

# Scale of nutrient patchiness mediates resource partitioning between trees and grasses in a semi-arid savanna

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## Summary

1. Scaling theory predicts that organisms respond to different scales of resource patchiness in relation to their own size. We tested the hypothesis that the scale of nutrient patchiness mediates resource partitioning between large trees and small grasses in a semi-arid savanna.

2. In a factorial field experiment, *Colophospermum mopane* trees and associated grasses were fertilized at either a fine or coarse scale of patchiness with nitrogen (N), phosphorus (P) or N + P. The growth of marked tree shoots, herbaceous biomass and leaf N and P concentrations were monitored for 2 years following fertilization.

3. Responses of trees were partly scale dependent. Tree leaf N concentration and shoot length relatively increased with fertilization at a coarse scale. Tree leaf mass decreased when P was supplied at a fine scale of patchiness, suggesting intensified grass competition.

4. Phosphorus fertilization increased leaf P concentrations more in grasses than trees, whereas N fertilization increased leaf N concentration moderately in both trees and grasses. Herbaceous above-ground biomass around focal trees was negatively correlated with tree size when fertilized with N, suggesting intensified tree competition.

5. *Synthesis.* Our results support the hypothesis that trees benefit more from nutrients supplied at a relatively coarse scale of patchiness. No direct responses of grasses to scale were detected. In trees, the scale effect was surpassed by the effect of sample year, when rainfall varied.

**Key-words:** determinants of plant community diversity and structure, herbaceous, heterogeneity, mopane, nitrogen, phosphorous, soil fertility, water availability, woodland

## Introduction

Ecologists increasingly realize that resource partitioning between coexisting species can be explained not only by the overall availability of resources but also by how resources become locally available over time and in space (Ritchie & Olff 1999; Hutchings, John & Wijesinghe 2003; Cromsigt & Olff 2006). Scaling theory predicts that organisms respond to different scales of resource patchiness in relation to their own size:

large organisms respond to coarser scales of resource patchiness and small organisms to finer scales of patchiness (Ritchie & Olff 1999; Hutchings, John & Wijesinghe 2003). Moreover, the new ‘heterogeneity paradigm’ in biodiversity conservation entails that managers should promote a high spatial heterogeneity in, for example, savanna-grassland systems to maintain a high species richness and herbivore biomass (du Toit, Biggs & Rogers 2003; Cromsigt, Prins & Olff 2009). If the scale of spatial resource heterogeneity is important, as scaling theory predicts, scale should also be considered when promoting heterogeneity.

Scaling law has been rarely addressed with plants, although we know that plants differ markedly in size and vary in

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nutrient uptake, biomass accumulation and root vs. shoot allocation patterns when the same amount of nutrients is supplied in patches of different sizes (Hutchings, John & Wijesinghe 2003; Kume, Sekiya & Yano 2006). Here we report on a field experiment where nutrients were supplied at different scales of patchiness to trees and grasses in a semi-arid savanna ecosystem, to test the general hypothesis that trees profit from patchiness at larger and grasses from patchiness at smaller scales.

Savannas are ideal for such a test because they consist of a continuous layer of small herbaceous plants (mainly grasses) interspersed by large woody plants (hereafter trees) (Scholes & Archer 1997; Sankaran, Ratnam & Hanan 2004) and have a heterogeneous distribution of resources in both space and time (Belsky, Mwonga & Duxbury 1993; Ludwig *et al.* 2004; Levick & Rogers 2008). In savannas, spatial heterogeneity in soil nutrient availability may scale from kilometres (e.g. geomorphological differences in soils), to metres (e.g. soils beneath large trees, Ludwig *et al.* 2001; Treydte *et al.* 2008; soils associated with termite mounds, Grant & Scholes 2006) to centimetres (e.g. dung and urine patches, Cromsigt & Olf 2006). Despite considerable research effort, the factors and mechanisms governing resource partitioning between trees and grasses in savannas are still poorly understood (Scholes & Archer 1997; House *et al.* 2003; Sankaran, Ratnam & Hanan 2004; Bond 2008). Models explaining tree-grass coexistence based on vertical partitioning of mainly soil water resources between trees and grasses have been invoked in the past (Walter 1971; van Wijk & Rodriguez-Iturbe 2002; van Langevelde *et al.* 2003; Sankaran, Ratnam & Hanan 2004). We are, however, unaware of studies specifically exploring *horizontal scale* differences in resource patchiness as a potential axis for resource partitioning between trees and grasses in savannas.

A potential problem with interpreting the responses of coexisting trees and grasses to the scale of resource heterogeneity is to separate intrinsic responses of either growth form to scale (e.g. root proliferation in enriched patches) from tree-grass competition effects. Trees and grasses are likely to differ in their relative N and P requirements (Ratnam *et al.* 2008). If varied in a generally nutrient-poor environment, changes in N vs. P supply may shift the competitive balance between trees and grasses, as nutrient requirements are met. Fertilization experiments revealed that grasses are strongly co-limited by N and P in savannas (Penning de Vries & Djitéye 1982; Donaldson, Rootman & Grossman 1984; Ludwig *et al.* 2001; Snyman 2002; Fynn & O'Connor 2005; Craine, Morrow & Stock 2008). Trees, for which far less information is available (Bond 2008), are expected to be generally less dependent on P than grasses (except N-fixing trees, Ratnam *et al.* 2008). A high P supply is required to sustain rapid protein synthesis, hence to uphold a fast relative growth rate (Elser *et al.* 2007). In comparison with grasses, the higher biomass allocation to structural tissue in trees prohibits a fast relative growth rate in trees. Tropical lowland grasses (as in our study area), following the C-4 photosynthetic pathway, also have a higher nitrogen-use efficiency, which lowers its relative dependency on N availability (Ehleringer & Monson 1993; Craine, Morrow & Stock 2008). By varying the nutrient type independently in a scale

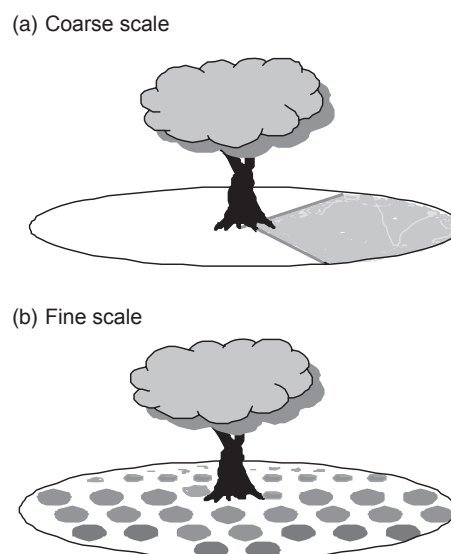
experiment, additional insights into the source (intrinsic scale responses vs. competition effects) of tree vs. grass responses may be revealed.

In our experiment, the scale of nutrient patchiness and the availability of N and P were manipulated independently in the field. Scale treatments differed in that the same amount of nutrients was supplied in either one large patch (coarse scale) or several small patches (fine scale). Both scales covered the same fertilized area, thus the local rate of fertilization was kept constant (Fig. 1). We tested the following specific hypotheses: (i) in terms of above-ground growth and leaf nutrient concentrations, trees respond more strongly (positively) to soil nutrients supplied at the coarse scale of patchiness and, conversely, grasses respond more strongly (positively) to nutrients supplied at the fine scale of patchiness; and (ii) grasses respond relatively more to P fertilization, whereas trees respond more to N fertilization.

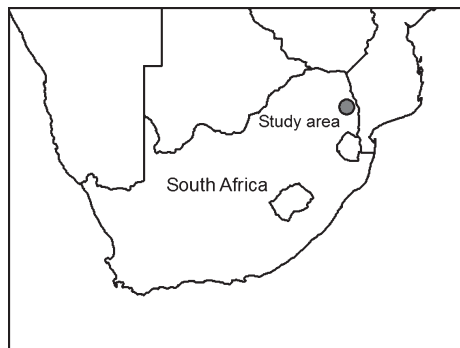
## Materials and methods

### STUDY AREA

The study was conducted in the Klaserie Private Nature Reserve (KPNR, situated in the south-eastern Lowveld of South Africa (24°13'2''S; 31°15'59''E; Fig. 2). The KPNR is part of the Greater Kruger system, which includes the Kruger National Park (KNP). The woody stratum at the study site is dominated by the tree form of *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard, whereas a mixture of grass species including *Urochloa mosambicensis* (Hack.) Dandy, *Bothriochloa radicans* (Lehm.), *Digitaria eriantha* Steud., *Panicum maximum* Jacq. and various non-graminoid herbaceous species dominated the continuous herbaceous layer of medium height. The woody component at the study site was selectively thinned in 1989 by cutting trees with chainsaws and treating stumps with a target-selective herbicide. The resulting open woodland with scattered mature



**Fig. 1.** An illustration of the differences between coarse-scale (a) and fine-scale (b) nutrient heterogeneity treatments to which mature *Colophospermum mopane* trees were subjected. The fertilized areas (grey) in both coarse and fine scales cover a third of a 5-m radius area around tree stems. Fine-scale patches ( $n = 52$ ) were c. 0.8 m in diameter.



**Fig. 2.** The study area in north-eastern South Africa. Eighty trees and their associated herbaceous plants, scattered over a  $0.4 \times 1.5$  km area, were subjected to different fertilizer treatments in the Klaserie Private Nature Reserve.

*C. mopane* trees was created in an attempt to supposedly improve habitat conditions for sable antelope (Colin Rowles, personal communication). This offered a unique opportunity to study tree–grass interactions, as inter-tree competition was largely eliminated (inter-tree distance increased from *c.* 8 m to  $> 40$  m post-clearing).

The soil in the study area is derived from granite-gneiss and is nutrient-poor (Venter, Scholes & Eckhardt 2003). This was confirmed by chemical analysis of topsoil (0–15 cm depth) samples analysed according to standard methods by the laboratory of the Agricultural Research Council in Pretoria, South Africa. The topsoil in the study area contained on average ( $\pm$ SE)  $0.084 \pm 0.004\%$  total N ( $n = 20$ ),  $1.11 \pm 0.07\%$  total C ( $n = 20$ ) and  $5.26 \pm 0.52$  mg kg<sup>-1</sup> extractable P ( $n = 20$ ). The C:N ratio of soils was on average  $13.1 \pm 0.5$ . The topsoil pH (water) in similar vegetation ( $< 5$  km S) ranged from 6.2 to 6.3 and the aluminium availability from 7 to 8 mg Al kg<sup>-1</sup> soil; therefore, phosphorus immobilization by precipitation is unlikely (Brady & Weil 2002).

The long-term (1997–2007) mean annual rainfall in the study area is 460 mm year<sup>-1</sup>. About 80% of the annual rainfall is received between October and the end of March. The rainfall received during the study period was 469 mm during the 2005/2006 season (July to end June), 328 mm during the 2006/2007 season and 348 mm from July 2007 to end February 2008 (when the last measurement was taken). The latter season represents average rainfall conditions for this period.

Large herbivore species occurring in the KPNR include African elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, white rhino *Ceratotherium simum*, African buffalo *Syncerus caffer*, Burchell's zebra *Equus burchelli*, blue wildebeest *Connochaetes taurinus*, greater kudu *Tragelaphus strepsiceros*, waterbuck *Kobus ellipsiprymnus* and impala *Aepyceros melampus*. Herbivore densities, however, were low at the study site, presumably because of the dominance of unpalatable species such as *Bothriochloa radicans* in the grass layer (open subhabitat) and the low tree density. Large herbivore dung densities, an indicator of area use (Augustine 2003), in the 5-m radius areas around trees (mean = 2.2 dung piles per tree, range = 0–19.0 dung piles per tree) were not related to treatments (full factorial ANOVAS,  $P > 0.05$ ) at the end of the experiment for all species combined, or for common individual species such as buffalo (mean = 0.7 dung piles per tree,  $P > 0.05$ ), impala (mean = 0.4 dung piles per tree,  $P > 0.05$ ) or elephant (mean = 0.5 dung piles per tree,  $P > 0.05$ ). This suggests that herbivores were not (yet) responding to treatments.

The last fire at the study site was in 1999 (Colin Rowles, personal communication). Fire as a factor of the tree–grass dynamics is therefore not further considered.

## TREATMENTS

Eighty *C. mopane* trees were selected in a  $0.4 \times 1.5$  km area and were allocated to five geographic blocks. The blocks corresponded to subtle differences in topography (crest and midslope positions). Trees ranged in height from 4.2 to 8.6 m and the diameter of canopies from 2.3 to 9.2 m. The horizontal canopy cover calculated from the diameter measurements ranged from 7 to 66 m<sup>2</sup> (5–84% of the 5-m radius treatment area). The inter-tree distance was on average 44 m.

A three-way factorial design was followed with N and P fertilization (present vs. absent) and the spatial scale (fine vs. coarse) at which nutrients were supplied as factors. Nutrient treatments consisted of (i) control, (ii) fertilization with 785 g N per tree, (iii) fertilization with 523 g P per tree and (iv) fertilization with 785 g N and 532 g P per tree. Nitrogen was supplied as a commercial ammonium nitrate fertilizer (28% N) and P as superphosphate (10.5% P). These loads correspond to local fertilizer concentrations of 30 g N m<sup>-2</sup> and 20 g P m<sup>-2</sup>, respectively, which is high compared with, for example, the annual nitrogen mineralization rate of only 5.8 g N m<sup>-2</sup> measured for a comparable broad-leafed savanna in the KNP (Scholes *et al.* 2003). In a typical cattle dung patch, however, nutrients are supplied at concentrations exceeding 100 g N m<sup>-2</sup> and 25 g P m<sup>-2</sup> (Williams & Haynes 1995). Nitrogen concentrations in urine patches may exceed 50 g N m<sup>-2</sup> (Saarijärvi & Virkajärvi 2009). For mega-herbivores such as elephant, and species that create latrines or middens (e.g. impala and white rhino, Miller 1996; Waldram, Bond & Stock 2008) local nutrient concentrations may even be higher, suggesting that our local N and P concentrations were realistic.

The spatial-scale treatments consisted of two different patch configurations in which nutrients were supplied. In both cases, a third of the surface area covered in a 5-m radius around tree stems was fertilized, with the difference that in the coarse-scale treatment one pie-shaped patch was fertilized, whereas in the fine-scale treatment 52 evenly spaced circular patches with a diameter of 80 cm each were fertilized (Fig. 1). Therefore, local N and P fertilizer concentrations were the same in both scale treatments, namely, 30 g N m<sup>-2</sup> and 20 g P m<sup>-2</sup>, respectively. The fertilizer was applied in December 2005 through early January 2006. Respective controls were assigned to fine- and coarse-scale treatments. Two replications were allocated per block, which yielded a total of 10 replications (total  $n = 80$ ).

## MEASUREMENTS

At the start of the experiment, four shoots per *C. mopane* tree were randomly selected in the 1.5- to 2.5-m height stratum and marked with aluminium rings. *Colophospermum mopane* is deciduous and new leaves are formed on new-season shoots. During the mid (January to March) growing seasons of 2006/2007 and 2007/2008, the length of all newly produced twigs was measured and totalled per shoot. All leaves produced per shoot were counted. During the 2006/2007 season, some *C. mopane* reproduced and the presence or absence of pods was recorded. At the start of the succeeding 2007/2008 rainy season, a *C. mopane* seedling cohort established in the study area. During February and March 2008, live seedlings (cotyledons still present) were counted in three 1-m<sup>2</sup> quadrates stratified at a radius of *c.* 2.5 m around tree stems. The density of seedlings was averaged per tree (seedlings per tree).

The herbaceous above-ground biomass was determined in the 5-m radius area around focal tree species during the mid growing seasons of 2006/2007 and 2007/2008 using a standard disc pasture metre (DPM) (Bransby & Tainton 1977; Zambatis *et al.* 2006). Thirty readings were stratified around focal tree stems in all treatments.

The calibration curve of Zambatis *et al.* (2006), determined for similar swards in the Kruger National Park (its boundary *c.* 50 km E), was used to convert average DPM readings to above-ground herbaceous biomass (kg DM ha<sup>-1</sup>).

For leaf quality determination of *C. mopane* trees, 10 fully expanded leaves were randomly plucked from the 1.5- to 2.5-m height stratum per tree, excluding leaves on marked shoots, during the wet seasons of 2006/2007 and 2007/2008. Leaf samples were contained in open paper bags and stored in a well-ventilated room until further processing. Samples were subsequently dried to constant weight at 60 °C, weighed and ground through a 1-mm sieve. For grass leaf N and P concentration measurements, dominant grass species contributing *c.* 30% or more of the total herbaceous biomass were sampled during the 2006/2007 wet season for a subset of trees. A random selection of tufts per species was clipped close to the ground with shears and the material contained in open paper bags per species. For coarse-scale treatments, the dominants in both treated and untreated fractions were sampled and separately analysed. This allowed the calculation of an area-corrected response in leaf N and P concentration for coarse-scale treatments. In total, 90 grass samples were sampled. Leaf samples were analysed at the REG Laboratory of Wageningen University, the Netherlands. N and P concentrations were measured with a Skalar San-plus auto-analyser (Novozamsky *et al.* 1983).

#### STATISTICAL ANALYSES

Five experimental trees were pushed over by elephants (no relation to treatments) and were subsequently excluded from the data set. For the tree data, linear mixed models with N fertilization, P fertilization and scale as fixed factors in a full factorial design were used. The year of measurement was entered as the repeated effect and trees were treated as subjects in the analyses. An autoregressive covariance matrix was assumed for the repeated measures. To test whether tree responses were related to tree size, tree cover was entered as covariate in models. Response variables consisted of leaf N and P concentrations (arcsine transformed), annual shoot length increment, number of leaves per shoot and shoot diameter of marked shoots and mean leaf mass (logarithmically transformed; Field 2005). Geographic block was entered as a random effect in models.

The pod production (presence/absence) data in relation to treatments (scale, N and P fertilization) were tested with a full factorial Generalized Linear Model. For the response variable, a binomial probability distribution was assumed and an identity link function was used. A univariate general linear model was used to test for treatment (N, P and scale) effects on *C. mopane* seedling density (square root transformed; Field 2005).

Average grass leaf N and P concentrations per tree were calculated from the different species sampled per tree. In the case of coarse-scale treatments, values for the fertilized (third) and non-fertilized (two-thirds) areas were calculated separately. Full-factorial ANOVAs were used to test for treatment effects on average leaf N and P concentrations (omitting non-fertilized coarse-scale values) and area-corrected coarse-scale N and P concentrations (using values from fertilized and non-fertilized areas). Concentrations were arcsine transformed and tree cover was entered as a covariate, as tree size may influence soil fertility (Ludwig *et al.* 2004). ANOVAs were also used to test for common species responses to treatments.

Herbaceous above-ground biomass data were significantly related to tree cover in both years. However, a significant N × Tree cover interaction (linear mixed model,  $F_{2,73} = 3.7$ ,  $P = 0.029$ ) indicated that the assumption of homogeneous regression slopes was violated (Field 2005). Therefore, Pearson correlation analyses were used to

describe the tree cover–grass biomass relationships for the different treatment groups. Bonferroni corrections were used to detect significant differences between groups.

All analyses were performed in SPSS v. 15 (SPSS Inc., Chicago, USA).

## Results

#### TREE RESPONSES TO SCALE

Consistent with our hypothesis, we found that the length of *C. mopane* tree shoots was on average 35% longer in the coarse-scale treatments than in fine-scale treatments in the second 2007/2008 season (Fig. 3). No scale-related differences occurred during the first 2006/2007 season (Fig. 3), when shoot length growth was suppressed (333 mm shoot<sup>-1</sup>) compared with the vigorous growth measured in the second 2007/2008 season (570 mm shoot<sup>-1</sup>; Fig. 3). *Colophospermum mopane* leaf N concentration was on average 4% higher (contrast,  $P < 0.05$ ) in coarse-scale treatments than in fine-scale ones (Table 1, Fig. 3).

The mean leaf mass of trees in P-fertilized, fine-scale treatments was lower (Year × P × Scale interaction; Table 1) than the leaf mass of P-fertilized, coarse-scale treatments in the first 2006/2007 season (Fig. 3). This effect disappeared in the second season when leaf mass was not affected by scale (Fig. 3).

Leaf number per shoot, shoot diameter and leaf P concentration were not affected ( $P > 0.05$ ) by the spatial scale at which nutrients were supplied to trees (Table 1, Fig. 3).

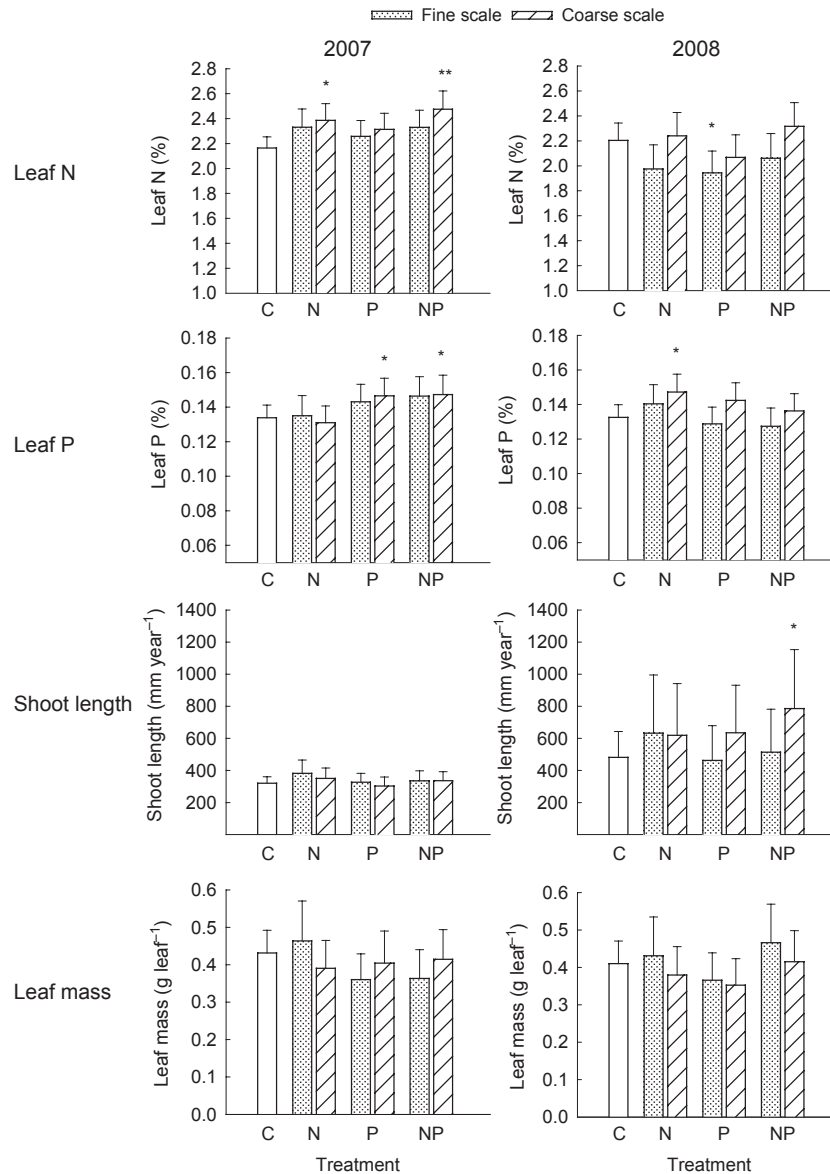
#### TREE REPRODUCTIVE RESPONSES

The proportion of trees bearing pods was neither affected by the spatial scale at which nutrients were supplied to trees (Wald chi-square = 1.045,  $n = 75$ ,  $P > 0.05$ ), nor affected by scale interactions with N (Wald chi-square = 0.175,  $P > 0.05$ ) or P (Wald chi-square = 0.091,  $P > 0.05$ ). Compared with controls, N fertilization decreased the proportion of trees bearing pods (0.66 vs. 0.43, Wald chi-square = 4.475,  $n = 75$ ,  $P < 0.05$ ). P fertilization did not affect the proportion of trees bearing pods (Wald chi-square = 0.605,  $n = 75$ ,  $P > 0.05$ ).

The average density of *C. mopane* seedlings (seedlings m<sup>-2</sup>) in three 1-m<sup>2</sup> quadrates spaced around trees was not affected by the scale of nutrient supply or affected by scale interactions with either N or P (ANOVA,  $P > 0.05$ ). Seedling density was also not affected by N fertilization (ANOVA,  $P > 0.05$ ), but seedling densities in treatments supplied with P were lower (T-test,  $t = 2.067$ , d.f. = 73,  $P < 0.05$ ) than in treatments not fertilized with P (1.2 vs. 2.3 seedlings m<sup>-2</sup>).

#### GRASS RESPONSE TO SCALE

Grasses were mostly unresponsive to scale. The P × Scale interaction (Table 2, *U. mosambicensis*; Appendix S1 in Supporting Information) indicated that the leaf P concentration of grasses growing within coarse-scaled fertilized patches (one-third of 5-m radius area) was relatively increased by P



**Fig. 3.** Responses of *Colophospermum mopane* trees not fertilized (C) or fertilized in December 2005 with nitrogen (N), phosphorus (P) or a combination of N and P (NP). Fertilizer was supplied either in a single patch (coarse scale) or distributed over 52 small patches (fine scale). Response variables, measured in 2 consecutive years (2006/2007 and 2007/2008) during the wet season, consisted of: leaf N and P concentrations, annual shoot length increment per tree and the mean leaf mass per tree. Back-transformed means and 95% confidence levels are given. The variation attributed to a random block factor has been accounted for (marginal means). Asterisks above bars indicate significant least square differences from control values: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

fertilization compared with fine scale, P treatments (representing whole 5-m radius area, Fig. 4, Appendix S1). However, the scale effect became insignificant (ANCOVA,  $F_{1,11} = 0.5$ ,  $P > 0.2$ ) when leaf P concentrations were corrected for the concentrations of grasses in the unfertilized two-thirds in the coarse-scale treatment. Thus, the high leaf P response of grasses in large fertilized patches did not offset the lower, but widespread response of grasses in fine-scale treatments, which otherwise would have opposed our expectations.

The scale of nutrient patchiness did not affect herbaceous above-ground biomass or grass leaf N concentrations (Fig. 5).

#### TREE VS. GRASS RESPONSES TO NUTRIENT TYPE

Leaf N and P concentration data supported the hypothesis that trees are relatively more responsive to N, and grasses relatively more responsive to P additions. Tree leaf N concentration responded positively (+5%) to N fertilization, but leaf P concentrations did not show a consistent response (between subject effect,  $P > 0.05$ ) to P fertilization (Table 1, Fig. 3). In fact, relative to controls, *C. mopane* leaf N concentration was suppressed (−10%) by P-only fertilization in the 2007/2008 season (Fig. 3). Conversely, grass leaf P concentration responded strongly to P fertilization (+120%), whereas the

**Table 1.** Linear mixed model statistics (*F*-ratios) for *Colophospermum mopane* leaf nitrogen (N) and phosphorus (P) concentrations, leaf number per shoot, mean leaf mass, annual shoot length and diameter of shoots (dependent variables) as affected by N and P fertilization supplied at two scales of patchiness (fixed factors)

Source	Leaves ( <i>F</i> -ratios)				Shoots ( <i>F</i> -ratios)	
	Nitrogen	Phosphorous	Number per shoot	Mean mass	Annual shoot length	Shoot diameter
<b>Within subjects</b>						
Year	27.3***	2.4	0.6	0.0	77.8***	75.0***
Year × N	2.3	0.3	0.0	1.4	1.3	0.0
Year × P	5.6*	11.4**	0.1	1.3	0.6	1.7
Year × Scale	0.3	1.5	1.1	0.4	5.7*	2.7
Year × P	7.3**	3.1	0.1	1.6	0.1	3.6
Year × N × Scale	2.2	0.9	0.0	0.6	0.2	0.8
Year × P × Scale	0.5	0.7	0.8	4.1*	0.8	0.7
Year × N × P × Scale	1.6	1.0	2.7	0.0	0.5	0.1
<b>Between subjects</b>						
N	6.0*	0.5	1.3	1.1	3.4	0.4
P	0.0	0.9	0.0	1.9	0.0	0.2
Scale	4.3*	0.8	0.7	0.9	3.6	0.4
N × Scale	2.8	0.0	1.1	0.2	0.6	0.0
P × Scale	1.0	1.0	0.0	1.8	0.0	0.6
N × P	1.3	1.0	0.5	1.4	0.1	0.1
N × P × Scale	0.4	0.2	0.3	0.0	1.4	0.2
<b>Covariate</b>						
Canopy cover	1.6	0.4	0.3	0.2	0.4	0.8

Sampling was repeated in 2 consecutive years (within-subjects factor). The projected cover of trees was entered as a covariate in models to test for tree size effects on variables.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

grass leaf N concentration responded moderately to N fertilization (+ 23%; Table 2).

Tree growth measures were mostly unaffected by nutrient additions, except for a relative decrease in individual leaf mass in trees fertilized with P in the fine-scale configuration in the first 2006/2007 season (Year × P × Scale interaction; Table 1).

The above-ground herbaceous biomass was negatively correlated with tree canopy cover in both seasons (2006/2007 season, Pearson,  $r = -0.29$ ,  $n = 74$ ,  $P = 0.014$ ; 2007/2008 season  $r = -0.30$ ,  $n = 74$ ,  $P = 0.010$ ). Lower herbaceous biomass was associated with larger trees. N fertilization, however, influenced the relationship between tree cover and herbaceous biomass. Herbaceous biomass was negatively correlated with tree cover in the N fertilizer treatments (2006/2007,  $r = -0.48$ ,  $n = 37$ ,  $P = 0.003$ ; 2007/2008,  $r = -0.48$ ,  $n = 36$ ,  $P = 0.003$ ; Fig. 5), but not correlated in non-N treatments ( $P > 0.1$ ). This suggests that herbaceous biomass was increasingly suppressed as tree size increased, but only when fertilized with N.

## Discussion

### SPATIAL SCALE INFLUENCES RESOURCE USE IN SAVANNA TREES

Our data partly support the predictions by Ritchie & Olff (1999) and Hutchings, John & Wijesinghe (2003) that the scale of resource patchiness has consequences for resource partition-

ing between coexisting plant species that vary in size, that is, trees and grasses in savannas. Under the study conditions, scale modified resource use in trees, although scale effects were surpassed by sample year differences (probably due to rainfall variation) (Table 1).

Most previous studies on resource partitioning between trees and grasses have focused on soil water partitioning in the vertical dimension (Knoop & Walker 1985; Scholes & Archer 1997; Sankaran, Ratnam & Hanan 2004), but our results showed that resource heterogeneity in the horizontal dimension can also have important implications for resource use in trees and perhaps partitioning of resources between trees and grasses.

The second-year results support the first expectation that trees benefit more from nutrients supplied at the coarse scale than fine scale of nutrient patchiness: tree leaf N concentrations were higher and shoot length increased (and likely shoot biomass, which is strongly correlated with shoot length in tested African woody species; see Rooke *et al.* 2004) in coarse-scale treatments relative to fine-scale treatments. It is generally accepted that water availability primarily determines the coexistence of savanna trees and grasses (Walter 1971; Knoop & Walker 1985; Scholes & Archer 1997; van Wijk & Rodriguez-Iturbe 2002; Sankaran, Ratnam & Hanan 2004; Sankaran *et al.* 2005), with nutrients only modifying the effects of water (Sankaran, Ratnam & Hanan 2004; Sankaran *et al.* 2005; van der Waal *et al.* 2009). Drought in the first sample year might have obscured scale effects in the first season, although tree leaf

**Table 2.** ANOVA test statistics ( $F$ -ratios) for mean leaf nitrogen (N) and phosphorus (P) concentrations of grasses (dependent variables) as affected by different types of fertilizer (N, P or N + P) supplied at two spatial scales of patchiness in a 5-m radius area around focal *Colophospermum mopane* trees (fixed factors)

Source	Leaf concentration ( $F$ -ratios)	
	Nitrogen	Phosphorous
N	10.2**	4.8
P	0.0	57.2***
Scale	0.3	0.2
N × Scale	2.3	1.2
P × Scale	0.4	5.2*
N × P	0.4	4.2
N × P × Scale	0.4	0.0
Canopy cover (covariate)	4.7	1.1

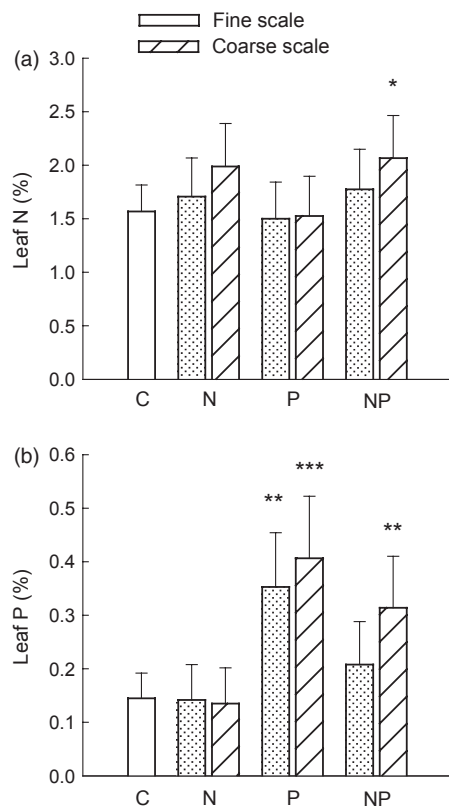
The projected tree cover of trees was included as a covariate in the analyses.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

size was suppressed in the fine-scale, P treatment. Drought might also explain the much lower shoot growth during the first year compared with the second year (Fig. 3), suggesting that water availability was more important than either nutrient (N or P) availability or the scale of patchiness at which nutrients were supplied.

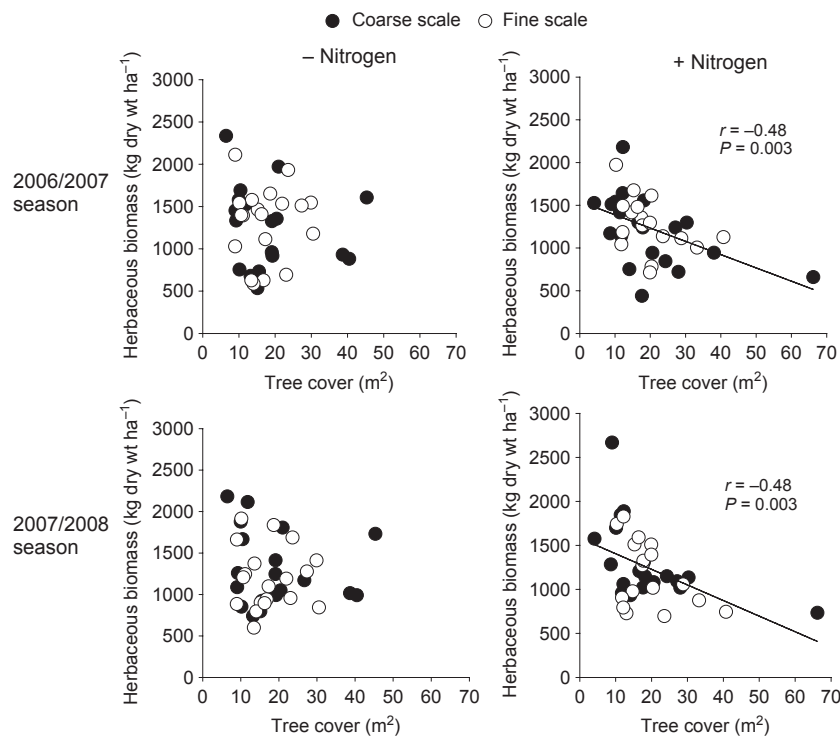
The scale-mediated responses observed in *C. mopane* trees may have been caused by either intrinsic plant responses to resource heterogeneity or may reflect competition effects of the coexisting grasses, which may have benefited more from the fine-scale nutrient supply. Experiments elsewhere have demonstrated that individual plants benefit more where the same amount of nutrients is supplied in single patches scaled to the root system of plants, rather than configured in many small patches (Hutchings, John & Wijesinghe 2003), or homogeneously distributed (Birch & Hutchings 1994; Fransen, de Kroon & Berendse 1998). Decreased performance in fine-scale nutrient environments (relative to plant root system size) may be related to the inability of plant roots to accurately match the fragmented spatial configuration of nutrient-rich patches, which incur additional physiological costs to plants (Hutchings, John & Wijesinghe 2003; Kume, Sekiya & Yano 2006). Applied to trees in our experiment, this would mean that *C. mopane* made more efficient use of nutrients supplied in coarse-scale treatments and less in the fine-scaled treatments.

The differences in tree response between the scale treatments tended to be more pronounced where P was supplied (with or without additional N) when compared with the N-only treatment. If trees have relatively higher N and grasses higher P requirements, as our data suggest, then one interpretation would be that the negative tree responses in the fine-scale, P treatments were at least partially due to intensified grass competition, lowering resource availability for trees in these treatments. Given their smaller root systems, grasses probably experienced more heterogeneous soil nutrient conditions in the fine-scale treatment compared with the coarse-scale treatment. In the coarse-scale treatment, grasses experienced mostly a



**Fig. 4.** Responses of (a) leaf nitrogen (N) concentration and (b) leaf phosphorus (P) concentration of grass swards associated with single *Colophospermum mopane* trees in relation to no fertilization (C) and fertilization with N and/or P, which were supplied either in a single patch (coarse scale) or distributed over 52 small patches (fine scale). The leaf N and P concentrations represent mean values of the dominant grass species sampled per tree. In coarse-scale treatments, values represent only grasses within fertilized patches, whereas a random sample was taken in the fine-scale treatments. Back-transformed (marginal) means and 95% confidence limits are given. Means were evaluated at a tree cover of 14.6 m<sup>2</sup>. Asterisks above bars indicate significant least square differences from control values: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

high or a low homogeneous soil nutrient supply. It follows that if grasses responded (e.g. by enhancing nutrient uptake) to soil heterogeneity, which is expected in fast-growing plants with high tissue turnover rates (Fransen, de Kroon & Berendse 1998; Kembel & Cahill 2005; de Kroon & Mommer 2006), then overall the nutrient uptake by grasses should be higher in the fine-scale treatments relative to coarse-scale treatments (Birch & Hutchings 1994; Hutchings, John & Wijesinghe 2003). Increased nutrient uptake may increase the competitiveness of grasses, as was suggested for suppressed *C. mopane* seedlings in fertilized tree seedling–grass plant mixtures (van der Waal *et al.* 2009). Although we did not find direct scale-related responses in grasses, it is still possible that an herbaceous above-ground biomass response to fertilization was offset by a weak (statistically undetectable) increase in grass consumption by grazers responding to the elevated leaf nutrient (i.e. P) concentrations. In any case, increased grass competitiveness in the fine-scale, P-fertilized treatment might explain the reduced leaf mass of *C. mopane* trees relative to



**Fig. 5.** The relationships between *Colophospermum mopane* tree canopy cover and the above-ground biomass of herbaceous plants in a 5-m radius area around tree stems for trees fertilized and not fertilized with nitrogen (N) at a coarse scale (solid circles) and a fine scale (open circles) of nutrient patchiness. The herbaceous biomass was determined in the two seasons (2006/2007 and 2007/2008) following fertilization. The data show that herbaceous biomass is increasingly suppressed when trees (and swards) are fertilized with N.

controls. Indeed, the capability of grasses to suppress mature trees is well-established (Knoop & Walker 1985; Stuart-Hill & Tainton 1989; Riginos 2009).

#### DIFFERENTIAL RESPONSES OF TREES AND GRASSES TO N AND P ADDITIONS

Supporting our second hypothesis, the *C. mopane* trees appeared to have relatively greater N than P requirements under the prevailing study conditions. Although *C. mopane* trees responded positively to N additions, trees tended to respond negatively to P-only additions, probably because grass competitiveness locally intensified, especially where nutrients were supplied at a fine scale. In a pot experiment, Ferwerda *et al.* (2005) found that *C. mopane* seedling growth was unresponsive to P fertilization, in spite of very low P background levels in the growth medium (i.e. 2.1 g P m<sup>3</sup>). These seedlings were responsive to N additions. Abundant N apparently also increased tree competitiveness with grasses. The negative relationship between tree cover and herbaceous biomass when fertilized with N suggests that the competitiveness of trees intensified with respect to grasses, but that the magnitude of the competition effect depended on tree size (Stuart-Hill & Tainton 1989).

In contrast to trees, grasses in our study showed a remarkable ability to accumulate P, but not N, in their leaves. Dominating P resources might have given grasses a competitive advantage over trees. In support, the mean leaf mass of *C. mopane* was decreased in the fine-scale, P-only treatment in

the first 2006/2007 season where tree leaf N concentrations were also reduced in the second 2007/2008 season. The lack of a strong N response in grasses may have been reinforced by the fact that many grasses in the 5-m radius area were beneath tree canopies. Ludwig *et al.* (2004) demonstrated that grasses are relatively more P limited under the canopies of large trees where soil N tend to accumulate (Treydte *et al.* 2008). High supplies of P often stimulate root growth relative to shoot growth (Salisbury & Ross 1994). Even if no response in above-ground biomass was observed, it is possible that grass roots in P treatments proliferated, increasing the competitiveness of grasses with regard to trees. This might also explain the lower tree seedling density in P-fertilized treatments.

#### EFFECTS ON TREE RECRUITMENT

Tree seedling recruitment, widely accepted to regulate tree cover in dry savannas (Sankaran *et al.* 2005; Sankaran, Ratnam & Hanan 2008), may be constrained at the seed, emergence or seedling establishment stages. Pod production and tree seedling density were not affected by scale in our study, whereas nutrient availability affected pod production (fewer trees reproduced when fertilized with N) and tree seedling densities (decrease with P fertilization). Direct scale effects on the small tree seedlings (< 0.15 m height) are unlikely; establishing in either small or large fertilized patches makes little difference. However, *C. mopane* seedlings are strongly suppressed by grass competition (van der Waal *et al.* 2009), and *C. mopane*



seedling survival is naturally low or zero beneath mature *C. mopane* trees (Mlambo, Nyathi & Mwenje 2007), thus tree seedlings may be indirectly affected by tree or grass competitiveness responses to scale. The lack of a seedling response to scale might therefore mean that either tree and grass competition effects were balanced across scale treatments or scale effects were statistically not detectable in our study.

### Implications for savanna systems

This study demonstrated that the local scale of nutrient patchiness influenced resource use by trees, which benefited more at the coarser scale of nutrient patchiness. Indirect evidence suggests that grasses may have benefited (intensified competitiveness) at the fine scale of patchiness. If grasses indeed respond to finer scales than trees, the local scale of patchiness may provide an additional axis along which coexisting trees and grasses partition resources in savanna systems. Recent studies on wild grazers by Cromsigt *et al.* demonstrated that local differences in resource heterogeneity may also mediate resource use by herbivores (Cromsigt & Olff 2006, 2008; Cromsigt, Prins & Olff 2009). The local scale of resource patchiness should thus also be considered when promoting a high spatial heterogeneity to conserve biodiversity (du Toit, Biggs & Rogers 2003; Cromsigt, Prins & Olff 2009).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** The leaf N and P concentration responses of the three most dominant grass species to different fertilizer and scale of patchiness treatments.

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