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The Ecology of Oncosperma horridum on Siberut Island, Indonesia

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Oncosperma horridum (Griff.) Scheff. is one of five species in the genus *Oncosperma*, which ranges from Ceylon to the Philippines and belongs to the large and diverse subfamily Arecoideae. The genus appears not to have a center of radiation, although the perhumid zones of Malesia possibly support a greater number of species than have been described. Two species, *O. horridum* and *O. tigillarium* (Jack) Ridl., occur in Malesia, with *O. fasciculatum* Thw. recorded from Ceylon and *O. gracilipes* Becc. and *O. platyphyllum* Becc. from the Philippines.

Members of the genus *Oncosperma* are usually tall, clustering, spiny palms with distinct crown shafts and pinnately divided leaves. *O. horridum* may reach 20 m or more in height and clusters may have up to 15 major stems. It is a widespread species, being the single representative of the genus in inland lowland and sub-montane rainforests of the Malay Peninsula, Sumatra, Borneo and the Philippines. It is not found in Java or the Lesser Sunda Islands. Usually *O. horridum* is confined to forests below 450 m, but occasionally may be seen at 900 m (Whitmore 1973).

This study was undertaken on the island of Siberut, the largest of the Mentawai chain which lie 140 km off the west coast of Sumatra. *O. horridum* (local name *ari ribuk*) is one of the most conspicuous forest components of many parts of the island, and fulfills many basic needs of the indigenous people (House 1983). The species thrives at low elevations and in the relatively aseasonal climate of Siberut. *O. tigillarium* replaces *O. horridum* near the coast on sandy beach-derived deposits and along the tidal stretches of large rivers.

This paper presents preliminary observations on apparently edaphically determined micro-habitat preferences of *O. horridum* on Siberut.

The Study Site

The study site is located in more or less undisturbed lowland tropical rainforest (sensu Whitmore 1975) in central Siberut, in the upper reaches of the Saibi River. Climatic conditions are truly tropical, with more than 4,000 mm of rain a year (>100 mm in every month) and mean monthly maximum daily temperature of 30° C. The forest at the study site contains four floristically and structurally distinct sub-types; *O. horridum* was common in three, namely Mixed forest (no dominant tree family), Dipterocarp forest (Dipterocarpaceae dominant) and Myrtaceous forest (Myrtaceae dominant). *O. horridum* was very infrequent in permanently inundated inland swamp forests. Mixed forest is found on flat ground and low hills and has a high species diversity. Individual tree species are locally common but this represents patchy, contagious tree species distribution rather than seral or climax dominance. Myristicaceae, Euphorbiaceae, Dipterocarpaceae, Lauraceae and Ebenaceae are the commonest tree families. Dipterocarp forest, occurring on higher hills and clay ridges away from centers of habitation is somewhat poorer in tree species, with a distinct dominance of species of Dipterocarpaceae, notably of *Dipterocarpus* and *Shorea.* Flacourtiaceae, Myristicaceae and Sapotaceae may be locally co-dominant. Myrtaceous forest is found on steep sided sandstone ridges and is dominated by *Tristania whiteana* Griff. Other species from both Mixed and Dipterocarp forests are present but in low numbers. Myrtaceous forest has the lowest species diversity of the three sub-types.

Parent rock materials throughout the study site are sedimentary series of Tertiary or pre-Tertiary origin, being micaceous sandstones and shales. Derived soils are deeply weathered and form two types: heavy, sticky clays and porous sandy loams. The high rainfall and erodibility of the soils have resulted in a rugged, dissected landscape with steep sided gullies and little flat ground. Soil slip and small landslides are common in wet weather. Inundation of low-lying areas is frequent during the two equinoctial wet seasons of April–May and September–January.

Procedure

The data presented here have been taken from 8 study plots, five located in Mixed forest, two in Dipterocarp forest, and one in Myrtaceous forest. Plot sizes ranged from 0.16 to 0.24 ha (mean plot size 0.21 ha). Discrete clumps of *O. horridum* were counted and the size of each clump in terms of the number of stems with conspicuous leaf scars and developed crown shafts were noted. The number of single, juvenile stems not associated with large clumps was also counted. Juvenile stems close to a clump (i.e. at distances equal to or less than that of the radius of the clump) were counted as being of that clump and likely to be suckers rather than seedlings.

Soils were sampled from each plot, the site of each pit chosen randomly. Samples taken from two or three depths (range 2–75 cm) were analyzed separately to give surface and mean profile values. Chemical and physical analyses were performed on air-dried samples. Exchangeable bases were extracted with neutral normal NH_4OAc, and cation exchange capacity determined by replacing exchanged ammonium salts with normal KCl at pH 2.5. pH was measured on a 1:5 soil water mix. Total N was determined by the Kjeldahl method, and loss on ignition measured by weight loss after ignition at 475° C for 8 h. The physical structure of the soils was determined by removal of clay using ultrasonics and sedimentation, and sand content measured by sieving and washing.

Other environmental plot characteristics recorded were the mean relative crown density of trees, assessed subjectively on two 3-point scales to accommodate size and compactness/openness of individual tree crowns, the density of trees >50 cm gbh, and the total basal area of trees >50 cm gbh.

Results

The densities of mature clumps and single juveniles, and the mean clump size and range of clump sizes are shown in Table 1. Table 2 shows the results of the chemical and physical soil analyses, and the tree density, crown density and basal area of plot trees are shown in Table 3. The effects of the measured edaphic and environmental parameters on the density and size of *O. horridum* have been assessed using simple correlation statistics (Table 4). The sample from which the correlations have been calculated is small ($n = 7$), and so the strict statistical significance of the values of r are limited. However, the results in Table 4 do show definite responses by *O. horridum* to small variations in habitat conditions.

Several interrelated soil factors, combined, appear to be responsible for determining palm densities; *O. horridum* shows a preference for coarse textured, well drained soils of low fertility (plots M2, M5, D2 and MY), behavior which parallels that

Table 1. Densities and sizes of O. horridum in study plots.

	M1 Flat	M2 Gentle	M4 Flat	M5 Steep	D1 Gentle	D2 Gentle	MY Steep
No. clumps ha^{-1}	13	16	6	19	10	22	15
Mean no. stems $clump^{-1}$	3.8	4.4	4.8	4.3	3.9	2.3	2.1
Range stems $clump^{-1}$	1–9	1–10	1–8	1–10	1–10	1–5	1–5
No. juveniles ha^{-1}	—	21.5	—	—	8.2	6.2	9.2

M = Mixed forest; D = Dipterocarp forest; MY = Myrtaceous forest.

of *O. tigillarium* near the coast, and avoids poorly drained clayey substrates with subsurface mineral flushing and possible occasional flooding (plots M1, M4). The influence of slope on soil texture and water holding capacity determines, in part, the levels of available mineral nutrients: soils on slopes tend to be coarser and better drained than those on flat ground where run-off has created accumulations of small soil particles. The mean palm density on flat ground is 9.5 clumps ha^{-1}; that on slopes is 16.4 clumps ha^{-1}.

Of the three major soil minerals measured, Mg^{++} appears to be most influential, high surface levels of which correspond to low densities. Similarly, overall soil fertility is negatively correlated with palm density. Surface mineral levels appear to be more influential than the general nutrient status of the whole soil profile; most *O. horridum* feeding roots are probably close to the soil surface, in common with many rainforest plants.

Trends in the size of individual plants are less significantly correlated with edaphic parameters, and because of a weak negative correlation between palm density and size ($r = -0.53$), most of the trends are opposite to those for palm density. High soil mineral status thus allows for fewer but larger plants.

Table 2. Results of chemical and physical analyses of study plot soils.

Plot		pH	% Moist	Bulk Density g ml^{-1}	% l.o.i.	Meq 100 g^{-1} Exch Ca^{++}	Exch Mg^{++}	Exch K^{+}	TEB	CEC	% N	% Fine Sand	% Silt	% Clay
M1	surface	4.7	4.6	0.87	5.7	0.7	1.1	0.3	2.1	21.6	0.2	22	32	46
	mean	5.0	6.6	0.96	4.9	0.6	1.3	0.4	2.3	27.4	0.1			
M2	surface	4.2	4.5	0.67	22.5	0.1	0.7	0.5	1.3	35.3	0.7	58	21	19
	mean	4.5	3.6	0.75	14.8	0.1	0.3	0.3	0.7	22.3	0.5			
M4	surface	4.8	10.0	0.86	4.8	5.6	2.7	0.4	8.7	41.8	0.2	9	31	60
	mean	4.9	10.5	0.90	4.3	4.8	2.7	0.5	8.0	42.2	0.2			
M5	surface	4.4	3.4	0.73	16.7	0.5	0.7	0.5	1.7	23.7	0.6	52	27	18
	mean	4.6	2.2	0.88	6.9	0.2	0.3	0.2	0.7	11.4	0.3			
D1	surface	4.8	7.3	0.66	23.5	4.4	2.5	0.7	7.6	39.8	0.9	16	35	48
	mean	4.8	7.6	0.83	10.5	1.5	1.5	0.4	3.4	37.3	0.4			
D2	surface	4.9	5.3	0.70	18.9	0.1	0.4	0.4	0.9	16.7	0.5	8	21	71
	mean	4.8	4.7	0.80	11.7	0.1	0.4	0.3	0.8	13.6	0.3			
MY	surface	4.5	2.9	0.82	12.2	0.3	0.7	0.4	1.4	20.2	0.4	63	19	15
	mean	4.8	2.1	0.94	7.6	0.1	0.4	0.2	0.7	11.9	0.2			

N.B. Na^{+} levels were too low to be of significance.

Table 3. Environmental parameters of the study plots.

Plot	Tree Density (Trees ha^{-1})	Mean Crown Density	Basal Area (m^2 ha^{-1})
M1	208	0.75	31.22
M2	363	1.40	41.03
M4	156	0.63	21.25
M5	276	1.03	30.52
D1	156	0.65	26.97
D2	333	1.33	48.43
MY	467	2.09	36.19

The independent variables of tree density, crown density and tree basal area do not exert significant influences on palm density or size. At high tree densities and crown densities (these are closely correlated: $r = 0.99$), where competition for light may be assumed to be intense, palm densities do not drop, suggesting some degree of shade tolerance by young palms. Both tree density and basal area are negatively correlated with soil fertility (vs. total exchangeable bases: $r = -0.77$ and -0.80 respectively).

Discussion

The preference that *O. horridum* exhibits for soils of low fertility contrasts with the behavior of the bertam palm (*Eugeissona tristis* Griff.) in Malayan rainforests (Fong 1977). The densities of this palm increase with cation exchange capacity; it is an opportunistic species of relatively short life span that rapidly colonizes canopy gaps, whereas *O. horridum* is a long lived species reproducing beneath a closed canopy. A greater limiting factor to *O. horridum* may be soil drainage quality; the palm cannot tolerate soils that may be saturated for long periods each wet season, hence its scarcity in permanent swamp forests. It does not develop aerial adventitious breathing roots as do many palms of wet soil habitats. *O. horridum*, in common with other large clustering palms, may overcome apparent low nutrient levels by self-mulching; copious leaf litter from several palm crowns falls either within the clump or at its base, providing the surface feeding roots with newly released nutrients, preventing excessive surface mineral leaching, and reducing competition from juveniles of other plants.

The abundance of *O. horridum* in parts of Siberut suggests that conditions for its establishment and growth are extremely favorable. Much higher clump densities than given in Table 1 were observed within the study site: an estimated 61 clumps

Table 4. Values of correlation coefficient r.

		Clumps ha^{-1}	Stems $Clump^{-1}$
1. *Edaphic*			
Bulk density	surface	−0.14	0.18
	mean	−0.37	−0.13
pH	surface	−0.09	−0.13
	mean	−0.48	−0.21
% moisture	surface	−0.75	0.43
	mean	−0.80	0.47
% fine sand[a]	surface	0.34	−0.07
% silt[b]	surface	−0.75	0.50
% clay[c]	surface	−0.18	−0.06
Exch. Ca^{++}	surface	−0.86*	0.51
	mean	−0.83*	0.53
Exch. Mg^{++}	surface	−0.91***	0.54
	mean	−0.89**	0.50
Exch. K^{+}	surface	−0.14	0.25
	mean	−0.86*	0.50
T.E.B.	surface	−0.87*	0.61
	mean	−0.87*	0.54
C.E.C.	surface	−0.78	0.74
	mean	−0.90**	0.61
Loss on ign.	surface	0.45	−0.11
	mean	0.47	−0.17
% N	surface	0.23	0.05
	mean	0.25	0.05
C:N	surface	0.84*	−0.67
2. *Environmental*			
Tree density		0.62	−0.67
Crown density		0.52	−0.71
Basal area		0.85*	−0.64

* $p < 0.02$; ** $p < 0.01$; *** $p < 0.005$.
[a] 20–250 μ; [b] 2–20 μ; [c] <2 μ.

ha^{-1} were found in a Mixed forest plot close to plot M2. Wherever *O. horridum* is present as tall, mature plants the crowns form an important component of the main rainforest canopy layer. It is sometimes seen as an emergent where the surrounding canopy has been disturbed. As with many much rarer rainforest plants, *O. horridum* shows some degree of site specificity, although this appears as changes in density and size rather than presence or absence. There are no data in the literature with which to compare these high densities; certainly Ashton (1964) found *O. horridum* to be rare and scattered in the mixed Dipterocarp forests of Brunei, and the species is not conspicuously common in either lowland Central Malayan or West Sumatran rainforests (pers. obs.).

A number of factors may account for the abundance of *O. horridum* on Siberut. There is a high tree fall incidence caused by high rainfall, unstable soils on steep slopes, occasional earth tremors, and wind storms (but not cyclones) coincident with the equinoctial wet seasons. Canopy conditions are therefore relatively unstable, and although *O. horridum* is not a true gap exploiter, it does appear to be able to take advantage of disturbance to the canopy. Seeds are not seen to germinate in open, sunny conditions, and young plants show yellowing on sudden exposure to full sun after a tree fall. However, this shade requirement for establishment and early growth seems to be gradually lost as the palm grows into the main tree canopy, and some exposure is necessary for flowering and successful fruit set. Seedlings were not found beneath mature clump canopies; whether an allelopathic mechanism operates is not known, but *O. horridum* crowns do exert a significant effect over general rainforest regeneration. The continuously shed and heavy litter and dense array of palm crowns casting heavy shade creates a poor environment for seed germination and seedling establishment; those seedlings that do germinate are likely to be damaged or smothered by further fall of palm leaves. Seeds of *O. horridum* itself are probably widely dispersed by long-distance travellers such as fruit pigeons, hornbills, macaques and gibbons.

Oncosperma horridum is an extremely important palm to the indigenous Mentawaian people (House 1983). The present level of use may assist the maintenance of palm populations. The felling of one or two mature stems from a clump of six or seven does not adversely affect the clump if basal buds are not damaged, and may release these from inhibition and thus prolong the life of the clump.

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