### CHAPTER 5

HERBACEOUS SWAMP VEGETATION OF THE MARKHAM VALLEY

A knowledge of the ecology of contemporary aquatic vegetation is an essential prerequisite to the palaeoecological study of any swamp or lacustrine system. Macroscopic and microscopic plant remains comprise the greater part of most organic deposits and changes in their assemblages can reveal information on the hydrology and nutrient status of the lake or swamp. However, such potential can be realised only with a sound understanding of the ecology of the component species, both individually and collectively.

There is a paucity of such ecological data from tropical freshwater habitats in general, and from those of the Australasian region in particular. Although the state of knowledge has improved since the review by Walker and Gregory (1965), most accounts present a geographical-scale synthesis without comprehensive floristic data or quantitative estimates of species importance (e.g. Taylor, 1959, Holloway *et al.*, 1973, and Paijmans, 1976).

More detailed, and of necessity localised, ecological studies exist (Wade and McVean, 1969, Flenley, 1972, and Hope, 1976b) but these are of sub-alpine and highland bogs under climatic and other environmental conditions very different from those prevailing in the lowlands. The most comparable data may therefore come from north-east Queensland, Australia, where Kershaw (1978) has studied a wide range of aquatic vegetation types from three sites on the Atherton Tableland. The swamp vegetation of four sites in the Markham Valley was investigated as a basis for the interpretation of modern and past swamp communities. Systematic ecological sampling was restricted to Lake Wanum, the largest site and that with the greatest diversity of herbaceous swamp vegetation. At the other three sites, the Erom-Erom lakes, Redhill swamp and Yanamugi lake, partial species lists were compiled and the vegetation associations described subjectively.

## SURVEY OF HERBACEOUS SWAMP VEGETATION AT LAKE WANUM

A survey was made of the two main herbaceous swamp areas at Lake Wanum, the south swamp (Plate 5.1) and the western margin of the north-east bay. Six transect lines were laid subjectively to include what appeared to be the major vegetation associations. Of the transects across the south swamp, A and F were aligned approximately north-south, transect B south-west to north-east, and transect C south-south-west to north-north-east. In the northeast bay, transect D followed the alignment of the western end of stratigraphic transect 'A' (see Fig. 3.3), transect E being parallel and about 40 m to the north. Fifty-eight quadrats 1.5 m square were set at regular intervals of 20 m, or in the north-east bay 10 m, along these transects. All vascular plant species encountered were collected for identification. A total enumeration of each quadrat was made, the percentage cover of each taxon being estimated on a five-point scale:

+ presence only, cover less than 5%
1 cover 5 - 24%
2 cover 25 - 49%
3 cover 50 - 74%
4 cover 75 - 100%

The score for each quadrat was not constrained to total four or less, since many minor species might occur, and distinct layering

was often present in the vegetation. The growth habit of each individual taxon was noted, as was the average shoot height of emergent plants, and evidence of flowering or spore production. In addition to the vegetation observations, the percentage of bare ground and open water in each quadrat was estimated and the approximate water depth determined using coring rods as probes.

The complete floristic data for all swamp quadrats are shown in Table 5.1. Taxa encountered, but not sampled in any quadrat include Ficus drupacea, Hyptis capitata, ?Sarcocephalus sp. (21053)<sup>1</sup>, ?Anthocephalus cadamba (21074) and Metroxylon sagu. Two additional quadrats located in the damp grasslandswamp boundary recorded the grasses Themeda australis, Phragmites karka, and Coelorhachis rottboellioides, the sedge Fimbristylis dichotoma, ferns Cyclosorus sp. (21050) and Stenochlaena palustris, and herbs Uraria lagopodioides, Premna herbacea, Ipomoea gracilis, Pouzolzia hirta, and Euphorbia hypericifolia.

### ANALYSIS OF SWAMP QUADRAT DATA

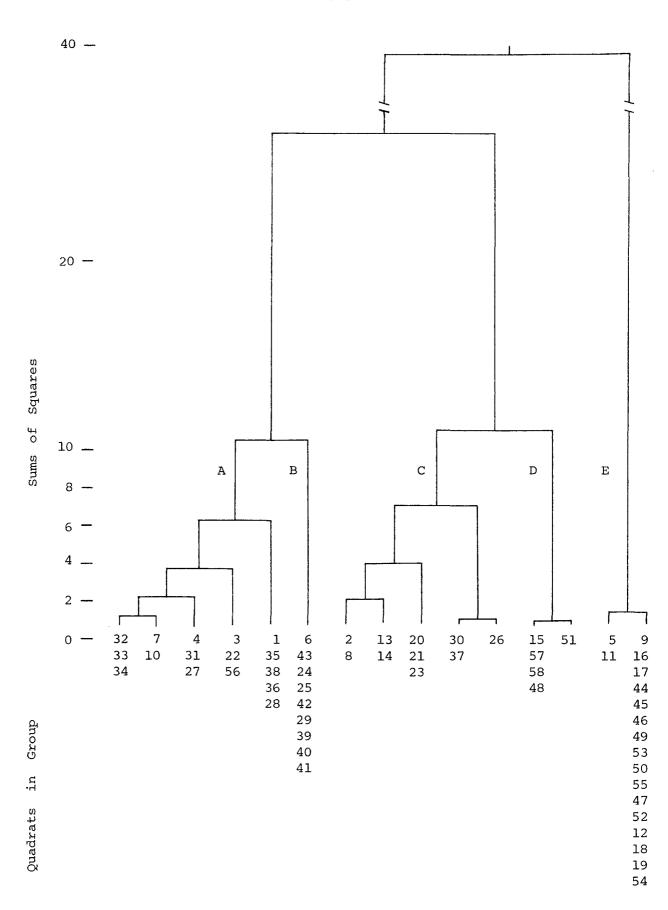
In order to erect a numerically based classification of the herbaceous swamp vegetation, a multivariate analysis was performed on the floristic data of Table 5.1. All values recorded as '+' were first set to 0.5. The technique of sumsof-squares analysis (program SSA) presented by Orloci (1975) was then employed. This hierarchical polythetic clustering method uses the coefficient of Euclidian distance as a similarity measure for the formation of groups. The coefficient, calculated by program EUCD, may be derived from either

<sup>&</sup>lt;sup>1</sup> ANU collection number. Voucher specimens are in the Herbarium, Botany Division, Lae, with selected duplicates at the Herbarium Australiense, CSIRO, Canberra.

specie				_ · · ·		
ds	e Area v		В	SOUTH SWAMP	1 F 1	NORTH-EAST BAY
uog	Transect	A	В	C	±	
Come	Quadrat No.	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0			5 5 5 3 5 5 5 7 8	678901233355333 678901233355333
• 1	NELUMBO NUCIFERA	0+002+4	+ 1 + 3 3 1 1 0 2 2 4 4 2	20++10001+444423	4 + 3 2 3 3 1 0 0	
• 2	NYMPHOIDES INDICA	0 + 0 0 2 0 0	0 0 0 0 + 0 + 0 0 0 0 0 0 0	00+000000+000000	0 0 0 0 0 0 0 0 0	10++100000+0
3	NYMPHAEA PUBESCENS	0000000	0000+11000000	0 0 0 + 0 0 0 0 0 0 0 0 0 + 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
4	NYMPHAEA SP. (21060)	0 0 0 0 0 0 0	0 0 0 0 0 + + 0 0 0 0 0	0 0 0 + 0 0 0 0 0 0 0 0 0 0 0 0 0	0 11 0 11 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
5	NYHPHUIDES SP. (21059)	0 0 0 0 0 0 0	0 0 0 + + 1 + 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0
• 6	CERATOPHYLLUM DEHERSUM	0000+04	+ 0 0 2 + + 0 + 0 0 1 + 0	+ 0 0 0 + 0 + + 0 0 0 0 0 0 0 0 0	0 0 0 0 + 0 0 0 0	0 0 0 + 0 0 0 0 0 0 + 0 0
, 1	VALLISNERIA SP. (21020)	0000000			0 0 0 0 0 0 0 0 0	+ 0 U U U U U U U U U U U U U U U U U U
• 8	NEPHROLEPIS HIRSUTULA	30+1004	000000000000000	0+000000000000000	0 0 0 0 0 0 0 0 0	1 + 1 + 0 1 + 2 + 2 + 0 3
• 9	STENOCHLAENA PALUSTRIS			0 + 0 0 0 0 0 + 0 + 0 0 0 + + 0 1	1	0+0001121+001
• 10	CYCLOSORUS SP. (21050)	001+000		010000+++0000000	0 0 0 0 0 0 1 + +	
11	CERATOPTERIS THALICTROIDES	0000000	+	000000000+000000	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0
12	ACROSTICHUM AUREUM	0000000	0000020000000	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0
13	MICROSORIUM SP. (21067)	0000000			0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 + + + 0 0 +
• 14	HYPOLYTHUN NEMORUM	1012021	0000+00000000	0 + + 2 3 3 4 4 2 3 0 0 0 0 0 0	0+00001+1	01+5+5+111++1
15	CYPERUS PLATYSTYLIS	0 2 0 0 0 0 0	10000000000000	00+0000000000000	000000000	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
16	CYPERUS POLYSTACHOS	0+0000			0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
17	ELEDCHARIS DULCIS	00000+0	1	0 0 0 0 0 0 0 0 0 + 0 0 0 0 0 0	1 1	0000000000000
18	SCIRPUS GROSSUS	0000000		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 + 0 0 0 0 0 0 0
19	FUIRENA CILIARIS	0000000		000000000000000000	0 0 0 0 0 0 0 0 0	000000+000000
• 20	LEERSIA HEXANDRA	0000000		100000000+000+30	+ 2 + 0 + + 1 3 4	
51	SACCIDLEPIS HYDSURDIDES	0000000		0 + + 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
22	SACCTULEPIS INDICA	0000000		00000000000000000	0 0 0 0 0 0 0 0 0	0 + 0 0 0 0 0 0 0 0 0 0 0
53	PHRAGHITES KARKA	0000000		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	02+000000	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
24	LUDHIGIA OCTOVALVIS	0 + 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 + 0 0 0 0 + 0 0 0 0 0 0
25	LUDWIGIA HYSSOPIFOLIA	0 + 0 0 0 0 0		00000000000000000	0 0 0 0 0 0 0 0 0	0000000000000
56	PANDANUS SP. (21062)	0000000		2030000000000+00	0 0 0 0 0 0 0 0 0	00000000000000
27	ALSTONIA SPATHLATA	000+000		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
58	UNCARIA GAMBIR	00+0001		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 + +	0 0 0 0 0 0 0 0 0 + 0 0 0 0
59	COLOCASIA SP. (21055)	0000000	100000000000000	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
30	HERRENIA GEMELLA	0000000	+ 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0	000000000000
31	IPOHOEA GRACILIS	0000000		+ 0 0 0 0 0 0 0 0 0 0 0 0 0 + 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0
32	CAYRATIA TRIFULIA	0000000	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 + + 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0
33	ARACEAE SP. (21064)	0000000		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0	2 + 0 0 0 0 0 0 0 0 0 0 0
34	MARSDENIA SP. (21066)	0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 + + 0 0 + 0 0 0 0 0 0
35	NEPENTHES MIRABILIS	0000000		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
36	SPATHOGLOTTIS PLICATA	0000000		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0	000000+000000
37	THRIXSPERMUN AMPLEXICAULE	0000000	00000000000000000	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	00000000	000000000+0000

TABLE 5.1. Floristic and cover-abundance data from herbaceous swamp quadrats at Lake Wanum

FIGURE 5.1. Dendrogram of sums-of-squares analysis on floristic data from Lake Wanum, normalised by quadrat



,		GROUP A	GROUP B	GROUP C	GROUP D	GROUP P	
		888888888888888888888888888888888888888	8 8 8 8 8 8 8 8 8	883888888	4 8 7 7 8	8 9 1 2 8 3 8 4 8 8 9 8 9 8 3 3 3 3 3 3 3 3 3 3 3 3 3 3	
1	NELUNBO NUCIFERA		* * 1 1 *	+ + 1122+		2 1 3 3 2 2 4 4 4 4 4 4 4 3 4 3 2 3 3	
ş	NYNPHOIDES INDICA			* . * * 1 1 *		2. •	
3	NYMPHAEA PUBESCENS	• • • • • • • • • • • • • • • • •	• • • • • • • • • •	11		• • • • • • • • • • • • • • • • • • • •	
4	HYNPHAEA SP. (21060)	• • • • • • • • • • • • • • • •				• • • • • • • • • • • • • • • • • • • •	
5	NYMPHDIDES SP. (21059)	• • • • • • • • • • • • • • • •		1 *			
6	CERATOPHYLLUM DEMERSUN		• • • • • • • • •		• • • • •	* . 2 * 1 * • • • • • • • • •	
7	VALLISMERIA SP. (21020)	• • • • • • • • • • • • • • •					
8	NEPHROLEPIS HIPSUTULA	3 + 1 + , + + 1 1 + 2 + 2 - 3 ,	*			• • • • • • • • • • • • • • • • • • •	
9	STENOCHLAENA PALUSTRIS	+ 1 1 2 4 + + , 1 1 2 1 + , 1 +	*		1 * * * *		
10	CYCLOSORUS SP. (21050)			• • • • • • • • • •			
11	CERATOPTERIS THALICTROIDES	•••••••••••	• • • • • • • • •	· • • • • • • • • • •	••••	• • • • • • • • • • • • • • • • • • • •	
12	ACROSTICHUH AUREUN	• • • • • • • • • • • • • • • •	• • • • • • • • • •	•• <sup>2</sup> •••••			
13	HICROSORIUH SP. (21067)	· · · · · · · · · · · · · · · · · · ·	* * * * * * * * * *	•••••	•••••	• • • • • • • • • • • • • • • • • • •	
14	HYPOLYTRUM NEMORUN	1121+1+2+111+11	2 2 3 2 3 4 1 2 3			• • • • • • • • • • • • • • • • • • •	
15	CYPERUS PLATYSTYLIS	• • • • • • • • • • • • • • • • • •	• • • • • • • • • •	21		••••	
16	CYPERUS POLYSTACHDS			•••••••			
17	ELEDCHARIS DULCIS		* • • • • • • • •	• • • • • • • • • •			
18	SCIRPUS GROSSUS			• • • • • • • • • •			
19	FUIRENA CILÍARIS			• • • • • • • • • •			
50	LEERSIA HEXANDRA		• • • • • • • • •	1	33834	, , , , , , , , , , , , <del>, , + + , + +</del>	
51	SACCIDLEPIS HYDSURDIDES Saccidlepis indica			• • • • • • • • • •			
25 23	PHRAGMITES KARKA		• • • • • • • • • •	•••••			
24	LUDWIGIA OCTOVALVIS	· · · · · · · · · · · · · · · · · · ·	* * * * * * * * * *	* * * * * * * * * * *		• • • • • • • • • • • • • • • • • • •	
25	LUDWIGIA HYSSOPIFOLIA			* • • • • • • • • •		• • • • • • • • • • • • • • • •	
26	PANDANUS SP. (21062)						
21	ALSTONIA SPATULATA				1		
28	UNCARIA GAMBIR						
29	COLOCASIA SP. (21055)						
30	HERREHIA GENELLA						
31	IPOHDEA GRACILIS						
32	CAYPATIA TRIFOLIA					• • • • • • • • • • • • • • • • • • • •	
33	ARACEAE SP. (21064)						
34	HARSDENIA SP. (21066)						
35	NEPENTHES MIRABILIS						
36	SPATHOGLOTTIS PLICATA				1	1	
37	THRIXSPERMUM AMPLEXICAULE		•••••				

TABLE 5.2. Herbaceous swamp data matrix grouped by sums-of-squares analysis, normalised by quadrat

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the raw data, or from normalised quadrat vectors (the 'chord' distance). Normalisation sets the sum of all vectors to unity, thus effectively comparing relative rather than absolute abundance of taxa between quadrats. Unfortunately, no facility is available for normalisation of data on the basis of within-taxon rather than within-quadrat vectors. An 'inverse' (taxon-grouping) analysis of the raw data produced an unsatisfactory dendrogram showing excessive 'chaining' of the more abundant commonly occurring taxa only. The quadrat groups, or vegetation associations, formed are therefore interpreted subjectively on the basis of apparent similarities in the floristic and environmental attributes.

Sums-of-squares analysis was performed on three versions of the floristic data set: the raw data, the normalised data, and a subset of the normalised data. This last group of eight taxa represents the 'common' species, defined as those with ten or more occurrences. The subset also happens to include the most generally abundant, or physiognomically dominant, taxa. Analysis of the full, normalised data appears to give the most tractable classification of the vegetation. The dendrogram of quadrat groupings thus produced is shown in Fig. 5.1 and their floristic composition is displayed in Table 5.2. Five groups of quadrats are defined at the sums-of-squares value 10:

Group A: Deep-water, floating root-mat, association

This group of 16 quadrats is characterised by the cooccurrence of three species: the large sedge Hypolytrum nemorum, the erect fern, Nephrolepis hirsutula, and the straggling fern Stenochlaena palustris. Associated with these species in the denser stands are *Microsorium* sp. (21067), also an erect fern, and several dicotyledons, amongst them *Nepenthes mirabilis*, and *Uncaria gambir*. The orchids *Spathoglottis plicata* and *Thrixspermum amplexicaule* are often found along the margins of the floating root-mat islands. This association predominates in many areas where the water is deeper than 2 m, although vegetation of somewhat similar floristic composition may occur in shallower water. It is, however, the only association consistently found in water deeper than 4 m, and may occur in areas up to 8 m deep.

Group B: Shallow water, Hypolytrum nemorum, association

Quadrats in this group are dominated by dense tussocky stands of *Hypolytrum nemorum* with shoots up to 2 m above water level. The only widespread associates are *Nelumbo nucifera* and the submerged *Ceratophyllum demersum*, found in open water between the *Hypolytrum* tussocks, although *Stenochlaena palustris* is locally common. This vegetation is characteristic of many areas with a water depth of about 1.5 m. Two quadrats (29 and 39) from areas of floating root-mat in deeper water consist of similar, almost monospecific *Hypolytrum* stands, and are classified with this association.

### Group C: Mixed aquatic association

The 10 quadrats of this group are floristically diverse, and heterogenous in their species composition. *Nelumbo nucifera*, *Nymphoides indica* and *Hypolytrum nemorum* are frequent occurrences, although none dominates. *Cyperus platystylis, Pandanus* sp. (21062) and *Araceae* sp. (21064) are locally abundant. A number of quadrats from the submerged margin of floating root-mats are also included in this group. With the exception of these sites, the association is generally found in water 1 m to 2 m deep.

Group D: Leersia hexandra root-mat association

A small but distinctive group of five quadrats dominated by *Leersia hexandra* comprise this association. This grass often forms a low floating root-mat in areas shallower than 2.5 m. *Stenochlaena palustris*, though never abundant, is a consistent associate.

Group E: Nelumbo nucifera open water association

The 18 quadrats of this large association are characterised by almost pure stands of *Nelumbo nucifera* in otherwise open water, typically 1.5 m deep. Other species, in particular floating-leaved and submerged aquatics, occur, but none is common. *Leersia hexandra* is found in some quadrats.

Analysis of the non-normalised raw data produces a slightly different allocation of quadrats to groups (Fig. 5.2). At the sums-of-squares value 100, four groupings are recognised. Floristic groups B, the *Hypolytrum nemorum* association, and D, the *Leersia hexandra* association remain unchanged. However, quadrats of the heterogenous group C, the mixed aquatic association, become equally redistributed between groups A, the deep-water root-mat, and E, the *Nelumbo nucifera* associations.

A third analysis, using the normalised records of the 'common' species only, results in the classification shown in Fig. 5.3. At the sums-of-squares value 12, group D is the only one to remain totally intact. The quadrats of group C again become redistributed, this time between groups B and E. Quadrats 4, 27 and

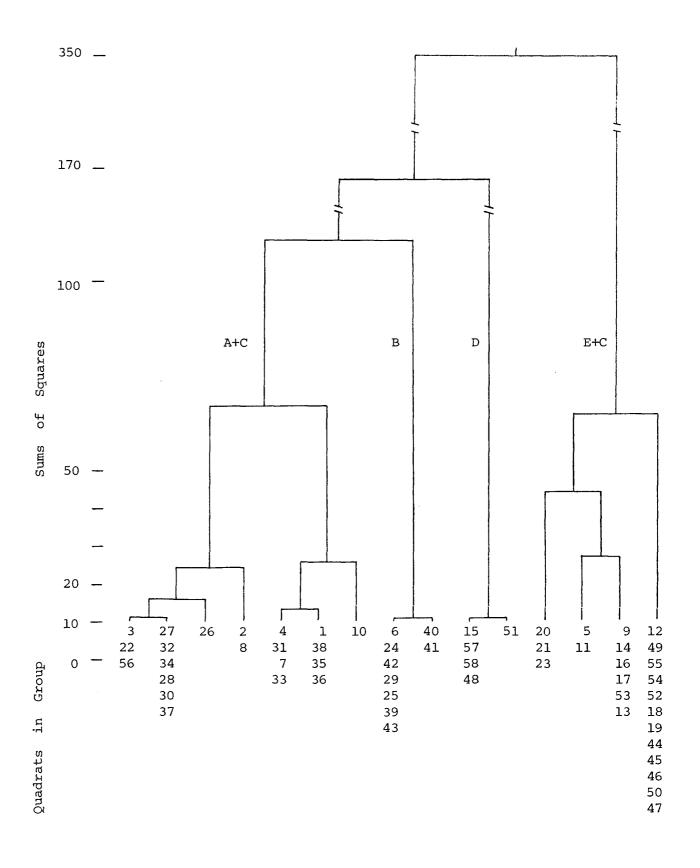
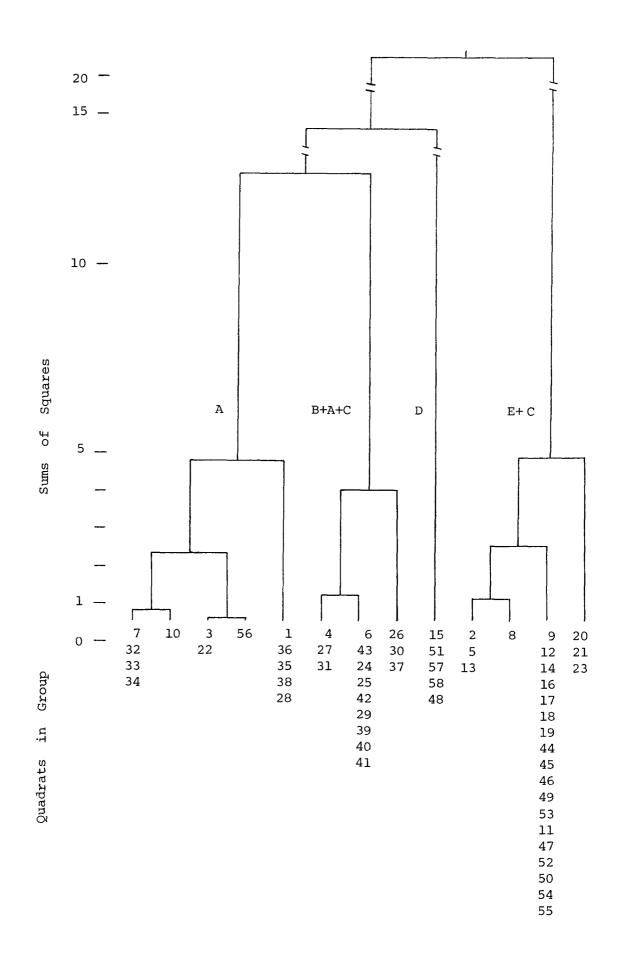


FIGURE 5.3. Dendrogram of sums-of-squares analysis on floristic data from Lake Wanum, common taxa only, normalised by quadrat



31 with their relatively high values for *Hypolytrum* are allocated to group B, the *H*. *nemorum* association, rather than to the floristically more diverse association of group A.

Despite these differences, the major features of the floristic classification remain intact. This suggests that the classification is relatively robust and insensitive to minor differences in the analytical technique. Four or five main vegetation associations occur, of which four can be defined by the small number of species that dominate them floristically and physiognomically.

# THE DISTRIBUTION OF HERBACEOUS SWAMP ASSOCIATIONS IN THE LAKE WANUM AREA

The herbaceous swamp associations described above frequently occur in small scale mosaics, and are therefore difficult to map. This is especially true in the south swamp area of Lake Wanum where all associations are represented to some extent. The Nelumbo nucifera association, group E, occurs here over a wide area (Plate 5.2), and also along the southern and eastern shores of the lake. Group C, the mixed aquatic association is also predominant in the south swamp. The Leersia hexandra floating rootmat association, group D, is also more common in the south swamp, although small areas do occur in the vegetation of the north-east The shallow water Hypolytrum nemorum association of group B bay. dominates large areas of the south swamp but is also found along the eastern shore of the lake, and forms the small islands of vegetation in the middle of the north-east bay. The generally deeper water of the western margin of the north-east bay is dominated by the floating root-mat vegetation of group A (Plate 5.3). All but two quadrats sampled from the area fall into this association.



PLATE 5.1. The extensive south swamp of Lake Wanum. Grasscovered Mount Ngaroneno (alt. 340 m) is visible to the northwest.



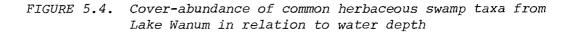
PLATE 5.2. Hypolytrum nemorum and Stenochlaena palustris encroaching on open water stands of Nelumbo nucifera, south swamp, Lake Wanum.

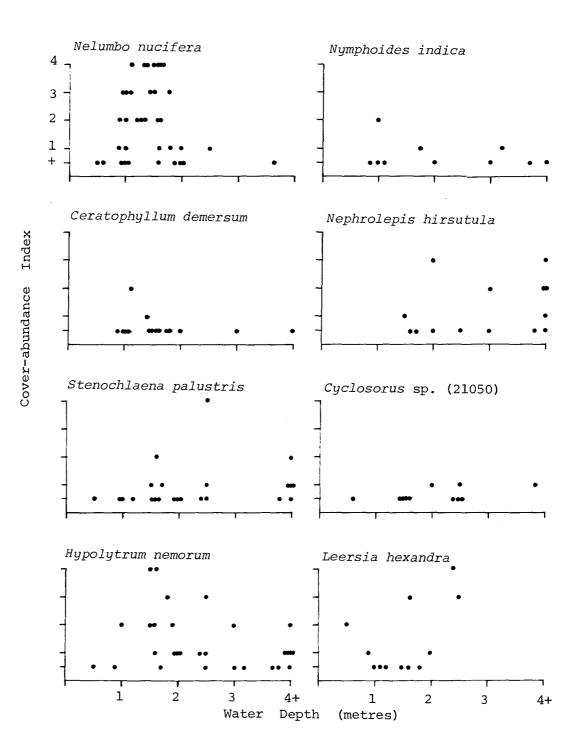


PLATE 5.3. Floating root-mat vegetation in deep water at the western margin of the north-east bay, Lake Wanum. The sedge Hypolytrum nemorum and erect fern Nephrolepis hirsutula dominate the mat. Stenochlaena palustris, a straggling fern, is also seen.



PLATE 5.4. Aquatic vegetation at the northern end of Yanamugi. Nymphoides indica covers much of the open water less than 3 m in depth. Sago palm, Metroxylon sagu, is visible in the right background.





Associations similar to those recognised at Lake Wanum appear to make up the herbaceous swamp vegetation around the Erom-Erom lakes. Here, the slope of the shoreline is gradual, and a distinct zonation of vegetation is apparent. Waterlogged grassland with such species as *Coelorhachis rottboellioides* gives way to a floating *Leersia hexandra* root-mat, similar to group D. Other taxa may be present, including species of *Sacciolepis*, and the twining *Merremia* sp. (21165). Isolated shoots of *Nelumbo nucifera* may also occur, and in deeper water the species forms an almost monospecific association, similar to that of group E at Lake Wanum. The area between each of the small lakes and the riparian forest of Oomsis Creek is occupied by dense herbaceous swamp vegetation. Although these areas were not surveyed, they appear to be dominated by *Hypolytrum nemorum*, either rooted or in floating vegetation similar to groups B and A at Lake Wanum.

#### ENVIRONMENTAL DETERMINANTS OF VEGETATION DISTRIBUTION

As indicated above, the major environmental factor controlling the distribution of the various herbaceous swamp associations is water depth. In some areas zonation of vegetation is related to increasing water depth. More usually, a mosaic of vegetation associations occurs and it becomes more difficult to assess the influence of the water depth on their floristic composition. The edges of floating root-mats can form a shallow 'microenvironment' in otherwise deeper water.

The abundance of each of the 'common' species in relation to water depth is shown in Fig. 5.4. Some of the taxa can be seen to occupy fairly restricted depth ranges, whilst others are more ubiquitous.

Most occurrences of Nelumbo nucifera are recorded from 0.75 m to 2 m of water, the two data points from deeper areas being associated with the edge of floating root-mat communities. The species is least common in the deep water root-mat association of group A. Nymphoides indica although never abundant is found growing in up to 5 m of water. It is surprisingly infrequent in shallow places dominated by Nelumbo nucifera. The widespread Hypolytrum nemorum exhibits a bi-modal distribution. The first abundance peak is associated with the quadrats of group B where the sedge dominates, and the second coincides with the deep water floating root-mat association of group A. The co-dominants of H. nemorum in this association, Nephrolepis hirsutula and Stenochlaena palustris show similar abundance patterns, although neither is as common as H. nemorum in shallow water. Nephrolepis hirsutula is almost entirely restricted to the quadrats of group A, and was not recorded growing in areas of water shallower than 1.5 m. Stenochlaena palustris is present throughout all groups although is more common in floating root-mat vegetation. In the quadrats sampled, Leersia hexandra is restricted to water shallower than 2.5 m. Cyclosorus sp. (21050) occurs in quadrats of group A in the south swamp with water depths generally of less than 2.5 m. However it is totally absent from this association in the northeast bay, where the water is deeper than 4 m. Its place appears to be taken by Microsorium sp. (21067), restricted to the group A quadrats in this area. Although often free-floating, Ceratophyllum demersum is commonly associated with shallow water areas less than 2 m deep.

The availability of shelter from wind and wave action may also affect the distribution of some species. *Nymphoides indica* and *Eleocharis dulcis* are seldom found in exposed situations, but tend to congregate in between tall stands of other vegetation.

The composition of the substrate provides a further factor that may influence the distribution of a species. The south swamp is largely underlain by minerogenic grey clay, as are the shallow margins of the south and east shores of the lake. In the north-east bay the substrate is predominantly organic. Differences in the vegetation and floristics of the two areas have been described above, and some may reflect the contrasting substrates. Kershaw (1978) recorded Nymphaea gigantea only from sites lacking a large accumulation of organic material, and suggested that the species might require a mineral substrate. At Lake Wanum, Nymphaea pubescens and Nymphaea sp. (21060) are present in the vegetation of the south swamp, but not in that of the north-east bay. However, the great difference in general water depth rather than their contrasting substrates probably accounts for the major variations in herbaceous swamp vegetation between these two areas.

HISTORICAL CHANGES IN HERBACEOUS SWAMP VEGETATION AROUND LAKE WANUM

The existence of a chronological series of aerial photographs of the lower Markham Valley makes it possible to trace recent changes in the herbaceous swamp vegetation around Lake Wanum.

The earliest photographs available are those reproduced in the wartime Allied Geographical Section terrain studies handbooks and reports (A.G.S. 1942, 1943*a*, 1943*b*, 1943*c*). Oblique aerial photographs dated February and March 1943 indicate the extent of herbaceous swamp along the southern margin of the lake to be very similar to that of 1974. However, no open water is visible in Lake Erom-Erom 1, apparently a swamp at that date. A series of vertical aerial photographs dated September 1956<sup>1</sup> show similar features although there appears to have been slight encroachment of swamp vegetation into the open water of the south-east corner of Lake Wanum. Substantial islands of vegetation are present in the centre of the north-east bay, and a swamp remains on the site of Erom-Erom 1.

The most dramatic changes are documented by a run of photographs from November  $1969^2$ . A vast encroachment of vegetation into open water along the southern and eastern margins is shown extending towards the 4 m bathymetric contour (Fig. 3.2). Many of the small embayments along the north shore of the lake are also vegetated, and there is an extension of the swamp islands in the north-east bay. The open water of Lake Erom-Erom 3 is also reduced by swamp growth. However, at Lake Erom-Erom 1, a considerable body of open water is visible for the first time.

Large scale vertical photographs of sections of Lake Wanum taken during 1971 indicate a reversal of previous conditions. The south-east corner of the lake<sup>3</sup> is still considerably infilled with what appear to be stands of *Nelumbo nucifera*. However, some

<sup>&</sup>lt;sup>1</sup> CAJ 53-5053 NADZAB 25 000 ft. 27 September 1956

<sup>&</sup>lt;sup>2</sup> QASCOPHOTO NG 99 2163 25 000 ft. 30 November 1969

<sup>&</sup>lt;sup>3</sup> QASCOPHOTO NG 155 8729 6 500 ft. 27 July 1971

tracts of open water are once again present, especially along the eastern shore. A photograph<sup>1</sup> of the north-west area suggests a slight diminution of aquatic vegetation cover in some of the embayments.

Ground and aerial observations made during 1974 and 1976 indicated the area of open water in Lake Wanum to be very similar to that in 1943. The south-east corner was again free of swamp vegetation, and the islands in the north-east bay were noticeably less extensive than in 1956 or 1969. Lake Erom-Erom 1 contained much open water, as in 1969, although between 1974 and 1976 there appeared to be a slight increase in the area of *Nelumbo nucifera* in the eastern branch.

Most of the observed vegetation changes could be explained by fluctuation in the water level of Lake Wanum and the Erom-Erom lakes. The extension of *Nelumbo nucifera* and other vegetation into the areas indicated in 1969 would require a drop in the lake level to at least 2 m below that of 1974. Evidence does exist for a recent slight rise in water level. Dead *Phragmites karka* stems may be found in areas of open water where the grass does not now grow. Numerous dead trees occur along the margin of the swamp forest and around the shores of the lake, presumably killed by inundation. A small decrease in the level of Lake Wanum was recorded between 1974 and 1976. During 1974, the outlet to Comsis Creek flowed constantly, whereas 18 months later the channel was found dry and overgrown.

 $^{1}$  QASCOPHOTO NG 144 4747 10 000 ft. 21 March 1971.

The opposite directions of apparent water level change in Lake Wanum and Lake Erom-Erom 1 suggest that local hydrological conditions are more important than any general climatic effects. Factors possibly influencing local hydrology are multifarious and almost impossible to quantify. Considerable extension of the Gabensis cocoa plantation immediately adjacent to the Lake Wanum south swamp took place between 1956 and 1969. Resulting erosion may have had a direct effect on the swamp forest or on the hydrology of Oomsis Creek. The suggested increase in water level of Lake Erom-Erom 1 could have been caused by further impoundment by the extensive swamp vegetation between the lake and Oomsis Creek.

One other biotic factor may be of importance in recent vegetation change. Lake Wanum is now well stocked with *Tilapia mossambica* despite heavy exploitation by the local inhabitants. These exotic fish were introduced into the lake by the D.A.S.F., reportedly during 1966, and their increasing population may have made some impact on the swamp and aquatic vegetation.

Whatever the causes, the evidence documents considerable and rapid change in swamp vegetation over the last few decades. The vegetation associations appear dynamic rather than successional, responding to minor changes in environmental conditions. This conclusion becomes of great importance when attempting to reconstruct the development of the swamp vegetation over a much longer time-scale.

## THE VEGETATION OF REDHILL SWAMP

The vegetation of Redhill swamp differs from that of the lake marginal areas of Lake Wanum and Erom-Erom. At Redhill there is practically no open water and the basin appears fairly shallow.

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The stratigraphy (Chapter 3) suggests that much of the swamp is floating on at least 3 m of water. Examination of the vegetation showed it to be a well developed root-mat association with a floristic composition similar to that of group A at Lake Wanum. The co-dominants of this group, *Hypolytrum nemorum*, *Stenochlaena palustris* and *Nephrolepis hirsutula* are all present. However, the floating vegetation of Redhill is more complex both floristically and physiognomically than that of Lake Wanum. The herbaceous vegetation may be up to 3 m high and many additional species are found including *Alstonia spatulata*, a small tree with a balsa-like trunk and root-system, and the sago palm, *Metroxylon sagu*.

The gentle slope of the south-eastern edge of the swamp basin provides a habitat for shallow water and periodically inundated vegetation. Within the perennial swamp are found, along with the species named above, Alstonia scholaris, Nepenthes mirabilis and Dysophylla verticillata. Also included in the swamp margin and periodically waterlogged grassland areas are Lycopodium cernuum, Coelorhachis rottboellioides, Alyxia floribunda and Coleus scutellarioides. In the damp shrubby grassland fringing the swamp Timonius timon and Ilex arnhemensis are very common, and Terminalia, Trichospermum, Schuurmansia henningsii and Desmodium gyroides are also encountered.

There is no evidence for any major change in the swamp vegetation from the aerial photographs available for 1956 and 1971. This is not surprising since, if as suggested most of the swamp is floating, only extreme changes in the hydrology would be reflected by visible changes in the vegetational associations.

### SWAMP AND AQUATIC VEGETATION AT YANAMUGI

The largest area of swamp vegetation at Yanamugi is the *Metroxylon sagu* dominated association to the north of the lake. *Phragmites karka* is also common in this area. In water deeper than c. 1.2 m the sago swamp gives way to a zone of *Eleocharis dulcis* whilst in open water up to 3 m deep *Nymphoides indica* dominates (Plate 5.4).

There is little swamp vegetation along the western and eastern shores of the lake where the slope of the basin is steeper (Fig. 4.2). However, other small areas of herbaceous swamp vegetation occur along the shallower margins of the lake. A bay in the south-east corner is dominated by the emergent aquatic herbs *Polygonum attenuatum* and *Phyla nodiflora*, as well as *Phragmites karka* and *Eleocharis dulcis*.

In areas of open water Nymphoides indica is the most common floating-leaved hydrophyte, although Nymphaea pubescens is also found. The submerged aquatics Najas graminea and Ceratophyllum demersum occur in water up to 4.2 m deep.

Small areas of floating root-mat vegetation exist in sheltered embayments along the south-west shore of the lake. Species forming these associations include Acrostichum aureum, Ceratopteris thalictroides, ?Scirpus grossus and several grasses, probably Leersia hexandra and species of Sacciolepis. Scattered individuals of Metroxylon sagu, Stenochlaena palustris and Nephrolepis occur in shallow water or periodically inundated situations around the lake. Available aerial photography<sup>1</sup> reveals no appreciable change in swamp and aquatic vegetation between 1962 and 1971.

SWAMP VEGETATION OF THE MARKHAM VALLEY AND OTHER TROPICAL AREAS

It would be improper to generalise about lowland freshwater swamp communities in Papua New Guinea on the basis of four localised sites, only one of which has been studied in any detail. However, tentative comparisons can be made both between the different sites in the Markham Valley, and with similar environments in other tropical areas.

The vegetation associations of Lake Wanum and the Erom-Erom lakes appear very similar, reflecting their proximity and identical geology. The differences between these two sites and Redhill swamp may result from several factors. The latter's location on the boundary of the granodiorite and metamorphic rocks may give rise to the suggested shallower basin morphometry and perhaps even to differing nutrient supply to the swamp.

Yanamugi is very different from the other sites in its geology, morphometry, sedimentology and climatic regime. Two of the major dominant species in the Lake Wanum area, *Hypolytrum nemorum* and *Nelumbo nucifera*, are missing from the swamp vegetation at Yanamugi and two others, *Stenochlaena palustris* and *Nephrolepis hirsutula*, are much less common. Nevertheless, the vegetation is otherwise floristically and physiognomically fairly similar, with the *Metroxylon sagu* palm and various swamp grasses being more abundant.

<sup>1</sup> C.A.J. 195 LERON 5031 25 000 ft. 1 February 1962 QASCOPHOTO C.A.J. 1284 ONGA 1284 23 000 ft. 25 May 1969 QASCOPHOTO MARKHAM VALLEY NG 138 1578 10 000 ft. 22 January 1971

There are very few similarities between the lowland swamps studied and the alpine and sub-alpine bogs of Papua New Guinea and West Irian described by Wade and McVean (1969) and Hope (1976b). These communities are structurally very different, and do not possess any species in common with the lowland sites. The few congeneric plants are mainly grasses and sedges.

At Kayamanda, an extensive valley swamp at a lower altitude (2 500 m), Walker (1972a) identifies 15 floristic groups falling into 8 major vegetation units. Only four species recorded, Lycopodium cernuum, Sacciolepis indica, Phragmites karka and Dysophylla verticillata, and six genera including four sedges, Nymphoides and Polygonum are common to the Markham Valley. No floating vegetation was encountered, although the northern sector of the swamp around Lake Ipea was not sampled. Flenley (1972) describes floating vegetation from nearby Lake Inim (2 550 m) although the floristic composition differs totally from that found in the lowland sites studied.

In contrast, striking similarities exist between the swamp and aquatic vegetation of the Atherton Tableland (alt. 750 m) north-east Queensland (Kershaw, 1978) and that of the Markham Valley. Six species (Ceratophyllum demersum, Cyperus platystylis, Eleocharis dulcis, Leersia hexandra, Nymphoides indica and Ludwidgia octovalvis) and six additional genera found at these sites are also recorded from the Markham Valley. Kershaw (1978) recognises three ecologically definable communities: free water dominated by Nymphoides indica, Cyclosorus gongylodes dominated floating root-mat, and fixed root-mat comprised of tussocks of Blechnum indicum. These communities appear structurally similar to three of the vegetation associations defined at Lake Wanum. In both areas, ferns play an important role in the swamp vegetation. *Cyclosorus* species are frequently found in herbaceous swamp areas of Papua New Guinea (Paijmans, 1976) and occur at Lake Wanum. *Stenochlaena palustris* is a widespread inhabitant of swamp forest and mangrove communities of south-east Asia (Holttum, 1932) and Papua New Guinea (Paijmans, 1976) although it is not found in northern Queensland.

The herbaceous swamp vegetation of the four sites investigated exhibits basic similarities both in floristic composition and physiognomy. Differences tend to be expressed floristically rather than structurally, even though the missing species may be important dominants in other sites. Floristic and structural similarities between these swamps and related environments in northern Queensland and south-east Asia appear much greater than those between lowland and high-altitude sites within New Guinea.