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Edaphic Controls on Sedge Invasion in a Tropical Wetland Assessed With Electromagnetic Induction

ABSTRACT

Invasion of sedge in the wetlands of Trinidad is causing an increase in wetland dry season fires and a reduction in coastal pasture, adversely affecting the livelihoods of people living and working in the wetlands. The purpose of our research was to determine if soil properties and water quality could help to explain why the area of sedge is expanding. We conducted an observational study, using geophysical methods and standard sampling techniques to determine the relationship between grass and sedge zonation and soil properties and water quality. Our findings showed that both electrical conductivity of soil solution at saturation (ECe) and surface water electrical conductivity (ECw) were significantly higher ($P<0.05$) in sedge communities than in grass communities (mean ECe sedge = 4.4 dS/m; mean ECe grass= 3.7 dS/m; mean ECw sedge= 0.5 dS/m; mean ECw grass= 0.2 dS/m). Our interpretation is that changes to the local hydrology by channelizing and levying rivers, reducing wetland flooding, is enhancing saline intrusion and facilitating the invasion of brackish water sedge species into non salt-tolerant grassland areas.

Abbreviations: ECa, apparent electrical conductivity; ECe electrical conductivity of soil solution at saturation; EMI, electromagnetic induction; VWC, volumetric water content.

INTRODUCTION

Wetlands are important ecological habitats that provide a range of important ecosystem functions and services including, coastal defence, spawning grounds and C stores (Dugan, 1993). Wetlands are being degraded by landuse change, however, with an estimated loss worldwide of 50% of those that existed in 1900 (Dugan, 1993, Organisation for Economic Co-operation and Development, 1996). Conversion to agriculture is considered to be the major factor determining loss globally, with increasing portions of the tropics and subtropics undergoing agricultural conversion. It has been estimated that by 1985 56–65% of available wetlands had been drained for intensive agriculture in Europe and North America, 27% in Asia, 6% in South America and 2% in Africa, a total of 26% loss to agriculture worldwide (Organisation for Economic Co-operation and Development, 1996). Given the importance of wetlands there is significant effort being spent on management and restoration in some areas, but this requires developing a good understanding of the ecohydrology of wetland ecosystems.

In Trinidad, wetlands show distinctive plant zonation. The natural regional zonation found in the Godineau wetland would be mangrove closest to the ocean in saline waters, then sedge in brackish waters, and finally grasses furthest inland in non-saline environments. There has been a substantial invasion of sedges into abandoned agricultural land and grassland ecosystems observed in the Godineau area (Fig. 1), especially since engineering works were undertaken in the 1960's to control annual flooding. These invasive sedges pose an increasing fire hazard for the mangrove ecosystem, and reduce the area of diverse grassland and palatable forage for animal production within the wetland (Brooks et al., 2004). As a result of these issues, and an interest in better managing the wetland, knowledge of the causes of sedge expansion within the Godineau wetland are of policy and management interest.

Wetlands are considered to be physically stressful habitats for plants because ecological alterations can result in vegetation changes within a relatively short period of time. The principal factor controlling wetland function is its hydrological regime (Gosselink and Turner, 1978; Carter et al., 1979). Ecological alterations can occur as a result of human management interventions in the wetland's hydrological regime, for example, through drainage. The frequency and duration of tidal inundation are often responsible for the vegetation patterns present in a lot of wetlands delineating between high lands and low lands (Vince and Snow, 1984). Tidal inundation influences edaphic factors such as soil salinity, redox potential and oxygenation, and soil physicochemical properties, which play an important role in determining plant community composition, productivity and zonation (Adams, 1963; Mahall and Park, 1976a, 1976b; Adam, 1990; Callaway et al., 1990; Pennings, 1992). It creates an inverse relationship between competitive ability and stress tolerance, resulting in competitively superior plants occupying the least stressful zones of the wetland, displacing competitively inferior plants to more stressful zones (Bertness et al., 1992, 2002). These competitive or invasive plants, often act as ecosystem engineers altering flow, light and sediments (Judd et al., 2007) and reducing biodiversity. The invasiveness of a species, therefore, can be the result of wetland nutrient enrichment, altered hydrology, altered soil chemistry or introgressive hybridization among native genotypes and cultivars (Galatowitsch et al., 1999).

A plant species is considered invasive when it is relatively new to a particular area and has a large impact on the new environment. These plants can rapidly disperse via diffusion and saltation and maybe categorized as either long or short distance colonizers (Davis and Thompson, 2000). There have been many reports of sedges invading into natural areas such as grasslands and wetlands (Carter et al., 1996; Rosen et al., 2006; Bryson et al., 1996; Jacono, 2001). The invasion of the sedge (*Eleocharis mutata* L.) Roem. & Schult. (scallion grass) in particular have been reported in the coastal fresh marsh of Brazonia National Wildlife Refuge in Texas (Rosen and Jones, 2004). *Eleocharis mutata* and *Cyperus articulatus* L. are the dominant plant species, rapidly expanding in the Godineau wetland, Trinidad.

Soils and their properties, along with the hydrology, play a distinctive ecosystem role in determining wetland zonation patterns. Because tidal inundation plays a pivotal role in plant productivity and expansion, quantifying the edaphic dynamics using a suitable method will increase our understanding of the vegetation patterns and dynamics in the wetland. Traditional methods used to determine the edaphic factors that influence plant patterns are usually intensive, invasive, time and cost inefficient, and may not always be the most practical for incessantly flooded tropical wetlands. Geophysical techniques such as electromagnetic induction (EMI) offer the possibility of collecting dense spatial measurement coverage, combining sufficient spacing, extent, and support (i.e. scale triplet, Blöschl and Grayson, 2000) to capture the small-and large-scale variability of soil properties across a field site (Robinson et al., 2008). EMI-based apparent soil electrical conductivity (ECa) measurements have been used by researchers attempting to infer different soil properties; soil ECa is related to clay mineralogy, soil volumetric water content (VWC), soil water electrical conductivity, soil depth, and temperature (Friedman, 2005) and has often been used in soil mapping by correlating signal response with soil variables of interest (Hendrickx and Kachanoski, 2002; Lesch et al., 2005; Triantafilis and Lesch, 2005; Bréchet et al., 2012), or using time-lapse approaches to understand hydrological dynamics(Robinson et al., 2009; Moffet et al., 2010; Robinson et al., 2012).

Many researchers (e.g., Williams and Hoey, 1987; Kitchen et al., 1996; Wolf et al., 1998; Ceuppens and Wopereis, 1999; Hopkins and Richardson, 1999; Paine et al., 2004; Mansoor et al., 2006) have used different geophysical survey methods for monitoring the spatial and temporal variability of abiotic factors in estuarine ecosystems. Relatively little work (Moffett et al., 2010) has been conducted using geophysical imaging to quantify soil properties and processes for understanding plant zonation, especially in the tropics.

In this study, we hypothesize that sedge dominance in a tropical wetland is caused by the magnitude of ecological changes due to soil salinization at a given point in time and space. By using EMI imaging and soil and water sampling, we investigated the major factors influencing zonation and sedge dominance within the tropical wetland. The objectives of the study were to:

(i) ascertain differences in soil properties between grass and sedge communities
(ii) test the difference in water quality between sedge and grass communities
(iii) determine the relationship between EMI signal and plant community zonation, and
(iv) determine the soil properties contributing to EMI response.

By using both soil sampling and EMI we could test whether the EMI signal can be used as a reliable way of identifying distinctive soil zones related to specific plant communities. If so, EMI could be used in reconnaissance survey to identify the soil zones most suitable for planting specific plant communities in habitat restoration.

MATERIALS AND METHODS

Location and Climate

The Godineau wetland is located in the South Oropouche watershed on the south western coast of Trinidad lying roughly between 10º 13-15′ N and 61º 30-32′ W. The climate in and around the South Oropouche watershed is much the same as the rest of the island which has a warm, humid tropical climate consisting of both wet and dry seasons (Water Resources Agency of Trinidad, 2001). The wet season occurs from June to December while the dry season occurs from January to May (Fig. 2). Similar to other humid tropical climates, during the wet season in the South Oropouche watershed, ground water storage accumulates, raising the water table and resulting in maximum run-off from the land towards the end of the wet season. When the dry season sets in, and terrestrial runoff is reduced, and saline water penetrates further inland through rivers, underground channels, and surface water. The average annual rainfall for the entire island is approximately 2000 mm and average temperature is 25^{0}C with evapotranspiration rates that may be as high as 60% of rainfall received in some parts of the island (Water Resources Agency of Trinidad, 2001).

Figure 1 shows a map of the entire wetland area. In the 1960’s this area was covered much more extensively by mangrove habitats, as determined from aerial photographs. Efforts were then made to ‘reclaim’ this area for agricultural production. The South Oropouche River was levied to prevent flooding, and a flood barrier with sluice gates was built to prevent saline water intrusion through the mangrove forest (Fig. 1). The mangrove forest was cleared, and arable agriculture and native grassland extended into this zone. Arable agriculture wasn’t a success and the area was left to grassland and cattle grazing. Progressively, the grassland has been displaced by sedge, and according to local knowledge, the sedge is now extending beyond its previous limits into areas that have always been grassland. This invasion by sedge poses both a fire risk and reduces the habitat for cattle grazing affecting local incomes.

We chose a study site on the interface between the sedge and grass communities exhibiting strong plant zonation. The study site, a portion of a small watershed, lies behind the village of Woodland (Fig. 1), in the Godineau wetland, approximately 100 m wide by 150 m in length. The soils within this region are Entisols, belonging to the Caroni peaty clay and the Godineau clay series and are characterised as acid sulphate soils (Juman and Sookbir, 2006) developed on peaty clay parent material, although we found no evidence of acid sulphate properties at our site. The topography of the area is generally flat, as these soils are found on the intermediate flood plains of the South Oropouche River system with impeded drainage, as evidenced by ground water gleying.

The dominant vegetation species that occur in distinct monocultures are grasses [Gramineae: *Paspalum fasciculatum* Willd. Ex Flugge and *Hymenachne amplexicaulis* (Rudge) Nees] and sedges (Cyperaceae: *Cyperus articulates* and *Eleocharis mutata*), as identified by staff members at the National Herbarium of Trinidad and Tobago. Textbook literature on the grasses indicates they are not salt tolerant but like wet clay soils; in particular, *Hymenachne amplexicaulis* is a fresh water grass that is semi-aquatic and likes long periods of fresh water inundation, typically months (Bogdan, 1977, Skerman and Riveros, 1990). The sedges are both brackish water species but may also be found in saline environments (Tucker 1983, Ravi and Mohanan, 2002 and Giesen et al., 2006).Another species found on the site were *Thalia trichocalyx* Ganep (Marantaceae). The vegetation species were distributed mostly along a gradient, with sedges toward the coast and grasses inland (Fig. 3). The majority of the study site is dominated by monospecific stands of *Eleocharis mutate*; these sedges give way to a grassland zone progressing inland. In scattered patches within the study site, *Thalia trichocalyx* were also found. It is believed that competitive interaction takes place at the community boundaries where both grasses and sedges dominate under conditions they are best adapted to (Pennings and Callaway, 1992).

Topographic, Electromagnetic Induction and Vegetation Surveys

For the topographic survey, a total station, range-pole and prism were used with a vertical datum. The total station comprising of a theodolite and an electronic measuring device (Trimble M3) was set up over a known datum point to determine coordinates by establishing a direct line between two points. Angles and distances were measured from the total station to the points on the field site under survey. The resulting topographic data were used to generate elevation maps of the field site.

Electromagnetic-induction was used to map the bulk soil electrical conductivity (ECa) of the study site non-invasively using the DUALEM-1S, a field computer (Archer Ultra Rugged Field PC, Juniper Systems) and GPS-BT GPS Receiver (Royal Tek, Kuei Shan). The DUALEM instrument is~1 m in length and has a receiver on one end and a transmitter on the other end from which ground conductivity is determined. Magnetic field loops are generated from the energized transmitter coil, which creates current loops in the ground; these in turn produce secondary magnetic fields. The receiver measures the combination of the primary and secondary magnetic fields, the magnitude of which is related to the ECa of the material at low induction numbers (Mc Neil, 1980). Different receiver coil orientations allow measurements to be integrated across different depths. Measurements sensitive to the upper 0-0.75 m and the lower 0.75-1.5 m can be obtained with a 1.0-m distance between coils in low conductivity materials (Abdu et al., 2008). The instrument is capable of taking 3600 measurements h^{-1} at a 1-s logging interval.

The DUALEM-1S instrument was held parallel to the ground (approximately 0.2 m above ground) using the vertical coil orientation. Measurements were made by navigating the wetland field site in a predetermined grid-like pattern. The grid-like EMI survey route was created by traversing the field site horizontally, then vertically at ~10 m distances between the grid (Fig 3A). EMI maps were then created by interpolating the data using kriging, following quality assurance/quality control procedures. The wetland field site was submerged at various times during the study period due to the amount of rainfall received (Fig. 2). The EMI mapping of the Godineau field site was conducted during the months of May, June and July of 2009 when the wetland was dry (rainfall in May = 71 mm, June = 91 mm, July= 275 mm) and in August 2009 when the wetland was submerged (rainfall in August = 341 mm) to capture the full range of soil moisture wetness. The precipitation recorded in 2009 for the 3 dry mo amounted to 436 mm and for the submerged 1 mo, 341 mm. In 2010, EMI mapping was conducted for the month of February when the wetland was dry, with the total precipitation recorded for that month being 2 mm indicating a very severe dry season in comparison to 2009 which had a wet dry season (Fig. 2).

A vegetation survey was carried out by visually observing community extents while delineating them by GPS to plot different plant boundaries. Five plant habitats were identified, Sedge EM (dominated by *Eleocharis mutata*), Sedge CA (dominated by *Cyperus articulatus*), Grass PF (dominated by *Paspalum fasiculatum*), Grass MA (dominated by *Hymenachne* *amplexicaulis*) and Thalia TT (*Thalia trichocalyx*); which were later being grouped into two habitat types of grasses and sedges. By means of a stratified random sampling method, a 1-m^2 quadrat was lowered at different georeferenced locations within a specific plant habitat type and the percentage cover was estimated and recorded, producing a total of 238 locations.

Water Quality Sampling

The surface water quality of the study site was measured using a Horiba water quality checker during the wet season when the site was inundated due to fresh water inputs as a result of rainfall events and surface runoff. Measurements were made at georeferenced locations recorded using a GPS receiver and a field computer. In total, 239 randomly located samples were tested for pH, conductivity, dissolved oxygen O_2, temperature and turbidity within the grass and sedge vegetation zones.

Soil Sampling and Analysis

A simple random sampling design was employed to collect soil samples that were representative of the entire field site. Sample locations were randomly selected for each vegetation block, with 46 locations recorded. After collecting the ECa data using the EMI for each sample location, a gouge auger was used to manually collect soil samples from depths of 0 to 0.3 m. Duplicate samples were collected at each sample location, each of which was immediately sealed in Ziploc plastic bags to prevent moisture loss.

The soil samples were transported back to the laboratory, and subsamples were promptly weighed (fresh mass) and analyzed for soil water content and bulk density by recording the dry mass after oven drying at 105^{0}C to constant weight. The remaining samples were air dried, crushed and passed through a 2- mm sieve for soil physical and chemical analyses. Hygroscopic water content was determined by oven drying the sample and allowing it to equilibrate at 50% ambient laboratory relative humidity following the method described in Wuddivira et al. (2012). Particle size analysis was performed using the hydrometer method after organic matter removal (Gee and Bauder, 1986). Soil solution electrical conductivity (ECe), pH and redox potential were measured from a saturated soil-water paste extract (Rhoades et al., 1999). A dry combustion method using a CHNS analyzer (Perkin Elmer) was used to determine the total carbon content in the soil samples (Nelson and Sommers, 1996).

Data Analysis

Before interpolation by Gaussian kriging, the non-normal ECa data were normal score transformed (Goovaerts, 1997). Semi-variograms were analyzed to determine the correlation structure that underlies the spatial prediction for the kriging of these values.

Simple kriging is used in the Gaussian method; after kriging the normal score transformed, interpolated data were then back-transformed to the original distribution. The elevation and electrical conductivity data sets were kriged and their values used to determine relationships with other variables.

Summary statistics were obtained for the data and the Sharpiro-Wilk test was used to test the normality of the data for each soil and water parameter (Table 1) in the grass and sedge habitats. All of the soil and water quality parameters were found to be normally distributed at the 0.05 level of significance within the field site. Apparent electrical conductivity, however, had to be logarithmically transformed before the application of the statistical techniques and parametric analysis such as regression and t-tests.

RESULTS AND DISCUSSION

Vegetation Patterns in the Study Site

The three surveys (EMI, vegetation and topographic) carried out on the field site were necessary to characterise the vegetation in terms of their location within the field site (Fig. 3). The EMI surveys and the subsequent interpolated maps generated characterized the spatial and temporal variation of ECa on the field site for the area shown in Fig. 3A. The vegetation grid revealed distinct vegetation monocultures at the field site (Fig 3B), where *Eleocharis mutata* habitats occupied 38% of the field site, *Paspalum fasiculatum* occupied 10%, *Hymenachne amplexicaulis* 46%, *Thalia trichocalyx* 5% and *Cyperus articulatus* 2%. Elevation has been hypothesized as being a major control of the vegetation patterns that develop in wetlands (Silvestri et al., 2005) because of the processes it influences. These processes include salinization, time of inundation, redox potential, and moisture saturation which are important for plant growth and productivity. The elevation ranged from 0.0-0.7 m from the datum, with the higher elevations found in the red areas (Fig. 3C) occupied predominantly by grasses, while the lower elevations in the blue areas were occupied predominantly by sedges and some grasses. Distinct vegetation monocultures were found at the Godineau field site zoned according to elevation (Fig. 3D). The grasses *Hymenachne amplexicaulis* (mean = 0.4 m) and *Paspalum fasiculatum* (mean = 0.3 m) were found on the highest elevation ranges, while the sedges *Eleocharis mutata* (mean = 0.2 m) and *Cyperus articulatus* (mean = 0.2 m) occupied the lowest elevation ranges. *Thalia trichocalyx* (mean = 0.3 m) was found in mid elevations respective to the grasses and sedges.

Influence of Edaphic Factors on Vegetation Distribution

We performed t-tests comparing the mean values of the soil and water quality parameters for the grass and sedge communities. These revealed that there were statistically significant differences between the grass and sedge communities (Table 2). Results showed that ECe (P = 0.05), dry bulk density (P = 0.02) and VWC (P = 0.05) were all significantly higher in the sedges than in the grasses. The mean ECa of the soil was significantly higher in the sedges (3.0dS m^{-1}, P = 0.01) than in the grasses (2.0dS m^{-1}). Sedges thrived better in saturated areas that were higher in salt content than grasses and may have a competitive advantage in these areas as they are more salt tolerant (Table 2). The data suggests that soil salinity and moisture regime are the drivers of the plant zonation within the site. The grasses are mostly constrained to drier areas, which are slightly saline, with lower soil ECe (average = 3.7 dSm^{-1}) whilst the sedge communities are in wetter more moderately saline soils (average = 4.4 dS/m^{-1}) Table 2. Given the respective ECe values conversion to osmotic pressure (OP) using $OP=0.036\times ECe$ (dS/m^{-1}) gives average osmotic pressures of 0.13 and 0.16 MPa for the grass and sedge communities respectively. As the soil dried from ~0.8 at saturation to 0.3 m^3m^{-3} in the dry season, we might expect these osmotic potentials to more than double, which in combination with the matric potential would produce soils with very negative tensions. Various researchers (Dunham, 1989; Hook and Burke, 2000 and Onkware, 2000) also found strong correlations between these soil parameters and vegetation distribution in wetlands. Soil texture was found to be uniform across the field and therefore was not a contributing factor to plant zonation in the Godineau wetland. It was clear, however, that the sedges were better able to tolerate salt stress than the grass species, as reported in similar findings by Bernhardt and Kropf (2006) in Mediterranean systems and in keeping with the grasses not being salt tolerant and the sedges being brackish water species.

Surface water is largely responsible for the import and export of salts on the site. Some species of sedge are known to have salt glands, allowing them to excrete salt (Hutterer and Albert, 1992). We theorised that if these sedges could secrete salt it could result in further salinization of the surface water and provide a competitive advantage over salt- intolerant grasses. The results of the t-test for each water quality parameter are presented in Table 3. The t-test revealed that there were significant differences between the grass and sedge communities for all mean water quality parameters at the 0.01 level. These results may suggest that the sedges are modifying their immediate environment, probably through salt secretion, suiting their survival needs as a means of interspecific competition. Based on the results of the current study, grasses were more sensitive to salinity, being better adapted to areas of lower soil salinity, which were also drier (higher elevation), and areas of fresher surface water quality. The sedges on the other hand were better adapted to areas of higher salinity and moisture at lower elevations.

Geophysical Survey Results

Previous studies have shown that seasonality is a major cause of variation in salinity within tidal wetlands (Callaway et al., 1990; Moffett et al., 2010). We expected the same in the Godineau wetland with its clear wet and dry seasons. The time lapse EMI maps of the Godineau field site showed that the magnitude of ECa values in the field site had a clear seasonal change, but that the spatial pattern remained similar (Fig. 4). Analysis revealed that within the field site, the months of May 2009 with 71 mm of rainfall (mean ECa=1.9 dS/m^{-1}; SD = 0.6) and February 2010 with 2 mm of rainfall (mean ECa=2.0 dS/m^{-1}; SD = 0.8) had the lowest mean ECa values. The ECa increased for the wetter months, with June mean ECa= 2.1 dS/m^{-1}; SD = 0.9; August mean ECa= 2.2 dS/m^{-1}; SD =0.7; and July with a mean ECa=2.3 dS/m^{-1}; SD =0.8) at the peak of the wet season. The general trend among months when compared with rainfall patterns revealed lower ECa levels towards the end of the dry season (May) and as it got wetter, higher ECa values during the wet season (June, July and August) when floodwaters uniformly covered the field site to a depth of ~0.5 m. The increasing soil water content was responsible for the higher ECa during the wet season; after the wet season (February), ECa values gradually decreased as the soils dried out.

The temporal stability of the average of the five ECa maps allowed us to plot the spatial locations with the consistently greatest and smallest ECa values (Fig 4). The standard deviation allowed us to determine areas with high variability. A plot of the temporal stability standard deviation vs. the temporal stability mean ECa of the five EMI maps indicated that there was no correlation between variability and ECa zone location. The temporal stability average ECa levels for the field site ranged from -1.5 to +1.5 dS/m^{-1} above and below the mean. The sedges dominated in those areas that had consistently higher ECa, while the grasses in those with consistently lower ECa.

Edaphic Factors as a Function of Apparent Electrical Conductivity

Regression analysis was used to determine the relationship between soil factors and the ECa signal. The regression of ECa signal against soil parameters revealed that ECe (saturated soil paste extract) was the dominant parameter affecting the signal (Fig 5A); this is expected in saline soils, especially these wetland soils where water content and texture do not vary greatly spatially. The linear dependence of ECa on ECe (Fig 5A) yielded a significant relationship between the two sets of values within the field site (r^2= 0.5):

$$ECe = 1.61 \times ECa$$

(2)

Similar significant relationships between ECa and ECe were also reported by Herrero et al. (2003).

Dovaik et al. (2010) reported that elevation is a contributor and a control for the development of soil salinization in the field. The scatter plot of temporal stability mean ECa values of the five EMI maps, with the zero mean adjusted to 2.1 dS/m^{-1}, against height within the field site revealed that the relationship between ECa and elevation was non-linear (Fig. 5B). A strong relationship was observed to exist for which an exponential regression model ($y= 3.6253e^{-2.234x}$, $r^2= 0.8$) gave the best fit to the data. Gokalp et al. (2010) also observed that higher values of ECa were found on lower elevations. This is an indication that topography was an important factor controlling the salinity patterns that created the observed spatial variability of ECa within the field site. Hence the vegetation patterns are dependent on salinity which depends on the microtopography.

Vegetation Pattern Dependence on Apparent Electrical Conductivity (ECa)

The advantage of using the EMI was that it allowed us to explore the relationship between all the plant communities and the signal response, which acted as a surrogate for ECe. Measuring soil properties is time consuming and expensive, whereas EMI measurements are quick, non-invasive and cheap once the capital outlay has been expended. The EMI measurements allowed us to further explore the relationship with the smaller plant habitats. The ECa values for each plant community for the months with the highest (July) and lowest (May) mean ECa as well as the temporal stability mean ECa values of the five EMI maps were presented in Fig. 6. The five plant habitats identified had distinctive ECa niches resulting in a clear hierarchical pattern. This general observation also revealed that the sedge *Cyperus articulatus* was found in the niche with the highest average ECa value in both in July (mean ECa = 3.6 dS/m^{-1}; SD = 0.3) when the ecosystem was at its maximum wetness and May (mean ECa =2.8 dS/m^{-1}; SD = 0.2) when the ecosystem was at its minimum wetness. Another species of sedges (*Eleocharis mutata*) was found in the second highest ECa niche July (mean ECa= 2.9 dS/m^{-1}; SD = 0.6) and May (mean ECa= 2.3 dS/m^{-1}; SD = 0.4). Other plant communities including grasses were found to be dominant under lower ECa levels. *Thalia trichocalyx*, which was present only in small areas, occupied a niche between the sedges and grasses and was located in spatial locations between the two communities in July (mean ECa =2.1 dS/m^{-1}; SD = 0.6) and May (mean ECa=1.7 dS/m^{-1}; SD = 0.4). The grass *Paspalum fasciculatum* was in a similar niche to that of *Thalia trichocalyx* in July (mean ECa= 2.1 dS/m^{-1}; SD = 0.7) and May (mean ECa=1.8 dS/m^{-1}; SD = 0.4), but the grass (*Hymenachne amplexicaulis)* occupied the distinctively lowest niche in July (mean ECa=1.8 dS/m^{-1}; SD = 0.7) and May (mean ECa= 1.5 dS/m^{-1}; SD =0.5) (Fig 6).

For ECa maps to be helpful in site-specific management, they should be time stable spatially regardless of external factors (Hartsock et al., 2000; King et al., 2001; Nehmdahl and Greve, 2001). The temporal stability mean ECa for each plant type showed the same hierarchical patterns for the plant types (Fig. 6). All these initial results for a tropical wetland are promising in terms of demonstrating the potential application of EMI for management. This information is useful both for management and for potential restoration. It means that ECa maps can be used to determine the spatial extent of the salinity; moreover, time lapse EMI maps could be used to determine if the saline areas are increasing or decreasing and reveal how much remediation of soils in terms of leaching of salts is required for restoration. The results, along with the known management history of the area, can help us to piece together why the habitat has changed so much and sedge invasion is occurring. The construction of dykes and levees along the South Oropouche River has changed the hydrology of the area. The salinity levels are perhaps low enough to allow the sedge to dominate over mangrove, but too high for grasses. Moreover, it is likely that the management, with reduced leaching, evapoconcentration of salts, and sedges that can engineer their environment by removing salt from the soil and releasing it to surface water through salt glands all combine to exacerbate the spread of soil salinity. As a result, the sedge is invading into areas formally dominated by grasses.

Improved management or restoration options for this wetland to remove the fire threat of sedge might include enhanced management to either return it to grassland or allow it to return to mangrove. Removal of the levees combined with cutting of the sedge may allow it to return to a saline mangrove environment, while maintaining the levees but diverting more wet season fresh water runoff into the wetland may help to wash out more salt and so allow grasses to return. Maintaining the status quo is likely to result in the continued invasion of sedge until a new dynamic equilibrium is reached.

CONCLUSION

Our study shows that tropical wetland plant zonation patterns are dependent on patterns of soil salinity, which themselves are dependent on other factors such as soil wetness and elevation. The results indicate that saline niches exist that are more suited to sedges, that grasses are more suited to low-salinity environments, and that the zonation patterns largely follow the salinity, which largely follows the topography. Our results demonstrate that EMI signal response is dependent on soil solution ECe in these environments and that the signal can be used as a surrogate for ECe. EMI maps can be used to test the relationship between the spatial EMI response and the plant community zonation. This has potentially important applications in wetland management and restoration because EMI can be used to delineate zones of salinity that would form niches specific to certain plant species, it could also be used to determine the changes in the spatial patterns of salinity caused by management changes leading to enhanced or reduced leaching of salts by fresh water.

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Table 1. Shapiro-Wilk normality test results for soil parameters.

Parameters	Grass community W (p-value)	Sedge community W (p-value)
Soil		
ECe (dS m^{-1})	0.97 (0.61)	0.96 (0.61)
Log ECa (dS m^{-1})	0.95 (0.17)	0.92 (0.08)
Clay (%)	0.93 (0.05)	0.93 (0.13)
Sand (%)	0.93 (0.06)	0.94 (0.25)
Dry bulk density (g/cm^{-3})	0.95 (0.20)	0.93 (0.12)
VWC (m^3 m^{-3})	0.97 (0.51)	0.96 (0.46)
pH	0.98 (0.76)	0.94 (0.25)
Redox (mv)	0.97 (0.60)	0.95 (0.33)
C (%)	0.96 (0.47)	0.95 (0.33)
S (%)	0.95 (0.28)	0.97 (0.75)
Water quality		
ECw (dS m^{-1})	0.95 (0.21)	0.98 (0.79)
pH	1.00 (1.00)	0.97 (0.22)
DO (mg^{-1})	0.96 (0.29)	0.96 (0.14)
Temperature (ºC)	0.97 (0.66)	0.98 (0.60)

+ECe, Electrical conductivity (soil extract); ECa, apparent electrical conductivity; VWC, Volumetric water content; C, Carbon; S, Sulphur; ECw, Electrical conductivity (surface water); DO, Dissolved oxygen

±*P* values in parentheses.

Table 2. Results of a t-test for soil parameters comparing sites under sedge and grass.

	t-test result	**Grass** **Mean (Stdev)**	**Sedge** **Mean (Stdev)**
ECe (dS m^{-1})	t = -2.0 df = 39.07 p = 0.05 *	3.7 (1.07)	4.4 (1.2)
Log ECa (dS m^{-1})	t=-2.7 df = 35.21 p=0.01**	0.3 (0.1)	0.4 (0.1)
Clay (%)	t = -0.9 df = 42.10 p = 0.35	80.9 (3.4)	81.8 (3.1)
Sand (%)	t = 0.9 df = 39.91 p = 0.40	18.7 (3.0)	18.0 (3.0)
Dry bulk density (g/cm^{-3})	t = -2.4 df = 36.47 p = 0.02 *	0.5 (0.1)	0.6 (0.1)
VWC (m^3 m^{-3})	t = -2.1 df = 31.65 p = 0.049 *	0.3 (0.1)	0.3 (0.1)
pH	t = -1.5 df = 41.00 p = 0.14	3.7 (0.2)	3.8 (0.2)
Redox (mV)	t = 1.4 df = 40.75 p = 0.16	195.5 (13.1)	189.8 (13.6)
C (%)	t = -1.2 df = 42.11 p = 0.23	4.2 (0.1)	4.4 (0.7)
S (%)	t = -0.7 df = 42.70 p = 0.50	0.3 (0.1)	0.3 (0.1)

*Significant at $P \leq 0.05$.
**Significant at $P \leq 0.01$.ECe
+Electrical conductivity (soil extract); Log ECa, log distribution of the apparent electrical conductivity; VWC, Volumetric water content; C, Carbon; S, Sulphur; ECw, Electrical conductivity (surface water); DO, Dissolved oxygen
± Mean with standard deviation in parentheses

Table 3. Results of a t-test results for water quality parameters comparing sites under sedge and grass communities.

	t-test result	Grass Mean (Stdev)	Sedge Mean (Stdev)
ECe (dS m^{-1})	t=33.2 df = 71.79 p < 2.20E-16 ***	0.2 (0.03)±	0.5 (0.05)
pH	t = 10.5 df = 66.39 p = 8.35E-16 ***	6.0 (0.1)	6.3 (0.2)
DO (mg^{-1})	t = -14.5 df = 30.86 p = 2.44E-15 ***	5.2 (1.4)	1.2 (0.5)
Temperature (^{o}C)	t =-10.6 df = 55.44 p = 5.51E-15 ***	27.7 (0.7)	26.2 (0.6)

***Significant at *P* <0.001.

+ECe, Electrical conductivity (soil extract); DO, Dissolved oxygen

±Mean with standard deviationin parentheses.

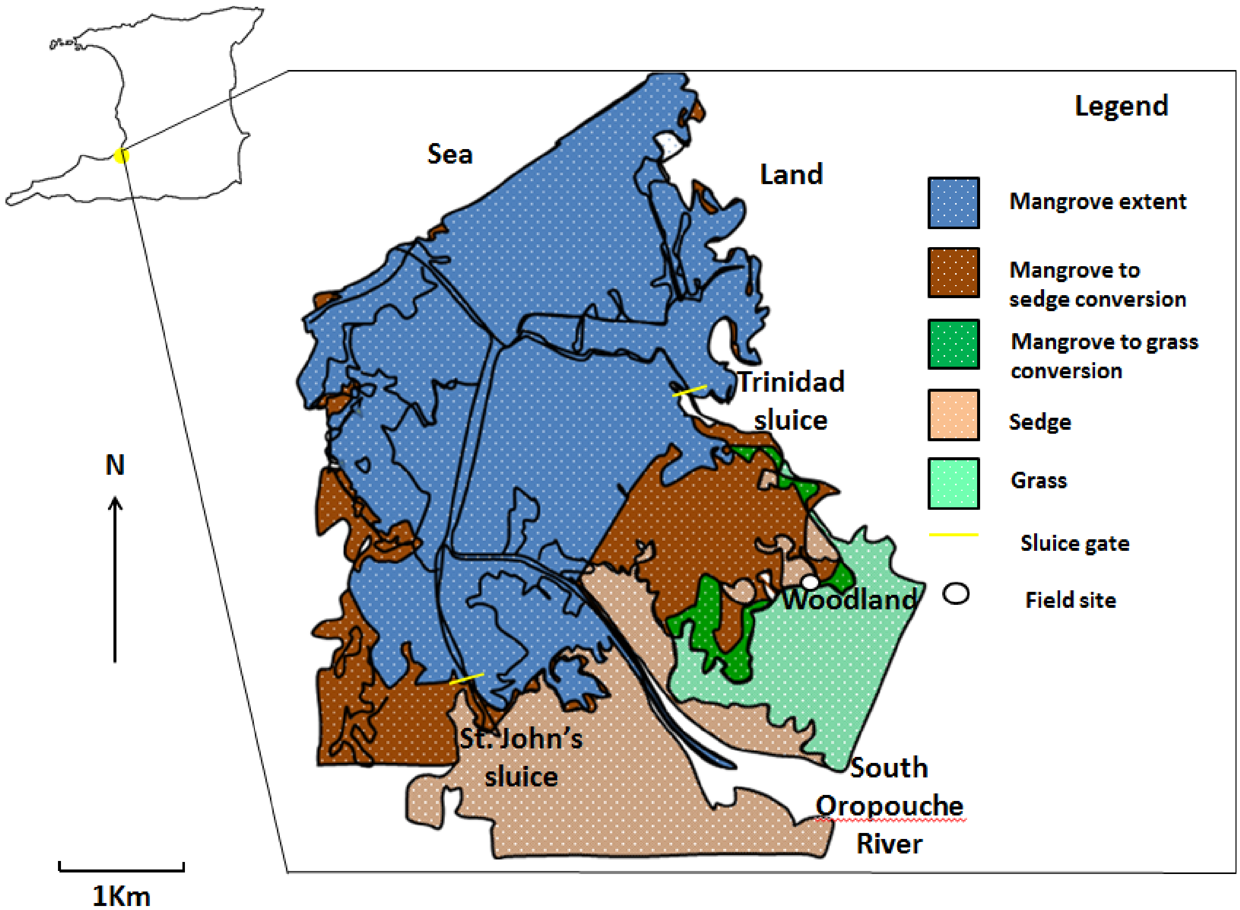

Fig 1. Outline of the Godineau wetland showing large-scale vegetation conversion between the years 1962 -2003.

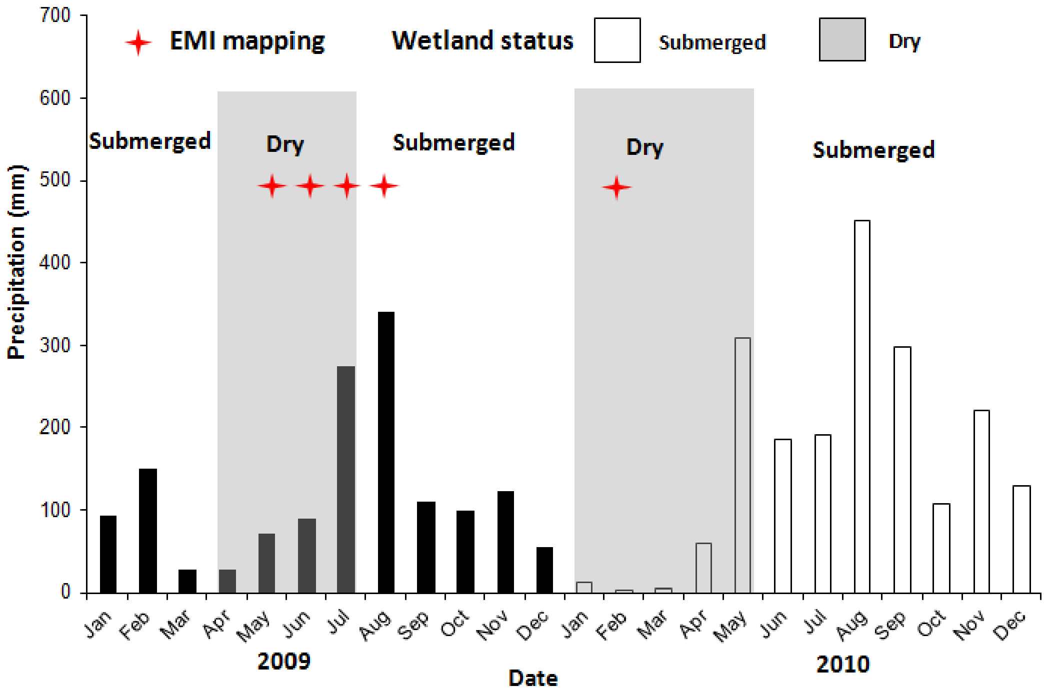

Fig 2. Monthly precipitation for 2009 and 2010 with the red stars showing the months when electromagnetic induction (EMI) mapping was conducted. The grey box indicates when the soil surface was dry, white when it was submerged.

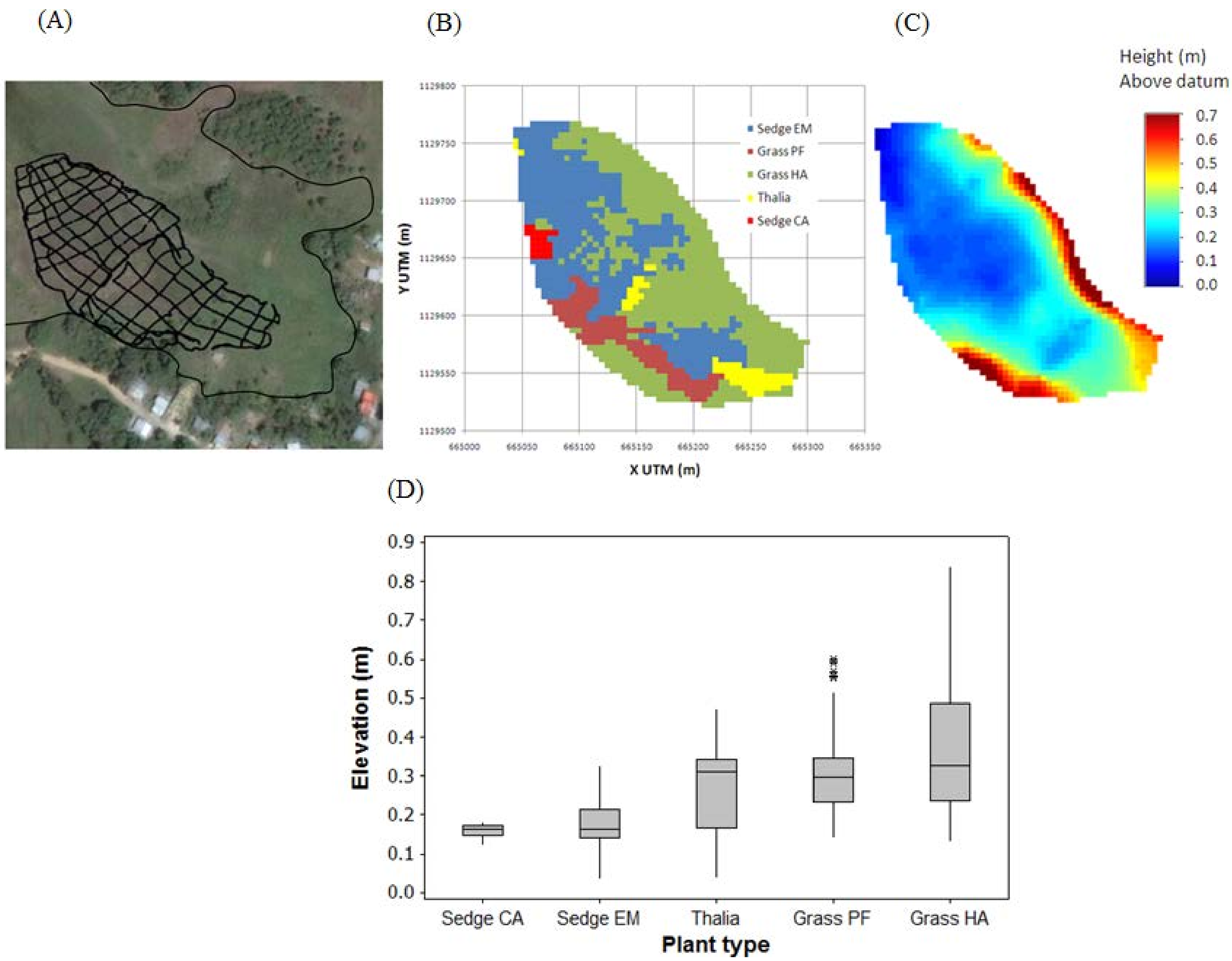

Fig 3. (A) Aerial photo of the Godineau wetland with the electromagnetic induction (EMI) survey route superimposed, (B) the dominant plant community distribution scaled to a 5m grid and (C) the kriged map of elevation to a common datum for the site, (D) boxplots of the dominant plant types vs. elevation. CA, *Cyperus articulatus*; EM, *Eleocharis mutata*; HA, *Hymenachne amplexicaulis*; PF, *Paspalum fasciculatum*; Thalia, *Thalia trichocalyx*. Asterisks in panel D represent outliers.

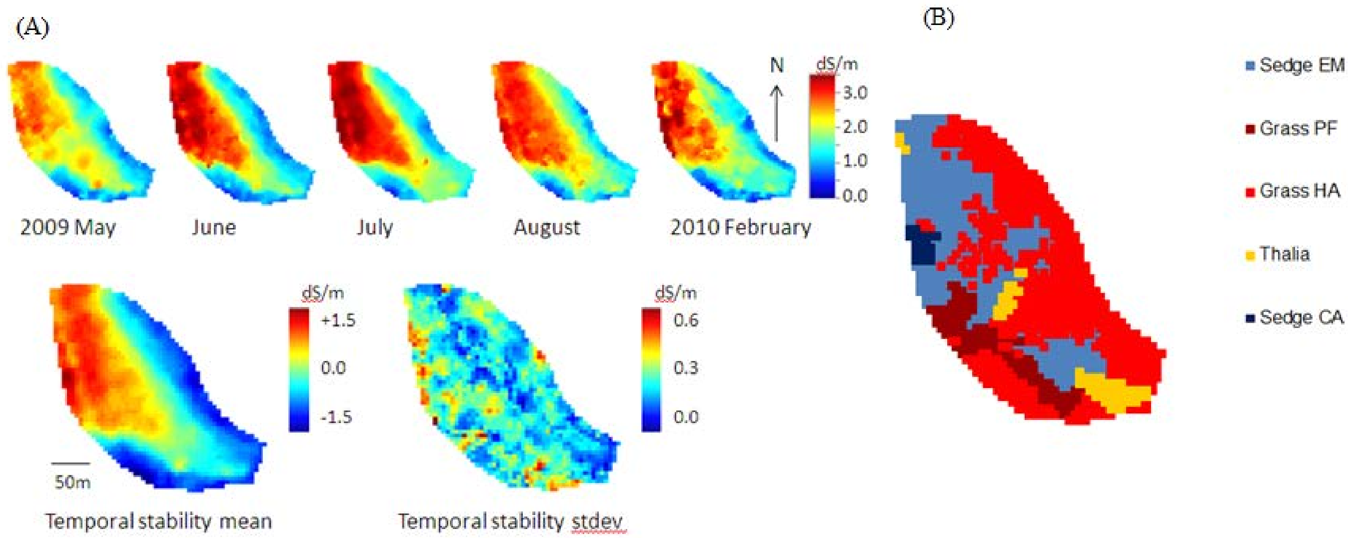

Fig 4. (A) Time lapse electromagnetic maps of Godineau field site for May 2009 to February 2010 with the temporal stability mean and standard deviation underneath for the five maps (B) plant community distribution across the field site: CA, *Cyperus articulatus*; EM, *Eleocharis mutata*; HA, *Hymenachne amplexicaulis*; PF, *Paspalum fasciculatum*; Thalia, *Thalia trichocalyx*.

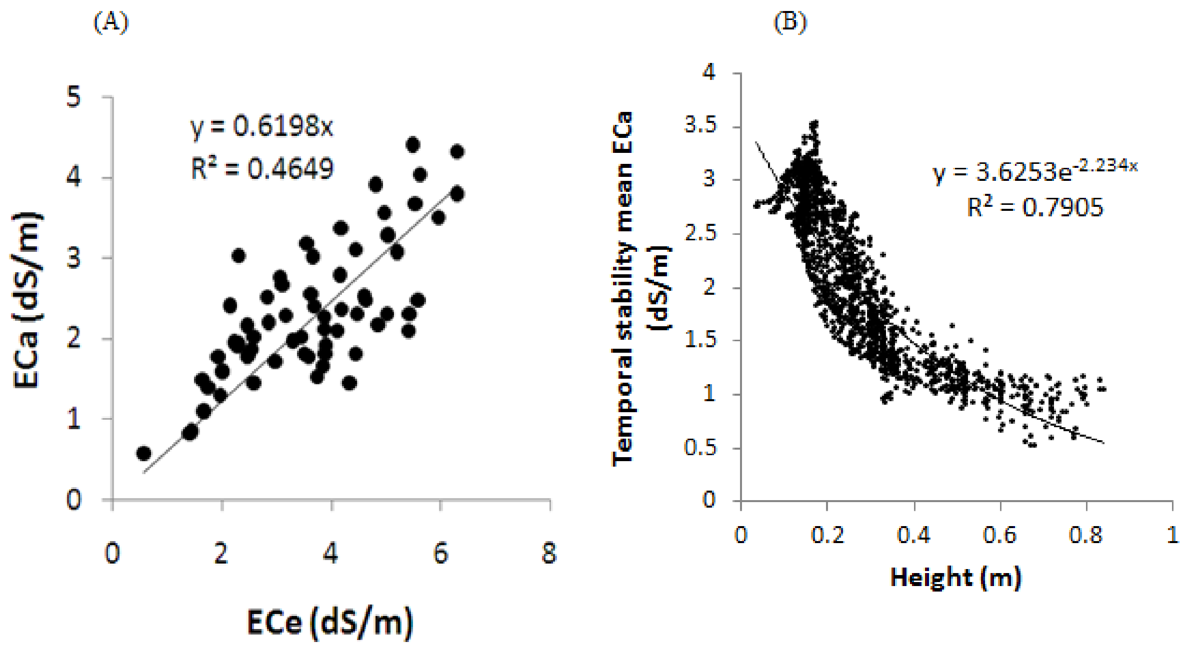

Fig 5. A) Electromagnetic induction (EMI)-based apparent electrical conductivity (ECa) as a function of extract electrical conductivity (ECe), and (B) ECa temporal stability average of the five EMI maps vs. ground elevation above the site datum.

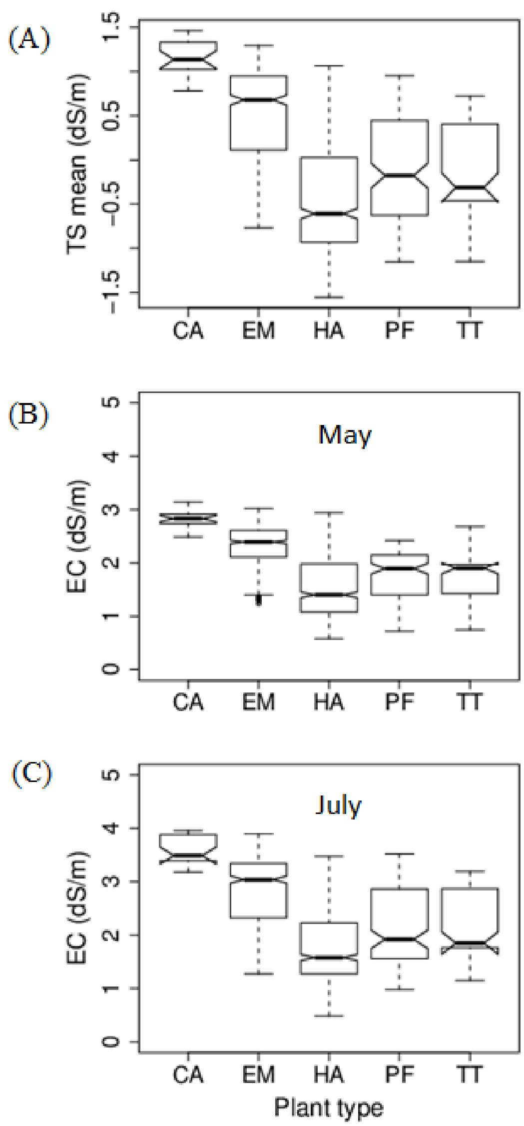

Fig 6. (A) EMI apparent electrical conductivity (ECa) temporal stability plot for the different communities showing the deviation from the temporal stability mean. Distribution of ECa signal with the dominant plant species for the months of (B) May (minimum ECa) and (C) July (maximum ECa). CA, *Cyperus articulatus*; EM, *Eleocharis mutata*; HA, *Hymenachne amplexicaulis;* PF, *Paspalum fasciculatum;* TT, *Thalia trichocalyx*.