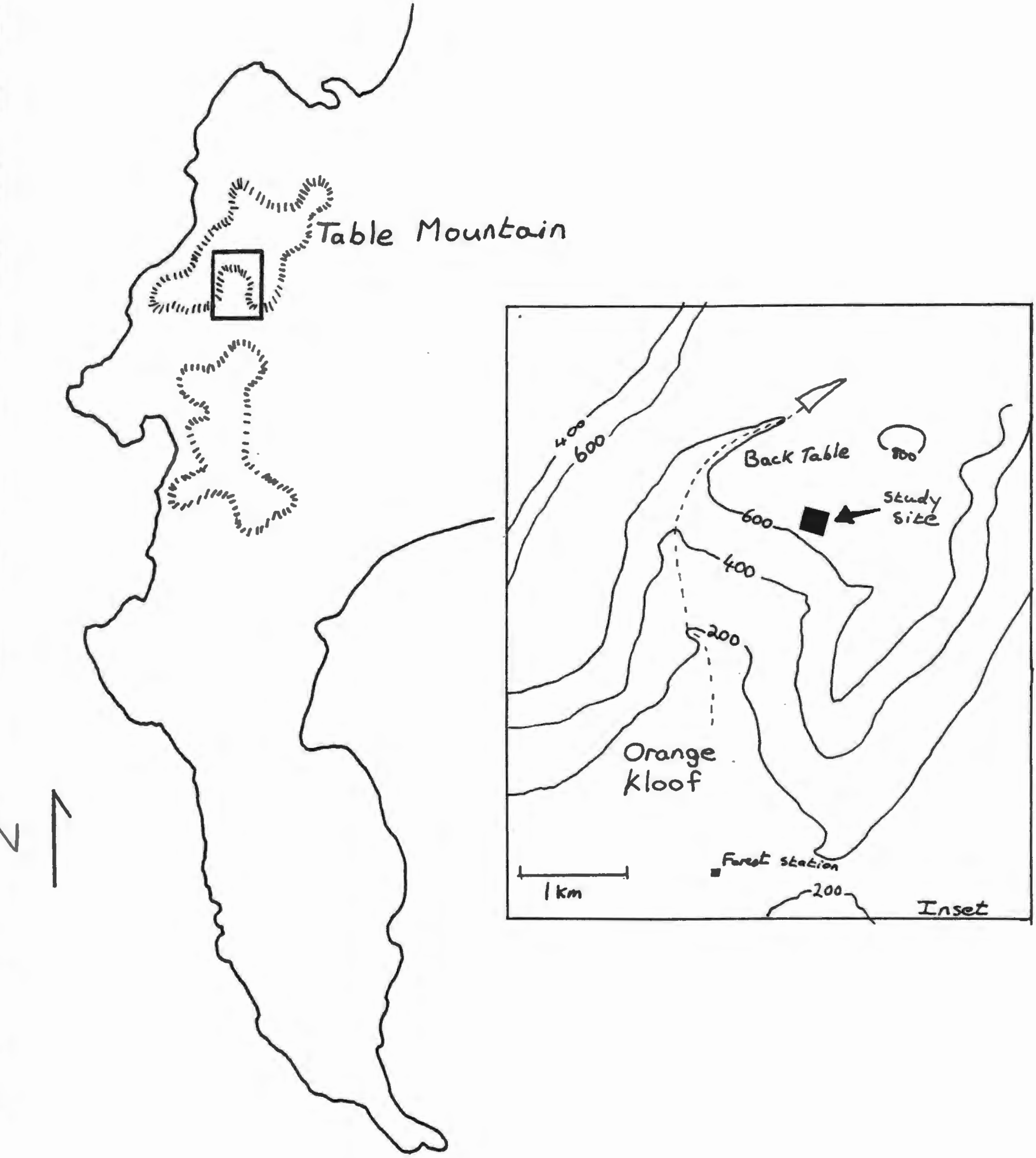

Fig. 1. Location of study site on the Cape Peninsula

## Materials and Methods

### Study site

The study was conducted above Orange Kloof at the southern end of the Table Mountain massif, Cape Town, South Africa (33° 59' 1 S., 18° 24' 7 E) (Fig. 1). The area used for the study falls within the Table Mountain Nature Reserve, and is administered by the Municipality of Cape Town. The site slopes (0.5-1°) westward, and is roughly 728 m above sea level. The soil is a mixture of peat and Table Mountain Sandstone and is approximately 40-120 cm deep. The site is mid-slope but poorly drained and was waterlogged during the heavy rains. The site is exposed to strong winds and is frequently covered in mist. Most of the precipitation falls during winter between April and August and the summer is usually hot and dry (Fig.2).

The site was dominated by *Erica hispidula* a low shrub (0.5 m), *Penaea mucronata*, *Tetratria flexuosa Thamnochortus gracilis*, *Leptocarpus membranaceus* and *Chondropetalum* sp.

### Selection of species

Three known forest pioneers: *Rapanea melanophloeos* (L.) Mez, *Kiggelaria africana* L. and *Cunonia capensis* L. were selected for their ability to colonize fynbos. The study specifically examined the post fire survival of *R.melanophloeos* and *K.africana*. *Cunonia capensis* saplings were used only to compare fire parameters. All species were present immediately adjacent to the study area. Four sizes were selected of the *R.melanophloeos* and three sizes of the *K.africana* (size classes were determined by height and bag size), *Cunonia* saplings were all of the same size. All the plants were acquired from nurseries in plastic bags, containing a silt and loam substrate mixture. A total of 15- 25 saplings were planted per size class, for both *R. melanophloeos* and *K. africana* and a total of 20 *C.capensis* saplings were planted. All saplings received adequate supplies of water during the hot weather before the

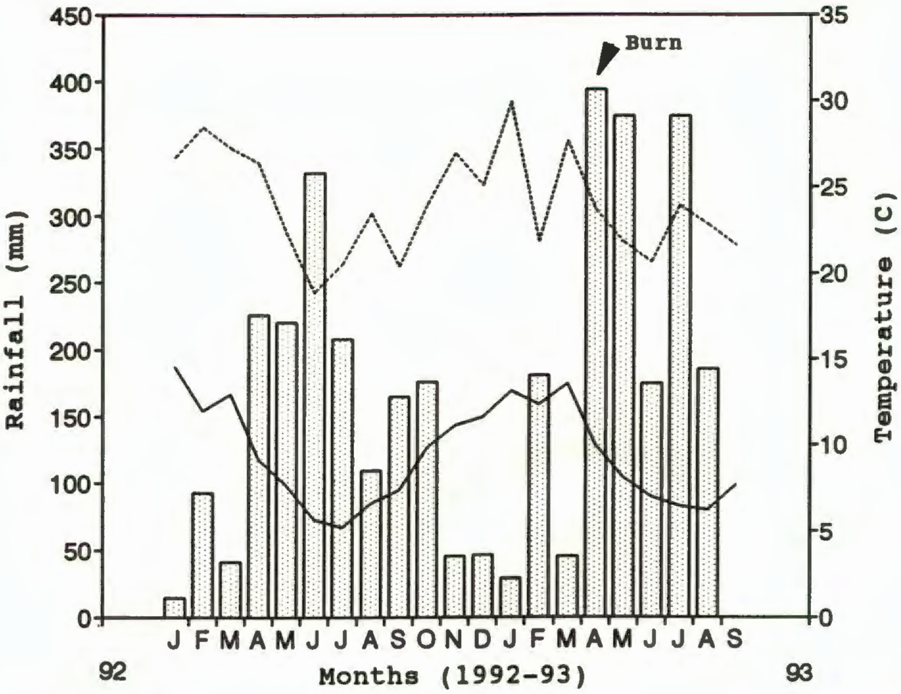

**Fig. 2.** Mean monthly maximum and minimum temperatures and monthly precipitation from stations close to the study site. (temperature data comes from Kirstenbosch N.B.G. and precipitation is recorded at the De Villiers Reservoir, less than 1 km from the site).

**Fig. 3.** Randomized grid layout of *R.melanophloeos* stand, each sapling is 1 meter apart.

burn and no plants died from water stress.

## Project design

This study took advantage of prior knowledge of a controlled burn on the back table of Table Mountain, which took place on the 28th of April 1993. Saplings of each species were planted in separate but adjacent sites, to simplify planting, removing and monitoring procedures. Each site was divided into one metre square grids, which left enough space between plants to prevent physical interactions, and allow the spread of the fire through the fynbos shrubs (Fig. 3). At each grid intersection a sapling was planted. A completely randomised layout was used at each site. Plants from each size class underwent three treatments.

A) Five individuals from each size class were removed before the fire and then replanted immediately after the fire. These control plants (unburnt) could indicate if sapling mortality was caused by environmental factors besides fire. Plants were left in plastic bags with the bottom removed, to prevent root damage during removal and replanting.

B) Another 5 individuals per species, per size class were not planted and their roots were analyzed for total nonstructural carbohydrates.

C) The remaining 5-15 plants were left in the soil to be burnt by the fire. Physical dimensions of height and basal diameters at 1cm above ground were taken for all plants.

## Fire behaviour and weather

The windspeed was estimated using a fan anemometer with cumulative counter. This was done before and after the fire and held about 1.7 m above the ground. Wet and dry bulb temperatures were recorded before the fire. Rate of spread was estimated from a video taken of all the plots during the fire. Flame length was determined from video footage and photographs, taken during the fire.

Interpretations based on the specific effects of fire on a particular vegetation need to include estimates of fire intensity. Fynbos fire intensity has been empirically related to flame length (Van Wilgen et al.1985), providing a useful indication of fire behaviour in the field. Van Wilgen et al.(1985) suggest that in fynbos field estimates of fire intensity from flame length should use Chandler's et al (1983) formula:

$$\mathbf{I} = 3(10\mathbf{h})^2$$

where **I** is fire intensity (Kw $m^{-1}$) and **h** is flame length (m), as it accounts for +/- 20% of the variation within the intensity range of interest.

As fire intensity can vary within three orders of magnitude in a small spatial scale (van Wilgen et al. 1985), separate estimates of fire intensity were calculated for all 11 m by 6 m plots containing trees of the same species. On the day of the fire fuel properties were made as homogenous as possible, by placing branches of surrounding shrubs in stands between the saplings.

## Post fire monitoring

Cambium mortality was measured by staining stem tissue with tetrazolium, in the first week after the fire. Living cells are made visible by reduction to insoluble pink and red formazan in the presence of a colourless tetrazolium salt (Kramer and Kozlowski 1979). A small wedge of stem tissue 4 cm above the ground was cut out and stained with 0.5 M tetrazolium in a Petri-dish for 20 min. Saplings which had wedges of tissue staining red were scored as surviving the burn. Those which had no stain were presumed to have dead cambial tissues.

Flame damage was assessed for every individual by recording the minimum height of visible discoloration on the stem. Unfortunately the percent canopy burnt was not measured as strong winds after the fire defoliated burnt and unburnt saplings. Plants were checked monthly for/ any visible sign of regrowth was taken as a positive sign. At the end of the experiment the rootstock cambium of those plants which had not resprouted was penetrated to determine whether the plants still had living underground tissue (a green cambium indicated intact meristem). Following which the impact of fire on all the trees was categorised into three response groups:

1) killed by fire (no living root tissue),
2) alive but had not resprouted (living root tissue),
3) successful resprouting (buds or leaves).

Measurements of bark thickness were taken after the fire to test the possible relationships with basal diameter and stem height.

### TNC analyses

Five unplanted *R.melanophloeos* and *K.africana* trees (per size class) were transported to the laboratory for the determination of nonstructural carbohydrate levels in the roots (treatment B). The soil was washed away from the roots which were severed and frozen in liquid nitrogen to arrest enzyme activity. In a frozen state the roots were placed in brown paper bags and oven dried at 60°C until constant dry weight. Dry samples were weighed and ground using a Wiley mill (20 mesh). A sub-sample for each individual was selected and milled to a finer particle size (40 mesh). Samples were stored in a desiccator containing silica gel, until further analysis.

The milled samples of root tissues were analyzed for total nonstructural carbohydrates (TNC) using a modified Weinmann method (Smith 1981). The enzyme amyloglucosidase (Sigma Chemical Co.) was used to hydrolyse the starch, instead of mylase. Reducing power was measured using the Shaeffer Sommogyi copper-iodometric titration method described by Heinze and Murneek 1940 (in Smith 1981), with gelatinized starch solution as the indicator. TNC content is expressed as percent dry mass and TNC pools calculated by the multiplication of TNC concentration with root dry weight. These values give an accurate indication of starch and sugar content.

## Discriminant Analysis

Discriminant Analysis (DA) was used to determine whether the variables measured could successfully predict pre-defined fire response groups (i.e. survival\ mortality). A discriminant function analysis tries to produce functions from variables used so that the best possible match to *a priori* groups are made (Klecka 1980). DA estimates discriminant functions for classifying future observation of resprouting ability on the basis of individual predictor variables (Klecka 1980). Discriminant functions scores were calculated from the first unstandardized discriminant coefficient and used to compute the position of the data in discriminant space. The following predictor variables were used for each sapling; stem height, basal diameter, minimum burn height and tetrazolium score. The classification accuracy rate is the proportion of correct classifications by the discriminant functions. This rate is compared to an estimated probability of survival for the entire population. If the predictor variables clarify the pre-defined groups, linear regression will indicate which variables are the most accurate. The classification accuracy can be seen by plotting the position of the data cases in discriminant space, using variable's which are highly correlated to the first discriminant function score (Klecka 1980). Statgraphics statistical package was used for all these analyses.

## Results

The head fire (Fig. 4) was of a low intensity typical of burns at the beginning of autumn, as weather conditions were mild (Table 1.) and heavy rains had fallen earlier in the month (Fig.2). Despite the damp conditions the fire behaviour varied within and between the different stands (Fig.4)(Table 2). Flames in the *R.melanophloeos* stand destroyed only about half the canopy of the larger leaves (Figs 4 & 5). The fire was generally more intense in the *K.africana* than *R.melanophloeos* stand (Table 2.), and the *C.capensis* stand experienced the most severe flames (front cover), with mean fire intensities almost ten fold, and maximum fire intensities three fold that in the *R.melanophloeos* stand.

**Table 1.** Weather conditions on the day of the fire.

| Temperature (C) | Humidity (%) | Wind velocity ($m.s^{-1}$) |
|---|---|---|
| 15.5 | 67 | 1.1 S.E |

**Table 2.** Individual stand fire behaviour parameters for the three forest tree pioneers.

| Spp in plot | Rate of fire spread ($m.s^{-1}$) | Mean flame length (m) | Mean fire intensity (Kw $m^{-1}$) | Max. fire intensity (Kw $m^{-1}$) |
|---|---|---|---|---|
| *Rapanea* | 0.15 | 0.50 | 75 | 558 |
| *Kiggelaria* | 0.25 | 0.70 | 147 | 972 |
| *Cunonia* | 0.17 | 1.45 | 631 | 1875 |

**Fig. 4.** Head fire moving through the *R.melanophloeos* stand.

**Fig. 5.** Unburnt (controls) and burnt *R.melanophloeos* on the day following the fire, note that all the fynbos surronding the trees has been burnt.

## Post fire responses

*R.melanophloeos* and *K.africana* that survived the fire resprouted shoots from unburnt sections on the stem often from below ground. The first resprouting (from the base) began three months after the fire in mid-July. By the end of September most of the plants which had survived the fire had resprouted. All the unburnt plants which had lost their leaves resprouted from bud initials located on branches. The high fire intensity in the *C.capensis* plot scorched the stems black to the ground, very few leaves remained on each tree. After five months only two *C.capensis* individuals reprouted from the root stock.

Table 3 illustrates that post-fire survival of *K.africana* and *R.melanophloeos* is probably determined by the degree of damage to cambial tissue. Tetrazolium is ~~very~~ a very accurate predictor of mortality but not of regrowth (Table 3).

**Table 3**. Predictions based on cambium condition (dead or alive) immediately after the fire vs observations of mortality and resprouting five months later. (sample size; *K.africana* (42), *R.melanophloeos* (38).

| Species | Mortality | | Survival | |
|---|---|---|---|---|
| | predicted | observed | predicted | observed |
| *Kiggelaria* | 21 | 20 | 21 | 13 |
| *Rapanea* | 13 | 10 | 25 | 14[a] |

[a] significantly different to the predicted response (Chi squared=4.05, p=0.05).

## Analysis

Interpretation and classification of observations was done using three fire response groups (1= killed by fire, 2 = alive but not sprouting, 3= sprouting). The first unstandardized coefficient of discrimination accounted for the classification of alive and dead groups.

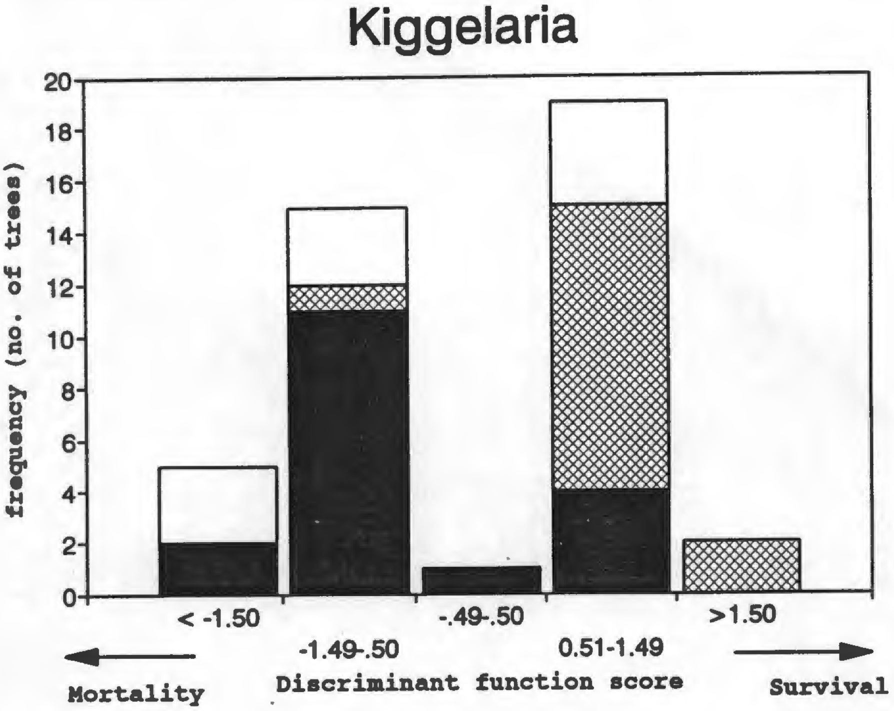

Fig. 6. Frequencies of *K.africana* predicted vs observed response to fire using discriminant function analysis: 1) shaded bars = plants killed by fire, 2) empty = alive but not resprouting, 3) crosshatch = resprouting, 4) total bar = predicted response, (Wilks lambda= 0.4711, Chi squared= 28.225, p ≥ 0.004, df=8).

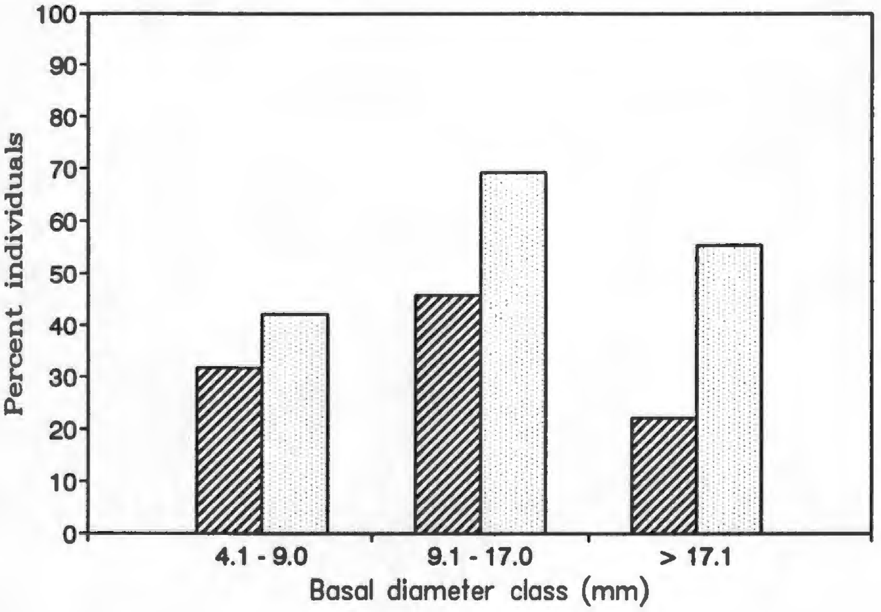

Fig. 7. Structural profile of burnt *K.africana* trees, and the percent survival after fire in each basal diameter size class (lines = % that have resprouted, light shading = % which survived fire but had not resprouted).

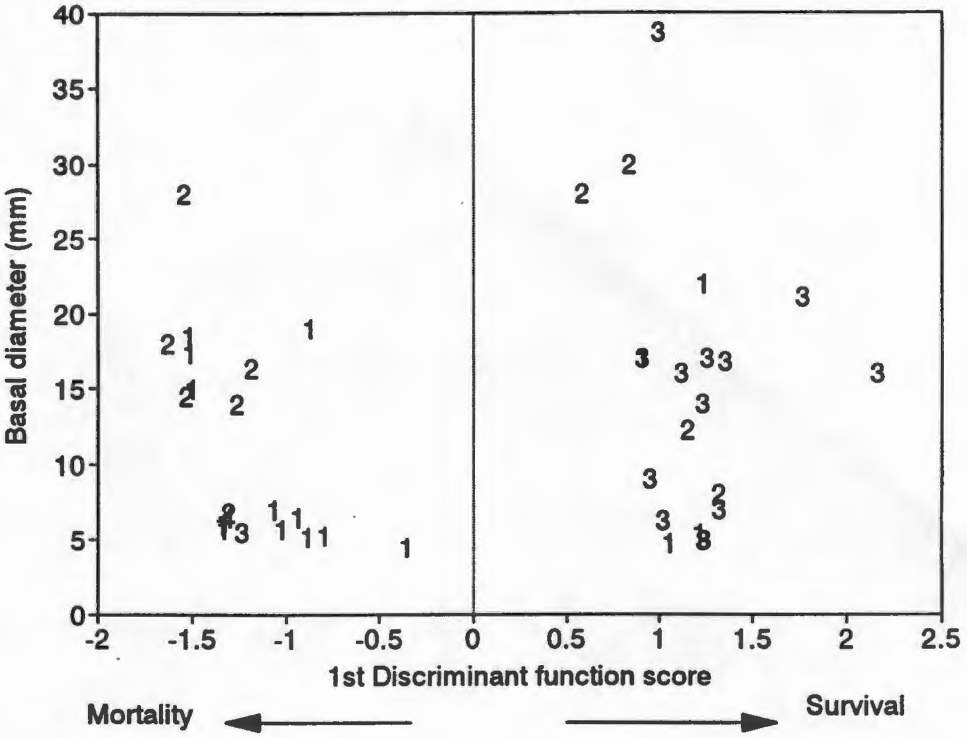

**Fig. 8.** Predicted classification of *K.africana* trees into survival and mortality groups from the discriminant function score and basal diameter. ( 1= killed by fire, 2= alive but not resprouting, 3= resprouting), note correlation n.s),(sample size= 42).

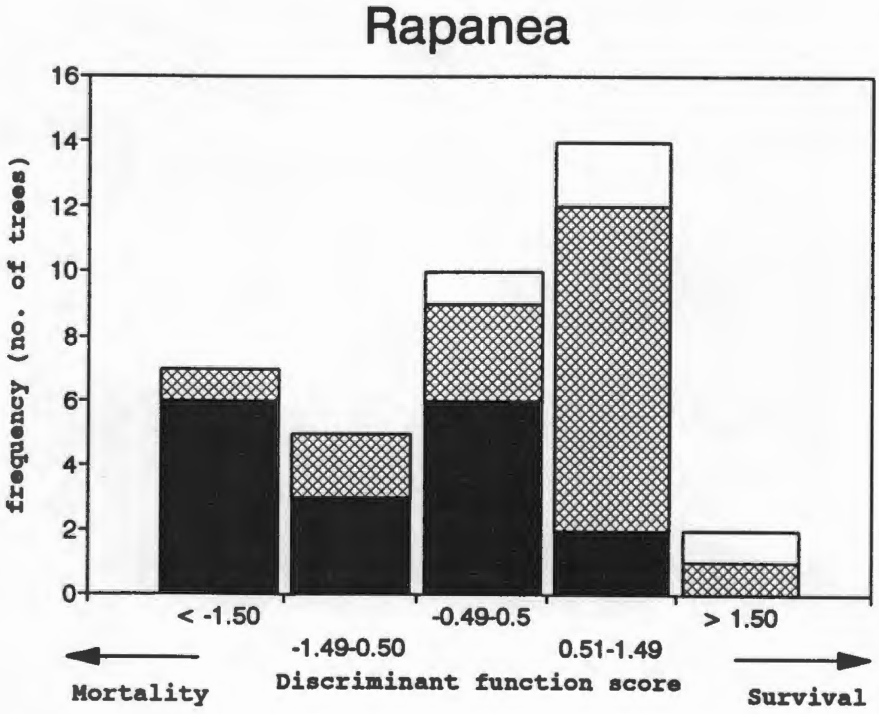

**Fig. 9.** Frequencies of *R.melanophloeos* predicted vs observed repone to fire using discriminant function analysis: 1) shaded bars = plants killed by fire, 2) empty = alive but not resprouting, 3) crosshatch = resprouting, 4) total bar = predicted response, ($p \geq 0.077$, df=8).

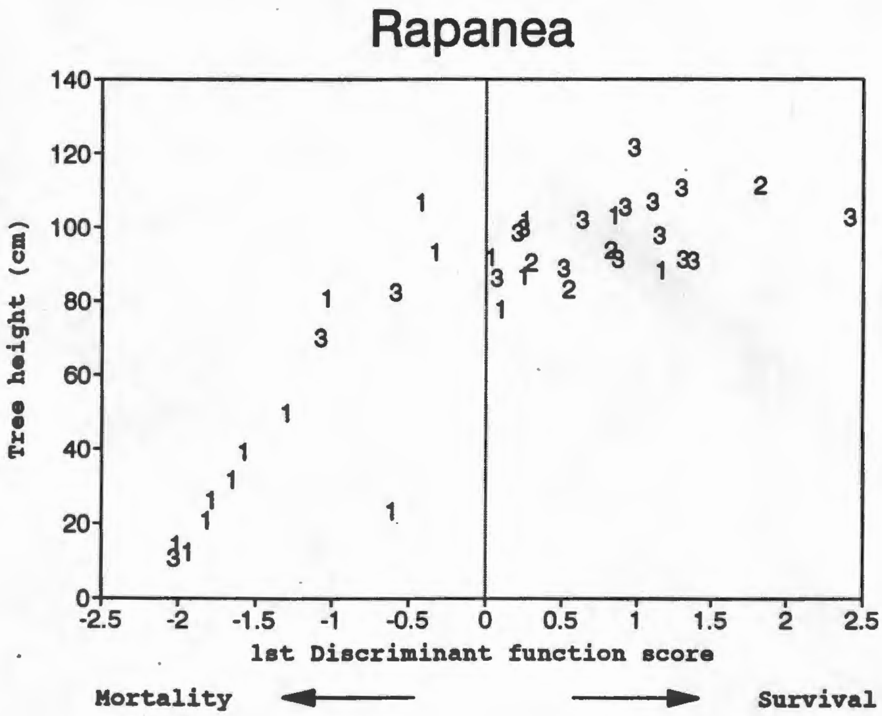

**Fig. 10.** Predicted classification of *R.melanophloeos* trees into survival and mortality groups from the discriminant function score and tree height. ( 1= killed by fire, 2= alive but not resprouting, 3= resprouting), (r= 0.854, df=38) .

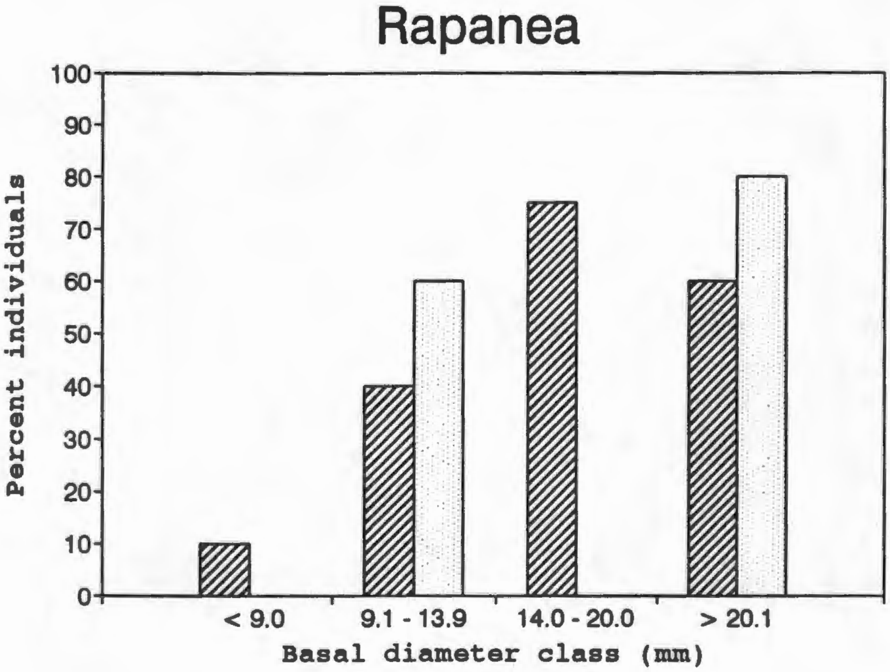

**Fig. 11.** Structural profile of burnt *R.melanophloeos* saplings, and the percent survival after fire in each basal diameter size class (lines = % that have resprouted, light shading = % which survived the fire but had not resprouted~~).~~ % that had resprouted).

### *K.africana*

The DA classification of *K.africana* saplings significantly discriminated (Wilks lambda= 0.4711, Chi squared= 28.225, $p \geq 0.0004$; df=8) between all three groups from the variables measured (Fig. 6). Thirty percent of *K.africana* saplings less than 9 mm in basal diameter sprouted after the fire (Fig. 8), most of these sprouters were predicted to survive the fire (Fig 7). Only 20% of saplings greater than 17.1 mm in diameter sprouted shoots, whereas 50% had survived the fire (Fig. 7). DA incorrectly classified 30% of these larger individuals in to the survival group. Stem height is a week but the most accurate pre-burn variable predictor of mortality (Table 4: Appendix. 2). Information of cambial mortality from tetrazolium staining correctly predicted the post-fire status of 79% of all *K.africana* saplings. (Table 3).

### *R.melanophloeos*

DA classifications of the saplings predicted response to fire was not significant ( $P \geq 0.07786$, df 8). However DA did separate resprouting from dead *R.melanophloeos* individuals (Fig. 9). DA was unable to separate the group of plants which were still alive but had not resprouted (group 2) from those that had survived the fire. The critical size of fire survival is a basal diameter ≥ 14cm as these saplings had a 0.78 (df. 24) probability of surviving the fire and 0.66 probability of sprouting shoots within the first 5 months after the fire (Fig. 11). Differences in the frequency of mortality are also related to stem height, with successful sprouters being taller than 85 cm (Fig 10). Tree height ($r=0.854$) and basal diameter ($r=0.8287$) are accurate morphological features for predicting pre-fire mortality (see Table 5. Appendix 2). Tetrazolium staining ($r=0.8492$) is also an accurate predictor of cambium survival but not of the saplings resprouting potential (Table 3). Basal diameter is an accurate predictor of bark thickness ($r=0.528$; $p=0.005$; df.17), those saplings with bark thicker than 0.8 mm had a higher probability of fire survival (Fig. 12).

The measurement (minimum height of burn on the stem) which was used to document the specific effects of fire intensity on each sapling, was a poor predictor of mortality, probably because in most cases the stems of *K.africana* and *R.melanophloeos* were singed shades of

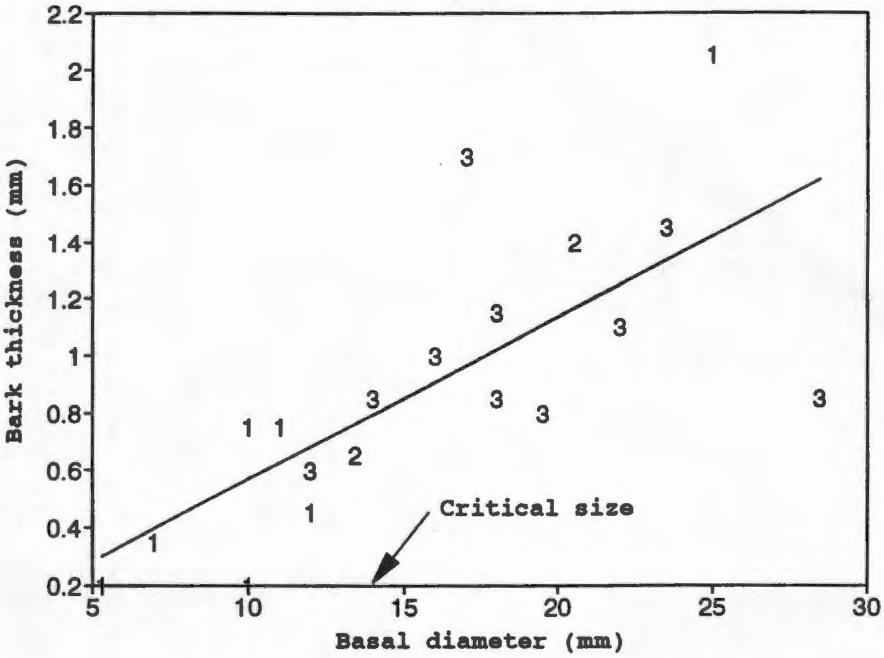

**Fig. 12.** Relationship between bark thickness and basal diameter of *R.melanophloeos*, showing the critical size for a 0.66 probability of resprouting. ($y = 0.1x - 0.684$, $r=0.528$, $p \geq 0.005$).

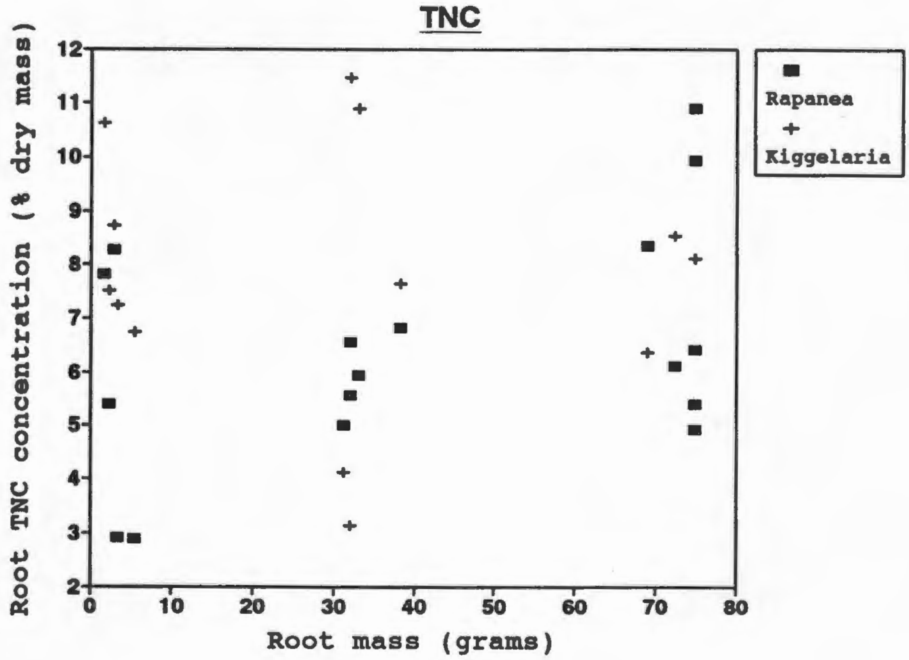

**Fig. 13.** Relationship between root wood nonstructural carbohydrate concentration and root mass for the two forest precursors.

grey and were not charred black as *C.capensis*.

Storage reserves

TNC concentrations in the roots of both species are very similar, ranging between 2.8-11.5 % dry mass, for small and large individuals (Fig. 13). Neither species showed any indication of an ontogenic shift in the concentration of root carbohydrates with plant size. In general larger trees of both species contain more starch and sugar reserves in their rooting systems, than smaller individuals (Fig. 14).

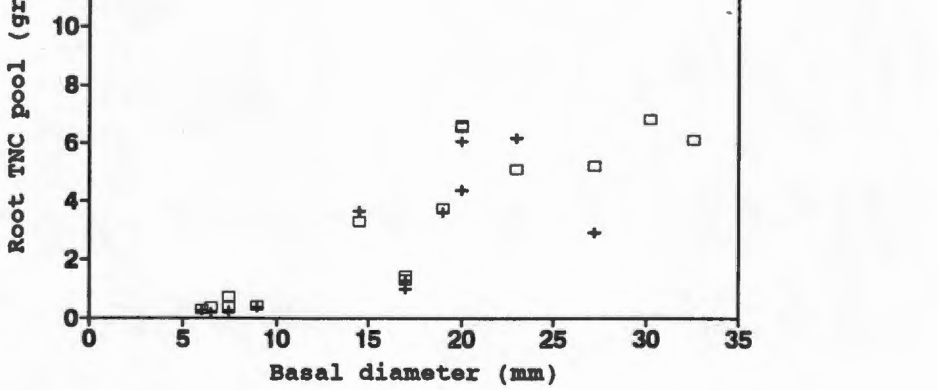

**Fig. 14.** **Relationship between plant size and root total nonstructural carbohydrates pool for** ***K.africana*** **and** ***R.melanophloeos*** **two forest precursors.**

## Discussion

There are a number of potential sources of variation that may affect observed mortality and classification by DA. These include choice of variables, characteristics of the fire, bark thickness and insulating properties of the bark, crown function and pre-fire vigour. The strong correlation between the first discriminant function score and cambium mortality (measured by tetrazolium staining) observed for both species hindered the separation of observed responses into the three distinct groups (Fig.6,9). The lack of a separate type 2 response group maybe a result of DA's interpretation of the dichotomous cambium response score into survival or death, with no distinct third group.

Fire behavioral characteristics are described by fire intensity, flame height and rate of spread (Table 2). Broad estimates of fire intensity in this study suggests that mortality should be generally higher in the *Kiggelaria* than *Rapanea* stand which holds true (Figs 8 & 11). Furthermore fire behaviour may explain why relatively fewer small less than < 9.1 mm diameter and more larger *K.africana* saplings were killed (Fig. 8). Small *K.africana*'s could have escaped the scorching of high flames which does less damage to plants close to the ground, and more damage to taller plants in head fires (Trollope 1984).

While *K.africana* showed no sign of size dependence for sapling survival (Figs 7), *R.melanophloeos'* potential to resprout after fire appears to be size dependent (Figs 10,11). These different patterns of survival suggests that fire intensity is the dominant factor governing post fire response of *K.africana*, as neither tree height or basal diameter are reliable predictors of cambium mortality. On the other hand pre-burn variables of basal diameter and stem height are accurate predictors of the post-fire mortality and survival of *R.melanophloeos* saplings and therefore can be used for field estimates of sapling survival under similar burn conditions (Appendix 3).

Bark thickness is a another variable which accurately predicts *R.melanophloeos* cambium mortality (Fig. 14), as thicker bark decreases the heat transfer to the cambium reducing flame injury to meristematic tissue (Frost 1984). However Ryan and Reinhardt (1988) caution against using bark thickness as a measure of the thermal properties associated with the bark, as thermal properties also depend~~ent~~ on the structural and chemical characteristics of the bark. Nevertheless bark thickness squared was the best pre-fire tree morphological variable for predicting cambial survival in a mixed conifer shelterwood Ryan and Steele (1989).

As no association exists between root TNC concentrations and sapling size, thus the ability of *R.melanophloeos* and *K.africana* to resprout following this fire appears to depend on the survival of cambial tissue (Table 3). Frost (1984) suggests that the tendency of plants to sprout does not only depend on survival of cambium tissue but also on the extent to which dormant buds on the stem and root crown have survived undamaged (i.e the existence of bud banks in meristematic tissue). The bud banks of *Quercus coxifera* L. a diciduous tree have been estimated by the number of pre-fire stems, which indicates this species post-fire sprouting potential (Malanson and Trabaud 1988). The destruction of above ground bud initials may explain why fewer saplings resprout than were predicted (Table 3), although the ability of plants to resprout from below ground tissue suggests that some small plants may only be able to sprout from the root crown.

The ability of all unburnt defoliated saplings to sprout shoots indicates that post burn growing conditions (waterlogging) did not affect sprouting. The production of new growth by many small burnt *K.africana* saplings indicates that the absence of TNC from above ground biomass did not limit the production of new shoots, despite the fact that root TNC reserves are the only source for respiration, growth and development after fire. The inability of small *R.melanophloeos*' seedlings to resprout is probably related to fire intensity which denatures the cambium preventing the formation of new shoots and not to shortage of starch reserves, as TNC concentrations did not differ significantly among saplings of different sizes (Fig. 13). The large range in TNC concentrations between plants of the same size may be due to sampling bias, or that allocation patterns to roots and shoots may change as plants grow larger, but as no TNC analysis was carried out on the above ground biomass, allocation patterns were not determined. The TNC concentrations in the roots of both spp are similar to other woody evergreen species in chaparral and matorral (Shaver 1981).

So far the evidence supports fire intensity as the overwhelming determinant of fire survival. Studies by Trollope (1984) have highlighted the importance of season of burn as a major determinant of woody species survival in savannas. Summer burns seem to have little impact on the ability of woody plant to resprout, however woody species are less tolerant to fire at the end of the dry season (Trollope 1984). It has been suggested that plants are more susceptible to fire as the production of new leaves has depleted the plants stored nonstructural carbohydrates and the plant has to draw on depleted storage reserves for regrowth. TNC concentrations are generally a good indicator of sprouting potential of *Quercus gambelii* Nutt. a deciduous tree (inhabiting the grassland of North western America), as storage reserves have seasonal cycles of accumulation peaking at the end of spring, and are low during autumn (Harrington 1989). Thus trees burnt at the beginning of spring had the lowest concentrations of TNC and the smallest regrowth potential (Harrington 1989). Seasonal shifts in TNC concentrations of *R.melanophloeos* and *K.africana* (two evergreen trees) are not expected to have much influence their sprouting potential, as seasonal variations in carbohydrate reserves are much smaller in evergreen than deciduous trees (Kramer and Kozlowski 1979).

Although carbohydrates may not constrain sprouting immediately after fire, the failure of the plant to resprout will mean that reserves present will be utilized for respiration and not replaced (as no carbon is being fixed). Thus plants which are still alive but have not resprouted may well die from the lowering of the water table during the summer drought (Manders et al 1992), if they are not able to produce new fine root material to enhance nutrient and water uptake (Kramer and Kozlowski 1979).

## Conclusion

The findings of this study provide further evidence that fire intensity is the overriding variable determining forest-fynbos boundaries. Although it seems that none of the species examined had reached a critical size where they were immune from the effects of fire intensity. The high sprouting rate after a low intensity burn suggests that forests would have occupied wider distributions in times when disturbance by fire was less intense. Low intensity fires will encourage forest nucleation and subsequent habitat amelioration suggested by Manders and Richardson (1992). If fynbos is protected from burning for a period exceeding 50 years (such as Orange Kloof), forest species will establish in fynbos and gradually change habitat conditions so that fuel levels no longer favour hot burns. Hence management strategies which favour cool controlled burns after the first rains have fallen, will facilitate the establishment and expansion of forest patches which will eventually exclude fynbos.

More empirical work is needed to determine; 1) whether saplings which survived the fire and did not resprout will be able to survive the summer drought, and 2) what the are growth rates for forest species in the open, as this data will improve predictions of mortality based on plant size. To determine whether sprouting is bud limited, future research should look at the locality of dormant buds and in relation to plant architecture in combination with patterns in reserve accumulation before the burning, and utilization during regrowth.

## Acknowledgements

This study would not have been possible without the generous assistance and motivated co-operation of Ms. K. Maze and the forestry personal at the Orange Kloof forest station and the donation of saplings from Kirstenbosch (N.B.G.) and Orange Kloof (Cape Town municipality) nurseries. I would like to thank; Francois van der Hyden for explaining TNC analytical procedures and commenting on a rough draft and William Bond for healthy supervision through all stages of the project and for clearing my fascination with fire.

**References**

Bond W.J. Unpublished manuscript.

Bowden B.J. 1991. *Fire response within the family Proteaceae: A comparison of plants displaying the seeder and resprouter mode of recovery.* unpublished phd thesis. University of W.Australia.

Chandler C. Cheney D., Tomas D. Trabaud L. and Williams C. 1983.
Fire in forestry Vol 1. *Forest Fire Behaviour and Effects* . Wiley New York.

Frost P.G.H. 1984. The response of organisms in Fire-Prone Environments. (In. *Ecological effect of Fire in South African ecosystems.* P.de V.Booysen and N.M.Tainton). Springer-Verlag. 149-176.

Geldenhuys C.J. 1987. *Bergwinds litterfall and fire.* Research review, South Afircan Forestry Research Institute 1986/1987. Government Printer.Pretoria.

Granger J.E .1984. Fire in Forests. (In. *Ecological effect of Fire in South African ecosystems.* P.de V.Booysen and N.M.Tainton). Springer-Verlag. 149-176.

Harrington M.G. 1989. Gambel oak root carbohydrate response to spring, summer, and fall prescribed burning. *Journal of Range Management.* 41(6) :504-7.

Kramer P.J. and Kozlowski T.T. 1979. *Physiology of woody plants.* Academic Press. Inc. New York.

Klecka W.R. 1982. *Discriminant Analysis.* Sage publications, London.

Malanson G.P and Trabaud L. 1988. Vigour of post-fire resprouting by *Quercus coxifera* L. *Journal of Ecology* 76:351-365.

Manders, P.T. 1990. *Journal of Vegetation Science.* 1:491-498

Manders, P.T. and Richardson, D.M. 1992 Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management.* 48:277-293

Manders, P.T. and Richardson, D.M. and Masson P.H. 1992. Is fynbos a stage in succession to forest? Analysis of perceived ecological distinction between two communities. (In *Fire in South Afirican mountain fynbos.* Van Wilgen B.W., Richardson, D.M Kruger F.J. & Hensbergen van H.J eds). Springer-Verlag.

Mckenzie B. Moll E.J., and Campbell B.M. 1977. A phycological study of Orange Kloof, Table Mountain, South Africa. *Vegetatio,* 34:41-53.

Pate S.J., Meney K.A and Dixon K.W. 1991. Contrasting growth and morphological characteristics of fire sensitive (Obligate seeder) and fire-resistant (resprouter) species of Restionaceae (S.Hemisphere Restiads) from Southwestern Australia. *Australian Journal of Botany.* 19:505-25.

Reinhardt E.D and Ryan K.C. 1989. *Estimating tree mortality resulting from prescribed fire.* Forest site Preparation and range Improvement, Symposium proceedings.

Ryan K.C.; and Reinhardt E.D. 1988. Predicting the postfire mortality of seven western conifers. *Canadian Journal Forestry Research.* 18:1291-97.

Ryan K.C. and Steele B.M. 1989. Cambium mortality resulting from broadcast burning in mixed conifer shelterwoods. Presented at the 10th Conference on Fire and Forest meteorology, April 17-21, Canada.

Shaver. G.R. 1981. Mineral nutrient and nonstructural carbohydrate utilization. (In. *Resource use by chaparral and matoral,* P.C. Miller ed). Springer-Verlag.

Smith D. 1981. ***Removing and Analysing Total Nonstructural Carbohydrates from plant tissue.*** University of Wisconsin Press. College of life Sciences Publication.

Trollope W.S.W. 1984. Fire in Savanna. (In. Ecological effect of ***Fire in South Afirican ecosystems.*** P.de V.Booysen and N.M.Tainton). Springer-Verlag. 149-176.

Van Daalen H. 1981. The dynamics of the indigenous forest-fynbos ecotone in the southern Cape. *South African Forestry Journal.* 119:14-23.

Van Wilgen B.W. 1982. Some effects of post fire age on the aerial plant biomass in fynbos (macchia) vegetation of South Africa. *Journal of Ecology*, 70, 211-225.

Van Wilgen B.W., Le Maitre D.C. & Kruger F.J. 1985. Fire behaviour in South African fynbos (machia) vegetation and predictions from Rothermel's fire model. *Journal of Applied Ecology*, 22, 207-216.

Van Wilgen B.W., Higgins K.B. & Bellstedt D.U. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in fire prone fynbos shrublands of South Africa. *Journal of Ecology*, 78, 210-222.

## Appendix 1.

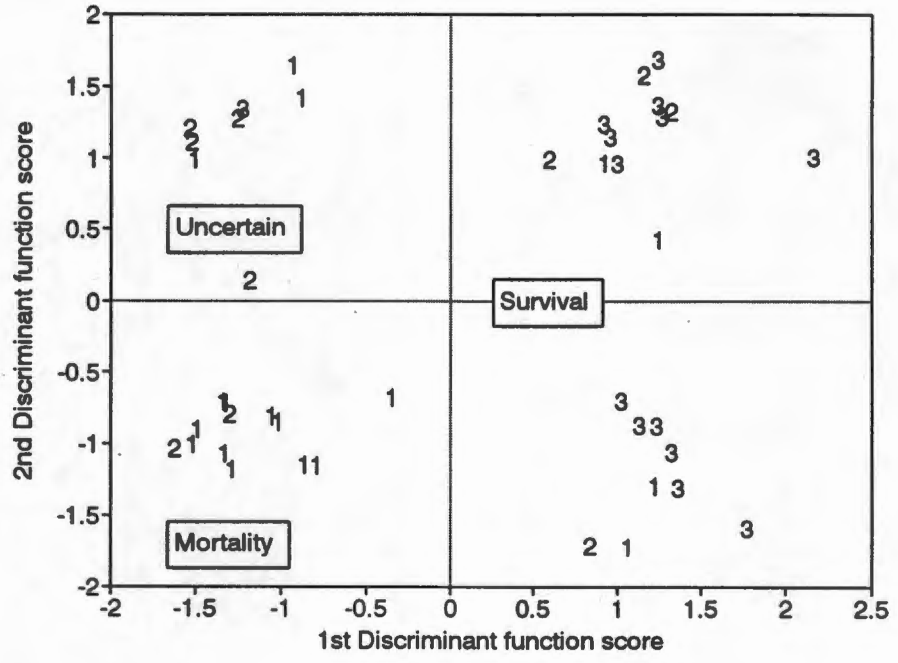

**Fig. 15.** Classification of *K.africana* saplings fire condition after fire in discriminant function space. (Wilks lambda= 0.4711, Chi squared= 28.225, $p \geq 0.004$, df=8), ( 1= killed by fire, 2= alive but not resprouting, 3= resprouting), (sample size= 42).

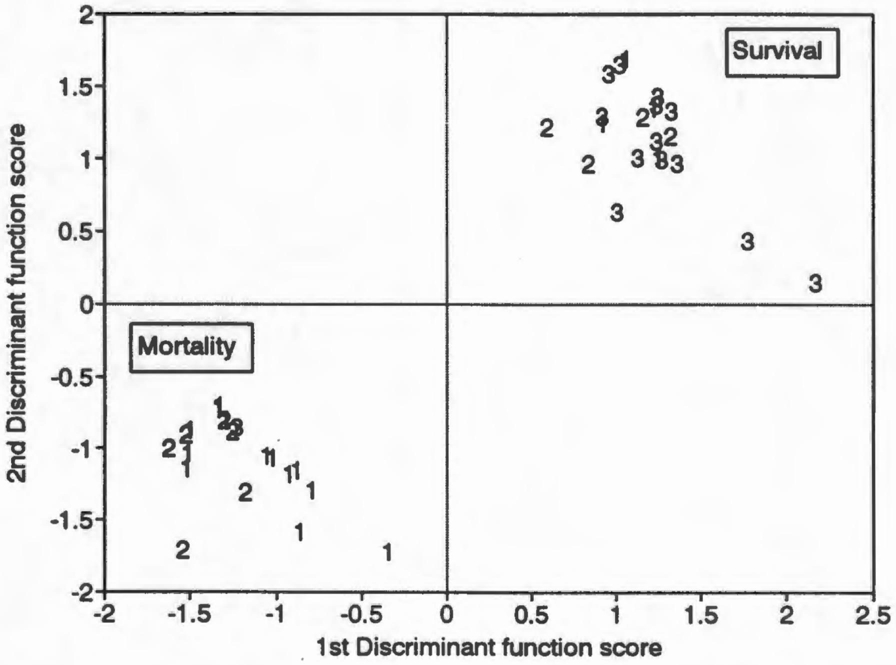

**Fig. 16.** Classification of *R.melanophloeos* saplings fire condition after fire in discriminant function space. ($p \geq 0.077$, df=8), ( 1= killed by fire, 2= alive but not resprouting, 3= resprouting), note correlation n.s),(sample size= 38).

## Appendix 2.

**Table 4.** Correlation matrix regression (Pearson product r) of variables predicting the post-fire response of *K.africana* (Dbh= basal diameter; Tet = Tetrazolium score; Brnht = minimum height of burn; Disc = Discriminant function (sample size = 38)

| Variable | Height (cm) | Dbh (cm) | Tet. | Brnht (cm) | 1st Disc |
|---|---|---|---|---|---|
| Dbh (cm) | 0.8708$^{c}$ | | | | |
| Tet. | 0.3391$^{a}$ | n.s | | | |
| Brnht (cm) | 0.3208$^{a}$ | n.s | n.s | | |
| 1st Disc | 0.3180$^{a}$ | n.s | 0.9644$^{c}$ | 0.4051$^{b}$ | |
| 2nd Disc | n.s | n.s | 0.9501$^{c}$ | n.s | 0.8647$^{c}$ |

Probability level

$^{a}$=.05 ; $^{b}$=0.01; $^{c}$=.00001

**Table 5** Correlation matrix regression (Pearson product r) of variables predicting the post-fire response of *R.melanophloeos* (abbreviations same as Table 4 )(sample size 38).

| Variable | Height (cm) | Dbh (cm) | Tet. | Brnht (cm) |
|---|---|---|---|---|
| Dbh (cm) | 0.7355$^{c}$ | | | |
| Tet. | 0.6686$^{c}$ | 0.4928$^{b}$ | | |
| Brnht (cm) | n.s | n.s | n.s | |
| 1st Disc | 0.8539$^{c}$ | 0.8287$^{c}$ | 0.8492$^{c}$ | 0.3858$^{a}$ |

## Appendix 3.

**Table 5.** A guide to predicting pre-fire tree survival following a cool autumn burn in mountain fynbos using morphological variables of *R.melanophloeos* (bark thickness mm).

| Tree height (m) | Chance of survival % | Basal diameter (cm) | Chance of survival % |
|---|---|---|---|
| < 0.5 | 10 | < 1.5 ( < 0.8) | 30 |
| 0.5-1 | 50 | ⩾1.5 ( ⩾ 0.8) | 66 |
| ⩾ 1 | 60 | | |