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Influence of Large Seasonal Water Level Fluctuations and Human Impact on the Vegetation of Lake Tonle Sap, Cambodia

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Lake Tonle Sap, the largest inland water body in Southeast Asia, encompasses unique ecosystems and wildlife adapted to large seasonal fluctuations in water level. The permanent waterlogged area of the lake is encircled by a vast floodplain, the inundated woodland being dominated by *Barringtonia acutangula* (Lecythidaceae), probably a major vegetation type of this ecotone, although human impact has degraded the floodplain vegetation and developed forest is restricted to a narrow band along the shore in the lowest water season. The aspects of seasonally inundated vegetation (i.e., variations in physiognomy, species composition, stratification, and distribution) on the coastal side of the floodplain (approximately 4 km in depth), located adjacent to the southern part of Siem Reap, was analyzed. Quantitative data for phytosociological evaluation were collected at 67 quadrats (10 m × 10 m each) during the low water seasons in 2005 and 2006, the sampling plots being classified by Two-Way Indicator Species Analysis (TWINSPAN) and ordinated by Detrended Correspondence Analysis (DCA). Two vegetation zones (i.e., extensive cropland and disturbed woodland), seven vegetation types (i.e., "Cultivated field," "Fallow field," "Shrub," and "Tall-shrub" in the extensive cropland zone and "Scrub," "Open forest," and "Closed forest" in the disturbed woodland zone), and vigorous invasion and/or regeneration of *Barringtonia acutangula* over the study area were identified. Human impact (e.g., plowing, burning, and cutting for firewood) seemed to be inversely related to both duration of flooding and maximum water depth and to be the main cause of degradation of seasonally inundated vegetation.

1. Introduction

Lake Tonle Sap, the largest inland water body in Southeast Asia and the natural reservoir of the Mekong River, has been found to contain unique wildlife and ecosystems adapted to its large seasonal fluctuations in water level (Mekong River Commission 1997; CNMC/NEDECO 1998a,b). In the highest water season (October–November),

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the waterlogged area expands to four times the size of that in the lowest water season (April–May), the maximum depth reaching to more than 8 m from a minimum of about 1 m. The lake (including its floodplain) also plays an important role in the everyday life of local people, and in the economy and culture of Cambodia, being a major source of fish, wood, fertile agricultural land, and some natural resources (CNMC/NEDECO 1998a,b; Bailleux 2003).

Unfortunately, during the past approximately 50 years, most areas of floodplain vegetation have been severely disturbed by human activities. At the same time, scientific research, such as biological inventories, phytosociological analyses, life history investigations of adapted species, and hydrological surveys, have fallen behind. For example, only a few studies have been conducted on the flora and vegetation of the floodplain (McDonald et al. 1997; Sokhun 1997; CNMC/NEDECO 1998b), although researchers have indicated that floodplain vegetation was an important factor in (1) fish habitat and breeding sites, (2) biological productivity and water purification, and (3) the high biodiversity.

The remnant forest fringing the shore in the lowest water season is the standout vegetation of the floodplain, *Barringtonia acutangula* (Lecythidaceae), which is dominant and grows to a maximum height of about 15 m (maximum DBH, about 55 cm), in addition to stunted examples of *Diospyros cambodiana* and *Coccoceras anisopodum* (McDonald et al. 1997). On the other hand, large areas of the floodplain are covered with various vegetation types, including woodland, scrub, shrub, meadow, aquatic herbaceous communities, and cultivated fields, and are recognized as mosaics of these types.

In the present study, we analyzed aspects of the seasonally inundated vegetation (i.e., variations in physiognomy, species composition, stratification, and distribution) on the coastal side of the floodplain (about 4 km in depth), being our first step toward the scientific evaluation of the lake ecosystem for its preservation, conservative management and use of its biological resources.

2. Study Area

The study area was adjacent to the southern part of Siem Reap, Cambodia, situated on the northwest side of Lake Tonle Sap (13°16′ N, 103°49′ E; about 1–6 m a.s.l.; Fig. 1). As in the other lakeside lowlands, the flooding pulse, originating mainly in the Mekong River, took place in April–May, increasing sharply before decreasing in October–November. In the study area, floodwaters reached about 8 km inland from the shore of the permanent lake at their peak. Accordingly, both maximum water depth and duration of flooding gradually changed from south to north, microscale landform undulations (e.g., banks, channels and shallow ponds) probably influencing site conditions. The climate of terrestrial areas surrounding the floodplain was seasonal dry tropical, with the result that in the dry season (corresponding to low water level in the lake) many plants, especially those growing on the upper floodplain, seemed to suffer from drought conditions (McDonald et al. 1997). Annual mean temperature was 28.2°C, with only 12% of annual precipitation (1425 mm/year) falling during the dry season in Siem Reap(MRCS 2003). The surface soil of the floodplain was reddish-brown or yellowish-brown soft sandy clay and clayey sand. Soil

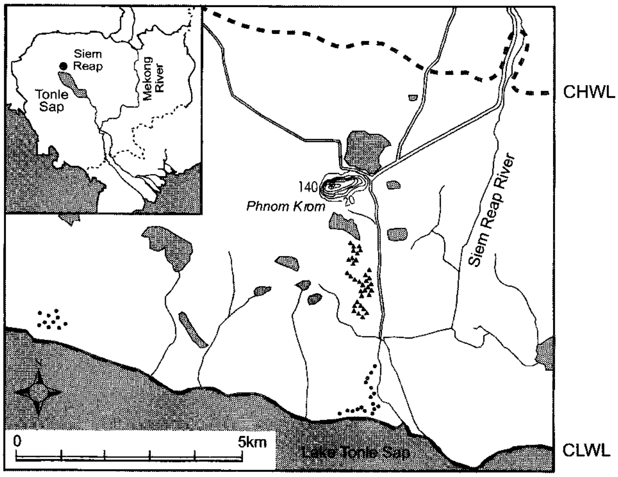

FIG. 1. Location of the study area (*upper left*) and 67 quadrats for phytosociological survey: ▲, quadrats of extensive cropland zone; •, quadrats of disturbed woodland zone; *CHWL*, coastline at the highest water level; *CLWL*, coastline at the lowest water level

deposition was estimated to be minute, owing to the seasonal rising and receding of the high volume of lake water.

Natural vegetation and landform conditions characterized the coastal side of the study area (about 4 km in depth), the upper reaches on the other hand having been largely reclaimed as paddy fields, enclosed by artificial banks and channels of various sizes. Reasons why local people have not caused large-scale modifications to the original inundated vegetation on the coastal side are though to be (1) the woodland, especially the forest consisting of stunted *Barringtonia acutangula* and *Diospyros cambodiana*, is essential for weakening waves and currents surging from the permanent lake to the littoral zone where they normally persist during the flood season, and (2) the location is unsuitable for agricultural use because of the long duration of submergence and its distance from villages (McDonald et al. 1997; CNMC/NEDECO 1998a,b). During the low water season, the various vegetation types already described can be distinguished physiognomically within the study area.

3. Methods

3.1. Survey Procedures

The phytosociological field surveys were carried out in the low water seasons (February–August) of 2005 and 2006. After general observations of the floodplain vegetation, we established 67 quadrats (10 m × 10 m each) on the coastal side of the floodplain, covering the major vegetation types (see Fig. 1). In each quadrat, the height and coverage of each layer (tree, short-tree, shrub, and herb), and species name and dominance sensu Braun-Blanquet (1964) for every component species, were checked. Maximum height and diameter at breast height (DBH) were measured by measuring poles and diameter tape, and the location of the quadrat determined by GPS (Global Positioning System) (GPSMAP76; GARMIN Corporation) for calculating the distance from the coastline at the lowest water level (CLWL). Voucher herbarium specimens were collected for each of the 122 plant species recorded (including unidentified species of low frequency and dominance).

3.2. Data Analysis

Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979) and Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) were used to analyze vegetation data. After omitting rare species that had been recorded less than three times, a data matrix consisting of 67 sampling plots versus 89 indicator species was prepared, the calculation being performed by PC-ORD for Windows Version 4.00 (McCune and Mefford 1999). In TWINSPAN, pseudospecies cut levels were set at 0, 1, 5, 25, 50, and 75, according to the dominance scale of Braun-Blanquet (1964) for each layer.

The following parameters were used to assess species richness and diversity of vegetation type: density of species (total number of species per quadrat), Simpson diversity index (*D'*; Simpson 1949), Shannon diversity index (*H'*; Shannon and Weaver 1949) and Pielou evenness index (*J'*; Pielou 1975).

4. Results

4.1. Classification of Seasonally Inundated Vegetation

Using TWINSPAN, 67 phytosociological samples were classified into two categories in the first division and eventually into seven categories in the third division (Fig. 2). The former was clearly characterized by the location of stands in the study area, the latter varying in respect to physiognomy, species composition and vegetation strati-

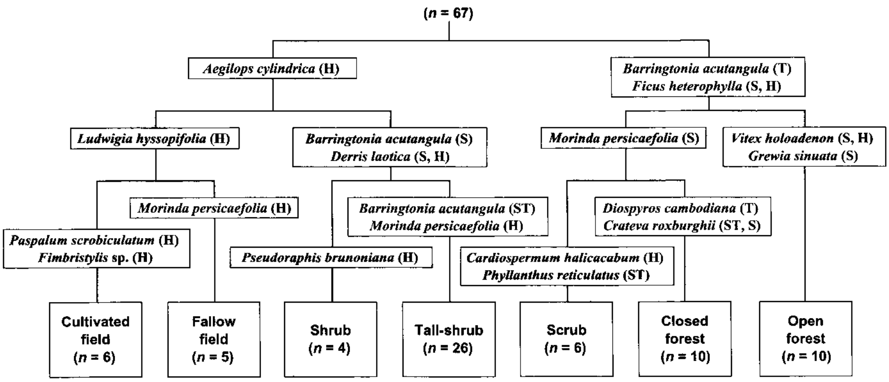

FIG. 2. Two-Way Indicator Species Analysis (TWINSPAN) dendrogram of 67 quadrats identifying seven vegetation types with indicator species listed at divisions. The number of quadrats in each vegetation type is indicated in *parentheses*. Abbreviations following species names are layers to which indicator species belonged: *T*, tree layer; *ST*, short-tree layer; *S*, shrub layer; *H*, herb layer

TABLE 1. Comparison of the mean distance from CLWL, mean height of vegetation, mean density of species (/100 m^2), and diversity indices among seven vegetation types

Vegetation types	Number of quadrats	Mean distance from CLWL (km)	Mean height of vegetation (m)	Mean density of species (/100 m^2)	Simpson D'	Shannon H'	Pielou J'
Cultivated field	6	4.1	0.3	11.2	0.577	2.103	0.887
Fallow field	5	4.5	1.1	13.0	0.333	1.171	0.456
Shrub	4	3.4	3.8	13.5	0.395	1.340	0.515
Tall shrub	26	3.6	6.3	15.9	0.428	1.559	0.567
Scrub	6	0.9	6.9	8.8	0.356	1.122	0.516
Open forest	10	0.2	10.8	8.0	0.390	1.177	0.583
Closed forest	10	0.6	13.8	8.0	0.439	1.354	0.658

CLWL, coastline at the lowest water level

fication (Fig. 1, Table 1, Table 2). Therefore, they were regarded as vegetation zones and vegetation types, respectively.

4.1.1. Vegetation Zones

Vegetation zones consisted of extensive cropland occupying the upper part of the study area (about 2–3 km in depth) and disturbed woodland fringing the coastal side of the study area (about 1–2 km in depth).

Stands of extensive cropland (n = 41) were separated from those of disturbed woodland (n = 26) by reference to *Aegilops cylindrica* (herb layer), a pioneer grass in seasonally dry habitats, as the indicator species (Fig. 2), and characterized by the growth of (1) similar pioneer herbaceous species such as *Melochia corchorifolia, Ludwigia hyssopifolia, Fimbristylis* sp., and *Lindernia crustacea*; (2) pioneer or early successional lianas such as *Derris laotica, Merremia hederacea, Phyllanthus reticulatus, Gmelina asiatica*, and *Hiptage triacantha*; and (3) pioneer or early successional woody shrubs and short-trees such as *Mimosa pigra, Croton krabas*, and *Hymenocardia wallichii* (Fig. 2, Table 2). This vegetation zone was subdivided into four categories of vegetation types (Fig. 2), both the mean distance from CLWL and mean density of species in stands in extensive cropland being larger than those in stands in disturbed woodland, while the mean vegetation height was lower (Table 1). The landscape of the extensive cropland was a mosaic of cultivated fields, abandoned fields of various successional stages, and agricultural infrastructure such as banks, channels, shallow ponds, and footpaths (Photo 1).

The indicator species utilized for the disturbed woodland were *Barringtonia acutangula* (tree layer) and *Ficus heterophylla* (shrub and herb layers). Tree and short-tree species such as *Diospyros cambodiana, Coccoceras anisopodum*, and *Crateva roxburghii*, shrubs such as *Morinda persicaefolia* and *Grewia sinuate*, and lianas such as *Combretum trifoliatum* and *Vitex holoadenon* occasionally accompanied these (Fig. 2, Table 2, Photo 2). This vegetation zone was subdivided into three vegetation types (see Fig. 2), "Scrub" indicating transitional vegetation over a wide area between the extensive cropland and seasonally inundated forest. The density of thick trees tended to increase toward the coastal side of the study area, whereas "Closed forest,"

TABLE 2. Synoptic table of indicator and preferential species in the seven vegetation types by Two-Way Indicator Species Analysis (TWINSPAN)

Vegetation types		Cultivated field	Fallow field	Shrub	Tall shrub	Scrub	Open forest	Closed forest
Number of quadrats		6	5	4	26	6	10	10
Mean density of species		11.2	13.0	13.5	15.9	8.8	8.0	8.0
Paspalum scrobiculatum	G	IV_{+}	-	-	I_{+}	-	-	-
Oryza sativa	G	II_{+}	-	-	-	-	-	-
Sesbania roxburghii	H	I_{+}	-	-	I_{+}	-	-	-
Aeschynomene indica	H	I_{+}	-	-	I_{+}	-	-	-
Passifora foetida	L	II_{+}	I_{+}	-	I_{+}	-	-	-
Cyperus pilosus	G	I_{+}	II_{+-1}	-	I_{+-1}	-	-	-
Brachiaria reptans	G	III_{+}	I_{+}	-	I_{+}	-	-	-
Nymphoides indica	H	III_{+}	III_{+}	1_{+}	-	-	-	-
Melochia corchorifolia	H	IV_{+}	III_{+-1}	-	I_{+}	-	-	-
Ludwigia hyssopifolia	H	V_{+-1}	III_{+-1}	1_{+}	I_{+}	-	-	-
Fimbristylis sp.	G	V_{+}	II_{+-3}	1_{+}	I_{+}	-	-	-
Lindernia crustacea	H	III_{+}	II_{+}	2_{+}	I_{+}	-	-	-
Aegilops cylindrica	G	III_{+}	III_{+}	3_{+}	IV_{+-1}	-	-	-
Mimosa pigra	S	III_{+}	III_{+}	4_{+-3}	IV_{+-2}	I_{+}	-	-
Pseudoraphis brunoniana	G	II_{+}	V_{+-5}	4_{1-5}	III_{+-3}	-	III_{+-1}	-
Derris laotica	L	II_{+}	I_{+}	1_{+}	V_{+-3}	III_{+-1}	-	-
Merremia hederacea	L	V_{+-1}	V_{+-4}	4_{+}	IV_{+-3}	IV_{+}	V_{+}	-
Barringtonia acutangula	T	V_{+}	V_{+-3}	4_{+-5}	V_{+-5}	V_{+-5}	V_{+-5}	V_{+-5}
Morinda persicaefolia	S	III_{+}	V_{+-1}	3_{+-2}	V_{+-2}	V_{1-5}	IV_{+-2}	V_{1-5}
Combretum trifoliatum	L	I_{+}	IV_{+}	3_{+-3}	IV_{+-3}	V_{+-2}	II_{+-1}	III_{+-2}
Phyllanthus reticulatus	L	I_{+}	IV_{+-3}	4_{+-2}	V_{+-5}	V_{+-1}	-	-
Gmellina asiatica	L	-	III_{+-1}	2_{+}	IV_{+-3}	III_{+-1}	-	-
Croton krabas	ST	-	III_{+}	4_{+}	IV_{+-3}	I_{+}	-	-
Hymenocardia wallichii	ST	-	II_{+}	-	II_{+-1}	I_{+}	-	-
Hiptage triacantha	L	-	II_{+}	2_{+-1}	IV_{+-2}	-	I_{+}	-
Dalbergia entadoides	L	-	-	1_{1}	III_{+-2}	-	-	-
Ipomoea aquatica	L	-	-	2_{+}	II_{+}	-	-	-
Ludwigia adscendens	H	-	-	-	I_{+-1}	-	-	-
Uvaria pierrei	S	-	-	-	I_{+-2}	-	-	-
Brownlowia paludosa	ST	-	-	-	II_{+-1}	I_{1}	-	-
Acacia thallandica	L	-	-	-	III_{+-2}	-	I_{2}	-
Cardiospermum halicacabum	H	-	-	-	I_{+}	V_{+}	I_{+}	-
Vitex holoadenon	L	-	-	2_{+-1}	IV_{+-5}	II_{2}	V_{2-5}	III_{1-2}
Crateva roxburghii	ST	-	-	-	I_{+}	I_{1}	III_{+}	V_{+-2}
Ficus heterophylla	S	-	-	-	-	IV_{1-2}	V_{+-1}	II_{+-1}
Diospyros cambodiana	T	-	-	-	-	I_{1}	I_{2}	V_{+-4}
Grewia sinuata	S	-	-	-	-	-	IV_{1-3}	I_{+}
Coccoceras anisopodum	T	-	-	-	-	-	-	II_{1-3}
Xanthophylum anisopodum	T	-	-	-	I_{+-1}	-	-	I_{4}

Roman numbers are appearance frequency; I, 1%–20%; II, 21%–40%; III, 41%–60%; IV, 61%–80%; V, 81%–100%

Symbols following appearance frequency indicate Braun-Blanquet's dominant scale (+, 1, 2, 3, 4, 5)

Growth forms; G, graminoids; H, herbs; S, shrubs; ST, short-trees; T, trees; L, lianas

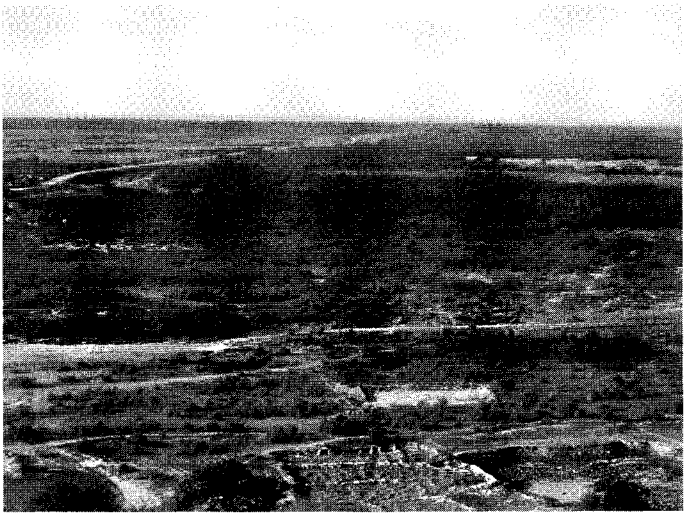

PHOTO 1. Landscape of the extensive cropland zone in the lowest water season (May 2005)

PHOTO 2. Landscape of the disturbed woodland zone in the highest water season (November 2003)

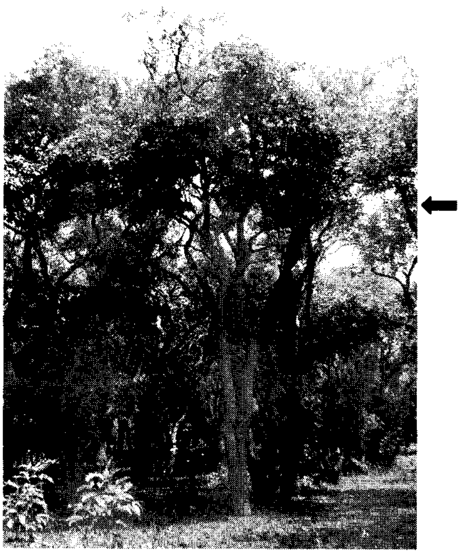

Photo 3. Aspect of emergent "Closed forest" fringing the shore in the lowest water season (February 2005). *Arrow* indicates the highest water level in the flood season

the most developed stage with the highest (mean height, 13.8 m) and most continuous (mean coverage, 92%) canopy, was only found on the coastal side located far from villages (Fig. 1, Table 1, Photo 3).

4.1.2. Vegetation Types

Seven categories of vegetation types, classified by TWINSPAN, included "Cultivated field," "Fallow field," "Shrub," and "Tall-shrub" in the extensive cropland zone and "Scrub," "Open forest," and "Closed forest" in the disturbed woodland zone (see Fig. 2). Vegetational characteristics of each type are summarized next.

"Cultivated field" ($n = 6$) was almost entirely occupied by paddy fields located in the comparatively high elevation area of the floodplain (waterlogged period, September–January) and cultivated extensively during the early part of the dry season. Under wet soil conditions just before flooding, the mean vegetation height was 0.3 m and the mean herb layer coverage scarce (2%). On the other hand, this type included large numbers of herbaceous species, such as *Merremia hederacea, Ludwigia hyssopifolia, Fimbristylis* sp., *Paspalum scrobiculatum, Melochia corchorifolia, Brachiaria reptans, Lindernia crustacea,* and *Aegilops cylindrica* (see Table 2). Current-year seedlings and/or sprouts of woody plants (e.g., *Barringtonia acutangula, Mimosa pigra,* and *Morinda persicaefolia*) and water plants (e.g., *Nymphoides indica* and *Pseudoraphis brunoniana*) also emerged (Table 2), the large variations in species composition among quadrats increasing the species diversity indices (see Table 1).

"Fallow field" ($n = 5$) referred to cultivated fields that had been abandoned for relatively few years and were characterized by a herb layer only, the mean height and coverage of recovered vegetation being greater than those of "Cultivated field" (1.1 m and 73% in the former, respectively). Herbaceous species, such as *Pseudoraphis* *brunoniana* and *Merremia hederacea*, and seedlings and/or sprouts of *Barringtonia acutangula*, *Combretum trifoliatum*, and *Phyllanthus reticulatus* occurred more frequently (Table 2), although *Paspalum scrobiculatum* was not recorded. Stands of this vegetation type were scattered in the upper part of the study area, the mean distance from CLWL being 4.5 km (Table 1).

"Shrub" ($n = 4$) was characterized by a shrub layer in which *Barringtonia acutangula* dominated (mean height, 3.8 m; mean coverage, 75%) and a large number of liana species flourished (Table 2). Shrubby species, such as *Mimosa pigra*, *Morinda persicaefolia*, and *Croton krabas*, and liana species, such as *Phyllanthus reticulatus*, *Combretum trifoliatum*, *Vitex holoadenon*, *Hiptage triacantha*, and *Merremia hederacea*, also occurred in the canopy. In the herb layer, *Pseudoraphis brunoniana* dominated and *Aegilops cylindrica*, *Lindernia crustacea*, and current-year seedlings of *Barringtonia acutangula* were occasionally recorded (Table 2). The distributional pattern of "Shrub" was mosaic in the "Cultivated field" range and sometimes comprised large patches.

In general, "Tall-shrub" ($n = 26$) was also a crowded vegetation type, with flourishing liana species as found in "Shrub." The height of the former reached to 6.3 m on average (Table 1), the maximum DBH in each quadrat attaining between 11.9 cm and 26.7 cm. Scattered individuals of *Barringtonia acutangula* were predominant in the canopy (note: in the present study, we regarded this developing foliage not as a shrub layer but as a short-tree layer), accompanied by *Croton krabas* and many woody liana species, such as *Phyllanthus reticulatus*, *Dalbergia entadioides*, *Gmelina asiatica*, *Combretum trifoliatum*, *Vitex holoadenon*, and *Acacia thailandica* (Table 2). Shrub and herb layers were composed of *Morinda persicaefolia*, *Derris laotica*, *Croton krabas*, *Hiptage triacantha*, *Mimosa pigra*, *Hymenocardia wallichii*, *Merremia hederacea*, *Pseudoraphis brunoniana*, and *Aegilops cylindrica*. The mean number of emergent species in a single quadrat (15.9 species/100 m^2) was the largest among the seven categories of vegetation types recognized (Table 1). Moreover, large numbers of indicator and preferential species overlapped with those of other vegetation types (see Table 2). "Tall-shrub" was widely distributed over the middle part of the study area (mean distance from CLWL, 3.6 km; Table 1), accompanied by phenomena such as isolated stands created by reclamation and degraded stands by selective logging. Therefore, from the point of view of vegetation succession, "Tall-shrub" was considered as a transitional stage between shrub and forest, showing relatively high species diversity (see Table 1) under varying human impacts.

"Scrub" ($n = 6$) was physiognomically a dense, shrubby vegetation located in the disturbed woodland zone (mean height of vegetation, 6.9 m; mean distance from CLWL, 0.9 km; Table 1). Compared floristically with "Tall-shrub" and "Shrub," "Scrub" was characterized by (1) disappearance or decrease in dominance of many herbaceous and liana species (e.g., *Aegilops cylindrica*, *Pseudoraphis brunoniana*, *Hiptage triacantha*, *Dalbergia entadioides*, and *Acacia thailandica*); (2) emergence of important species of seasonally inundated forest (e.g., *Ficus heterophylla* and *Diospyros cambodiana*); (3) frequent growth of *Cardiospermum halicacabum*, a perennial herb species; and (4) lower density of species (8.8 species/100 m^2; see Table 2). Predominant species coinciding with those of "Tall-shrub" were *Barringtonia acutangula*, *Combretum trifoliatum*, *Vitex holoadenon*, and *Phyllanthus reticulatus* in the short-tree layer and *Morinda persicaefolia*, *Gmelina asiatica*, *Derris laotica*, and *Merremia hederacea* in the shrub and herb layers.

The canopy of "Open forest" reached to 10.8 m on average ($n = 10$; Table 1), the stunted examples of *Barringtonia acutangula* (maximum DBH, 27.6–46.8 cm) having abundantly extended crowns (mean coverage of tree layer, 67%). Short-tree and shrub layers, which frequently appeared as dense bushes or blankets of foliage, contained *Morinda persicaefolia* and species characteristic of disturbed woodland zones, such as *Vitex holoadenon*, *Ficus heterophylla*, *Grewia sinuate*, and *Crateva roxburghii* (see Table 2). On the other hand, the herb layer was poor (mean coverage, 22%) under dark conditions, and several species such as *Merremia hederacea* and *Pseudoraphis brunoniana* were infrequently recorded. Species density was only 8.0 species/100 m^2. "Open forest" occurred along the shore of the lowest water season (mean distance from CLWL, 0.2 km; Table 1), a habitat in which waterlogged conditions continued for about 6 months, from the end of July to early in February. Stumps left over from selective logging were apparent, and branches had also been cut by local people for firewood and fish-catching materials, even in the flood season.

"Closed forest" ($n = 10$) was the most developed stand of seasonally inundated forest; namely, the mean canopy height (13.8 m, Table 1) and coverage (92%), and maximum DBH in each quadrat (38.9–63.5 cm), were greater than those of "Open forest," although species density (8.0 species/100 m^2), species indices, and locations of stands (mean distance from CLWL, 0.6 km) were similar between the two vegetation types (Table 1). The dominant canopy species was *Barringtonia acutangula*, accompanied by water-durable trees (*Diospyros cambodiana*, *Coccoceras anisopodum*, and *Xanthophyllum glaucum*) and the liana *Combretum trifoliatum* (Table 2). In the short-tree layer, a small number of *Vitex holoadenon* and *Crateva roxburghii* occurred (mean coverage, 13%), the shrub layer being almost entirely occupied by *Morinda persicaefolia* (mean coverage, 75%). The herb layer was also poor, including primarily *Morinda persicaefolia*, *Vitex holoadenon*, and *Crateva roxburghii* (mean coverage, 10%). In the present study, "Closed forest" was infrequently found, occurring as remnant patches far from villages (about 7 km west from main sampling area; see Fig. 1).

4.2. Ordination of Seasonally Inundated Vegetation

The ordination of 67 quadrats on the two principal axes of DCA is given by Fig. 3, in which seven categories of vegetation types classified by TWINSPAN were overlaid. Table 3 shows correlations between DCA scores and parameters of stand characteristics.

Axis 1 (eigenvalue, 0.794) had negative correlations with vegetation height and tree layer coverage (Table 3; $P < 0.001$, Spearman's ranking correlations). Additionally, Axis 1 also had positive correlations with species density, short-tree layer coverage, Shannon H, and distance from CLWL (Table 3; $P < 0.05$, Spearman's ranking correlations). Axis 2 (eigenvalue, 0.427) had negative correlations with tree layer coverage, short-tree layer coverage, and vegetation height (Table 3; $P < 0.05$, Spearman's ranking correlation), but a positive correlation with Shannon H' (Table 3; $P < 0.05$, Spearman's ranking correlation).

Along Axis 1, seven vegetation types roughly followed the order "Closed forest", "Open forest", "Scrub", "Tall-shrub", "Shrub", "Fallow field", and "Cultivated field" (Fig. 3). Comparing the distributional ranges of the vegetation types on the two prin-

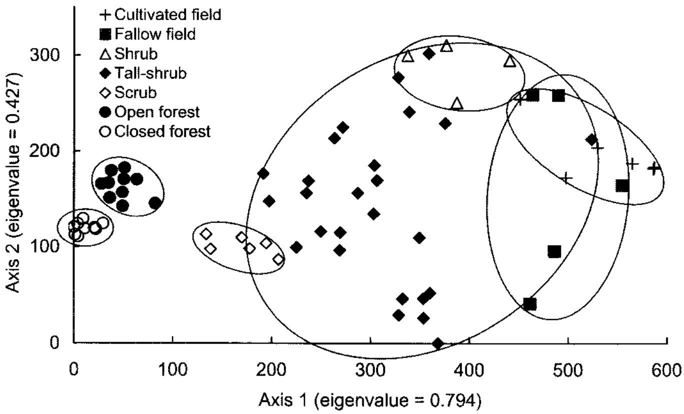

FIG. 3. Detrended Correspondence Analysis (DCA) ordination of 67 quadrats. The different vegetation types classified by TWINSPAN are *overlaid* and *encircled*

TABLE 3. Correlations between DCA scores and parameters of stand characteristics

Parameter	Axis 1	Axis 2
Height of vegetation	−0.942***	−0.315**
Density of species	0.447***	0.200
Simpson *D′*	0.088	0.220
Shannon *H′*	0.242*	0.266*
Pielou *J′*	−0.126	0.139
Coverage of T	−0.728***	−0.873***
Coverage of ST	0.390**	−0.331*
Coverage of S	−0.018	−0.098
Coverage of H	0.144	0.233
Distance from CLWL	0.803***	0.061

T, tree layer; ST, short-tree layer; S, shrub layer; H, herb layer; CLWL, coastline at the lowest water level

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; Spearman's ranking correlations

cipal axes, three vegetation types constituted a disturbed woodland zone, which was characterized by the existence of a tree and/or short-tree layer and a limited number of woody species adapted to long-term inundation, closely clustered.

5. Discussion

5.1. Structure of Seasonally Inundated Vegetation

Seasonally inundated vegetation covering the vast floodplain of the study area was clearly affected by flooding stress and man-made disturbances. CNMC/NEDECO (1998b) listed up to about 200 vascular plant species in the Tonle Sap area, describing the introduced floodplain vegetation as comprising three major habitat types (McDonald et al. 1997): (1) short-tree and shrubland vegetation, covered by semicontinuous, locally homogeneous stands of short trees and large shrubs; (2) stunted swamp forest, comprising trees 7–15 m in height and dense gallery forests that commonly skirted the lake shoreline of the floodplain; and (3) aquatic herbaceous vegetation, being either floating or emergent (1–3 m tall). In the present study, based on phytosociological data from 67 quadrats (10 m × 10 m each), we recorded 122 vascular plant species and seven vegetation types on the coastal side of the floodplain (about 4 km in depth; about 1–6 m a.s.l.).

Of the 122 plant species, indicator and preferential species of the seasonally inundated forest, namely, "Closed forest" and "Open forest" in our study, were limited to taller trees such as *Barringtonia acutangula*, *Diospyros cambodiana*, *Coccoceras anisopodum*, and *Xanthophyllum glaucum*, shorter trees such as *Crateva roxburghii*, shrubs such as *Morinda persicaefolia*, *Ficus heterophylla*, and *Grewia sinuate*, and lianas such as *Vitex holoadenon* and *Combretum trifoliatum* (see Table 2). On the other hand, it should be noted that *Mimosa pigra*, a prickly woody shrub originating from tropical America, has spread extensively in the cropland zone. It is currently considered to be one of the most invasive and problematic species in the seasonally inundated vegetation (Tim et al. 2005).

Two types of wooded vegetation distinguished by McDonald et al. (1997), namely short-tree and shrubland vegetation, and stunted swamp forest, seemed to roughly correspond to "Shrub" + "Tall-shrub" and "Scrub" + "Open forest" + "Closed forest" in the present study, respectively. However, "Shrub" constituted crowded recovery areas neighboring "Cultivated field", and "Tall-shrub" consisted of 26 dense stands with large floristic and architectural variations in disturbed areas (see Table 1, Fig. 3). Because of stumps and selective cuts on branches, "Scrub" and "Open forest" are also implicated in degraded vegetation suffering from human impact. Therefore, these vegetation types, excepting "Closed forest", might be seminatural and still developing. Accordingly, to reconstruct the original vegetation structure of the inundated area, both distributional patterns along the waterlogged versus drought condition gradient, not subject to human impact, and regeneration traits for key species (see Table 2) should be examined carefully.

5.2. Importance of *Barringtonia acutangula*

The genus *Barringtonia* (Lecythidaceae) is distributed in tropical regions from East Africa to the Pacific Islands and frequently occurs in freshwater swamps near rivers and lakes (Payens 1967). In the lowland areas of Cambodia, *Barringtonia acutangula* is highly useful, providing firewood, edible young shoots, and medicinal bark, roots, and fruits (McDonald et al. 1997; Dy phon 2000; Kham 2004).

The present survey revealed that *Barringtonia acutangula* grew vigorously, becoming the dominant species in six vegetation types, excluding "Cultivated field". The species regenerated from seedlings (growing from floating fruits) and also sprouted from stumps or floated twigs, thereby achieving maturity even in interior sites in the extensive cropland zone. Considering these phenomena, it can be concluded that *Barringtonia acutangula* had originally prevailed even more than presently over the floodplain, and that an investigation of the life history strategies of this species should be a priority in the restoration of disturbed sites and the wise management of seasonally inundated vegetation.

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