Effects of *Acacia* invasion on leaf litter nutrient and soil properties of coastal Kerangas forests in Brunei Darussalam

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Abstract

Exotic *Acacia* were introduced to Brunei Darussalam in the 1990s for plantation forestry and land rehabilitation but are now regarded as invasive. We assessed the effects of *Acacia* on litter nutrient composition and soil physicochemical properties of Brunei's coastal Kerangas (heath) forests. Soil and litter samples were collected from ten 20 x 20 m plots in *Acacia*-invaded Kerangas forests (IKF) and ten uninvaded (UKF) plots. Soil samples were analyzed for pH, gravimetric water content and nutrient concentrations whereas litter samples were analyzed for total nutrients only. We recorded significantly higher concentrations of litter total N and P in the IKF than the UKF plots. In contrast, no significant differences were detected in soil properties, except for topsoil available P and subsoil exchangeable Ca which were both lower in the IKF plots. A significant positive correlation was detected between litter N and topsoil N in the IKF plots. We suggest that the fairly recent timescale of *Acacia* invasion (< 25 years) of the IKF sites resulted in the lack of significant increase of soil nutrients. In conclusion, *Acacia* invasion into Brunei's forests can potentially alter both leaf litter and soil physicochemical properties of Kerangas forests, in particular affecting nutrient availability. This alteration of ecosystem may further enhance the invasion success of *Acacia*, making restoration attempts more challenging.

Index Terms: alien invasive plants, heath forests, *Acacia mangium*, *Acacia auriculiformis*, nutrient cycling, ecosystem services

1. Introduction

Invasive plant species are a well-known threat to the biodiversity, services and functions of natural ecosystems.[1-3] The negative ecological effects of invasive plants are often irreversible and once established, invasives are typically difficult to control and eradicate.[4] One crucial factor for successful plant invasion is the ability of invasive plants to alter soil physicochemical properties and litter input, and modify decomposition rates and nutrient fluxes.[5-8] Such alterations often promote further spread of the invasive plant and competitive reduction of native species, resulting in changes in community structure over the long term,[9] and possibly even local extinction of native species.[2]

Among invasive plant species, *Acacia* species are widely regarded as one of the most successful alien species to have invaded many areas worldwide.[10-13] Although their centre of diversity and distribution is in Australia,[14,15] *Acacia* have been successfully planted in varying climatic conditions globally for commercial supply of tree products, as well as for land rehabilitation.[16,17] Similarly, *Acacia* were introduced to Brunei Darussalam, northwest Borneo in the 1990s to increase timber productivity and as roadside plantings,[18] but has since spread into disturbed forest habitats, in particular the coastal heath forests.[19-21]

As a nitrogen-fixing legume, *Acacia* are known to alter nutrient cycles[22,23] and modify litter and soil physicochemical properties.[24-26] Several studies in South African fynbos, Portugal coastal dunes, China and India have recorded three- to four-fold increases in litter mass in *Acacia*-invaded habitats compared to non-invaded ones,[25,27] and double the average N concentration in leaf litter and soil of invaded ecosystems.[11,28,29] The higher litter mass in *Acacia*-invaded habitats appear to enable more nutrients to be released during litter decomposition, leading to nutrient enrichment and eventually changing the nutrient quantity in invaded ecosystems.[24,27,30-32]

The detrimental effects of *Acacia* may be particularly significant in nutrient-poor tropical ecosystems, such as heath forests. Tropical heath (Kerangas) forests are rare in Brunei Darussalam[19,33] and their distribution throughout Borneo is now highly threatened by land conversion and habitat fragmentation.[33] With repeated fire incidences in coastal heath forests[21,33,34] coupled with the nitrogen-fixing capabilities of *Acacia*, there is increasing concern that *Acacia* invasion may modify the physicochemical properties of soils in invaded habitats.[35-37]

We investigated the effects of *Acacia* invasion on the soil physicochemical properties and litter nutrients in disturbed coastal Kerangas (heath) forests (KF) in Brunei Darussalam. Two research questions were formulated: (1) Does *Acacia* invasion alter the nutrient concentrations of leaf litter in coastal Kerangas forests? and (2) Does *Acacia* invasion alter soil physicochemical properties in coastal Kerangas forests?

2. Experimental approach

2.1 Study site

The study was conducted in coastal Kerangas forests surrounding Universiti Brunei Darussalam (4°58'30.37"N, 114°53'37.93"E), Brunei-Muara District. Ten plots (20 x 20 m) were established in *Acacia*-invaded Kerangas forests, located within a 200 ha area that was affected by forest fires in 2009 (henceforth referred to as invaded Kerangas Forest, IKF). Ten additional 20 x 20 m plots were established randomly in intact coastal, remnant Kerangas forests that have not experienced forest fires since 2009, referred to as uninvaded Kerangas forest (UKF) plots. Pairs of UKF plots were spaced along the coastline as a representative sample of the surrounding forest composition. Plots were set up at a minimum distance of 300 m apart from each other. UKF plots were located at distances of 300 m to 22 km from IKF plots, and reached 5 km inland (see ***Figure 1***). Within the 10 IKF plots, 1588 trees of ≥ 1 cm dbh were recorded, most of which were *Acacia* trees. In contrast, within the 10 UKF plots, 1286 trees were recorded, most of which were native heath tree species, in particular *Buchanania sessifolia*, and *Ixonathis reticulata* (RS Sukri, unpublished data).

2.2 Collection of litter and soil samples

Leaf litter and soil samples were collected from the IKF and UKF plots in early December 2013 to mid-February 2014, during the typical wet season for Brunei Darussalam.[38] Within each plot, leaf litter were collected using 0.25 m^2 quadrats at four points at the midpoint along the diagonals from the plot centre, and bulked to give one sample per plot. Similarly, soil samples at topsoil (0 – 15 cm) and subsoil (30 – 50 cm) depths were collected using a soil auger at four random sampling points per plot and bulked, giving a total of 20 topsoil samples and 20 subsoil samples.

2.3 Litter and soil analyses

Fresh soils were subsampled to determine soil pH and gravimetric water content (GWC).[39] Fresh soils were mixed with distilled water in a 2:1 water-to-soil ratio and pH measured using a benchtop pH meter (Hanna instruments Ltd, UK). For GWC, a 10g sample of fresh soil was oven-dried for 24 hours at 105^{o}C until a constant weight was obtained, weighed and GWC determined.[39] Soil organic matter was measured using a muffle furnace (Gallenkamp Size 2, Apeldoorn, Netherlands) set at 550°C for two hours.[39] The remaining fresh soil samples were air-dried at room temperature for two months. Air-dried samples were sieved through a 2.0 mm sieve, ground using a pestle and mortar and 200 g of the processed soil samples were further ground using a ball mill (Retch mixer mill mm 400, Germany) to obtain fine soil samples for nutrient and OM analyses. Three replicates from each soil depth (topsoil and subsoil) per plot were sub-sampled randomly for this purpose.

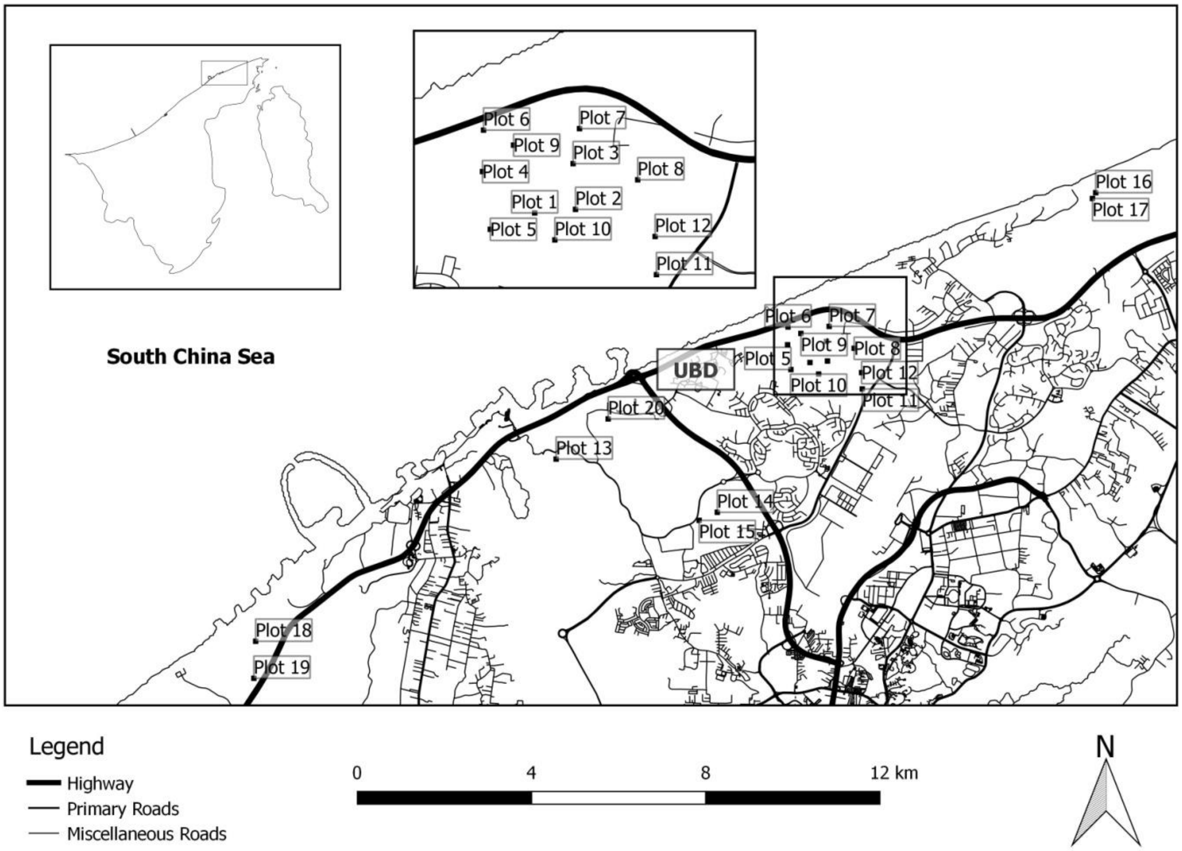

Figure 1. Map of study sites selected in Coastal Kerangas Forest, close to Universiti Brunei Darussalam (4°58'30.37"N, 114°53'37.93"E), Brunei Muara District. Ten 20 x 20 m plots were established within locations of disturbance caused by fire in 2009 (Plots 1- 10), and ten 20 x 20 m plots were established randomly within intact coastal Kerangas forests that have not experienced forest fires since 2009 (Plots 11-20).

Leaf litter samples collected were wiped clean using 70% ethanol to remove mineral soil and oven-dried at 60°C for 2-3 days to constant mass.[39] A total of 50 g litter samples per plot were subsampled and ground using a ball mill (Retch mixer mill mm 400, Germany) to fine powder. Three replicates of litter samples from each plot were used for nutrient analysis.

Ground soil samples were analyzed for the concentrations of total N, P, Mg, K, exchangeable Mg, Ca, K and available P, while ground leaf litter samples were analyzed for total N, P, K, Mg and Ca concentrations. Total N and P concentrations were determined using the Kjeldahl method by digesting each soil sample in concentrated sulphuric acid, and analyzed using a Flow Injector Analyser (FIAstar 5000, Hoganas, Sweden). For analysis of total Mg and K concentrations, air-dried soil samples were acid-digested using a microwave digestor (Multiwave 3000 Anton Paar, Austria) following Allen *et al*.[39] We attempted to analyse for total Ca in soil but the total Ca concentration levels were below the instrument's detection limit and thus were not included in the final data analysis. Concentrations of soil exchangeable Ca, Mg and K were extracted using 1 N neutral ammonium acetate.[40] Total and exchangeable Mg, Ca and K concentrations were measured using a Flame

Atomic Absorption Spectrophotometer (AAS; Thermo Scientific iCE 3300, Sydney, Australia). Soil available P concentrations were extracted using Bray's solution (0.03 N ammonium fluoride in 0.025 N HCl) and mixed with ascorbic acid and molybdate reagent.[39] The absorbance of each solution was read at 880 nm wavelength using UV-spectrophotometer (UV-1800, Shimadzu, Kyoto, Japan).

2.4 Statistical analysis

All statistical analyses were conducted using R 3.2.2 software.[41] Differences in litter nutrient properties and soil physicochemical properties between the IKF and UKF plots (n = 10 samples each) were determined using t-tests. Assumptions of normality and equality of variances were checked, and where necessary, response variables were $\log_{10}$ transformed. For the concentrations of Total K, the non-parametric Mann-Whitney U test was used. GWC and OM values were arc-sine transformed prior to the t-tests. Simple linear regressions were also used to assess the relationships of total N and total P in the topsoil with litter N and litter P, respectively.

3. Results

3.1 Differences in leaf litter properties between Acacia invaded Kerangas forest (IKF) plots and uninvaded Kerangas forest (UKF) plots.

Leaf litter from the IKF plots was significantly higher in total dry mass, as well as in total N and P concentrations, than litter from the UKF plots ($p < 0.05$; see ***Table 1***). In contrast, total Ca concentrations was significantly higher in litter from the UKF plots than the IKF plots ($p < 0.05$; see ***Table 1***), but total K and total Mg concentrations did not differ.

3.2 Differences in soil physicochemical properties between Acacia invaded Kerangas forest (IKF) plot and uninvaded Kerangas forest (UKF) plots

Available P concentrations in topsoil were significantly lower in the IKF plots than in the UKF plots ($p < 0.001$; see ***Table 1***). However, no significant differences in available P concentrations in subsoils were detected ($p > 0.05$) between the UKF and IKF plots. Concentrations of exchangeable Ca in subsoil were significantly higher in the UKF than the IKF plots ($p < 0.01$; see ***Table 1***), but topsoil exchangeable Ca concentrations were not significantly different ($p > 0.05$). There were no significant differences in the concentrations of other soil nutrients (Total N, P, Ca, Mg, K and exchangeable Mg and K) either in topsoil or subsoil samples from the UKF and IKF plots. Similarly, no significant differences were detected in GWC, OM content and pH for topsoil and subsoil in the IKF and UKF plots (see ***Table 1***).

3.3 Relationships between leaf litter nutrient (N and P) and topsoil nutrient properties

Litter N concentrations were highly significantly and positively related to topsoil N concentrations in the IKF plots ($R^2 = 0.41$ $p = 0.001^{**}$; see ***Figure 2***). However, there were no significant linear relationships between the litter N and topsoil N concentrations in the UKF plots, and no significant litter P-topsoil P relationships were detected in either the IKF or UKF plots ($p > 0.05$; see ***Figure 2***).

4. Discussion

4.1 The effects of Acacia invasion on leaf litter and soil physicochemical properties

Leaf litter dry mass at the invaded Kerangas forest (IKF) plots were significantly higher than at the uninvaded Kerangas forest (UKF) plots. This is consistent with the findings of similar studies conducted in South African fynbos, coastal dunes in Portugal, China and India where litter mass values were three to four times greater in *Acacia*-invaded areas compared to non-invaded areas.[25,27-29,42,43] Higher litter mass indicates higher litterfall production in the IKF plots, and this can potentially lead to nutrient enrichment as more nutrients may be released during litter decomposition.[24,27,30-32,44] Indeed, we recorded significantly higher litter N and P concentrations from the IKF plots (see ***Table 1***). Moreover, as a nitrogen fixing species, *Acacia* produce phyllodes with higher N content than native tropical trees.[45]

Table 1. Summary of litter properties and soil physicochemical properties for top soil (0-15cm depth) and subsoil (15-30cm) depth of Invaded Kerangas forest (IKF) and uninvaded Kerangas forest (UKF) in Brunei. Litter and soil nutrients are expressed as mg g^{-1}, Gravimetric water content (GWC) and Organic matter (OM) in %. Significant differences were detected at α = 0.05 level. (ns - not significant; *p < 0.05; **p < 0.01;***p < 0.001).

Component	Variables	Habitat		p value
		IKF	UKF	
Litter	Total N	10.07 ± 1.16	7.91 ± 0.74	*
	Total P	1.57 ± 0.08	1.16 ± 0.12	**
	Total K	0.58 ± 0.09	0.57 ± 0.08	ns
	Total Ca	1.76 ± 0.19	2.96 ± 0.44	**
	Total Mg	1.17 ± 0.18	1.13 ± 0.15	ns
Topsoil	Total N	0.87 ± 0.10	1.05 ± 0.13	ns
	Total P	0.03 ± 0.003	0.04 ± 0.01	ns
	Total K	1.11 ± 0.30	1.39 ± 0.42	ns
	Total Mg	0.13 ± 0.02	0.26 ± 0.09	ns
	Exchangeable K	0.07 ± 0.01	0.09 ± 0.02	ns
	Exchangeable Ca	0.02 ± 0.002	0.02 ± 0.003	ns
	Exchangeable Mg	0.02 ± 0.003	0.07 ± 0.04	ns
	Available P	0.18 ± 0.003	0.22 ± 0.005	**
	GWC	31.9 ± 2.81	35.49 ± 3.54	ns
	pH	4.59 ± 0.04	4.51 ± 0.06	ns
	OM	4.87 ± 0.55	5.38 ± 0.51	ns
Subsoil	Total N	0.27 ± 0.06	0.37 ± 0.11	ns
	Total P	0.04 ± 0.01	0.04 ± 0.01	ns
	Total K	1.23 ± 0.36	1.83 ± 0.51	ns
	Total Mg	0.14 ± 0.03	0.46 ± 0.23	ns
	Exchangeable K	0.05 ± 0.01	0.06 ± 0.02	ns
	Exchangeable Ca	0.02 ± 0.002	0.03 ± 0.002	**
	Exchangeable Mg	0.01 ± 0.002	0.08 ± 0.07	ns
	Available P	0.22 ± 0.004	0.23 ± 0.004	ns
	GWC	21.15 ± 3.69	20.38 ± 2.92	ns
	pH	4.87 ± 0.06	4.70 ± 0.10	ns
	OM	2.83 ± 0.26	2.95 ± 0.41	ns

Despite the higher N concentrations in the IKF leaf litter, we did not detect a significant increase in soil N concentrations in the IKF plots. This is contradictory to the results of other *Acacia* invasion studies that have all detected increased soil N concentrations under *Acacia* invasion.[25,27,42,46] In Brunei Darussalam, Matali and Metali[47] recorded significantly higher total N concentrations and lower GWC, total Ca, K and exchangeable Ca concentrations in *Acacia* plantation soils than in nearby intact Kerangas forest soils. In contrast, we did not detect significant changes in soil physicochemical properties in our IKF plots, except for lower available P and exchangeable Ca concentrations in the IKF plots.

We suggest that our findings may be partly a reflection of the invasion time scale in these coastal KF habitats. *Acacia* invasion may be regarded as a fairly recent event in Brunei's coastal KF landscape, as the start of invasion is thought to have occurred in the 1990s.[18] The effects of *Acacia* on soil nutrient properties may take time to be significantly effective and can become more profound after a longer period of invasion.[29,48] Concentrations of C and N in *Acacia longifolia*-invaded soils in Portuguese coastal dune systems were higher in areas long invaded (>20 years) than in recently invaded areas (>10 years).[29] Similarly, *Acacia saligna* invasion in South African fynbos appeared to alter N-cycling regimes in poor nutrient soils through long term invasion of well over three decades.[25]

Further, our IKF plots were established within coastal Kerangas habitats which experienced forest fires in 2009. As fires are known to cause volatilization of many soil nutrients including N,[29,49,50] there would have been considerable loss of nutrients during those fire events. Similarly, lower C and N pools were detected in a burned plot in a Mediterranean coastal dune ecosystem, reflecting nutrient loss from the initial fire event coupled with repeated fire occurrence.[29] In that dune ecosystem, both C and N pools have since increased as a result of *A. longifolia* invasion.[29] Thus, *Acacia* invading these burnt Kerangas habitats would need time to recover from the initial and substantial loss of soil nutrients. We suggest *Acacia* invasion into burnt Kerangas habitats[19] would eventually increase soil N concentrations in our IKF plots more than that in the UKF plots.

It is also possible that the lack of increased soil nutrients in the IKF plots may be partly due to the allelopathic ability of *Acacia*,[51,52] which is known to affect decomposition processes and slow down the release of nutrients from decomposed leaf litter into soils. The lack of a significant increase in soil N pools by litter of *Acacia dealbata* in the Iberian Peninsula, Portugal was attributed to the presence of secondary compounds in *A. dealbata* litter that inhibit microbial activity.[53] Moreover, rapid mobilization of nutrients to plant biomass and leaching of nutrients in sandy Kerangas habitats may also lead to further lowering of soil nutrient concentrations.[45]

It should be highlighted that the distance between the IKF and UKF plots differed, as the IKF plots were closer together compared to the UKF plots which were more spread out along the coastline. However, we suggest that any distance effects would be minimal as the whole of this coastal landscape has the same underlying sandy heath soils.[21]

4.2 The relationship between litter and soil nutrient concentrations

We detected a highly significant positive correlation between litter N and topsoil N concentrations in the IKF plots. This finding highlights the role of litter input in the availability of soil nutrients, as topsoil nutrients in particular are highly influenced by litter quality.[54,55] Our findings indicate the potential of *Acacia* invasion in altering soil properties such as total soil N particularly through the process of nutrient enrichment from their N-rich litter. Studies of other *Acacia* species in South Africa and China have recorded increased input of N into soil through higher litterfall rates, in combination with N rich litter from the invasive *Acacia* species.[25,27,46] Enrichment of N in soil may generate negative feedback that increases the competitive superiority of invasive species, promoting further invasion and subsequently resulting in changes to the community composition of invaded habitats.

5. Conclusion

In conclusion, our study recorded increased total N and P concentrations in the litter of *Acacia*-invaded coastal Kerangas forests, and a significant relationship between litter N and topsoil N concentrations in these invaded habitats. Our findings suggest that successful *Acacia* re-invasion of the IKF plots after fires and its competitive superiority can be attributed to present status of low topsoil N contents present in these Kerangas habitats due to the short invasion time period.

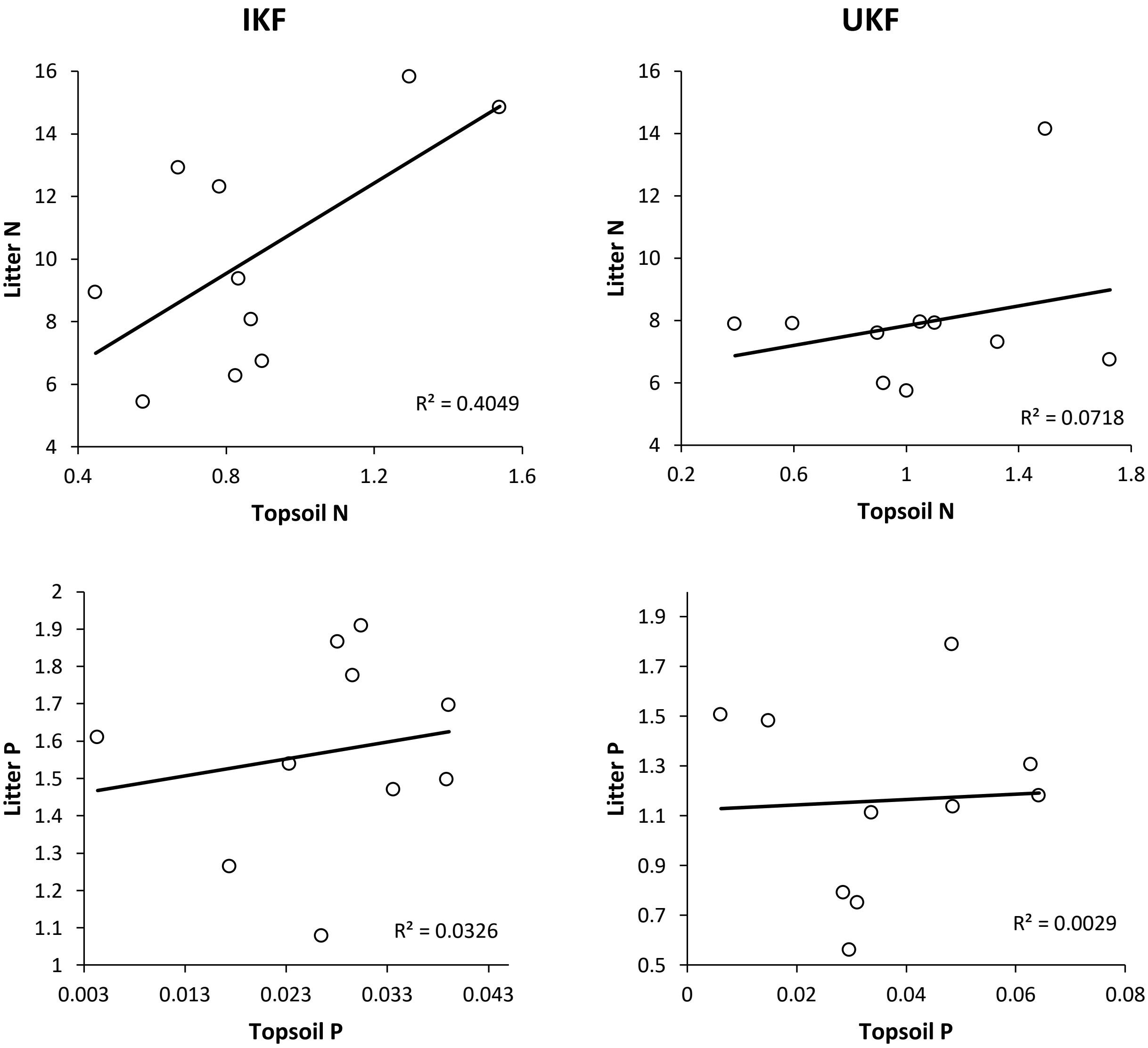

Figure 2. Simple linear regressions between litter nutrients (Tot N and Tot P) against topsoil nutrients (Tot N and Tot P) from the IKF (n = 10) and UKF (n = 10) plots.

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