

Juggling carbon: allocation patterns of a dominant tree in a fire-prone savanna

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Abstract In frequently burnt mesic savannas, trees can get trapped into a cycle of surviving fire-induced stem death (i.e. topkill) by resprouting, only to be topkilled again a year or two later. The ability of savanna saplings to resprout repeatedly after fire is a key component of recent models of tree–grass coexistence in savannas. This study investigated the carbon allocation and biomass partitioning patterns that enable a dominant savanna tree, *Acacia karroo*, to survive frequent and repeated topkill. Root starch depletion and replenishment, foliage recovery and photosynthesis of burnt and unburnt plants were compared over the first year after a burn. The concentration of starch in the roots of the burnt plants ($0.08 \pm 0.01 \text{ g g}^{-1}$) was half that of the unburnt plant ($0.16 \pm 0.01 \text{ g g}^{-1}$) at the end of the first growing season after topkill. However, root starch reserves of the burnt plants were replenished over the dry season and matched that of unburnt plants within 1 year after topkill. The leaf area of resprouting plants recovered to match that of unburnt plants within 4–5 months after topkill. Shoot growth of resprouting plants was restricted to the first few months of the wet season, whereas photosynthetic rates remained high into the dry season, allowing replenishment of root starch reserves. ^{14}C labeling showed that reserves were initially utilized for shoot growth after topkill. The rapid foliage recovery and the replenishment of

reserves within a single year after topkill implies that *A. karroo* is well adapted to survive recurrent topkill and is poised to take advantage of unusually long fire-free intervals to grow into adults. This paper provides some of the first empirical evidence to explain how savanna trees in frequently burnt savannas are able to withstand frequent burning as juveniles and survive to become adults.

Keywords *Acacia karroo* · Fire · Non-structural carbohydrates · Resprouting · Topkill

Introduction

Savannas are characterized by a continuous grass layer and a discontinuous tree layer and are amongst the most fire-prone ecosystems in the world (Mouillot and Field 2005). In mesic savannas, fire-intervals can be as short as 1–3 years (Trollope 1984; Bond and Midgley 2000). The potential for frequent fires in savannas results from the coincidence of a continuous highly flammable grass sward and warm dry periods in the winter months (Mouillot and Field 2005). The fires are typically grass-fuelled surface fires and rarely spread through the canopies of the trees. Thus, as trees grow taller and reach above the flame-zone, they are more likely to escape from being topkilled by fire (Trollope 1984; Glitzenstein et al. 1995; Williams et al. 1999). Generally, it is only once they have escaped the so-called fire-trap that they become reproductively mature (Archibald and Bond 2003). However, the short intervals between fires in mesic savannas allow few opportunities for trees to grow to such a height so as to escape from the fire-trap.

Many savanna trees survive for decades in a stunted non-reproductive form by repeatedly resprouting from surviving

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belowground structures after their aboveground parts have been killed by fire, i.e. topkill (Bond and van Wilgen 1996; Gignoux et al. 1997). This ability of savanna trees to persist indefinitely in a transition stage between adolescence and maturity may be key to the co-existence of trees and grasses in savannas (Higgins et al. 2000; Hanan et al. 2008). Higgins et al. (2000) suggested that frequent fires inhibit the recruitment of adult trees and thus prevent trees from dominating the landscape to the point of grass exclusion. However, frequent fires do not exclude savanna trees. The juvenile trees are able to resprout repeatedly after topkill and take advantage of rare fire-free periods to grow into adults (Higgins et al. 2000).

Resprouting plants rely on carbohydrate reserves to support growth and respiration until the plant has recovered enough leaf area to once again actively support these costs (Chapin et al. 1990; Iwasa and Kubo 1997). In resprouter woody plants, root starch is depleted during post-disturbance aboveground regrowth and is later replenished once the plant has recovered enough photosynthetic biomass (Miyanishi and Kellman 1986; Bowen and Pate 1993; Canadell and Lopez-Soria 1998). It is equivocal whether reserves are used primarily as substrate for new growth or to supply the energy required to initiate growth and maintain surviving tissues (Hoffmann et al. 2000; Wildy and Pate 2002). However, it is clear that aboveground recovery is slow if the plants are topkilled when their root reserves are low (Landhäusser and Loeffers 2002).

A plant without sufficient reserves to maintain the existing root system after topkill will lose belowground gains between topkill events due to root die-back (Landhäusser and Loeffers 2002). With very frequent fires, as in mesic savannas, a plant without reserves would struggle to grow large enough to escape from being topkilled as both aboveground and belowground growth gains would be lost after each fire. However, with sufficient belowground reserves, a plant can sustain the existing root system after aboveground death (Landhäusser and Loeffers 2002; Langley et al. 2002). The incremental gains belowground during inter-fire periods may progressively support faster stem growth between fires, thus improving the probability of the plant growing large enough to escape from being topkilled (Bond and van Wilgen 1996; Bond and Midgley 2000).

Numerous studies have been carried out on the role of carbohydrate reserves during the resprouting of shrubs (Miyanishi and Kellman 1986), particularly Mediterranean-type shrubs (Bowen and Pate 1993, Canadell and Lopez-Soria 1998; Cruz et al. 2003). However, relatively few studies have focused on savanna trees (Hoffmann et al. 2000), despite the prevalence of resprouting trees in savannas (Trollope 1984; Gashaw et al. 2002; Bond and Archibald 2003). Generally, savanna trees only mature once they have grown to a size where they are unlikely to be topkilled,

whereas shrubs mature while they are still vulnerable to topkill (Bond and van Wilgen 1996). Fires are also much more frequent in mesic savannas (1–3 years) than they are in Mediterranean-type shrublands (10–30 years) (Bond and van Wilgen 1996). Thus, savannas trees not only have less time to recover between fires than Mediterranean-type shrubs, but they also have to grow faster between fires if they are to mature. In addition, resprouting savannas trees have to compete with a rapidly regenerating grass sward (Scheiter and Higgins 2007). In mesic savannas, the resprouting trees need to recover the aboveground parts necessary to support the plant, outgrow competitors and replenish reserves within 1–3 years. Thus, to survive frequent and repeated fires, the savanna trees will constantly need to juggle carbon between root storage and shoot growth (Bond and Midgley 2000).

This study investigated the carbon allocation and biomass partitioning patterns that enable a mesic savanna tree to survive frequent and repeated topkill. We hypothesized that savanna tree saplings might use reserves extensively to fund rapid regrowth after topkill, but that they would replenish the reserves between topkill events. Alternatively, the saplings might use root starch reserves conservatively after fires, so that some reserves remain in the case of another topkill event. To test these hypotheses, we examined resprout growth, starch utilization and the recovery of *Acacia karroo* Hayne for a year after topkill. We also compared the leaf area and photosynthetic capacity of post-fire resprouting saplings and unburnt saplings of *A. karroo* as an indication of the photosynthetic capacity of the resprouting plants. This was followed by a greenhouse-based ¹⁴C-labeling experiment to determine the extent to which shoot growth of *A. karroo* during resprouting relied on root reserves and whether the surviving root was supported by new photosynthates or stored carbohydrates.

Methods

Study site and species

The fieldwork for this study was conducted in a 1-ha fenced enclosure (28.20161°S, 32.04218°E, elevation 140 m a.s.l.) in the Gunjaneni area on the eastern border of the Hluhluwe-iMfolozi Park (HiP) in KwaZulu–Natal, South Africa. The vegetation of the park is predominantly fine-leaved *Acacia* savanna (Whateley and Porter 1983). Between 1956 and 1996, the mean fire-return-interval for the park was 4 years, whereas the median fire-interval was 1.3 years, with more than 90% of fires occurring between June and September (i.e. in the dry season) (Balfour and Howison 2001). The mean rainfall (2002–2006) within 5 km of the site was 620 mm, with approximately 70% falling

between October and March. The tree component in the enclosure was dominated by *A. karroo* and *A. nilotica*. The shrub layer was dominated by *A. caffra* and *Dichrostachys cinerea*. The grass sward was dominated by *Cymbopogon excavatus*, *Eragrostis curvula* and *Themeda triandra*. One-half of the plot was burnt on 30 August 2005 so as to allow for the comparison of unburnt and burnt resprouting plants. Prior to this, the plot had last burnt in 2001. Within each half, burnt and unburnt plants were selected at random for each of the various experiments using a wandering quarter method (Catana 1963).

The Hluhluwe form of *A. karroo* (Barnes et al. 1996) is a prolific resprouter, with the mortality of burnt populations less than 1% greater than that of unburnt populations (MacDonald 1980). In one of the few post-fire censuses conducted in HiP, the mortality of *A. karroo* was found to be only 2.3% 1 year after the fire, whereas the mortality rate of unburnt *A. karroo* plants over the same period was 1.6% (MacDonald 1980). Typically, numerous coppice shoots emerge from the root crown of the plant within weeks after a fire; these persist for months to years until a single shoot becomes dominant, and the plant takes on a single stemmed form. After repeated fires, the saplings develop swollen taproots which show the scars of previous topkilled stems. During the transition stage between a sapling and a young adult, the Hluhluwe form of *A. karroo* is slender and sparsely branched and is rarely reproductive. Once the adults have grown out of the so-called fire-trap, they become more branched and reproductively mature (Archibald and Bond 2003). *Acacia karroo* has been singled out as one of the most important grassland invaders in South Africa in general (O'Connor 1995; Hoffman and O'Connor 1999; Hoffman et al. 1999) and in HiP specifically (Skowno et al. 1999; Bond et al. 2001), where it seems particularly well adapted to tolerate frequent fire (Bond et al. 2001; Archibald and Bond 2003; Walters et al. 2004).

Aboveground recovery and biomass partitioning of burnt plants

The stem diameter and length of the each of the coppicing shoots of 30 resprouting *A. karroo* saplings were recorded in October 2005, January 2006, April 2006 and August 2006. Plant height for each sapling was also recorded. These values were analyzed using repeated measures analyses of variances (ANOVAs) followed by Tukey HSD Tests (Statistica ver. 7.0; StatSoft, Tulsa, OK). The stem and leaf masses of the resprouting plants were determined allometrically based on stem volume. Stem volume was calculated as the volume of a paraboloid using the length and basal diameter of the stem. To determine the allometric relationship between stem volume and stem and leaf mass, additional shoots were measured, harvested, separated into stem

and leaf material, dried at 70°C for 72 h [Fig. S1 and Table S2 in the [Electronic Supplementary Material \(ESM\)](#)] on each of the sampling occasions. The October 2005 stem and leaf mass estimates were made using the January 2006 regression equations. The estimates of stem and leaf mass were converted into carbon units based on the carbon concentration in the stem and leaves. The total carbon concentrations in the leaf and stem tissues were determined using a Thermo Flash EA 1112 series elemental analyzer (Thermo Electron, Milan, Italy). Sub-samples (2.2 mg) of dried leaf and stem samples were weighed into 8 × 5-mm tin capsules (Elemental Microanalysis, Devon, UK) and combusted in the elemental analyzer.

In addition to these aboveground measurements, the root crown diameter of the plants, taken at 10 cm below the surface, were measured 2 weeks after the fire in September 2005 and again at the end of the study in August 2006.

Root starch depletion and replenishment

The pattern of root starch depletion and replenishment during aboveground recovery was tracked by harvesting the top 30 cm of the taproot (measured from the lowest submerged stem scar) of unburnt and burnt resprouting *A. karroo* saplings in December 2005, February 2006 and August 2006. On each sampling occasion, the taproots of 15 unburnt individuals and 15 resprouting individuals were excavated. The taproots of six individuals were harvested in July 2005 as an indication of pre-fire root starch concentrations. After excavating, the roots were dried at 70°C for 5 days, weighed, milled and analyzed for root starch content. Starch in sub-samples (50 mg) of dried, ground root material was hydrolyzed to glucose using the amyloglucosidase–alpha-amylase method described by McCleary et al. (1997). The glucose concentration of the resulting solution was determined colorimetrically using the phenol–sulphuric method described by Dubois et al. (1956). Prior to the starch determination, soluble sugars were removed from the sub-sample by washing the sub-sample in hot (80°C) 80% ethanol (v/v).

To test whether there was a significant difference between the root starch concentration of the burnt and unburnt plants collected in different months, we used a factorial ANOVA (Statistica ver. 7.0) with the harvest date and the treatment (burnt or unburnt) included as categorical predictors, and root starch concentration as the response variable. The starch content of the roots (g starch per root) was converted to carbon equivalents by multiplying by 0.4, which is the proportion of carbon per unit of starch (C₆H₁₂O₆)_n.

Leaf area recovery

Changes in the leaf area of 22 burnt and 23 unburnt plants were tracked for approximately 1 year after the August

2005 fire. The leaf area of the plants was calculated as a function of the total leaf mass of the plants [resprouting plants: leaf area (cm^2) = $68.7 \times$ leaf mass (g), $r^2 = 0.91$, $n = 22$, $P < 0.001$; unburnt plants: leaf area (cm^2) = $48.9 \times$ leaf mass (g), $r^2 = 0.92$, $n = 25$, $P < 0.001$]. The total leaf mass of unburnt saplings was determined from an analysis of digital photographs of the intact plants with the background blocked out by a white screen. The images were analyzed using Adobe Photoshop ver. 7.0 (Adobe Systems, San Jose, CA) where the number of pixels associated with leaves was converted to leaf mass using a regression equation that was established at the beginning of the study ($r^2 = 0.93$, $n = 19$, $P < 0.001$).

Photosynthesis measurements

Diurnal light-saturated photosynthetic rates (A_{max}) of leaves of ten unburnt and ten resprouting plants were measured on four occasions between October 2005 and August 2006. The diurnal responses were measured at 2-h intervals from 0900 to 1600 hours on fully expanded sunlit leaves located near the apex of the shoot or branch using a LI-6400 gas analysis system (LICOR, Lincoln, NB) with a 2×3 -cm cuvette with a LED light source (LICOR 6400 02B). A single leaf on each plant was used throughout the day and harvested at the end of the day. The area of the leaves was determined by scanning the leaves with a desktop scanner and analyzing the images in Adobe Photoshop ver. 7.0. All of the plants sampled had a known pre-fire height of between 1 and 2 m. The measurements were made with CO_2 in the reference chamber set to 400 ppm and the leaf temperature set to the ambient air temperature at the time of day. The relative humidity within the cuvette was allowed to vary with the ambient conditions. The light level inside the cuvette was set to the light saturation points of the leaves, which were 1250, 1500, 2000, and 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in October 2005, January 2006, May 2006, and August 2006, respectively. The light saturation point of the leaves in the different months were determined by plotting light response curves, as described later. The mean A_{max} of burnt and unburnt plants taken at different times of the year was compared using a factorial ANOVA (Statistica ver. 7.0) with the season and treatment (burnt or unburnt) included as categorical predictors.

The light response curves were plotted for three plants in each of the sampling months. For each light response curve, the photosynthetic rate of a leaf was recorded at various light levels, ranging from 0 to 2500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The temperature of the leaf was maintained at the temperature recorded at the start of the readings, which was generally between 26 and 28°C, and the CO_2 concentration inside the leaf chamber was kept constant at 400 ppm. At each light level, the leaf was allowed to acclimate for a minimum of

2 min and a maximum of 5 min before the readings were taken.

^{14}C -labeling experiments

For the labeling experiments, 32 *A. karroo* plants were grown from seeds collected in HiP. The seeds were grown for 16 months from November 2004 in acid-washed sand in 20-l bins in a glasshouse (University of Cape Town). Each plant was supplied with 400 ml 2 mM NaNO_3 Long Ashton nutrient solution (Hewitt 1966) three times a week and supplemented with water as needed. The ^{14}C labeling was conducted in February 2006, by which time the basal diameter of each of the plants was >1 cm, and the plants were between 0.8 and 1.2 m tall. Labeling was achieved by sealing intact shoots of the plants into polyethylene bags (volume of approx. 4 l) and releasing $^{14}\text{CO}_2$ into the bag by adding 1 ml of 10% (v/v) lactic acid to 120 μl of $\text{NaH}^{14}\text{CO}_3$ (40 μCi) (Amersham Biosciences, Buckinghamshire, UK).

To determine whether root reserves could be mobilized to support shoot growth, shoots of intact plants that had been labeled with ^{14}C were clipped at the base after a cold chase period of 2 days to allow the labeled assimilates to be transported to the belowground structures (Fig. S3a of the [ESM](#)). The aboveground material, harvested after the 2-day chase period, was separated into those leaves and stems supplied with ^{14}C and those that had not been supplied with ^{14}C . Over the next 6 weeks, as the plants resprouted, sets of four plants were harvested every 1.5 weeks and separated into coarse roots (diameter >3 mm), fine roots (diameter <3 mm), young shoot tips and the remainder of the shoot. The plant material was dried at 70°C for 72 h, weighed and ground to a powder using a Wiley mill (Arthur H. Thomas Co, Philadelphia, PA).

To determine when the export of current photoassimilates to the root system recommenced after topkill, plants were clipped at the base and allowed to coppice and produce new leaves before they were supplied with $^{14}\text{CO}_2$ (Figure S3b of the [ESM](#)). Sets of four plants were labeled at a time and harvested 2 days later. The first set of plants were labeled 1 month after the plants had been clipped and the next two labeling events followed at weekly intervals. Only the longest shoot of each plant was supplied with ^{14}C . The harvested material was dried, weighed and milled as described previously.

To analyze the ^{14}C activity of the samples, dried 50-mg sub-samples of ground plant material were oxidized in a Packard Tricarb Model 306 Sample Oxidizer (Packard Instruments, Downers Grove, IL), and the released ^{14}C was captured in 8 ml of Carbo-sorb (Perkin Elmer, Waltham, MA) with 12 ml of Permafluor (Perkin Elmer) and then counted using a Beckman LS 5000 TD liquid scintillation counter (Beckman Instruments, Fullerton, CA). The amount

of ^{14}C recovered in an organ or tissue was expressed either as the proportion of the total ^{14}C label recovered in the plant or as specific activity (Bq/g). The proportion of ^{14}C recovered in plants gives an indication of the total sink size of a particular organ, whereas the specific activity gives an indication of the sink strength of an organ.

Results

Recovery after topkill by fire

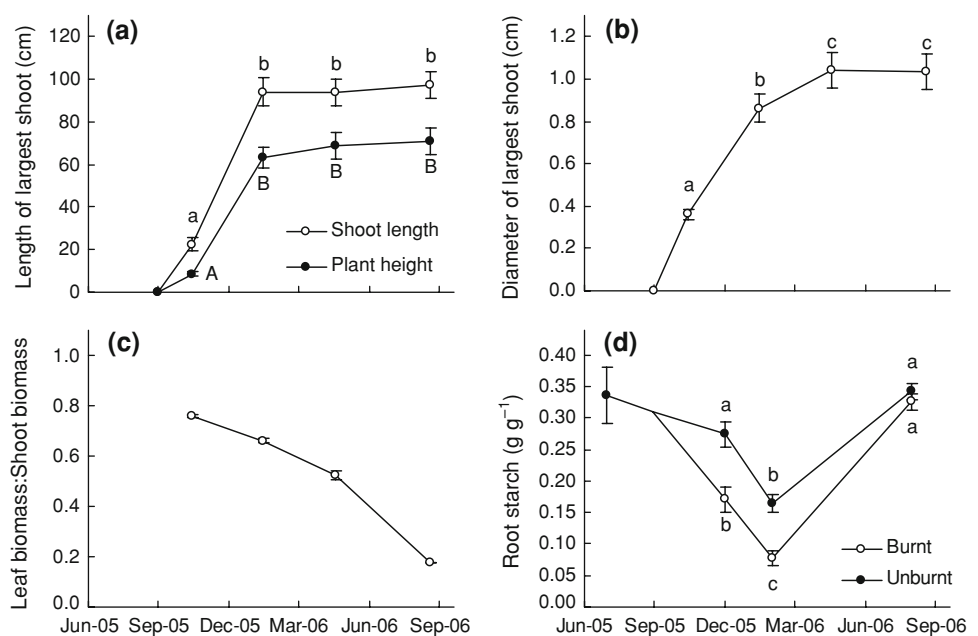
The recovery of the burnt plants was characterized by rapid height gain and shoot elongation (Fig. 1a) and more gradual shoot thickening (Fig. 1b) that continued into the dry season. The mean stem length of the largest shoot ($F_{3,78} = 143$, $P < 0.001$) of each of the burnt plants and the mean height of the plants ($F_{3,75} = 103$, $P < 0.001$) increased significantly between October 2005 and January 2006, but not after January. The mean stem diameter of the largest shoot of the burnt plants increased significantly between October 2005 and January 2006, and between January 2006 and April 2006 ($F_{3,78} = 98$, $P < 0.001$). Initially, resprouting plants invested heavily in leaf biomass, with leaves accounting for more than 75% of the total shoot biomass in October 2005, but leaf relative abundance decreased over time as the stems elongated and thickened (Fig. 1c).

Root starch concentrations of both the burnt and unburnt plants followed a seasonal cycle of depletion during the spring and summer (September–February) and replenishment through the autumn and into mid-winter (April–August; Fig. 1d). By

the end of the summer, the mean root starch concentration of unburnt plants was approximately 50% of the winter maximum, whereas the mean starch concentration of the burnt plants was approximately 25% of the winter maximum. Both the season ($F_{2,93} = 142$, $P < 0.001$) and the treatment, i.e. topkilled or unburnt, ($F_{1,93} = 24$, $P < 0.001$) significantly affected the mean root starch concentration of the plants. There was also a significant interaction between the two factors (season \times treatment, $F_{2,93} = 4.9$, $P = 0.009$), because the root starch concentration of the burnt plants recovered more rapidly than that of the unburnt plants. One year after the fire, the mean root starch concentrations of the burnt and unburnt plants were statistically similar according to the Tukey HSD pair-wise comparison ($P = 0.94$, for the two group means).

Root crown cross-sectional area of the burnt resprouting plants at the end of the study was linearly related to root crown cross-sectional area taken just 2 weeks after the fire ($y = 1.11x$, $r^2 = 0.98$, $n = 28$, $P < 0.001$, data not shown). Furthermore, the root starch content of resprouting plants recovered to pre-fire levels within the sampling period (Fig. 1d). Thus, it seemed justifiable to use final root starch content as a proxy for pre-fire starch content. We calculated root starch content as the product of root starch concentration and root mass. For each of the burnt plants, this value was compared to the estimated amount of carbon incorporated into shoot biomass to determine whether the above-ground growth could be accounted for by carbon reserves. Although the total shoot biomass accumulated over the year was positively correlated with the estimated total amount of starch the plants could store ($r^2 = 0.86$, $n = 27$, $P < 0.001$; Fig. 2a), the total amount of carbon incorporated into shoot

Fig. 1 **a** Plant height, shoot length, **b** stem diameter of the largest coppice shoots of the burnt plants, **c** the leaf to shoot biomass ratio of the burnt plants during resprouting, **d** the root starch concentrations of the burnt and unburnt plants (mean \pm standard error). The burn occurred on 30 August 2005. The letters indicate significant differences ($P < 0.05$) according to Tukey HSD Tests. In **a**, lowercase letters shoot length data, uppercase letters plant height data



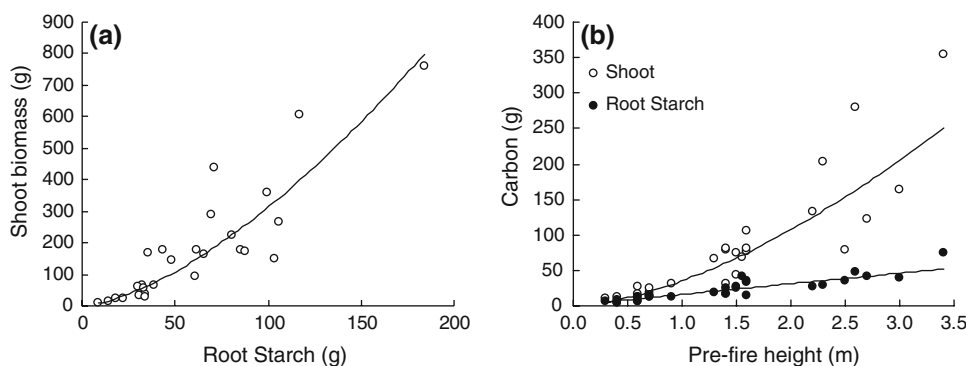


Fig. 2 **a** The root starch content in August 2006 was used as a proxy for the pre-fire starch content of the burnt plants and was found to be positively correlated to the total shoot biomass of the plants accumulated over the year after the fire ($y = 0.26x^{1.54}$, $r^2 = 0.86$, $P < 0.001$). **b** The carbon incorporated into shoot biomass over the year by the burnt plants was significantly larger than the amount of carbon they

were able to store as starch in their roots [separate slopes analysis of covariance (ANCOVA), $F_{1,50} = 8.6$, $P = 0.005$]. Both shoot production and root starch content and of resprouting plants were strongly correlated to pre-fire height ($y = 35.37x^{1.60}$, $r^2 = 0.86$, $n = 27$, $P < 0.001$, and $y = 16.20x^{0.95}$, $r^2 = 0.82$, $n = 27$, $P < 0.001$, respectively). All data were log transformed for the statistical analyses

biomass was significantly larger than that stored as starch (separate slopes ANCOVA, $F_{1,50} = 8.6$, $P = 0.005$; Fig. 2b).

The total leaf area of the plants followed a seasonal pattern, with maximum leaf area from mid-summer to the beginning of the dry season (January–April) and minimum leaf areas at the end of the dry season (i.e. in August)

(Fig. 3). The leaf area of the resprouting trees was positively correlated with the pre-fire height of the plants on all four sampling dates post-fire ($P < 0.001$, Fig. 3). By January 2006, 5 months after the fire, there was no significant difference in the total leaf area of burnt and unburnt plants that had been of similar size before the fire [analysis of

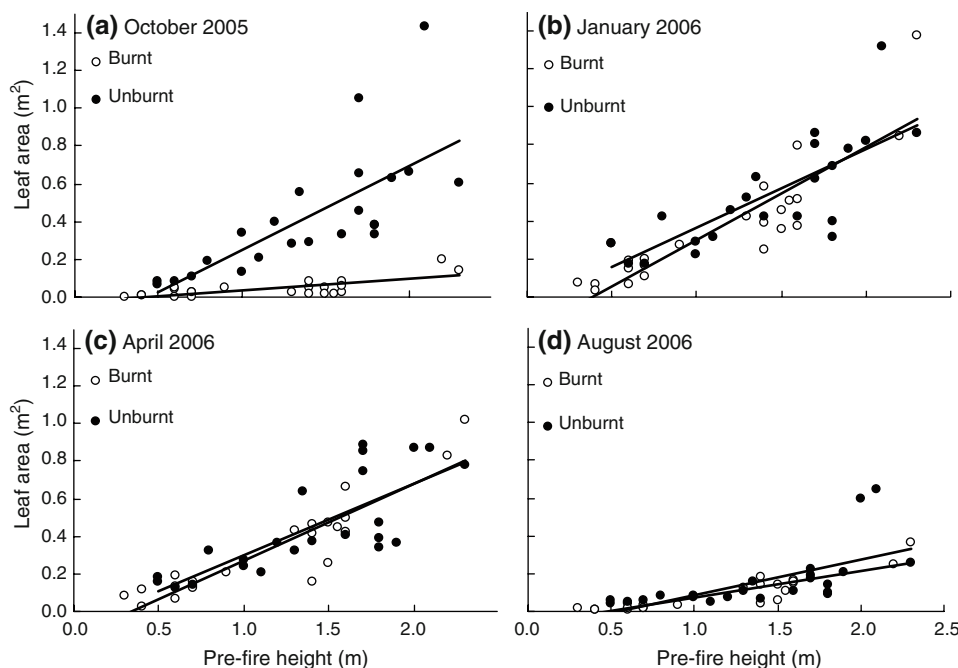


Fig. 3 For both the burnt resprouting plants and the unburnt plants, variation in leaf area was significantly correlated ($P \leq 0.001$) with the pre-fire height of the plants on all four sampling dates. For the burnt resprouting plants, the linear regression equations for leaf area (m^2) as a function of pre-fire height (m) were $y = 0.06x - 0.02$ ($r^2 = 0.52$, $n = 22$, $P < 0.001$), $y = 0.49x - 0.19$ ($r^2 = 0.79$, $n = 22$, $P < 0.001$), $y = 0.41x - 0.14$ ($r^2 = 0.83$, $n = 22$, $P < 0.001$) and $y = 0.14x - 0.07$ ($r^2 = 0.81$, $n = 22$, $P < 0.001$) for October 2005 (a), January 2006 (b), April 2006 (c) and August 2006 (d), respectively. For the unburnt

plants, the linear regression equations were $y = 0.44x - 0.20$ ($r^2 = 0.53$, $n = 23$, $P < 0.001$), $y = 0.41x - 0.05$ ($r^2 = 0.60$, $n = 23$, $P < 0.001$), $y = 0.38x - 0.08$ ($r^2 = 0.60$, $n = 23$, $P < 0.001$) and $y = 0.19x - 0.10$ ($r^2 = 0.41$, $n = 23$, $P = 0.001$) for October 2005 (a), January 2006 (b), April 2006 (c) and August 2006 (d), respectively. By January 2006, only 5 months after the fire, there was no significant difference in the total leaf area of the burnt resprouting plants and unburnt plants when controlling for pre-fire size (ANCOVA, $F_{1,42} = 0.8$, $P = 0.4$)

covariance (ANCOVA), $F_{1,42} = 0.8$, $P = 0.4$]. There was also no significant difference in the leaf area of burnt and unburnt trees in April 2006 (ANCOVA, $F_{1,42} = 0.3$, $P = 0.6$), nor in August 2006 (ANCOVA, $F_{1,32} = 0.7$, $P = 0.4$).

Photosynthetic rates of burnt and unburnt plants

A_{\max} of both the burnt and the unburnt plants increased rapidly from October to January and then declined into the dry season ($F_{3,272} = 106$, $P < 0.001$; Fig. 4). Overall, the light-saturated photosynthetic rate (A_{\max}) of the burnt plants was significantly greater than that of unburnt plants ($F_{1,272} = 4.3$, $P = 0.04$, Fig. 4). However, the Tukey HSD test revealed that the mean A_{\max} of the resprouting plants was significantly larger than that of the unburnt plants in October 2005 only, and not thereafter (Fig. 4).

^{14}C labeling of intact and resprouting plants

For the plants that were labeled with ^{14}C before they were topkilled, most of the ^{14}C recovered after 48 h was in the original aboveground biomass ($82 \pm 2\%$) (data not shown). Of this, the majority was recovered in the ^{14}C -fed leaves ($66 \pm 2\%$) and in the stem supporting these leaves ($12 \pm 1\%$) (data not shown). As the coppicing shoots grew, the proportion of ^{14}C in the shoots increased linearly ($r^2 = 0.95$, $n = 18$, $P < 0.001$; Fig. 5a), whereas the proportion of ^{14}C in the coarse roots decreased exponentially ($r^2 = 0.62$, $n = 18$, $P < 0.001$; Fig. 5a). As the new shoots elongated, the specific activity of the young shoot tips decreased rapidly according to a power function as the new shoots grew ($r^2 = 0.87$, $n = 10$, $P < 0.001$;

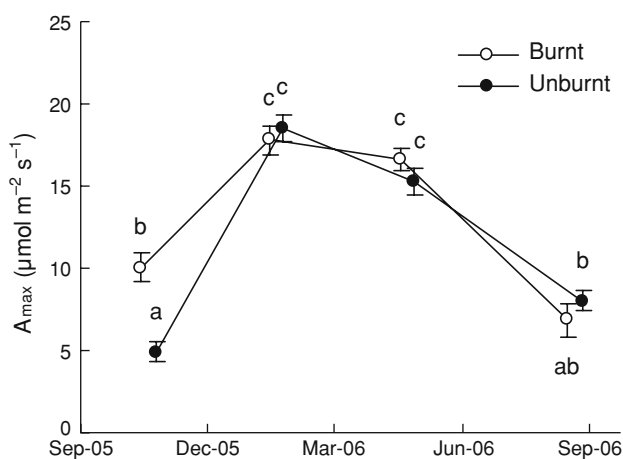


Fig. 4 The mean (\pm SE) light-saturated photosynthetic rates (A_{\max}) of burnt and unburnt saplings as recorded during the first year after the August 2005 fire. The mean A_{\max} of the resprouting plants was significantly larger than that of the unburnt plants in October 2005, but not thereafter. The letters indicate significant differences ($P < 0.05$) according to a Tukey HSD Test

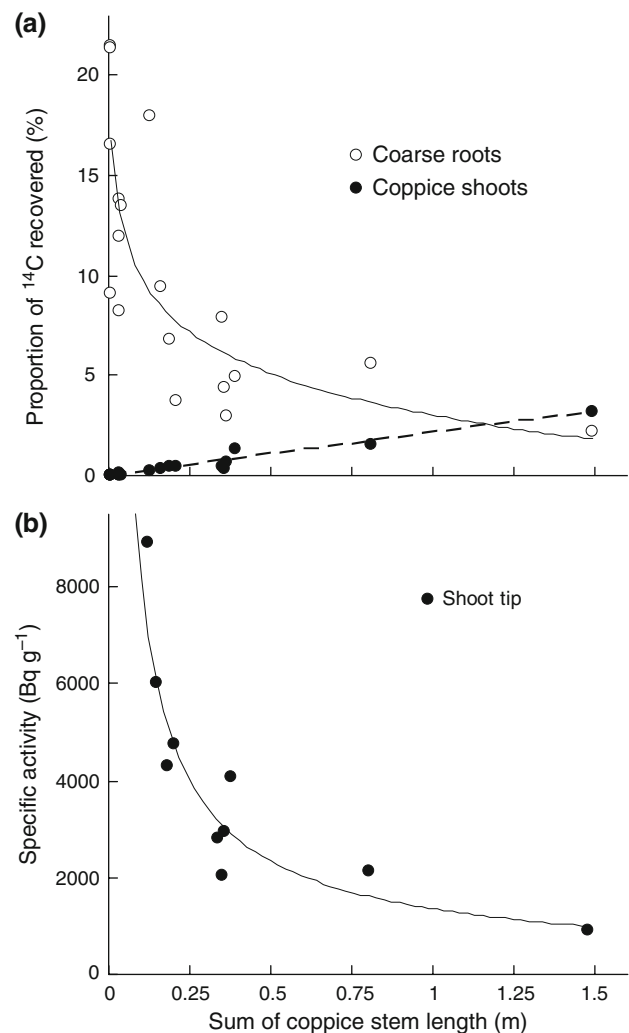


Fig. 5 **a** The proportion of ^{14}C recovered in the coarse roots and in the coppice shoots of the plants that were labeled with ^{14}C before they were topkilled. As the coppicing shoots grew, the proportion of ^{14}C in the coppicing shoots increased linearly ($r^2 = 0.95$, $n = 18$, $P < 0.001$), while the proportion of ^{14}C in the coarse roots decreased exponentially ($r^2 = 0.62$, $n = 18$, $P < 0.001$). **b** The standardized specific activity of the young shoot tips decreased rapidly according to a power function as the new shoots grew ($r^2 = 0.87$, $n = 10$, $P < 0.001$)

decreased rapidly following a power function ($r^2 = 0.87$, $n = 10$, $P < 0.001$; Fig. 5b).

For the plants that were labeled with ^{14}C while they were resprouting, almost all ($99.3 \pm 0.3\%$) of the label recovered in the tissues of the plants was in the aboveground parts (Fig. 6). Most of this label was in the ^{14}C -supplied leaves ($80 \pm 3\%$) and in the stem supporting these leaves ($13 \pm 2\%$) with the remainder in the tissue acropetal to the ^{14}C -supplied leaves ($6 \pm 3\%$) (Fig. 6a). The proportion of ^{14}C retained in the ^{14}C -supplied leaves was generally less for longer shoots than for shorter shoots; however, the correlation between coppice stem length and ^{14}C in this tissue was not statistically significant. The proportion of ^{14}C in the

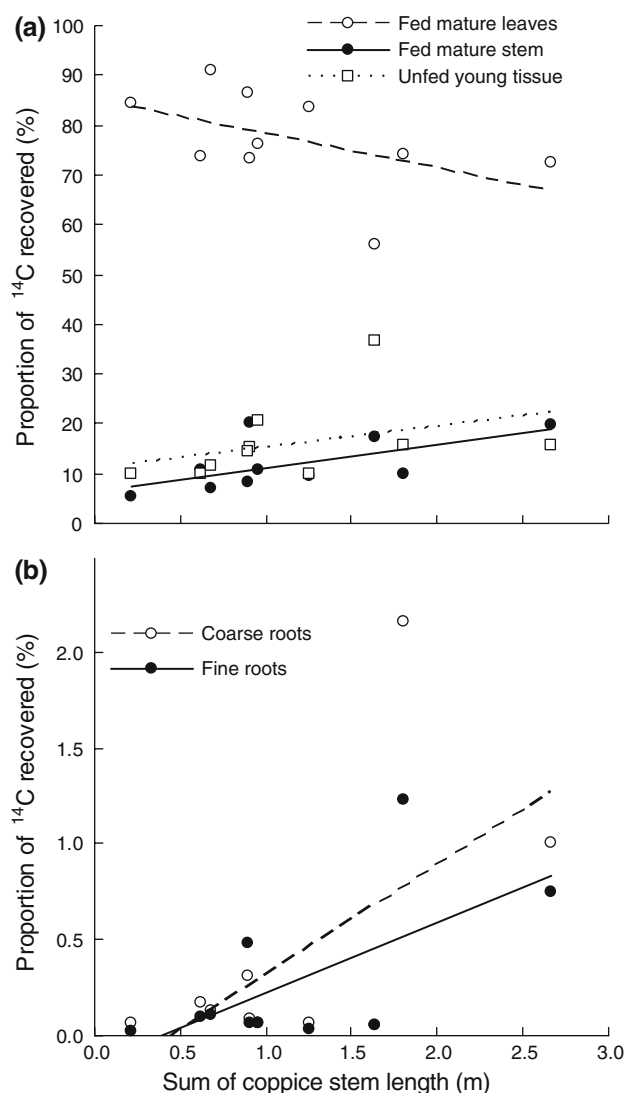


Fig. 6 The proportion of ^{14}C label recovered in the leaves that were supplied (fed) with $^{14}\text{CO}_2$, the stem supporting these leaves, and the young unfed shoot tip on the fed shoot (a), and in the coarse roots and the fine roots of the plants that were labeled while they were resprouting after being clipped at the base (b). The proportion of ^{14}C recovered in the stem supporting the fed leaves ($r^2 = 0.40$, $n = 10$, $P = 0.05$) and in the fine roots ($r^2 = 0.41$, $n = 10$, $P = 0.05$) increased significantly as the shoots elongated. The correlation between coppice stem length and ^{14}C in the ^{14}C -supplied leaves tissue was not statistically significant

stem supporting the fed leaves increased linearly as the shoots grew ($r^2 = 0.40$, $n = 10$, $P = 0.05$, Fig. 6a). The proportion of ^{14}C recovered in the fine roots also increased linearly as the shoot grew ($r^2 = 0.41$, $n = 10$, $P = 0.05$, Fig. 6b), but remained much lower than that recovered in the aboveground tissues. Over the duration of the experiment, the proportion of ^{14}C recovered in the tissues acropetal to the region supplied with $^{14}\text{CO}_2$ was $6 \pm 2.5\%$, whereas only $0.3 \pm 0.1\%$ was in the coarse roots and $0.4 \pm 0.2\%$ in fine roots.

Discussion

Savanna tree saplings can survive decades of topkill by fires with rare opportunities for growing tall enough to escape the flame-zone. Tree cover in savannas is highly variable in space and time depending, in part, on the frequency of sapling escape. This study investigated the carbon allocation and biomass partitioning that enable savanna saplings to survive recurrent and frequent topkill and eventually escape the fire-trap.

In this study, resprouting caused a sharp decrease in the root starch reserves of *A. karroo* saplings. The depletion of root reserves during resprouting has also been reported for woody plants in neo-tropical savannas (Miyanishi and Kellman 1986), Mediterranean-type ecosystems (Bowen and Pate 1993; Canadell and Lopez-Soria 1998) and North American forests (Landhäusser and Loeffers 2002; Langley et al. 2002). The root starch content of resprouting savanna shrubs (*Miconia albicans* and *Cildemia sericea*) was depleted by 30% compared to unburnt plants 1 year after a single fire and by 50% 1 year after five successive annual burns (Miyanishi and Kellman 1986). These two savanna shrub species needed 2 years after the burn to return to pre-fire root starch levels. By contrast, starch reserves of burnt *A. karroo* plants were replenished to match those of the unburnt plants within a single year after topkill (Fig. 1d). This implies that even annual fires would not decrease the resprouting vigor of *A. karroo* saplings.

During the first half of the growing season after topkill, the shoots of the resprouting plants elongated rapidly, and the plants allocated more biomass to leaf tissue than stem tissue (Fig. 1a, c). The plants also avoided excessive shading by grasses as they grew tall quickly (Fig. 1a). Root starch reserves were mobilized not only to initiate the first burst of growth but also to supplement current assimilation after leaf area had recovered (Fig. 3), as indicated by the continued depletion of starch throughout the growing season (Fig. 1d). After February, which marks the end of the summer and the wet season, shoot elongation ceased, whereas root starch replenishment commenced and continued into the dry season, as did shoot thickening, although at a slower rate (Fig. 1b, d). The allocation switch late in the wet season from shoot growth to belowground sinks recorded in this study is consistent with what has been reported for neo-tropical (Franco 1998; Hoffmann 2002) and Australian (Prior et al. 1997; 2004) savanna trees. Generally, growth ceases before photosynthetic activity in plants under stress (Lambers et al. 1998). In savannas, nutrient and water availability is generally greatest in the wet summer months (Bernhard-Reversat 1982; Scholes and Walker 1993). In the early resprouting stages, light-saturated photosynthetic rate (A_{max}) of the resprouting plants was higher than that of the unburnt plants (Fig. 4). This is

similar to the pattern reported for burnt and unburnt trees in Australian savannas (Cernusak et al. 2006) and North American prairies (McCarron and Knapp 2003). The difference in the A_{\max} of burnt and unburnt plants could be the result of improved resource availability because of the decreased grass sward and the input of N and P in the form of ash (McCarron and Knapp 2003; Cernusak et al. 2006). It could also be a consequence of the increased root:shoot ratio of the burnt plants, and thus increased resource availability per unit leaf (Castell et al. 1994; McCarron and Knapp 2003). Nevertheless, the enhanced photosynthetic activity of the resprouting plants likely contributed to the rapid recovery of the plants. Thus, the ability of resprouting *A. karroo* saplings to replenish depleted root starch reserves only 1 year after topkill might be explained by the rapid leaf canopy expansion of the resprouting plants in spring (Fig. 3), the enhanced photosynthetic activity at early resprouting stages (Fig. 4), and the maintenance of the canopy and some photosynthetic activity into the dry season (Fig. 4) sufficient not only to meet root respiration costs but also to continue the replenishment of the root starch reserves.

Up until January 2006, i.e. 5 months after the burn, root reserves were used as a source of carbon for growth and respiration. To estimate the proportion of carbon supplied from root reserves compared to current photosynthates, we calculated the amount of carbon assimilated using the leaf area (Fig. 3) and mean A_{\max} measurements (Fig. 4). We assumed that the plants were photosynthetically active between 0900 and 1600 hours only, had a constant photosynthetic rate throughout the day (mean A_{\max}) and that this varied linearly between sampling periods. Only the data for plants that had a pre-fire height of 1–2 m were included in the calculations. By the end of October, 2 months after the burn, approximately 40% of the root starch reserves had been mobilized (Fig. 1d), representing approximately 10 g of carbon (Fig. 2b), whereas only 4 g of carbon would have been assimilated. Thus, at this time, approximately 70% of carbon used by the plant would have been supplied by root starch reserves. By the end of January, 5 months after the burn, when approximately 75% of the root starch reserves had been mobilized (Fig. 1d), representing approximately 19 g carbon (Fig. 2b), approximately 120 g of C would have been assimilated through photosynthesis. Thus, by this stage, photoassimilates had supplied 85% of the carbon requirements of the plants, whereas root starch had supplied only 15%. After January, root starch reserves started to recover, and photoassimilates would have supplied carbon for both continued growth and root starch replenishment. Despite the strong and rapid increase in dependence on current photoassimilates with time after resprouting, the extent of regrowth was positively correlated with root starch reserves (Fig. 2a). However, this contribution of root

reserves to recovery over the entire growing season seems to be largely indirect. The reserves supplied the energy and substrate required for the rapid recovery of photosynthetic tissue at the start of the growing season, but this became the major source of carbohydrates fueling continued growth for the remainder of the growing season. This is consistent with what has been reported for seedlings of a Brazilian savanna tree species (Hoffmann et al. 2000) and a western Australian fire-adapted shrub (Wildy and Pate 2002). Hoffmann et al. (2000) reported that most of the shoot growth of resprouting Brazilian savanna *Kielmeyera coriacea* tree seedlings occurred after the decrease in reserves had already stabilized. Wildy and Pate (2002) reported that root starch contributed less than 10% to new shoot biomass of resprouting *Eucalyptus kochii*, a western Australian shrub, during the first year after topkill.

The results from the ^{14}C -labeling experiment performed in this study indicated that root reserves are mobilized not only to support the initial shoot elongation and foliage recovery but also to support respiration of the root system and the new shoots. The proportion of ^{14}C recovered in the coarse roots of resprouting plants labeled prior to topkill decreased exponentially, but the decrease was not matched by an increase in the ^{14}C in the coppicing shoots (Fig. 5a) or in the fine roots (data not shown). Presumably, a large proportion of this missing ^{14}C was consumed by respiration, probably in the relatively massive root rather than in the smaller resprouting shoots. Although the proportion of label recovered in the coppicing shoots of the plants that were labeled before they were topkilled was small, it steadily increased as the shoots grew (Fig. 5a), which indicates that stored assimilates continued to contribute to shoot growth even after the shoots were fairly well established. However, the specific (per gram) contribution declined rapidly as the shoots developed (Fig. 5b). The leaves on the older and longer shoots exported assimilates to their supporting stem in particular, but also acropetally to the shoot tip (Fig. 6a). Thus, the first few leaves and shoot tips would have been more dependent on reserve carbohydrates than the leaves and shoot tissue that developed later, as the contribution from reserves became diluted by current photosynthates.

The allocation of ^{14}C from $^{14}\text{CO}_2$ -supplied resprouting shoots to basipetal transport was negligible (Fig. 6b). The proportion of ^{14}C recovered in roots 48 h after the ^{14}C -labeling of intact plants was approximately 25% (Fig. 5a), whereas the proportion of ^{14}C recovered in roots 48 h after the ^{14}C -labeling of resprouting plants was less than 5% (Fig. 6b). Most of the photosynthates of mature leaves of coppicing shoots were retained in the leaves themselves, exported to the supporting stem, or transported acropetally to the developing shoot tip. In our study, basipetal translocation from coppicing shoots had not commenced 7 weeks

after coppicing. Over this period, root metabolism would have been entirely dependent on root reserves.

Root dieback can occur when root reserves are insufficient to support root metabolism after topkill (Landhäusser and Lieffers 2002). However, *A. karroo* saplings are able to retain large root systems after topkill, and we propose that this capability may be the key for their eventual escape out of the fire-trap. For trees that were less than 3 m tall, there was a strong correlation between pre-fire height, root reserves and new shoot production (Fig. 2), implying that as plants develop larger root systems and larger root reserves, they can recover faster after topkill. Thus, below-ground gains retained from one inter-fire period to the next also manifest an aboveground growth advantage, as was hypothesized by Bond and van Wilgen (1996), and the plant is more likely to grow large enough to escape topkill during future inter-fire periods. The rapid recovery of leaf area and the replenishment of reserves within a single year after topkill implies that the plants are well adapted to persist within the fire-trap indefinitely but that they are also poised to take advantage of unusually long fire-free intervals to grow out of the fire-trap, as predicted by Higgins et al. (2000).

The prolonged dependence of resprouting *A. karroo* on root reserves during the wet season and the replenishment of reserves over the dry season implies that the ability of the plants to recover after repeated topkill could be particularly vulnerable to browsing during the dry season. As in the case of topkill, recovery of *A. karroo* after defoliation is in part supported by carbohydrate reserves (Teague 1989). If the plants suffered substantial defoliation late in the growing season, they would have limited capacity to recover leaf area, and the loss of leaf area would presumably delay the replenishment of reserves and thus decrease their resprouting vigor if they were topkilled again.

This study focused on recovery after a single topkill event in the late dry season when root starch concentrations were at a maximum. It is possible that fires at a time when starch reserves were seasonally depleted would result in a more substantial decrease in the resprouting vigor of *A. karroo*. Topkill in the middle of the growing season, when starch root reserves were low, resulted in poor resprouting vigor of *Adenostoma fasciculatum*, a chaparral shrub, (Jones and Laude 1960) and saplings of north American hardwood trees (Kays and Canham 1991) and also poor root retention and root starch replenishment of *Populus tremuloides* saplings (Landhäusser and Lieffers 2002). However, topkill is generally more likely to occur in the dormant season (Trollope 1984; Higgins et al. 2000; Drewa 2003; Govender et al. 2006), when the grass sward is cured and highly flammable, than in the growing season, when the grass sward is green and less flammable. Nevertheless, a 30-year fire experiment in a loblolly pine plantation found

that summer burns were an effective management tool for manipulating the population density of understory hardwoods, which are topkilled by fire and resprout (Robbins and Myers 1992). Like *A. karroo*, these hardwoods partially deplete their starch reserves over the growing season (Robbins and Myers 1992). A suggestion for future research is to test the effect of summer burning or intensive late season browsing on the recovery rate of encroaching savanna woody resprouters like *A. karroo*.

Conclusion

This paper provides some of the first empirical evidence to explain how the dominant tree species in mesic savannas are able to withstand frequent burning as juveniles and survive to become adults. The paper also adds to the existing body of literature that emphasizes the importance of below-ground carbohydrate reserves for the survival of woody plants that experience frequent and severe aboveground damage in a wide range of habitats, from savannas (Miyaniishi and Kellman 1986) to Mediterranean-type shrublands (Bowen and Pate 1993; Canadell and Lopez-Soria 1998) to temperate forests of Japan (Kabeya et al. 2003). In this study, resprouting *A. karroo* saplings used starch reserves extensively after topkill. Root reserves maintained root function, after topkill, and supplemented the initial rapid recovery of the canopy, which then had the capacity to fund further growth as well as replenish exhausted starch reserves within the first year after topkill. Although saplings lose their aboveground parts after topkill, they retain the belowground gains from inter-fire periods. The larger root structures of these saplings have a positive effect on their aboveground growth rates and thus increase their chance of escaping the fire-trap and becoming adult trees.

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