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REPORT

The Flood Pulse as the Underlying Driver of Vegetation in the Largest Wetland and Fishery of the Mekong Basin

Mauricio E. Arias, Thomas A. Cochrane,
David Norton, Timothy J. Killeen, Puthea Khon

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Abstract The Tonle Sap is the largest wetland in Southeast Asia and one of the world's most productive inland fisheries. The Mekong River inundates the Tonle Sap every year, shaping a mosaic of natural and agricultural habitats. Ongoing hydropower development, however, will dampen the flood pulse that maintains the Tonle Sap. This study established the current underlying relationship among hydrology, vegetation, and human use. We found that vegetation is strongly influenced by flood duration; however, this relationship was heavily distorted by fire, grazing, and rice cultivation. The expected flood pulse alteration will result in higher water levels during the dry season, permanently inundating existing forests. The reduction of the maximum flood extent will facilitate agricultural expansion into natural habitats. This study is the most comprehensive field survey of the Tonle Sap to date, and it provides fundamental knowledge needed to understand the underlying processes that maintain this important wetland.

Keywords Cambodia · Ecohydrology · Wetlands · Tropical floodplain vegetation

INTRODUCTION

Wetlands are among the most productive and valuable ecosystems in the planet. They cover only 6 % of the earth's surface, but their role in providing services such as flood abatement, biodiversity, agriculture, and fisheries is disproportionally high (Junk et al. 2013). The delivery of these services is prevailed by the hydrology regime that wetlands are subject to. The seasonal hydrological regime of large floodplain wetlands—characterized by a strong and predictable unimodal pattern known as the Flood Pulse—was hypothesized as the driving force of major biogeochemical cycles and life-form adaptations (Junk et al. 1989). Research in the Amazon found that the most influential factors determining vegetation distribution and composition in large floodplains are: water level, flood duration, physical stability (sedimentation and erosion), succession, water chemistry, soils, and human impact (Junk and Piedade 1997; Worbes 1997; Ferreira and Stohlgren 1999; Parolin et al. 2004). In the Okavango Delta in Botswana, plant species composition was also found to be driven by flooding (Murray-Hudson 2009; Murray-Hudson et al. 2011), with inter-annual flooding frequency as the main driver of herbaceous plant distribution. The "wet-dry tropics" in the Northern Territory of Australia was also found to have a strong flooding seasonality responsible for the floodplains' biophysical patterns (Bowman and McDonough 1991; Finlayson 2005; Warfe et al. 2011). More recently, spatial patterns of plant species in the Everglades in Florida were shown to follow predictable distributions dictated by the hydroperiod regime (Foti et al. 2012). Despite geographical differences among large tropical wetlands, hydrology is the key factor in determining vegetation patterns and related ecological processes.

Among the world's large tropical floodplains, the Tonle Sap is arguably the one where the hydrology–ecology interaction has been studied the least (Junk et al. 2006; Kummu et al. 2006; Lamberts 2006; Parolin and Wittmann 2010). Nonetheless, a few field surveys in the floodplain have revealed important information about this interaction (McDonald et al. 1997; Hellsten et al. 2003; Araki et al. 2007). Plant richness is low compared to other tropical

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ecosystems, with 233 plant species identified within the three main natural habitats: gallery forest, shrublands, and aquatic herbaceous vegetation (McDonald et al. 1997). In addition to natural vegetation, different varieties of rice and other crops are major components of this ecosystem (Hellsten et al. 2003; Araki et al. 2007).

The Tonle Sap is the Mekong's largest and most important wetland because of its nutritional, cultural, and ecological contributions to Cambodian society. Eighty percent of the human-consumed protein in Cambodia comes from freshwater fish and other aquatic animals (Hortle 2007), a majority of which are caught in the Tonle Sap. More than 10 % of the country's population lives in the Tonle Sap region, and their agricultural, fishing, and trading livelihoods are intrinsically supported by the ecosystem (Keskinen 2006). The hydrology of the Tonle Sap is driven by the flood pulse from the Mekong River, which inundates the floodplain every year by up to 9 m over several months. This periodic and extensive flood pulse has shaped a mosaic of natural and agricultural habitats that—in combination with the replenishment of nutrients from the Mekong—sustain the primary production of this unique ecosystem.

The hydrology of the Mekong and the Tonle Sap is well understood (MRC 2005; Costa-Cabral et al. 2007), and it is now acknowledged that the historical flood regime is likely to change as a result of water resources infrastructure development and climate change (Xu et al. 2009; Grumbine and Xu 2011; Lauri et al. 2012). Large-scale modeling studies using limited field data predict that hydropower will impact the Mekong and Tonle Sap by dampening the seasonal water fluctuation, reducing sediment loads, shifting habitats spatial patterns, and blocking fish migration routes (Kummu et al. 2010; Arias et al. 2012; Lauri et al. 2012; Ziv et al. 2012). Field-based observations that relate the hydrology to ecosystem properties and human use are needed in order to validate the findings from modeling projections.

The main objective of this study was to identify the main drivers of vegetation characteristics in the Tonle Sap floodplain. Specifically, the following questions were addressed:

1. What is the relationship among hydrological indicators?
2. What is the influence of hydrological indicators on soils, human use, and current vegetation patterns?
3. What is the influence of hydrological indicators, soils, and human use on plant species composition?

MATERIALS AND METHODS

Field Sites Description

Field surveys were undertaken in three distinct sites around the lake (Fig. 1), providing a good representation of the different natural and agricultural vegetation that exist in the floodplain and covering all five provinces surrounding the lake (Kampong Chnnang, Pursat, Battambang, Siem Reap, and Kampong Thom). The study areas were chosen because they are under protection by the Cambodia Ministry of the Environment or Conservation International-Cambodia, both of whom facilitated logistics and field guidance. Two of the sampling areas, Stung Sen and Prek Toal, included core zones of the UNESCO Tonle Sap Biosphere reserve, which are described elsewhere (McDonald et al. 1997; Hellsten et al. 2003). The other study area, Kampong Prak, lies within the Biosphere reserve buffer zone in Pursat Province.

Vegetation and Soil Collection Procedure

A total of eight transects were surveyed across the floodplain. Each transect started at the edge of the lake and followed the elevation gradient to cover the largest range of flooding conditions and vegetation communities (Fig. 1). Overall, seventy-seven 100 m^2 plots were measured in transects covering a distance of 5–15 km, with field work carried out between March 2011 and March 2012.

Information on water regime, soil characteristics, vegetation, and human use were collected at each plot. GPS coordinates were recorded and present land use/land cover (LULC) was defined according to classes in existing maps (JICA 1999) and previous studies (McDonald et al. 1997; Hellsten et al. 2003; Araki et al. 2007). An index of human use was determined based on evidence of wood extraction, evidence of recent fire in vegetation and soils, and the presence of cattle. Surface soils (<30 cm) were described according to the Food and Agricultural Organization soil description guidelines (FAO 2006). Soil composite samples (500 g) from horizons A and B were collected in plastic bags for laboratory analyses. Particle size, pH, color, electrical conductivity, and nutrients were analyzed at Research Development International-Cambodia near Phnom Penh. Soil moisture and organic matter were analyzed at the Faculty of Agronomy of the Royal University of Agriculture (RUA) in Phnom Penh. Soil moisture was determined by weight difference after drying the samples at 105 °C for at least 24 h. Organic matter was estimated by the ignition loss method (weight loss of the soil after putting the samples in a muffle furnace at 600 °C for 5–6 h). Particle size fraction was determined using a hydrometer. pH and electrical conductivity were measured on a 1:5 by mass solution of soil to distilled water using a YSI handheld digital probe. Soil color was recorded for dry and wet samples using standard Munsell color charts. Nitrogen and potassium were analyzed using LaMotte colorimetric tests.

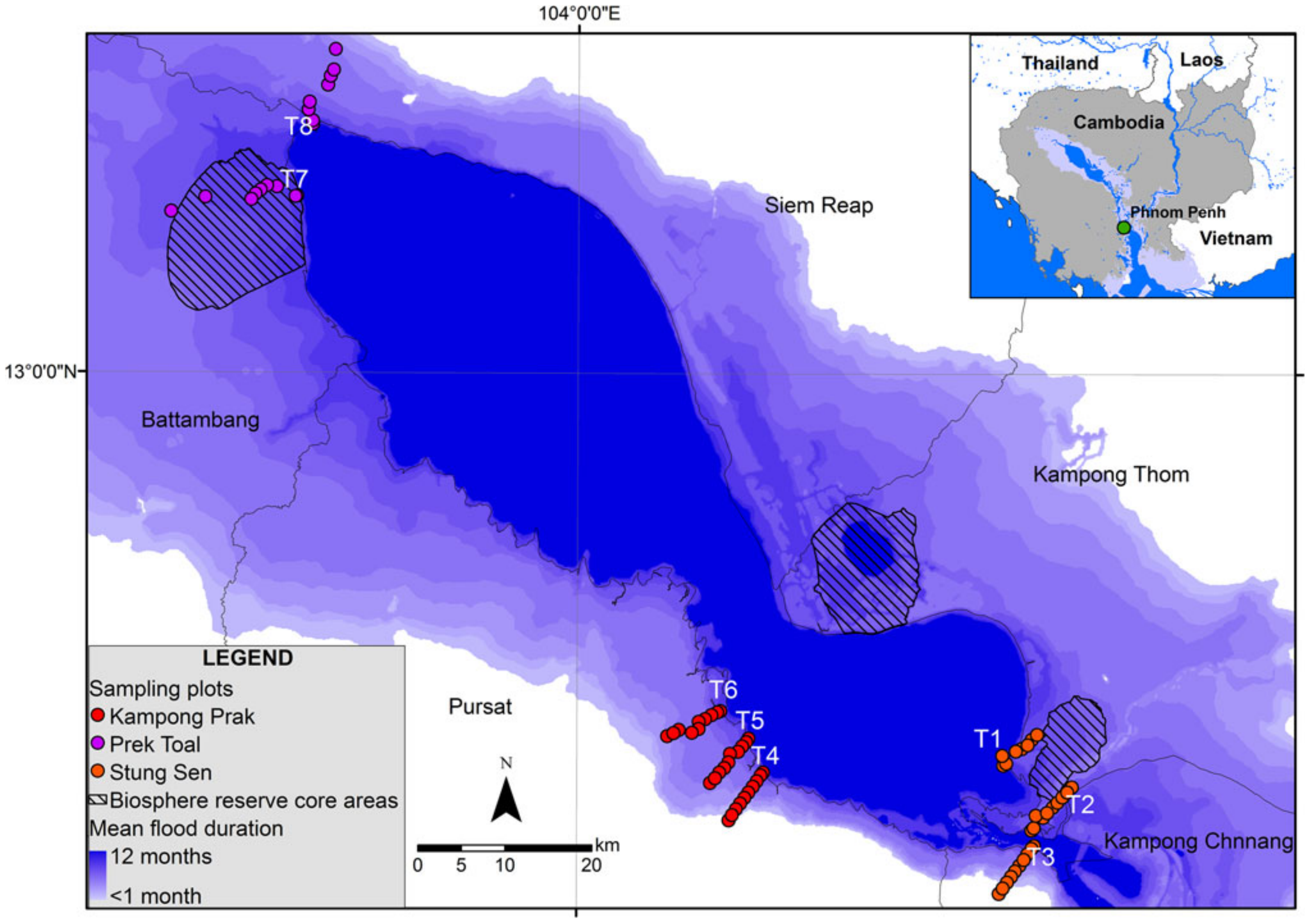

Fig. 1 Sampling plot locations along survey transects T1–T8 overlaid on an average annual flood duration grid

For vegetation sampling, plants were classified as either canopy or understory based on a diameter at breast height (DBH) threshold of 3.2 cm. At the canopy level, all trees, lianas, and large shrubs within the 100 m^2 plot were identified, DBH recorded, one wood core per species extracted, and maximum height per species estimated using a tangent height gauge. Canopy cover was measured with a canopy densiometer at the center of the plot facing each cardinal point. For measurements of the understory and ground vegetation cover, three 1 m^2 quadrants were randomly located within the larger plot. Understory cover was measured by placing the canopy densitometer at ground level, and ground vegetation cover was based on a visual estimate. All understory and ground plants on the three quadrants were identified, and measurements per species included: diameter at ground level, height, stems count or ground coverage, and wet weight using an analog ±10 g scale. Cover and biomass of standing litter in the 1 m^2 quadrants were also measured to provide an indicator of the litter available to the aquatic phase just before flooding. Selected samples of the harvested vegetation and litter were taken to RUA to determine moisture content. Plants were given unique identities in the field using a reference guide compiled from names, photographs, and descriptions from previous field visits, and from previous study by Dy Phon (2000), McDonald et al. (1997), and Davidson (2006). Plant specimens were pressed and taken back to Phnom Penh for identification at the National Herbarium of Cambodia at the Royal University of Phnom Penh. 10 of the 88 plant species encountered were not identified to the species level, and therefore a unique id (using the family name when known) was used for subsequent analyzes.

The vegetation information collected in the field was used to estimate above ground biomass (AGB) per unit area. AGB of woody vegetation at the canopy level (trees, lianas, and large shrubs) was estimated with an allometric equation for tropical dry forest (Chave et al. 2005), which estimates AGB as a function of wood density, tree height, and DBH. No allometric relationships for understory plants existed for the Tonle Sap, so we obtained understory AGB by harvesting 242 samples of vegetation in 1 m^2 subplots and developing allometric equations for shrubs and herbaceous vegetation as a function of diameter, height, stem count, and/or coverage.

Hydrological Data

Mean annual flood duration, flood frequency, and maximum water depth were used as surrogates of hydrological conditions for establishing relationships to soil, human use, and vegetation. Records of daily water level since 1997 exist at Kampong Luong (N12° 34.598 E104° 12.472, Fig. S1 in the Electronic supplementary material). There is a strong linear relationship between water levels at Kampong Luong and water levels in the Tonle Sap River at Prek Kdam (40 km away from Phnom Penh; Inomata and Fukami 2008), and we used this relationship to extend the Kampong Luong time series back to 1986. The hydrological patterns observed during 1997, 1998, and 2000 are representative of the average, dry, and wet conditions, respectively, of the contemporary water level patterns (Kummu and Sarkkula 2008; Arias et al. 2012). Water levels were used in combination with a digital elevation map with a 100 m horizontal resolution to create maps of annual flood duration (number of days per year with standing water) and flood frequency (fraction of years when flooding occurs). A detailed methodology of how flood duration and frequency maps were created, and a validation of this flood mapping method is provided elsewhere (Arias et al. 2012). These hydrological parameters were then determined for each survey plot by overlaying the GPS coordinates on the maps and matching the flood duration and frequency values to the survey points using GIS zonal statistics tools. Moreover, water depth was measured directly at each of the survey plots with a Dr Lange HT 1 probe and/or a Speedtech Instruments water depth probe within 23 days of the peak of the wet season in October 2011. Records at Kampong Luong were used to correct the field measurements to represent the maximum water level during the season. Maximum water levels during the 2011 wet season were similar to levels from 2000, the largest ever measured on the lake.

Statistical Analyses

Prior to carrying out any statistical inferences, measured datasets were checked for normality using histograms, qq plots, and the Shapiro–Wilk test. To fulfill normality conditions, a square-root transformation was applied to AGB, height, litter cover, ground cover, understory cover, canopy cover, species richness, and soil pH data. In order to explore the relationship among hydrological indicators, linear relationships among hydrological indicators (flood duration, flood frequency, maximum water level) and soil moisture were evaluated with Pearson correlations (*r* values) using pairwise comparisons. The relationship between soils and hydrology was also examined via Pearson correlations, but in addition, principle components (PCs) were calculated to determine the main gradients of variance among soils. The impact of clearance (presence of recent crops and fire) on vegetation structure (height, canopy cover, and AGB) and its spatial distribution along the flooding gradient were examined using analysis of variance (ANOVA). The role of hydrology and soils in predicting vegetation structure was evaluated by linear models for all possible interactions among flood duration and soil PCs. The linear models were compared according to the predictability (r^2 coefficients) and the model's certainty (*p* value). Plots outside the seasonal floodplain (permanent lake and village crops not flooded during October 2011) were excluded from both the ANOVA and the linear models. All statistical analyses were done using the software R 2.13.1 (http://www.r-project.org/).

The influence of flood duration, soils PCs, and human use on plant species composition was analyzed using two ordination techniques: detrended correspondence analysis (DCA) and detrended correspondence canonical analysis (DCCA). DCA is an indirect gradient technique in which the underlying structure of the plant species composition is extracted and compared with environmental gradients; in contrast, DCCA is a direct gradient technique in which the axes of plant species composition variation are constraint by selected environmental variables (Ter Braak 1986). Similarities in the results from the DCA and DCCA imply that the intrinsic variance in plant species composition is caused by the measured environmental variables. Both techniques were applied using the software CANOCO (Lepš and Šmilauer 2003) with the same input data: one matrix of species presence/absence per plot, and another matrix with measured environmental variables from each plot. The predictability of these techniques was assessed via Eigenvalues of plot scores (a measure of how much variation is explained along the gradient axes in standard deviation units), species–environment correlations (linear correlations between the environmental gradients and the species composition axes), and interset correlations (linear correlations between the environmental data and the plot scores of plant species; Ter Braak 1986). The environmental variables were analyzed in two different groups: one with flood duration, soils PCs, and human use (a value between 0 and 3 based on the presence of fire, agriculture, and/or cattle), and another with biological-based variables (AGB, height, litter cover, ground cover, understory cover, canopy cover, and species richness). Plots outside the seasonal floodplain and plots with only one plant species were excluded from the analyses as they formed outliers in the ordinations.

RESULTS

A summary table was prepared (Table 1) in order to provide a general description of hydrological patterns, soil

Table 1 Mean and standard deviation (in parenthesis) of computed flood duration and field observations for each habitat

Habitat	*n*	Flood duration (days)	Water max depth (m)	Soil moisture (%)	Clay (%)	Sand (%)	Soils organic matter (%)	Species richness	Key plant species	Ground cover (%)	Canopy cover (%)	Max height (m)	Total AGB (kg/m^2)	Clearance[a]
Open water	2	335 (43)	9.5 (0.2)	49 (1)	33 (4)	56 (5)	1.7 (0)	0 (0)	NA	0 (0)	0 (0)	0 (0)	0 (0)	NA
Aquatic grassland	4	277 (35)	8.9 (0.3)	33 (13)	41 (5)	31 (9)	10.3 (3.9)	3 (2)	*Brachiaria mutica*	70 (5)	3 (5)	1.7 (0.6)	0.9 (0.3)	0
Open forest	8	240 (48)	8.4 (0.6)	30 (7)	46 (9)	38 (11)	10.2 (5.0)	5 (2)	*Barringtonia acutangula*	35 (28)	30 (31)	8.2 (4.4)	2.3 (1.7)	3
Closed forest	19	229 (46)	7.6 (0.7)	24 (10)	49 (8)	31 (11)	8.5 (2.1)	6 (2)	*Barringtonia acutangula*	20 (12)	63 (23)	11.2 (3.9)	3.1 (3.1)	4
Shrubland	12	210 (40)	6.9 (0.8)	21 (7)	54 (14)	32 (12)	11.4 (4.0)	4 (2)	*Vitex holoadenon*	23 (10)	58 (16)	4.4 (1.7)	1.4 (1.9)	4
Grassland	6	208 (12)	8.0 (0.3)	24 (8)	50 (9)	32 (13)	9.0 (3.1)	5 (2)	*Mimosa pigra*	46 (25)	13 (11)	3.4 (3.7)	0.6 (0.4)	5
Tall shrubland	12	149 (26)	5.2 (1.2)	16 (6)	34 (11)	44 (11)	9.4 (2.6)	9 (2)	*Hymenocardia wallichii*	19 (8)	61 (14)	6.6 (2.1)	2.0 (1.4)	3
Receding rice	2	137 (13)	5.3 (0.3)	26 (1)	30 (13)	56 (12)	5.8 (4.7)	8 (0)	*Oryza sativa*	55 (1)	0 (0)	3.4 (4.0)	0.7 (0.1)	2
Floating rice	3	110 (23)	4.4 (0.7)	14 (7)	36 (18)	47 (14)	5.5 (4.0)	4 (4)	*Oryza sativa*	5 (8)	0 (0)	0.3 (0.3)	0.0 (0.0)	3
Abandoned field	3	69 (20)	2.6 (0.8)	6 (1)	21 (5)	45 (11)	4.3 (2.5)	3 (2)	*Cynodon dactylon*	27 (17)	0 (0)	1.2 (0.9)	0.4 (0.5)	0
Village crop	2	24 (33)	0.0 (0.0)	4 (0)	5 (0)	80 (0)	2.2 (2.5)	4 (0)	*Cocos nucifera*	22 (32)	36 (51)	13.6 (6.2)	14.7 (14.1)	2
Wet season rice	4	10 (17)	0.8 (0.9)	4 (1)	12 (4)	55 (21)	2.3 (1.8)	1 (0)	*Oryza sativa*	6 (6)	1 (3)	0.0 (0.0)	0.0 (0.1)	4

AGB Above ground biomass

[a] Number of plots where clearance (fire or agriculture) was observed

characteristics, and vegetation communities along the flooding gradient. In addition, detail information from each of the survey plots is provided in the Supplementary information Electronic supplementary material (Tables S2–S4). All the transects started at an elevation of approximately 1.5 m above sea level (asl; measured at Hatien, Vietnam), which is the mean water surface elevation during the dry season, and the highest elevation surveyed was 11.5 m asl, well above the maximum water level recorded (10.3 m asl). The average terrain slope was 0.06 %, varying from 0.01 to 0.14 %. Greater habitat and plant species variation was associated with stepper slopes, while transects with flattest terrain had the most contiguous stands of seasonally flooded trees and shrubs. At elevations below 2 m asl (flood duration between 8 and 10 months annually), soils were predominantly sandy clays and vegetation communities include aquatic grasslands and gallery forest with little understory coverage (open forest) and a moderate number of plant species (average 3–5 per 100 m^2). Between 2 and 5 m asl (flood duration 5–8 months y^{-1}) soils were mainly clays, and vegetation communities included closed forest with understory, shrublands, and grasslands with an average of 4–6 species per 100 m^2. Four of the 5 seasonally flooded grasslands had evidence of fire in recent years. Between 5 and 9 m asl (flood duration 1–5 months y^{-1}), soils ranged from clay loams to loams, and vegetation gradually transitioned into a mosaic of natural and agricultural communities, with tall shrublands, floating and recession rice fields, and abandoned rice fields. Because of the mixed habitat types and human uses, this region had the most variation in species richness, with 9 ± 2 species per 100 m^2 in tall shrublands to 3 ± 2 per 100 m^2 in the abandoned fields. Above 9 m asl, natural flooding from the Tonle Sap lasts a maximum of 1 month annually, and it remains dry for at least 3 in every 10 years. Therefore, this upper part is dominated by conventional rice paddies and village crops that cannot tolerate long and deep flooding; rainfall and irrigation are the primary means of water for agriculture in this region. Soils in this area had a sandy loam texture and village crops at the floodplain boundary were mainly citrus, mangos, cashews, and sugar palm, among others.

ANOVA tests showed that there are no significant differences in canopy height, canopy cover, or aboveground biomass among the 3 survey sites (aka., Stung Sen, Kampong Prak, and Prek Toal). There appears to be differences in species richness at the 95 % confidence level between Stung Sen (2.1 ± 0.6) and Kampong Prak (2.6 ± 0.8), but species richness in Prek Toal (2.2 ± 0.6) was not significantly different from the other two. Overall, 25 of the 88 plant species encountered were present in all 3 regions, and another 15 were found in at least two sites.

Table 2 Pair-wise Pearson correlation coefficients (*r*) among hydrological indicators. $p \leq 0.001$ for all correlations

	Max water depth	Flood frequency	Soil moisture
Flood duration	0.88	0.61	0.71
Max water depth	–	0.59	0.79
Flood frequency	–	–	0.55

Relationship Among Hydrological Indicators

As expected, there is strong correlation among different hydrological indicators in the Tonle Sap. Analysis of maximum water depth, mean annual flood duration, flood frequency, and dry season soil moisture revealed significant ($p \leq 0.001$) correlations for all plausible one-to-one relationships (Table 2). The strongest correlation was between maximum water depth and flood duration ($r = 0.88$). Flood frequency had the lowest correlation to the other hydrological parameters (0.55–0.61), mainly because most of the wetland area floods every year and the distribution of flood frequency values is quite skewed. Given the strong relationship among the three hydrological indicators, subsequent analyses are presented only for mean annual flood duration, which is the variable that most directly represents seasonal flooding patterns.

Influence of Annual Flood Duration on Soils

Nine of the soils parameters analyzed were found to be significantly correlated with flood duration (Table 3). Strongest correlations ($p \leq 0.001$) were found with clay content (0.56), electrical conductivity (0.70), sand content (−0.48), and mottles content (0.40). The variability among all of the 16 soil variables was summarized via principle component analysis (PCA), which explained 64 % of the variance into four PCs (Table S5 in the Electronic supplementary material). The 1st PC explained 24 % of the variance among all soils data and showed a strong correlation with flood duration ($r = 0.73$, $p \leq 0.001$). The soil attributes with the strongest weightings on the 1st PC were: clay content, sand content, organic content, electrical conductivity, and soil moisture. Moreover, the 2nd, 3rd, and 4th PCs explained 19, 12, and 9 % of the soils data variance, respectively, and although the 2nd and 3rd PCs were also significantly correlated to flood duration, the relationships were much weaker and less significant than for the 1st PC.

Influence of Annual Flood Duration on Human Use

The difference in the mean flood duration between cleared and non-cleared plots was significant ($p \leq 0.001$). Vegetation

Table 3 Pair-wise Pearson correlation coefficients (r) between soil properties and flood duration

Soil property	Pearson's r
Clay content	0.56***
Plant available water	0.21
pH	0.22
N content	0.18
Sand content	−0.48***
Color dry soil	0.24*
K content	−0.32**
Electrical conductivity	0.70***
Organic matter content	0.36**
Silt content	−0.18
Color wet soil	0.23*
Moisture content	0.71***
A horizon depth	0.09
Organic layer depth	−0.16
Mottles content	0.40***

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$

clearance occurred preferentially in areas that flood on average 5 ± 2 months y^{-1}, whereas areas that flood for longer time (7 ± 2 months y^{-1}) were predominantly used for selected wood harvesting and complete vegetation clearance was thus rare.

Influence of Annual Flood Duration and Soils on Vegetation Structure and Species Richness

Mean annual flood duration and soil properties play a significant role in determining canopy height, canopy cover and AGB (Table S6 in the Electronic supplementary material). However, statistical models yielded low to moderate r^2 coefficients. Among response variables, canopy height showed the most significant r^2 coefficients, while AGB yielded the least significant relationships. The strongest r^2 was the model of canopy height as a response of flood duration, and the 2nd, 3rd, and 4th PC of soils ($r^2 = 0.593$). The 1st PC of soils was excluded from this analysis because of its high correlation with flood duration.

Plots of vegetation characteristics as a response of annual flood duration suggest that the underlying relationship between vegetation and flood duration is complex (Fig. 2). The mean and standard deviation of canopy height tended to increase with flood duration, with a maximum of 8.4 ± 4.3 m at plots flooded 6–7 months annually (Fig. 2a). Species richness followed a unimodal trend, with a maximum number of species occurring in plots flooded 3–4 months annually, and then decreasing toward both drier and wetter plots (Fig. 2b). A very similar unimodal pattern was followed by the presence of the most abundant trees and shrubs in the floodplain, with the main difference being that the occurrence of these species clearly peaked in plots flooded 7 months annually (Fig. 2c).

Influence of Annual Flood Duration and Other Drivers on Plant Species Composition

Strong correlations (0.87 and 0.80) between the 1st and 2nd axes of the DCA and the DCCA suggest that the variables analyzed were good descriptors of the intrinsic variance in species composition. For the environmental variables (annual flood duration, soil PCs, and human use), we found the strongest correlations with the 1st gradient axis to be with flood duration (0.68 and 0.84 in the DCA and the DCCA, respectively; Table 4). We infer that the 1st axis is a good representation of seasonal flooding patterns in the floodplain. Species–environment correlations with the 1st axis were 0.75 and 0.92 in the DCA and the DCCA, respectively. For the biological variables, we found good interset correlations between the 1st axis and litter cover, subcanopy cover, and herbs AGB. Species–environment correlations for the 1st axis were 0.84 and 0.92 in the DCA and the DCCA, respectively. Species–environment correlations with the 2nd axis were 0.72 and 0.82, while the Eigenvalues were 0.41 and 0.35 in the DCA and DCCA, respectively.

DISCUSSION

Most of what is written about the Tonle Sap's vegetation is based on conceptual models (McDonald et al. 1997; Hellsten et al. 2003) or highly localized observations (Araki et al. 2007). The information in these reports was valuable in scoping our study, but did not identify the main drivers of vegetation characteristics. In this paper, we present a comprehensive record of biophysical characteristics, and present evidence that these characteristics are linked to hydrological indicators and human use.

Water depth and annual flood duration provided the most discerning information on hydrological conditions within each plot, whereas flood frequency provided the least because most plots are inundated every year. This parameter, however, is the main factor distinguishing conventional rice paddies and village crops from the rest of the habitats that flood every year. Annual flood duration was responsible for the greatest variance among soil characteristics, a relationship consistent with other large tropical wetlands (Bowman and McDonough 1991; Furch 1997; Mubyana et al. 2003).

The conversion of natural vegetation by fire and human use also was correlated to flood duration: In seasonally flooded habitats, inundated for at least 7 months every year,

Fig. 2 Response of vegetation characteristics to annual flood duration. *Error bars* in **a** and **b** represent 1 standard deviation from the mean value. *Histograms* in **c** depict the most abundant plant species in the survey

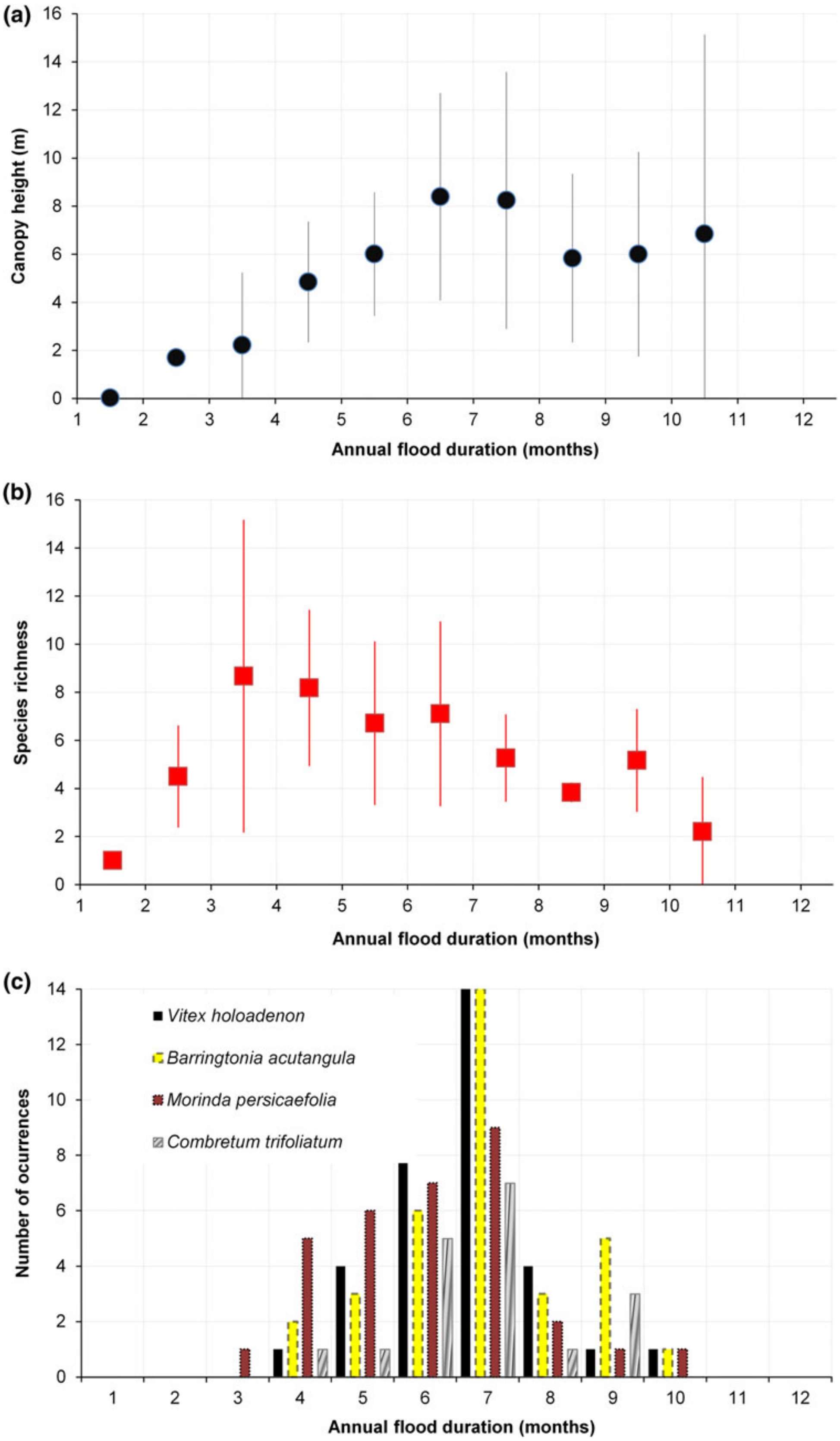

Table 4 Summary of detrended correspondence analysis for non-constrained (DCA) and constrained (DCCA) presence/absence of plant species

	1st axis		2nd axis	
	DCA	DCCA	DCA	DCCA
Environmental variables				
Correlation between axes site scores	0.80		0.87	
Eigenvalues[a]	0.41	0.55	0.72	0.16
Species–environment correlations[b]	0.75	0.92	0.54	0.61
% variance species–environment[c]	25.6	49.2	14.8	13.8
Interset correlations[d]				
Flood duration	0.68	0.84	0.15	−0.12
Human use	−0.04	0.01	0.19	0.16
Soils 1st PC[e]	0.57	0.68	0.19	−0.02
Soils 2nd PC	0.18	0.20	−0.06	−0.05
Soils 3rd PC	0.47	0.62	0.41	0.34
Soils 4th PC	−0.07	−0.24	−0.04	0.13
Biological variables				
Correlation between axes site scores	0.93		0.73	
Eigenvalues	0.72	0.54	0.41	0.35
Species–environment correlations	0.84	0.92	0.72	0.82
% variance species–environment	24.7	25	14.6	21.7
Interset correlations				
Litter cover	−0.62	−0.65	−0.14	−0.20
Ground cover	0.28	0.31	0.24	0.10
Understory cover	−0.64	−0.73	0.12	0.11
Canopy cover	−0.73	−0.83	0.08	0.08
AGB canopy	−0.05	−0.17	0.38	0.42
AGB shrubs	−0.52	−0.47	−0.22	−0.28
AGB herbs	0.64	0.76	0.13	−0.06
Vegetation height	−0.41	−0.52	0.39	0.36
Species richness	−0.48	−0.38	−0.37	−0.58

PC Principal component, *AGB* Above ground biomass

[a] A measure of how much variation is explained along the gradient axes, in standard deviation units

[b] linear correlations between the environmental gradients and the species composition axes

[c] % of variance on species composition caused by the environmental gradient along each axis

[d] Linear correlations between the environmental data and the plot scores of plant species

vegetation clearance occurred mainly due to fires in grasslands, whereas agriculture was the principal factor in areas flooded for less than 5 months annually. Fires are known to occur in the floodplain during the dry season and they probably start both naturally and intentionally (Campbell et al. 2006). Whichever the cause, the opening of these areas creates an opportunity for uses such as water buffalo grazing and rice paddies, which subsequently reduce the chances of the natural re-vegetation of burned areas. It is important to note that the Tonle Sap is a unique ecosystem where seasonal flooding limits human use; nearly 6000 km^2 of floodplain are covered with natural vegetation, and if there was no seasonal flooding, all of this area would have been converted to rice paddies centuries ago.

Flood duration was found to be closely related to vegetation structure and species richness. Data summarized in Table 1 reveals patterns of species richness, canopy cover, and maximum height along the flooding gradient; yet, these relationships show complex responses to flooding (Fig. 2; Table S6 in the Electronic supplementary material). Vegetation communities and species in other large tropical wetlands have been shown to be non-uniformly distributed along the hydrological regime (Milzow et al. 2010; Todd et al. 2010; Foti et al. 2012), and this could be a fundamental factor in the resulting nonlinear relationships between vegetation properties and hydrology. We infer that the complexity of vegetation properties in the Tonle Sap is strongly influenced by the interplay between human use and hydrology. Maximum values of vegetation properties appear at a region of intermediate disturbance where the non-flooded phase is long enough to promote the growth of natural rooted vegetation, but where the water during the flooded phase is too deep for rice cultivation.

Soil attributes, including clay content, sand content, and organic matter content, were associated with particular habitats, which is consistent with preliminary observations of the Tonle Sap (Hellsten et al. 2003) and general patterns observed in the Amazon (Cochrane and Cochrane 2010). The variation in these soil attributes was found to be correlated with flood duration, and we thus infer that the hydrological gradient is one of the primary mechanisms linking soils with vegetation. There are also feedback mechanisms in which vegetation influence soils in the long term, including suspended sediment trapping and litter fall, but more studies are needed to evaluate the significance of these processes.

Results from the ordination showed that average annual flood duration was the best descriptor of plant species composition among non-biological environmental variables, whereas canopy cover and herbaceous AGB were the best descriptors among biological variables. In addition to illustrating the influential role of flood duration in plant species composition, the results from our ordination analyses point out that there is a selected number of environmental and biological variables that best describe the spatial distribution of plant species through the Tonle Sap, including annual flood duration, maximum annual water depth, clay content, sand content, potassium soil content, canopy cover, litter cover, and herbaceous AGB. This subset of variables is less than a third of the total we investigated, and we recommend that further studies prioritize some of these variables while expanding the sampling sites.

In summary, our results show that despite the complexity and intense human use of this ecosystem, the flood pulse is the underlying driver of its habitats and vegetation communities by creating the main gradient of soil characteristics, limiting the area cleared for agriculture, influencing vegetation structure, and shaping the composition of plant species. The physiological adaptations and life histories of the floodplain's natural vegetation are largely

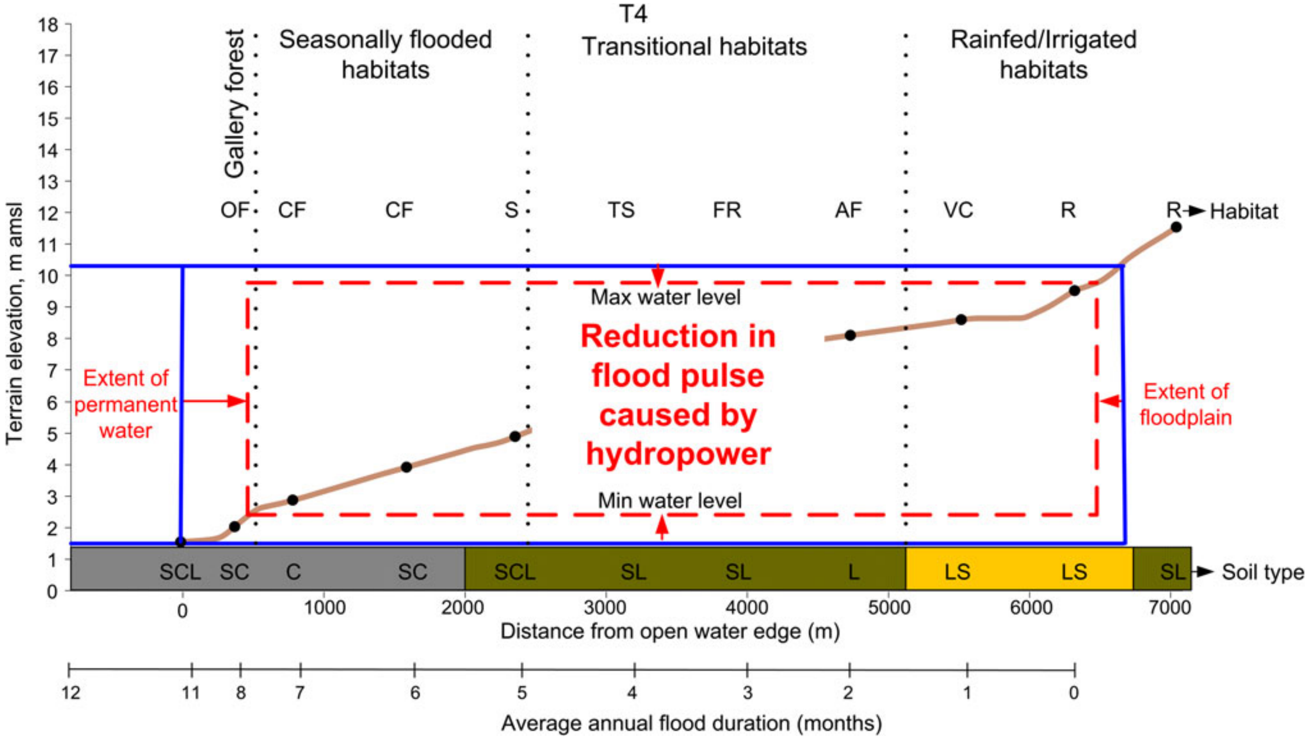

Fig. 3 Projected changes from hydropower in annual minimum and maximum water level and flood extent on elevation profile of transect T4. *Blue lines* indicate the historical min/max water levels and flood extend, whereas the *red dashed lines* indicate the projected conditions under a future hydropower scenario. The *thick brown line* is terrain elevation, *black dots* over it are sampling plot locations, and *capital letters* represent habitat or soil types. Habitat groups based on Arias et al. (2012) and changes in water levels based on maximum hydropower potential in the Mekong Basin (Lauri et al. 2012). *C* Clay, *SC* sandy clay, *SCL* sandy clay loam, *SL* sandy loam, *L* loam, *LS* loamy sand, *OF* open forest, *CF* closed forest, *S* flooded shrubland, *TS* tall shrubland, *FR* floating rice, *AF* abandoned field, *VC* village crop, *R* wet season rice

unknown and further research on this subject would greatly improve our knowledge on the ecohydrology of this wetland.

Implications of Hydrological Changes Caused by Hydropower

The ongoing development in the Mekong Basin will impact the flood pulse of the Tonle Sap by decreasing the extent of maximum flooding and increasing the extent of the permanent lake (Kummu and Sarkkula 2008; MRC 2010; Arias et al. 2012). Expected changes in the Mekong will increase the dry season water levels by 80–90 cm and reduce wet season levels by 40–50 cm (Lauri et al. 2012; Fig. 3). Because of the extremely flat terrain, the reduced seasonal water fluctuation will cause horizontal shifts of more than 500 m horizontally, resulting in a system-wide decrease of seasonal floodplain area (aka., habitats that flood every year) from 10 187 to 7994 km^2 (−22 %). This modified flood gradient will likely change soil and vegetation properties over the long term. Changes in texture, moisture, and organic content of floodplain soils are expected. Nearly all of the existing forests in the coastal zone, which have the largest biomass and canopy cover of all seasonally flooded vegetation communities, could be permanently inundated. Due to the reduction in seasonal flood extent, land clearance will be favored in additional 1300 km^2, reducing the buffer between agricultural fields and natural vegetation communities.

Hydrological disruptions, together with a fast growing population and recent changes in the Tonle Sap management scheme (Keskinen and Varis 2012), will provide major challenges in the way natural resources are sustainably used in the Tonle Sap. Other basin-wide impacts from hydrological disruptions, including reduced sediment loads (Kummu et al. 2010) and blocked fish migration routes (Ziv et al. 2012), will further compromise the Tonle Sap's ecological productivity. Understanding the factors that drive this ecosystem is an essential step for developing mitigation strategies to ensure that the Tonle Sap continues to be a productive ecosystem, but further work linking hydrological and biological characteristics with ecosystem processes and services is needed.

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AUTHOR BIOGRAPHIES

Mauricio E. Arias is a doctoral candidate in Civil and Natural Resources Engineering at the University of Canterbury (New Zealand). His research interests focuses on the interaction of hydrology, ecology, and human use of freshwater ecosystems.

Address: Department of Civil and Natural Resources Engineering, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand.

Thomas A. Cochrane (✉) is a Senior Lecturer in Civil and Natural Resources Engineering at the University of Canterbury. His research interest includes hydrological modeling, soil and water conservation, impacts of water infrastructure development, and integrated catchment analysis. He is the principal investigator of the CEPF funded project of which this research is part of.

Address: Department of Civil and Natural Resources Engineering, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand.
e-mail: tom.cochrane@canterbury.ac.nz

David Norton is a Professor of the New Zealand School of Forestry at the University of Canterbury. His research interests include conservation biology, especially fragmentation and restoration ecology, significance assessment and threatened plant conservation; forest ecology, especially forest pattern and dynamics.

Address: New Zealand School of Forestry, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand.

Timothy J. Killeen is the Senior Director of Carbon and Commodities at WWF. He has a wide range of expertises in biodiversity conservation, ecosystem ecology, and climate change studies.
Address: Carbon and Commodities Program, World Wildlife Fund, 1250 24th Street N.W., P.O. Box 97180, Washington, DC 20090-7180, USA.

Puthea Khon is a postgraduate student in environmental science at the Faculty of Mathematics, Sciences and Engineering, Pannasastra University of Cambodia. He has carried out field research in the Tonle Sap in diverse fields including water quality, sanitation, and biology.
Address: Faculty of Mathematics, Sciences and Engineering, Pannasastra University of Cambodia, No. 184, Maha Vithei Preah Norodom, Phnom Penh, Cambodia.