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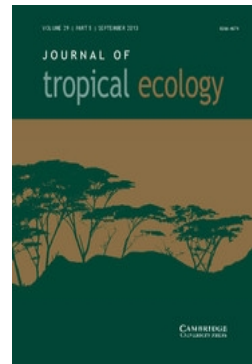
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SHORT COMMUNICATION

Termites facilitate root foraging by trees in a Bornean tropical forest

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Abstract: Plants can develop novel adaptations for nutrient acquisition in nutrient-limited ecosystems. These adaptations include colonization by roots of tree trunks and logs that can act as nutrient reservoirs. Termites may facilitate this root colonization by digging tunnels and accelerating decomposition in logs and tree trunks. We measured the frequency with which above-ground tree root colonization co-occurs with the presence of termites or their tunnels inside living trees above 20 cm dbh ($n = 178$) and dead tree trunks and logs at least 15 cm in diameter ($n = 146$) in a Bornean tropical forest. Roots above the soil surface co-occur with termite tunnels 39% more frequently than expected by chance in trunks of living trees and 17% more frequently than expected by chance in logs. By categorizing logs according to hardness through ease of penetration, we found that softer logs at a late stage of decay did not show co-occurrence of termite activity and roots to the same extent as harder logs. This suggests that trees forage where termites have removed physical barriers to colonization. In this fashion, termites may accelerate nutrient cycling in tropical rain forests.

Key Words: Borneo, Brunei, decomposition, facilitation, foraging, rain forest, roots, termites

Tropical rain forest (TRF) plants have evolved novel adaptations for above-ground nutrient acquisition in areas where soil nutrient supply cannot meet the demand of high plant productivity. For example, some trees use adventitious roots to capture nutrients from epiphytes and patches of detritus suspended in tree cavities (Nadkarni 1981). Pitcher plants *Nepenthes* spp. acquire nitrogen from captured insects and some epiphytes receive nutrient subsidies from arthropod excreta (Schulze *et al.* 1997, Thompson 1981). In addition, plants may acquire nutrients by colonizing living and dead plant matter (Benzing 2008).

Termites are one group of arthropods important to nutrient cycling. They may alter the spatial distribution of nutrients through excreta rich in nitrogen from their diet or their nitrogen-fixing symbiotic microbes (Brody *et al.* 2010). Termites modify their environment physically by constructing tunnels and digesting wood (Ferreira *et al.* 2011, Maser & Trappe 1984). Fallen trees with tunnels created by termites or other insects are softer, wetter and have higher microbial activity, nitrogen fixation rates,

and exchangeable and mineralizable nitrogen than those without insect tunnels (Maser & Trappe 1984).

Termites interact with plants in many ways, increasing soil fertility (Brouwer *et al.* 1992, Evans *et al.* 2011) and primary productivity (Arshad 1982). However, we know of no study showing that plant roots forage preferentially where termites are active. In a Bornean TRF, we tested whether above-ground roots are more likely to occur in logs (including standing dead trees) or living tree trunks when termites or their tunnels are present. We predicted trees would increase investment in roots where termites have been active.

We worked at the Kuala Belalong Field Studies Centre (KBFSC) in Ulu Temburong National Park, Brunei Darussalam (4°30'N 115°10'E). The park is dominated by primary lowland dipterocarp rain forest on steep sandstone ridges and shale valleys with orthic Acrisol soils (Ashton 1964, Sukri *et al.* 2012). Mean annual rainfall is *c.* 5080 mm without a distinct dry season (Osunkoya *et al.* 2007). Ulu Temburong exhibits high primary productivity and high nutrient leaching (Ashton 1964, Ross & Dykes 1996). Cranbrook & Edwards (1994) provide details of the biology and natural history of the area.

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Between 15 January 2013 and 21 January 2013 we surveyed all trees greater than 20 cm diameter at breast height (dbh) and all logs with a diameter greater than 15 cm that were within 2 m of either side of the Ashton Trail on the west bank of the Belalong River at KBFSC. We noted the presence or absence of termites, termite tunnels and tree roots growing within surveyed logs or trees. We surveyed each tree or log for 5 min.

For each tree we determined termite presence, the presence of invading roots on the trunk, termite tunnel presence and whether invading roots penetrated the trunk. We measured dbh at 1.3 m above the supporting buttresses. We confirmed tunnel presence by identifying tunnel openings on tree trunks and excavating them by removing bark for a length of 30 cm or until we discovered live insects. We confirmed termite presence only by discovery of live termites inside excavated tunnels. We assumed tunnels devoid of other wood-boring insects (e.g. carpenter ants or beetles) were termite-born. This is valid given the high abundance of termites within the soil macro-invertebrate fauna at KBFSC (1500 m⁻²; Jones 1996). We considered only tree roots, defined as extending from the ground and possessing root hairs, in order to exclude epiphytes and climbers. Above-ground tree roots are more indicative of termite-assisted foraging than the roots of epiphytes or climbers as the latter two are by definition found above ground. We categorized roots as either surface roots on the bark or penetrating roots under the bark or entering termite tunnels on the surface of the trunk. If more than one type of root was present, we only considered penetrating roots for our analyses.

For a haphazardly selected 50-cm-long section of each log, we determined the maximum diameter, termite presence, termite tunnel presence, root presence, log hardness and shortest distance to the soil surface. We defined termite tunnels as for tree sampling, although tunnels were excavated to different depths dependent on substrate hardness. We categorized roots as either surface roots that were on the bark surface, or penetrating roots under the bark, in excavated tunnels, or inside soft decayed material. We classified log hardness as hard, medium, or soft based on the average depth of penetration for ten repeated strikes with a 10-cm steel spade around the sampled area, with an average penetration of less than 1 cm classified as hard, up to half of the spade length as medium, and more than half of the spade length as soft. We assigned a negative distance to the soil surface for partially buried logs and a distance of zero for logs touching the surface.

We tested for associations between the presence and absence of roots with both termites and their tunnels in both logs and trees by testing the frequency of their co-occurrence using chi-square goodness-of-fit tests. Because larger trees and logs have a larger surface area, the probability of co-occurrence between any two features

(including roots and termites, or roots and tunnels) on larger trees and logs is increased. Therefore, we performed additional chi-square tests using only trees and logs below the median dbh and diameter, respectively, to confirm that any co-occurrence between roots and termites was not driven solely by this sampling effect. We also compared the prevalence of roots, termites and tunnels in different hardness categories using a three-sample test for equality of proportions. We used R (version 2.15.2) for all statistical tests.

Roots beneath the bark surface of living trees co-occur with tunnels 39% more often than expected at random ($\chi^2_3 = 26.2$, $P < 0.001$). Of the 107 trees surveyed, 46 exhibited both termite tunnels and roots, 33 exhibited neither, while only 21 and seven trees exhibited only tunnels or only penetrating roots. The frequency of co-occurrence is 80% greater than expected when analysing only trees below the median dbh (14 trees exhibited both tunnels and penetrating roots, 21 exhibited neither, seven exhibited only tunnels and four exhibited only penetrating roots), indicating that this co-occurrence is not driven by a sampling effect of larger trees possessing a larger sampling area (trees smaller than median dbh: $\chi^2_3 = 12.3$, $P < 0.01$). Although termites and roots co-occurred 46% more often than expected at random, the relationship between these two attributes was not significant ($\chi^2_3 = 6.27$, $P = 0.10$).

The association between the presence of tunnels and roots beneath the bark surface of logs was also significant, with co-occurrence in 89 of 146 logs surveyed, or 17% more often than expected ($\chi^2_3 = 25.3$, $P < 0.001$). The relationship remains significant when considering only logs at or below ground level ($\chi^2_3 = 20.1$, $P < 0.001$) or above ground ($\chi^2_3 = 8.79$, $P < 0.05$). Termite and root presence were also significantly associated in logs, co-occurring in 64 of 146 logs surveyed, or 16% more often than expected ($\chi^2_3 = 7.82$, $P < 0.05$). Notably, this relationship remains significant in logs at or below ground level ($\chi^2_3 = 8.26$, $P < 0.05$), but not in logs where the sampling area was not in contact with the soil ($\chi^2_3 = 4.06$, $P = 0.26$), supporting the hypothesis that logs in contact with the soil are more accessible to roots.

We found a significant relationship between tunnels and roots for hard logs (24% more often than expected, $\chi^2_3 = 15.0$, $P < 0.005$) and medium logs (17% more often than expected, $\chi^2_3 = 9.1$, $P < 0.05$), but not for soft logs ($\chi^2_3 = 1.4$, $P = 0.70$). Softer logs are likely more easily colonized by roots even in the absence of tunnel-boring insects. This is also supported by the increase in root presence with log softness, from 60% presence in hard logs to 85% in soft logs ($\chi^2_2 = 6.97$, $P < 0.05$), despite the proportion of logs with tunnels remaining unchanged across hardness categories ($\chi^2_2 = 0.0042$, $P = 0.998$). Finally, the proportion of soft logs with roots was significantly higher than the proportion of soft logs

with tunnels (85% of soft logs exhibited roots, while only 74% exhibited tunnels).

We suggest that termites facilitate root foraging in both logs and tree trunks, catalysing nutrient cycling at KBFSC by allowing roots to access nutrients in hard substrates that would otherwise be inaccessible until further decay. We believe the mechanism underlying this facilitation is two-fold: first, termites enrich the substrates they inhabit through their excreta and nitrogen-fixing symbionts (Yamada *et al.* 2006), and second, termites remove physical barriers to root invasion in hard substrates by tunnelling. There is also interaction between these two mechanisms, as tunnels allow water, microbes and fungi to access the interior of logs, resulting in yet higher nutrient concentration (Maser & Trappe 1984).

We failed to find a significant co-occurrence of termites with penetrating roots in tree trunks, although we expect this is due to the small number of live trees observed with termites. However, the association between tunnel and root presence in trees is representative of the effect of termites on root invasion. We also failed to find a significant co-occurrence between termites and roots in logs whose sampling area was detached from the soil. Detachment from soil likely presents a barrier to root entry into logs, even if termite activity makes the interior of such logs available. These exceptions do not disprove our general hypothesis that termites facilitate root foraging.

Substantial root colonization can occur in softer logs even in the absence of termite tunnels due to both the weaker physical barrier to invasion, and because of the accumulation of nutrients with time. Similarly, rotting logs and tree trunks may attract roots by serving as local water reservoirs (Amaranthus *et al.* 1989). Our results show that the facilitation provided by termite tunnels to roots is less important in softer substrates. Nevertheless, termites can also accelerate these broader mechanisms of substrate enrichment (Maser & Trappe 1984). We also cannot exclude the possibility that the stress of termite attack could reduce the chemical defences of living trees against root invasion. However, the association between root and termite presence in decaying logs indicates that termite tunnels have an effect independent of tree defences.

We suggest two avenues for future studies of termite–root interactions. First, nutrient concentrations in logs and trees with and without termites should be quantified to test whether termite excreta enriches substrates with nitrogen from their diet or their nitrogen-fixing symbiotic microbes (Brody *et al.* 2010). Second, longitudinal comparisons of root growth on artificially fertilized versus unfertilized logs and trees would provide a mechanistic approach to studying the observed root–termite association, and allow determination of whether termites primarily encourage root growth by physically or chemically altering the substrates they invade.

We have demonstrated a significant association between root invasion and both termites and their tunnels in trees and logs. We believe this is a heretofore undescribed adaptation by plants to low nutrient conditions of some TRF soils. By growing roots directly into logs and tree bark, plants can acquire nutrients before they are returned to soil, reducing the chance of nutrient leaching from the system (Nadkarni 1981). At the ecosystem scale, we predict that termite activity accelerates nutrient cycling in some TRFs, reducing nutrient leaching.

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LITERATURE CITED

- AMARANTHUS, M., PARRISH, D. & PERRY, D. 1989. Decaying logs as moisture reservoirs after drought and wildfire. Pp. 191–194 in Alexander, E. (ed.). *Stewardship of soil, air, and water resources, proceedings of Watershed 89*. United States Forest Service Publication R10-MB-77, United States Forest Service, Alaska Region, Juneau.
- ARSHAD, M. 1982. Influence of the termite *Macrotermes michaelseni* (Sjöst) on soil fertility and vegetation in a semi-arid savannah ecosystem. *Agro-Ecosystems* 8:47–58.
- ASHTON, P. S. 1964. *Ecological studies in the mixed dipterocarp forests of Brunei State*. Clarendon Press, Oxford. 74 pp.
- BENZING, D. H. 2008. *Vascular epiphytes: general biology and related biota*. Cambridge University Press, Cambridge. 359 pp.
- BRODY, A. K., PALMER, T. M., FOX-DOBBS, K. & DOAK, D. F. 2010. Termites, vertebrate herbivores, and the fruiting success of *Acacia drepanolobium*. *Ecology* 91:399–407.
- BROUWER, J., GEIGER, S. & VANDENBELDT, R. 1992. Variability in the growth of *Faidherbia albida*: a termite connection. Pp. 131–138 in Vandenbeldt, R. J. (ed.). *Faidherbia albida in the West African Semi-arid Tropics*. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India; and International Centre for Research in Agroforestry, Nairobi, Kenya.
- CRANBROOK, EARL OF & EDWARDS, D. S. 1994. *Belalong, a tropical rainforest*. Sun Tree Publishing, Singapore. 389 pp.
- EVANS, T. A., DAWES, T. Z., WARD, P. R. & LO, N. 2011. Ants and termites increase crop yield in a dry climate. *Nature Communications* 2:262.
- FERREIRA, E. V. D., MARTINS, V., INDA, A. V., GIASSON, E. & DO NASCIMENTO, P. C. 2011. Termites action on the soil. *Ciencia Rural* 41:804–811.

- JONES, D. T. 1996. A quantitative survey of the termite assemblage and its consumption of food in lowland mixed dipterocarp forest of Brunei Darussalam. *Monographiae Biologicae* 74:297–306.
- MASER, C. & TRAPPE, J. M. 1984. *The seen and unseen world of the fallen tree*. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-164. 56 pp.
- NADKARNI, N. M. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. *Science* 214:1023.
- OSUNKOYA, O. O., OMAR-ALI, K., AMIT, N., DAYAN, J., DAUD, D. S. & SHENG, T. K. 2007. Comparative height–crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. *American Journal of Botany* 94:1951–1962.
- ROSS, S. & DYKES, A. 1996. Soil conditions, erosion and nutrient loss on steep slopes under mixed dipterocarp forest in Brunei Darussalam. *Monographiae Biologicae* 74:259–270.
- SCHULZE, W., SCHULZE, E., PATE, J. & GILLISON, A. 1997. The nitrogen supply from soils and insects during growth of the pitcher plants *Nepenthes mirabilis*, *Cephalotus follicularis* and *Darlingtonia californica*. *Oecologia* 112:464–471.
- SUKRI, R. S., WAHAB, R. A., SALIM, K. A. & BURSLEM, D. F. 2012. Habitat associations and community structure of dipterocarps in response to environment and soil conditions in Brunei Darussalam, northwest Borneo. *Biotropica* 44:595–605.
- THOMPSON, J. N. 1981. Reversed animal–plant interactions: the evolution of insectivorous and ant-fed plants. *Biological Journal of the Linnean Society* 16:147–155.
- YAMADA, A., INOUE, T., WIWATWITAYA, D., OHKUMA, M., KUDO, T. & SUGIMOTO, A. 2006. Nitrogen fixation by termites in tropical forests, Thailand. *Ecosystems* 9:75–83.