

# Stability of wooded patches in a South African nutrient-poor grassland: do nutrients, fire or herbivores limit their expansion?

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**Abstract:** Patches of wooded vegetation in nutrient-poor grassland characteristically contain high soil moisture and nutrient availability compared with surrounding grassland. These ‘islands of fertility’ appear stable in size, suggesting that tree recruitment at the patch boundary is limited. We hypothesize that tree establishment in adjacent grassland is limited by (1) competition for resources, (2) fire or (3) herbivory. In a South African grassland, we measured moisture availability and conducted a bioassay experiment to analyse whether soil nutrient limits tree recruitment at the patch boundary. We thus measured nutrient concentrations of maize plants grown in patch, boundary and grassland soil. To investigate whether browsing or fire affected tree seedlings at the patch boundary, we burned plots including patches, and used fences to exclude browsers. Neither soil moisture nor nutrient availability at the boundary differed from inside the patches, suggesting that tree recruitment at the boundary is not resource limited. Both fire and browsing combined caused a significantly lower tree seedling growth at the patch boundary, suggesting that these two factors can impede tree recruitment. The balance between positive feedback mechanisms facilitating tree recruitment, and the negative impact of fire and browsing can explain the apparent stability of these islands of fertility.

**Key Words:** browsing, facilitation, fire, soil heterogeneity, soil moisture, soil nutrients, tree island, tree seedling

## INTRODUCTION

Patches of woody vegetation in nutrient-poor grasslands are a widespread phenomenon and important for biodiversity (Schade & Hobbie 2005, Schlesinger *et al.* 1996, Scholes & Archer 1997, Vetaas 1992). Within nutrient-poor grasslands, wooded patches are often linked to higher soil moisture and nutrient availability, creating so-called islands of fertility where organic matter and nutrients are high relative to areas outside the canopy. The establishment of trees in the adjacent grassland can be limited by competition for resources within the herbaceous layer, fire or herbivory (Belsky 1994, Bowman *et al.* 2004, Harrington 1991, Hodgkinson 1991, Ludwig *et al.* 2004a, Scholes & Archer 1997). It appears, however, that possibilities for woody plant recruitment (increase in density) and release (individuals

increase in size) under the tree canopy are often improved by positive feedback mechanisms (Escudero *et al.* 2004, Holmgren *et al.* 1997, Ludwig *et al.* 2004b). Nutrients drawn from deep horizons and laterally from areas beyond the tree canopy are mainly deposited beneath the canopy via litterfall and canopy leaching (Scholes 1990). Trees can increase the soil moisture availability through shading, which lowers soil temperature and reduces evaporation and water stress on understorey plants (Amundson *et al.* 1995, Belsky *et al.* 1989, Holmgren *et al.* 1997, Mordelet & Menault 1995). Moreover, large trees protect tree seedlings by reducing the effects of fire as they depress grass growth by competition for water, nutrients and light (Hochberg *et al.* 1994). Due to these positive feedback mechanisms, expansion of these wooded patches can be expected (Wiegand *et al.* 2005), but observations show relatively stable patches through time (Lejeune *et al.* 2002, 2004; Schlesinger *et al.* 1996). So far, the balance between these positive feedback mechanisms and the effects of fire and herbivory on tree recruitment and

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release at the boundary of these wooded patches has not been studied.

The apparent stability in size of the wooded patches suggests that net facilitation for tree recruitment and release does not occur at the boundary of the wooded patches. The question then is which factors cause this stability. We tested several hypotheses related to soil nutrient and moisture availability inside and outside wooded patches and the effects of fire and browsing. First, we examined nutrient and moisture availability in the soil inside and outside patches, to determine if soil conditions could potentially limit the expansion of the patches. Our hypothesis was that in the wooded patches nutrient content is higher than in the surrounding grassland. We tested the differences in soil nutrient availability in a bioassay experiment, measuring plant growth and nutrient responses to soil nutrient availability. Also, soil moisture content was hypothesized to be higher inside wooded patches than in the grassland. We expected that, at the patch boundary, soil moisture availability shows a sharp transition. Conditions just outside the patches are expected to resemble the grassland situation with high evaporation rates presumably induced by higher solar radiation.

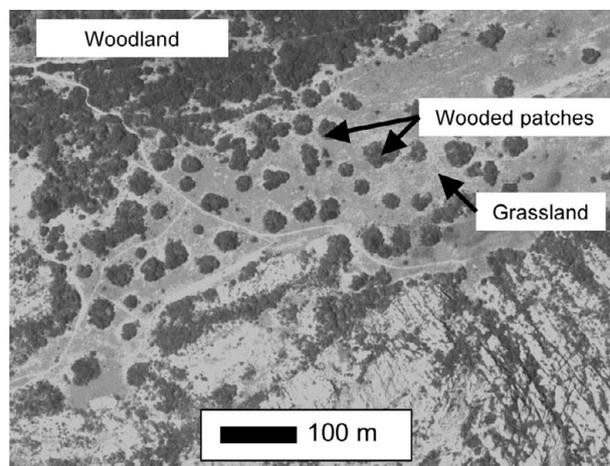
Second, we conducted a fire experiment and used differently sized fences to exclude browsing to investigate whether fire and/or browsing limits tree recruitment and release outside the patches. We expected that tree seedlings at the boundary of the patch experience high browsing pressure and are most prone to damage by fire. We hypothesized that the combination of fire and browsing reduces tree seedling release at the boundaries of the patches.

## MATERIALS AND METHODS

### Site description

Wooded patches of about 500 m<sup>2</sup> each occur in nutrient-poor grassland on large parts of the Soutpansberg (Figure 1). Based on aerial photos taken at 10-y intervals, the patches appear to have been stable in size for at least the last 49 y (K. Slager unpubl. data). Experiments were conducted at Lajuma Mountain Retreat (29°26'E, 23°01'S, altitude *c.* 1420 m asl) in the upper reaches of the Soutpansberg (South Africa) in the period from January until December 2004. The soil originates from weathered sandstone and quartzite and is well-drained. The average annual rainfall in this region is 730 mm during the wet, warm period, but varies a lot from year to year.

Wooded patches co-occur with active and abandoned termite mounds and are characterized by high tree species diversity. Approximately 70 species of tree have been recorded in the patches, including *Ekebergia capensis*

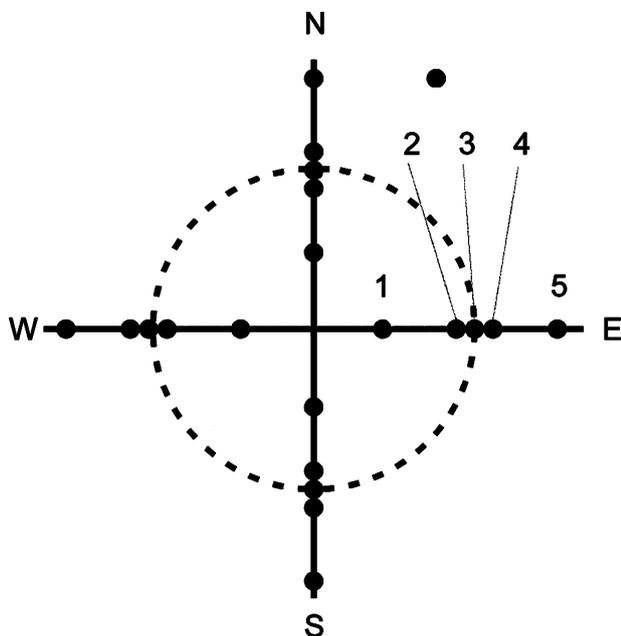


**Figure 1.** Wooded patches in nutrient-poor grassland and adjacent woodland in the study site at Lajuma Mountain Retreat, Soutpansberg, South Africa.

Sparrm., *Rothmannia capensis* Thunb., *Brachylaena transvaalensis* E. Phillips & Schweick., *Apodytes dimidiata* E.Mey. ex Arn., *Maerua caffra* (DC.) Pax, *Combretum molle* R.Br. ex G.Don, *C. kraussi* Hochst., *Rhus chirindensis* Baker f., *Olea capensis* L., *Acacia ataxacantha* DC., *Mimusops zeyheri* Sond. and *Cussonia spicata* Thunb. Smaller species and shrubs include *Canthium mundianum* Cham. & Schltld., *Maytenus undata* (Thunb.) Blakelock, *Eugenia natalitia* Sond., *Pterocelastrus echinatus* N.E.Br., *Tricalysia capensis* (Meisn. ex Hochst.) Sim, *Rhus lucida* L. and *Gymnosporia harveyana* Loes. Most of the species are characteristic of rocky ledges, forests or forest edges. The large trees growing here suggest that the patches have existed for a long time. Most species regenerate by seed but some, such as *Canthium mundianum*, also regenerate clonally. There were hardly any grasses present in the wooded patches. The patches are visited by several mammals, including common duiker (*Sylvicapra grimmia* L.), bushbuck (*Tragelaphus scriptus* Pallas), warthog (*Phacochoerus africanus* Gmelin), bushpig (*Potamochoerus larvatus* F. Cuvier) and kudu (*Tragelaphus strepsiceros* Pallas). Most of the woody species, including seedlings, growing on the edges of the patches show heavy browse marks up to a height of about 1.8 m. The boundary of the patches is characterized by a sharp transition zone from trees to grassland (Figure 1). The grass matrix consists of short acidophilic, unpalatable grass species, and is dominated by *Loudetia simplex* (Nees) C. E. Hubb. Grass biomass approximates 500 g m<sup>-2</sup>. The grassland area and the patches have certainly not burned over the past 10 y, but at unknown intervals before then.

### Soil nutrient and moisture content

To investigate nutrient and moisture availability of the soil in and around the patches, we selected randomly



**Figure 2.** Sample locations for soil nutrient and moisture availability per patch (circular dashed line) with 1 = inside patch, 2 = 1 m inside from the boundary, 3 = patch boundary, 4 = 1 m outside the boundary, 5 = grassland.

five patches for the experiments. Per patch, four transects were designed from the centre of the patch into the grassland directed to the north, south, east and west (Figure 2). Along each transect, soil was sampled. Samples 1 and 2 were taken at 5 m and 1 m respectively from the boundary inside the patch, sample 3 at the boundary, and samples 4 and 5 at 1 m and 5 m respectively from the boundary in the grassland, resulting in 20 samples per patch. The patch boundary is defined here as the line encircling a patch, beyond which the tree stems hardly ever occur, but where grasses and tree seedlings co-occur; this is most often a very clear line or narrow (<1 m) band. The patch boundary was often under the canopy edge of large trees. We also sampled the soil in nearby closed woodland for comparison with patch soil. From the woodland, five samples were taken at 20-m intervals.

We measured soil moisture content in both the wet and dry period to test our hypothesis on the soil moisture availability for plants. To prevent large differences in soil moisture content due to evaporation because of increasing solar intensity during the day, we sampled during the morning (in dry weather, between 9h00 and 11h00). During the dry period (April), soil samples from 0–30 cm deep were extracted at each sample location with an auger and immediately sealed to prevent water loss. During the early wet period (November), we measured soil moisture content only inside the patch (location 1), at each aspect at the boundary of the patch (location 3), and in the grassland (location 5). We measured soil moisture

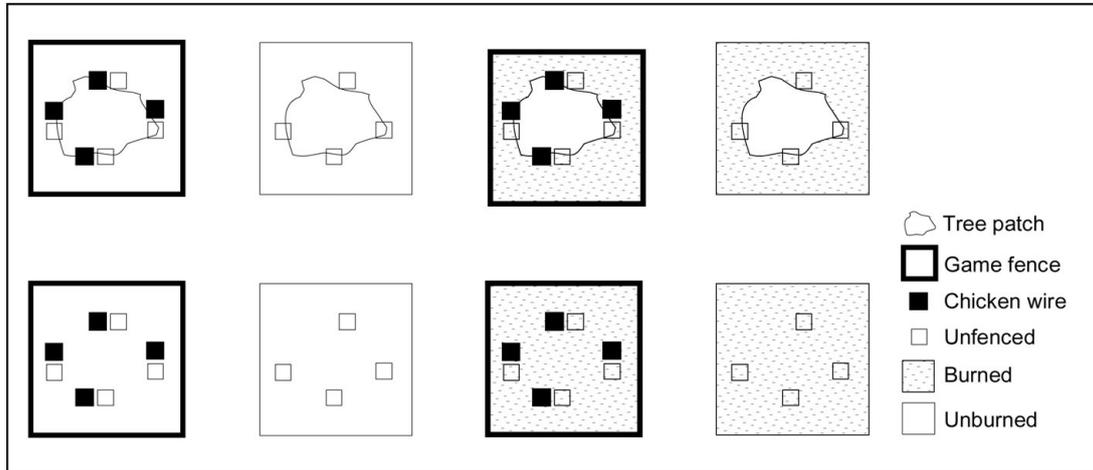
content gravimetrically after removing organic matter manually, by determining the difference between wet (fresh samples) and dry soil. The samples were dried in an oven for 48 h at 105 °C.

To test the hypothesis on soil nutrient availability for plants, we conducted a bioassay experiment rather than measuring nutrient levels in the soil. Another set of soil samples from 0–30 cm deep was taken at the sample locations. Soil was first sieved and large particulate organic matter was eliminated by hand. Plant bags were filled with the remaining soil and placed in a nursery. In each bag (20 bags per patch), four maize (*Zea mays* L.) seeds were sown. Watering occurred with a sprinkler system, every second day. The amount of light and water that each bag received could not be completely controlled. Therefore, each week the bags were rotated so that none of the bags would stay longer than 1 wk in a favourable or unfavourable position. The two best-performing maize plants in each bag were maintained, to prevent unsuccessful maize plants from negatively influencing the outcome. After 5 wk, the height of the tallest maize plant was measured. The above-ground part of the plants was weighed, dried in an oven for 48 h at 70 °C, and weighed again.

The nutrient concentration of the leaves of these plants were analysed by digestion with  $H_2SO_4$  (sulphuric acid) and  $H_2O_2$  (hydrogen peroxide) (for detailed description of the method, see Temminghoff *et al.* 2000). From the leaf samples, %N, %P, %K, %Ca, %Mg and %Na of dry matter were measured. Besides the bioassay experiment, we also analysed the soil taken from the sample locations 1, 3 and 5, and determined soil % total N, % total P and pH ( $H_2O$ ).

### Browsing and fire

To test the effect of browsing and fire on tree seedlings at the boundary of the patches, we selected eight plots of  $35 \times 35$  m: four plots including one wooded patch each, and four plots in the grassland. The latter were dominated by the grass species *Loudetia simplex*, and some ferns were present. We applied two treatments, fencing and fire, which resulted in plots (1) without fire and without browsers, (2) without fire but accessible for browsers, (3) with fire and without browsers, and (4) with fire and accessible for browsers (Figure 3). Game fences with a height of 2 m excluded large browsers, but not baboon and rodents. We thus fenced subplots of  $1 \times 1$  m with chicken wire (mesh size of  $1 \text{ cm}^2$  and height of 1.4 m, Figure 3) to also exclude small browsers. Within the four fenced plots, eight subplots were selected: four were fenced with chicken wire and four were the controls. We also selected four subplots as controls in the four unfenced plots. The subplots were situated at the patch boundary equally distributed facing north, east, south and west. The tree



**Figure 3.** Overview of eight  $35 \times 35$ -m plots for the fencing and fire experiment, of which four were selected around a wooded patch and four in the grassland, resulting in plots (1) without fire and without browsers, (2) without fire but accessible for browsers, (3) with fire and without browsers, and (4) with fire and accessible for browsers. Within the four fenced plots, eight  $1 \times 1$ -m subplots were selected: four were fenced with chicken wire and four were the controls. Also, four subplots were selected as controls in the four unfenced plots. The subplots were situated at the patch boundary equally distributed facing north, east, south and west.

seedlings in all subplots were identified and individually monitored for 2 mo in the wet season for changes in height (expressed as % of the starting height).

We burned four of the eight  $35 \times 35$ -m plots on 5 October 2004, with fire breaks in place. The air temperature was  $18^\circ\text{C}$  and the wind direction was north-east. The fire was lit on the downwind side with a backfire. After the fire had spread a few metres inwards and on the flanks, the head fire was lit.

Fire intensity was measured through quantifying the evaporation of water from cans during the fire (Trollope 1998). These cans were attached to poles at ground level, at grass canopy level, and at 1 m above the grass canopy level, both in the grassland and at the boundary of the patches. Control cans with water were placed outside the fire zone to correct for water loss by evaporation without burning. Water content loss from fire was determined through a priori and a posteriori measurement of can water content. We measured the maximum height of the flame by using three poles with a height of 5 m. Each pole was encircled with cotton strings every 25 cm. The highest string that was affected by the flames indicated the maximum flame height.

We measured soil moisture content gravimetrically 50 d after burning in the burned and unburned plots, using 70 soil samples from 0–30 cm deep, which were immediately sealed to prevent water loss. The samples were weighed, dried in an oven for 48 h at  $105^\circ\text{C}$ , and weighed again.

### Statistics

Data on soil moisture, nutrient availability and the growth of tree seedlings were first tested for normality and

homogeneity of variances, and logarithmic or square-root transformation if possible. For the experiment with fire and fencing, we had four replicates per treatment (four sites where patches were burned, four sites where patches were not burned, four sites with patches fenced with game fence, four sites with patches without game fence). Each site had four plots with and four plots without chicken fencing, and the measurements of each of these four plots were lumped per site. For normally distributed data, t-test and ANOVA with the post-hoc Tukey test were used. Non-parametric analysis of variance with a non-parametric multiple comparison (Zar 1996) was performed in cases where the data were not normally distributed.

## RESULTS

### Soil moisture content

During the dry period, grassland soil samples contained significantly less water than the samples from 1 m outside the patch and from the samples inside the patch (ANOVA,  $n = 20$  for each location, except for location 3 with  $n = 19$ ,  $F = 18.5$ ,  $P < 0.0001$ , Table 1). Samples from inside the patches had significantly higher moisture content. The influence of aspect in which the samples were taken was tested for sample locations 2–4 close to the patch boundary, as these locations are most likely to be influenced by aspect. Samples from the north side contained less moisture (4%) than those from the south side (5%), other aspects showing intermediate values (ANOVA,  $n = 14$  for north and  $n = 15$  for east, south and west,  $F = 2.84$ ,  $P < 0.05$ , Table 1), as the southern side receives most shade.

**Table 1.** Soil moisture content of soil samples (mean ± SE) per sample location (averaged over aspect) and per aspect (averaged over sample locations) in the dry period (April), and in the wet period (November). Data were tested with ANOVA and grouped with the post hoc Tukey test, letters indicate significant differences. Location 1 = inside patch, 2 = 1 m inside, 3 = boundary, 4 = 1 m outside, 5 = grassland. N = north, E = east, S = south, W = west.

Dry period	
Sample location	
1	6.4 ± 0.4 (c)
2	4.7 ± 0.3 (b)
3	4.3 ± 0.3 (ab)
4	4.3 ± 0.3 (ab)
5	3.5 ± 0.2 (a)
Aspect	
N	3.9 ± 0.3 (a)
E	4.7 ± 0.4 (ab)
S	5.3 ± 0.2 (b)
W	4.3 ± 0.3 (ab)
Wet period	
Aspect	
N	6.8 ± 0.2 (abc)
E	7.1 ± 0.2 (bc)
S	7.6 ± 0.3 (c)
W	6.2 ± 0.4 (ab)

During the wet period, we found similar trends for the soil moisture content just outside the patches (ANOVA, n = 6 for N, E, grassland and inside patch, n = 5 for S and W, F = 23.8, P < 0.0001, Table 1). Soil moisture content inside the patch was significantly higher then, compared to soil moisture content at the boundary of the patch and in the grassland.

**Soil nutrient availability**

The maximum height of the maize plants in the bioassay experiment was not significantly different between the patches (mean ± SE = 17.8 ± 0.84 cm), which indicates that patches had similar soil properties (ANOVA, n = 19

for patch A, D, and E and n = 20 for patch B and C, F = 0.44, P > 0.05). Maize plants on soil from inside the patch and 1 m inside from the boundary grew significantly taller than plants in samples taken from the grassland (n = 20 for location 1–5 and n = 5 in woodland, F = 8.06, P < 0.0001, Table 2). Also, maize plants in soil from the woodland were significantly taller than plants growing in soil taken from the grassland.

Maize plants that grew on soil from inside the patches, and from woodland, showed higher N levels than maize plants that grew in soil from outside the patches (ANOVA, n = 13 for location 1, n = 15 for 2, n = 11 for 3 and 4, n = 7 for 5 and n = 5 for woodland, F = 5.68, P < 0.0001, Table 2). Plants that grew in soil from 1 m inside the boundary still contained higher %N than maize plants growing in soil from the grassland. Similarly, K levels were significantly lower in the plants on soil from grassland than in the plants growing on soil from most other locations (F = 8.13, P < 0.0001, Table 2). However, an opposite trend was shown for P, being significantly higher in maize plants on soil taken in the grassland than in maize plants that grew on soil from elsewhere (F = 4.08, P < 0.0001, Table 2). Ca levels between the plants growing in soil from patches showed little variation, but were lower in plants growing in soil from grassland compared with those in soil from the woodland (F = 2.57, P < 0.05, Table 2). For %Mg and %Na, no differences were found between the locations (0.5 ± 0.04 and 0.006 ± 0.0009 respectively).

N levels within soil samples from inside the patches were higher than within samples from the boundary and grassland (ANOVA, n = 5 for all locations, F = 18.9, P < 0.0001, Table 3), and a similar contrast in N was found between woodland and grassland soil samples. In contrast to P levels in maize plants, %P of the soil in the patches and in woodland was significantly higher than in the grassland (n = 5 for all locations, F = 8.53, P < 0.001, Table 3). The pH did not differ between soil samples taken inside the patches, at the boundary and in the grassland, whereas the soil samples taken in the woodland had a significantly higher pH (n = 5 for all locations, F = 9.68, P < 0.001, Table 3).

**Table 2.** Maximum height of and nutrient concentrations in maize plants growing in the bioassay experiment (mean ± SE) per sample location. Concentrations of nitrogen (%N), phosphorus (%P), potassium (%K) and calcium (%Ca) are given in % of dry matter. All data tested with ANOVA and grouped with the post-hoc Tukey test, letters indicate significant differences. Location 1 = inside patch, 2 = 1 m inside boundary, 3 = boundary, 4 = 1 m outside boundary, 5 = grassland, WL = woodland.

Sample location	Max height (cm)	%N	%P	%K	%Ca
1	18.7 ± 0.92 (b)	3.18 ± 0.13 (b)	0.22 ± 0.01 (a)	3.46 ± 0.29 (b)	0.71 ± 0.03 (ab)
2	20.0 ± 0.64 (b)	2.92 ± 0.20 (ab)	0.24 ± 0.02 (a)	3.96 ± 0.35 (bc)	0.58 ± 0.04 (ab)
3	17.3 ± 0.74 (ab)	2.59 ± 0.15 (ab)	0.26 ± 0.03 (ab)	3.22 ± 0.35 (b)	0.65 ± 0.07 (ab)
4	17.2 ± 0.83 (ab)	2.40 ± 0.08 (a)	0.27 ± 0.02 (ab)	2.81 ± 0.47 (b)	0.59 ± 0.07 (ab)
5	13.3 ± 0.38 (a)	2.27 ± 0.17 (a)	0.35 ± 0.03 (b)	1.08 ± 0.10 (a)	0.48 ± 0.12 (a)
WL	20.4 ± 1.69 (b)	3.02 ± 0.15 (ab)	0.24 ± 0.02 (a)	5.38 ± 0.20 (c)	0.87 ± 0.09 (b)

**Table 3.** Nitrogen and phosphorus concentrations, and pH (H<sub>2</sub>O) in the soil samples (mean ± SE). All data were tested with ANOVA and grouped with the post-hoc Tukey test, letters indicate significant differences. Location 1 = inside patch, 3 = boundary patch, 5 = grassland, WL = woodland.

Sample location	%N	%P	pH
1	0.15 ± 0.01 (c)	0.045 ± 0.002 (b)	5.01 ± 0.19 (a)
3	0.09 ± 0.01 (ab)	0.035 ± 0.001 (ab)	4.83 ± 0.06 (a)
5	0.06 ± 0.01 (a)	0.030 ± 0.003 (a)	4.70 ± 0.04 (a)
WL	0.12 ± 0.01 (bc)	0.041 ± 0.002 (b)	5.58 ± 0.14 (b)

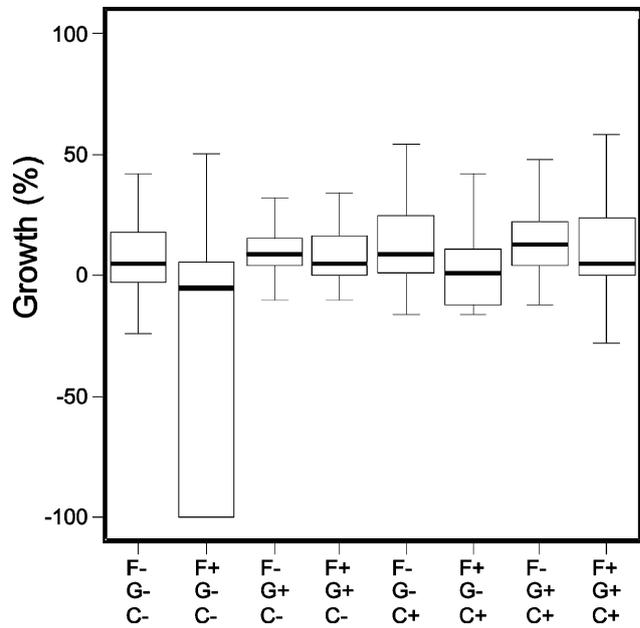
**Browsing and fire**

Fire (F) and fencing with game fence (G) and chicken wire (C) significantly affected the growth of the tree seedlings (non-parametric analysis of variance; see Table 4 for test statistics). Fire alone could partly explain the differences in tree seedling growth at the boundary of the patches, as there was a significantly lower growth in burned plots without browsers than in unburned plots without browsers (F+G-C- versus F-G-C-, where + refers to the presence of the treatment and - to its absence) (Figure 4). Also, game fencing could partly explain the differences as a significantly lower seedling growth was found in burned plots without game fences than in burned plots with game fences, both without chicken wire (F+G-C- versus F+G+C-) and with chicken wire (F+G-C+ versus F+G+C+). Since we found significantly lower seedling growth in burned plots without game fences than in burned plots with game fences (F+G- versus F+G+, irrespective of chicken wire fencing), large herbivore browsing does contribute to suppressing seedling growth. We found that seedlings were significantly smaller in the burned plots without game fence and chicken wire (F+G-C-), and taller in the burned plots with game fence and chicken wire (F+G+C+). Hence, both small and large browsers caused browsing damage to the tree seedlings.

Evaporation during fire was significantly higher in the grassland than at the boundary of the patch. This was the

**Table 4.** Results of the non-parametric analysis of variance of the growth of tree seedlings in plots with different treatments: fire and no fire, with and without game fencing, and with and without chicken wire (see Figure 3 for experimental design) (n = 278). \*P < 0.001.

Factor	χ <sup>2</sup>
Fire	20.8*
Game fence	162*
Chicken wire	40.3*
Fire × Game fence	150*
Fire × Chicken wire	271*
Chicken wire × Game fence	131*



**Figure 4.** Growth of tree seedlings as % of height measured at the beginning of the experiment (median and quartiles). Tested with non-parametric analysis of variance and grouped with the non-parametric multiple comparison test (Zar 1996). Due to the significant interactions (Table 1), all combinations of treatments were compared with the non-parametric multiple comparison test. The letters indicate significant differences. Treatments: C+ = fenced with chicken wire, C- = no chicken wire, G+ = fenced with game fence, G- = no game fence, F+ = fire, F- = no fire.

case for measurements at canopy height (1.69 ± 0.15 ml at the boundary versus 2.37 ± 0.17 ml in the grassland; t-test, t = 2.97, df = 22, P < 0.01) and at 1 m above canopy height (0.73 ± 0.16 ml at the boundary versus 1.29 ± 0.22 ml in the grassland; t-test, t = 2.07, df = 22, P < 0.05), but not at ground level (1.53 ± 0.12 ml at the boundary versus 1.67 ± 0.17 ml in the grassland; t-test, t = 0.645, df = 22, P = 0.526). Average flame height in the grassland was 1.02 ± 0.51 m. Flame height at the boundary of the patches was not measured, but observations showed that flames were much lower and quenched towards the boundaries. There was a significantly lower soil moisture content in plots that were burned (5.03% ± 0.21%) compared with plots that were not burned (7.17% ± 0.22%), 50 d after burning (t-test, t = 7.07, df = 68, P < 0.0001).

**DISCUSSION**

In this paper, we show that both soil moisture and nutrient availability inside the wooded patches is significantly higher than in the grassland. As soil moisture availability is a critical factor for determining the development of woody vegetation in (semi)arid regions (Davis *et al.* 1999, Fensham & Holman 1999, Scholes & Archer 1997),

and plant productivity is controlled by soil nutrient status, especially when rainfall reaches 700–900 mm  $y^{-1}$  (Scholes 1990), our results suggest that conditions for tree recruitment are better inside the wooded patch than outside. These results agree with other studies that show the phenomenon of the islands of fertility (Escudero *et al.* 2004, Hibbard *et al.* 2001, Mordelet *et al.* 1993, Schade & Hobbie 2005, Schlesinger *et al.* 1996). We suggest that these wooded patches accumulate nutrients and thus maintain locally high soil fertility in an otherwise nutrient-poor grassland matrix. This accumulation might take place by the trees (horizontally or vertically) or animals (faeces: Georgiadis 1989, termite mounds: Smith & Yeaton 1998). Further research could distinguish between these different factors. Cook & Dawes-Gromadzki (2005) used naturally occurring stable isotopes to understand heterogeneity in the transfer and capture of resources across banded vegetation in arid and semi-arid landscapes. Similar isotope techniques have been applied in the past to assess historic vegetation changes in savannas (Boutton *et al.* 1998), and could be used here to analyse carbon  $^{13}C/^{12}C$  ratios as an index for C3:C4 (woody plant:grass) ratios with soil depth, assessing whether the patches are perhaps forest relicts or grass invaders (Liao *et al.* 2006).

We found no differences between the soil moisture content in the grassland and just outside the patch in the dry period, but there were differences during the wet period. Apparently, moisture availability is strongly improved only in the centre of the patch, probably due to shading provided by the tree canopy, the presence of termite mounds inside the patches, lateral rooting of adult trees in the wooded patches (Scholes 1990). On hot days, differences can probably become more extreme and more critical, especially on the northern side of the patches. Here, competition for soil moisture with the herbaceous layer will be stronger and could cause high mortality among tree seedlings (Harrington 1991, Walker *et al.* 1981). Although we did not find significant differences in soil moisture content at the boundary of the wooded patches, the differences in soil moisture content between the patch and the grassland during the wet season might be enough to prevent tree recruitment (Pulido & Diaz 2005) on the northern side of the patches, since tree seedlings are much more sensitive to water stress than adult trees. Based on our measurements and the prevailing rainfall regime, however, we argue that it is unlikely that soil moisture availability limits the expansion of the wooded patches.

Between the locations around the patch boundary and inside the patch, we found no differences in height of the maize plants and the majority of the measured nutrients, but there were differences in nitrogen availability. Nitrogen availability was found to be significantly higher inside the wooded patch than at the boundary, both in the

soil as well as in the leaves of the maize plants. Although the availability of both nitrogen and phosphorus were highest in the soil from inside the patch, high phosphorus concentration was found in maize plants growing in soil from the grassland. An explanation for the contradiction between the available phosphorus and the phosphorus taken up by the plants might be that phosphorus inside the patch is less easily taken up than phosphorus in the grassland.

From the fire experiment, it appeared that the direct effects of fire on trees, i.e. damage and top kill, were minimal around the wooded patch because the fire tended to die out here. This is most likely due to the low amount of fuel load (grass biomass) and high percentage of bare soil close to the boundary of the patches. This reduced fuel load could be due to competition for nutrients, water or light with the trees (Ludwig *et al.* 2004a, b), or to herbivores that were attracted by the tree seedlings at the boundary of the patches and also forage on the surrounding vegetation (Palmer *et al.* 2003). Fire intensity was indeed found to be significantly higher in the grassland than around the patches, as we approximated fire intensity by the amount of water evaporated due to the fire. We found that soil moisture availability is reduced 50 d after fire, probably due to a subsequent decrease in grass cover and biomass which results in a higher exposure to solar radiation and wind, which in turn increases evaporation rates (van de Vijver 1999).

The separate effects of fire and fencing could partly explain the difference in tree seedling growth at the boundary of the patches, as woody plant seedlings were significantly smaller in the burned plots without game fence and chicken wire. These results suggest that the combination of fire and browsing is responsible for the difference in seedling growth after 2 mo. Both small and large browsers caused browsing damage to the tree seedlings. The interactions of browsing and fire can be explained by the attraction of browsers to post-fire high-quality regrowth of the vegetation (Gureja & Owen-Smith 2002, van de Vijver 1999). As especially tree seedlings are vulnerable when very young, we mainly focused on the effects of our treatments in the first year. Despite the short time span of the study, we did obtain significant results, and we do not expect that more years of observation will lead to different ecological processes taking place.

We can conclude that positive feedback mechanisms may act under the tree canopy of wooded patches, enhancing conditions for tree recruitment and release by promoting soil moisture and nutrient availability and reducing fire impact. These facilitative effects do also occur at the boundary of the wooded patches as we found that soil nutrient availability in the boundary zone did not differ from the centre of the patch. Neither soil moisture nor nutrient availability at the boundary differed from inside the patches, suggesting that tree

recruitment at the boundary is not limited by resources. We can further conclude that the combined effect of browsing and fire act as mechanisms to impede the recruitment of tree seedlings and release of young trees at the boundary of the patches. The balance between positive feedback mechanisms facilitating tree recruitment, and the negative impact of fire and browsing suppressing tree establishment can explain the apparent stability of the islands of fertility. Here, browsing and fire might counter frequently observed increases in woody cover in grassland (Hibbard *et al.* 2001, van Langevelde *et al.* 2003).

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