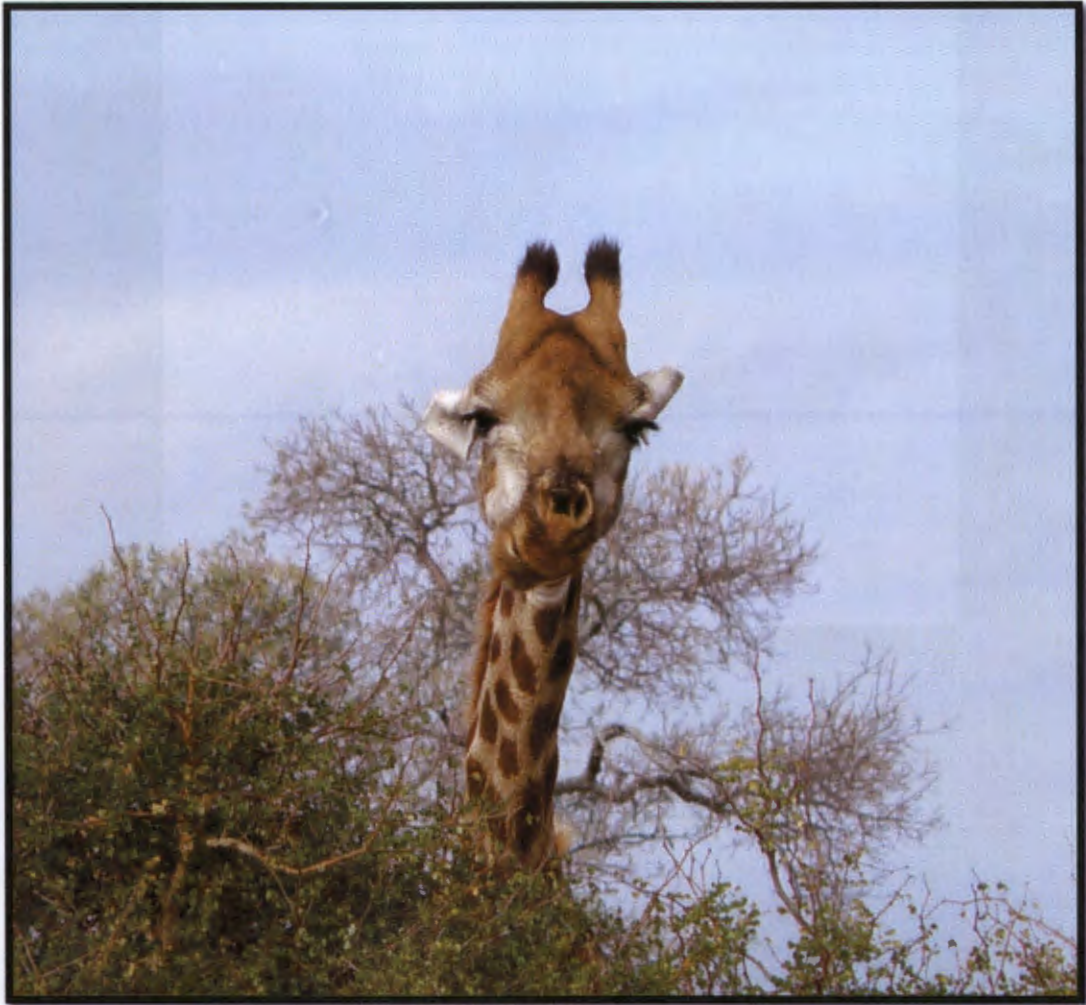




**Does Tree size matter? Giraffe influence on African Savanna
ecosystem properties**

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the requirements for the award of an honours degree in botany

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Abstract

Trees alter the environment by affecting microclimate, soil properties and adding structural complexity to an otherwise single stratum system. It is known that the herbaceous understory of Savanna ecosystems is most productive at intermediate tree density, where the shade and nutrients from the tree are more influential than the competition with the tree. Tree density varies in savannas due to disturbances, such as fire and herbivory. Yet, disturbances do not only alter density but can affect entire tree structure. It has been found that chronic ungulate browsing influences whole tree size, as well as canopy size and shape. Giraffe in south of Kruger National Park browse heavily on *Acacia nigrescens* found on basalt-derived soils. I studied the influence of trees above the giraffe browse trap (>6 m) as opposed to trees in the browse trap (< 6 m) on savanna ecosystem properties. I compared grass biomass, soil moisture, soil organic matter, soil carbon and soil nitrogen beneath tall trees vs. short trees, as well as in the open vs. underneath trees. Ecosystem properties were estimated and compared between a giraffe impacted to a giraffe absent area. Giraffe impacted area overall yielded lower grass biomass, soil moisture, soil nitrogen and soil carbon. The consequence is a trophic cascade of events from increased giraffe decreasing fires and in turn increasing tree density and hence carbon sequestration. As giraffes replace a single large tree by several small trees, shows that their population size is key determinant of ecosystem properties.

Keywords

herbaceous productivity; canopy effects; megafauna herbivory; *Acacia nigrescens*; carbon sequestration, Kruger National Park

Introduction

Savannas are distinguished from grasslands by the presence of trees and from closed woodlands and forest by a continuous grass layer. When trees colonize grasslands they alter their environment by affecting microclimate, soil properties and by adding structural complexity to an otherwise single stratum system (Belsky and Amundson 1992, Belsky 1994, Belsky *et al.* 1989, Vetaas 1992). Trees therefore contribute to spatial heterogeneity and indirectly to biodiversity of savanna ecosystems.

Trees influence the understory environment in various ways. Depending on tree density, rainfall and soil fertility, trees either compete with the herbaceous understory or increase the understory productivity (Belsky *et al.* 1993, Knoop and Walker 1985, Mordelet and Menaut 1995, Moro *et al.* 1997, Treydte 2007). Average herbaceous-layer productivity in arid regions of Africa is higher in savannas with low tree density than in grasslands or woodlands (Belsky and Amundson 1992). The herbaceous understory is most productive at intermediate tree density, where the shade and nutrients from the tree are more influential than the competition with the tree (Belsky 1994).

Tree canopies cast a shade creating a microclimate in their immediate surroundings. By reducing the solar radiation reaching the understory, trees decrease average soil temperatures and evapotranspiration of the herbaceous layer and increase moisture of the surface soil by hydraulic lift (Belsky and Amundson 1992, Belsky 1994, Ludwig *et al.* 2001). Furthermore, the soil under trees has higher water infiltration rates and water holding capacity (Vetaas 1992).

Soils under savanna tree canopies have increased nutrients, increased levels of organic matter and higher microbial biomass (Belsky and Amundson 1992, Belsky *et al.* 1989, Ludwig *et al.* 2004, Moro *et al.* 1997, Vetaas 1992). Nutrients increase below the tree crown due to an increased amount of animal droppings, leaf litter and wind transported materials forming 'islands of fertility' (Belsky 1994). Faunal density is higher below tree canopy as they provide protection from the sun, browsing opportunities for herbivores and perches for birds.

Tree density varies in savannas due to disturbances, such as fire and herbivory (Higgin *et al.* 2007, Levick *et al.* 2009, Roques *et al.* 2001, Sankaran *et al.* 2005, Scholes and Archer 1997). Yet disturbances not only alter density but can also affect

entire tree structure. Browsers alter the composition and density of shrub and tree strata in savannas and chronic ungulate browsing influences whole tree size, as well as canopy size and shape (Fornara and Du Toit 2007). Fire and smaller ungulate species reduce the release of saplings to larger size classes, whereas giraffe and elephants impact mature trees by either destruction or suppression (Pellew 1983). The fact that giraffes are almost exclusively browsers ranging over large areas can have landscape scale effects on tree composition and distribution, particularly on acacias (Bond and Loffell 2001, Pellew 1983).

Past research has mainly focused on tree density, leaving the influence tree size has on nutrients, especially carbon, soil moisture and understory productivity an open question.

Soil is the largest pool of terrestrial organic carbon in the biosphere, storing more carbon than is contained in plants and the atmosphere combined (Jobbagy and Jackson 2000). Trees are key component of stored carbon, and thus important in the potential for savanna ecosystem to act as carbon dioxide (CO₂) sink in the effort to curb global warming. The amount of organic carbon in the soil is affected by plant production, so that smaller trees might sequester less carbon.

I wished to determine the potential impact of a single species of megaherbivore, *Giraffa camelopardalis*, has on ecosystem properties through its effect on tree size and shape.

I hypothesise that a larger tree will increase the herbaceous understory productivity and forage quality relative to smaller trees and that giraffe, by suppressing tree height and canopy size, could change the savanna ecosystem. This study may be relevant to the management of savanna parks by helping to indicate the ecosystem impacts of a single large mammal species.

The aim was to determine the effects of tree size on understory productivity by evaluating the grass biomass and species composition. Furthermore, I wished to examine soil properties such as soil moisture, carbon and nitrogen content under trees below and above giraffe browse height and to use these to estimate potential ecosystem properties without giraffe impact.

Materials and Method

Sampling Site

The study took place in the south of the Kruger National Park, South Africa (22°20'S–25°30'S and 31°50'E–32°00'E, Figure 1). Mean monthly temperatures are between 26 °C and 17.5°C and rain falls mainly in the summer months between October and April with the highest rainfall in December and January. Sampling was limited to the basalt plains in the region of lower Sabie (Site M) and in the Satara area (Site S). Mean average rainfall in both areas varies with lower Sabie receiving approximately 525 mm precipitation per year, whereas Satara only receives 489 mm of rain per year.

The south of the park appears to be most heavily impacted by giraffe browsing (personal obs. and personal comm.). Soils in both sampling regions are dark clays of basaltic origin and the most common tree species found here are *Acacia nigrescens*, *Sclerocarya birrea* subs. *caffra*, *Lannea schweinfurthii* var. *stuhlmanii*, and *Gymnosporia senegalensis*.

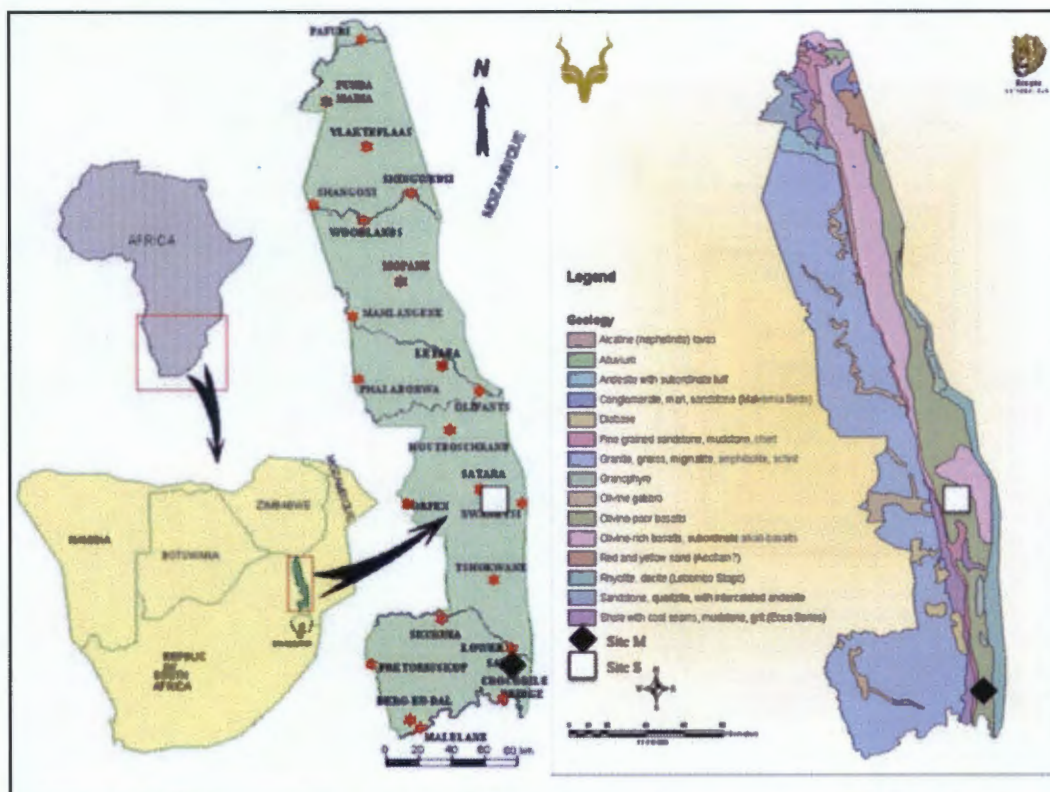


Figure 1: Map of Kruger National Park, depicting the geology with sample Site M and Site S (from http://www.sanparks.org/parks/kruger/conservation/scientific/maps/maps_environment.php).

Sampling procedure

Exclosure sites were used to sample for tree densities as well as size in the absence of herbivory while adjacent sites were the main focus of sampling. The Makohlolo exclosure is located near lower Sabie, and the Buffalo exclosure near Satara.

Data were collected during the dry season in June/July 2010, selecting *Acacia nigrescens* over a range of size classes and local densities. Trees were sampled by walking in a predetermined direction and choosing every third small or medium individual, whereas every large tree in the area was selected. In lower Sabie 37 trees of which 18 trees were taller than 6 m and in Satara 30 trees of which 19 were taller than 6 m were selected.

Tree height, stem radius, maximum canopy width and its perpendicular length, height of the maximum canopy spread and distance to the nearest tree were recorded. Heights were measured using an inclinometer and lengths using a tape measure.

Canopy area was calculated using the formula for area of an oval:

$$A = \pi ab$$

where a and b are half of the two canopy width dimensions

Sampling was located at half canopy radius and in adjacent open areas in three directions (Figure 2). Soil samples were taken from the surface layers by hammering in a soil borer of 5.3 cm diameter and 10 cm length. The soil was weighed in the field using a portable scale. Biomass of the herbaceous layer was estimated non-destructively using a disk pasture meter and grasses under each disk were classified using Van Outshoorn (1992). To obtain the standing biomass in kg/ha the following equation from Zambatis et al. (2006) was used:

$$y = [31.716 (0.3218^{1/x}) x^{0.2834}]^2$$

where y= biomass in kg/ha

x= Disk pasture meter reading in cm

In each exclosure a 100 x 50 m plot was marked and *Acacia nigrescens* counted, as well as their canopy size measured. The stand basal area of *Acacia nigrescens* in exclosures as well as outside of exclosures was measured using a Bitterlich wedge.

A pit in the open landscape at both ^{Acacia} sampling sites was dug to 60 cm to obtain bulk density down the profile.

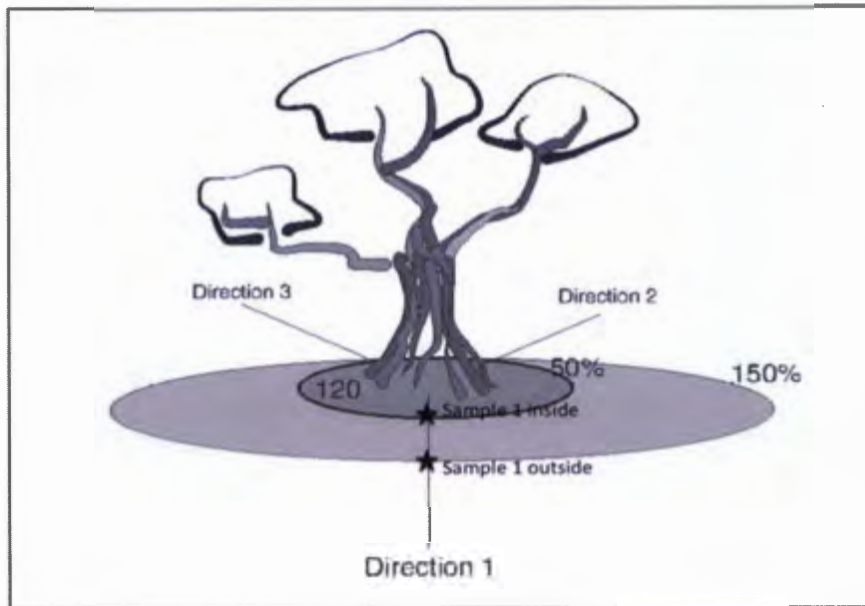


Figure 2: Sampling procedure under *Acacia nigrescens* (50% canopy radius) and away from *Acacia nigrescens* (150% canopy radius) in three directions of 120° to each other.

Laboratory analysis

Soil samples were dried in a drying oven at 70° C for at least 48 hours and reweighed to deduce the moisture content. Soil organic matter was determined via combustion of samples in a muffle furnace at 450° C for at least 5 hours. Percent soil organic matter was calculated as

$$\% \text{ OM} = \frac{A - B}{A} \times 100$$

where A = mass before burning in g

B = mass after burning in g

Soil samples were ground in a mill and analysed by a Finnigan Matt 252 Mass spectrometer (UCT) for percentage carbon and percentage nitrogen.

Statistical analysis

Statistical analyses were performed using STATISTICA 9 (StatSoft, Inc 2009). Tree height was correlated with stem diameter and canopy area to determine whether the independent variables were allometric to each other and therefore interchangeable. Percent organic matter was correlated with percent carbon to deduce their relationship. The dependent variables of both sites were compared with a t-test to detect whether they could be combined into one site.

The dependent variables examined were grass biomass, soil moisture, soil organic matter, soil carbon and soil nitrogen. Dependent variables were tested for normality and homogeneity of variances. Two comparisons were conducted: under tree compared with away from tree and secondly, in browse trap compared to out of browse trap. The browse trap is the maximum height to which giraffes browse which, following Bond and Loffel (2001) was set to 6 m. For parametric data a t-test for independent samples was used whereas for nonparametric data a Mann Whitney U test was performed. Furthermore, correlations were drawn with tree height as the independent variable and biomass, soil moisture, soil carbon and soil nitrogen as dependent variables. To test for normality of each correlation, residuals were plotted. If no pattern was observed normality of the data was assumed.

Potential Ecosystem Properties

To estimate the impact giraffes are having on the ecosystem I needed mean tree density and mean canopy area of tree per hectare in enclosure and outside of enclosure. Together with the mean property (e.g. carbon) in weight (T or kg) per hectare outside of the enclosure, comparisons between giraffe impacted area and giraffe free area were made.

To obtain the soil property in weight (T or Kg) per hectare I needed to calculate bulk density of the soil. This was done by dividing the mass of the soil of the first 10 cm from the soil profile (in g) by the volume of the soil core borer (in cm^3) and multiplied by 1000 to obtain the density in kg per m^3 . To calculate the kg of soil property per m^2 under each tree, as well as away the following equation was used:

$$\text{Property (kg/m}^2\text{)} = \frac{\%P}{100} \times \text{bulk density} \times \text{depth}$$

where % P = the percent of the property

bulk density = top 10 cm of soil in kg m^{-3}

depth = depth of the soil profile in m, which in this case is to 0.1 m

The potential property (e.g. carbon) in a hectare could be compared to the actual property using the following equation:

$$P \text{ (kg/ha)} = \text{Area under tree (m}^2\text{)} \times P_1$$

where Area under tree = trees per ha \times mean canopy area (m^2)

P_1 = mean property

To calculate the total weight per hectare of the property in question, I added the result of away from trees to those from under trees. The tree density in burnt as well as unburnt plots was used to evaluate the influence of fire by actual tree count in half hectare of an experimental burn plot in Satara landscape.

Results

Allometry

There is a correlation between tree height with stem diameter and canopy area ($R^2=0.816$ and $R^2=0.675$ respectively; Figure 3). However, between tree height of 5 -10 m the relationships changes from linear to exponential. As the tree increases in height the canopy increases more rapidly in stem diameter and canopy area.

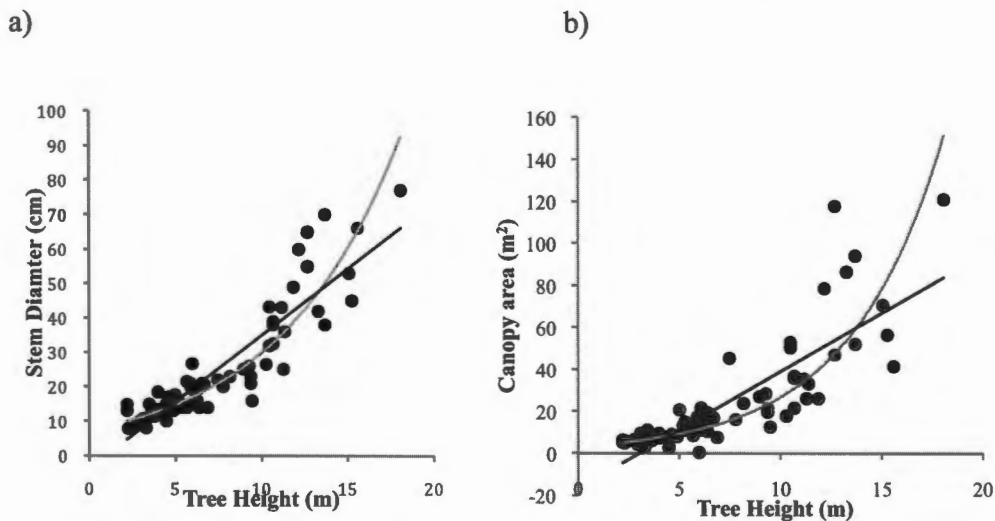


Figure 3: a) Correlation between tree height and stem diameter ($R^2=0.816$, $p<0.001$) and b) tree height and canopy area ($R^2=0.675$, $p<0.001$).

The two sampling sites cannot be pooled, as the properties were significantly different. Therefore they were treated separately in all further analysis. Sample size for comparing properties under trees to properties away from trees for Site M was 37 ($n_1=37$, $n_2=37$, $df=72$) and for Site S was 30 ($n_1=30$, $n_2=30$, $df=58$). Comparing properties under trees taller than 6 m to properties under trees smaller than 6 m had a sample size of 18 and 19 respectively for Site M ($n_1=18$, $n_2=19$, $df=35$). Site S had a sample size of 19 larger than 6 m and 11 smaller than 6 m ($n_1=19$, $n_2=11$, $df=28$).

Herbaceous Biomass

The grass biomass of Site M was significantly higher under trees than away from trees (mean under 3098.11 ± 929.26 kg ha⁻¹, mean away 2439.88 ± 913.03 kg ha⁻¹, $t=3.0734$, $p<0.01$). The same was observed for Site S, with the biomass being significantly higher under trees than in the open (mean under 2931.62 ± 1332.15 kg ha⁻¹, mean away 2295.29 ± 920.95 kg ha⁻¹, $t=2.15$, $p<0.05$). Furthermore, at Site

At Site M the grass biomass under trees that had escaped the giraffe trap (> 6 m) was significantly lower than trees that were smaller than 6 m (mean >6 m $2632.63 \pm 763.33 \text{ kg ha}^{-1}$, mean <6 m $3539.09 \pm 868.79 \text{ kg ha}^{-1}$, $t = -3.36$, $p < 0.01$). At Site S the grass biomass under trees that had escaped the giraffe trap does not significantly differ from trees in the trap (mean >6 m $2839.26 \pm 1327.06 \text{ kg ha}^{-1}$, mean <6 m $3091.165 \pm 1390.06 \text{ kg ha}^{-1}$, $t = -0.49$, $p = 0.626$). A correlation analysis shows that as tree height increases, grass biomass decreases (Site M: $R^2 = 0.162$, $p < 0.05$, Site S: $R^2 = 0.074$, $p = 0.147$; Figure 4).

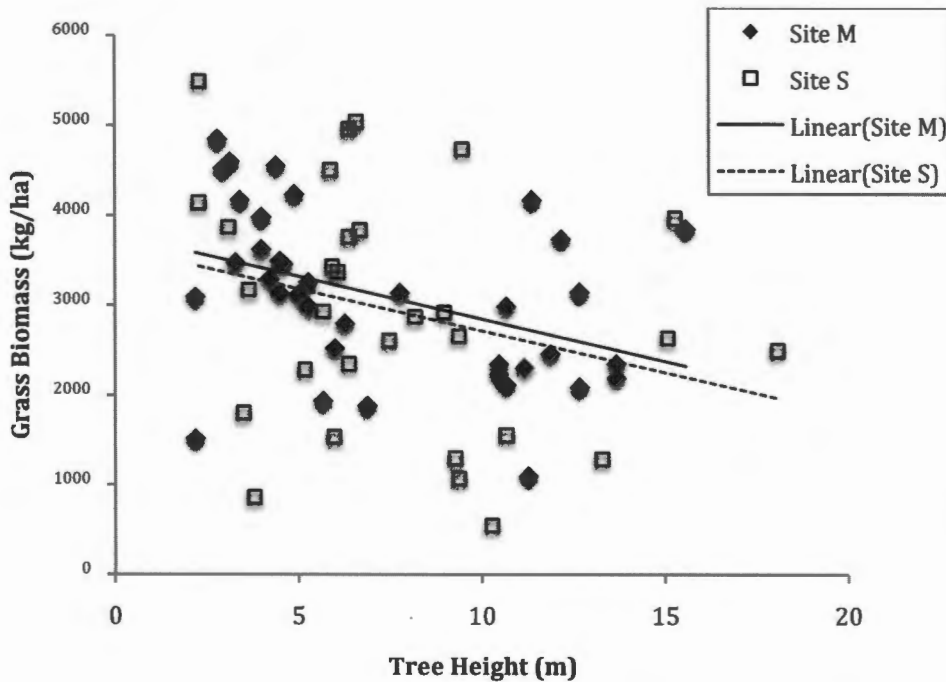


Figure 4: Correlation of grass biomass and tree height for both Site M ($R^2=0.162$, $p < 0.05$) and Site S ($R^2=0.074$, $p=0.147$).

Herbaceous Species Composition

At Site M there was a higher diversity of grasses found away from trees than under trees (Table 1). *Themeda triandra* and *Panicum maximum* dominated both under trees and away from trees. However, the frequency of *Panicum maximum* was reduced by almost half in the open where *Urochloa mosambicensis* was common. *Bothriochloa radicans* increased more than fourfold from under trees to outside, as did another *Panicum* sp. Species which were only found away from canopy cover included *Aristida* sp., *Panicum coloratum*, *Eragrostis superba* and *Heteropogon contortus*.

Site S showed a similar pattern with higher grass species diversity away from trees than under tree canopy (Table 1). *Panicum maximum* dominated under trees whereas *Bothriochloa radicans* dominated the outside, although was common under tree canopy. Other species found under trees included *Themeda triandra*, *Digitaria eriantha*, *Eragrostis cilianensis*, *Urochloa mosambicensis*, *Setaria sphacelata*, *Eragrostis* sp. and *Aristida* sp. Species found away from tree canopy cover included, *Cenchrus ciliaris*, *Eragrostis superba*, *Heteropogon contortus* and *Chloris virgata*.

Grass species composition did not change much from small trees to larger trees. The species that were generally found under small trees were also found under large trees. The only visible effect on grass species composition was the presence of a tree canopy and not the size of the tree or its canopy.

Table 1: Frequency grass species occurred and total number of species (N) under a tree and away from a tree in Site M and S.

	Site M		Site S	
	under	away	under	away
<i>Themeda triandra</i>	78	88	32	13
<i>Panicum maximum</i>	105	40	68	12
<i>Urochloa mosambicensis</i>	9	47	3	7
<i>Bothriochloa radicans</i>	2	26	52	78
<i>Aristida</i> sp.	-	8	8	16
<i>Panicum coloratum</i>	-	1	-	-
<i>Panicum</i> sp.	4	17	-	-
<i>Eragrostis superba</i>	-	14	-	1
<i>Heteropogon contortus</i>	-	2	-	1
<i>Digitaria eriantha</i>	-	-	14	16
<i>Eragrostis cilianensis</i>	-	-	9	15
<i>Cenchrus ciliaris</i>	-	-	-	3
<i>Setaria sphacelata</i>	-	-	4	-
<i>Chloris virgata</i>	-	-	-	4
<i>Eragrostis</i> sp.	-	-	5	21
Total N	5	9	9	12

Soil Moisture

The soil moisture content under trees did not significantly differ from the soil moisture content away from trees for both sites (Site M: mean under 9 ± 1.26 %, mean away 8.96 ± 1.78 %, $t = 0.12$, $p = 0.91$; Site S: mean under 11.36 ± 2.89 , mean away 10.59 ± 3.11 , $t = 0.99$, $p = 0.33$). Trees taller than 6 m had significantly higher moisture content than smaller trees at Site M (mean >6m 9.48 ± 1.44 %, mean <6m

8.54 ± 0.87%, t=3.36, p< 0.05). The difference in soil moisture content at Site S was not significant, nonetheless taller trees yielded higher moisture content than smaller trees (mean>6m 12.06 ± 2.93, mean<6m 10.15 ± 2.48, t= 1.81, p = 0.08). As the trees increase in height the soil moisture content under the trees increased (Site M: $R^2=0.142, p<0.05$, Site S: $R^2=0.085, p=0.118$; Figure 5).

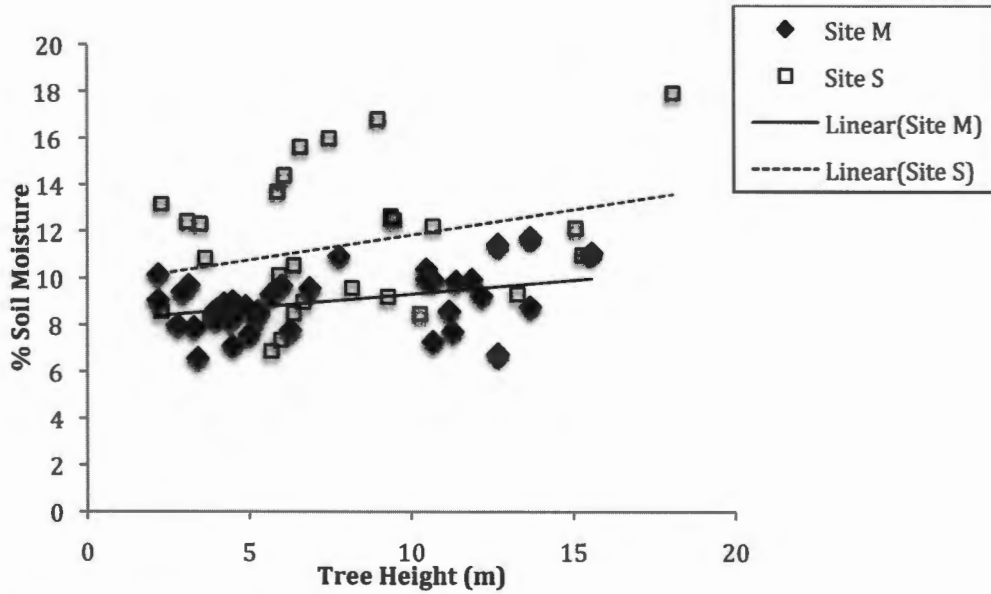


Figure 5: Correlation of soil moisture content with tree height of Site M ($R^2=0.142, p<0.05$) and Site S ($R^2=0.085, p=0.118$).

Organic Matter and Carbon Content

The correlation shows that percent carbon is approximately a third of percent organic matter ($R^2 = 0.634$, $p < 0.05$; Figure 6).

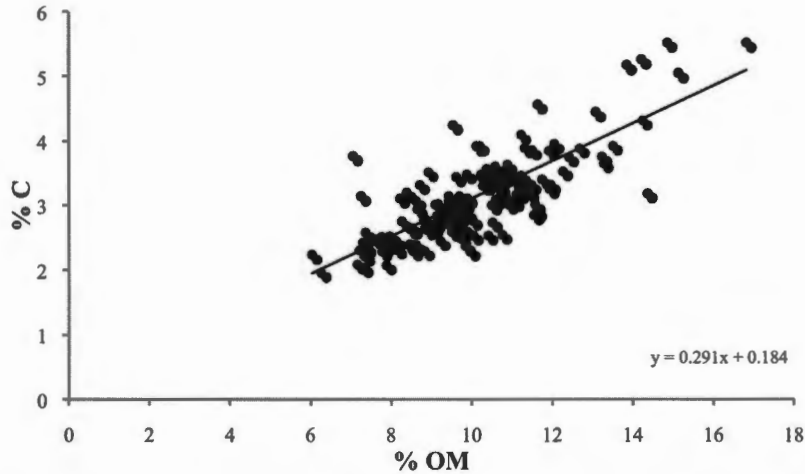


Figure 6: Correlation between the % organic matter obtained via combustion and % carbon from spectrometer ($R^2 = 0.634$, $p < 0.05$).

The percent of organic matter in the soil at both sites differed greatly under trees to away from trees, with the percent of OM being higher under trees (Site M: mean under 11.48 ± 1.93 %, mean away 9.82 ± 1.24 %, $t = 4.42$, $p < 0.001$; Site S: mean under 10.11 ± 1.54 %, mean away 8.49 ± 1.54 %, $t = 4.06$, $p < 0.001$). The soil organic matter under trees larger than 6 m was significantly higher than organic matter under smaller trees (mean >6m 12.22 ± 2.3 %, mean <6m 10.78 ± 1.17 %, $U = 105.00$, $Z = 1.99$, $p < 0.05$). In Site S a similar pattern was found with the percent of organic matter in soil under larger trees being higher than the percent of organic matter under small trees (mean >6m 10.53 ± 1.47 %, mean <6m 9.38 ± 1.43 %, $t = 2.081$, $p < 0.05$). With an increasing tree height, the percent of organic matter in the soil increased (Site M: $R^2 = 0.22$, $p < 0.01$, Site S: $R^2 = 0.183$, $p < 0.05$; Figure 7).

The percentage of carbon in the soil under trees was significantly higher to the percentage of carbon found in soils away from the trees (Site M: mean under 3.51 ± 0.79 %, mean away 3 ± 0.45 %, $t = 3.37$, $p < 0.01$; Site S: mean under 3.19 ± 0.56 %, mean away 2.7 ± 0.68 %, $t = 3.03$, $p < 0.01$). At Site M the percentage of carbon in soil was significantly higher under tall vs. small trees (mean >6m 3.9 ± 0.93 %, mean <6m 3.13 ± 0.37 %, $Z = 1.99$, $p < 0.05$). However, the percentage of carbon in soils at Site S did not differ significantly but were higher under tall trees (mean >6m 3.26 ± 0.6 ,

mean < 6m 3.07 ± 0.5 , $t = 0.88$, $p = 0.38$). As for percentage organic matter the percentage of carbon increased as the height of trees increased (Site M: $R^2 = 0.349$, $p < 0.001$, Site S: $R^2 = 0.113$, $p = 0.069$; Figure 8).

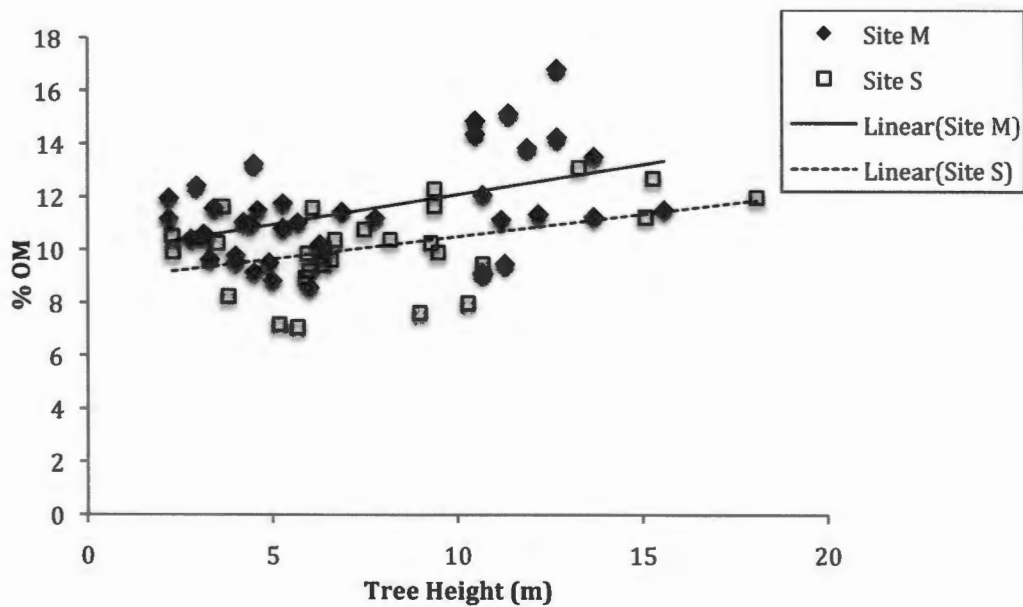


Figure 7: Correlation of percent organic matter with tree height for Site M ($R^2 = 0.22$, $p < 0.01$) and Site S ($R^2 = 0.183$, $p < 0.05$).

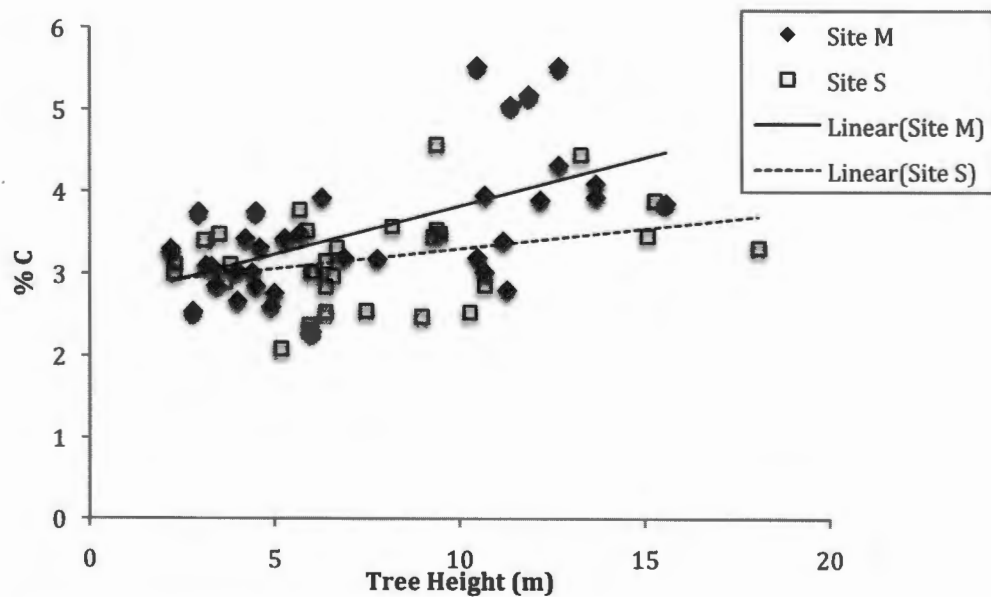


Figure 8: Correlation of percent carbon with tree height for Site M ($R^2 = 0.349$, $p < 0.001$) and Site S ($R^2 = 0.113$, $p = 0.069$).

Nitrogen

The percent of soil nitrogen was significantly higher under than away from trees (Site M: mean under 0.276 ± 0.054 %, mean away 0.212 ± 0.027 %, $t = 6.39$, $p < 0.001$; Site S: mean under 0.249 ± 0.044 %, mean away 0.236 ± 0.047 , $t = 5.42$, $p < 0.001$). Yet, the percent of nitrogen in soils below trees larger than 6 m was only significantly higher at Site M ($Z = 2.628$, $p < 0.01$) and not at Site S ($t = 0.76$, $p = 0.45$). For both Site M and Site S as the tree height increased the percent of nitrogen in the soil tended to increase (Site M: $R^2 = 0.3465$, $p < 0.001$; Site S: $R^2 = 0.180$, $p < 0.05$; Figure 9).

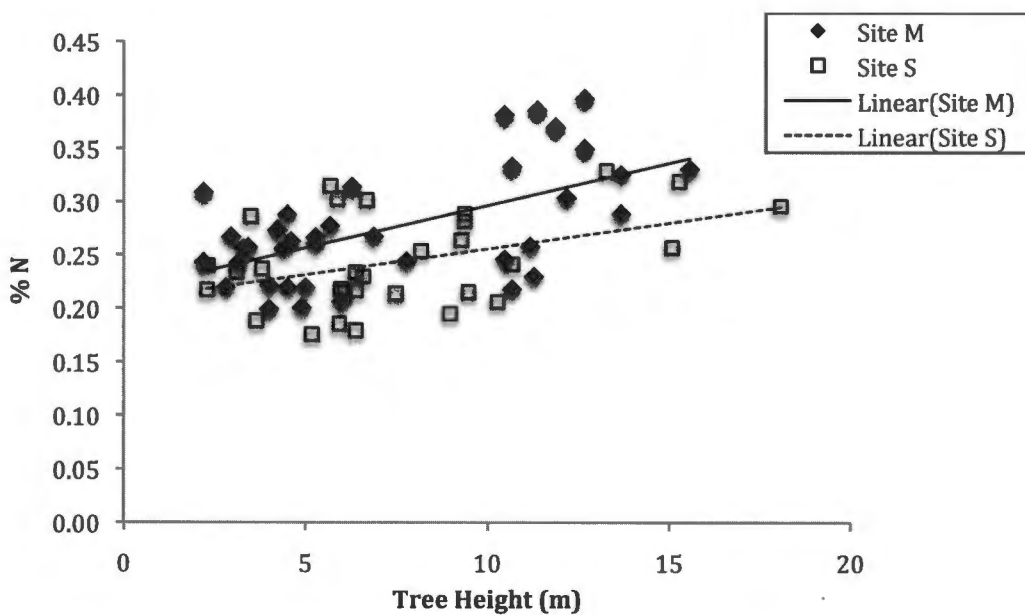


Figure 9: Correlation of percent nitrogen with tree height for Site M ($R^2 = 0.346$, $p < 0.001$) and Site S ($R^2 = 0.180$, $p < 0.05$).

Potential Ecosystem Properties

Tree density in burnt plot ranged from 100 - 140 trees per hectare and in unburnt plot over 200 per hectare. Mean canopy area in enclosure was 50 m² for trees taller than 6 m, whereas outside of enclosure it was 10 m². Bulk density for Site S was 1912.262 kg m⁻³ and in Site M bulk density was 1837.79 kg m⁻³.

Mean grass biomass under tall trees (>6m) was 2706.53 kg/ha, under small trees (<6m) was 3384.04 kg/ha and in the open was 2381.23 kg/ha. Mean moisture in soil under tall trees was 20.34 kg/m², under small trees 14.29 kg/m² and 18.34 kg/m² in the open. Mean soil carbon under tall trees was 6.704 kg/m², 5.816 kg/m² under small trees and 5.341 kg/m² in the open. Mean soil nitrogen was 0.449 kg/m² under tall trees, 0.455 kg/m² under small trees and 0.367 kg/m² in the open. The weights of properties in 1 hectare plot are shown in Table 2.

Table 2: Potential ecosystem properties between giraffe and no giraffe impacted savanna in a burnt and unburnt plot of 1 hectare.

	Soil Carbon (T/ha)		Soil Nitrogen (T/ha)		Soil Moisture (T/ha)		Grass Biomass (T/ha)	
	giraffe absent	giraffe present	giraffe absent	giraffe present	giraffe absent	giraffe present	giraffe absent	giraffe present
burnt	60.225-62.95	53.88-54.07	4.078-4.24	3.76-3.79	193.4-197.41	179.31-177.69	2.54-26.61	2.48-2.52
unburnt	67.04	54.36	4.49	3.85	203.44	175.27	2.71	2.58

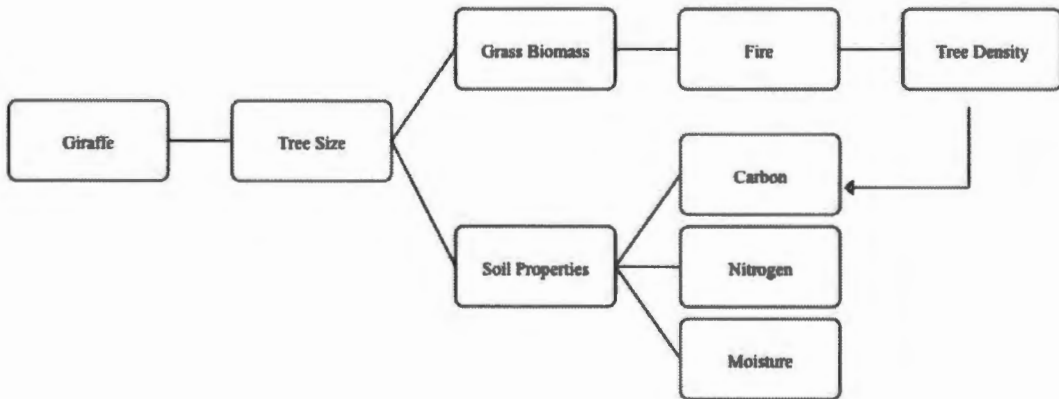


Figure 10: Inferred causal relationship driving ecosystem properties in the Kruger National Park.

Discussion

Giraffes are a conspicuous feature in most contemporary African savanna parks, not only in their towering presence but also by the landscape scale effects they have on tree populations. It is very unlikely that factors other than giraffe have caused the pattern of suppressed tree growth seen on *Acacia nigrescens*. No terrestrial mammal in South Africa, other than the elephant removes foliage at heights greater than ± 3 m. Once trees have escaped the fire and smaller ungulate browse trap they are faced with megaherbivores who keep their size in check. Although occasional elephant browsing or damage was observed, most elephants avoided vicious *Acacia nigrescens* and rather appear to concentrate on broad-leaved tree species.

Observing *Acacia nigrescens* inside and outside of exclosures the impact becomes evident. Trees found inside the exclosures are 'relaxed', opposed to trees outside the exclosures which are shorter than 6 m and subjected to giraffe browsing (Figure 11). Furthermore, the relationship between tree height to canopy size outside of the exclosure is exponential (Figure 3b) from ± 7 m upwards indicating that as the trees escape the giraffe browse trap they 'relax' and increase their canopy area. This tree suppression can be seen across the whole landscape, indicating the large-scale effect giraffes can have.



Figure 11: Left, a 'relaxed' *Acacia nigrescens* found inside the exclosure. Right, a *Acacia nigrescens* impacted by giraffe, outside of exclosure. Note the structural differences between the two trees.

I questioned the effects reduced tree size may have on ecosystem properties, such as soil moisture, soil carbon, soil nitrogen and in turn on the herbaceous productivity. Overall a tree taller than 6 m yielded higher soil moisture, nitrogen and carbon than a smaller tree. This is especially interesting when considering which properties are most influential on herbaceous productivity. Larger trees may be invaluable as means to decrease evapotranspiration not only due to shade but also by increasing soil moisture content. Many studies have highlighted the importance of reduction of solar radiation as well as air and soil temperatures underneath tree canopy (Belsky et al. 1989, Belsky et al. 1994, Moro et al. 1997, Vetaas 1992, Weltzin and Coughenour 1990). However, recent research in this field has found that soil nitrogen availability is the most important factor affecting nutrient quality of grasses (Mbatha and Ward 2010). Grass species found under tall trees did not differ from those found under small trees, which indicates that the nutritional value and moisture content of the soil plays a minor role in influencing grass species composition or biomass.

However, the grass biomass under taller trees was less than that of smaller trees. Observing the smaller trees in the field it became noticeable that they had a cage-like architecture. Grasses growing underneath and in between this cage of sharp thorns were not browsed, and because it was before the fire season had not yet been reduced. The lack of grazing and fire is one explanation for higher biomass of grasses underneath smaller trees opposed to larger trees. Furthermore, the more frequent presence of *Bothriochloa radicans*, *Urochloa mosambicensis* and *Aristida* sp. away from trees indicates a history of heavy grazing away from tree canopy.

Higher grass biomass found under small trees, increasing the fuel load for fire. This shows how there is a relationship between the herbivore and fire, soil properties and subsequently tree density and carbon sequestration. A giraffe influences the occurrence of fire and hence tree density (Figure 10), similarly how the wildebeest population irruption that followed disease (rinderpest) eradication in the Serengeti ecosystem lead to a widespread reduction in the extent of fire and an ongoing recovery of tree population (Holdo *et. al* 2009). When estimating the weight of a property in a giraffe impacted or giraffe absent plot it became evident the potential role giraffes play in an ecosystem. The content of nitrogen, moisture and carbon in the soil was less in a giraffe impacted site (Table 2). Although overall grass biomass under small trees is higher, when comparing grass biomass in one hectare of giraffe

impacted vs. giraffe absent plot the biomass of grass in the giraffe absent plot is higher (Table 2). These findings are important in the trophic cascade effects a single species may have on the savanna ecosystem (Figure 10). Giraffes reduce tree size, which over large area reduces grass biomass, reducing fire occurrences. A reduction of fire events increases tree density (Bond *et al.* 2003), which leads to more carbon being sequestered. Secondly, tree size affects soil properties (Figure 10) and estimates indicate smaller amounts of soil carbon, soil nitrogen and soil moisture in giraffe impacted areas. So while giraffes indirectly increase carbon sequestration by decreasing fuel load, they also decrease soil properties and decrease carbon sequestration by suppressing tree size. This is only a first broad estimation of the large-scale impacts a single browser has on ecosystem properties. However, since giraffes replace a single large tree by several small trees, shows that their population size is a key determinant of ecosystem properties and should not be ignored.

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