



Coastal Freshwater Wetland Plant Community Response to Seasonal Drought and Flooding in Northwestern Costa Rica

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Abstract Wetlands in tropical wet-dry climates are governed by distinct and extreme seasonal hydrologic fluctuations. In this study, we investigated the plant community response to seasonal flooding and drought in Palo Verde Marsh, Costa Rica. Climate change models for the region predict reduced rainfall and a drier wet season which would likely alter seasonal hydrologic cycles and prompt vegetation change. We quantified compositional change following disturbance emphasizing seasonal differences in plant life-form abundance across life history stages via standing vegetation, seed bank, and seedling recruitment measurements. Whereas the dry season standing vegetation was dominated by emergent species, aquatic species (floating-rooted, free-floating, and submerged life forms) were more dominant during the wet

season. Seed bank and seedling recruitment measurements indicated that many species are resilient with life history traits that enable them to respond rapidly to extreme hydrologic filters. Interestingly, species richness was highest during seasonal flooding. Our results highlight the importance of early-wet season rainfall for plant regeneration and community change. Our findings also indicate that a drier future would likely have a large impact upon wetland plant communities with a decrease in species richness and an increase in the abundance of drought-tolerant emergent species.

Keywords Climate change · Palo Verde National Park · Plant life forms · Seasonal hydrology · Seed bank · Tropical dry wetland

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Introduction

In tropical wet-dry climates, ecosystem properties are greatly defined by seasonal differences in abiotic conditions (Murphy and Lugo 1986; Bullock et al. 1995). Wetlands located in such climates are often flooded during the wet season and, subsequently, exposed to drought-like conditions during the dry season (Middleton 1999). These distinct and extreme seasonal cycles produce pronounced seasonal fluctuations in wetland water and oxygen availability which greatly dictate ecosystem functioning (e.g., productivity, decomposition, nutrient cycling) and compositional change (Junk 1997; Baldwin and Mitchell 2000; Mitsch and Gosselink 2007; Reddy and DeLaune 2008).

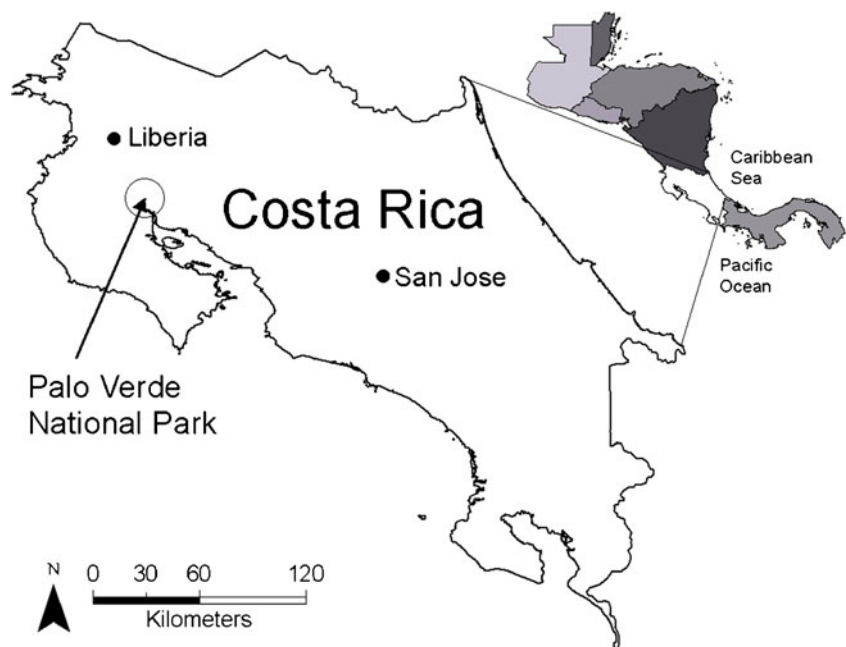
Plant community change in tropical seasonally-flooded wetlands is regulated by the environmental filters associated with flooding and drawdown cycles (Brock and Rogers 1998; Middleton 1999; Finlayson 2005). These environmental

filters create a dynamic plant community, particularly when combined with the diverse and relatively frequent disturbances that impact these ecosystems (e.g., herbivory, fire, hurricanes, anthropogenic management). As a result, many of the plant species found in tropical seasonally-flooded wetland plant communities are highly resilient (Brock and Rogers 1998; Brock et al. 2003); they have adaptations and life history traits that enable them to rapidly revegetate after disturbances and also tolerate or avoid the pronounced and fluctuating aerobic/anaerobic environmental filters. The seeds of most plant species in these wetlands germinate primarily during drawdown conditions and most of the post-disturbance plant community recruitment occurs during the dry season (van der Valk and Davis 1978; Middleton 1999; Casanova and Brock 2000). Well-studied plant communities in tropical seasonally-flooded wetlands include those in the Amazonian floodplains (Junk and Piedade 1997; Piedade et al. 2010), the Northern Tablelands of New South Wales-Australia (Casanova and Brock 2000), Kakadu National Park- Australia (Finlayson and Woodroffe 1996; Finlayson 2005), Keoladeo National Park- India (van der Valk et al. 1993; Middleton 1999), and the Kafue Flats- Zambia (Howard 1985).

In Central America, the seasonally-flooded freshwater wetlands in and around Palo Verde National Park (PVNP; Costa Rica; see Fig. 1 for location) are among the most dynamic, ecologically important, and diverse wetlands in the region. PVNP wetlands have been collectively designated a Ramsar Wetland of International Importance. Only a handful of studies have examined the plant community present in PVNP wetlands (Hernández Esquivel 1990; Crow 2002; Trama et al. 2009). Palo Verde Marsh is one

of the largest wetlands within PVNP. In this study, we examined the influence of distinct and extreme seasonal flooding and drought cycles upon the plant community in Palo Verde Marsh with an emphasis on seasonal differences in plant life-form abundance across life-history stages. We conducted surveys of the wet and dry season standing vegetation, the seed bank, and in situ seedling recruitment. Since the impact of seasonal flooding on wetland plant communities is often most evident after disturbance, we created gaps in the wetland vegetation via the mechanical removal of emergent vegetation and monitored the subsequent plant community change. We expected that due to the multiple and diverse disturbances that impact Palo Verde Marsh, the plant community would have a large and diverse seed bank, and we hypothesized that, for most species, seed bank germination would be higher when soils were freely drained and not flooded. We expected that the intense environmental filters associated with drawdown and flooding would greatly define the seasonal plant assemblages, and hypothesized that the dry and wet season plant assemblages would differ in composition and richness. We sought to identify species only present during one of the two seasons (wet versus dry) likely due to their inability to persist during the anaerobic conditions present in the wet season or the intense water-limitation found during the dry season; we hypothesized that the abundance and species richness of aquatic life forms (i.e., floating-rooted, free-floating, and submerged species) would be higher in the wet season than dry season and the abundance and species richness of emergent life forms would be higher in the dry season than wet season.

Fig. 1 Map identifying the location of Palo Verde National Park within Costa Rica and Central America



Methods

Study Area

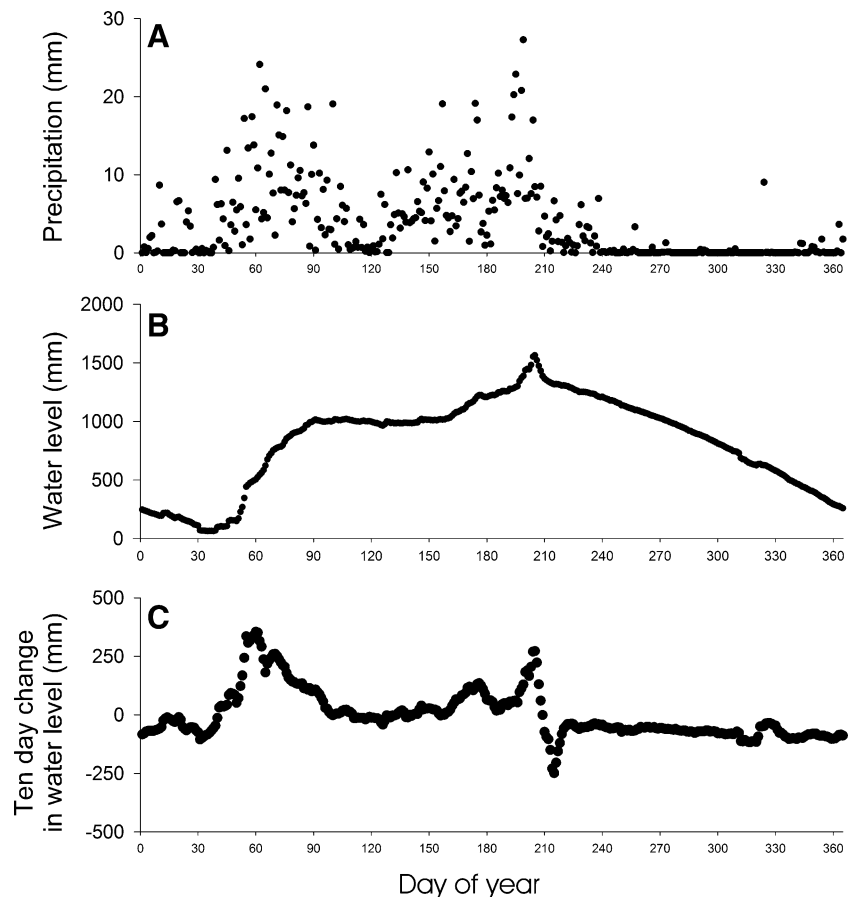
Palo Verde Marsh (~1,250 ha; 10°20'35" N, 85°20'25" W; called Laguna Palo Verde in Spanish) is a coastal freshwater wetland located in the lowlands of the Tempisque River Watershed in the Province of Guanacaste (northwestern Costa Rica; see photos in Fig. 2a-f). The climate in this region is tropical and very seasonal with distinct and extreme wet and dry seasons that greatly define ecosystem processes (Holdridge 1967; Daubenmire 1972; see photos in Fig. 2a-f). Areas upland and adjacent to Palo Verde Marsh contain tropical dry forest which is perhaps the most extensively studied ecosystem in the area (Janzen 1983; Murphy and Lugo 1995; Powers et al. 2009). Near Palo Verde Marsh, the Tempisque River meets a large estuary (the Gulf of Nicoya; see Vargas 1995), and the section of the river immediately adjacent to the marsh is tidally influenced. The estimated elevation in the marsh ranges between about 1.3 and 2.1 m above sea level (Guzmán Alvarez 2007). Although small portions of the marsh are open to tidal exchange via openings in a natural levee that separates the marsh from the river (Trama 2005), our study area is tidally influenced only during very extreme storm events.

The soils in the freshwater wetlands in and around Palo Verde National Park are primarily Vertisols (Loaiciga and Robinson 1995), which allow minimal infiltration, expand during the wet season, and contract during the dry season (Fig. 2d,e). Wet season surface water runoff from the adjacent forests is the predominant hydrologic input to Palo Verde Marsh. During the wet season (~May–November), Palo Verde Marsh will fill to a typical maximum water depth of about 1.5 m (Fig. 3a,b,c); although, intense tropical storm activity occasionally results in short-term water levels greater than 1.5 m. The mean \pm SE, minimum, and maximum annual cumulative precipitation within Palo Verde National Park between 1921 and 1999 was 1,271 \pm 131, 717, and 2,201 mm, respectively (data obtained from on-site OTS records; Osland et al. 2011). The mean annual precipitation for the entire Tempisque River Watershed between 1921 and 1999 was estimated to be 1,817 mm (Mateo-Vega 2001). The majority of this precipitation occurs during the wet season (with a bimodal distribution; Fig. 3a). During the dry season (~December–May), the water level decreases due to drought conditions (high evapotranspiration rates that exceed the rainfall) until much of the marsh has no standing water at the end of the dry season; however, complete drawdown can be prevented in some years by small rainfall events during the last few

Fig. 2 Photos of a panoramic view of Palo Verde Marsh and the Tempisque River (a); wet season plant communities highlighting the free-floating and floating-rooted species *Neptunia natans* and *Nymphaea* spp. [(b) and (c), respectively]; and the dry season highlighting soil contraction and little vegetation [(d), (e) and (f)]. In (f), small seedlings are germinating in cracks but not on the soil surface which is a common occurrence during the intense dry season



Fig. 3 Mean daily precipitation (a), water level (b), and ten day change in water level (c) at Palo Verde Marsh for a 5 year period (2003–2008). Day 1 is equivalent to April 1st



months of the dry season (March–April). Note that the data presented in Fig. 3 were collected from a relatively deep area of the marsh, and higher areas of the marsh can be without standing water for an additional 1 to 3 months.

Experimental Design

Since the impact of seasonal drought and flooding on the Palo Verde Marsh plant community is most evident after disturbance, our compositional and in situ seedling recruitment analyses utilize data collected from 30 20-m² plots (circular plots with a radius of 2.52 m) where the dominant vegetation (*Typha domingensis*) was removed via mechanical disturbance in a randomized block design (i.e., 15 blocks; two plots per block). A randomized block design was selected because the edaphic and hydrologic variability at the site were unknown when we initiated the study. The blocks were all located within areas previously dominated by *T. domingensis*, and, together, the 15 blocks covered an area roughly 2.5 km by 0.5 km. Within each 20-m² plot, three 1-m² permanent quadrats were randomly established for the standing vegetation and in situ seedling recruitment surveys (total # of 1-m² quadrats=90).

The mechanical disturbance was applied via a local method called fangueo, where a tractor with metal paddle

wheels is used to crush and remove wetland vegetation (see McCoy and Rodriguez 1994; Trama et al. 2009; Osland et al. 2011). Although tractor use has the potential to alter soil and seed bank properties (Froud-Williams et al. 1984; Lowery and Schuler 1991; Kozłowski 1999), a concurrent study found no short-term impact of fangueo on several soil and seed bank properties in Palo Verde Marsh (Osland et al. 2011).

The seed bank analyses used data derived from sampling that also occurred in 30 20-m² plots established in a randomized complete block design with two plots per block using the same blocks as the compositional surveys. However, since the seed bank sampling was planned in coordination with another study that assessed the impact of cattail removal (Osland et al. 2011), the plot layout for the seed bank sampling was slightly different. In addition to sampling from 15 of the 30 20-m² plots used for compositional analyses (i.e., one of two plots within each block), samples were also collected from a third 20-m² plot established within each of the 15 blocks. This additional plot was located in areas where *Typha* had not been removed. Due to the brief amount of time between vegetation removal and seed bank sampling (i.e., two months), the seed bank assemblages in these two areas (*Typha* removed and *Typha* not removed) were not

different (Osland et al. 2011) and the data from these treatments were pooled. In situ seedling recruitment, seed bank, and standing vegetation measurements were initiated 2, 3, and 5 months after vegetation removal, respectively. Seed bank samples were collected 2 months after vegetation removal.

Seed Bank and Seedling Recruitment

A seedling emergence study was conducted in the lathehouse at the OTS' Palo Verde Biological Station. Within each 20-m² plot, two composite samples were collected. Each composite sample contained 11 mixed cores that were haphazardly collected to 5-cm depth within each 20-m² plot (cores were 4.6 cm in diameter; total volume and area for each composite sample was 914 cm³ and 183 cm², respectively). The total number of pre-composite cores collected within each 20-m² plot was 22, and the total number of pre-composite cores collected for the study was 660. These pre-composite cores rendered 60 composite samples. In the lathehouse, each composite sample was placed in a 2-cm layer on top of a 5-cm layer of sterilized potting soil in flats that were 25-cm long×20-cm wide×10-cm deep. Each duplicate composite was assigned to one of two water level treatments: flooded or drawdown. In the flooded treatment, the water level was maintained 3 cm above the soil surface. In the drawdown flats, the soil was kept moist but not flooded. In order to account for contaminant seeds, eight control trays were included in the experimental design (four drawdown and four flooded); however, we lost two controls due to interference by iguanas. Emerging seedlings were identified and counted on seven dates between May and September, 2007. Seed bank densities on a per m² basis were calculated by scaling up from the area represented by each composite sample (i.e., the area represented by the 11 cores present in each composite sample- 183 cm²); the total number of seeds present in each composite sample was multiplied by 54.70. In addition to quantifying seedling emergence in the lathehouse, we also measured in situ seedling recruitment during the dry season (April 2007) by identifying and counting the number of seedlings that germinated in our 1-m² field plots.

Plant Community Composition

Within each 1-m² quadrat, we identified and estimated the percent cover of each species present. Cover was estimated to the nearest 1% for abundant species (i.e., species with cover greater than ~5%) and to the nearest 0.1% for less abundant species (i.e., species with cover less than ~5%). For species identification, we relied primarily upon Crow (2002) and Hammel et al. (2004). For statistical

analyses, we used the means from the three nested and randomly assigned 1-m² quadrats to represent the community found in the larger 20-m² plots. We compared percent cover data from the first wet season (June and September 2007) and the second dry season (April 2008). The cover data was classified according to the common life forms present in the wetland [i.e., emergent, free-floating, floating-rooted (sometimes also called floating-leaved or rooted floating-leaved by others), and submerged] and also used to calculate species richness and diversity (using the Shannon-Wiener index with the use of the relative percent cover of species *i* to represent *p_i* in the calculations).

Data Analyses

To compare wet and dry season plant community characteristics, we used mixed factor analyses of variance (ANOVA) models with block as a random effect and season (wet or dry) as a fixed effect. Our response variables were life form (i.e., emergent, free-floating, floating-rooted, and submerged) relative abundance (i.e., cover) and species richness. These analyses were conducted using PROC MIXED in SAS Version 9.1.3 (SAS Institute, Cary, NC, U.S.A.).

To illustrate differences in plant community composition between the dry and wet seasons, a nonmetric multidimensional scaling (NMS) analysis (Kruskal 1964; Mather 1976; McCune and Grace 2002) was performed using PC-ORD Version 4 (MjM Software, Gleneden Beach, OR, USA; McCune and Medford 1999). Prior to analysis, we relativized the species cover data by species maxima and removed rare species which were defined as species present in less than 5% of the plots. The resultant matrix contained 22 species and 82 plots. Bray-Curtis dissimilarity coefficients were used to quantify plant species compositional distance (Bray and Curtis 1957). In order to determine the appropriate number of dimensions to include in the analysis, we used a stepdown procedure to compare the number of dimensions with the corresponding change in final ordination stress. We initially evaluated six axes using 100 runs with real data, a stability criterion of 0.00001, a maximum of 400 iterations, and a Monte Carlo test with 150 randomizations to determine whether the resultant axes were stronger than those identified by chance (McCune and Grace 2002). Based upon this procedure, a three dimensional analysis was deemed optimal and resulted in a final stress of 18.0, a *P* value of 0.007, and a final instability of 0.00001 after 112 iterations. This ordination was rotated 30° to load the strongest secondary matrix variables (water depth and emergent vegetation cover) on the horizontal axis. To compare the wet and dry season plant communities, we used Multi-Response Permutation Procedure

(MRPP) with Bray-Curtis dissimilarity as the distance measure and $n/(\sum n)$ to weight groups. We also calculated indicator values for the 22 common species for each season via indicator species analysis (INSPAN) (Dufrene and Legendre 1997) using PC-ORD. Indicator values represent the percent of perfect indication for a given group and is the product of the relative abundance and relative frequency of each species within each community. A Monte Carlo test was conducted to identify significant indicator values. Sørensen's index of similarity (Sørensen 1948) was used to calculate site-level similarity between the standing vegetation, seed bank, and in situ seedling recruitment.

Results

Seed Bank and in Situ Seedling Recruitment

The majority of the species and individuals that were observed in the in situ seedling surveys were classified as emergents (Fig. 4a,b,c; Tables 1 and 2). The site-level species richness from the in situ seedling recruitment measurements was 14 species. The mean \pm SE and maximum plot-level seedling recruitment density was 106.1 ± 24.2 and 536 individuals/m², respectively. The site-level seed bank species richness was 24 and 11 species for the drawdown and flooded treatments, respectively. Whereas the mean \pm SE and maximum plot-level seed bank density for the flooded treatment was 510.3 ± 95.2 and 2,093 individuals/m², respectively, the mean \pm SE and maximum plot-level seed bank density for the drawdown treatment was 1960.2 ± 200.7 and 5,145 individuals/m², respectively. In both the flooded and drawdown seed bank treatments, emergent life forms had a higher relative abundance and species richness than the aquatic life forms (Fig. 4a,b).

Common species that emerged from the seed bank, listed by decreasing abundance, include *Ceratopteris pteridoides* (note this is an aquatic fern with reproduction from spores), *T. domingensis*, *Nymphaea* spp., *Ceratophyllum muricatum*, *Echinodorus paniculatus*, *Solanum campechiense*, *Cyperus articulatus*, and *Eichhornia crassipes* (Table 2). Although most species germinated preferentially in the drawdown treatment, the only abundant species to germinate equally well in the flooded treatment was *Echinodorus paniculatus* (Table 2). The only species that germinated preferentially in the flooded treatment was *Najas arguta* (Table 2). Common species that germinated during our in situ seedling recruitment surveys at the end of the dry season, listed by decreasing abundance, were *T. domingensis*, *Nymphaea* spp., *Neptunia natans*, *E. crassipes*, *C. articulatus*, and *S. campe-*

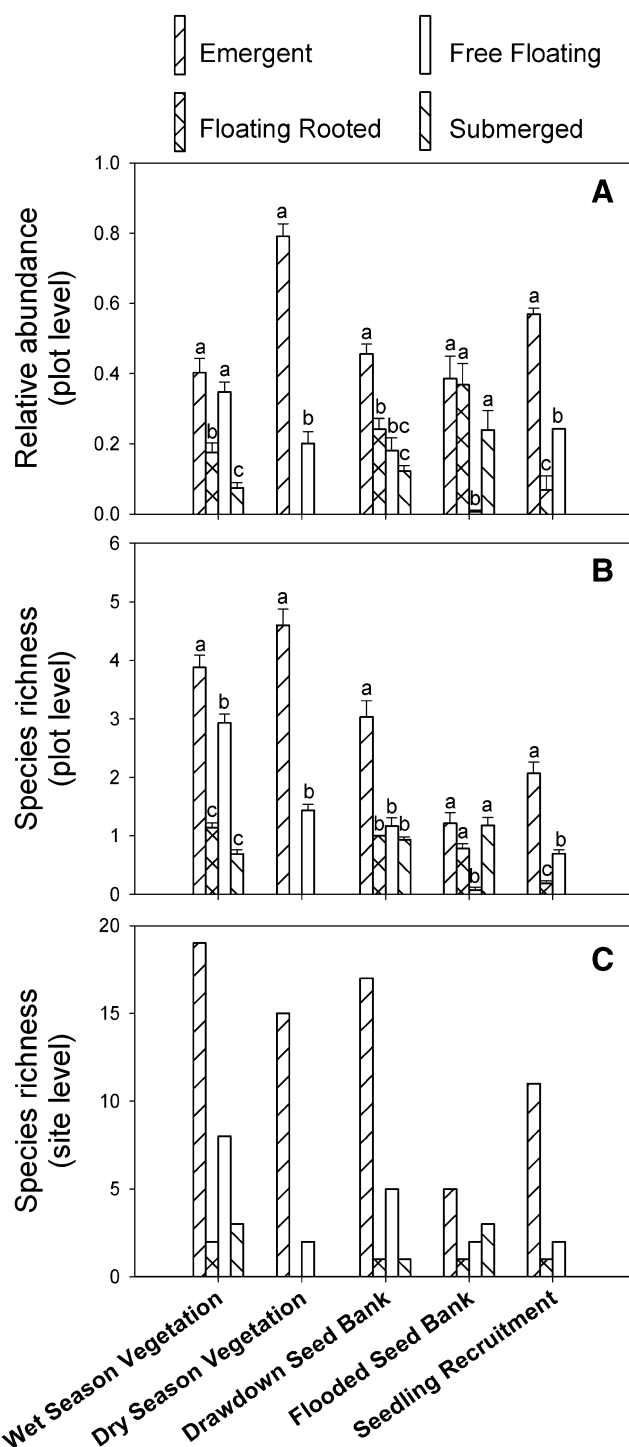


Fig. 4 A comparison of four plant life forms found in various components of the plant community using measures of (a) relative abundance at the plot level, (b) species richness at the plot level, and (c) species richness at the site level. Different letters indicate significant differences between life forms within each component of the plant community

chiense (Table 2). Interestingly, many of the seedlings that germinated in the field during the dry season, germinated in cracks formed by soil contraction (Fig. 2f).

Table 1 Species-specific standing vegetation, seed bank, and in situ seedling recruitment data. For the standing vegetation, the results of an indicator species analysis (INSPAN) of the 22 common species are shown. The indicator values represent the percent of perfect indication for either the wet or dry season plant community. INSPAN *P* values are shown for the wet season species. For the seed bank data, the mean \pm SE seedling

density is shown for each treatment along with the corresponding results from *t*-tests between the two treatments. For the seedling recruitment data, the mean \pm SE seedling density is shown. Species codes can be used to interpret the NMS ordination in Fig. 5. The life form abbreviations indicate the species' predominant life form as follows: E = emergent, FF = free-floating, FR = floating-rooted, and S = submerged

Species	Code ^a	Life Form	Standing Vegetation			Seed Bank			Seedling recruitment density (individuals/m ²)
			Wet season indicator value	Dry season indicator value	<i>P</i>	Drawdown seed bank density (individuals/m ²)	Flooded seed bank density (individuals/m ²)	<i>P</i>	
<i>Aeschynomene sensitiva</i>	AeSe	E	14	0	NS	0	0	–	0.07 \pm 0.03
<i>Cyperus articulatus</i>	CyAr	E	12	20	NS	32.8 \pm 16.3	0	0.05	2.43 \pm 1.44
<i>Cyperus gigantea</i>	CyGi	E	1	8	NS	0	0	–	0
<i>Echinochloa colona</i>	EcCo	E	8	23	NS	0	0	–	0.07 \pm 0.04
<i>Echinodorus paniculatus</i>	EcPa	E	26	20	NS	182.4 \pm 47.9	199.3 \pm 51.5	NS	0.98 \pm 0.26
<i>Eichhornia crassipes</i>	EiCr	FF	11	27	NS	29.2 \pm 12.2	2.0 \pm 2.0	0.03	3.02 \pm 1.88
<i>Eleocharis mutata</i>	ElMu	E	17	0	0.04 ^b	0	0	–	0.09 \pm 0.06
<i>Hymenachne amplexicaulis</i>	HyAm	E	14	65	0.003 ^b	9.1 \pm 5.9	0	NS	0.51 \pm 0.12
<i>Lemna aequinoctialis</i>	LeAe	FF	78	0	\leq 0.0001	18.3 \pm 8.4	0	0.04	0
<i>Najas arguta</i>	NaAr	S	19	0	0.02 ^b	0	29.5 \pm 5.3	$<$ 0.0001	0
<i>Neptunia natans</i>	NeNa	FF	73	22	\leq 0.0001	1.8 \pm 1.8	0	NS	6.71 \pm 1.91
<i>Nymphaea amazonum</i>	NyAm	FR	88	0	\leq 0.0001	432.3 \pm 80.9 ^c	138.3 \pm 32.3 ^c	$<$ 0.01 ^c	25.74 \pm 7.60 ^c
<i>Nymphaea pulchella</i>	NyPu	FR	26	0	0.007 ^b				
<i>Oxycarium cubense</i>	OxCu	E	0	40	\leq 0.0001	0	0	–	0
<i>Paspalidium geminatum</i>	PaGe	E	20	7	NS	5.5 \pm 3.1	0	0.08	0.04 \pm 0.03
<i>Paspalum vaginatum</i>	PaVa	E	18	30	NS	3.7 \pm 2.5	2.0 \pm 2.0	NS	0.30 \pm 0.10
<i>Poaceae spp.</i>	Pospp3	E	2	13	NS	0	0	–	0
<i>Solanum campechiense</i>	SoCa	E	0	33	0.0002	42.0 \pm 17.9	0	0.02	1.93 \pm 0.54
<i>Thalia geniculata</i>	ThGe	E	15	0	NS	0	0	–	0
<i>Typha domingensis</i>	TyDo	E	7	64	0.002	456.0 \pm 50.7	88.9 \pm 44.6	NS	64.11 \pm 19.80
<i>Utricularia gibba</i>	UtGi	S	47	0	\leq 0.0001	0	2.0 \pm 2.0	NS	0
<i>Wolffiella welwitschii</i>	WoWe	FF	81	0	\leq 0.0001	0	0	–	0
<i>Bacopa repens</i>	–	E	–	–	–	5.5 \pm 5.5	9.8 \pm 6.3	NS	0
<i>Bergia capensis</i>	–	E	–	–	–	23.7 \pm 13.6	0	NS	0
<i>Ceratophyllum muricatum</i>	–	S	–	–	–	202.4 \pm 26.5	32.8 \pm 6.8	$<$ 0.0001	0
<i>Ceratopteris pteridoides</i>	–	FF	–	–	–	465.2 \pm 155.3	1.5 \pm 1.5	$<$ 0.01	0
<i>Ludwigia inclinata</i>	–	E	–	–	–	21.9 \pm 11.3	0	0.06	0
<i>Pistia stratiotes</i>	–	FF	–	–	–	0.9 \pm 0.9	0	NS	0
<i>Spermacoce assurgens</i>	–	E	–	–	–	5.5 \pm 4.0	3.9 \pm 3.9	NS	0
Unknown species (6 total)	–	E	–	–	–	22.0 \pm 9.4	0	–	0

NS refers to indicator values that are not significant

^a codes are only shown for species present in at least 5% of the plots

^b denotes indicator values that are not significant after a Bonferroni correction

^c *Nymphaea* seedlings could not be identified to the species level during the seed bank and seedling measurements

Plant Community Composition

The wet and dry season plant assemblages were significantly different (Fig. 5; Fig. 6; Table 2; Table 2; MRPP, wet

vs. dry, $A=0.05$, $P<0.00001$). The NMS ordination in Fig. 5 illustrates the compositional differences associated with seasonal flooding and drought. Common species present during the wet season include *N. natans*, *Nymphaea*

Table 2 Comparison of life form relative abundance and species richness (plot level) between the wet season and dry season plant communities. Significant *F* values are denoted by asterisks (*** *P*<0.001, ** *P*<0.01, * *P*<0.05)

Source	<i>F</i> _{1,72}
Emergent relative abundance	41.9***
Emergent species richness	7.3**
Floating-rooted relative abundance	20.4***
Floating-rooted species richness	105.4***
Free-floating relative abundance	7.1**
Free-floating species richness	46.6***
Submerged relative abundance	15.3***
Submerged species richness	50.0***

amazonum, *Utricularia gibba*, *Paspalum vaginatum*, *E. crassipes*, *Hymenachne amplexicaulis*, and *Nymphaea pulchella* (Fig. 6; Table 2). Common species present during the dry season include *H. amplexicaulis*, *T. domingensis*, *P. vaginatum*, *N. natans*, *E. crassipes*, *C. articulatus*, and *Paspalidium geminatum* (Fig. 6). Interestingly, plot-level species richness and diversity were greater during the wet season (Fig. 4b; Fig. 5). The site-level species richness was also greater during the wet season (32 and 17 species for wet season and dry season, respectively; Fig. 4c). The site-level species richness for the entire study was 40 species.

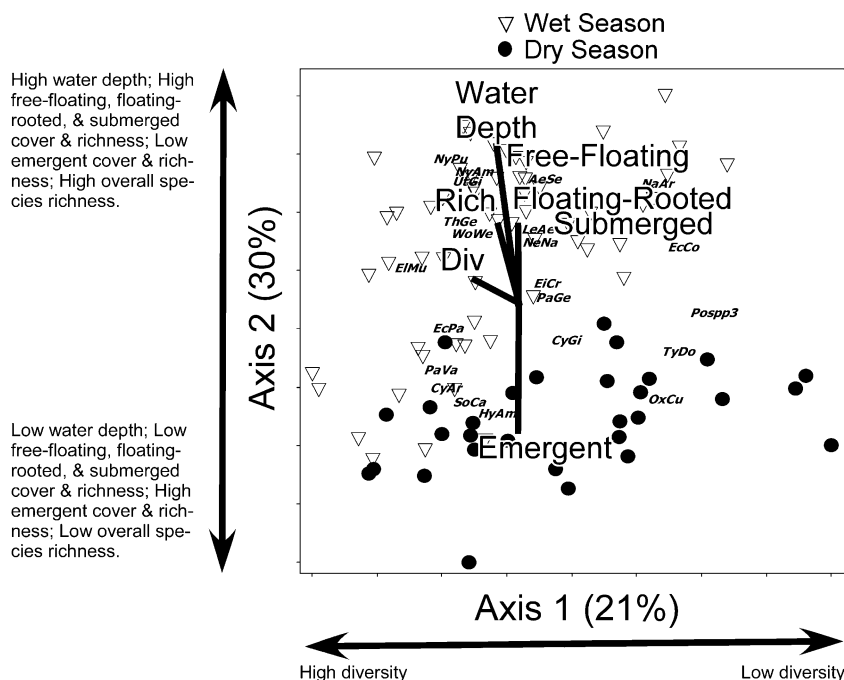
Whereas emergent species relative abundance and richness were greater during the dry season, the relative abundance and richness of free-floating, floating-rooted, and submerged species were greater during the wet season (Fig. 4a,b,c; Fig. 5; Table 2). We examined relationships

between compositional space and the following variables: water depth, species diversity (Shannon *H'*), species richness, and also the percent cover and species richness of plants with the four life forms of interest (i.e., emergent, free-floating, floating-rooted, or submerged). The proportion of the compositional variance represented by the three axes included in the analysis was 66% (Axis 1: 21%, Axis 2: 30%, and Axis 3: 15%). Water depth, species richness, and the percent cover and richness of free-floating, floating-rooted, and submerged life forms were all positively correlated with Axis 2 (water depth [$\tau=0.61$]; species richness [$\tau=0.40$]; free-floating richness [$\tau=0.43$]; free-floating cover [$\tau=0.24$]; floating-rooted richness [$\tau=0.40$]; floating-rooted cover [$\tau=0.46$]; submerged richness [$\tau=0.47$]; and submerged cover [$\tau=0.37$]; where τ is Kendall's tau rank correlation coefficient). In contrast, emergent richness and cover were negatively correlated with Axis 2 ([$\tau=-0.31$] and [$\tau=-0.55$], respectively). Species diversity was the only variable that was correlated to Axis 1 [$\tau=-0.26$].

Indicator species analysis identified eight species that were present during the wet season and absent during the dry season (indicator values of zero in the dry season column in Table 2). In contrast, only two species that were present during the dry season were not observed during the wet season (indicator values of zero in the wet season column in Table 2). The following five species were significant indicators of the wet season plant community: *Lemna aquinoctialis*, *N. natans*, *N. amazonum*, *U. gibba*, and *Wolffiella welwitschii* (significant wet season *P* values in Table 2).

The following species were present and relatively common in all three components of the plant community (standing

Fig. 5 A comparison of plant community composition during the wet and dry season. This is a nonmetric multidimensional scaling (NMS) ordination of individual plots in species space. Whereas the individual plot treatments are denoted by symbols, the species centroids are denoted by four letter species codes that can be interpreted with Table 2. Dark lines radiating from the center represent the strength and direction of correlations between secondary matrix variables and NMS scores. The text to the left and bottom of the joint plot provide interpretation of the secondary matrix correlations (secondary matrix abbreviations: Div = species diversity; Rich = species richness)



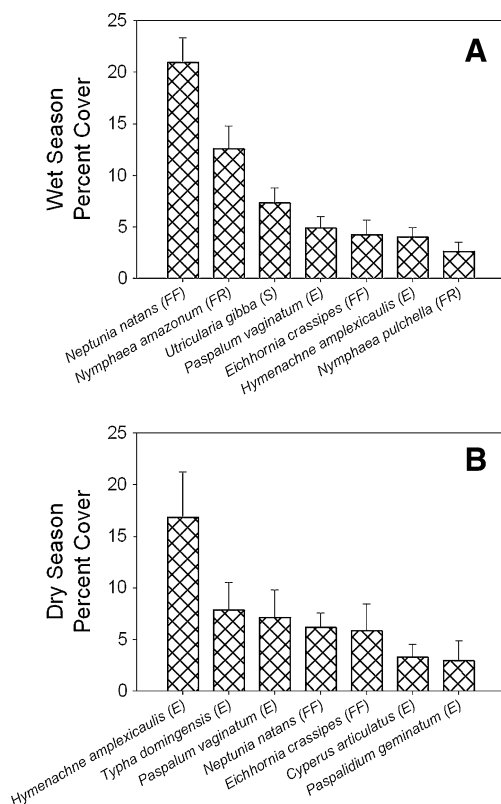


Fig. 6 Plant species with the highest percent cover measurements during the (a) wet season and (b) dry season. The letters in parentheses indicate the species' predominant life form as follows: E = emergent, FF = free-floating, FR = floating-rooted, and S = submerged

vegetation, seed bank, and in situ seedling recruitment): *C. articulatus*, *E. paniculatus*, *E. crassipes*, *H. amplexicaulis*, *N. natans*, *Nymphaea* spp., *P. vaginatum*, and *T. domingensis* (Table 2). *Ceratopteris pteridoides* and *C. muricatum* were two species that were abundant in the seed bank but not common in the standing vegetation. *Neptunia natans* was a species that was abundant in the standing vegetation and seedling recruitment surveys but not in the seed bank investigation. The Sørensen index of similarity between the wet season standing vegetation and the drawdown seed bank, flooded seed bank, and in situ seedling recruitment was 59, 41, and 61%, respectively. The Sørensen index of similarity between the dry season standing vegetation and the drawdown seed bank, flooded seed bank, and in situ seedling recruitment was 50, 28, and 65%, respectively.

Discussion

Impact of Drought and Flooding on the Seed Bank and In Situ Seedling Recruitment

Freshwater wetlands located near the Pacific coast of Central America are visibly impacted by seasonal fluctua-

tions in water and oxygen availability associated with distinct and extreme wet and dry seasons. In seasonally-flooded wetlands, seed banks usually play an important role in determining the plant community response to water level fluctuations and disturbances (van der Valk and Davis 1978; van der Valk 1981; Middleton 1999). Disturbances (e.g., fire, herbivory, hurricanes, anthropogenic management) create gaps which are then typically colonized from the seed or vegetative propagule bank preferentially during drawdown conditions. Our results indicate that the seed bank at Palo Verde Marsh is relatively large (i.e., high density). The mean seed bank density found in this study (1,960 individuals/m² during drawdown conditions) is comparable to results from monsoonal wetlands in Keoladeo National Park, India (1,100–3,100 individuals/m²; Middleton et al. 1991) and the Nyl Flooplain, South Africa (1,300 individuals/m²; Brock and Rogers 1998) but less than densities found in the Magela Creek Floodplain, Australia (8,000–15,400 individuals/m²; Finlayson et al. 1990). As in most seasonally-flooded wetlands, most species in the Palo Verde Marsh seed bank germinated better when the soil surface was moist but not flooded. Hence after a disturbance, most of the recruitment is likely to occur at the beginning of the wet season; personal observations by MJO and EG indicate that the largest recruitment events occur during the transition period between the dry and wet season and in response to the first small rainfall events of the wet season. Large rainfall events at the start of the wet season lead to low recruitment due to rapid flooding.

In both the seed bank and seedling recruitment studies, cattail (*Typha domingensis*) and water lily (*Nymphaea* spp.) were among the three most abundant taxa (Table 2). A study examining *Typha* dominance at Palo Verde indicated that without gap-creating disturbances (e.g., herbivory, fire, hurricanes, anthropogenic management) flood-tolerant emergent species like *Typha* would probably become dominant during both the wet and dry seasons and result in more similar wet and dry season assemblages (Osland et al. 2011). Yet with disturbance, seasonal flooding and drawdown cycles are accompanied by distinct seasonal cycles in plant assemblages.

Impact of Drought and Flooding on Plant Life Form Relative Abundance and Species Richness

In order to cope with the fluctuating oxygen and light gradients associated with changing water levels, wetland plant communities contain species with a diverse array of morphological and physiological adaptations. Perhaps the simplest classification of wetland plant species with such adaptations is based upon life forms (i.e., emergent, free-floating, floating-rooted, and submerged; sensu Sculthorpe 1967). In many wetlands, the relative abundance of these

simple life form groupings is dictated by water level (e.g., Cherry and Gough 2006; Yuan et al. 2007). Not surprisingly, life form group relative abundance in Palo Verde Marsh is dictated by seasonal water level fluctuations. During seasonal drawdown, the relative abundance and species richness of emergent species is greater than during flooding (Fig. 4 and Table 2). In contrast, the relative abundance and species richness of the more aquatic life forms (i.e., submerged, free-floating, and floating-rooted) is greater during flooding periods than during seasonal drawdown.

Drought and Flooding as Environmental Filters That Dictate Seasonal Plant Assemblages

In seasonally flooded wetlands like Palo Verde, seasonal flooding typically acts as an environmental filter constraining the number of species that are present during flooded and drawdown conditions (van der Valk 1981; Keddy 1992; Middleton 1999). The plant community at Palo Verde Marsh is no exception; flooding and drawdown cycles act as environmental filters resulting in distinct dry and wet season assemblages. Interestingly, species richness was greater during the wet season. In many ecosystems, species richness is negatively correlated to stress and, in wetland ecosystems, the anaerobic conditions associated with flooding are often more stressful than drawdown conditions leading to decreased richness during flooding. Yet, the lower dry season species richness at Palo Verde Marsh indicates that the intense dry season conditions (i.e., high temperatures and low water availability) may be more stressful for a greater number of species than the anaerobic conditions associated with flooding during the wet season.

A Drier Wet Season: Implications for Wetland Plant Communities

Central America has been identified as one of the most prominent tropical climate change “hot-spots” because climate change models for the region consistently predict reduced rainfall and drier conditions during June and July which is the start of the wet season (see Giorgi 2006; Neelin et al. 2006; Rauscher et al. 2008; Maurer et al. 2009). A prolonged dry season (or a drier start to the wet season) will have a tremendous impact upon drought-stressed terrestrial and aquatic ecosystems in the region (e.g., Engelbrecht et al. 2007; Touchon and Warkentin 2009; Nahlik and Mitsch 2011). Our results indicate that plant community composition and plant-dependent ecosystem functions in the region’s wetlands are defined by the rapid flooding that typically occurs at the start of the wet season. Rapid flooding associated with heavy rainfall at the onset of the wet season enables flood-tolerant plant

species and life forms to persist. We expect that climate-change induced reductions in flooding at the start of the dry season would likely allow emergent and less flood-tolerant species to become dominant as their growth rates are able to keep up with the reduced increases in water level. Such a regime shift would also likely impact the prominent avian populations in the region which rely upon a mosaic of open water and vegetation (Osland et al. 2011).

Conclusions

The wetlands of PVNP are collectively designated a Ramsar Wetland of International Importance and are among the most dynamic, diverse, and ecological important wetlands in Central America. In this study, we characterized the wetland plant community response to hydrologic fluctuations associated with the distinct and extreme wet and dry seasons in Palo Verde Marsh. Like most seasonally flooded wetlands, the majority of plant species in Palo Verde Marsh seed banks germinated preferentially during drawdown conditions and most of the plant community recruitment occurred during the dry season. Our results indicate that many of the plant species found in Palo Verde Marsh are resilient with adaptations and life history traits that enable them to rapidly revegetate after disturbances and also tolerate or avoid the pronounced and fluctuating environmental filters associated with seasonal flooding and drought. Yet, our results also highlight the importance of rainfall at the onset of the wet season. Climate change projections for the region predict reduced rainfall and flooding during this period of limited water availability which will likely alter wetland plant communities in the region.

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