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Effects of water and nutrient addition on the coppice growth response of cut *Terminalia sericea*

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The ability of a woody plant to coppice and remain vigorous largely depends on the severity of disturbances, resource availability and the mobilisation of stored reserves. There is limited information about the role played by resource limitation on the recovery of cut trees. This study investigated the effects of water and nutrient supplementation on coppice growth responses of resprouting cut trees in a semi-arid savannah in South Africa. Cut trees were exposed to different levels of water and nutrient (nitrogen and phosphorus) supplementation over a period of 2 years in a factorial experimental design. We hypothesised that adding water and nutrients would result in an increased coppice growth response and replenishment of stored structural reserves. Adding water and nutrients significantly increased shoot diameter, shoot length and resprouting ratio for the initial 12 months after cutting but not stored structural reserves. Such a response pattern suggests that the initial growth of resprouting shoots may be strongly resource-limited, while resources are concentrated on supporting fewer resprouting shoots compared to a higher number.

Conservation implications: If practicing rotational tree harvesting, trees resprouting in resource-poor locations need a longer resting period to recover stored reserves and to also recover lost height after cutting.

Introduction

Plants are subjected to various forms of disturbances and stresses that affect their growth, production and survival. When recovering lost biomass after a disturbance, resource availability and exposure to further disturbances limit the full recovery of plants growing in a disturbed ecosystem (Hoffmann, Schroeder & Jackson 2002; Holdo, Holt & Fryxell 2009). Thus, there is a need to understand the importance of tree resource use as well as the factors that affect tree recovery as influenced by climatic factors. An understanding of how disturbances and resource availability interact will have further management implications for the long-term productivity and sustainability of woody vegetation (Neke 2004; Neke, Owen-Smith & Witkowski 2006; Pote *et al*. 2006). As a result of exposure to disturbances, coppicing (resprouting) may be central to the survival and resilience of trees in disturbance-prone systems (Avohou *et al*. 2011). Coppicing can be defined as the production of vegetative shoots at the base of the stem or sprouts arising from a stump, resulting in the emergence of new shoots from the stump or roots (Hardesty 1984; Laureysens *et al*. 2003; Van Wyk & Van Wyk 1997).

Following a disturbance event, an increase in nutrient and water availability stimulates growth rates and allocation to storage in resprouting organs (Cruz *et al*. 2002; Sankaran, Ratnam & Hanan 2008). This is supported by the study of Cruz *et al*. (2002), who suggest that resprout growth is limited by the low amount of moisture during the early stages of regeneration. In other instances, an increase in water and nutrient availability after a disturbance may increase woody plant vegetation, leading to bush encroachment and therefore reducing biodiversity and the overall productivity of the ecosystem (Ward 2005). For example, water availability was shown to be positively correlated with regeneration in *Acacia tortilis* (Forssk) in Tunisia (Noumi *et al*. 2010) and in *Populus tristis* Fisch and *Populus balsamifera* in the USA (Dickmann, Nguyen & Pregitzer 1996).

Nutrients play a key role in replenishing depleted stored nutrient reserves of plants after a disturbance such as tree cutting (Bowen & Pate 1992) and their interaction with moisture affects coppice regrowth (Castell & Terradas 1994). Because nitrogen (N) in the remaining plant parts is used for reconstructing new tissue, adding more N increases root N storage for later use after a disturbance (El Omari *et al*. 2003; Kabeya & Sakai 2005). More N also increases concentrations of photosynthetic enzymes, which in turn cause a higher rate of photosynthesis in leaves (Chapin III

1991). In fertilised resprouting *Erica australis* L. Com., trees grew faster and produced higher biomass than un-fertilised trees 2 years after fertiliser application in Spain (Cruz *et al*. 2002). Nutrient addition also increased both diameter and height of *Betula pendula* Roth. and willow (*Salix* spp.) stands in Finland (Hytonen & Kaunisto 1999).

It has been suggested that stored carbohydrate reserves and surviving meristems are the most important resources controlling resprouting after disturbances, with differences in soil nutrient levels also affecting stored carbohydrate reserves (Bellingham & Sparrow 2000; Bond & Midgley 2001; Kabeya & Sakai 2005). For example, carbohydrate reserve concentration in resprouting *Quercus crispula* Blume was positively correlated to resprouting shoot length and leaf number (Kabeya *et al*. 2003), while starch concentrations in roots of coppicing *Salix viminalis* L., were higher in trees that received higher levels of N compared to plants that received lower levels (Fircks & Sennerby-Forsse 1998).

Surprisingly, little is known about the regeneration strategies of woody species in tropical and subtropical savannahs (Neke 2004; Pote *et al*. 2006). This is because most studies have focused on ecosystems that differ markedly from African woodlands, such as temperate ecosystems (Wilson 2002). Such ecosystems differ in terms of the seasonality and distribution of rainfall, tree population structure, moisture levels and tree densities. Most studies on tree responses have also strongly focused on the effects of varying resource levels on seedling growth and survival (Cheng & Fuchigami 2002; Druege *et al*. 2000; Kraaij & Ward 2006; Scogings & Mopipi 2008; Wendler & Millard 1996; Wilson & Witkowski 1998), rather than mature and established trees. Knowing such information will provide clues for understanding mechanisms underlying a tree's regrowth strategies after a disturbance. Also, such information would assist in evaluating how changes in resource availability may impact a community exposed to different disturbance types and frequencies.

This study was carried out to investigate how the addition of water and nutrients interact to influence tree regrowth (in terms of shoot production, shoot length and diameter, and resprout ratio) as well as the total non-structural carbohydrate (TNC) storage capacity after cutting. The following question was asked: how do varying levels of water and nutrient supplementation influence the coppice response and stem TNC reserves of cut trees? It was hypothesised that supplementing resprouting trees with water and nutrients would increase coppice response and would also result in higher TNC levels in supplemented trees compared with unsupplemented trees.

Research method and design

The study site and the experimental design were described previously (Moyo, Scholes & Twine 2015b); a brief description of both the site and the design follows.

Setting

The experiment was conducted at the Wits Rural Facility (WRF), a 350-ha research station in the central savannah lowveld region of Limpopo Province, South Africa (24° 30′ S; 31°06′ E). The study site is semi-arid, with a mean annual rainfall of ~650 mm, concentrated in the summer season (between October and April) (Figure 1b) (Kaschula, Twine & Scholes 2005a; Neke *et al*. 2006; Shackleton 1997). The study spanned a 2-year period, starting at the end of the dry season of 2010 (September 30), during the period when trees begin leaf-flush, and ending in September 2012 (Moyo, Scholes & Twine 2015a; Moyo *et al*. 2015b).

Design

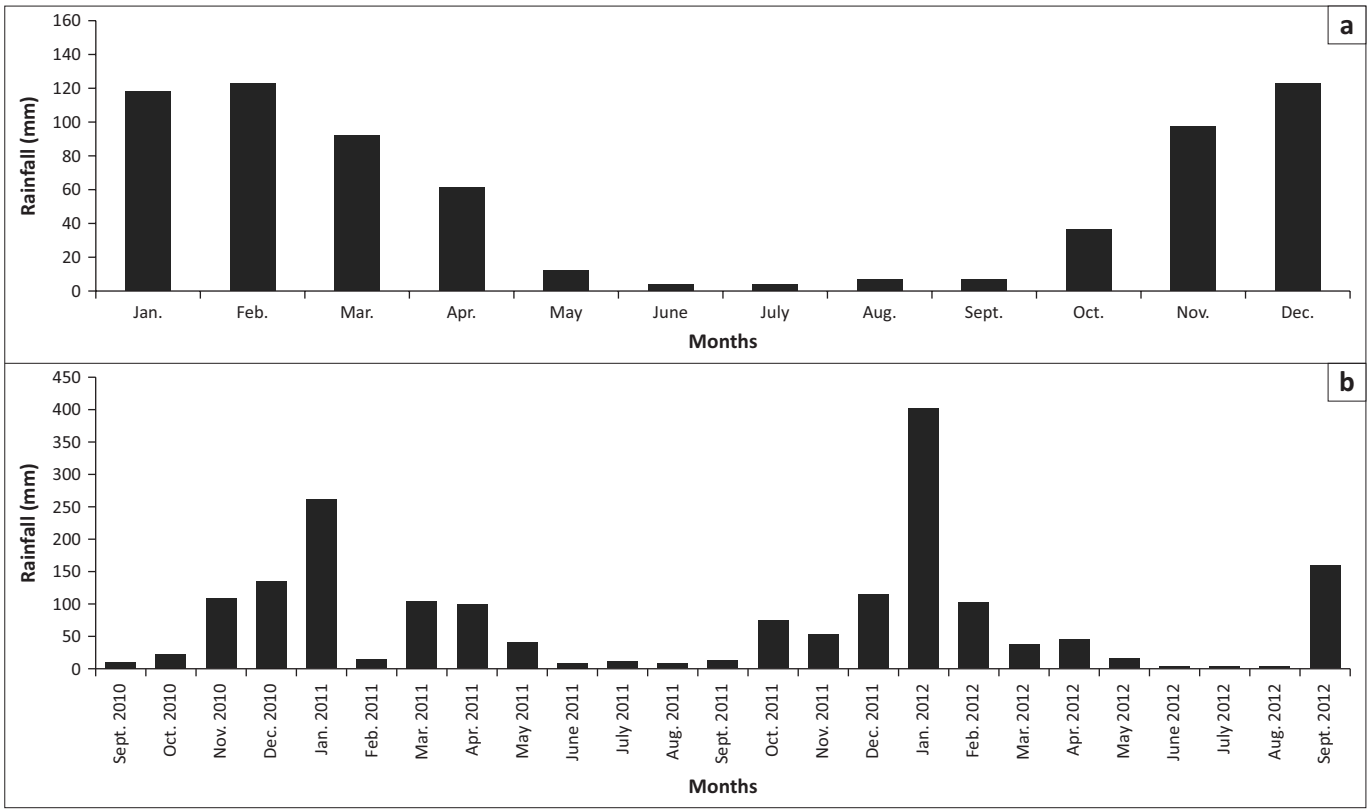
A 3 × 3 factorial experiment (nine plots in each site) replicated in three sites, was established in September 2010 to determine the effects of water and nutrient additions on the coppice response of *Terminalia sericea*. All three sites were on the slope crests. Therefore, they had shallow, coarse-textured and dystrophic soils (Neke 2004; Shackleton 1997; Shackleton 1999) (Moyo *et al.* 2015). Plots within a site were separated by a distance of approximately 15 m, with a density of approximately 1400 trees per ha. Ten trees were selected per plot (with a distance of about 2 m separating each tree from the adjacent one) with the number totalling 270 for the experiment. While root systems of *T. sericea* extend horizontally, this distance was considered adequate to avoid uptake of water and nutrients by the neighbouring trees.

Trees were cut at a standard height of approximately 25 cm from the ground, because research has shown that cutting height influences coppice response (Ibrahima *et al*. 2007; Kaschula, Twine & Scholes 2005b; Khan & Tripathi 1986; Shackleton 1997) (Moyo *et al.* 2015b). A 30-cm radius was marked around each tree, and grass was cleared to reduce competition for water and nutrients. Long-term average monthly (18 years) rainfall data (Figure 1) from the WRF records were used to derive monthly water treatments. Water addition treatments were as follows (Moyo *et al.* 2015b):

- No water addition (W_0) – no water additions throughout the study.
- Low (W_+) – trees were supplemented with an amount of water 0.5 times the long-term mean rainfall for that month.
- High (W_{++}) – trees were supplemented with the long-term mean rainfall for that month (Moyo *et al.* 2015b).

This monthly amount of rainfall was then divided by four to obtain weekly amounts for supplementing trees for a period of about 18 months beginning in September 2010. Water was applied next to the base of each stump using a watering can (Moyo *et al.* 2015b).

For the experimental plots that had nutrient additions, nitrogen (N) and phosphorus (P) were supplied using a commercial fertiliser in the form of ammonium phosphate, with a total of 80 kg N ha^{-1} for the high–fertiliser addition



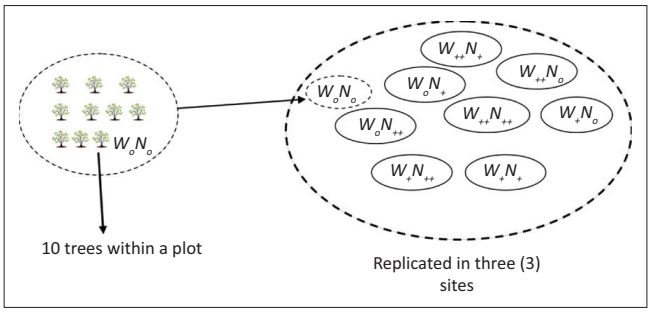
Source: Data courtesy Dr Wayne Twine

FIGURE 1: (a) Long-term mean monthly rainfall distribution (1992–2010) for the Wits Rural Facility and (b) cumulative monthly rainfall data for the duration of the study period (September 2010 – September 2012). January 2012 received exceptionally high amounts of rainfall compared to other January figures for the past 18 years.

treatment and 40 kg N ha^{-1} for the low–fertiliser addition treatment. Considering that the amount of fertiliser was added once at the beginning of each of the two growing seasons during the study (therefore, twice during the study – in October 2010 and October 2011), this amount (160 kg N ha^{-1} in total was added) was regarded as a high rate of N application in several studies (Le Roux & Mentis 1986; Mbatha & Ward 2010; Tilman 1987) (Moyo *et al.* 2015b). Fertiliser was added after the first rains fell in October 2010 and also in October 2011. Fertiliser application was done in split applications compared to a single application to avoid, over the course of the wet season, possible leaching of fertiliser through rainfall and added water if applied all at once. A commercial dry fertiliser blended as 4:3:4:1 (N, P, K, and Zn) and mixed according to 120 g/kg N and 90 g/kg P was purchased. Fertiliser additions, calculated according to N and P on the commercial fertiliser, were as follows (Figure 2):

- No fertiliser addition (N_0) – no fertiliser additions throughout the study.
- Low (N_+) – 0.13 g of N and 0.1 g of P per tree.
- High (N_{++}) – 0.27 g of N and 0.2 g of P per tree (Moyo *et al.* 2015).

The dry fertiliser was applied by coring a hole next to the base of the stump with a diameter of 3 cm and a depth of about 10 cm and depositing the fertiliser into the hole. The assumption was that all the fertiliser added using this method was utilised exclusively by the fine tree roots with loss, if any, of approximately the same for the treatments that received fertiliser addition (Moyo *et al.* 2015b).



W, water treatment; N, nutrient addition.

FIGURE 2: Factorial experiment designed to investigate the influence of water and nutrient additions on the coppice response of harvested trees.

A combination of the treatments, for example, $W_{++}N_0$ would mean the treatment is high water addition (W_{++}) and no nutrient addition (N_0).

Morphological measurements

From each resprouting stump, the following variables were measured per stump on a monthly basis: (1) total number of shoots, (2) resprout shoot diameter (measured above the resprouting zone) and (3) resprout shoot length. For (2) and (3), the leader shoot showing the greatest length was selected and marked using strings.

Shoot production was calculated as the number of shoots produced per unit area of stump basal area. The tree's original stump diameter was measured at the beginning of the experiment and used together with resprout shoot diameter

to calculate the resprout shoot diameter as a ratio of the original tree's stump diameter. This was termed the resprout ratio.

Total non-structural carbohydrate sampling and determination

To obtain an indication of TNC dynamics in *T. sericea* and also to understand how adding water and nutrients affected TNC levels, all trees exposed to treatments as illustrated in Figure 2 were sampled for stem TNC levels twice during the course of the study:

- after a year of treatment application (30 September 2011)
- after 18 months of treatment application, that is, at the end of the wet season (30 April 2012).

Three trees per treatment were sampled using an increment borer (4.3 mm diameter) to extract two 3-cm-long wood cores from the stumps. Before storing the cores in airtight plastic bottles, the outer tree bark was immediately removed from cores after sampling. Core samples were then bottled and placed inside a freezer. Drying of samples was done at 65 °C for 2 days (assumed dry) and samples were ground using a coffee grinder before finer grinding through a 40-µm mesh Wiley mill screen, at the University of Florida, USA (Moyo, Scholes & Twine 2015a). A composite sample for each treatment was obtained after grinding. The TNC was determined on a dry weight basis using the anthrone method described by Edwards, Downie & Clingeleffer (2011). The TNC values reported here are the sum of the soluble (glucose and sucrose) and insoluble (starch) fractions (Moyo *et al*. 2015a).

For comparison, cores from three non-harvested and unsupplemented trees, about 20 m from the experimental sites, with the same diameter (measured 25 cm above ground) were sampled for TNC analysis.

Confounding effects

Because of the presence of antelopes at the study site, the possibility of browsing after tree cutting was very high. The proportion of shoots that were browsed was estimated by counting the total number of shoots resprouting per stump, at the time of recording morphological changes, together with the total number of shoots browsed. The browse proportion was then calculated as the number of browsed shoots relative to the total number of shoots resprouting per stump, and expressed as a percentage. The browse proportion was compared across all the treatments for the duration of the study.

Analyses

The data were partitioned into two 12-month time intervals to test for the effects of water and nutrient additions on cut trees using linear mixed models implemented in Statistical Analysis Software (SAS) with proc generalised linear model. The September 2010 to September 2011 interval represented the end of the initial 12 months while the September 2011 to September 2012 interval represented the second 12-month period. Prior to analysis, the total number of shoots, shoot diameter and length data were log-transformed because data were not normally distributed. For the number of shoots, a generalised linear mixed model was fitted using an underlying Poisson distribution with a logit link, which included the fixed effects of treatment. In addition, random effects in terms of site and tree within site were included in the model. All models were fitted using the procedure GLIMMIX as implemented in SAS v. 9.2 (SAS Institute, Cary, NC, USA) (Moyo *et al*. 2015a).

Significance of fixed effect terms were evaluated with an approximated *F*-test, with mean comparisons between treatment regimens obtained using least square means with Dunnett's T3. The simple means comparison (unprotected) was used to obtain the level of significance for the total number of shoots. The effects of water and nutrient addition on coppice response (shoot diameter and length) and TNCs were analysed using analysis of variance, and Dunnett's T3 test was used for mean comparison at $p < 0.05$ (Moyo *et al*. 2015a).

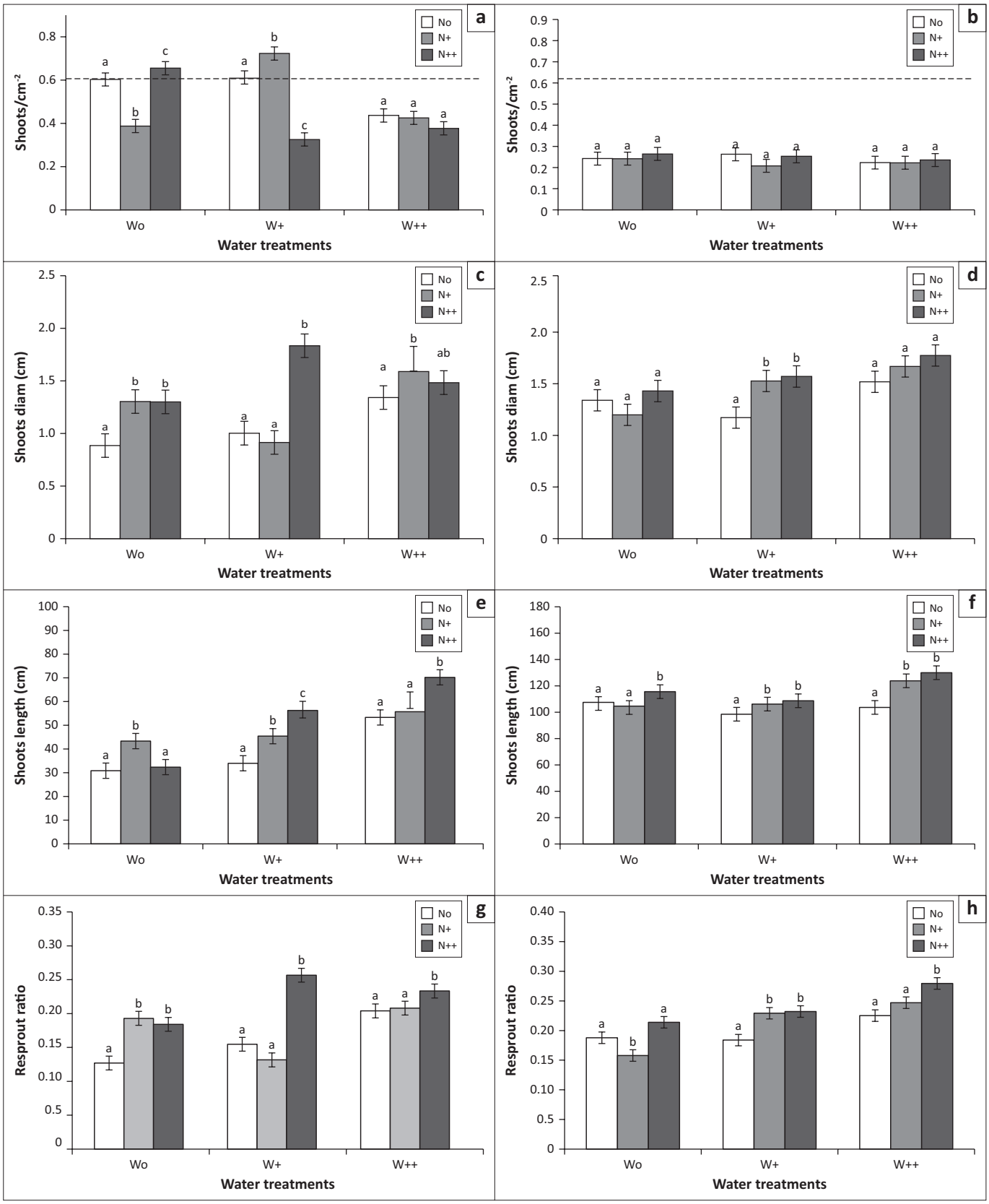
Results

Effects of water and nutrient additions on coppice response

Twelve months after trees were cut (September 2011), in the no–water addition treatment (W_0), shoot production was significantly higher when water was interacting with high nutrient addition (W_0N_{++}) than the other nutrient addition treatments. Shoot production was lowest when water was interacting with high nutrient addition, in the low–water addition treatment (W_+N_{++}) (Figure 3a). There were no significant differences in shoot production in the W_{++} treatment interacting with nutrient treatments in September 2011. The second year after cutting (September 2012), there were no significant differences in shoot production in all water treatment levels interacting with nutrient addition treatments. Between the sampling dates, shoot production reduced markedly across all treatments (Figure 3a).

A year after trees were cut and under W_0, W_0N_0 recorded the lowest shoot diameter compared to W_0N_+ and W_0N_{++} (Figure 3b). For the W_+ treatment, shoot diameter was significantly higher under the W_+N_{++}, compared with W_+N_0 and W_+N_+. For the W_{++} treatment, significantly higher shoot diameter was only noted when water was interacting with lower nutrient addition ($W_{++}N_+$) compared to $W_{++}N_0$, and not when compared with $W_{++}N_{++}$. The second year after cutting, there were no significant differences in shoot diameter in the W_0 and W_{++} treatments interacting with nutrient addition treatments, while in the W_+ treatment, W_+N_+ and W_+N_{++} recorded significantly higher shoot diameter than W_+N_0 (Figure 3b).

A year after cutting, under W_0, shoot length was highest under no nutrient addition (W_0N_0); in both the W_+ and W_{++}



The small letters compare treatment effects across September 2011 while the block letters compare effects across September 2012.

The asterisks indicate treatment differences between the two time points (September 2011 and September 2012).

The means are represented with standard error bars.

(a and b), The dashed line indicates the drop in shoot production across treatments and between the two time points (September 2011 and September 2012).

(a, c, e, g), September 2011; (b, d, f, h), September 2012.

W, water treatment; N, nutrient addition.

FIGURE 3: Effects of water and nutrient addition on (a and b) shoot production (calculated as number of shoots per unit area of original stump circumference cm^2), (c and d) shoot diameter, (e and f) shoot length and (g and h) resprout ratio (calculated as the ratio of the tree's original stump diameter to that of the leader shoot resprout diameter) between September 2011 and September 2012.

treatments, shoot length was lowest at the high–nutrient addition level (W_+N_{++} and $W_{++}N_{++}$). The second year after cutting and under W_0, shoot length was highest under high nutrient addition (W_0N_{++}), while under W_+ and W_{++}, shoot length was lowest under no nutrient additions (W_+N_0 and $W_{++}N_0$) (Figure 3c).

A year after cutting, resprout ratio was significantly lowest for W_0N_0 and highest under W_0N_{++} and $W_{++}N_{++}$ for the respective water treatments. For the W_0 treatment in September 2012, resprout ratio was lowest in W_0N_+, while highest for the $W_{++}N_{++}$ under the W_{++} (Figure 3d).

Interactive effects of water and nutrient additions on coppice response

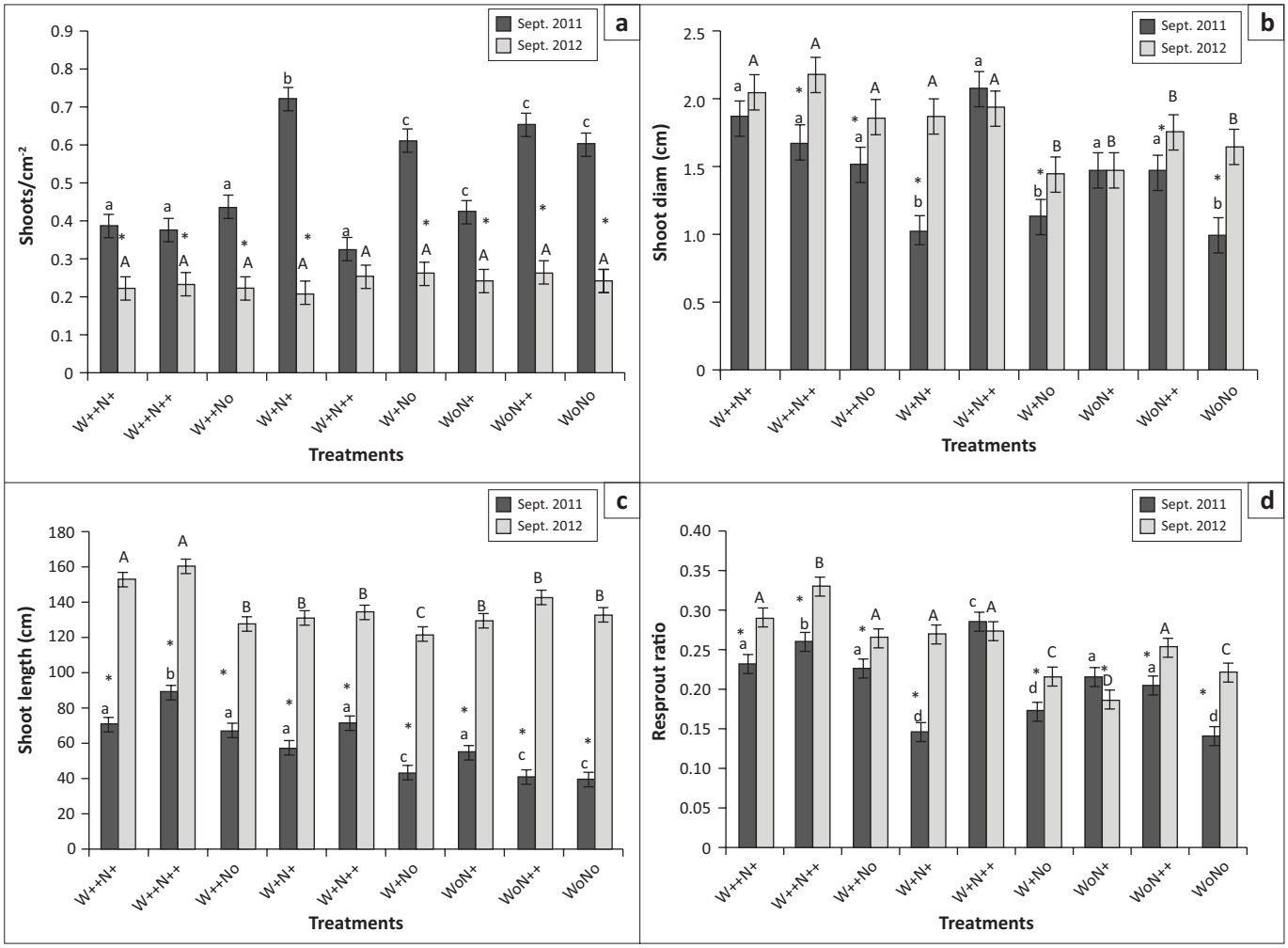
A year after cutting, shoot production was highest when water and nutrient additions were low (W_+N_+), with no significant differences observed 2 years after the trees were cut (Figure 4a). In September 2011, shoot diameter was significantly highest under the W_+N_{++}, with W_+N_0 recording the lowest shoot diameter in September 2012 (Figure 4b). In September 2011, shoot length was significantly higher under the $W_{++}N_{++}$, while in September 2012, $W_{++}N_{++}$ and $W_{++}N_+$ recorded the highest shoot length (Figure 4c). The resprout ratio was significantly highest for the $W_{++}N_{++}$ for both the sampling dates, that is, September 2011 and 2012 (Figure 4d).

Effect of water and nutrient additions on stem total non-structural carbohydrate levels

Supplementing cut trees with water and nutrients had no significant effect on stem TNC concentration for both sampling dates (September 2011 and April 2012) (Table 1). Uncut trees recorded significantly higher TNC levels compared to unsupplemented trees (W_0N_0) in September 2011.

Confounding effects: Browsing

Browsing (percent of shoots browsed per stump) on resprouting trees was widespread in both growing seasons during the study, although it was lower in the second



The small letters compare treatment effects across September 2011 while the block letters compare effects across September 2012.

The asterisks indicate treatment differences between the two time points (September 2011 and September 2012).

The means are represented with standard error bars.

W, water treatment; N, nutrient addition.

FIGURE 4: Effects of water and nutrient interaction on (a) shoot production (calculated as the number of shoots per unit area of original stump circumference cm^2), (b) shoot diameter, (c) shoot length and (d) resprout ratio (calculated as the ratio of the tree's original stump diameter to that of the leader shoot resprout diameter) between September 2011 and September 2012.

TABLE 1: Differences in total non-structural carbohydrate (mg g^{-1} DW) levels between September 2011 and April 2012 as a function of water and nutrient additions.

Treatment	September 2011	April 2012
W_0N_0	52.37[a] (10.8)	38.01[a] (11.9)
W_0N_{++}	51.96[a] (13.5)	24.79[a] (10.7)
W_0N_+	60.71[ab] (16.2)	34.44[a] (12.5)
$W_{++}N_0$	68.62[ab] (13.7)	38.96[a] (7.8)
$W_{++}N_{++}$	65.00[ab] (13.8)	46.54[a] (17.4)
$W_{++}N_+$	65.77[ab] (39.2)	29.2[a] (17.2)
W_+N_0	63.80[ab] (19.3)	30.88[a] (21.8)
W_+N_{++}	66.67[ab] (10.1)	43.6[a] (19.9)
W_+N_+	58.16[ab] (12.9)	44.88[a] (19.6)
Non-harvested*	74.48[b] (24.3)	43.09[a] (14.4)

Sample means are represented with standard deviations.

Letters are for treatment comparisons within each time-point. Different letters indicate significant differences within one time point.

W, water treatment; N, nutrient addition.

*, Non-harvested refers to trees that were not cut and not supplemented with either water or nutrients at the time of sampling.

compared to the first. There were no significant differences (F = 1.57, p = 0.167) in browsing proportion across all treatments during the study.

Discussion

Water and nutrient addition had initial significant effects on shoot production, while, as hypothesised, the addition of water and nutrients resulted in significant increases in resprout shoot diameter and shoot length. Contrary to the hypothesis, adding water and nutrients did not result in significant increases in stem TNC levels at both sampling dates, September 2011 and April 2012.

Effects of water and nutrients on coppice response of cut trees

High water and nutrient addition had a significant effect on shoot production after 12 (but not after 24) months. The differences in tree responses can possibly be attributed to the higher amount of rainfall received in the 2012 rainfall season compared to the 2011 season, contributing to treatment effects being non-measurable in 2012. Alternatively, this pattern could also be interpreted as generally the speeding up of the resprouting process because resprouting trees start off with many small shoots and, over time, tend to invest in fewer and larger shoots. Therefore, the effect of water and nutrients could have been to speed up the rate at which this shift in allocation happens.

Similar nutrient addition effects have been reported when there was an increase in the above-ground shoot production in *Pinus taeda* L., *Pinus elliottii* and *Liquidambar styraciflua* L. (Albaugh *et al*. 2004; Cobb *et al*. 2008), in *Populus deltoids* Bartr. and *Planatus occidentalis* L. (Coyle & Coleman 2005), and shoot biomass and growth in *Quercus macrocarpa* Michx. and northern pin oak *Quercus ellipsoidalis* E. J. Hill (Davis *et al*. 1999).

Shoot length and diameter for trees supplemented with water and nutrients were significantly higher in the $W_{++}N_{++}$ treatment between September 2011 and September 2012. Under high soil moisture conditions, there is a general increase in sprouting vigour leading to the transfer and supply of growth promoters such as auxins, cytokinins and gibberellins (Ferm & Kauppi 1990). This is not the case when there is very low soil moisture (Liu & Dickmann 1996). Consequently, adding water for this study may have led to an overall increase in cell division and resprouting shoots exhibit stronger apical dominance, resulting in higher average shoot diameters and lengths compared to W_0N_0 trees.

It has been proposed that fertiliser addition increases foliar N concentrations as well as chlorophyll levels, leading to an increase in photosynthetic efficiency (Scott *et al*. 2004). In this study, nutrient addition possibly resulted in increased leaf area (Ewers *et al*. 1999), thus increasing the surface area for elevated photosynthetic activity. This may have contributed to an increase in shoot elongation and shoot thickness. Results from this study are similar to those obtained by Osman and AboHassan (2010), when shoot production and resprout shoot length increased after the addition of N and addition of P to *Rhizophora mangle* L. (Lovelock *et al*. 2004). In addition, current findings are also supported by results from the addition of N to thinned *P. taeda*, which increased resprout diameter and length (Sayer *et al*. 2004).

In line with this study's findings, shoot diameter and height were higher in *Pinus ponderosa* Dougl. ex P. Laws. and C. Laws, which received N addition compared to trees which received no additions (Tingey *et al*. 1996), with both height and diameter growth in fertilised stands doubling in comparison to the non-fertilised stands in Norway spruce (*Picea abies* [L.] Karst.) (Bergh *et al*. 1999).

An overall reduction in the number of shoots for all treatments at the beginning of the wet season in September 2012 implies that there was self-thinning. Between September 2011 and September 2012, there was over 50% reduction in the number of shoots in all treatments. While self-thinning could be viewed as a way of reducing high respiration demands associated with high leaf material, this growth pattern was observed even on supplemented trees. Findings from this study could possibly mean that resource availability does not necessarily control self-thinning, that is, self-thinning may, in fact, be controlled within the trees and not by environmental factors.

Effect of water and nutrients on stem total non-structural carbohydrate levels

Adding water and nutrients had no significant effect on stem TNC levels at both time points. This was surprising given that an increase in soil moisture and nutrient levels through resource additions on the same trees extended leaf survival early into the dry season (Moyo *et al.* 2015), thereby possibly extending the period of photosynthesis for trees supplemented. Such an extension of the period of photosynthesis maintained greater leaf area, possibly leading

to higher carbon assimilation in supplemented trees. This was in comparison to unsupplemented trees, which had leaf survival that only lasted to the end of the growing season, thereby photosynthesising for a shorter period. Given this, the expectation was that these phenological shifts in the dry season (September 2011) extended the photosynthetically active period so that supplemented trees rely less on stored reserves for regrowth compared to unsupplemented trees.

Because TNC concentrations in tree tissues are considered a measure of carbon storage or a demand for growth (Druege *et al*. 2000; Kabeya & Sakai 2005; Sakai & Sakai 1998), the lack of significant effects the addition of water and nutrients may indicate that the carbon demand in resprouting trees, even for supplemented trees which had a longer period to photosynthesise, was exceeding the supply from photosynthesis alone, as stored TNC were mobilised for growth. Resprouting trees appear to continuously draw from stored reserves.

Findings from this study are different to work on *Q. crispula* Blume, where root TNC levels were higher after resource addition (Kabeya & Sakai 2005). Similar to findings from this study, other studies also found that N additions had no effect on carbohydrate reserves in beech (*Fugus sylvatica* L.) (Pahlsson 1992), while it had little effect on starch levels for Chrysanthemum cuttings (Druege *et al*. 2000).

In protected areas such as game reserves and conservation areas, a fire can open up patches of land (Ward 2005), exposing seeds and seedlings to resources such as light and nutrients. Such disturbances, coupled with the fluctuation in rainfall distribution in semi-arid areas (Scholes & Archer 1997), create bush encroachment patches absent when no fire events or disturbances occur (Ward 2005). In agreeing with this study's findings, this is true when considering the quick recovery of shoot length and diameter in *T. sericea* after a cutting event. This quick recovery may eventually result in this species encroaching large areas of land, thus reducing the biodiversity and species distribution of the herbaceous vegetation.

Browsing proportion was the same across all treatments, implying that while browsing may have influenced shoot length and, possibly, the number of shoots produced as well as total biomass produced, the influence was evenly spread across all the treatments. Therefore, browsing did not unduly influence the relative differences in the variables measured between treatments.

Water and nutrients were supplemented through addition immediately adjacent to the tree stump. Water addition may have facilitated nutrient uptake, and we assumed that this type of water and nutrient addition enhanced the tree's ability of fine roots to absorb most of the resources added. The mean annual rainfall in the study area (650 mm per annum) lies between the upper and lower limits of the study species range. Considering that *T. sericea* adapts well to droughts (Griffiths 1959), the rainfall in the area is intermediate when compared to the lower limit of the species range. For a tree species adapted to growing in a resource-poor environment, this may mean that the weaker effects of water addition in the second season may have been a result of the study species' allocation of resources towards storage, instead of growth, as suggested by Witkowski, Mitchell and Stock (1990). Such allocation may help explain the low effectiveness of high water addition on coppice regrowth during the second season of growth.

Conclusion

This study demonstrated that resprouting is water and nutrient limited in cut trees and that resource addition does not replenish the stem carbon storage. The results suggest that water is limiting for resprout shoot diameter and length, but not for shoot production and stem storage carbohydrates. Results from this study thus support the hypothesis that supplementing cut trees with water and nutrients increases coppice growth, but this effect holds primarily only for the first growing season after cutting, with the effect declining over time. Results from a follow-up study also suggest that even though a tree supplemented with water and nutrients may end up photosynthesising for a longer period compared to an unsupplemented tree, this does not necessarily change the tree's reliance on stored carbon reserves for regrowth early in the growing season.

Total number of shoots produced displays clear self-thinning and it is interesting to note that water and nutrient additions do not impact this self-thinning. This suggests that self-thinning may be light related and is not positively related with resource availability. Future research could focus on how adding water and nutrients changes the balance of TNC in roots and stems, and not only the stem TNC as covered in this current study. Cutting of trees at shorter intervals, for example, logging and short coppice rotation can be done in environments that have higher water and nutrient levels, because a quicker recovery of lost biomass is expected in resource-rich environments compared to resource-poor environments (Moyo *et al.* 2015). In an ecosystem where competition for food is high and resources for plant growth are limited, new leaves can be a major source of food at a time when most herbivores struggle to fulfil their nutritional needs, especially at the end of the dry season. Therefore, this would ensure that herbivores are assured of a food source, because cattle have been shown to browse more than graze during the dry season (Katjiua & Ward 2006). In order to reduce the possibility of this study species encroaching large areas, disturbances such as hot fires, which burn and open up large patches, should be controlled. This is because hot fires open up large patches, leading to vigorous resprouting of this species, which may threaten biodiversity in the long run.

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Competing interests

The authors declare that they have no financial or personal relationships which may have inappropriately influenced them in writing this article.

Authors' contributions

H.M. was responsible for designing the study, field work and data collection including the analysis and writing up of the paper. M.C.S. guided the first author and read drafts of the paper, while W.T. also read and corrected drafts of the paper as well as formulated the study design.

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