Fire Induced Topkill in an African Acacia: is hydraulic failure in the stem a possible reason ?

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of the University of Cape Town

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Abstract

A common consequence of the effects of savanna fires on trees is topkill. Topkill is the death of the canopy structure of a tree. This death is predominately motivated through the direct burning of the canopy and the death of cambium cells. However, in low intensity fire, the flames are not always able to make contact with the canopy but will cause cambium death in the tree bole and in turn creating a girdling effect. Reports suggest that immediate leaf drop off is experienced by acacia trees after a low intensity burn. This drop off could potentially be a result of hydraulic failure. Field and laboratory based test with vary degrees of heat application to the stem of *Acacia karroo* indicate that hydraulic failure did not take within the initial day after burning. Stomatal conductance, transpiration and cellular water content were expected to show the first signs of failure. However, in the severest burn, leaf drop off and topkill only resulted after two weeks of burning. Therefore, the death of the trees was a result of cambium death a phloem malfunction and not immediate hydraulic failure. The leaf drop off in the field observations and previous studies are probably a result of heat damage to the leaves from the burn.

Key-words: fire effects, savanna, *Acacia karroo*, cambial damage, topkill, plant hydraulics.

Introduction

The vegetation of the savanna biome is characterized by a herbaceous, generally graminoid ground layer (0.5 – 2 m tall), which is over shadowed by a patchy canopy of woody trees (2 – 10 m tall) (Scholes, 1997). A key element of the biomes ecology is fire. Fire has an important effect on the structure of the plant communities and dictates the composition, abundance and demography of those subjected to its disturbance (Bond and van Wilgen, 1996). The interval between fires can range from 1 to 30 years. In comparison to the fynbos biome, where intervals between 5 to 40 years occur, fire occurrence in savannas is higher (Bond and van Wilgen, 1996) and poses a significant constraint on individual persistence.

The ability to persist in a frequently changing system is important for long lived species. Graminoids with fast growth rates and their ability to rapidly resprout post fire allows them persist in a highly disturbed environment. Trees are different as they have slower growth rates and they have to compete with graminoids (Walter, 1971 in order to escape from the critical fire zone, an area 2m above ground level (Scholes. 1997). However, trees are able to successfully persist in situations of repeated burning which would decimate other vegetation types (Trollope, 1984; Gignoux *et al.*, 1997; Hoffmann and Solbrig, 2003). This persistence is a result of the ability to resprout at the base of the stem when all other components of the stem and branches have been permanently damaged, otherwise known as topkill (Trollope, 1974, 1984).

Topkill can result from death of the terminal buds and cambium death in the trees canopy. The threshold temperature for cambial tissue is 60 ^{0}C (Uhl and Kaufmann, 1990), when this temperature is reached or exceed cambium death is imminent. The high temperatures (>600^0 C) created by fire occur predominantly between 0.1 and 2m above the ground, with the highest temperature occurring at 60 cm above ground. Beyond 2m, a sharp decline in temperature occurs (Miranda *et* al., 1993; Mercer and Weber, 2001).

Tree height is therefore a critical determinant in avoiding topkill as a result of the lower flame temperatures above 2m. In *Acacia karroo* there is a negative correlation between height and the vulnerability for topkill (Trollope, 1984).Therefore taller individuals have a greater probability of avoiding topkill than small trees.

Not all fires in the savannas have the intensity and flame height to cause direct topkill in trees that exceed the height of the fire zone. Low intensity fires might not cause direct damage to the canopy but they can inflict topkill indirectly through damage to the main stem (Gignoux *et al.*, 1997; van Mantgem and Schwartz, 2003). This indirect damage comes when temperatures in the in the bole exceed 60^0C. The heat stress will cause cambium death, resulting in stem girdling and consequently topkill (Uhl and Kaufmann, 1990; Dickenson and Johnson, 2001; van Mantgem and Schwartz, 2003). In order to avoid this, savanna species increase bark thickness. Bark provides the insulating layer against the protrusion of high temperatures further into the bole of the tree (Uhl and Kaufmann, 1990; Pinard and Hoffman, 1997; van Mantgem and Schwartz, 2003). Larger stems posses a larger bark layer than small stems (Gignoux *et al.*, 1997; Jackson *et al.*, 1999).This larger stem then reduces the ability of heat to successfully penetrate the cambium within the stem.

Cambium death in the basal stem of trees from heat damage can be viewed in the same manner as stem girdling. Girdling a stem prevents the flux of photosynthates from the tree canopy to the roots, while enabling water transport in the reverse direction through the xylem (Baldwin, 1934; Hogberg *et al.*, 2001). Death from girdling is not immediate and occurs when a large build of photosynthate occurs in the leaves and the roots are starved of carbohydrates for a sufficient period. Therefore if a tree were to experience a low intensity fire where cambium damage to the basal stem is incurred, the canopy leaves are unlikely to immediately drop off .However, field observations have recorded leaf drop off with in two days in *Acacia karroo* following a low intensity fire. Balfour, (2005) showed that that localized basal stem heat applications in *Acacia karroo* resulted in the shedding of leaves within a couple of days post treatment. This phenomenon suggests that there may be a more immediate response of heat damage through hydraulic dysfunction.

In order for the conductive tissue to be effective, the xylem conduits must exist under tension (Tyree and Sperry, 1989). This tension creates renders the conducting vessels vulnerable to injury through the development of embolisms and potential cavitation. Cavitation arises through the formation of air bubbles in the conduits as a result of water induced stress or temperature changes (Tyree and Sperry, 1989). Several studies on the effects of xylem freezing have indicated that xylem frozen under tension will create extensive embolism through the formation of air bubbles in the sap (Langan *et al.*, 1997; Lemoine *et al.*, 1999). No data exists on the impacts of increased stem temperatures on xylem embolism. However, it is possible that a water column under tension and subjected to increased temperatures will produce embolisms, cavitation and potentially permanent damage to the xylem conduits. The impacts of heat protrusion from a fire into the bole of a tree could then potentially have a temporary or permanent negative affect on the plants hydraulics, therefore providing an answer to the sudden leaf shedding experience by some savanna trees species post fire. We hypothesize that the sudden leaf drop off experienced by some savanna trees after a low intensity burn is result of hydraulic malfunction.

We studied the influence of localized heating and girdling on the basal stems of *Acacia karroo* on water relations and gaseous exchange. Three experiments were conducted with varying degrees of damage application. Within each experiment, three treatments were applied, girdling, burning and burning plus girdling. The plant water status and gaseous exchange were monitored via the changes in relative leaf water content, photosynthesis, stomatal conductance and transpiration. The loss of conductive tissue was measured in the burnt treatments.

Materials and Methods

Acacia karroo was chosen for all experimentation. Three separate experiments were carried out on the species. Plants were selected within the size range commonly experiencing top kill under natural conditions. Stem diameters ranged from 16. 2 to 26.5 mm (at 30 cm above the ground) .Their height ranged from 1.5 to 2.5 m.

Field Experiment

The field experiment was carried out in the Hluhluwe-Umfolozi reserve in north eastern Kwa-Zulu Natal in the month of April. Three treatments were applied, girdle, burn and girdle plus burn with a control. The girdling involved the removal of a 5 cm section of bark 30 cm above ground. Burning was conducted with the flame from a butane torch. The flame, approximately 20 cm in length was rotated around the stem for 30 seconds. The flame was placed 5 cm from the stem placed 5 cm from the stem at 30 cm above the ground. In the girdle plus burn treatment the flame was applied directly to the xylem. The leaf photosynthetic gaseous exchange readings were taken prior to treatment, one hour and 24 hours after treatment. Three fully developed leaves on different branches in the canopy of each tree where chosen for gaseous exchange measurements. This was done on order to cover all potential effects on the canopy.

Pot Experiments

The pot experiments were conducted in a greenhouse at the University of Cape Town. Temperatures in the greenhouse were kept constant at 25°C and the trees used were watered daily. The experiments were conducting between the June and September. 60 and 90 second burns were implemented. In the 60 second burn, only a burn treatment with a control was initiated. The butane torch was applied for 60 seconds on half of the stems circumference. The gaseous exchange readings were taken pre-treatment and then

1, 2, 3, 5, 8 and 20 days there after on fully developed leaves. Five leaves on separate branches were used in the measurements .On every measurement the relative water contents of leaf samples from the same branches were calculated. In the 90 second burn, three treatments were applied, girdled, burn and girdle plus bun with a control. In the burn treatments, the butane torch was rotated around the stem for 90 seconds. The gaseous exchange readings were taken pre-treatment and then 1, 6, 11, 17 and 25 days there after. Three leaves on separate branches were monitored. The relative water content measurements were conducted from these same branches. The loss of conductive area was measured on the individuals from the burnt treatment.

Experimental Stem Heating

The temperatures reached in the centre of a stem during a 90 second burn around the stem were measured with a k-type thermocouple (Inconel Corporation). An *A. karroo* stem, 1,9 cm in diameter was cut. The thermocouple was inserted into the centre of the stem, parallel to xylem vessels. The temperatures were then recorded every 10 seconds for four minutes.

Photosynthetic Leaf Gaseous Exchange

A LI-6400 portable infra-red gas analyser (LI-COR Biosciences Inc., Nebraska, USA) was used to measure photosynthetic assimilation (A), transpiration rate (E), stomatal conductance (G_s), intercellular CO_2 (C_i) and leaf temperature of A. *karroo* in each experiment. The light intensity in the Licor 2 X 3 cm cuvette (Licor 6400-02) was set at 1500 μmol m^{-2} s^{-1}.A high flow rate of air through the cuvette (500 μmol s^{-1}) ensured that gas exchange properties rapidly equilibrated and measurements were generally taken within 2 minutes. All measurements were taken prior to midday.

Relative Leaf Water Content

The relative water content of the leaves in experiments two and three were calculated using the method of Barrs and Weatherley, (1962). The time taken to reach maximum turgid weight for this species was calculated to be 3.5 hours. The fresh weight, turgid weights were measured and then they were oven dried at 80 ^{0}C for 24 hours and their dry weight measured. The relative water content was then calculated using the following equation:

RWC (%) = [(fresh weight - dry weight) / (turgid weight - dry weight)] * 100

Loss of Conductive Tissue

The percentage loss of conductive area was determined using the staining techniques modified from Sperry *et* al., (1988). Individuals from the 90 second rotational burn treatment were selected for the analysis. Each stem consisted of a control and treatment stem section. The control section was located 10 cm below the burn scar, while the treatment section included the scar and the area above. When harvesting each section, the stems were emerged in water and trimmed initially, 10 cm below the control section and 10 cm above the treatment section. The single stem piece was then cut into two sections with each section being 20 cm in length. Each section was then trimmed on alternate ends until a final segment of 14. 2 cm was obtained. To ensure an accurate measurement of permanently blocked xylem, the stem segments were flushed at a pressure of 151 kPa for one hour .The segments were then attached to a tubing system that allowed 0.5 % (*w*/w) Safaranin dye in 5 mM KCl to be drawn through the xylem for 20 minutes. An endpoint of each segment was removed and the stained xylem area was measured using a digital camera (C- 730 Ultra Zoom Camedia , Olympus America Inc. , New York, USA) and image analysis software (Image v. 1.61 National Institute of Health Bethesda, Maryland, USA). The loss in conductive tissue was formulated through the comparison of active xylem tissue (stained area) to total xylem area and expressed as a percentage.

Data Analysis

A one-way ANOVA with the treatment as a factor (4 levels) was carried out on the gaseous exchange and relative water content data on the last set of readings in each of the experiments. Multiple comparisons were made using the Tukey's LSD posteriori tests. All analyses are reported at $\alpha = 0.05$. The analyses were conducted using STATISTICA©. V. 7.0 package (Statsoft, Inc. Oklahoma, USA)

Results

Field Experiment

The three treatments exhibited similar trends in photosynthetic rate (A), transpiration (E) and stomatal conductance (Gs) in the two measurements taken post treatment (Figure 1). No significant differences were found between treatments in each of the gaseous exchange variables, photosynthetic rate ($F = 2.0582$, $p > 0.05$); transpiration rate ($F = 0.0783$, $p > 0.05$) and stomatal conductance ($F = 0.2996$, $p > 0.05$).However, the burnt plus girdled treatment did exhibit a continuous decline in photosynthetic rate and stomatal conductance over the 24 hours .This result and the fluctuations in measurements of the other treatments are a result of changes in climatic conditions as readings were taken over two days. One month after the administration of the treatments, most of the trees in the treatments had experienced topkill. Below the point of damage (girdle/burn), the trees had begun to resprout.

Pot Experiments

The changes in gaseous exchange experienced between the control and burnt treatments in the 60 second burn followed similar patterns over the twenty day period (Figure 2). The photosynthetic, transpiration and stomatal conductance measurements showed similar changes. Analysis of the final readings revealed no significant differences between the control and burnt trees. This was the case in all of the gaseous exchange variables. However, a clear separation between the burnt and control trees occurred two days post treatment with regard to gaseous exchange. This separation remained between them for the 20 days of analysis and is most visible in the stomatal conductance measurements. The fluctuation in the variables over the analysis is a result of changes in the outside climatic conditions. The drastic decline in transpiration two days after the applications is a result of an uncontrollable rise in temperature within the greenhouse. The relative water contents (Figure 2) of the leaves from both sets of trees reflected a sharp decrease day after application. This decline was reflected more in the burnt trees and created a clear separation between them and the controls in the following weeks. After 20 days there was no significant difference between them. Upon further examination none of the burnt trees had experienced topkill after the 20 days but there were small shoots appearing below the burn scar.

In the 90 second burn, differences in gaseous exchange between the treatments were visible and became clear in the second day post treatment (Figure 3). Among the treatments, the burnt followed by the girdled plus burnt trees exhibited the largest declines in gaseous exchange. An exception to this is in the stomatal conductance measurements where all treatments showed an increase initially. From day five to the final readings, each treatment experienced topkill in certain individuals. Linked with this was the appearance of shoots below the burn scar. The girdle plus burnt trees where the first die and after 17 days none were alive. This decline and eventual death is reflected in the decrease in gaseous exchange and relative leaf water content. However, the decline in relative water content was delayed compared to the gaseous exchange. Death in the burnt trees was slower with the first tree only dying after 17 days. This slow decline is well represented in the photosynthetic readings where a constant decline occurred from day five. The girdled trees did show a decrease in photosynthetic rate between the final two readings, however, only one individual died during the experiment. The one-way ANOVA of last readings indicated that there were significant differences between the treatments in gaseous exchange and water content.

The xylem staining analysis (Table 1) indicated that there was a significant loss in conductive xylem area above the burn scar for the burnt treatments The burnt sections lost between 93 and 87. 6 percent of their conducting area, in comparison to their total xylem area. The control sections did show a small percentage of area that was no longer considered to be functional.

Heating Trial

The time-temperature (Figure 4) profile formulated form the 90 second burn shows that there was a sharp increase in temperatures within the first minute. Between 40 and 80 seconds from the start of burning, the temperature in the centre doubled. After 90 seconds, temperatures in excess of 90°C were recorded. Once the heat source was removed, the temperatures continued to rise for another minute, to a maximum of 104°C, cooling then began to take place three minutes. However the stem remained fairly warm for some time afterwards.

Discussion

The objective of this study was to assess the effect of increased temperatures within the xylem column, on the gaseous exchange and hydraulic characteristics in *Acacia karroo.* The results from the field experiment indicated that there were no significant changes in photosynthesis, transpiration and stomatal conductance in all three treatments over a 24 hour period (Figure 1). Balfour, (2005) conducted a similar experiment with same burning time and observed rapid leaf loss in the first two days of burning. However, our results did not show immediate changes. This is in particular reference to the transpiration and stomatal conductance measurements in the gaseous exchange and water relations of the trees, which could have attributed to potential leaf loss. So xylem malfunction did not immediately result. Therefore we were unable to replicate the findings of Balfour, (2005) to extent that rapid changes occurred .Yet damage to the cambium and phloem tissues was certainly incurred as topkill along with shoot formation below the burn scar were observed after a month

Following the finding from the field experiment we initiated a pot experiment where the applied burning time was increased to 60 seconds and focused on half on the stem (Figure2). Post treatment analysis was conducted for a 20 day period and included a focused analysis of the celluar water content of the leaves through measurement of leaf relative water content. However, the increased heat application and monitoring time did not make difference. The burnt trees showed no significant changes in the three gaseous exchange variables and relative leaf water content after the 20 days. Not even the terminal buds which are feed by the outer layer of xylem and should be the first affected, experienced any wilting (Tyree and Zimmermann, 2002).The fluctuations observed over the analysis are merely a result of temperature and light changes in the greenhouse from the prevailing climatic conditions.

Possible reasons for the inability to replicate the immediate effects that Balfour, (2005) are the variations in stem diameter and the inability to generate sufficient heat for hydraulic malfunction to occur. The residence time for air temperatures $> 60^{o}C$ in savanna fires have been recorded for between 20 and 270 seconds (Miranda *et al.*, 1993).The time required for temperatures to reach beyond 60°C, the requirement for cell death in the tree bole can range from seconds to minutes and is dependant on bark thickness and bole diameter (Uhl and Kaufmann, 1990; van Mantgem and Schwartz, 2002; Hoffmann and Solbrig, 2003). Therefore the temperatures created from the 30 and 60 seconds burns were perhaps not generating enough heat. The heating trial (Figure 4) indicated that a 90 second burn, generated temperatures in excess of 90°C and maintain them at this level for a few minutes. Consequently we decided to conduct an increased burn time of 90 seconds around the circumference of the tree.

The results from the increased burn time continued reflected no immediate changes in gaseous exchange and relative leaf water content within the first week of analysis. However, the trees in all treatments did show an eventual decline that was previously not evident in the previous experiments. Between the burnt and girdled plus burnt, the latter treatment was the first to show decreases after a week. This slightly more immediate response is a combination of girdling and direct damage to the xylem column. As the bark was removed, damage to the xylem did take place. However, these trees only showed a negative response to the treatment after five days. Therefore the xylem that was damaged was not sufficient for drastic changes in water relations to take place or that there was a large enough reserve of water in the stem structure above. If the burning was to have had an immediate effect, a rapid decrease in stomatal conductance would have occurred. Stomata close when a water deficit exists in the xylem column and in turn reduces the plant transpiration. Cochard *et al.*, (2002) found in Walnut (*Juglans* x *nigra*) trees that increased stress in the xylem vessels, through water depravation, resulted in a rapid closure of the stomata. Consequently the transpiration would be reduced and further formation of embolisms and cavitation prevented (Jones and Sutherland, 1991; Hinckley and Braatne, 1994). However, the results from the conductive tissue analysis are contrastingly different

The xylem above the burn scars indicated a significant loss in conducting area. This loss could only have been attributed to the cause of death in the burnt treatments if the stomatal conductances and transpiration rates decline immediately. However, this did not occur and the resulting permanent blockages in the xylem are most likely a consequence of the overall death of the trees from cell death. When cell death occurs and topkill results, the effected tissues including the xylem vessels will dry out. van Doorn and Cruz, (2000) found that when xylem conduits in Chrysanthenum (*Dendranthema grandiflora*) stems were dried out they became blocked due to potential oxidative reactions in the vessels. Therefore the resulting blockages above the burn scar where cell death occurred where a feature of the topkill experienced and not heat damage.

Although the burning treatment did not influence the hydraulics of the trees it did have a girdling effect on the trees. The heat from the burn severed the pathway of cambium and phloem between the roots. Therefore this resulted in the build up of photosynthates in the leaves and root starvation (Baldwin, 1934; Hogberg *et al.*, 2001). With time this eventually resulted in topkill. The delayed effects between the two burning treatments, burn and girdle plus burn illustrate the importance of bark in preventing topkill occurring as a result of stem damage (Uhl and Kaufmann, 1990; Pinard and Huffman, 1997; Gignoux *et al.*, 1997).

Conclusion

The immediate leaf drop from observed in Bafour, (2005) and field observations are not a result of heat damaged incurred to the xylem conduits. The transpiration rates and stomatal conductance's of the burnt trees did not decline rapidly when the same and increased heating treatments were applied. The observed leaf drop offs are more likely are result of the leaves being scorched with regard to the field observations. In the case of Balfour, (2005) it was a possibly a case of absolute decimation of the stems through intense burning .Our results suggest that topkill results from cambium death a phloem damage as noted in other stem heating experiments (Uhl and Kaufmann, van Mantgen and Schwartz, 2002. However, the study does illustrate the importance of bark protecting the bole of the tree and the extreme ability of *A. karoo* to persist when topkill is induced (Trollope, 1974).

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Figures

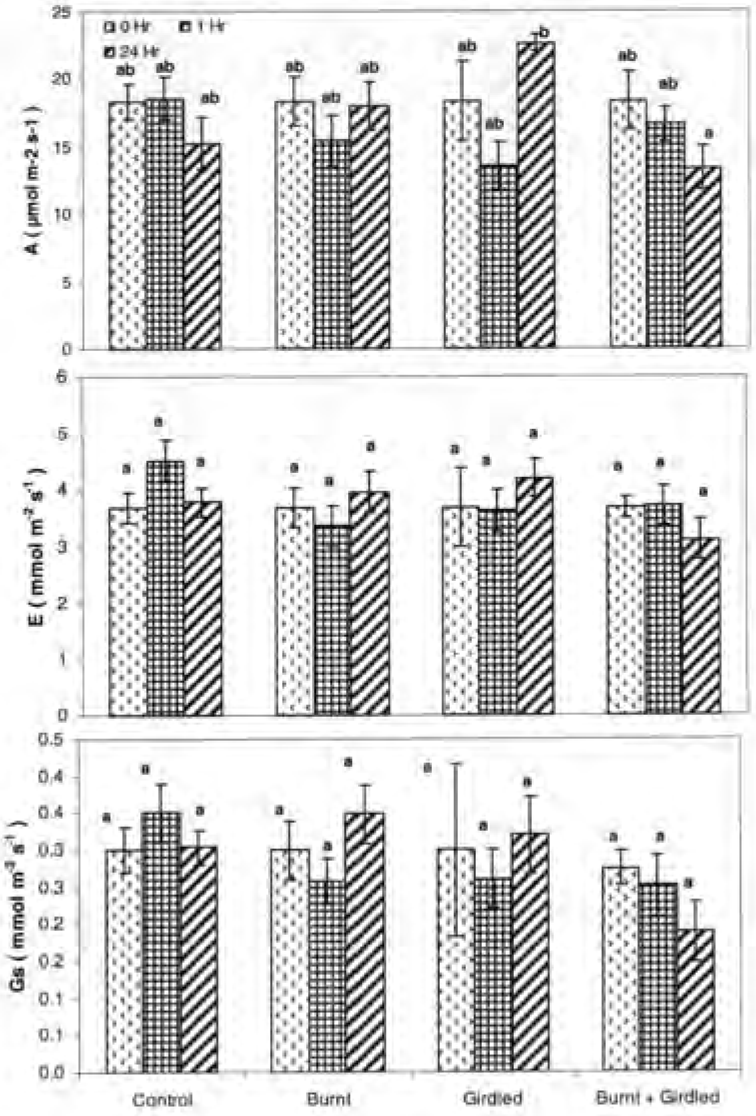

Figure 1: The comparative changes within 24 hours in photosynthetic rate (A); transpiration (E); stomatal conductance (Gs) in *A. karroo* trees, from burnt, girdled and burnt plus girdled treatments . A 30 second rotational burn was applied to the burning treatments. The results from the ANOVA indicate no significant differences between the treatments.

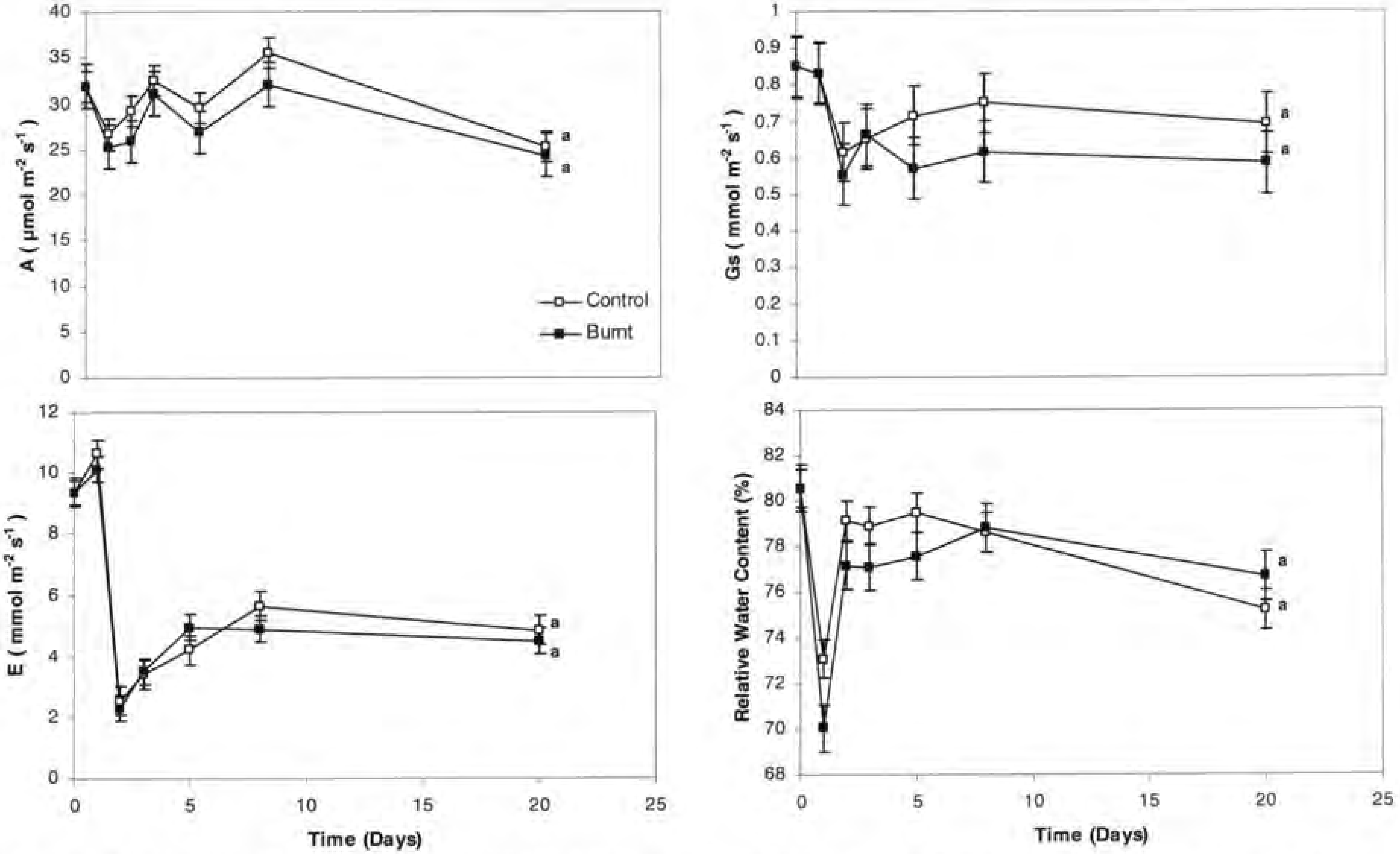

Figure 2: The comparative changes in photosynthetic rate (A); transpiration (E); stomatal conductance(Gs); relative water content over a 20 day period in *A. karroo* tree . One treatment, where half of the stem was burnt for 60 second. The results from the ANOVA indicate no significant differences between the treatments.

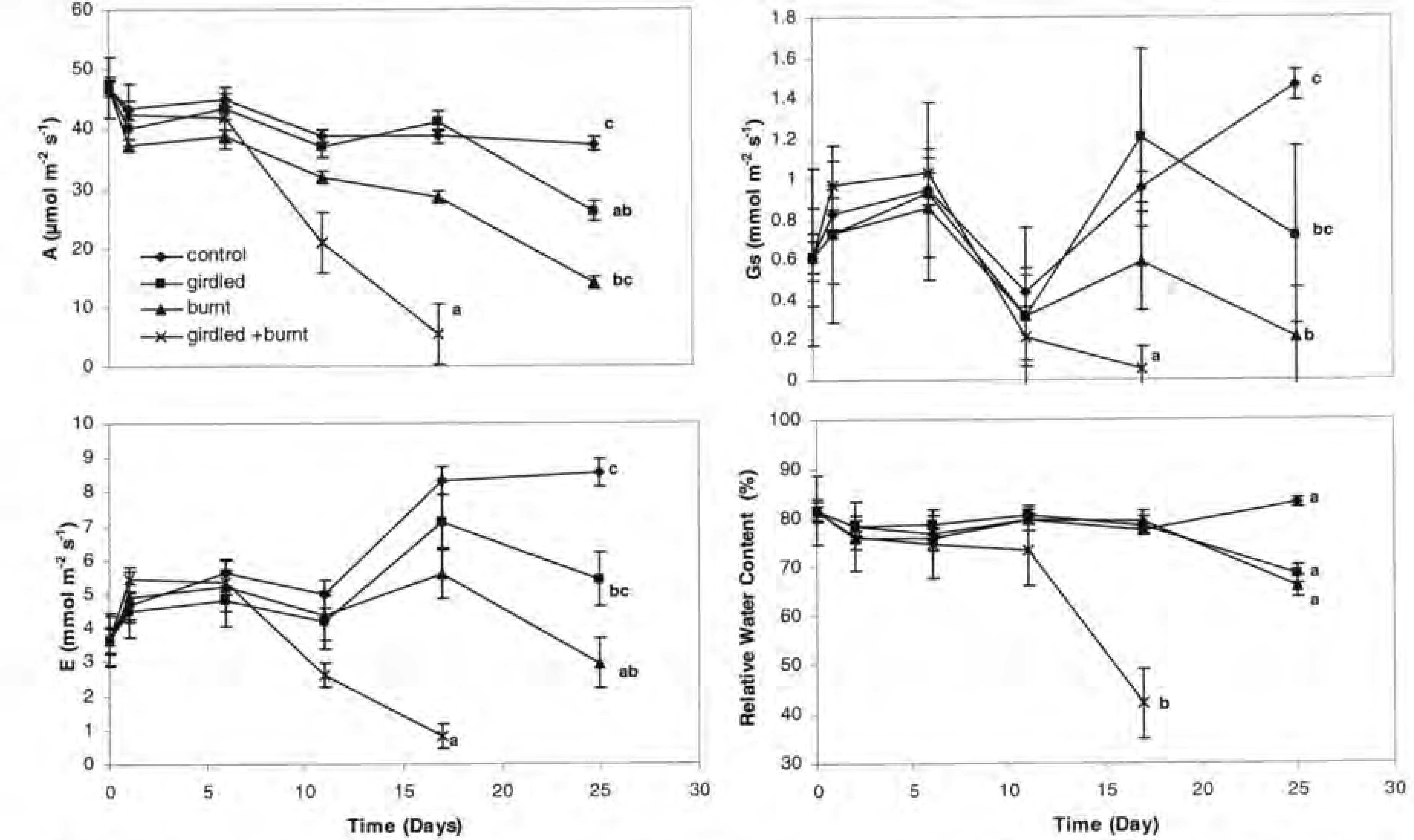

Figure 3: The comparative changes in photosynthesis (A); transpiration (E); stomatal conductance (Gs) and relative water content over a 25 day period in *A. karroo* tree. Three treatments where a 90 second rotational burn was applied to the around the stem. The difference in significance for day 25 readings were determined with a one-way ANOVA followed by post hoc Tukey LSD at $p < 0.05$. different letters indicate differences in significance.

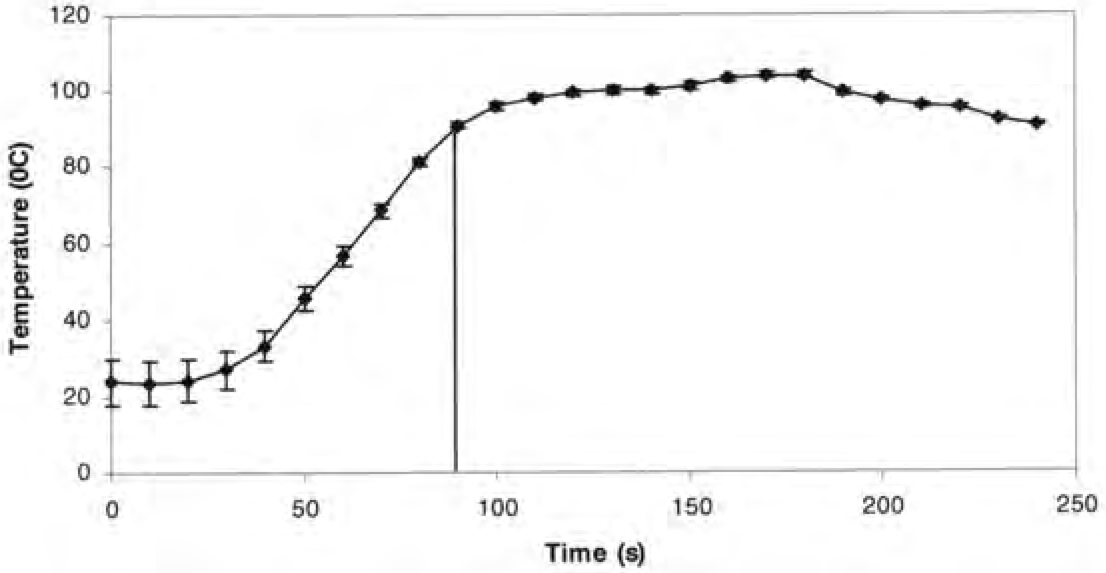

Figure 4 : The time temperature profile for *A. karroo* stem when a heat source from a butane torch was applied for 90 seconds in a rotational motion around the stem. The solid vertical line indicates 90 seconds.

Tables

Table 1: The comparison between the total xylem area and the active conducting area below the burn scar (control) and above the burn scar (burnt) in three trees that experienced a 90 second rotational burn around the stem at 30 cm above ground. The area conducting in relation to the total xylem area is expressed as a percentage conducting area. The differences between conducting areas of the sections was significant ($t = 2.93$, $p < 0.05$).

	Control	**Burnt**
Total Xylem Area (mm^2)	146.67	122.67
Conducting Area (mm^2)	107.50	11.00
Conducting Area (%)	73.45	9.58