



Insect outbreaks alter nutrient dynamics in a southern African savanna: patchy defoliation of *Colophospermum mopane* savanna by *Imbrasia belina* larvae

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ABSTRACT

Invertebrate herbivore outbreaks have important impacts on system biogeochemical cycling, but these effects have been poorly documented in African savanna ecosystems. In semi-arid African savannas, outbreaks of the lepidopteran *Imbrasia belina* (mopane worm) affect discrete patches of the dominant *Colophospermum mopane* trees; larvae may completely defoliate trees for up to six weeks during each of the early and late growing seasons. We studied the impact of mopane worm outbreaks on the availability of nitrogen (N), phosphorus (P), and potassium (K) within mopane savanna by quantifying major nutrient pools in defoliated and non-defoliated savanna patches, including leaves, leaf litter, worm frass, and the soil beneath trees. Within an outbreak area, approximately 44 percent of trees were infested, supporting ~29,000 worms/ha, leading to ~640 kg/ha dry weight frass deposition at 1.4 g of frass/day-individual (fourth or fifth instar), compared with an average 1645 kg/ha dry weight of leaf on trees most of which should be deposited by litterfall at the end of the growing season. Frass had twofold higher P, 10 percent higher K, but equivalent N content than litter. Taking frass and litter deposition together, the N, P, and K contents added due to the outbreak event at our study site were 0.88, 5.8, and 2.8 times those measured in non-outbreak patches, a pattern which was reflected in the nutrient contents of soil surfaces beneath defoliated trees. Invertebrate herbivory appears to be an important driver for mopane savanna but has been largely neglected.

Key words: invertebrate herbivory; lepidopteran outbreak; mopane worm; nitrogen; phosphorus; potassium; Venetia Limpopo Nature Reserve.

AFRICAN SAVANNAS ARE TYPIFIED BY A MIXTURE OF GRASS AND TREES whose structure, composition, and functioning are determined primarily by plant-available moisture and available nutrients and secondarily by fire and herbivory (Frost *et al.* 1986, Sankaran *et al.* 2004, Bond 2008, Staver *et al.* 2009, Lehmann *et al.* 2011). Research on herbivores in protected savannas has predominantly focused on the iconic, rich community of large mammalian grazers, mixed feeders, and browsers that can markedly affect savanna functioning through altering nutrient dynamics (Augustine *et al.* 2003, Augustine & McNaughton 2004, 2006, Sankaran *et al.* 2008). However, the impact of invertebrate herbivory on ecosystem functioning may match or exceed that of their mammalian counterparts in African savannas. Larval irruptions of *Cirina forda* (Saturniidae) defoliate more than a third of the leaf biomass of its main host *Burkea africana* (Scholtz 1976), grasshoppers may consume as much grass as wildlife grazers in the Serengeti (Sinclair 1975), and termite biomass (70–100 kg/ha; Wood & Sands 1978) exceeds that of large mammals (10–80 kg/ha; Bell 1982) with termites removing up to 15,000 kg/ha of litter to a colony per annum (Dangerfield *et al.* 1998). Despite these long-standing examples, the influence of invertebrate herbivores on biogeochemical cycling in African savannas is not well known.

Insect herbivory is well recorded elsewhere to affect woody plants and ecosystem functioning. Specifically, temporary population outbreaks of lepidopteran species may result in complete defoliation and even mortality of woody host species (Mattson & Addy 1975, Ritchie *et al.* 1998, Christenson *et al.* 2002, Kurz *et al.* 2008). Invertebrate herbivory of woody plants can affect plant chemistry (Freeland & Janzen 1974, Findlay *et al.* 1996), chemistry of throughfall (Tukey & Morgan 1963), and nutrient content of leaves and litter (Klock & Wickman 1978, Risley 1986, Risley & Crossley 1988, Seastedt *et al.* 1988, Belovsky & Slade 2000), all factors which can affect rates of litter decomposition (Chapman *et al.* 2003). During outbreaks, large volumes of fast-decomposing frass and insect cadavers are deposited to the soil. These fluxes tend to enhance soil nutrient content and redistribute resources to biogeochemical pools which may or may not be available to plants (Hollinger 1986, Hunter 2001, Lovett *et al.* 2002, Frost & Hunter 2004). As similar effects might be anticipated in African savannas, a first motivation for this study was to assess the extent of influence of a conspicuous, abundant insect herbivore on nutrient dynamics.

The effects of mammalian herbivory on nutrient cycling in African savannas may provide insights for cases of intensive insect herbivory such as lepidopteran outbreaks (Scholtz 1976). Grazing mammalian herbivores can increase foliar N in areas they frequent by excreting N in forms easy for plants to take up (Ruess & McNaughton 1987, Frank & Evans 1997) and

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returning more labile substrates that are readily mineralized (Frank *et al.* 2000, Hamilton & Frank 2001, Johnson & Matchett 2001). Grazers may also increase N loss through the pathways of leaching, volatilization, and denitrification (Frank & Evans 1997, Frank & Zhang 1997). The sum effect is an increase in N cycling (Frank & Groffman 1998, Augustine & McNaughton 2006, Frank 2008) which is reflected by enriched ^{15}N in systems with intense grazing (Frank & Evans 1997, Frank *et al.* 2000, Coetsee *et al.* 2011). Similarly, browsing may result in altered chemical composition of foliage (du Toit *et al.* 1990, McNeil & Cushman 2005, Scogings *et al.* 2011) that may promote 'browsing lawns' (Fornara & Du Toit 2007). Browsing and grazing, however, may lead to decreased ecosystem N indirectly through altered litter quality by decreasing the abundance of plant species with N-rich tissues (Ritchie *et al.* 1998, Sirotinak & Huntly 2000). Herbivory may also influence root exudates and carbon allocation, which influences the activity of the soil biotic community and consequently nutrient supply (see Bardgett *et al.* 1998 for a review).

The effects of mammalian grazing and browsing on other minerals are not clear; increased grazing led to a decreased amount of soil P in Sahelian rangelands (Hiernaux *et al.* 1999). The long-term exclusion of herbivores in Ugandan woodland resulted in an increase in woodiness with an increase in the labile fractions of organic and inorganic P but a slight decline in total P and dramatic increases in Ca, K, and Mg (Hatton & Smart 1984).

Colophospermum mopane (mopane) savanna covers 555,000 km² of southern Africa (Mapaure 1994). Mopane is the main host for the lepidopteran *Imbrasia belina* Westwood 1849 (mopane worm), whose outbreaks can completely defoliate extensive tracts of woodland after six weeks during the early growing season and occasionally for a second period later in the growing season (van Voorthuizen 1976, Dithlogo 1996). Defoliation during outbreaks impairs subsequent foliar regrowth although tree mortality has not been reported (Hrbar *et al.* 2009). The sum effect of outbreaks of native lepidopteran species is often mutualistic and involves a recharge of the cycling nutrient pool with increased productivity over the long term (Mattson & Addy 1975, Belovsky & Slade 2000). Mopane worms are a valuable protein source to local communities; however, populations are in decline in southern Africa due to overharvesting; a number of areas that used to have regular outbreaks have not experienced an outbreak for several years (Akpulu *et al.* 2009, Gondo *et al.* 2010).

The main aim was to investigate how mopane worms affect cycling of three key plant nutrients, namely N, P, and K. We hypothesized that (1) more nutrients are returned to the soil in areas defoliated by worms, because frass will have higher levels of nutrients than litter, as leaves resorb nutrients before senescence, whereas larvae eat leaves when green. (2) As a consequence, soil nutrient levels will be elevated in outbreak areas where frass is deposited. To evaluate these hypotheses, we parameterized key ecosystem pools and fluxes for infested and non-infested patches, including mopane leaf biomass, leaf nutrient content, nutrient deposition from litter vs resorption prior to

litterfall, mopane worm biomass, worm frass production, and frass nutrient content.

METHODS

STUDY AREA AND SPECIES.—We conducted this study in the Venetia Limpopo Nature Reserve (VLNR) and an adjoining property Hackthorne (approx. 22°16'S; 29°20'E) at about 600 m above sea level. Mean annual rainfall of this semi-arid region is about 370 mm, with a coefficient of variation of 36 percent (O'Connor 2015). Rainfall for the study's wet season (2013/14) was 267 mm. Rainfall occurs mainly as convective events during summer (November to April). The growing season (summer) is hot, and the dry season (winter) is mild. Mean monthly maximum and minimum temperatures recorded at Musina (80 km east) are, respectively, 32°C and 20.3°C for January and 24.7°C and 7.2°C for July (Smit & Rethman 1998). The relatively flat study area is covered in deep (up to 1.2 m; weak orthic A horizon <10 cm deep), red sandy loam (6–12 percent clay) soils of the Hutton Ventersdorp 3200 or Hutton Stella 3100 forms (Botha 1994). The area supports Musina Mopane Bushveld (Rutherford *et al.* 2006) dominated by *Colophospermum mopane*, *Combretum apiculatum*, and *Grewia flava* commonly referred to as 'sandveld' (O'Connor 1992). Mopane is the most abundant species and is uniformly distributed throughout the vegetation type. The VLNR has existed since 1991 when livestock was replaced by low densities of wildlife including elephant (*Loxodonta africana*) (O'Connor 2015). Fire has not occurred since 1948 (MacGregor & O'Connor 2002).

Colophospermum mopane is a deciduous, broad-leaved legume occurring on fertile and dystrophic soils (O'Connor 1992, Rutherford *et al.* 2006). This species is not known to nodulate (Tuohy *et al.* 1991), but N-fixing actinomycetes may form an association (Burbano *et al.* 2015). It is usually monodominant thereby exerting a strong influence on biogeochemical cycling through its seasonal pattern of leaf flush, leaf fall, and decomposition (Dekker & Smit 1996). Mopane is the main host for the lepidopteran *Imbrasia belina* (Saturniidae) whose short-lived adult moths usually appear after the first rains and lay 30–300 eggs on leaves that hatch 10 days later (van Voorthuizen 1976, Dithlogo 1996). Larvae undergo five instar stages of development over six weeks during which each larva may consume >40 g of dry leaf material and gain 4000 times its original mass (Styles 1994, Akpulu *et al.* 2009) and then pupate in soil beneath a tree. Depending on rainfall, a second generation may emerge about March and follow the same developmental process. Pupae enter diapause during winter to emerge the following summer. The caterpillar stage can be classed as an outbreak owing to their occurrence in very large numbers over a short period of time (Dithlogo 1996), which enables their harvesting by rural communities (Akpulu *et al.* 2009). Mopane is also a staple dietary item for African elephants (Smallie & O'Connor 2000, Hrbar *et al.* 2009), but it is rarely used by other mammalian browsers.

Worm outbreaks occurred across a large region (>2000 km²) in December 2013 and April 2014. We selected a single study area of approximately 5 km² with uniform soils and vegetation

on the VLNR and Hackthorne to minimize the influence of soil variation on nutrient measures. We used the first outbreak to quantify both worm and tree populations and sample soil. We determined frass production and examined the influence of frass on soil using the second outbreak.

NUTRIENT INPUTS INTO THE SOIL.—To determine whether more nutrients are returned in frass vs. leaf litter, we studied (A) production of mopane leaf biomass; (B) nutrient content of green and senescent leaves; (C) frass production by mopane worms; and (D) nutrient content of frass. We assumed all available leaf biomass becomes litter based on observed complete leaf fall in these savannas (Dekker & Smit 1996).

We determined mopane leaf biomass per area during the first outbreak. We measured mopane density along five transects of 100×4 m located systematically across infested and unaffected savanna. For each tree encountered, we measured tree height, height of maximum canopy diameter, height of lowest leaf-bearing shoots and on two perpendicular axes; maximum canopy diameter and basal diameter. We measured each tree height, height of maximum canopy diameter, height of lowest leaf-bearing shoots, maximum canopy diameter on two perpendicular axes, and basal diameter on two perpendicular axes. We calculated canopy volume per tree from these measures using BECVOL (Smit 1996). We estimated mopane leaf biomass per tree using an allometric regression equation specific for mopane relating leaf dry mass (g) to canopy volume (cm^3): $\ln y = -4.165 + 0.711x$ (BECVOL; Smit 1996, Smit & Rethman 1998). We calculated average leaf biomass per unit area by summing per-tree leaf biomass for each transect. To determine nutrient content of mopane leaves, we collected and air-dried to constant weight well-illuminated green leaves on a tree (north side, outer canopy) and recently abscised (senescent) leaves beneath trees separately from each of ten widely separated trees not bearing mopane worms. We analyzed a 10 g subsample from each tree for K and P using the dry ashing method (Palic *et al.* 1998). We analyzed a 2 g subsample for total N using a combustion method with a Leco Nitrogen Analyser FP 528 (LECO Corporation, St. Joseph, Michigan, U.S.A.).

Nutrient resorption efficiency (NRE) is the proportion of nutrients returned to the tree prior to leaf senescence. We calculated the NREs for each of N, P, and K using the following formula (Aerts 1996):

$$\text{NRE} = \frac{(\text{Nutrient}_{\text{growing green}} - \text{Nutrient}_{\text{senescent}})}{\text{Nutrient}_{\text{growing green}}} \times 100$$

where NRE is a percent, and $\text{Nutrient}_{\text{growing green}}$ and $\text{Nutrient}_{\text{senescent}}$ are the respective nutrient concentrations of green and senescent leaves.

We determined potential frass production by estimating worm density in an outbreak area and daily production of frass per worm. We determined worm density during the first outbreak along ten 100×4 m transects (five transects the same as those used for estimating leaf biomass); two observers counted worms on each mopane tree. We estimated frass production per worm under controlled conditions using worms from the second

outbreak. On five separate trees in an enclosed area protected from large mammals, we placed 1×1 m sealed shade-netting bags (following the method of Ghazoul *et al.* 2006) filled with ten third instar worms each over a leafy branch (younger instars were not available). We inspected bags twice daily to ensure all worms were alive and to relocate bags and worms to a new branch when leaf material had fallen below 50 percent of the original amount to prevent frass production limitation from food availability. We collected and weighed dry weight frass from each bag every three days for 15 d at which time feeding activity ceased because worms were mature. We determined the nutrient content of frass by collecting approximately 20 g dry fresh frass from beneath the trees sampled for soil nutrients and analyzing N, P, and K contents in the same manner as leaves were analyzed.

SOIL NUTRIENT CONTENT.—After the first defoliation event, we collected soil samples from each of ten pairs of defoliated and non-defoliated trees of similar size within 25 m of one another. We used bulk density (BD) to convert nutrient data from a weight to an area basis (g/m^2) (Brady & Weil 2008). To determine BD, we extracted litter-free soil cores (2.8 cm radius, 5 cm depth), oven-dried them at 60°C to constant mass, and calculated the ratio between oven-dried soil mass (g) and field-moist soil volume (cm^3) (Boone *et al.* 1999). We collected composite soil samples for nutrient analyses from four subsamples at depths of 0–1 and 1–5 cm at each tree. We concentrated our sampling effort in the top 5 cm of soil as we did not expect worms to enrich deeper soil layers, and tree litter does not typically affect deeper soil layers in savannas (Coetsee *et al.* 2010). We air-dried samples for 72 h and sieved them through a 1-mm sieve. We determined total soil N by total combustion at Bemlab (Pty) Ltd., Somerset West, South Africa, using a Leco Nitrogen Analyser FP 528 (LECO Corporation). We determined P and K contents by extraction with one percent citric acid and analysis using a Thermo ICP iCAP 6000 Series Spectrometer (Thermo Fisher Scientific, Surrey, U.K.).

STATISTICAL ANALYSIS.—We compared differences in soil nutrient content between infested and uninfested trees using bulk density to calculate nutrient content on an area basis. To test whether shallow soil layers had higher nutrient content between trees with and without frass, we compared shallow samples (0–1 cm) and deeper soils (2–5 cm) and used a mixed effects model (lme4 package in R, Bates *et al.* 2015) including treatment (infestation), depth, and their interaction as fixed effects and soil pit as a random effect to account for potential non-independence between values in the same pit. We evaluated model fit by graphical residual analysis (*i.e.*, visual estimation of residuals to look for heteroscedasticity, evidence of curvature, temporal correlation, and non-normality of errors). We obtained *P*-values for fixed effects using the car package in R (Fox & Weisberg 2011).

RESULTS

SOIL NUTRIENT INPUTS.—The study area supported an average of 1150 mopane trees/ha (500–18,000 trees/ha) bearing an

estimated average of 1645.3 kg/ha (SE \pm 137.47 kg/ha) of dry leaf biomass. Within the outbreak area, on average, worms occurred in 44 (SE \pm 1.8) percent of trees. Each tree contained approximately 54 (SE \pm 7.35) worms, resulting in 28,945 (SE \pm 6807) worms/ha (Table 1). Fourth- and fifth instar worms produced 1.42 g of frass/day or 22.05 g for the period studied. Thus, 640 (SE \pm 150) kg/ha was the average amount of frass produced by the last two instar stages during the studied outbreak (Table 1).

Frass contained 1.5-, 13.6-, and 5.9-fold greater N, K, and P content than leaf litter, respectively. However, more total litter weight is returned to the soil than frass in this system. Using the average amount of frass produced per hectare (Table 1) and average infection rate (44 percent of trees), the total amount of nutrients returned in frass and litter would be 9.42 kg/ha N, 7.94 kg/ha K, and 2.24 kg/ha P. In the absence of an outbreak (all leaf material becomes litter), 16.40 kg/ha N, 1.50 kg/ha K, and 1.00 kg/ha P would be returned to the soil. At the landscape scale, nutrients added during the outbreak event at our study site were thus 0.88, 5.8, and 2.8 times the respective N, P, and K content compared to when no outbreak had taken place. Comparison of nutrient content between leaf litter, green, and senescing leaves indicates that, prior to leaf senescence, trees resorb 24 percent of N, 51 percent of K, and 56 percent of P (Table 2).

SOIL NUTRIENT CONCENTRATIONS.—Nutrient concentrations of soils (uncorrected for bulk density) are shown in Table 3 to allow comparison with published sources. Surface soils (0–1 cm depth) beneath uninfested trees contained higher N contents ($X^2 = 5.3$, $P < 0.0001$), P ($X^2 = 26.0$, $P < 0.0001$), and K ($X^2 = 13.9$, $P < 0.0001$) than underlying soil (1–5 cm depth). By contrast, soils beneath infested trees showed no difference in soil N content ($X^2 = 0.01$, $P > 0.05$) (Fig. 1A), higher K content up to 5 cm depth ($X^2 = 7.34$, $P < 0.007$) (Fig. 1B), and increased P at a depth of 0–1 cm but not of 1–5 cm ($X^2 = 4.37$, $P = 0.03$ for the main effect of treatment and $X^2 = 14.9$, $P = 0.0001$ for their interaction) (Fig. 1C).

DISCUSSION

At the landscape scale, N returned to soils was similar between an area where a moderate outbreak was taking place and where no outbreak was taking place (10% less in the outbreak region). We expected worms to increase N deposition through frass and cadavers, as previous work has shown that up to 70% of N and P flow through frass and insect remains during California oak moth *Phryganidia californica* outbreaks (Hollinger 1986). We also expected green leaf fragments (greenfall) from worm feeding with elevated N values due to lack of resorption during herbivory. Green leaf fragments shed during ‘messy’ feeding by lepidopteran larvae were found to contain twice the nutrient content of senescent leaves (Risley 1986, Risley & Crossley 1988). Regardless of the amounts of N returned to soil in litter and frass, soils had similar N values (for N, hypothesis 2 did not hold). Elsewhere, lepidopteran outbreaks have resulted in an increase in soil N content in wet environments (Fogal & Slansky 1985, Hollinger 1986, Chapman *et al.* 2003, Frost 2005, Uselman *et al.* 2011), but not in a dry environment, where frass stayed undecomposed on the soil surface (Hunter 2001).

We tentatively suggest two mechanisms to explain similar soil N between trees with and without frass deposition. First, similar soil N levels may be the result of differences in retention of frass and litter N. Lovett *et al.* (2002) compared the fate of labeled N added in gypsy moth frass vs. that added in litter in defoliated mixed oak forest. About 80 percent of ^{15}N was recovered when N was added in litter as most of this N remained in undecomposed leaf tissue. About 40 percent of ^{15}N was recovered when N was added in frass. Most of the frass N was recovered from soil organic matter after rapid immobilization by soil microbes. Second, there may not have been enough time between addition of frass and sampling to reflect changes in N. Herbivore-mediated changes in litter quality were slow to influence ecosystem N elsewhere (Belovsky & Slade 2000). Unfortunately, we have no values to compare foliar N in mopane trees leafing out after litterfall vs. those after being defoliated.

TABLE 1. Frass produced per ha computed by counting all trees and worms in ten 50 \times 4 m transects

Transect	Trees/ transect	Trees with worms (%)	Worms/ transect	Average number of worms per tree	Worms/ha	Frass dropped (kg)	Frass/ha (kg)
1	34	35	492	41	24,600	10.9	544
2	34	35	777	65	38,850	17.2	859
3	10	50	284	57	14,200	62.8	314
4	15	40	265	44	13,250	58.6	293
5	15	47	340	49	17,000	75.1	376
6	13	38	139	28	6,950	30.7	154
7	30	53	562	35	28,100	12.4	621
8	21	48	684	68	34,200	15.1	756
9	36	50	1113	62	55,650	24.6	1230
10	26	46	1133	94	56,650	25.0	1252
Mean	23	44	579	54	28,945	33.2	640

TABLE 2. Nutrient content of immature green mopane leaves, senescent leaves, dropped leaves, and mopane worm frass collected from beneath trees (mean \pm SE; N = 10 for each category)

	N (mg/g)	K (mg/g)	P (mg/g)	N:P
Green leaves	24.5 \pm 0.88	22.7 \pm 0.69	3.8 \pm 0.17	6.4 \pm 0.19
Senescing leaves	18.6 \pm 0.95	11.1 \pm 0.37	1.7 \pm 0.08	11.3 \pm 0.63
Leaf litter	9.97 \pm 0.68	0.9 \pm 0.17	0.6 \pm 0.07	16.6 \pm 1.15
Frass	14.8 \pm 0.91	12.4 \pm 0.97	3.50 \pm 0.48	4.2 \pm 0.65

Soil P content was in general higher at our site than recorded for a similar site in Zimbabwe (15.1–38.9 ppm vs. 7.8–15.8 ppm; Mlambo *et al.* 2005), while values for soil K content under grass (0.16 vs. 0.17–0.20 me/100 g) and under trees were comparable (0.3–0.47 vs. 0.19–0.63 me/100 g). Phosphorus affects shoot and root growth as well as seed development of plants (Hodges 2010). Soil P content under trees increased following defoliation by mopane worms in shallow soil but decreased in deeper soil. Frass added substantial amounts of P to soils and frass N:P ratios were low, indicating more P in relation to N was added in frass. P resorption was more efficient than N resorption resulting in less P being returned in leaf litter.

Mlambo and Nyathi (2008) showed that the total amount of N returned to soil in mopane leaf litter is about ten times that of P. Accordingly, recycling of P in frass should return much more P to the soil than when P is returned in litter. Elsewhere, lepidopteran outbreaks (Hollinger 1986) or insect herbivory (Seastedt & Crossley 1984, Schowalter *et al.* 2011) resulted in up to a doubling in the flow of phosphorus. The high P levels in frass were reflected only in the surface (0–1 cm) soil and not in deeper soil (1–5 cm). We propose that this may possibly be attributable to both low mobility of P (Hodges 2010) and its rapid and effective uptake by the vesicular–arbuscular mycorrhizal associations of mopane roots (Högberg 1986) facilitated by deposition of frass directly above the root zone.

The presence of mopane worms had a more pronounced effect on soil K than on N or P at our study site. Knowledge about the effect of insect herbivory on potassium is largely lacking. Seastedt *et al.* (1983) found increased leaching of K and lower foliar K contents when black locust (*Robinia pseudo-acacia*) and red maple (*Acer rubrum*) were defoliated with herbicide to mimic insect herbivory. In contrast, Nef (1988) found increases in foliar K of poplars (*Populus* spp.) in response to insect defoliation, and Grace (1986) found increased quantities of K in litter-fall when Pennsylvania oak forest was defoliated by gypsy moth (*Lymantria dispar*). Raffa *et al.* (1998) found no changes in foliar levels of red pine (*Pinus resinosa*) K in response to defoliation by sawfly (*Neodiprion lecontei*). K is also known to be very prone to

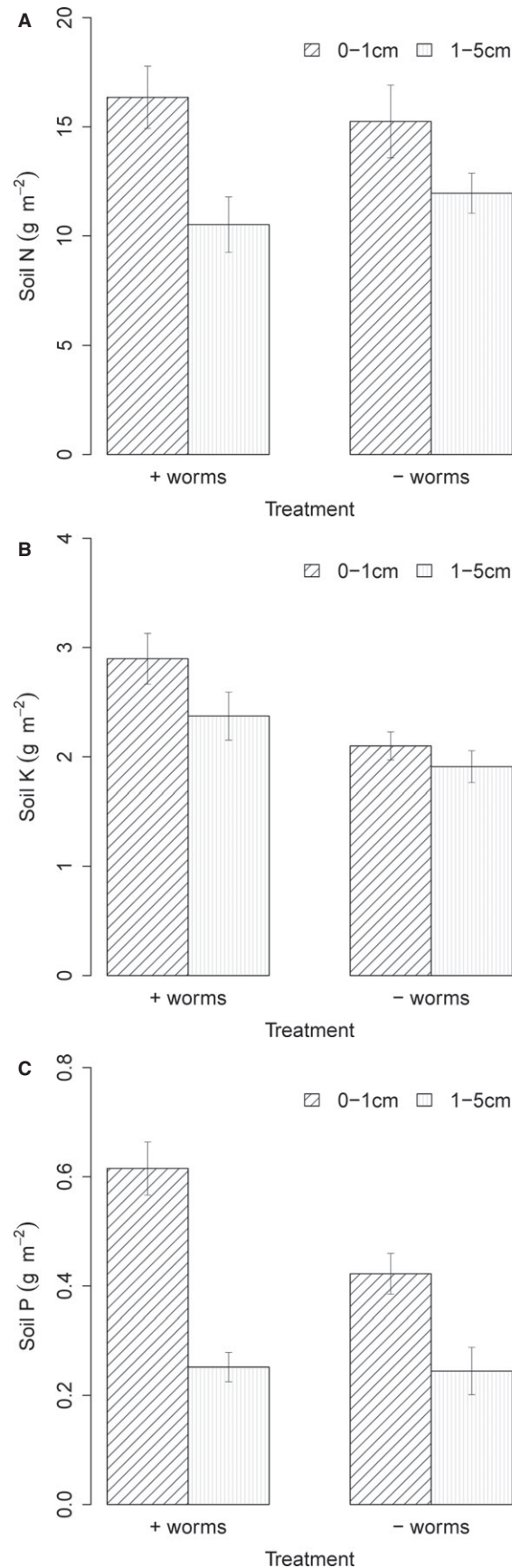


FIGURE 1. Influence of the presence vs. absence of worms on soil nutrient content by soil depth (0–1 vs. 1–5 cm) beneath mopane canopies for (A) nitrogen (N); (B) potassium (K); and (C) phosphorus (P). Bars represent S.E., N = 10 per category

TABLE 3. Nutrient content comparing soils beneath canopies either with or without worms present and away from canopies (mean \pm SE)

Treatment	Depth (cm)	Nitrogen (%)	Potassium (me/100 g)	Phosphorus (ppm)
Grass	0–1	0.05 \pm 0.005	0.15 \pm 0.03	30.5 \pm 15.5
	1–5	0.05 \pm 0.004	0.16 \pm 0.03	32.2 \pm 22.5
Tree + worms	0–1	0.10 \pm 0.008	0.47 \pm 0.03	38.9 \pm 3.18
	1–5	0.07 \pm 0.008	0.38 \pm 0.03	16.0 \pm 1.85
Tree – worms	0–1	0.09 \pm 0.008	0.33 \pm 0.02	25.8 \pm 2.33
	1–5	0.07 \pm 0.006	0.30 \pm 0.02	15.1 \pm 2.79

leaching from foliage; Seastedt and Crossley (1984) suggest that K losses by foliar leaching may increase 100% with a modest increase in herbivory and is most strongly affected by insect herbivory, while N and P are more influenced by detritivores. It is difficult to judge how these divergent effects on foliar and litter K translate into effects in soils, as we could find no previous work documenting insect defoliation effects on soil K.

The following nutrient flows were not taken into account: loss of worms to natural mortality especially by bird predation (Gaston *et al.* 1997), estimated as 4–95 percent in Botswana, depending on instar and site (Dithlogo 1996); nutrient addition from worm cadavers (Hunter 2001); green leaf fragments shed during ‘messy’ feeding containing twice the nutrient content of senescent leaves (Table 2), commonly observed for lepidopteran larvae (Risley 1986, Risley & Crossley 1988); and loss of leachate containing especially potassium from sheared green leaves (Seastedt *et al.* 1988). Elsewhere, insect cadavers decompose faster than litter and their nutrients increase decomposition rate of leaf litter (Schowalter & Crossley 1983, Seastedt & Crossley 1984). However, nutrient inputs from frass appear to be substantially greater than omitted inputs based on leaf biomass consumed (Dithlogo 1996).

CONCLUSION

Our results indicate that mopane worms may affect nutrient cycling, especially that of K and to a lesser extent of P. Premature litterfall due to herbivory should increase cycling of nutrients back to the soil as trees have time to resorb significant levels of K and P before natural senescence in the absence of herbivory. We propose that high litterfall nutrient K and P, together with more K and P in frass than senesced litter, account for higher soil K and P values when mopane worms are present. Accordingly, hypotheses 1 and 2 hold for K and P. Our study has generated the questions: What is the maximum amount of frass that can be produced by mopane worm? What are the effects of insect frass on inorganic N? What are the effects of defoliation on root exudation and C dynamics? How would greenfall affect decomposition of frass? How do differences in soil nutrient values translate in regrowth quality after defoliation? How does mopane manage to sustain high foliar N levels while resorbing low levels of N before senescence?

Mattson and Addy (1975) proposed that insect browsers are regulators of primary productivity ensuring consistent long-term production. Insect outbreaks are characteristic of systems where bottlenecks in the flow of nutrients are created through pronounced climatic variability, exacerbated by low soil fertility, in which an outbreak serves to recharge the cycling nutrient pool. We do not know how altered nutrient dynamics by mopane worm may affect long-term mopane productivity. However, Styles (1994) calculated that, during an outbreak of mopane worms, worms were capable of consuming ten times the amount of mopane tree leaf biomass over six weeks than 14 elephant bulls could consume over a year, producing 3.5 times more dung. Invertebrate herbivory is deserving of greater attention in African savannas—an emerging conclusion also for Neotropical savannas (Costa *et al.* 2008).

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p725tq4> (de Swardt *et al.* 2018) and archived with South African National Parks <http://data.knp.sanparks.org/sanparks/metacat/judithk.111607.1/sanparks>

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