NOTE

DROUGHT - INDUCED MORTALITY IN TROPICAL HEATH FOREST

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Tropical heath forest is strikingly different in flora, structure, and physiognomy from lowland evergreen rain forest. It develops on coarsely textured, podzolized sands throughout the humid tropics, although it is rare in Africa. In Borneo it is called kerangas, an Iban term for land which will not grow rice (Whitmore 1984).

A major unresolved question in tropical ecology is whether the distinctive features of heath vegetation are due mainly to nutrient deficiency or the periodic water shortages which characterize sandy soils (Whitmore 1989). Some investigators emphasize the role of water stress (Brunig 1971, Kruger 1979), others the importance of nutrient limitation (Loveless 1962, Beadle 1966, Specht 1979), while still others suspect an interaction between water regime and nutrient availability (Medina & Cuevas 1989). Waterlogging, hydrogen ions and phenolic acids may also have toxic or inhibitory effects on heath vegetation (Armstrong 1981, Proctor et al. 1983).

A severe drought provided an opportunity to compare the effects of water stress on tree survival in dipterocarp and heath forests in Brunei. In 1992 the sliding thirty-day total of rainfall at Sungai Liang (4° 40' 37"N, 144° 29' 21" E) remained less than 100 mm from late January through mid-April (83 days) except for a four-day period in February (unpublished records of the Meteorological Service, Department of Civil Aviation of Brunei Darussalam). By late March the crowns of some saplings and understory trees in heath forest at Badas F.R. (Forest Reserve, 14 km from Sungai Liang) were devoid of living leaves, whereas moderate wilting of seedlings and herbs was the worst symptom observed in dipterocarp forest at Andulau F. R. (3 km from Sungai Liang). In late May it was clear that the desiccated trees at Badas had died and we decided to count dead stems in dipterocarp and heath forest.

Four permanent 1-ha plots in these two forest formations have been established by the Biology Department of Universiti Brunei Darussalam at Andulau F. R. (Compartment 7), Bukit Sawat Research Forest (Gazette Plan 793, Lot 5651),

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Badas F. R. (Gazette Plan 302, Lot 3661), and Ladan Hills F. R. (Compartment 57). Six $10 \times 10 m$ subquadrats were selected by stratified random sampling to ensure representative areal coverage in each plot. In these subquadrats all free-standing trees and palms at least 1 cm in diameter at breast height (DBH at 1.3 m) were enumerated by diameter class, and stems with dry inner bark were scored as dead. The censuses were done on 11 July 1992 at Andulau and Badas and on 15 July at Ladan Hills and Bukit Sawat.

As expected (Whitmore 1984), the densities of trees <5 cm DBH was 40-100% greater in heath than in dipterocarp forest, but larger trees occurred at similar densities in our samples of these two forest formations (Table 1). Both relatively and absolutely, the number of dead trees of 1-5 cm DBH was substantially greater in heath forest at Badas than at the other three sites. Similarly high mortality was experienced by *Pinanga*, the only palm in our Badas samples.

Interpretation of these results is complicated by the absence of comparable data prior to the incidence of drought. The sudden onset of mortality with no

Table 1. Total free-standing trees and palms and the percentage dead (mean \pm s.e.m.) in six 10 \times 10 m subquadrats at four sites

	Dipterocarp forest						Heath forest					
	Andulau			Ladan Hills			Badas			Bukit Sawat		
Trees, >1 to <5 cm												
Total	50.3	±	9.4	46.2	±	3.8	95.8	±	7.7	69.8	±	17.4
% dead	0.4	±	0.3	0.3	±	0.3	11.3	±	1.5	0.0	±	0.0
Trees, ≥5 to <10 cm							٠					_
Total	11.2	±	1.4	8.0	±	1.2	11.8	±	0.7	11.2	±	1.3
% dead `	3.3	±	3.3	2.1	±	2.1	1.1	±	1.1	1.9	±	1.9
Trees, ≥10 cm												
Total	5.2	±	1.1	5.3	±	1.0	5.7	±	0.7	7.7	±	1.0
% dead	0.0			0.0			0.0			0.0		
Palms, ≥1 to <5 cm						•			•			
Total	0.3	±	0.2	0.0			8.0	±	4.2	0.0		
% dead	0.0		,		_		24.2	±	11.7		-	

Note: Size, classes are based on DBH. Mortality was averaged for occupied subquadrats only.

evident disease symptoms and the survival of all *Pinanga* in the moistest subquadrat (as indicated by topography and vegetation) strongly implicate drought as the cause of tree death at Badas. One might argue that dead stems would persist longer in heath forest because their putatively greater content of secondary chemicals would resist decomposition (cf. Janzen 1974), but this is countered by the absence of dead stems at Bukit Sawat.

Our finding that drought-induced mortality was concentrated in the smaller size classes at Badas contrasts with that of Leighton & Wirawan (1986) for dipterocarp forest in Kalimantan. It is, however, consistent with a suggestion from Newbery's (1991) ordination analysis of heath forests that canopy trees experience different regimes of water and nutrient stress than smaller tree species which may be more shallow rooted.

In the absence of soil moisture measurements, we can only speculate why mortality of small trees in heath forest at Bukit Sawat was not high like at Badas. The topography at Bukit Sawat is more undulating than the mostly flat terrain at Badas, but dead stems were not obviously more common on the higher areas at Bukit Sawat. Possibly some subterranean feature improves the water supply at Bukit Sawat during drought. The forest at Bukit Sawat was very selectively logged in the late 1960s, but its present structure resembles that at Badas except for the absence of large emergent Agathis borneensis. Perhaps transpiration from the overstory at Bukit Sawat was therefore lower and moisture stress for understory plants during the drought was reduced compared with Badas. Unfortunately, this idea could not be tested because areas outside the plot at Badas with an overstory structure like that at Bukit Sawat were destroyed by fire during the drought (Becker & Wong 1992). Our observations are important in suggesting that there is biologically significant intersite variation in the moisture regimes of tropical heath forest occurring on similar parent material (raised Pleistocene terraces).

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