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GENERAL WETLAND SCIENCE

Water Level and Salinity Drive Community Structure of Culturable Baldcypress (*Taxodium distichum*) Endophytes in Southern Louisiana

Elizabeth R. Kimbrough[1] · Mae L. Berlow[2] · Sunshine A. Van Bael[1]

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Abstract
Little is known about effects of salinity and flooding on plant symbionts, including baldcypress trees *(Taxodium distichum)*, the dominant trees in many swamp ecosystems in the southeastern US. In this study, we characterize the culturable fungal and bacterial endophytes in the roots and leaves of baldcypress trees at four sites with varying levels of salinity and flooding regimes in southeastern Louisiana. Both salinity and flooding (water level) contributed to endophytic community composition of leaves and roots. We found that diversity and endophyte isolation frequency were higher in roots than in leaves, with leaf bacteria being almost negligible. Our study demonstrates a connection between environmental variables, plant symbionts, and a key restoration species. This work may help in predicting future outcomes of sea level rise for endophytes communities in baldcypress and other wetland plants.

Keywords Cypress-tupelo swamp · Degradation · Endophytic bacteria · Endophytic fungi · *Eutypa lata* · Flooding · Salt

Introduction

Land use change, sea level rise, and associated changes in salinity, hydrology, and flood dynamics are global concerns. However, the effects are especially acute in coastal communities and subsiding areas near river deltas, as in southern Louisiana, where swamps and marshes are being degraded into marsh and open water (Shaffer et al. 2009). Little is known about effects of salinity and flooding on a key group of plant symbionts, the endophytes – microscopic fungi and bacteria that live asymptomatically within tissues of host plants (Porras-Alfaro and Bayman 2011). These microbial symbionts have been shown to increase host plants' resilience to biotic and abiotic stressors such as herbivory, disease, salinity, and temperature (Rodriguez et al. 1997; Redman et al. 2002; Rodriguez et al. 2009; Friesen et al. 2011; Redman et al. 2011). Endophytes have been found throughout the tissues of all plants examined to date (Friesen et al. 2011) including baldcypress trees *(Taxodium distichum)* (Kandalepas et al. 2010).

Baldcypress are the dominant trees in Cypress-Tupelo swamp ecosystems in the southeastern US. These deciduous conifers are crucially important to the Gulf Coast region as major buffers against storm damage and as focal restoration species (Shaffer et al. 2009). Because most plants have narrow salinity tolerances, baldcypress's ability to span freshwater to slightly brackish water (2 ppt salinity) and persist in variable flooding conditions (Allen et al. 1996) makes it an excellent candidate for studying interactions between salinity levels, flooding, and plant endophytes.

In this study, we characterized the culturable fungal and bacterial endophytes in the roots and leaves of baldcypress trees at four sites with varying levels of salinity and flooding in Southeastern Louisiana. Understanding the factors that structure microbial community composition has been the focus of much research over the past decades (Christian et al. 2015). Previous studies have demonstrated that endophyte community composition is influenced by plant organ (i.e. root,

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✉ Elizabeth R. Kimbrough
lizkimbrough@gmail.com

[1] Department of Ecology and Evolutionary Biology, Tulane University, 6823 St. Charles Avenue, New Orleans, LA 70118, USA

[2] Department of Biological Sciences, University of Tennessee, Knoxville, 1406 Circle Dr, Knoxville, TN 37996, USA

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stem, leaf, etc.) and environmental variables (Compant et al. 2010; Zimmerman and Vitousek 2012; Higgins et al. 2014; de Souza et al. 2016). For wetland plants, however, we do not know how interactions among environmental variables influence symbiont communities, including those variables associated with sea level rise. We predicted that baldcypress roots and leaves would harbor diverse (species rich) communities of culturable endophytes and that differences in the community diversity, isolation frequency, and composition would be driven by plant organ, salinity, and flooding. Our work on baldcypress endophyte communities explores the connection between the environment, plant symbionts, and a key restoration species, and may help in making predictions about the effects of sea level rise on wetland endophyte communities.

Methods

Study Sites/Sampling

In October 2014, we harvested root and leaf tissue from 12 mature *T. distichum* trees (>20 m height) from four unique sites ($n = 48$) along a degradation gradient in southern Louisiana (Table 1). We sampled apparently healthy leaves and roots from three locations on each tree. All trees within a site were ~100 m apart from each other and inundated with water, having roots completely submerged at the time of collection. Degree of degradation was determined by flooding regime, salinity, and anthropogenic access/disturbance. Permanently flooded and impounded sites were designated as more degraded than periodically flooded sites; and brackish sites were more degraded than fresh sites. The four sites, listed from the healthiest to most degraded, are: Tickfaw (TF), a periodically flooded freshwater swamp within the Tickfaw River floodplain; Jean Lafitte (JL), a permanently flooded freshwater site in Jean Lafitte National Historical Park and Preserve; Honey Island Swamp (HI), a permanently flooded freshwater swamp site along the Pearl River; and Bonnet Carre Spillway (LP), a brackish site on Lake Ponchartrain that is permanently inundated (Table 1). Salinity data for each site was collected from the USGS Coastwide Reference Monitoring System (CRMS) website (Steyer 2010) and is the average of the measurements taken monthly 1 year prior to our collection dates.

Culturing

Samples were placed on ice and transported into refrigeration at Tulane University for processing following well-established protocols (Arnold et al. 2003) within 48 h of collection. For leaves, a sterile blade was used to remove leaf tips and the remaining tissues were cut into 2 mm long leaflet

Table 1 Salinity, flooding regime, and degradation of four sites in southern Louisiana

Site	Mean Salinity /Salinity Range(ppt)	Flooding Regime	Degree of Degradation
Tickfaw (TF)	Fresh (0.1 ppt)/(0–0.2 ppt)	Periodic	LOW: apparently healthy trees of varying ages, closed to heavy foot traffic
Honey Island (HI)	Fresh (0.2 ppt)/(0.1–0.5 ppt)	Permanent	LOW-MEDIUM: apparently healthy trees of varying ages, along a flowing river, visited by humans
Jean Lafitte (JL)	Fresh (0.6 ppt)/(0.3–1.0 ppt)	Permanent	MEDIUM: healthy adult trees with no young trees established, water impounded, few human visitors
Lake Pontchartrain (LP)	Brackish (1.3 ppt)/(0.8–1.7 ppt)	Permanent	HIGH: no young trees established, flowing water along the Bonnet Carre spillway in a high use area, near an elevated highway

pieces and then surface sterilized via serial immersion in 95% ethanol (10 s), 10% Clorox (5.25% NaOCl-; 2 min), and 70% ethanol (2 min). For roots, apparently healthy, fine roots were selected, cut into 2 mm length sections and serially immersed in 70% ethanol (10 s), 50% Clorox (2 min), and sterile water (2 rinses). A surface sterilization control plate was used for each plant in this collection to be sure that surface sterilization was complete. For each individual tree, 32 surface sterilized sections of roots and 32 sections of leaves were randomly selected for plating on growth media. Of these 32, 16 pieces were plated on 2% malt agar (2% MEA: 20 g of Difco Malt Extract and 20 g of Difco Agar per L of deionized water) which is selective for fungi (Fröhlich and Hyde 1999). The remaining 16 pieces were plated on a non-salt containing nutrient agar (BD Difco Nutrient agar containing: beef extract 3 g/L, peptone 5 g/L, agar 15 g/L) which is selective for bacteria. The total sampled was $n = 768$ leaf and root pieces plated to screen for fungal abundance and $n = 768$ leaf and root pieces plated to screen for bacterial abundance. Plates were sealed, incubated at room temperature, and monitored daily for 5 weeks for emergent fungi and bacteria. Emergent fungal and bacterial colonies were counted and isolated into pure cultures. Isolates were photographed and preserved in 50% glycerin and water, respectively, in the Van Bael laboratory at Tulane University.

Sequencing

Up to 50% of the surviving symbionts at each site were randomly selected for Sanger sequencing. Total genomic DNA was extracted using a MoBio Ultraclean DNA Isolation Kit. For fungi, we used primers ITS1F and LR3 to amplify the nuclear ribosomal internal transcribed spacers (nrITS) and 600 bp of the large ribosomal subunit (partial LSU) as a single fragment (nrITS-partial LSU) following Higgins et al. (2011). For bacteria, we used primers 27F and 1492R to amplify the 16S rDNA gene DNA. All PCR products were submitted to Beckman Coulter Genomics for Sanger sequencing. Sequence editing was carried out with Sequencher v5.0 (Gene Codes Corporation, Ann Arbor, MI). Sequences with 97% similarity were considered to be representative of the same operational taxonomic unit (OTU). Representative sequences of each OTU were compared to NCBI archives through BLAST searches to assign putative taxonomic identities using Geneious version r9 (http://www.geneious.com, Kearse et al. 2012). Voucher cultures of all OTUs were archived in the Van Bael lab at Tulane University, under accession numbers 1182–1750. Accession numbers for sequences deposited in the NCBI Genbank are: MK036892-MK036991, as well as KY765153, KY765188, KY765159, KY765161, KY765168 referenced in Washburn and Van Bael (2017).

Environmental Data

Environmental data for each site was collected from the USGS Coastwide Reference Monitoring System (CRMS) website (Steyer 2010). Using google maps, we selected the CRMS stations that were within 3 miles of the collection sites. For the sites Lake Ponchartrain, Tickfaw, Honey Island and John Lafitte we used data from CRMS stations 6299, 0046, 6088, and 0234, respectively. The following environmental variables were used and accounted for data collected over a 1-year period prior to our plant tissue sampling date: site, date of collection, average salinity, maximum salinity, average water level, minimum water level, maximum water level, average temperature, minimum temperature, maximum temperature, tidal amplitude, and average time flooded.

Statistical Methods

Endophyte isolation frequency (EIF) was measured as a proportion of root/leaf pieces which grew a symbiont into culture over the total number of pieces plated in growth media and compared via Mann-Whitney U tests in PAST (PAlaeontological STatistics). All alpha diversity metrics were created with Fisher's Alpha (FA). We used Bray-Curtis dissimilarity to compare community composition and to assess among community (beta) diversity. We conducted a db-RDA in the R package *vegan* (Oksanen et al. 2016) to determine which environmental variables best explained the endosymbiont communities (in Bray-Curtis dissimilarity matrix format). We used the ordistep function to select from the environmental data variables. The anova function was used to determine the significance per variable that contributed to the model (Table 2).

Results

We cultured 364 bacterial and fungal endophyte isolates from leaves and roots of 48 *T. distichum* trees from southern Louisiana. We acquired DNA sequences from a subset of 151 isolates: 113 fungal and 38 bacterial sequences, representing 43 fungal and 17 bacterial OTUs (Supplementary Table S1 and S2). All species names are putative taxonomic identities based on 97% sequence similarity. The most common fungal species were *Eutypa lata*, which is a known pathogen in sugarcane (*Saccharum* sp.) and grapes (*Vitis vinifera*) (Erincik et al. 2001) and *Metarhizium brunneum*, a fungal strain which is used as a biocontrol. The most common bacterial species were *Bacillus ceres,* a plant growth promotor known to increase salt tolerance in safflower (*Carthamus tinctorius*) plants (Reyad et al. 2017) and *Bacillus aryabhattai,* a plant growth promoting rhizobacteria (Park et al. 2017).

Table 2 ANOVA results based on R capscale model selection of all environmental variables. Bold indicates significance

Organ	Symbiont Type	Max Water Level (F, p)	Average Salinity (F, p)
Roots + Leaves	Bacteria + Fungi	F = 3.02, ***p* = 0.001**	F = 1.64, ***p* = 0.041**
Roots + Leaves	Bacteria	F = 0.79, $p = 0.671$	F = 0.93, $p = 0.585$
Roots + Leaves	Fungi	F = 4.59, ***p* = 0.002**	F = 1.77, $p = 0.092$
Roots + Leaves	Fungi (*Eutypa lata* excluded)	F = 2.08, ***p* = 0.007**	F = 1.66, ***p* = 0.044**
Roots	Bacteria + Fungi	F = 1.56, ***p* = 0.032**	F = 1.46, ***p* = 0.058**
Roots	Bacteria	F = 0.79, $p = 0.390$	F = 0.93, $p = 0.522$
Roots	Fungi	F = 2.16, ***p* = 0.011**	F = 1.68, $p = 0.065$
Leaves	Bacteria + Fungi	F = 2.43, $p = 0.065$	F = 2.63, ***p* = 0.052**

Plant Organ

Endophytic diversity, as calculated by Fisher's Alpha, was seven times higher in roots (FA = 27.70) than in leaves (FA = 3.51). We observed a greater EIF of culturable endophytes in the roots than in the leaves of baldcypress (Mann Whitney U = 2225.5, $n = 98$, $p < 0.001$) (Fig. 1).

Site

Among sites, Jean Lafitte had the highest diversity of endophytes (Fisher's Alpha: HI =12.50, JL = 29.18, LP = 12.66, TF = 8.83). Tickfaw and Lake Ponchartrain significantly differed from one another in EIF (Mann Whitney, U = 2225, $n = 98$, $p = 0.035$) and fungi were isolated more frequently than bacteria across all sites (Mann Whitney, U = 3920, $n = 98$, $p = 0.047$) (Fig. 1).

Environmental Data

Maximum water level and average salinity in the year prior to collection explained a significant amount of variation in the culturable endophyte communities (F = 3.02, $p < 0.001$); (F = 1.64, $p < 0.041$) (Fig. 2). For root communities alone, the maximum water level explained a significant amount of variation within the culturable endophyte communities (F = 1.56, $p < 0.032$) and average salinity was found to improve the model during model selection (F = 1.45, $p < 0.058$). Within cultured fungal communities (excluding bacteria), maximum water level in the year prior to collection explained a significant amount of variation in community composition (F = 4.59, $p < 0.02$).

Discussion

Diversity and Isolation Frequency

We found that diversity and isolation frequency of culturable endophytes in baldcypress were greater in roots than in leaves. Leaf bacterial diversity and EIF were quite low when compared to studies on other conifers and other deciduous temperate trees examining both leaves and roots (Izumi et al. 2008; Wilson 2015). This is the first study done on the leaves of a tree that is both deciduous and a conifer (and having high level of phenolic terpenoid compounds present in leaves (Falk and Wolkenstein 2017)) and we speculate that these factors could have some influence on the dearth of endophytes found. However, this could also be attributed to the difficulties of using culture-based methods to survey bacterial communities.

The leaf endophyte community was dominated by the putative fungal pathogen, *Eutypa lata* (Erincik et al. 2001). The greater endophytes isolation frequency observed at Tickfaw can also be attributed to the presence of *E. lata,* which comprised 52 of the 112 isolates. Even though we collected fungi from apparently healthy leaves, the *E. lata* isolates may actually represent pathogens, as *E. lata* is a known generalist pathogen infecting sugar cane, grapes, and woody fruit trees such as *Prunus sp.* (Lecomte et al. 2000). Further investigation into the relationship between *E. lata* and baldcypress is needed.

Environmental Variables

Both salinity and flooding (water level) contributed to endophytic community composition of baldcypress endophytes. Microbes have variable tolerances to salt, and only certain microbes are able to persist when conditions become more saline (Chowdhury et al. 2011). Changes in salinity alter the community composition of bacteria in soil samples and increases in salinity of 5% or more significantly decreased the genetic diversity of bacteria in soil samples (Omar et al. 1994). Fungal diversity and community composition are also altered in the presence of NaCl (Ke et al. 2013). For arbuscular mycorrhizal fungi, the presence of NaCl delayed germination of spores and reduced overall hyphal growth, the potential mechanism being the diversion of energy from metabolism to osmoregulation (Juniper and Abbott 2006). Because many plants draw upon the rhizosphere/soil microbiome to assemble their own microbiomes (Compant et al. 2010), changes in the soil microbiome due to salinity shifts could be responsible for

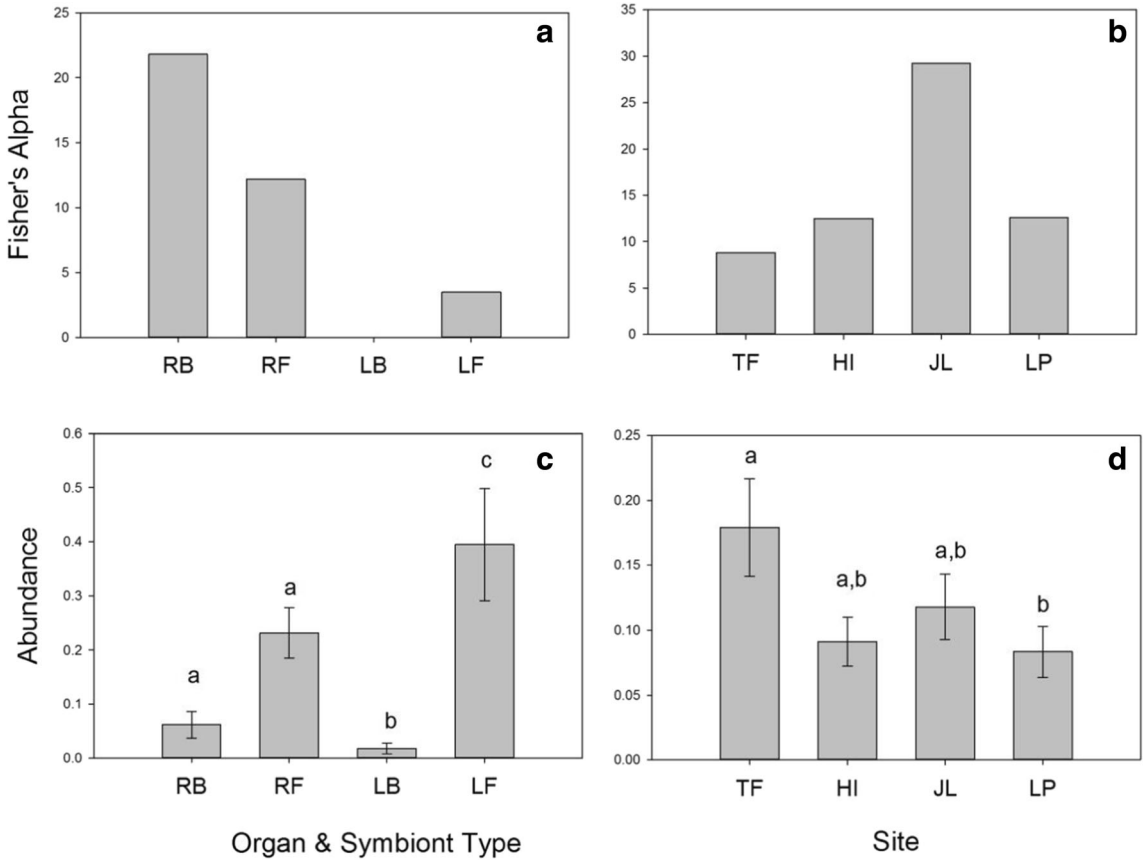

Fig. 1 Plant organs and sites differed in endophyte isolation frequency and diversity of endophytes (Organs: root bacteria = RB, root fungi = RF, leaf bacteria = LB, leaf fungi = LF; Sites: Tickfaw = TF, Honey Island = HI, Jean Lafitte = JL, Bonnet Carre Spillway at Lake Ponchartrain = LP). **a** Diversity (measured by Fisher's Alpha) was highest in roots and for root bacteria. **b** Among sites, diversity was highest at Jean Lafitte, the least disturbed area. **c** Endophyte isolation frequency (abundance, mean ± standard error) was highest for leaf fungi and **d** at Tickfaw, the least degraded site. Lower case letters show which groups are significantly different using a Bonferroni correction ($p<0.05$)

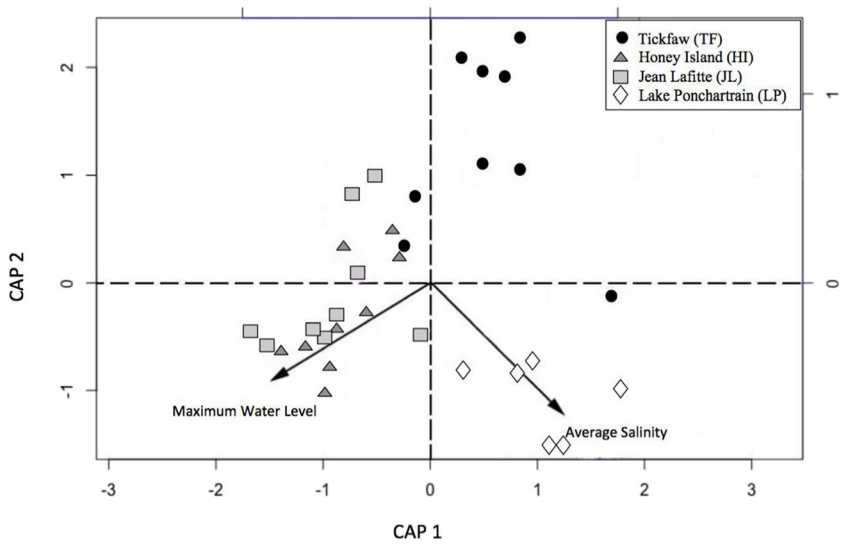

Fig. 2 Sites differed in community composition of endophytes. Salinity and maximum water level described significant variation with community composition. Each data point represents the microbial community composition (of fungi and bacteria combined) of one tree and is based on Bray-Curtis similarity of communities at the OTU level. Vectors indicate the weight and direction of those environmental variables that were best predictors of endophyte community composition as suggested by the results of the db-RDA

the change in plant microbial communities, particularly for root endophytes, which recruit microbes from the rhizosphere and soil in closest proximity to the roots.

Salinity and flooding have known negative effects on baldcypress physiology individually, and these effects are increased in combination, demonstrating an interactive effect which may influence baldcypress populations (Allen et al. 1996; Krauss et al. 1998, 1999). Some research supports the idea that with increased depth and duration of flooding, baldcypress growth declines and mortality is increased (Souther and Shaffer 2000), potentially due to a decrease in oxygen and nutrient availability (Conner and Day Jr. 1992). These changes in plant physiology may influence the tree's recruitment of endophytes or have weakened the tree's defenses to pathogens, thus influencing endophyte community assembly.

Limitations

Though our study utilized agar media recipes consistent with many other endophyte studies (Arnold et al. 2003; Mighell and Van Bael 2016; Kandalepas et al. 2015) the richness, source (plant vs. animal) and composition of nutrients could bias the selection of microbial isolates. Overall, culture-based work provides a very limited view of the endophyte community, as it is estimated that only a fraction of microbes, especially bacterial, can be grown in culture (Izumi et al. 2008; Ulrich et al. 2008). Future work should focus on using an amplicon-based approach to better assess true diversity. This study also failed to account for plant genotypes, which can be highly variable among baldcypress (Allen et al. 1996). Gehring et al. 2017 demonstrated that an interaction between plant genotypes and their mycorrhizal fungal symbiont community was important for drought tolerance in pine trees and that mycorrhizal community composition was strongly driven by plant genetics. Interactions between plant genotype, endophytic communities, and environmental stress should be examined in situ or tested experimentally using advanced molecular methods.

Conclusion

Our study demonstrates a connection between environmental variables, plant symbionts, and a key restoration species. Baldcypress' culturable endophyte community composition was associated with both salinity and flooding. As coastal ecosystems change due to sea level rise, subsidence, and human activities, we can expect variability in water levels and greater saline incursions into previously freshwater areas. It is possible that the observed clines in salinity and differing hydrological regimes at these sites can be used to predict future outcomes of sea level rise for baldcypress endophytes and endophyte communities in other wetland species.

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