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Sapling survival in a frequently burnt savanna: mobilisation of carbon reserves in *Acacia karroo*

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Abstract In frequently burnt savannas, saplings face the formidable challenge of both recovering from, and eventually growing tall enough to escape from, frequent fire damage. The aim of this study was to explore how saplings allocate carbon to achieve these ends through carbon partitioning, storage and remobilization. Lignotuber total non-structural carbohydrate (TNC) concentrations and δ^{13}C values of *Acacia karroo* (Fabaceae; Mimosoideae) were determined in plants from two different juvenile stages. These were one year after a fire when the plant consisted of numerous leafy shoots or coppices ("coppicing" stage), and three years after a fire when the plant consisted of one pole-like stem ("Gulliver" stage). Gulliver lignotubers were found to have significantly larger TNC pools (150 g vs. 97 g) and larger TNC concentrations (33% vs. 24%, w/w) than coppice lignotubers showing that post-coppice Gullivers recharged TNC in the lignotuber. δ^{13}C values from the stems of plants in the Gulliver stage were significantly enriched (>1‰) in ^{13}C compared to both coppicing ($P < 0.01$) and adult ($P < 0.05$) plants. Changes in both the amount of stored carbon and in the δ^{13}C values indicated dependence on stored carbon reserves, and partially heterotrophic growth for initial resprouting. The plants appeared to use both current photosynthate and stored carbon reserves for growth of the Gulliver stem. The use of stored carbon is hypothesized to promote fast stem growth rates to a height where saplings escape fire injury.

Keywords *Acacia karroo* · Resprouting · Total nonstructural carbohydrates · Stable carbon isotope · δ ^{13}C · Heterotrophic · Fire ecology · Savanna

Introduction

A common attribute of woody plants occurring in areas prone to high disturbance is the ability to resprout after disturbance (Bellingham and Sparrow 2000; Bond and Midgley 2003). Sprouting of woody plants is an adaptive trait which enables survival after considerable damage from fire or physical disturbance (Hodgkinson 1998) by initiating new vegetative growth from roots or stems (Bond and Midgley 2001). The ability of woody plants to repeatedly resprout after frequent burning is dependent upon carbohydrate reserves, which are replenished between burns (Hoffmann et al. 2000). In order to resprout after injury a plant needs surviving meristems and

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stored reserves to support growth (Vesk and Westoby 2004). The allocation of resources to storage carries a cost which must be traded off against costs of growth and/or reproduction (Bond and Midgley 2001, 2003). Many plant species resprout from specialized below-ground organs such as the lignotuber, which act as a reservoir of dormant buds, carbohydrates and mineral nutrient reserves (James 1984; Cruz and Mereno 2001). These carbohydrates are thought to be mobilized during resprouting, thereby acting as the main supply of carbon for regrowth during the early stages after a disturbance (Miyanishi and Kellman 1986; Bowen and Pate 1993; Van der Heyden and Stock 1996; Canadell and López-Soria 1998).

The role of stored carbon in resprouting of woody plants has not been well quantified, and is usually based on the observation that depletion of carbon reserves is accompanied by failure to resprout (Miyanishi and Kellman 1986; Bowen and Pate 1993; Canadell and López-Soria 1998). Foliage removal treatments which reduce carbohydrate levels in above and below ground plant parts restrict coppice shoot growth (Kays and Canham 1991; Erdmann et al. 1993; Tschaplinski and Blake 1994; Van der Heyden and Stock 1996), demonstrating a dependence on carbohydrate storage. A number of studies have, however, failed to demonstrate a direct relationship between nonstructural carbohydrate reserves and regrowth (Cruz and Moreno 2001; Cruz et al. 2003). Schutze, Cramer and Bond (unpublished data) used a ^{14}C labelling experiment to demonstrate the dependence of the initial coppice growth on underground stored carbon in *Acacia karroo*. They found that post clipping regrowth contained labelled ^{14}C which can only have come from underground starch reserves. This supports the hypothesis that starch reserves are used to support regrowth after a fire.

Many studies on stored carbon allocation to post-disturbance growth have focused on Mediterranean type shrubby species (Bowen and Pate 1993; Bell et al. 1996; Bell and Pate 1996; Bell and Ojeda 1999; Verdaguer and Ojeda 2002) and a few on temperate forest species (Kays and Canham 1991). The role that carbon reserves play in post-burn regrowth of savanna species has received very little attention. In mesic savannas fires are more frequent than in shrublands (several fires in a decade compared to once in one to several decades) and the costs of sprouting are likely to be even greater (Vigilante and Bowman 2004). Post-fire resprouting savanna saplings need to replenish their depleted carbohydrate reserves in order to be prepared for the next fire, but they must also grow tall enough to escape the flame zone before they grow to mature, fire-proof adult sizes. Just how they accomplish this is virtually unstudied. As for Mediterranean ecosystem shrubs, many saplings in frequently burnt savannas produce swollen roots or stem bases, referred to as lignotubers. Many also develop pole-like sapling architectures which facilitate bolting to fire-tolerant heights (Boaler 1966; Gignoux et al. 1997; Archibald and Bond 2003). Bolting behaviour is well known for conifers in frequently burnt habitats such as *Pinus palustris* in the south-eastern United States (Wahlenberg 1946) and *P. merkusii* in south-east Asia (Stott 1988). However, unlike the conifers, savanna saplings can be top-killed many times, persisting for decades before escaping to grow into adults, or dying (Trollope 1984; Menaut et al. 1990; Higgins et al. 2000). We hypothesised that to survive frequent fires savanna saplings would have to store carbon in the roots to subsidise rapid re-sprouting after a burn. To grow tall enough to eventually escape the flames, saplings would also need to allocate stored carbon to rapid stem growth. Where fires are frequent, as in many mesic savannas, this juggling trick would need to be repeated year after year.

It has been shown that stable carbon isotopes can be used as a tool to trace growth based on stored carbohydrates (=heterotrophic plant growth) as distinct from growth based on current photosynthesis (=autotrophic) (Terwilliger and Huang 1996; Brugnoli et al. 1988; Brugnoli and Farquhar 2000; Damesin and Lelarge 2003; Helle and Schleser 2004; Kagawa et al. 2006). It is thought that discrimination takes place during the export and/or transport of sugars (Badeck et al. 2005). Transitory starch accumulation and remobilization probably governs the diel rhythm of δ^{13}C in organic matter exported from leaves, which when integrated over a day results in carbon exported from the leaf being enriched with ^{13}C (Gessler et al. 2007, 2008). Consequently, all organic matter formed by incorporating these exported sugars becomes enriched in δ^{13}C relative to the starting material (Kühn et al. 1999; Sturm and Tang 1999; Damesin and Lelarge 2003; Hobbie and Werner 2004; Kagawa et al. 2006). For example, in a study of temperate deciduous trees, Helle and Schleser (2004) found a marked increase in δ^{13}C in early season tree rings when stored carbon was utilized for growth, but a decrease as the season progressed and trees switched to current photosynthate.

This study aimed to elucidate the dependence of a common resprouting South African savanna species, *A. karroo*, on stored carbon after fire. To achieve this, stable carbon isotope values, total nonstructural carbohydrates, lignotuber size and plant size were measured in saplings at different post-burn intervals and adult *A. karroo* plants.

Materials and methods

Site description

The study was undertaken in the Hluhluwe-Umfolozi Park in KwaZulu Natal, South Africa in the "Corridor" section of the park (S 28.26963°, E 31.94231°). The area has an elevation of approximately 273 m above sea level with an average annual rainfall of 637 mm per annum over the previous three years. The long-term average annual rainfall for this elevation in the Hluhluwe-Umfolozi Park is estimated to be 780 mm per annum (Balfour and Howison 2001). The average annual rainfall for the three years prior to the analyses indicated that 2001 and 2002, receiving 575 and 500 mm, respectively, were dry years while 2003, in which 836 mm fell, was a relatively wet year, well above the long-term average.

Acacia karroo is a common tree in the mesic savannas of Hluhluwe. In the first few months after a fire, top-killed plants send out numerous coppice shoots. By the second year after a burn, a marked asymmetry develops among resprouting stems in many saplings. One stem usually grows taller than the others, forming a pole-like stem and the shorter coppices begin to die off (Maze 2001). We refer to multi-stemmed plants as "coppice" and pole-form plants as "Gullivers" (Bond and van Wilgen 1996). For this study, we compared saplings at the two different post-burn stages with adults that had grown taller than flame height. The first site was selected in an area that burnt one year prior to this study (8th August 2003) with all plants in the coppice stage. The second site was in an area that had burnt three years prior to the study (28th August 2001), where many of the plants had produced poles (the Gulliver stage). The third site had not been burnt for many years and supported a population of mature adults. The three sites were within 1 km of each other, and had similar rainfall and soil types.

Sample collection

All plant samples were collected towards the end of the dry season (August 2004). The coppicing plants were therefore precisely one year old, while the Gullivers were three years old. The presence of a charred plant skeleton indicated that each coppicing plant had been completely top-killed in the previous fire. Each of the Gullivers had no evidence of burnt branches or spines from the canopy to the base of the stem, showing that that it had not experienced a fire in its lifetime. The coppices had therefore grown through one full seasonal cycle while the Gullivers had grown through three full seasonal cycles before they were harvested. The height and basal diameters of ten *A. karroo* Gullivers were measured, their roots excavated; and the top 50 cm of the main root removed for starch and isotope analyses. The roots were stored on ice and then frozen on return from the field. A branch from the previous year's growth was collected from the canopy of each Gulliver and the pole stem of each plant was also sampled for isotope analyses. The height and basal diameter of the thickest coppice was measured for ten coppicing plants. All of the coppice shoots were clipped off at ground level and taken for analyses. The top 50 cm of the main root of the coppiced plants were removed, as described for the Gullivers. Five adult *A. karroo* plants of similar size were felled and a stem section of *ca.* 3 cm was taken from the stem at a height of *ca.* 1 m from the base. Only stems from adult trees were sampled for carbon isotope analysis in order to assess the longer-term isotope trends relative to the two early post-fire stages.

All excavated roots were sawn into *ca.* 2 cm thick discs and these discs were then chopped into small bits. The sawdust created from sawing each root into sections was collected for starch analysis. All plant material was dried in an oven to constant dry weight (*ca.* 72–96 h) at 80°C. The dry weight of total coppice material and of each root was recorded.

Stable carbon isotope analysis

Helle and Schleser (2004) found that δ^{13}C was at a maximum in young heterotrophic leaves shortly after bud burst and in the early wood of each tree ring, when growth depends on carbon reserves. Maximum values differed by up to 5‰ from minimum values recorded during autotrophic growth later in the growing season, whereas contiguous δ^{13}C values rarely differed from each other by more than 0.3‰. Following these results, we expected distinct differences in δ^{13}C for resprouting stem material derived from root reserves present before a fire compared to growth from post-burn photosynthate. To track changing isotopic composition, and therefore changing sources of carbon, we drilled a 1 mm diameter hole every millimetre along the radius of each sample disc. The shavings from drilling were collected for isotope analyses. A sub-sample of the sawdust collected from each root was milled in a ball mill (Retsch MM200, Haan, Germany) for isotope analysis. From each wood sample a 60–80 µg sub sample was weighed and combusted in an elemental analyzer (Model NA 1500; Carlo Erba, Milan Italy). Carbon isotope ratios of the generated CO_2 were determined using a Finigan Mat 252 Mass Spectrometer. δ^{13}C was referred to the Vienna Pee Dee Belemnite standard (VPDB): $\delta^{13}C\ (‰) = (R_S/R_{VPDB} - 1) \times 1000$, where R_S and R_{VPDB} are the molecular abundance ratios of carbon isotopes, $^{13}C/^{12}C$, of the sample and the standard VPDB, respectively.

Total nonstructural carbohydrate (TNC) analyses

TNC concentrations in the lignotubers of the Gullivers and coppicing plants and in the stems of the Gullivers were determined. Material used for TNC analysis was milled with a ball mill (Retsch MM200) and oven dried at 80°C. The colorimetric method described by Buysse and Merckx (1993) was used for the TNC analyses. Samples of 0.05 g of milled plant material were hydrolysed in 5 ml 3% (v/v) HCl solution in a boiling water bath for 3 h. The hydrolysis products were centrifuged, the supernatant decanted and made up to 50 ml with 80% (v/v) ethanol. Because sugar concentrations in this solution yielded absorbance readings above the linear portion of the standard curve an additional 1/5 dilution in 80% (v/v) ethanol was necessary. The samples, containing 150 µl of sugar solution, 150 µl of phenol solution made from 28% (w/w) phenol in 80% (v/v) ethanol and 750 µl of concentrated H_2SO_4 were allowed to stand for 15 min before their absorbances were measured at 490 nm using a spectrophotometer. Absorbances were converted to concentrations using both starch and glucose standards to determine the efficiency of digestion and the colorimetric procedure.

Statistical analyses

Data were log-transformed to meet ANOVA assumptions. One-way ANOVAs and Students *t*-tests were used to compare normally distributed data. Post-hoc comparisons were performed using the Tukey HSD tests. Where log transforms did not satisfy ANOVA requirements, non-parametric tests (Kruskal-Wallis and Mann-Whitney tests) were used. All statistical analyses were performed using Statistica Version 7 (StatSoft Inc).

Results

There were no differences in the size (Fig. 1) or dry weights (Table 1) of the main root (hereafter referred to as lignotuber) from Gullivers compared to those from coppicing plants and there was no correlation between lignotuber dry weight and plant height (Table 2). However, the total non-structural carbohydrate (TNC) concentrations and TNC contents of the Gulliver lignotubers were higher than those of the coppice lignotubers (Table 1). Furthermore, significant correlations were found between TNC concentrations and total TNC content with plant height and for TNC content with stem diameter (Table 2). Lignotuber dry weight was negatively correlated with TNC concentrations but was positively correlated with TNC content, indicating that the TNC content was strongly determined by the lignotuber size, rather than the lignotuber TNC concentration (Table 2). With three year's post-burn growth, the Gullivers had significantly larger stem diameters than the one-year post-burn coppicing plants (Table 1). Mean coppice stem diameter was half ~13 mm) that of Gulliver stem diameter (~26 mm). There was a highly significant correlation between stem diameter and plant height (Table 2). Despite the significantly higher Gulliver stem diameters there was no obvious difference in either size or structure of the top 50 cm of the rooting systems of the Gullivers compared to that of the coppicing plants (Fig. 1).

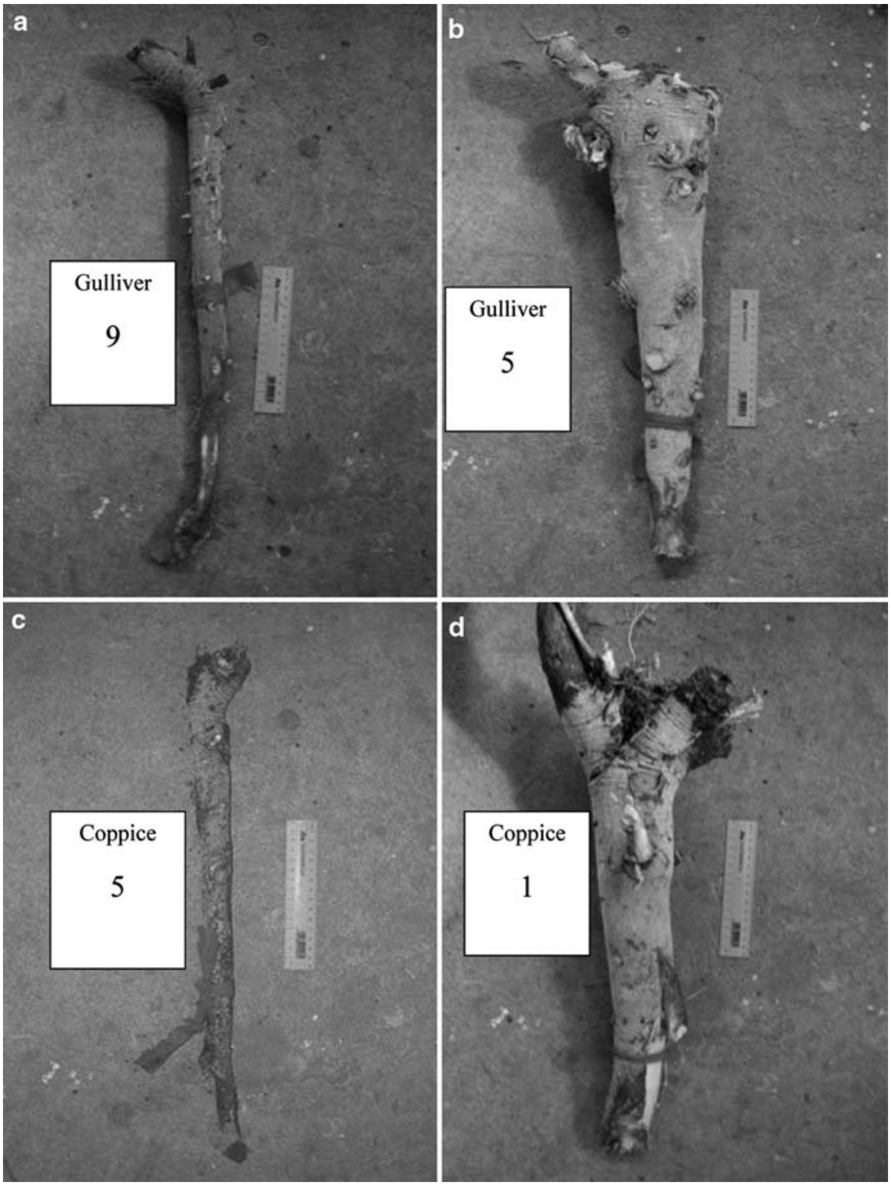

Fig. 1 The smallest (**a**) and largest (**b**) lignotubers from plants in the Gulliver stage and the smallest (**c**) and largest (**d**) lignotubers taken from the coppicing plants. The ruler in the picture is 15 cm in length

Table 1 Lignotuber dry weights, starch concentrations, and total starch pools of plants in the two post-burn stages: Gullivers three year post-burn with pole-like main stem; Coppice one year post-burn multi-stemmed shrubs (mean ± SE, $n = 10$)

	Gulliver	Coppice	*P*
Lignotuber dry weight (g)	538 ± 110	433 ± 60	0.413
TNC concentration (%)	32.8 ± 4	23.7 ± 2.1	0.059
TNC pool (g)	150 ± 19	97 ± 12	0.030
Stem diameter (mm)	25.6 ± 1.02	13.8 ± 2.03	0.000

Students *t*-tests were used for lignotuber dry weight, TNC concentration and TNC pool size while the Mann-Whitney U-test was used for stem diameter

The lack of strong seasonality in the growth patterns and wood deposition in the stems precluded the use of tree rings to establish the age of the adults. Thus, it was not possible to align the δ^{13}C sequences with the corresponding rainfall patterns. However, the growth estimated to cover the last 4–5 years (outer 8–10 mm of adult stems) showed no clear seasonal pattern in δ^{13}C values (Fig. 2). The δ^{13}C values across the radius of the Gulliver stems showed a clear pattern with relatively high δ^{13}C values (−26.5‰) at the centre of the stem that decreased by *ca.* 1‰ up to 4 mm from the centre and then increased again up to

Table 2 Correlations between biomass and TNC measures

	Stem diameter (m, at 5 cm)	Lignotuber dry weight (g)	TNC concentration (%)	TNC content (g)
Plant height (m)	0.78*	0.21 NS	0.44**	0.59***
Stem diameter (m, at 5 cm)		0.33 NS	0.25 NS	0.55***
Lignotuber dry weight (g)			−0.47**	0.76*
TNC concentration (%)				0.12 NS

The correlations were calculated by combining the data from the ten Gullivers and ten coppicing plants ($n = 20$). The numbers in each row are the correlation coefficients (r), *$P < 0.001$, **$P < 0.05$, ***$P < 0.01$, NS = not significant

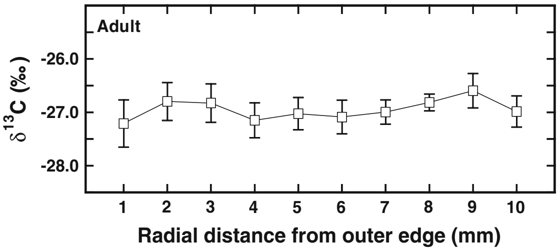

Fig. 2 δ^{13}C values for the outer 10 mm of growth from each adult stem ($n = 5$). Values are thus grouped and plotted from most recent growth to older growth. *Acacia karroo* stem diameter is estimated to increase at *ca.* 2.3 mm/year. The plotted values are therefore estimated to correspond to the last 4–5 years of growth before stem harvest

ca. 8 mm from the centre before decreasing towards the periphery by *ca.* 2–3‰ (Fig. 3a). The δ^{13}C values of the Gullivers were generally more positive than the average value for the adults. The δ^{13}C values of the coppices showed slight enrichment (0.5‰) between 0 mm and 1 mm from the centre and then decreased steadily towards the periphery to reach a final value of *ca.* −27.5‰ (Fig. 3b). The δ^{13}C values of the branches taken from the Gulliver canopies had consistently low δ^{13}C values of *ca.* −27.5‰ (Fig. 3c), relative to the average of the adults. The δ^{13}C values from the adult stems were relatively constant, ranging between −27.5‰ and −26.5‰ across the entire stem cross section (Fig. 3d).

The δ^{13}C values of each life history stage (coppicing, Gulliver and adult) were compared by combining the values of all plant parts sampled in each stage. The Gullivers were found to have significantly higher mean δ^{13}C values than the coppicing and adult plants, while there was no difference in δ^{13}C values between the coppicing plants and adults (Fig. 4). When each tissue type from each life history stage was compared separately, significantly more positive δ^{13}C values were found for the Gulliver stems compared to one year old branches from the Gulliver canopy as well as the adult and coppice stems (Fig. 5).

Discussion

The similar size and depth of the root systems of both the Gulliver and coppicing life forms indicates that the differences in shoot architecture were a function of post-burn age and not plant age. The differences in TNC concentrations and δ^{13}C values between the Gulliver and coppice life forms therefore reflect post-burn allocation and not ontogenetic differences in growth patterns. The negative correlation between TNC concentrations and lignotuber dry weight indicated that smaller lignotubers had higher TNC concentrations. A possible reason for this is that as the lignotuber increased in size after each successive fire, more woody material was laid down, thereby diluting TNC concentrations. The strong positive correlation between lignotuber dry weight and TNC content indicated that larger lignotubers were capable of storing more TNC, even though this TNC may have been stored at lower concentrations than in smaller lignotubers. Thus, as the plants got older the lignotubers got bigger and could contain more carbon reserves, allowing faster post-burn regrowth because of increased reserves for root maintenance and shoot construction.

A number of studies have successfully used ^{13}C isotopes to trace heterotrophic growth in woody plants (Gleixner et al. 1993, 1998; Jaggi et al. 2002; Helle and Schleser 2004; Kagawa et al. 2006). As far as we are aware, ours is the first study to report the use of carbon isotopes for exploring the use of stored reserves on post-burn sprouting. The observed pattern

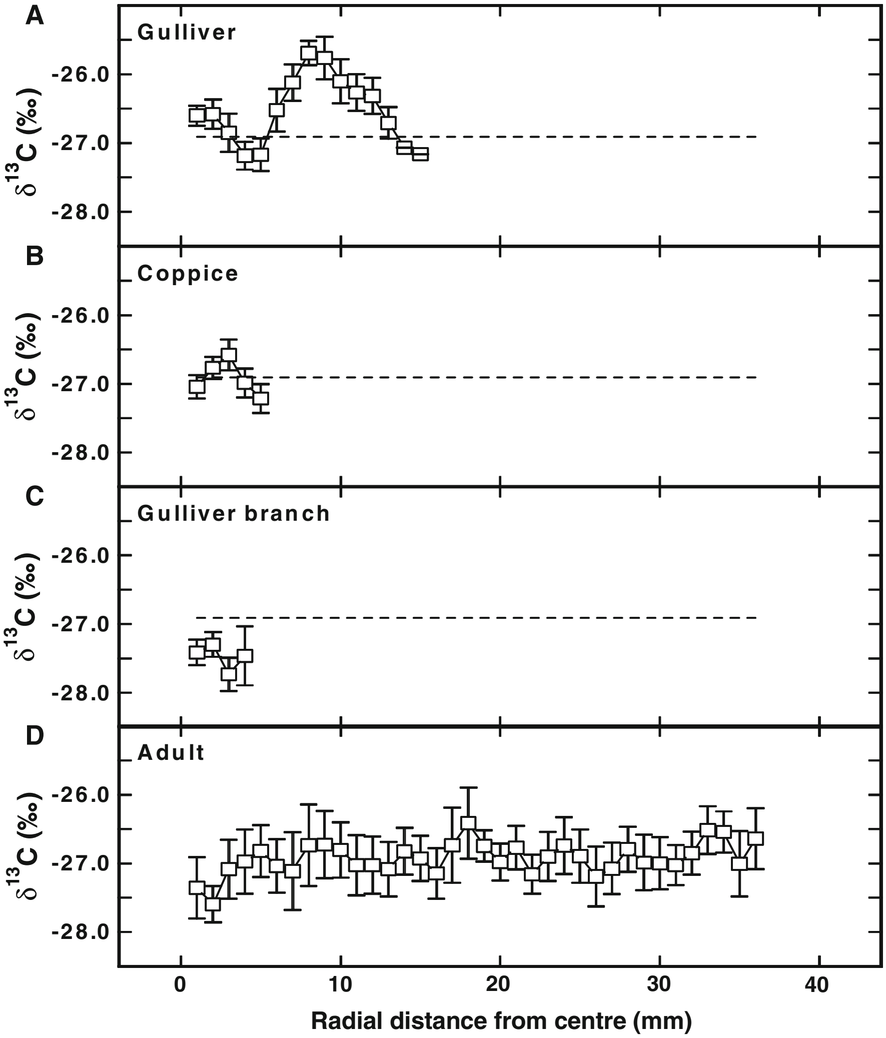

Fig. 3 δ^{13}C values (mean ± SE) from the centre (distance = 0 mm) of the stem across a radial section for (**a**) Gulliver stems ($n = 10$); (**b**) coppice stems ($n = 10$); (**c**) branches taken from the Gulliver canopies ($n = 10$); (**d**) adult stems ($n = 5$). The dashed line in panels A, B and C indicates the average δ^{13}C values for the adults, above which values the growth may be considered at be least partially heterotrophic on stored reserves. Samples were then taken at 1 mm intervals along the radius of the stem

in δ^{13}C across the Gulliver and coppice stem cross sections supports the hypothesis that stored reserves were the main source of carbon for initial post-burn re-sprouting (Figs. 3 and 6). The δ^{13}C values in these stages were enriched relative to those of sub-branches from the Gulliver canopy and also relative to the δ^{13}C values of the adults. This enrichment was followed by a gradual depletion in δ^{13}C in both the Gulliver and coppice stems, indicating a possible switch to increasingly autotrophic growth. During this "autotrophic" phase the coppices were probably recharging the lignotuber TNC content (shown in Fig. 6), as evident from the TNC data. In the first few months of post-burn growth, coppice shoot growth benefits from a lack of competition for light as a result of low grass cover after fire and ready access to water as a consequence of the deep roots of *A. karroo* compared to those of the grasses.

By the second year after a burn, one of the coppice stems develops to form the distinctive "pole" of the Gulliver stage (Maze 2001). The growth of the "pole" requires competitive re-allocation of resources from the lignotuber and/or from other coppice stems. That some of these resources are derived from the lignotuber is shown by the increase in δ^{13}C which occurred in the Gulliver stems while the δ^{13}C values of the coppice stems continued to decrease across the stem cross-sections (Fig. 3). The δ^{13}C values thereafter gradually decreased indicating a switch to increasingly autotrophic growth in the Gulliver with less and less dependence on stored carbon reserves. The coppice shoots, which die off as the shoots age (Maze

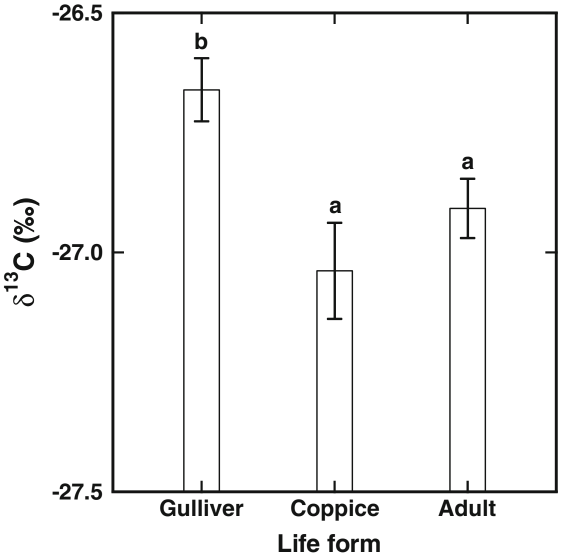

Fig. 4 δ^{13}C values (mean ± SE) for each of the three life history stages sampled. Values include all plant parts sampled for each stage. Kruskal-Wallis test: (H (2, $N = 417$) = 10.47, $P = 0.0053$). Different letters indicate significant ($P < 0.05$) differences between mean values

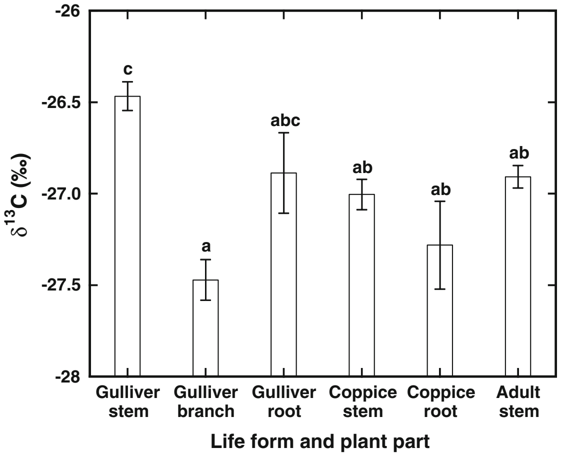

Fig. 5 δ^{13}C values (mean ± SE) for each plant part sampled in each of the three life-history stages. Significant differences were found between means (One-way ANOVA, $P < 0.0001$, df = 410). Different letters indicate significant ($P < 0.01$) differences between means using the Tukey HSD for unequal N (Spjotvoll/Stoline) post-hoc test

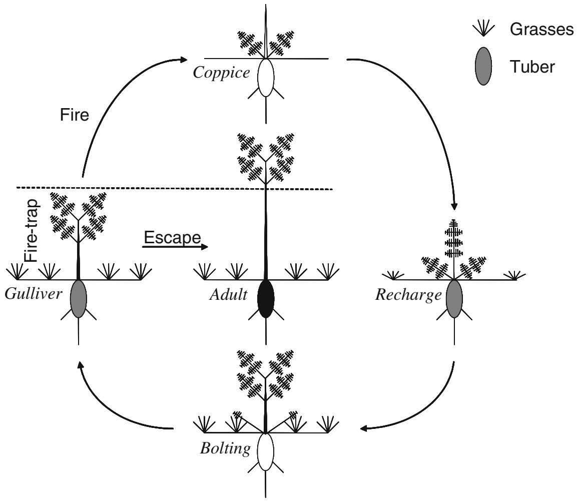

Fig. 6 Small trees within the "fire-trap" are likely to be damaged by fire. Resprouting follows "top-kill" of trees with sufficient carbohydrate reserves to allow heterotrophic "coppice" formation causing an initial increase in the δ^{13}C values. The coppice shoots "recharge" the stored carbon reserves causing a decrease in the δ^{13}C values. One of the coppice shoots grows rapidly to form the Gulliver, utilizing stored carbon from the lignotuber for this "bolting" phase and resulting in a second phase of increased δ^{13}C values. The smaller coppice shoots atrophy as the Gulliver bolts and the grass recovers; this is associated with a decrease in the δ^{13}C values as the Gulliver becomes fully autotrophic. With rapid growth and sufficient interval between fires the Gulliver becomes an adult and "escapes" the fire-trap, subject only to minor WUE associated fluctuations in δ^{13}C values. After the 'bolting' stage the plant begins to recharge underground lignotuber reserves. In the diagram the shading of lignotuber indicates supposed starch content for each phase

2001), are likely to continue replenishing TNC content of the root lignotubers during the pole-forming stage since root reserves in one year post-burn plants were still a third less than three year post-burn plants. Root reserves have to be replenished as "insurance" against failure of the pole to grow to a fire-proof stage before the next fire.

Helle and Schleser (2004), in their study of temperate deciduous tree growth, found much larger differences in δ^{13}C in early and mid season growth then between contiguous growth periods from which they inferred seasonal switches in the source of carbon. In our study, we infer switches from stored carbon to current photosynthate for different stages in post-burn recovery.

An alternative source of variation in δ^{13}C is temporal change in water use efficiency (WUE) (Francey and Farquhar 1982; Farquhar et al. 1989). We controlled for WUE effects on δ^{13}C by comparing isotope values with adult trees which had not resprouted as they were protected from fire. Thus, in these adult trees, the isotope signal would be most linked to annual variation in WUE. Adult values had a much narrower range of δ^{13}C across the stem sections than juveniles, indicating that inter-annual variation in WUE did not account for the variation in δ^{13}C values observed in juveniles.

Conclusion

The high root TNC concentrations (mean of 28.25%) similar to that of savanna species in Brazilian Cerrado (mean from four genera of 29.6%; Hoffman et al. 2004) and content found in the roots of *A. karroo* serve both to support initial coppicing and bolting of the main stem in this savanna tree species. Stored carbon thus supports both fire survival and sapling growth out of the flame zone in areas prone to frequent fires (Fig. 6). The isotope analyses support the hypothesis that plants in the Gulliver stage utilize stored carbon in order to achieve rapid growth rates of the main stem allowing them to eventually escape the fire kill zone generated by the grass layer. *Acacia karroo* is a major contributor to bush encroachment in Southern African savannas (O'Connor 1995; Chirara et al. 1998; Skowno et al. 1999; Moleele et al. 2002). A possible mechanism for these widespread increases can be linked to increasing atmospheric CO_2 concentrations (Bond and Midgley 2000). Increased CO_2 concentrations would be likely to increase the rates of and total supply of starch reserves to underground storage, which the results of this study have shown to be used to supplement rapid growth in the Gulliver life history stage. These effects would be greatest for species with a significant below-ground sink such as *A. karroo* (Fig. 1).

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References

Archibald S, Bond WJ (2003) Growing tall vs. growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. Oikos 102:3–14. doi:10.1034/j.1600-0706.2003.12181.x

Badeck FW, Tcherkez G, Nogués S, Piel C, Ghashghaie J (2005) Post-photosynthetic fractionation of stable carbon isotopes between plant organs—a widespread phenomenon. Rapid Commun Mass Spectrom 19:1381–1391. doi:10.1002/rcm.1912

Balfour DA, Howison OE (2001) Spatial and temporal variation in a mesic savanna fire regime: responses to variation in annual rainfall. Afr J Range Forage Sci 19:43–51

Bell TL, Ojeda F (1999) Underground starch storage in *Erica* species of the Cape Floristic Region- differences between seeders and resprouters. New Phytol 144:143–152. doi:10.1046/j.1469-8137.1999.00489.x

Bell TL, Pate JS (1996) Growth and fire response of selected Epacridaceae of South Western Australia. Aust J Bot 44:509–526. doi:10.1071/BT9960509

Bell TL, Pate JS, Dixon KW (1996) Relationships between fire response, morphology, root anatomy and starch distribution in South-West Australian Epacridaceae. Ann Bot (Lond) 77:357–364. doi:10.1006/anbo.1996.0043

Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. Oikos 89:409–416. doi:10.1034/j.1600-0706.2000.890224.x

Boaler SB (1966) The ecology of *Pterocarpus angolensis* in Tanzania. Overseas Research Publication 12. Ministry of Overseas Development, London

Bond WJ, Midgley GF (2000) A proposed CO2-controlled mechanism of woody plant invasion in grasslands and savannas. Glob Change Biol 6:865–869. doi:10.1046/j.1365-2486.2000.00365.x

Bond WJ, Midgley JM (2001) The persistence niche: ecology of sprouting in woody plants. Trends Ecol Evol 16:45–51. doi:10.1016/S0169-5347(00)02033-4

Bond WJ, Midgley JM (2003) The evolutionary ecology of sprouting in woody plants. Int J Plant Sci 164(3):S103–S114. doi:10.1086/374191

Bond WJ, van Wilgen BW (1996) Fire and plants. Chapman and Hall, London

Bowen BJ, Pate JS (1993) The significance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifolia* R.Br. (Proteaceae). Ann Bot (Lond) 72:7–16. doi:10.1006/anbo.1993.1075

Brugnoli E, Farquhar GD (2000) Photosynthetic Fractionation of Carbon Isotopes. In: Leegood RC, Sharkey TD, von Caemmerer S (eds) Photosynthesis: Physiology and Metabolism. Kluwer Academic Publishers, Netherlands, pp 399–434

Brugnoli E, Hubick KT, von Caemmerer S, Wong SC, Farquhar GD (1988) Correlation between the carbon isotope discrimination in leaf starch and sugars of C_3 plants and the ratio of intercellular and atmospheric partial pressures of carbon dioxide. Plant Physiol 8:1418–1424

Buysse J, Merckx R (1993) An improved colimetric method to quantify sugar content of plant tissue. J Exp Bot 44(267):1627–1629. doi:10.1093/jxb/44.10.1627

Canadell J, López-Soria L (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Funct Ecol 12:31–38. doi:10.1046/j.1365-2435.1998.00154.x

Chirara C, Frost PGH, Gwarazimba VEE (1998) Grass defoliation affecting survival and growth of seedlings of

Acacia karroo, an encroaching species in southwestern Zimbabwe. Afr J Range Forage Sci 15:41–47

Cruz A, Moreno JM (2001) Seasonal course of total non-structural carbohydrates (TNC) in the lignotuberous Mediterranean-type shrub *Erica australis*. Oecologia 128: 343–350. doi:10.1007/s004420100664

Cruz A, Pérez B, Moreno JM (2003) Resprouting of the Mediterranean-type shrub *Erica australis* with modified lignotuber carbohydrate content. J Ecol 91:348–356. doi: 10.1046/j.1365-2745.2003.00770.x

Damesin C, Lelarge C (2003) Carbon isotope composition of current-year shoots from *Fagus sylvatica* in relation to growth, respiration and use of reserves. Plant Cell Environ 26:207–219. doi:10.1046/j.1365-3040.2003.00951.x

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable isotopes in plant ecology. Annu Rev Ecol Syst 33:507–559. doi:10.1146/annurev.ecolsys.33.020602.095451

Ehleringer RE, Hall AE, Farquhar GD (1993) Stable Isotopes and Plant Carbon-Water Relations. Academic Press, San Diego

Erdmann TK, Nair PKR, Kang BT (1993) Effects of cutting frequency and cutting height on reserve carbohydrates in *Gliricidia sepium* (Jacq). Walp. For. Ecol. Manage 57:45–60. doi:10.1016/0378-1127(93)90161-F

Farquhar GD, Hubick KT, Condon AG, Richards RA (1989) Carbon isotope fractionation and plant water-use efficiency. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable Isotopes in Ecological Research, Ecological Studies No. 68. Springer, New York, pp 21–40

Francey RJ, Farquhar GD (1982) An explanation of $^{13}C/^{12}C$ variations in tree rings. Nature 297:28–31. doi:10.1038/297028a0

Gessler A, Keitel C, Kodama N, Weston C, Winters AJ, Keith H et al (2007) $\delta^{13}C$ of organic matter transported from the leaves to the roots in *Eucalyptus delegatensis*: short-term variations and relation to respired CO_2. Funct Plant Biol 34:692–706. doi:10.1071/FP07064

Gessler A, Tcherkez G, Peuke AD, Ghashghaie J, Farquhar GD (2008) Experimental evidence for diel variations of the carbon isotope composition in leaf, stem and phloem sap organic matter in *Ricinus communis*. Plant Cell Environ 31:941–953. doi:10.1111/j.1365-3040.2008.01806.x

Gignoux J, Clobert J, Menaut JC (1997) Alternative fire resistance strategies in savanna trees. Oecologia 110:576–583. doi:10.1007/s004420050198

Gleixner G, Danier HJ, Werner RA, Schmidt HL (1993) Correlations between the ^{13}C content of primary and secondary plant products in different cell compartments and that in decomposing Basidiomycetes. Plant Physiol 102:1287–1290

Gleixner G, Scrimgeour C, Schmidt HL, Viola R (1998) Stable isotope distribution in the major metabolites of source and sink organs of *Solanum tuberosum* L.: a powerful tool in the study of metabolic partitioning in intact plants. Planta 207:241–245. doi:10.1007/s004250050479

Helle G, Schleser GH (2004) Beyond CO2-fixation by Rubisco–an interpretation of 13C/12C variations in tree rings from novel intra-seasonal studies on broad-leaf trees. Plant Cell Environ 27:367–380. doi:10.1111/j.0016-8025.2003.01159.x

Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for tree- grass coexistence in savanna. J Ecol 88:213–229. doi:10.1046/j.1365-2745.2000.00435.x

Hobbie EA, Werner RA (2004) Intramolecular, compound-specific, and bulk carbon isotope patterns in C_3 and C_4 plants: a review and synthesis. New Phytol 161:371–385. doi:10.1111/j.1469-8137.2004.00970.x

Hodgkinson KC (1998) Sprouting success of shrubs after fire: height-dependent relationships for different strategies. Oecologia 115:64–72. doi:10.1007/s004420050492

Hoffman WA, Orthen B, Franco AC (2004) Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. Oecologia 140:252–260. doi: 10.1007/s00442-004-1595-2

Hoffmann WA, Bazzaz FA, Chatterton NJ, Harrison PA, Jackson RB (2000) Elevated CO_2 enhances resprouting of a tropical savanna tree. Oecologia 123:312–317. doi: 10.1007/s004420051017

Jaggi M, Saurer M, Fuhrer J, Siegwolf R (2002) The relationship between the stable carbon isotope composition of needle bulk material, starch, and tree rings in *Picea abies*. Oecologia 131:325–332. doi:10.1007/s00442-002-0881-0

James S (1984) Lignotubers and burls–their structure and ecological significance in Mediterranean ecosystems. Bot Rev 50:225–266. doi:10.1007/BF02862633

Kagawa A, Sugimoto A, Makimov TC (2006) Seasonal course of translocation, storage and remobilization of ^{13}C pulse-labeled photoassimilate in naturally growing *Larix gmelinii* saplings. New Phytol 171:793–804. doi:10.1111/j.1469-8137.2006.01780.x

Kays JS, Canham CD (1991) Effects of time and frequency of cutting on hardwood root reserves and sprout growth. For Sci 37(2):524–539

Kühn C, Barker L, Bürkle L, Frommer WB (1999) Update on sucrose transport in higher plants. J Exp Bot 50:935–953. doi:10.1093/jexbot/50.suppl_1.935

Maze KE (2001) Fire survival and life histories of Acacia and Dichrostachys species in a South African Savanna. Unpublished Master's thesis, University of Cape Town

Menaut J, Gignoux J, Prado C, Clobert J (1990) Tree community dynamics in a humid savanna of the Cote-d'Ivoire: modelling the effects of fire and competition with grass and neighbours. J Biogeogr 17:471–481. doi:10.2307/2845379

Miyanishi K, Kellman M (1986) The role of root nutrient reserves in regrowth of two savanna shrubs. Can J Bot 64:1244–1248

Moleele NM, Ringrose S, Matheson W, Vanderpost C (2002) More woody plants? The status of bush encroachment in Botswana's grazing areas. J Environ Manage 64:1244–1248. doi:10.1006/jema.2001.0486

O'Connor TG (1995) *Acacia karroo* invasions of grassland: environmental and biotic effects influencing seedling emergence and establishment. Oecologia 103:214–223. doi:10.1007/BF00329083

O'Leary MH (1981) Carbon isotope fractionation in plants. Phytochemistry 20(4):553–567. doi:10.1016/0031-9422(81)85134-5

O'Leary MH, Madhaven S, Paneth P (1992) Physical and chemical basis of carbon isotope fractionation in plants.

Plant Cell Environ 15:1099–1104. doi:10.1111/j.1365-3040.1992.tb01660.x

Rundel PW, Ehleringer JR, Nagy KA (1989) Stable Isotopes in Ecological Research. Springer-Verlag, New York

Skowno AL, Midgley JJ, Bond WJ, Balfour D (1999) Secondary succession in *Acacia nilotica* (L.) savanna in the Hluhluwe Game Reserve, South Africa. Plant Ecol 145:1–9. doi:10.1023/A:1009843124991

Stott PA (1988) The forest as phoenix: towards a biogeography of fire in mainland South East Asia. Geogr J 154:337–350. doi:10.2307/634607

Sturm A, Tang GQ (1999) The sucrose-cleaving enzymes of plants are crucial for development, growth and carbon partitioning. Trends Plant Sci 4:401–407. doi:10.1016/S1360-1385(99)01470-3

Terwilliger VJ, Huang J (1996) Heterotrophic whole plant tissues show more ^{13}C enrichment than their carbon sources. Phytochemistry 43(6):1183–1188. doi:10.1016/S0031-9422(96)00538-9

Trollope WSW (1984) Fire in Savanna. In: Booysen PdeV, Tainton NM (eds) Ecological effects of fire in South African ecosystems. Ecological studies 48. Springer-Verlag, Berlin, pp 149–176

Tschaplinski TJ, Blake TJ (1994) Carbohydrate mobilization following shoot defoliation and decapitation in hybrid poplar. Tree Physiol 14:141–151

Van der Heyden F, Stock WD (1996) Regrowth of a semiarid shrub following simulated browsing: the role of reserve carbon. Funct Ecol 10:647–653. doi:10.2307/2390175

Verdaguer D, Ojeda F (2002) Root starch storage and allocation patterns in seeder and resprouter seedlings of two Cape Erica (Ericaceae) species. Am J Bot 89:1189–1196. doi:10.3732/ajb.89.8.1189

Vesk PA, Westoby M (2004) Funding the bud bank: a review of the costs of buds. Oikos 106:200–208. doi:10.1111/j.0030-1299.2004.13204.x

Vigilante T, Bowman DMJS (2004) Effects of fire history on the structure and floristic composition of woody vegetation around Kalumburu, North Kimberley, Australia: a landscape-scale natural experiment. Aust J Bot 52:381–404. doi:10.1071/BT03156

Wahlenberg WG (1946) Longleaf pine: its Use, Ecology, Regeneration, Protection, Growth and Management. Charles Lathrop Pack Forestry Foundation, Wash. D.C