

Interspecific variation in the resprouting responses of *Acacia* species following simulated herbivory in a semi-arid southern African savannah

Humphrey Choeni and Allan Sebata*

Department of Forest Resources and Wildlife Management, National University of Science and Technology, PO Box AC 939, Ascot, Bulawayo, Zimbabwe

Abstract

Plants have evolved a diverse suite of tolerance traits against herbivory, including compensatory growth, increased photosynthesis and activation of dormant meristems. We studied the responses of five *Acacia* species to simulated herbivory in a semi-arid southern African savannah. We clipped terminal shoots of five juvenile *Acacia* species (*Acacia rehmanniana*, *A. nilotica*, *A. karroo*, *A. arenaria* and *A. gerardii*) to simulate herbivory. We then determined biomass change after 5 months and also counted the number of resprouts and measured their length and diameter. All clipped shoots produced resprouts, with all the *Acacia* species compensating for the lost biomass. We found considerable interspecific variation in the compensation for biomass lost to herbivory in the five *Acacia* species. Resprouts biomass ranged from two times in *A. arenaria* to four times that removed in *A. karroo*. *Acacia karroo* produced many resprouts, while *A. arenaria* produced very few resprouts (4 vs 15 resprouts). The relationship between the number of resprouts and their growth also varied among the different *Acacia* species. We conclude that the response of *Acacias* to herbivory ranges from prolific resprouters (such as *A. karroo*) to poor resprouters (e.g. *A. arenaria*).

Key words: biomass, compensatory photosynthesis, nutrient reserves, persistence, tolerance

Résumé

Les plantes ont développé différentes caractéristiques comme moyens de tolérance face à l'herbivorie, comme une croissance compensatoire, une meilleure photosyn-

thèse et l'activation de méristèmes dormants. Nous avons étudié les réponses de cinq espèces d'*Acacia* d'une savane semi-aride d'Afrique australe à une herbivorie simulée. Nous avons coupé les pousses terminales des juvéniles de cinq espèces d'*Acacia* (*Acacia rehmanniana*, *A. nilotica*, *A. karroo*, *A. arenaria* et *A. gerardii*) pour simuler l'herbivorie. Nous avons ensuite déterminé les changements de biomasse après cinq mois et compté le nombre de repousses dont nous avons mesuré la longueur et le diamètre. Toutes les pousses coupées ont produit des repousses, et toutes les espèces d'*Acacia* ont compensé la perte de biomasse. La biomasse des repousses allait du double de ce qui avait été enlevé pour *A. arenaria* au quadruple chez *A. karroo*. *Acacia karroo* a produit de nombreuses repousses alors qu'*A. arenaria* en a produit très peu (4 repousses vs 15). La relation entre le nombre de repousses et leur croissance variait aussi selon les espèces d'*Acacia*. Nous concluons que la réponse des *Acacia* à l'herbivorie va de prolifique (tel *A. karroo*) à médiocre (e.g. *A. arenaria*).

Introduction

The ability of plants to tolerate or compensate for herbivore damage is highly variable (Brody & Irwin, 2012). Plants have evolved a diverse suite of tolerance traits including compensatory growth, increased photosynthesis and activation of dormant meristems (Strauss & Agrawal, 1999; Tiffin, 2000; Cromsigt & Kuijper, 2011). Activation of dormant meristems is in response to the removal of terminal shoots that break apical dominance (Aarssen, 1995). The activated lateral meristems develop into new lateral shoots (hereafter referred to as resprouts), which compensate for the lost biomass.

*Correspondence: E-mail: allans20022002@yahoo.com

Biomass change can be used to quantify the compensatory responses of woody plants to herbivory (Belsky *et al.*, 1993; Strauss & Agrawal, 1999; Agrawal, 2000). Clipping experiments to simulate large ungulate herbivory in *A. xanthophloea*, *A. tortilis* and *A. hockii* (Pellew, 1983) and *A. drepanolobium* (Gadd, Young & Palmer, 2001) have shown that the production of resprouts fully compensates for losses in biomass.

In the semi-arid southern African savannah, *Acacias* are among the most abundant woody plants (Tsumele, Mlambo & Sebata, 2006). They are keystone species in maintaining biodiversity of these ecosystems and also provide important browse to large mammalian herbivores (Shaw, Keesing & Ostfeld, 2002; Hean & Ward, 2012). Although *Acacias* are generally good resprouters (Hean & Ward, 2012), interspecific variability might affect the dynamics of plant communities in which they dominate through influencing which species will persist or decline. Thus, an understanding of the resprouting abilities of different *Acacia* species will improve the management of ecosystems in which they are predominant.

The development of lateral buds into resprouts enables *Acacia* species to tolerate persistent herbivory (Augustine & McNaughton, 1998; Fornara & du Toit, 2007). The resprouts quickly replace lost photosynthetic tissue. However, the production of many resprouts is thought to negatively affect their size (Bergstrom, Skarpe & Danell, 2000).

We compared the responses of five *Acacia* species to shoot clipping and also studied the relationship between the number of resprouts and their length and diameter. Assuming that resource availability influences resprouting, species that produce fewer resprouts should be able to channel more resources to length and diameter growth. The two main questions addressed are as follows: (i) Does resprouting compensate biomass lost to herbivory in juvenile *Acacia* trees? and (ii) is there any relationship between the number of resprouts and their length and diameter?

Methods

The study was performed in a fenced site at the National University of Science and Technology in Bulawayo, Zimbabwe (20° 08'S, 28° 36'E, 1341 m above sea level). Mean annual rainfall was 600 mm (range: 325–915), with most of it falling during a single rainy season between October and April. Mean annual temperature was 23.6°C,

with October and July as the hottest and coldest months, respectively. The vegetation was deciduous open woodland with a tree crown cover of 30–40 per cent. The dominant woody species were *A. karroo*, *A. erioloba*, *A. nilotica*, *A. rehmanniana* and *A. robusta*.

Three 80 m × 30 m belt transects were set out within a flat and uniform area of *Acacia* dominated woodland, with a mean tree height of 1.58 m (SD = 0.34, $n = 43$). In each belt transect, three juvenile *Acacia* plants per species (*A. rehmanniana*, *A. nilotica*, *A. karroo*, *A. arenaria* and *A. gerardii*) were selected at random as described by Gliner and Morgan (2000). Each plant had a main stem diameter of between 3 and 5 mm. Terminal shoots were clipped (3 cm from tip) from 10 stems per plant in November 2011, before leaf flush, to simulate dry season browsing by medium-sized mammalian browsers using garden shears. The timing of damage is decisive in plant responses to herbivory, and late dry season clipping of woody plants has been reported to increase shoot biomass the following wet season (Bergstrom, Skarpe & Danell, 2000). All leaves and shoots were removed from each stem up to point of branching from main stem, and the removed plant biomass was weighed after oven drying at 60°C for 48 h. Individual woody plant branches are considered as autonomous (Riba, 1998). Each of the clipped stems was marked with paint. Another 10 stems were marked but left uncut. In March 2012 (5 months after clipping), the trees were revisited and the following variables were determined on resprouts located near the clipped area: resprout number, length, diameter and biomass after oven drying at 60°C for 48 h. Riba (1998) reported higher growth responses near the clipped area. Biomass change was determined as resprout biomass/removed biomass. A value above one represents overcompensation of browsed biomass and that below one undercompensation.

Statistical analysis

All data were normally distributed (Kolmogorov–Smirnov test) (SPSS, 2002). The response variables (biomass change, number of resprouts, length of resprouts and diameter of resprouts) were averaged for the ten stems per plant. The transect effect was not significant in all the variables (biomass change: $F_{2,42} = 0.08$, $P = 0.992$; number of resprouts: $F_{2,42} = 0.001$, $P = 0.999$; length of resprouts: $F_{2,42} = 0$, $P = 1.00$; diameter of resprouts: $F_{2,42} = 0.11$, $P = 0.989$), and thus, the test statistics were based on the averaged variable measurements.

A GLM univariate was carried out to test for the species effect on the response variables (biomass change, number of resprouts, length of resprouts and diameter of resprouts) using SPSS (SPSS, 2002). In each case, the other three variables were treated as covariates. When *F*-tests indicated significant differences, means were compared using *post hoc* Tukey HSD ($P < 0.05$).

Data on the number of resprouts were regressed against both length and diameter of resprouts for all trees surveyed, separately by species and then for all species pooled in SPSS command (SPSS, 2002). All tests were considered significant at the $P < 0.05$ level.

Results

No resprouting was recorded on stems that were not clipped. All the *Acacia* species resprouted following shoot clipping. Biomass change and number of resprouts were highest in *A. karroo* and lowest in *A. arenaria* (Table 1). *Acacia rehmanniana* had the longest and thickest resprouts (Table 1).

The biomass change varied among the species ($F_{4,37} = 9.99$, $P < 0.001$) (Table 1). The covariates (length of resprouts: $P = 0.243$; number of resprouts: $P = 0.140$; diameter of resprouts: $P = 0.222$) did not influence the species effect on the biomass change.

The number of resprouts varied among the species ($F_{4,37} = 717.87$, $P < 0.001$) (Table 1). The covariates (biomass change: $P = 0.140$; length of resprouts: $P = 0.882$; diameter of resprouts: $P = 0.237$) did not influence the species effect on the number of resprouts.

The length of resprouts varied among the species ($F_{4,37} = 409.95$, $P < 0.001$) (Table 1). The covariates (biomass change: $P = 0.243$; number of resprouts:

$P = 0.890$; diameter of resprouts: $P = 0.722$) did not influence the species effect on the length of resprouts.

The diameter of resprouts varied among the species ($F_{4,37} = 69.68$, $P < 0.001$) (Table 1). The covariates (biomass change: $P = 0.222$; number of resprouts: $P = 0.417$; length of resprouts: $P = 0.722$) did not influence the species effect on the diameter of resprouts.

The relationship between number and length of resprouts was not significant in all species except *A. nilotica* (Table 2). It was, however, significant for all the species pooled together. The number of resprouts had a positive relationship with length of resprouts in *A. nilotica* and for all the species pooled together.

Table 2 Relationships ($y = a + bx$) of number of resprouts (y) and length of resprouts (x) and diameter of resprouts (x) of five *Acacia* species ($n = 9$)

	<i>r</i>	<i>r</i> ²	Regression equation	
Number of resprouts vs length of resprouts				
<i>A. rehmanniana</i>	0.37	0.14	$y = 11.02 + 0.68x$	ns
<i>A. nilotica</i>	0.78	0.60	$y = -3.30 + 1.67x$	*
<i>A. karroo</i>	-0.20	0.04	$y = 18.78 - 0.18x$	ns
<i>A. arenaria</i>	-0.00	0.00	$y = 9.28 - 0.00x$	ns
<i>A. gerardii</i>	0.62	0.39	$y = 6.46 + 0.96x$	ns
All species (pooled)	0.70	0.49	$y = 7.58 + 0.62x$	***
Number of resprouts vs diameter of resprouts				
<i>A. rehmanniana</i>	-0.86	0.73	$y = 2.91 - 0.29x$	**
<i>A. nilotica</i>	-0.40	0.16	$y = 2.82 - 0.35x$	ns
<i>A. karroo</i>	-0.05	0.00	$y = 0.44 - 0.01x$	ns
<i>A. arenaria</i>	0.73	0.54	$y = -1.47 + 0.42x$	*
<i>A. gerardii</i>	-0.42	0.17	$y = 1.98 - 0.31x$	ns
All species (pooled)	0.19	0.04	$y = 0.31 + 0.01x$	ns

ns, not significant, * <0.05 , ** <0.01 , *** <0.001 .

Table 1 Mean ($\pm$ SE) biomass change, number of resprouts, length of resprouts (cm) and diameter of resprouts (cm) of five *Acacia* species in semi-arid southern Africa ($n = 9$)

	Biomass change	Number of resprouts	Length of resprouts	Diameter of resprouts
<i>A. rehmanniana</i>	3.46 ^a (± 0.05)	7.85 ^a (± 0.03)	16.37 ^a (± 0.05)	0.65 ^a (± 0.01)
<i>A. nilotica</i>	2.42 ^b (± 0.03)	7.27 ^b (± 0.01)	8.84 ^b (± 0.03)	0.28 ^b (± 0.01)
<i>A. karroo</i>	4.22 ^c (± 0.02)	14.56 ^c (± 0.06)	16.12 ^c (± 0.06)	0.35 ^c (± 0.01)
<i>A. arenaria</i>	2.14 ^d (± 0.01)	4.01 ^d (± 0.01)	9.26 ^d (± 0.02)	0.21 ^d (± 0.01)
<i>A. gerardii</i>	2.38 ^b (± 0.01)	5.23 ^e (± 0.01)	11.46 ^e (± 0.02)	0.36 ^c (± 0.01)
	$F_{4,40} = 983.83^{***}$	$F_{4,40} = 16,190^{***}$	$F_{4,40} = 9386^{***}$	$F_{4,40} = 348.75^{***}$

*** <0.001 . Means within each parameter for different browse species with different superscripts (a, b, c, d, e) differ significantly ($P < 0.001$), based on Tukey test.

Acacia rehmanniana and *A. arenaria* exhibited significant relationships between number and diameter of resprouts (Table 2). The number of resprouts in *A. rehmanniana* had a negative relationship with diameter of resprouts, while in *A. arenaria*, the relationship was positive.

Discussion

All clipped shoots produced resprouts with all the *Acacia* species compensating for the lost biomass. This concurs with reports of biomass compensation in other *Acacia* species following herbivory (du Toit *et al.*, 1990; Hean & Ward, 2012). Biomass compensation is a tolerance strategy (Haukioja & Koricheva, 2000). Compensatory growth occurs from activated dormant buds (Moncrieff *et al.*, 2012). Resprouting was in response to the removal of apical dominance, which triggered the activity of lateral meristems (Crawley, 1987; Agrawal, 2000). It is a strategy to produce cheap photosynthetic tissue to compensate for the lost biomass. Woody plant biomass compensation is considered a more efficient response to herbivory as it only involves activation of buds as compared to the use of constitutive defences (Baldwin, Sims & Kean, 1990). The ability of plants to regrow following browsing strongly depends on the amount of stored carbohydrates (Poorter & Kitajima, 2007), with repeated defoliation depleting carbohydrate pools. Under such conditions, woody plants invest in resprouts to quickly regain a positive carbon and nitrogen balance.

We found a considerable interspecific variation in the compensation for biomass lost to herbivory in the five African *Acacia* species. Resprouts biomass ranged from two times in *A. arenaria* to four times that removed in *A. karroo*. *Acacia karroo* also had the highest number of resprouts which was evidence of its prolific resprouting abilities, presumable because of its fast growth rate. On the contrary, *A. arenaria* produced very few resprouts (4 vs 15 resprouts). Plants vary widely in their ability to compensate for herbivore damage (McNaughton, 1983; Paige & Whitham, 1987). Woody species that produce few resprouts such as *A. arenaria* could in the long term fail to adequately replenish lost carbohydrate reserves and be lost from the ecosystem (du Toit *et al.*, 1990). On the contrary, the production of few resprouts could be beneficial to the plant as fewer stored carbohydrate reserves will be mobilized for regrowth.

Woody plants can quickly replace lost biomass and photosynthetic tissue through production of many large resprouts. However, resprouting depends on the

mobilization of stored carbohydrate reserves (Danell, Huss-Danell & Bergstrom, 1985). We expected the production of many resprouts to negatively affect their growth as represented by length and diameter. This was only true for the relationship between the number and diameter of resprouts in *A. rehmanniana*. Bergstrom, Skarpe and Danell (2000) in a shoot-clipping experiment to simulate browsing in *Combretum apiculatum* also reported an inverse relationship between the number of resprouts and their size. Conversely, there was a positive relationship between number and diameter in *A. arenaria* and between number and length of resprouts in *A. nilotica*. Interestingly, both species had the smallest resprouts length and diameter. This suggests that some *Acacia* species are capable of allocating carbohydrate resources to both number and growth simultaneously. Interspecific variability in the relationship between the number of resprouts and their growth could be attributed to differences in species-specific resource-allocation patterns.

We conclude that the response of *Acacias* to herbivory ranges from prolific resprouters (e.g. *A. karroo*) to poor resprouters (e.g. *A. arenaria*).

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