Casa abierta al tiempo
UNIVERSIDAD AUTÓNOMA METROPOLITANA

Doctorado en Ciencias Biológicas y de la Salud

UNIDAD IZTAPALAPA
DIVISIÓN DE CIENCIAS BIOLÓGICAS Y DE LA SALUD
POSGRADO DOCTORADO EN CIENCIAS BIOLÓGICAS Y DE LA SALUD

TESIS

"ESTUDIO DE LA INTERACCIÓN ENTRE *THALASSIA TESTUDINUM* Y *CAULERPA PASPALOIDES* EN LA RESERVA DE LA BIOSFERA DE LOS PETENES, CAMPECHE, MÉXICO."

PARA OBTENER EL GRADO DE

DOCTOR EN CIENCIAS BIOLOGICAS Y DE LA SALUD

PRESENTA

M. EN C. B. SERGIO ARMANDO FUENTES AGUEDA
Matricula: 2163802437
kamahl2004@gmail.com/ sfagueda87@xanum.uam.mx

ORCID: 0000-0003-3297-5104

DIRECTORA: MARGARITA ELIZABETH GALLEGOS MARTÍNEZ

JURADO
PRESIDENTE: DR. MARGARITA ELIZABETH GALLEGOS MARTÍNEZ
SECRETARIO: DR. JORDAN KYRIL GOLUBOV FIGUEROA
VOCAL 1: DR. MARÍA DEL CARMEN MANDUJANO SÁNCHEZ
VOCAL 2: DR. THOMAS A. FRANKOVICH
VOCAL 3: DR. ABEL SENTÍES GRANADOS

IZTAPALAPA, CIUDAD DE MEXICO A 24 DE MAYO, 2024

La presente investigación se realizó:

En el Laboratorio de Pastos Marinos de la Universidad Autónoma Metropolitana Unidad Iztapalapa, Departamento de Hidrobiología bajo la dirección de la Dra. Margarita Elizabeth Gallegos Martínez.

En el Laboratorio de Ecología y Evolución en el Instituto de Ecología de la Universidad Nacional Autónoma de México bajo la asesoría de la Dra. María del Carmen Mandujano Sánchez.

En el Laboratorio de Ecología y Taxonomía Vegetal de la Universidad Autónoma Metropolitana Unidad Xochimilco bajo la asesoría del Dr. Jordan K. Golubov Figueroa

El autor agradece al Consejo Nacional de Ciencia y Tecnología (CONACyT) por la beca otorgada para sus estudios de doctorado, con el número de registro 288716, que comprendió del periodo de 1 de septiembre del 2016 al 31 de agosto del 2020.

Al Comité de Apoyos Extraordinarios de Posgrado de la UAM por el apoyo extraordinario que otorgó desde septiembre 2020.

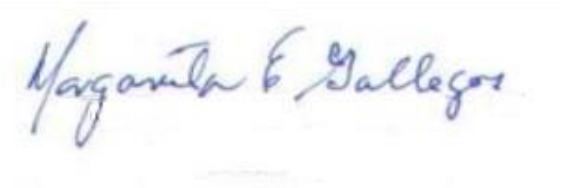
El Doctorado de Ciencias Biológicas y de la Salud de la Universidad Autónoma Metropolitana pertenece al Padrón de Posgrados de excelencia del CONACyT y, además, cuenta con apoyo del mismo Consejo con el convenio PFP-20-93.

El jurado designado por La Comisión Académica del Doctorado en Ciencias Biológicas y de la Salud, de la Universidad Autónoma Metropolitana aprobó la tesis que presentó:

M. en C.B. Sergio Armando Fuentes Agueda

Fecha de aprobación de la tesis: 24 de mayo del 2024

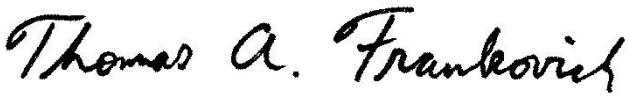
JURADO:



Presidente: Dr. Margarita Elizabeth Gallegos Martínez

Secretario: Dr. Jordan Kyril Golubov Figueroa

Vocal 1: Dr. María del Carmen Mandujano



Vocal 2: Dr. Thomas A. Frankovich

Vocal 3: Dr. Abel Sentíes Granados

Agradecimientos:

- A la Dra. Margarita Elizabeth Gallegos Martínez por la dirección de esta tesis.
- A la Dra. María del Carmen Mandujano Sánchez por la asesoría de la tesis.
- Al Dr. Jordan K. Golubov Figueroa por la asesoría de la tesis.
- Al Comité Tutoral conformado por la Dra. Margarita Elizabeth Gallegos, la Dra. María del Carmen Mandujano Sánchez Martínez y el Jordan K. Golubov Figueroa por la asesoría, desarrollo, apoyo y revisiones que dieron durante el doctorado.
- Al Jurado conformado por el Presidente Dr. Carlos Manuel Duarte Quesada, Dra. Margarita Elizabeth Gallegos Martínez, Secretaria Dra. María del Carmen Mandujano Sánchez, Vocal Dr. Thomas A. Frankovich, Vocal Dr. Jordan Kiril Golubov Figueroa y Vocal Dr. Abel Sentíes Granados.
- Al Representante de la Comisión Académica, Dr. Noé Manuel Montaño Arias por revisar esta tesis y ser parte del proceso pregrado.
- Al Programa de Doctorado en Ciencias Biológicas y de la Salud en la Universidad Autónoma Metropolitana por su apoyo y revisiones en el proceso.
- A la Universidad Autónoma Metropolitana por su apoyo en el uso de las instalaciones y los servicios otorgados durante la realización del doctorado.
- Al proyecto “Estado de salud, conservación y vulnerabilidad de los ecosistemas de pastos marinos del Litoral del Golfo de México”, con el patrocinio de la Secretaria de Energía, CONACYT (CISESE, CIGOM).
- A los integrantes del Laboratorio de Pastos Marinos de la UAM-I, les agradezco su apoyo y amistad durante este importante periodo de mi vida:

Hidrobióloga Gabriela Márquez Labastida por el apoyo en la logística de las salidas de campo, por la ayuda y complementación de los datos de biomasas de VAS y por el trabajo de laboratorio.

Hidrobiólogo Francisco Javier Ordoñez Gasca por el apoyo en la logística de las salidas de campo, por la ayuda y complementación de los datos de luz y nutrientes y por el trabajo de laboratorio.

Hidrobiólogo Ivanhoe Ricardo Herrera Moro Chao por la asesoría y apoyo en el área de parámetros fisicoquímicos asociados a pastos marinos y por los análisis

estadísticos, así como por su ayuda en campo, por la complementación de datos fisicoquímicos y por el trabajo de laboratorio.

Hidrobiólogo Omar López por su apoyo en campo, así como por la complementación de datos fisicoquímicos y por el trabajo de laboratorio.

Hidrobiólogo Eduardo Hernández Elizalde por su apoyo en campo, por la complementación de datos de materia orgánica y por el trabajo de laboratorio.

Hidrobióloga Yolanda Gabriela Valencia Vilchis por su apoyo en campo, por la complementación de datos de pigmentos fotosintéticos y por el trabajo de laboratorio.

Hidrobiólogo Alfredo Alcántara León por su apoyo en campo y por el trabajo en el laboratorio.

Ingeniero Ambiental Martín por su apoyo en campo y por el trabajo en laboratorio.

Bióloga Guillermina Avelino por su asesoría en la parte demográfica de pastos marinos, así como por la complementación de datos y por el trabajo de laboratorio.

M.C. Gilberto Hernández Cárdenas por su apoyo con los datos espaciales y por la elaboración del mapa de la zona.

M.C. Fernando Valdez Cruz por su asesoría en sedimentos y materia orgánica relacionados a la VAS, así como por el apoyo en campo, por la complementación de datos de sedimentos y por el trabajo de laboratorio.

M.C. Angélica Itai Mijangos Hernández por su asesoría en las condiciones de salud de los pastos marinos, así como por el apoyo en campo y por el trabajo de laboratorio.

M.C. Alma Delia Toledo Guzmán por su apoyo en los datos espaciales de las especies y la elaboración de mapas asociados a la eficiencia fotosintética.

M.C. Iliana Pérez Espinosa por su apoyo en los datos espaciales de las especies, en el campo y trabajo en el laboratorio.

- Al Biólogo José Alfredo Arévalo Ramírez de la UAM-X por la asesoría, revisión, correcciones y sugerencias en el área de Ecofisiología Vegetal.

- Al Dr. Abel Sentíes y al Dr. Kurt M. Dreckmann del Laboratorio de Macroalgas de la Universidad Autónoma Metropolitana Iztapalapa por la identificación de las especies algales.

- Al Dr. Carlos Canto del Instituto de Física de la UNAM por la asesoría en la creación de modelos de comportamiento y uso del programa Origin.

- A la Dra. Mariana Rojas Aréchiga por el apoyo y la logística en el laboratorio de Ecología y Evolución de la UNAM.

- A los miembros del Taller de artículos del Instituto de Ecología, UNAM, Joanne Peel, Donaji López, Omar Díaz Segura, Gabriel Urschid, Héctor Tapia, Juan Carlos Flores, Vania Olmos, Jessica Reyes, Sandra, Rosa, Cristina Ramírez, Omar Durán, Jerry, Linda Mariana, Esteban, Saldino, Isabel, Manuel, Mapa, Tania, Jazz, Pactli, Andrés, Pepillo y demás alumnos por las sugerencias y correcciones del proyecto.

- A Juan Chay y compañía, no sólo por trasladarnos a los puntos de muestreo en lancha, sino por la ayuda en el campo, por sus atenciones durante los muestreos y por la amistad que nos brindaron durante el proyecto.

- Al E.B.C. (Equipo de Buceo Ciencias) por los conocimientos y la preparación que me brindaron para bucear, ya que sin eso no hubiese sido posible realizar esta tesis.

- Al centro cultural polinesio Kalohi Kamahine dirigido por Alejandro Ocejo y Corina Ocejo e integrantes, por ayudarme en una etapa difícil y enseñarme que la danza y la vida tienen mucho en común.

- Al Lic. Adolfo por sus asesorías en la salud mental.

- Al Dr. Alexis Lodigiani por ayudarme con mi salud y recordarme que uno se impone los límites y decide superarlos o no.

- A mi familia por el apoyo que me brindaron durante el doctorado.

A la vida misma por ser mí maestra en sangre y carne.

RESUMEN

En todo el mundo se han estudiado los factores abióticos que establecen la distribución y abundancia de los pastos marinos en zonas tropicales; éstos son: la temperatura, la salinidad, la atenuación de luz, la composición del sedimento y la profundidad. Las interacciones entre pastos marinos y macroalgas se han definido como relaciones de competencia, ya que usan los nutrientes, la luz solar y el espacio de colonización como recursos comunes en los ambientes marinos. La parte biótica como las interacciones con otros elementos de la vegetación acuática sumergida no se ha abordado debido a su complejidad. El objetivo de este trabajo fue determinar y analizar el tipo de interacción que hay entre las especies de *T. testudinum* y *Caulerpa paspaloides* usando indicadores poblacionales, fisicoquímicos y de eficiencia fotosintética. Los monitoreos se hicieron en la Biosfera de los Petenes en tres praderas de Vegetación Acuática Sumergida (VAS) (monoespecífica de *T. testudinum,* una monoespecífica de *C. paspaloides* y mixta de ambas especies) en las temporadas de nortes, lluvias y secas desde 2016 a 2019. Se cuantificaron los factores fisicoquímicos en los tres sitios, la cantidad relativa de nutrientes en columna de agua e intersticiales y la eficiencia fotosintética que tienen ambas especies. Para estimar los efectos en el crecimiento de las interacciones entre especies se colectaron muestras de biomasa de *T. testudinum* y *C. paspaloides*, se determinó la tasa finita de crecimiento de ambas especies, así como su crecimiento por días. Se realizó un PCA para encontrar los factores más representativos que pueden tener una relación directa con el establecimiento y la abundancia de las dos especies. Se encontró que los factores fisicoquímicos que difieren en las praderas son la profundidad y el tamaño del grano. Sin embargo, las variables fisicoquímicas de temperatura y del Nitrógeno Inorgánico Disuelto (NID) eran diferentes a lo largo de las tres temporadas, siendo mayores en la temporada de lluvias. A pesar de esto, el crecimiento y establecimiento de ambas especies fue el mismo en praderas monoespecíficas, pero la eficiencia fotosintética de *C. paspaloides* fue menor en la temporada de lluvias y en las praderas mixtas. El PCA nos indica que los factores más importantes son la profundidad, las biomasas de ambas especies, las *Fv/Fm* de ambas especies y la presencia de otras macroalgas que conforman el factor 1 y la

temperatura, y el NID que conforma el factor 2. La presencia de *T. testudinum* y *C. paspaloides* se da principalmente por factores biológicos. Debido a que existe mínima competencia en praderas monoespecíficas, *T. testudinum* invierte los recursos en reproducción sexual y crecimiento horizontal; en cambio, en praderas mixtas los invierte en crecimiento vertical y formación de hojas. Sin embargo, *C. paspaloides* en praderas mixtas presenta dos temporadas de crecimiento, sugiriendo que la presencia de *T. testudinum* reduce los competidores y permite un mayor establecimiento de las especies. A pesar de que la mortalidad de *C. paspaloides* ocurre en la temporada de nortes esto permite el establecimiento de *T. testudinum*. Se sugiere que la adecuación de *T. testudinum* tiene una relación inversa a la de *C. paspaloides*, y que los aumentos en la temperatura y NID se asocian al aumento de macroalgas y al crecimiento.

Palabras clave: Interacciones, vegetación acuática sumergida, competencia, demografía, eficiencia fotosintética, pastos marinos, macroalgas.

ABSTRACT

Interactions between seagrasses and macroalgae have been defined as competitive relationships since they use nutrients, sunlight, and colonization space as limiting resources in marine environments. It is not known whether *Thalassia testudinum* is affected explicitly by its interaction with *Caulerpa paspaloides*.

The research aims to determine and analyze the type of interaction between of *T. testudinum* and *C. paspaloides* using population, physicochemical, and photosynthetic efficiency indicators. Monitoring was done in the Petenes Biosphere in three meadows (monospecific of *T. testudinum*, monospecific of *C. paspaloides,* and a mix of both species) in three seasons that differ climatically: dry, rains and "nortes" from 2016 to the year 2019. Biomass samples of *T. testudinum* and *C. paspaloides* were collected to estimate the effects of species interactions on growth, and the finite growth rate of both species and their growth per day in leaves were determined. The physicochemical factors at the three sites, the relative amount of nutrients in the water and interstitial column, and the quantum efficiency of both species were measured. For these parameters, PCA tests were performed to establish the most representative variables that have a direct relationship in the study. The fitness in monospecific meadows and mixed meadows for both species was the same, and the growing and abiotic variables that were different in the fields were depth and grain size. Temperature, nitrates, nitrites, and DIN were different during the seasons. Photosynthetic efficiency was lower in the mixed meadows of *C. paspaloides* during the rainy season, and *T. testudinum* was significatively lower in the rainy season in both meadows. The PCA indicates that the most important factors were water depth, biomass of both species, the *Fv/Fm* of both species, the presence of macroalgae, and the other factors were composed of temperature and NID. The presence of *T. testudinum* and *C. paspaloides* is mainly due to biological factors. In monospecific populations, due to the absence of competitors, the fitness of both species will be increased. However, the mortality of *C. paspaloides* was higher than the mortality of *T. testudinum* and allowed for the colonization of macroalgae. In shallow sites, *T. testudinum* grew favorably, and *C. paspaloides*, in deep places. Biomass samples

with high temperatures and NID were associated with an increase in macroalgae and the growth of *C. paspaloides* in mixed populations. Increase in nutrients and temperature could have a significative increase in *C. paspaloides* populations during the rainy season.

Keywords: Interactions, submerged aquatic vegetation, competition, demography, photosynthetic efficiency, abiotic factors.

1-. INTRODUCCIÓN

Las interacciones biológicas son las relaciones existentes entre los organismos de un ecosistema. Las podemos dividir en dos, las intraespecíficas que se dan principalmente entre individuos de la misma especie y las interespecíficas que se dan entre individuos de diferentes especies (Aschehoug et al., 2016). Las interacciones biológicas se pueden clasificar a partir de la relación que tienen los individuos; si ambos individuos se benefician uno al otro se le denomina mutualismo o comensalismo (Hacker y Gaines, 1997); cuando un individuo perjudica al otro y éste se beneficia se le llama parasitismo y, por último, si ambos individuos necesitan un recurso en común para sus funciones vitales y uno de ellos sufre una baja en su adecuación se le llama competencia (Tilman, 1994).

La competencia por recursos se puede definir como “la captura de recursos esenciales en un lugar limitado y común por individuos cercanos” (Aschehoug et al., 2016).Existen dos criterios para la captura de recursos en una competencia: ya sea que las plantas puedan capturar y usar los recursos antes que sus vecinos o que éstas puedan invertir estructuras que les ayuden a capturar y utilizar los recursos de forma eficiente, y como resultado generen un *trade-off* en la asignación de energía hacia diferentes partes de la planta; por ejemplo, generar hojas grandes y como consecuencia tener poco rizoma).

Cuando hay competencia por un recurso, otros recursos resultan afectados; por ejemplo, si un individuo llega a asimilar mejor la luz solar, que es un recurso que las plantas usan para la formación y el crecimiento de estructuras que asimilan los nutrientes como son las raíces, podrá absorber mejor el agua y los nutrientes en el suelo (Pugnaire y Luque, 2001). En el caso de que los recursos sean suficientes en el medio, se puede llegar a ver una coexistencia entre los dos individuos y éstos pueden interactuar entre sí sin afectar su crecimiento, reproducción o sobrevivencia (Tilman, 1982).

Para que una población pueda persistir es necesario que algunos parámetros demográficos se comporten de manera densodependiente, por lo menos en algún

momento o lugar (Hixon y Carr 1997). Sale y Tolimieri (2000) han llamado PEDDTOP ("persistence equals density dependence at some time or place") a esto, debido a que las condiciones en las que se desarrollan las poblaciones no permanecen constantes en el tiempo, lo que afecta a las tasas demográficas originando fluctuaciones en el tamaño poblacional. Hixon et al. (2002) mencionan que la regulación es esencial para la persistencia de las poblaciones y que la densodependencia es el único mecanismo posible, a través de la competencia y la depredación.

Para saber si existe una competencia o una coexistencia se ha propuesto el modelo de Lotka-Volterra, en el que se considera el crecimiento poblacional (*dN/dt*), el número de individuos (*N*) y la capacidad de carga (*K*) de ambas especies (Begon et al. 1996). A pesar de que el modelo solo indica el crecimiento logístico de una población, se puede integrar con otra variable que es la manera como otra población afecta a esta población, denominada "α" para la población 1 y "β" para la población 2, y con ello tener un modelo acoplado para ambas poblaciones:

$$\frac{dN}{dt} = rN\frac{(K-\alpha N)}{K}$$

$$\frac{dN}{dt} = rN\frac{(K-\beta N)}{K}$$

Por lo tanto, para conocer una interacción entre dos especies se necesitan conocer la dinámica poblacional de las poblaciones competidoras y la dinámica de los recursos que usan estas poblaciones para su adecuación (Begon et al. 1996).

1.1 Los pastos marinos

Los pastos marinos son angiospermas que realizan su ciclo de vida totalmente sumergidas en el fondo marino, y existen un total de 58 especies (Orth et al., 2006) a nivel mundial. A pesar de ser un grupo pequeño de plantas, las praderas de pastos marinos tienen gran importancia ecológica y biológica ya que, además de los arrecifes de coral y los manglares, son sistemas en los que hay una mayor producción primaria en el mar (500-4000 g carbón/m^2/año) (Duarte y Cebrian, 1996).

Proporcionan refugio, alimentación y protección, y son sitios de apareamiento, desove y crecimiento de numerosas especies de invertebrados marinos de importancia económica y ecológica, como bivalvos y crustáceos (Raz-Guzmán y Sánchez-Martínez, 2001).

En México existen 11 especies de pastos marinos y en la región del golfo de México y Caribe se desarrollan principalmente las especies *Thalassia testudinum* Banks ex König**,** *Syringodium filiforme* Kützing y *Halodule wrightii* Ascherson (Gallegos, 2010). Los pastos marinos crecen en poblaciones monoespecíficas y en poblaciones mixtas con otras especies de pastos marinos y/o con las macroalgas bentónicas, de éstas, las que más se han estudiado en cuanto a su relación con las praderas de pastos marinos son las pertenecientes al género *Caulerpa* J.V. Lamouroux (Levinton, 2009), de las cuales se tienen registradas 105 especies a nivel mundial y 18 en México, particularmente 16 en el Atlántico mexicano (Pedroche y Sentíes 2020).

1.2 Factores abióticos y bióticos en la vegetación acuática sumergida

La composición de las praderas de pastos y la fauna marina depende de las condiciones abióticas que la rodean, como son la temperatura, la salinidad, el movimiento del agua y los elementos esenciales (carbono, hidrogeno, oxígeno y nitrógeno) (Davis y Fourqurean, 2001) y (Reece, 2011). Las plantas adquieren estos elementos esenciales (CHON) de manera directa del medio a partir de la columna de agua y el agua intersticial en forma de nutrientes como el amonio, los nitratos y el fósforo y por la descomposición de materia orgánica por bacterias y otros organismos (Duarte, 1990).

El amonio es producido directamente de los desechos animales y de los cadáveres animales, y constituye una fuente importante de nitrógeno e hidrógeno para los pastos marinos (Sandoval-Gil, 2016). Por lo tanto, los pastos marinos actúan como biofiltros en el medio, absorbiendo el amoniaco y descomponiéndolo para sus funciones metabólicas, y puesto que los pastos marinos en su mayoría son longevos a comparación de las macroalgas, esto los hace biofiltros eficaces (de los Santos, et al. 2020). Nowicki y Nixon (1985); obtuvieron que en sedimentos lodosos el

amoniaco tiende a ser mayor, esto gracias a que hay más cantidad de materia orgánica y al tamaño del sedimento que atrapa el amonio, y los sedimentos arenosos tienen menor cantidad de amonio, ya que el tamaño del grano es más grande y libera el amonio a la columna de agua. También Nowicki y Nixon (1985) obtuvieron que en zonas profundas el amonio es mayor que en zonas someras, esto es porque, por la baja disponibilidad de luz en los sitios profundos, el amonio es sintetizado en menor proporción, pues por ausencia de este recurso, los organismos vegetales que descomponen el amonio no lo metabolizan de forma apropiada.

Los nitratos se pueden encontrar en forma natural en la lluvia y en la nitrificación de compuestos orgánicos (Moreno-Marín, 2016), aunque pueden producirse por exceso de fertilizantes y químicos de origen agrícola o ganadero. En este caso, el amonio se consume más que los nitratos, pero los pastos marinos pueden usarlos nitratos en la columna de agua, en especial en zonas con índices altos de CO^2, donde los nitratos se consumen a mayor taza de asimilación que el amonio (Sandoval-Gil, 2016). A pesar de que Nowicki y Nixon (1985) no encontraron una relación entre la temperatura y/o la luz con la cantidad de nitratos en el medio, observaron que la cantidad de nitratos intersticiales es mayor en los sedimentos arenosos que en los lodosos. Los nitratos se pueden clasificar en dos, los nitratos altos que son el nitrógeno producido por la materia orgánica que producen los seres vivos (desechos orgánicos, partes vegetales y/o cadáveres), que utilizan los organismos vegetales, y los nitratos bajos que son el nitrógeno residual resultado del consumo de materia orgánica por los microbios, que queda depositado en el sedimento. Los nitratos en grandes cantidades pueden ser tóxicos para la flora y fauna marina (Camargo et al., 2005). Las hojas de los pastos marinos tienen la capacidad de absorber los nitratos. Cuando hay una perdida foliar alta hay grandes pérdidas de nitrógeno en los pastos marinos, aunque cuando las hojas llegan al sedimento puede ser reabsorbido en las raíces (Terrados y Williams, 1997).

El fósforo es un nutriente asociado a desechos orgánicos y de agricultura, que es procesado por los organismos fotosintéticos para generar crecimiento y reproducción vegetativo alto. Cantidades altas de este nutriente dará como resultado la

eutrofización (Moosman et al., 2006). Libes (2009) señala que el fósforo es un nutriente que en exceso se asocia a ambientes anóxicos. Esto es porque en ambientes lodosos el fósforo es menos aprovechado que en los sedimentos arenosos. Esto se debe a que el tamaño del grano en los sedimentos arenosos es mayor y esto permite al fósforo viajar de modo más eficiente que en los sedimentos lodosos. Esto lo confirma Nowicki y Nixon (1985) donde encontraron que en sedimentos lodosos el fósforo es mayor que en sedimentos arenosos. Asimismo, que a mayor temperatura hay mayor cantidad de fósforo en los sedimentos.

El interés por estudiar los nutrientes relacionados con la VAS es detectar primero las zonas que sufren limitación de nutrientes y, por lo tanto, se reduce el establecimiento de los elementos de la VAS; por ejemplo, el incremento de nutrientes aumenta el crecimiento de macroalgas (Waycott et al., 2007) y es un indicador de deterioro ambiental o de influencia antrópica.

La composición del sedimento, así como su tamaño tiene una importancia en las praderas de pastos marinos. Los pastos marinos no solo abarcan parte de la columna del agua, sino que sus rizomas, dependiendo de la especie, pueden abarcar desde centímetros hasta metros de profundidad como es el caso de *T. testudinum.* Como se explicó anteriormente, los nutrientes no solo se encuentran en la columna de agua sino en el agua intersticial. La disponibilidad, el almacenaje y la pérdida de los nutrientes intersticiales dependerán del sedimento, sus características físicas y su composición. Por ejemplo, se ha investigado que la permeabilidad en los sedimentos arenosos es más alta, y como consecuencia tendrá diferentes características fisicoquímicas y la distribución de especies será diferente (Adhitya et al., 2016). En sedimentos de arcilla y limos el intercambio de nutrientes es menos frecuente debido al tamaño del sedimento que llega hasta micras, lo cual hace que estos sistemas tengan menos cambios químicos y biológicos (Bell y Hall, 1995).

Por lo tanto, en comunidades de VAS simples (compuesta de especies de pastos marinos colonizadores y macroalgas) composición del sedimento será poco compacta y de grano grueso, ya que no poseen sistemas rizoidales que descompongan el sedimento ni materia orgánica para el establecimiento de

microbiota, además de pérdida de nutrientes intersticiales como el nitrógeno y el fósforo, así que tenderá a tener especies de pastos marinos colonizadoras y macroalgas. Por el contrario, en sedimentos finos e irregulares en composición y más estratificados se podrán encontrar especies permanentes como *T. testudinum*. Las poblaciones de esta especie tenderán a tener mayor sistema rizoidal, una microbiota más desarrollada en el sedimento y, por ende, una descomposición más alta de sedimento como se observa en poblaciones recuperadas de pastos marinos (Marba et al. 2007).

1.3 Demografía en pastos marinos y macroalgas

Por definición, la demografía se encarga de describir los cambios numéricos en las poblaciones que se presentan, ya sea por factores bióticos y/o abióticos. Los cambios se representan por medio de la evaluación de la natalidad y la mortalidad de los individuos que las conforman, con base en las diferencias de edad y/o el estadio de desarrollo en el que se encuentran (Stearns, 1992). Además, también se encarga de describir y dar hipótesis de cómo son afectadas las poblaciones por las alteraciones del medio. Por lo tanto, los estudios de ecología poblacional permiten evaluar e investigar si las poblaciones están aumentando, disminuyendo o se encuentran en equilibrio numérico (Caswell, 2001) y señalar qué fenómenos biológicos o antropogénicos podrían alterar el comportamiento demográfico de las poblaciones (Glardon et al*.,* 2008).

La ecología de poblaciones tiene como objetivos entender cómo está formada una población, cómo es afectada por alteraciones en su medio, qué necesidades tiene y cómo funciona (Harper, 1977). Para ciertas poblaciones se pueden ver tendencias de la fluctuación cíclica, como ciertas tendencias dinámicas relacionadas con cambios ambientales, pero no completamente controlados por el medio ambiente (Duarte et al., 1994).

Existen dos tipos fundamentales de estudios demográficos: los estudios dinámicos, que consisten en el seguimiento de una cohorte de individuos a través de uno o varios años, y los estudios estáticos (varias cohortes), en los cuales se analizan únicamente la estructura de edades y la fecundidad en un momento dado (Harper, 1977; Silvertown, 1987).

Las tasas vitales de fertilidad y la supervivencia que se obtienen a partir del seguimiento de cada individuo, pueden resumirse y representarse de diferentes maneras, como en las tablas de vida, que permiten saber cómo sería la edad de la primera reproducción, mortalidad, natalidad, tasa de crecimiento, valor reproductivo y estructura poblacional (Harper, 1977; Silvertown, 1987).

En el caso de los organismos clonales (aquellos que producen secciones análogas [ramets] que actúan como un organismo independiente y separado del organismo (Harper, 1977) no es sencillo establecer la edad de los individuos y ésta no es siempre la variable que determina su comportamiento demográfico, como sucede con los corales, las plantas, las algas o los insectos con fases de desarrollo variables. En muchas ocasiones la edad resulta ser un indicador menos confiable por la variabilidad de crecimiento y desarrollo. Por ejemplo, en los corales *Pseudopterogorgia americana*, la edad establecida para individuos de 100 cm es de 14 a 60 años (Yoshioka y Yoshioka, 1991), por lo tanto, para estos corales es más significativo utilizar una clasificación por estadios en lugar de por edad. Esto sucede también con las plantas, en las que los estadios se definen más por su tamaño, altura o peso (Mandujano et al., 2007).

En pastos marinos y algas el registro de biomasa por metro cuadrado ha sido una herramienta útil para dar seguimiento de la supervivencia y el establecimiento de los individuos en una población (Phillips y Price, 2002, Van Tussenbroek et al., 2010). Sin embargo, se han diseñado métodos demográficos para medir e identificar el estado de las poblaciones de estas especies de una forma más directa y precisa, considerando que son especies con crecimiento modular. Para *T. testudinum* los haces verticales son un sinónimo de vástagos; para cuantificar la edad de cada haz vertical, el índice de plastocrono (Ip), que consiste en el número de hojas que produce un haz por año, es importante para establecer las edades que tienen los haces verticales de *T. testudinum* (Duarte et al. 1994). En cambio, ya que *C. paspaloides* es un organismo altamente clonal por su crecimiento cenocítico, los estolones y frondas pueden considerarse unidades demográficas para analizar las poblaciones de esta especie (Fuentes et al. 2014). Ya que ambas especies tienen diferentes historias de vida y son taxonómicamente diferentes, puede ser complicado comparar el crecimiento y establecimiento de ambas especies. Para esto existen estimadores de la adecuación que nos resumen si una especie crece, se mantiene o se reduce en el tiempo, y que se pueden estandarizar para cualquier especie biológica, como es el caso de la tasa finita de crecimiento (λ) (Mandujano et al., 2001), que es una relación del número o biomasa de los individuos en el tiempo.

1.4 Fotosíntesis en pastos marinos y macroalgas

Los elementos CHON (Carbono, Hidrógeno, Oxígeno y Nitrógeno) son importantes en el proceso de la fotosíntesis (Reece, 2011). El 40% de la fotosíntesis en el planeta se efectúa en los sistemas acuáticos-marinos; por lo tanto, junto con el fitoplancton, los pastos marinos son importantes como generadores de O_2 y sumideros de carbono (Falkowski y Raven, 2013).

En las praderas de pastos marinos la fotosíntesis puede alterarse por factores abióticos como, por ejemplo, a mayores profundidades y turbidez en el agua se ha registrado una producción menor de oxígeno en el medio y, por lo tanto, la fotosíntesis de los pastos marinos se afecta de manera negativa (Zimmerman, 2007).

La fotosíntesis puede registrase, por la medición directa de producción de oxígeno en un ambiente encerrado o por el registro de la eficiencia fotosintética (*Fv/Fm*). Para obtener la eficiencia fotosintética se usan métodos indirectos de la fluorescencia del cloroplasto (en el fotosistema II) saturándolo con luz y registrando la curva de saturación (Kalaji et al., 2014). Los cambios y las disminuciones de la eficiencia fotosintética se usan como indicadores de estrés y/o perturbaciones ambientales que afectan la fotosíntesis (turbidez, temperatura, pH, contaminación, etc.), indicándonos el estado de salud fisiológica de las plantas. Además, se ha encontrado que *Fv/Fm* se correlaciona de forma positiva con la tasa de asimilación de CO_2 y la de producción de O_2 (Lambers, 2008). Por lo tanto, la eficiencia fotosintética nos indica qué especies están estresadas y, por ende, predecir zonas de alto impacto ambiental. La norma establecida supone que los valores menores a 0.8 son una señal de estrés fotosintético y, por lo tanto, hay daño en el fotosistema II (Lambers, 2008). Las plantas subacuáticas tuvieron que adaptarse a una disminución de la luz disponible por lo que de manera natural sus requerimientos de luz son menores, (0.7 para *T. testudinum*, Enríquez et al. 2002 y 0.6 para macroalgas Biber et al., 2004).

Ya que las plantas viven en sistemas variables y se encuentran sujetas a factores que afectan su adecuación, hay mecanismos de regulación que les permiten adaptarse a estas condiciones adversas. En el caso del aumento o disminución de la

luz solar, ciertos pigmentos accesorios en los cloroplastos regulan la llegada de luz a través del fotosistema II y evitan el sobrecalentamiento y la desnaturalización de las proteínas de los cloroplastos en el caso de un aumento en la radiación (Lambers, 2008). Uno de estos procesos, el ciclo de las xantofilas, genera una conversión de anteraxantina a zeaxantina en ausencia de luz y una producción de anteraxantina en las hojas con excesos de luz. La cantidad de pigmentos accesorios son también herramientas para establecer la calidad de vida de la VAS en el medio acuático.

1.5 Las interacciones de pastos marinos y macroalgas

Las interacciones que tienen los pastos marinos y las macroalgas en ambientes nativos son de competencia por nutrientes, espacio en sustrato y por luz solar. Algunas de las estrategias que usan los pastos marinos es el crecimiento de hojas para poder captar mejor la luz y la asimilación de nutrientes en la columna de agua. Sin embargo, si en la comunidad hay macroalgas, éstas tendrán una mejor absorción de los nutrientes de columna de agua ya que compiten con los organismos epifitos y el fitoplancton (Fong y Harwell, 1994).

También Fong y Harwell (1994) dedujeron que en condiciones altas de irradiación solar y nutrientes intersticiales podrían tener un establecimiento y abundancia mayor en el sistema, y esto lo comparten con las macroalgas y otras especies de pastos marinos como *S. filiforme* y *H. wrightii*. Aunque, Biber et al. (2004) vieron que para las macroalgas en ambientes mixtos el recurso limitante será los nutrientes de columna de agua, por lo que son más relevantes en los sistemas de pastos marinos.

2-. ANTECEDENTES

Los estudios que han asociado la competencia entre pastos marinos con las macroalgas se han limitado a la disponibilidad de luz, al espacio y a los nutrientes que hay en el medio, como serían el Carbono y el Nitrógeno (Van Tussenbroek et al., 2010)

Ceccherelli y Cinelli (1997) describieron la competencia entre *C. taxifolia* y el pasto marino *Cymodocea nodosa* en el Mediterráneo*,* donde observaron que hay una interacción directa entre las dos especies, siendo afectada negativamente la cobertura de *C. nodosa* e indicando dos procesos de competencia: la obtención exitosa de los nutrimentos y su administración efectiva cuando están ausentes, en este caso sería la temporada de invierno.

Thomas (2003) observó que en Australia *Caulerpa taxifolia* presentaba estrategias de alelopatía al liberar sustancias toxicas como son sulfatos y caulerpina, lo que sugiere que hay una competencia entre estas dos especies. Identificó a la luz solar como el recurso limitante ya que observó que en hábitats cubiertos con *C. taxifolia* los niveles de eutrofización fueron altos.

Fong y Harwel (1994) describieron a la comunidad de la VAS que existe en Florida, EE.UU., definiendo factores biológicos y fisicoquímicos que afectan la supervivencia y el establecimiento de las especies que la conforman como *Thalassia testudinum*. Tanto el crecimiento como el establecimiento de *T. testudinum* es definido por habitar en aguas con temperaturas intermedias (25-32°C), salinidades intermedias (menos de 40), bajas concentraciones de nutrientes en columna de agua (menor a 1.5 mg) y altas concentraciones de nutrientes intersticiales (mayores a 2mg). En cambio, los factores que benefician el crecimiento y el establecimiento de las macroalgas en general, son temperaturas altas (mayores a 32°C), salinidad intermedia (menos de 40), alta concentración de nutrientes en columna de agua (mayores a 2mg). También Davis y Fourqurean (2001) registraron que las macroalgas están presentes en áreas nuevas ya que son las primeras en colonizar, en cambio en zonas más antiguas se encontraran pastos marinos que son especies más longevas y de crecimiento lento.

Otros estudios como los de Davis y Fourqurean (2001) han dado mayor peso a los nutrientes en agua y en sedimentos, siendo el Nitrógeno y Fósforo los más significativos para el establecimiento y a la abundancia de los elementos de la VAS. Sin embargo, en zonas tropicales se ha visto que estas interacciones no siempre son negativas, como por ejemplo en las zonas pantropicales, como lo reportan Meñez y Calumpong (1982), donde las algas consumen metales pesados y otros nutrientes que los pastos marinos no pueden consumir o incluso tienen aportes a la comunidad bentónica como proporcionar nutrientes.

En la zona de la Península de Yucatán, a diferencia de otras regiones del mundo, se presentan tres estaciones marcadas durante el año, una de lluvias fuertes de mayo a agosto (lluvias), otra de vientos fríos y fuertes que vienen del norte (nortes) de septiembre a noviembre y otra cuando no hay lluvias (secas), de diciembre a abril (CONAGUA, 2023. Las estaciones climáticas tienen efectos ecológicos en la zona; por ejemplo, la temporada de nortes afecta negativamente a la (VAS) de la zona, causando la desaparición de las especies vegetales tanto de algas como de algunas especies de pastos marinos (Fuentes et al., 2014).

En la Biosfera de los Petenes se ha registrado que *T. testudinum* es la especie más abundante tanto en cobertura como densidad. Esto permite suponer que las poblaciones son saludables, longevas y mejores competidoras. A pesar de que en el estudio no hay una clasificación de macroalgas, es más frecuente encontrar a *T. testudinum* creciendo con macroalgas que en poblaciones monoespecíficas (Pérez et al. 2019).

C. paspaloides es la especie más frecuente y abundante en la reserva y las poblaciones son abundantes en las áreas cercanas a los manglares en la costa de Campeche y presentan crecimiento y supervivencia alta (Fuentes 2015)**.** Aunque es más probable encontrar praderas monoespecíficas en el puerto y la zona hidroeléctrica de Campeche (Pacheco, 2009). A diferencia de otras especies de *Caulerpa*, a ésta no se le ha considerado como especie invasora, como es el caso de las costas del Mediterráneo, Australia o California. Fuentes (2015) sugirió que en la temporada de nortes, hay un efecto negativo en la adecuación de *C. paspaloides*, ya

que hay aumentos en la dinámica del agua, así como reducción de los nutrientes en columna de agua. Por esto se propuso la existencia de un ciclo para esta especie; crece y se desarrolla en la temporada de lluvias, sobrevive en los nortes y se inicia su reclutamiento y desarrollo en la temporada de secas. Sin embargo, no existe suficiente evidencia de este hecho.

Los estudios de las interacciones entre pastos marinos y algas son escasos y no se cuenta con información actualizada que permita entender los mecanismos que las determinan.

El objetivo general fue determinar y analizar el tipo de interacción que hay entre las especies de *Caulerpa* y de pastos marinos usando indicadores poblacionales, en este caso particular de *Thalassia testudinum* y *Caulerpa paspaloides* en la Biosfera de los Petenes. Por medio del análisis de factores bióticos (demografía, fotosíntesis y especies) y abióticos (nutrientes, sedimento y características ambientales).

Como objetivos particulares se tuvieron los siguientes:

- Describir la composición biológica de las praderas monoespecíficas y mixtas de *T. testudinum* y *C. paspaloides*.
- Describir las características fisicoquímicas que hay en praderas monoespecíficas y mixtas de *T. testudinum* y *C. paspaloides*.
- Evaluar la dinámica poblacional y crecimiento de *T. testudinum* y *C. paspaloides* en poblaciones monoespecíficas o mixtas.
- Evaluar el estado de salud de *T. testudinum* y *C. paspaloides* con parámetros de eficiencia fotosintética y de contenido de pigmentos.
- Evaluar qué factores fisicoquímicos pueden afectar el estado de salud de *T. testudinum* y *C. paspaloides.*

La hipótesis es que la relación entre *T. testudinum* y *C. paspaloides* es una relación de competencia donde *T. testudinum* tiene la ventaja por sus estrategias de permanencia y de eficiencia fotosintética.

También esta investigación pretende contestar las siguientes preguntas:

- ¿Cuáles factores (biológicos y abióticos) tienen un peso importante en esta interacción y el establecimiento de las especies?
- ¿Qué tipo de interacción tienen *T. testudinum* y *C. paspaloides?*

3-. MATERIALES Y MÉTODOS

3.1 Descripción del área de estudio

El estudio se realizó en la Reserva de la Biosfera de los Petenes que se encuentra en el sureste de México, abarca desde la ciudad de Campeche, en el estado de Campeche hasta Celestún, en el estado de Yucatán (20.8593° N, 90.3339° W). En "Los Petenes," *Thalassia testudinum* puede ser encontrada en coberturas monoespecíficas o mixtas, siendo registrada como la especie más frecuente a lo largo de la reserve, seguido de las especies *S. filiforme, H. wrightii* y una diversidad de macroalgas (Pérez et al*.*, 2019).

Esta zona se distingue por la presencia de islas de vegetación arbolada conocidas como petenes. Estas formaciones de vegetación están ubicadas en cuerpos de agua comúnmente formados por el manto freático que drena hacia el Golfo de México y tienen como vegetación predominante el manglar y la selva baja caducifolia. Las especies arbóreas más comunes de los petenes son: *Rhizophora mangle* L., *Avicennia germinans* L., *Laguncularia racemosa* L. Gaertn., *Manilkara zapota* P. Royen, *Ficus continifolia* Kunth, *Swietenia macrophylla* King, *Tabebuia rosea* a Bertol. DC, *Sabal yapa* (C. Wright. ex Becc., *Bravaisia berlandieriana* Nees T.F. Daniel, *Metopium brownei* Jacq. Urb., *Bursera simaruba* L. Sarg., *Annona glabra* L., *Pisonia aculeata* L. y *Acrostichum aureumen* L. (Zamora-Crescencio, 2015) (CONABIO, 2023).

Durante los años 2014 y 2015 se hicieron monitoreos piloto donde se registró y evaluó la cobertura relativa de "Los Petenes". Con base en estas observaciones, se eligieron tres zonas, una zona con cobertura relativa de 100% de *C. paspaloides* (Fig. 1 (3)), una con cobertura relativa de 100% de *T. testudinum* (Fig. 1 (1)) y una con cobertura relativa al 50% de las dos especies (Fig. 1(2)). Todos los análisis de cobertura y caracterización fisicoquímica de los sitios se llevaron a cabo durante el 2016 (noviembre), 2017 (marzo, julio, noviembre), 2018 (febrero, abril, junio, agosto, octubre) y 2019 (enero).

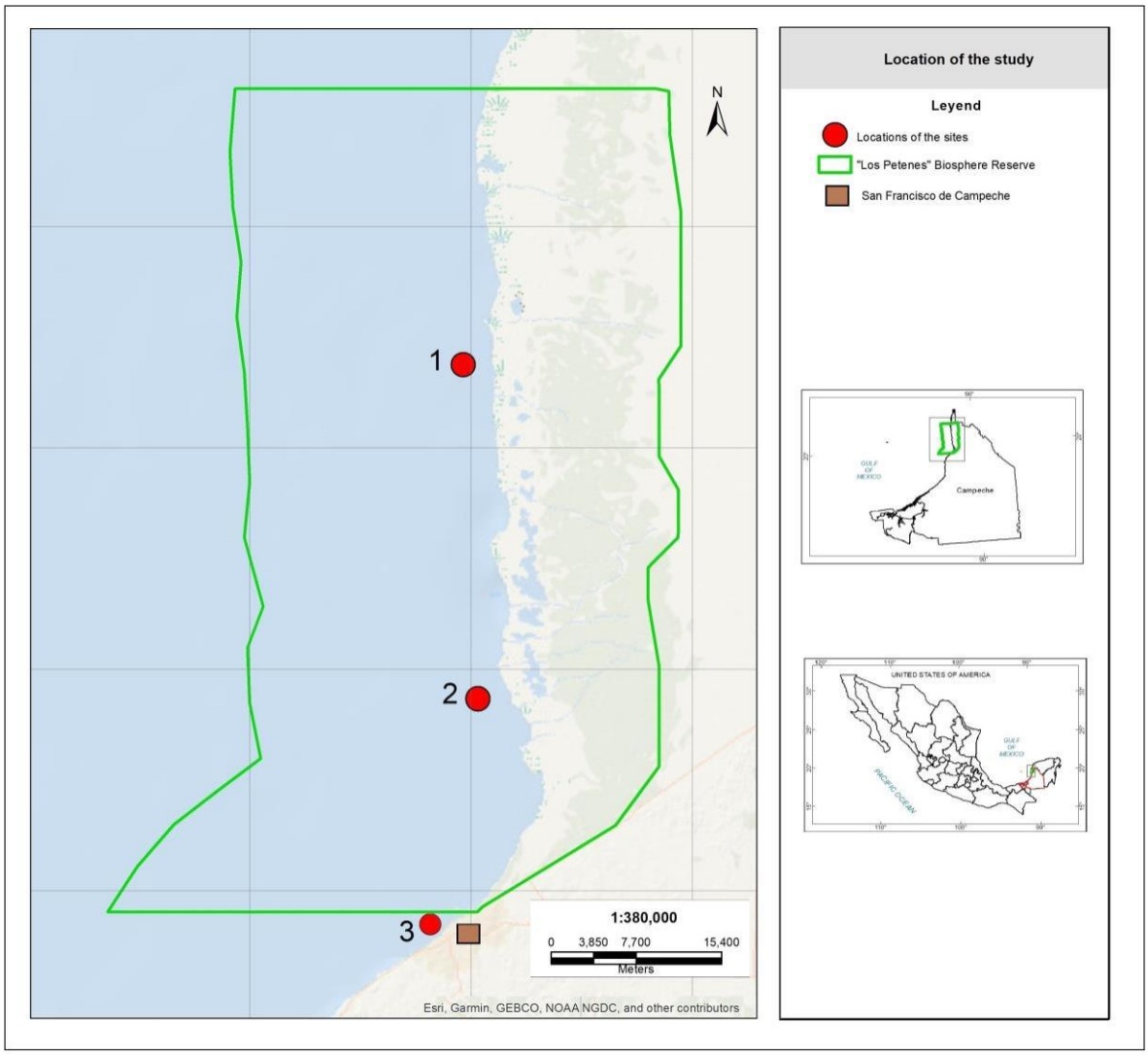


Figura 1-. Zonas de estudio para la caracterización de la vegetación acuática sumergida y fisicoquímica para los sitios de muestreo (1-. 100% de *T. testudinum*, 2-. 50% *T. testudinum* y 50% *C. paspaloides* y 3-. 50% *C. paspaloides*).

3.2 Registro de la Vegetación acuática sumergida

Para registrar la composición florística de la VAS en los tres sitios y observar cómo se desarrolla en un ciclo anual, se midió en cada uno de los tres sitios el porcentaje del área que abarcaban las especies subacuáticas en un cuadro de $0.5m^{2,}$ (10 cuadros por sitio).

Se colectaron núcleos de 10cm de diámetro aleatorios en los tres sitios desde el 2016 (noviembre), 2017 (marzo, julio, noviembre), 2018 (febrero, abril, junio, agosto,

octubre) y 2019 (enero). Cada núcleo colectado de biomasa de *T. testudinum*, se separó de las macroalgas que se encontraron, se secaron a 55°c por tres días y se pesaron. Así se obtuvo el registro relativo de biomasa de macroalgas y de *T. testudinum*.

3.3 Biomasa fitoplanctónica

La biomasa fitoplanctónica se obtuvo a partir de una muestra de agua (500ml), se filtró con filtros de 5 micras de espesor, se guardó el filtro en papel aluminio en frío y en un ambiente seco. En el laboratorio se desintegraron las muestras con acetona en tubos de ensayo de plástico y se centrifugaron a 5000 rpm para separar la masa fitoplanctónica del filtro. Se usó un espectrómetro HACH 3900 (HACH, 2015) para analizar la cantidad de masa fitoplanctónica representativa en la columna de agua.

3.4 Registro de las especies de macroalgas

Se colectaron muestras de macroalgas, se fijaron en alcohol al 80% y se analizaron e identificaron en el Laboratorio de Macroalgas Marinas y Salobres de la UAM-I.

3.5 Caracterización fisicoquímica de los sitios

Con una sonda multiparamétrico YSI (556-MPS) se registraron los valores de salinidad, temperatura, pH, conductibilidad, oxígeno disuelto y porcentaje de oxígeno. Se usó un disco se Secchi para medir la profundidad del sitio.

3.6 Nutrientes en columna de agua e intersticiales

Para el análisis de nutrientes se recolectó agua en la superficie del agua en frascos de 500ml (1 muestra por sitio). Con estas muestras se obtuvieron los nutrientes en la columna de agua (sílice, nitratos, nitritos, amonio y fósforo total).

Para el agua intersticial se colectaron núcleos de sedimentos (1 núcleo por sitio) y se separaron por estratos en el laboratorio: el sedimento del agua se separó por medio de una centrifuga a 1500RPM durante 30 min y en condiciones sin oxígeno. Con estas muestras de agua se obtuvieron amonio y fósforo total intersticiales.

Para cuantificar amonio se utilizaron 2ml de phenol-ethanol, 2ml de solución, sodio nitroprussido y 5ml de solución alcalina (trisodio citrato e hidróxido de sodio) para una cantidad de 50ml de agua. La lectura espectrofotométrica se hizo a 640nm.

Los nitritos se cuantificaron con 1ml de una solución de sulphanilamida para una cantidad de 50ml de agua y 0.1 de solución de naphthyl-ethylenediamina dihydorochlorida, después de 6 min de reposo. La lectura espectrofotométrica se hizo a 543nm.

Para nitratos se agregó 1ml de solución de diluto amonio clorido para 50ml de agua a través de una columna de solución. La lectura espectrofotométrica se hizo a 543nm.

Para fósforo total se agregaron 5ml de la solución conformada por molibdato de amonio (100ml), ácido sulfúrico (250ml), ácido ascórbico (100ml) y tartrato de antimonio (50ml) para una cantidad de 5ml de agua. La lectura espectrofotométrica se hizo a 885nm.

Para sílice se agregó en vasos de plástico 1.0ml de solución de molibdato de amonio, 200µl de ácido clorhídrico al 1:1, y 10 minutos después se agregó 300µl de ácido oxálico. La lectura espectrofotométrica se hizo a 410nm.

El análisis del tamaño del grano se analizó con la técnica de Folk (1974). Para ello se pesaron 15 gr de sedimento seco y se lavaron con peróxido de hidrógeno para eliminar la materia orgánica y posteriormente se tamizaron a través de diferentes tamaños de tamices para separar los sedimentos gruesos de los finos. Para terminar, se calculó el porcentaje de arenas, limos y arcillas.

La cuantificación de la materia orgánica que hay en el sedimento se llevó a cabo de acuerdo con la técnica de Dean (1974), Paez-Osuna et al. (1984) y Gaudette et al. (1974). El porcentaje de pérdidas por ignición se obtuvo después de calcinar el sedimento en crisoles en una mufla a una temperatura de 55°C por una hora. La diferencia en pesos antes y después de la calcinación se atribuye a la transformación de la materia orgánica de la muestra en CO^2 y H_2O.

3.7 Métodos demográficos de *Thalassia Testudinum*

Una vez al año entre 2017 y 2018, se colectaron muestras aleatorias (Fig. 1 (1 y 2)) por medio de un nucleador de acero inoxidable con un diámetro de 21 cm, una altura de 45.5 cm y un área conocida de 0.3m^2. Las muestras de cada nucleador se guardaron en bolsas de plástico para su limpieza y para el registro del número de haces verticales, número de internodos de rizoma y de haces verticales, de hojas, flores y frutos, de la biomasa total, aérea y subterránea, por muestra. La distribución de edades de las poblaciones se calculó con el número de hojas de cada haz vertical y para calcular la tasa de crecimiento vertical de los años 2017 y 2018, se usó una regresión entre el número de cicatrices de hojas y las hojas presentes y el tamaño de cada haz. Para el cálculo del crecimiento horizontal se usó una regresión del número de internodos del rizoma y se relacionó con el tamaño de cada rizoma. El número de hojas promedio se calculó a partir de las cicatrices foliares y se corroboró midiendo la distancia que hay entre cada cicatriz, para obtener el número de cicatrices por año se calculó el promedio de longitud de onda (Duarte et al. 1994). Para verificar la edad en años de un haz, se midió la distancia entre cicatriz de hoja de cada cicatriz floral (Marba et al. 1994). Con esto se hizo una relación con los IP y se determinó en cuántos años crece un haz.

Posterior a la cuantificación individual de las estructuras se clasificaron en biomasa aérea (hojas, haces verticales) y biomasa subterránea (rizomas, raíces, haces horizontales). Se secaron a una temperatura de 50°C por tres días y se pesaron. A todos los datos se les realizó una prueba de ANOVA para determinar si existen diferencias significativas en los años, en los meses y en las dos temporadas.

También se calculó la tasa de cambio en biomasa (λ poblacional) (Caswell, 2001): $\lambda = Nt+1/Nt$. En donde:

λ= tasa finita de crecimiento de biomasa

Nt=la biomasa en el tiempo t

Nt+1= la biomasa en el tiempo t+1

Por lo tanto, se calcularon los cambios en las tasas de biomasa entre los años.

Estas metodologías de demografía son las que utilizan Duarte et al. (1994) para calcular el intervalo de plastocrono, y Fuentes et al. (2014) para la evaluación de la tasa de crecimiento.

Para evaluar el crecimiento modular de *T. testudinum* se marcaron 50 haces verticales de *T. testudinum* en praderas monoespecíficas y en mixtas. Se hizo una perforación a la hoja de *T. testudinum* con una aguja y con un alambre brilloso se marcó el haz vertical. A los 90 días se recolectaron los haces marcados y se registró cuánto crecieron desde la cicatriz que dejó la aguja, de acuerdo con el método descrito por Zimmerman (1994). Para calcular la λ modular se usó la formula ($\lambda=N_{t+1}/N_t$) en donde:

λ= tasa finita de crecimiento modular

Nt=la longitud de la hoja en el tiempo t

N_{t+1}=la longitud de la hoja en el tiempo t+1

En este caso, la longitud después de la marca fue N_t ya que indica la longitud que se tuvo en el primer día y la longitud total fue (N_{t+1}), que representa la longitud que alcanzó 30 días después. La longitud de las frondas de *C. paspaloides* representó el estado de cada módulo. Esta metodología se adaptó a la utilizada por Duarte et al. (1994) para calcular el intervalo de plastocrono, y de Mandujano et al. (2001) para el marcado de módulos y la evaluación de la tasa de crecimiento modular.

3.8 Métodos demográficos de *Caulerpa paspaloides*

Para analizar el comportamiento demográfico *de C. paspaloides* se seleccionaron muestras aleatorias (Fig. 1 (2 y 3)) con cobertura del 100% de *C. paspaloides* dentro del cuadro de 0.5m^2 (diez muestras por sitio). Las muestras obtenidas se guardaron en bolsas de plástico herméticas y se registró el número de estolones y frondas completas e incompletas, así como el diámetro de cada estolón y el peso en g/m^2 para cada muestra.

Además, se calculó la tasa finita de cambio en biomasa (equivalente a una λ poblacional) (Caswell, 2001): $\lambda=Nt+1/Nt$

Por lo tanto, se calcularon los cambios en las tasas de biomasa entre los años y las temporadas.

Esta metodología de demografía de algas fue establecida por Fuentes et al. (2014) para *C. paspaloides.*

Se marcaron 50 frondas en praderas monoespecíficas y mixtas *C. paspaloides*. Las frondas marcadas con estos alambres fueron recolectadas 90 días después. Se aplicó la misma fórmula ($\lambda=N_{t+1}/N_t$), la longitud antes de la marca fue N_t, ya que indica la longitud que se tenía en el primer día y la longitud total fue (N_{t+1}), que representó la longitud que alcanzó a los 90 días. En este caso, la longitud de las frondas de *C. paspaloides* representa el estado de cada módulo. Para calcular la λ modular se usó la formula ($\lambda=N_{t+1}/N_t$) en donde:

λ= tasa finita de crecimiento modular

N_t=la longitud de la hoja en el tiempo t

N_{t+1}=la longitud de la hoja en el tiempo t+1

En este caso, la longitud después de la marca fue N_t ya que indica la longitud que se tuvo en el primer día y la longitud total fue (N_{t+1}) que representó la longitud que alcanzó 90 días después. En este caso, la longitud de las frondas de *C. paspaloides* representó el estado de cada módulo. Esta metodología se adaptó a la utilizada por Fuentes et al. (2014) y de Mandujano et al. (2001) para el marcado de módulos y evaluación de la tasa de crecimiento modular.

3.9 Caracterización de la luz en cada sitio

En cada sitio de estudio se registró la radiación fotosintéticamente activa (PAR, µmol/m^2/s) en la columna de agua con el LY-COR LI-193 desde la superficie (antes de tocar el agua), cubriendo el agua y, a partir de ahí, cada metro hasta el fondo.

Con este registro se calculó la pérdida de luz para cada sitio, por medio de la relación que hay entre la profundidad y el PAR.

Con los valores máximos y mínimos de PAR y un despeje de la ecuación de Lambert-Beer fue hecha para calcular el porcentaje de luz que hay en el fondo para cada sitio:

$I\ z / I\ 0 = e^{(-Kd * z)}$

$Porcentaje\ de\ luz\ en\ el\ fondo\ (\%) = e^{(-Kd * z)} * 100$

I z= PAR mínimo

I 0= PAR máximo

e = natural logaritmo base

K_d *= coeficiente de atenuación de luz*

z = profundidad

En cada sitio se colocó un aparato HOBO UA-002-64 en el fondo marino para detectar los cambios de luz**,** y se intercambiaron cada tres meses. Una vez que se colectó la información se descargó y analizó con el programa HOBOware.

3.10 Eficiencia fotosintética de *T. testudinum* y *C. paspaloides*

En cada sitio se colectaron 10 haces verticales de *T. testudinum* y 10 frondas de *C. paspaloides*. Cada muestra se colocó en oscuridad con aire constante por un tiempo mínimo de 30 min. En un cuarto oscuro se registró la respuesta fotosintética para cada haz vertical y cada fronda, mediante un fluorómetro (mini-PAM, Heinz Walz, Effeltrich, Alemania). Esta técnica permitió la descripción de la variabilidad espacio-temporal de la eficiencia fotoquímica del PSII (*Fv/Fm*).

3.11 Pigmentos fotosintéticos de *T. testudinum* y *C. paspaloides*

Se colectaron muestras de las hojas y frondas de las muestras usadas para medir eficiencia fotosintética, de 2018 a 2019 en las temporadas de secas, lluvias y nortes. Las muestras se guardaron en papel aluminio y en un contenedor con nitrógeno líquido. Las muestras se maceraron con una varilla de vidrio dentro del eppendorf con una sustancia de 2% de acetato de amonio 0.5M y aforadas a 2ml. Se guardaron en oscuridad por 24 hrs a -20°C. Los tubos se dejaron reposar a temperatura ambiente y sonificados a 3 min. Se sometieron a ultracentrífuga a 70000rpm durante 20min, se extrajo el sobrenadante y el líquido filtrado se puso en viales etiquetados que se guardaron a una temperatura de -20°C. Las muestras se procesaron en HPLC, usando una fase móvil (acetato de amonio 30% y metanol 70%) y acetato de amonio 0.5 M. Se obtuvo la cantidad de ng/cm² de violaxantina, antheraxantina, zeaxantina, clorofila a y clorofila b, ya que son los pigmentos responsables de la regulación de luz solar para evitar la oxidación de proteínas.

3.12 Análisis estadísticos

La cobertura de la VAS al ser por porcentajes, se analizó con una prueba de chi cuadrada para encontrar diferencias en las coberturas relativas de cada especie en cada pradera. Para encontrar dónde existen estas diferencias significativas entre la cobertura de especies se usaron pruebas de residuales.

Para las variables fisicoquímicas (fisicoquímicos, nutrientes, tamaño del sedimento y materia orgánica) y de biomasa fitoplanctónica se realizó una prueba no paramétrica (Wruskall-Wallis), ya que el número de datos es limitado (10 por sitio), para encontrar diferencias significativas en los sitios y en las temporadas (nortes, lluvias y secas).

Los datos morfológicos de *T. testudinum* (longitud de haces (cm), longitud de hojas (cm), número de internodos, longitud (cm), diámetro (cm) y número de rizomas y número de flores y cicatrices florales) fueron analizados con una ANOVA de dos vías para evaluar si hubo cambios en los datos morfológicos durante los años 2017 y 2018. Los otros datos morfológicos de *T. testudinum* (número de hojas, cicatrices de hojas, internodos y flores), por ser variables numéricas discretas, se realizaron con

un modelo lineal generalizado (GML) para encontrar diferencias significativas en las praderas (monoespecífica y mixta) y años (2017 y 2018). Se realizó la prueba *post-hoc* de Student para cada uno de los parámetros en los que se encontraron diferencias significativas.

Los datos morfológicos de *C. paspaloides* (el número de estolones, frondas completas e incompletas, diámetro de los estolones y peso en g/m^2) se analizaron con análisis de varianza (ANOVA) para identificar diferencias significativas en las praderas (monoespecífica y mixta), durante los años 2017 y 2018, y las temporadas (lluvias, secas, y nortes).

Se hizo una prueba de ANOVA multifactorial para evaluar si hubo cambios en la *Fv/Fm* en ambas especies tanto en los sitios como en las temporadas.

Los datos se registraron en porcentaje de pigmentos xantofilos (zeaxantina, antheraxantina y violaxantina) y clorofilas (a y b) y se analizaron en una prueba de Chi cuadrada para encontrar diferencias en la cantidad de pigmentos en las temporadas y en los sitios, y su correspondiente análisis de residuales.

Un análisis de componentes principales (PCA; Tabachnick and Fidell, 2019, STATISTICA 9.0) se hizo con los factores (Sitios 1, 2 y 3) y las variables de respuesta (profundidad, porcentaje de luz en el fondo, temperatura, salinidad, pH, Oxígeno disuelto, Nitrógeno inorgánico disuelto, Fósforo total, amonio y fósforo en agua intersticial y la *Fv/Fm*). Los factores con valores arriba de 0.63 se consideraron valores muy buenos (Tabachnick and Fidell, 2019).

Un análisis de componentes principales (PCA; Tabachnick and Fidell, 2019, STATISTICA 9.0, STATSOFT USA) se realizó con los factores (Sitio 1, 2 y 3) y las variables de respuesta (Biomasa de *C. paspaloides*, profundidad, temperatura, salinidad, pH, Oxígeno disuelto, Nitrógeno inorgánico disuelto, Fósforo total, amonio y fósforo en agua intersticial y la *Fv/Fm*). Los factores con valores arriba de 0.63 se consideraron valores muy buenos (Tabachnick and Fidell, 2019).

Para que el PCA fuera lo más completo posible se integró la biomasa de macroalgas y la de *T. testudinum*. Una vez que se conocieron las variables que se correlacionaron entre sí por medio del PCA en este estudio, se hizo un análisis de comportamiento de las variables más importantes con el programa Originpro 2016 (Multion, USA). El programa por medio de la opción “new layer axes graphics” acomoda las variables en las fechas de muestreo y las reacomoda en una gráfica para encontrar patrones en común o se comportan de forma aleatoria.

4-. RESULTADOS

4.1 Caracterización de la vegetación acuática sumergida y elementos biológicos en los tres sitios

El Sitio 1 registró 100% de *T. testudinum*; el Sitio 2 registró una cobertura relativa de 52% *T. testudinum*, 38% *C. paspaloides*, 5% macroalgas y 5% espacios en blanco; y el sitio 3 registró 5% *T. testudinum*, 81% *C. paspaloides*, 8% macroalgas y 6% espacios en blanco, en promedio. Se encontraron diferencias significativas entre los sitios 2 y 3 (χ^2 = 19.02, *g.l.*=3, p<0.01) y en el análisis de residuales se obtuvieron diferencias en la cobertura de *T. testudinum,* con una mayor presencia en el Sitio 1, y la cobertura de *C. paspaloides* en el sitio 3 (Fig. 2).

No se encontraron diferencias significativas en la cantidad de biomasa fitoplanctónica en las praderas ni entre las temporadas (H= 2.27, n=30, *g.l.*=2, p=0.32). En general, se tiene un promedio de 1.59 ±0.26 mg/m^3 en la zona.

Las especies de macroalgas que se registraron en los sitios 2 y 3 fueron las siguientes: *Derbesia marina* ((Lyngbye) Solier), *Avrainvillea levis* (M. Howe), *Caulerpa prolifera* ((Forsskål) J.V. Lamouroux), *Halimeda monile* ((J. Ellis y Solander) J.V. Lamouroux)), *Batophora oerstedii* (J. Agardh) y *Penicillus dumetosus* (J.V. Lamouroux) Blainville.

Tabla 1. Cobertura de la vegetación acuática sumergida para cada sitio

Sitio	***T. testudinum***	***C. paspaloides***	**Macroalgas**	**Espacio en blanco**	***p*>0.01**
1	100 %	NA	NA	NA	0.10
2	**52 %**	38 %	5 %	5 %	<0.01
3	5 %	**81 %**	8 %	6 %	<0.01

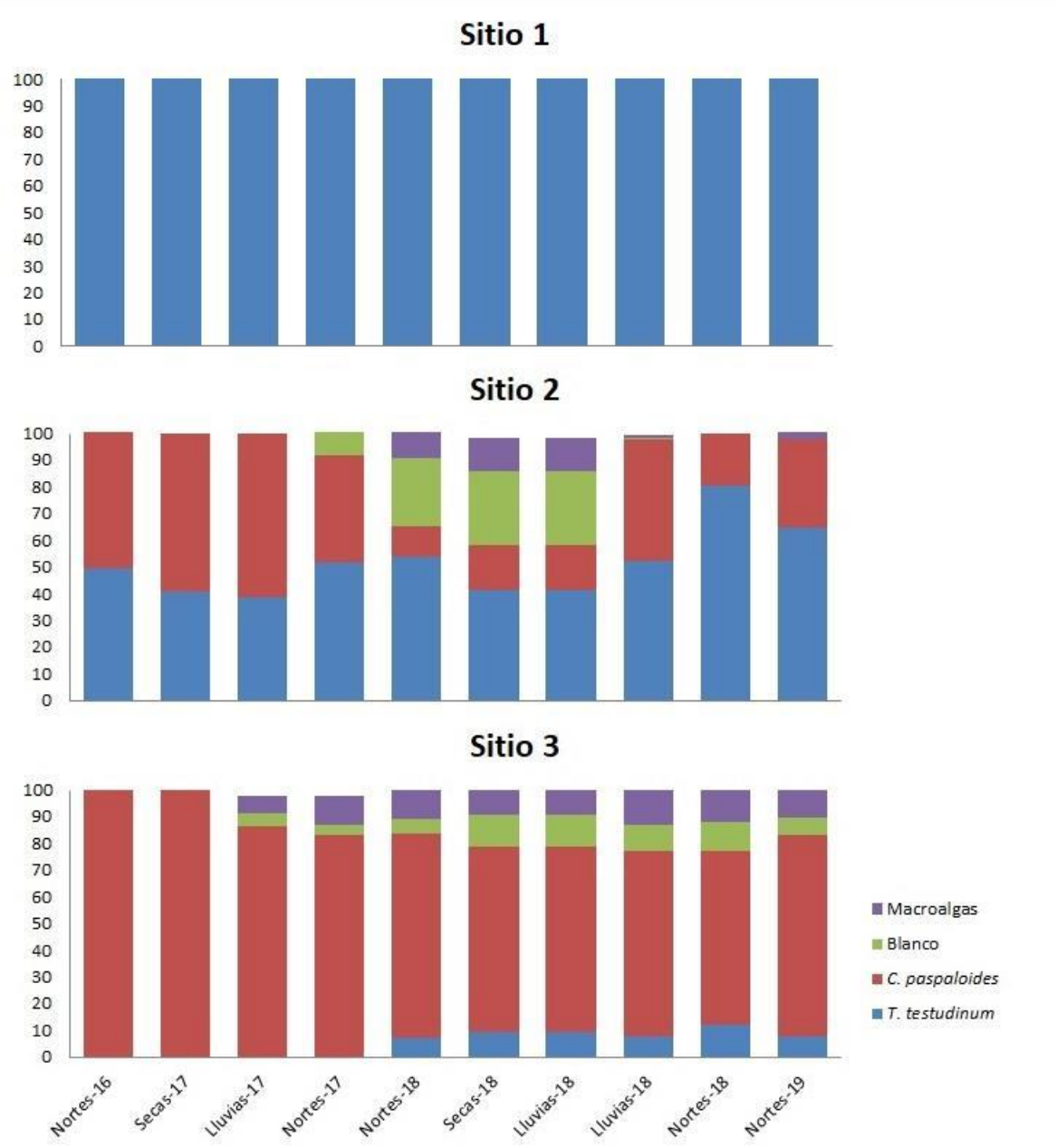


Figura 2-. Coberturas de la vegetación acuática sumergida de los 3 sitios a lo largo del muestreo.

4.2 Diferencias abióticas entre las praderas

Se encontraron diferencias significativas en la profundidad (H=21.84, n= 30, $g.l.$=2, p<0.01) y en el tamaño del grano (Mz) (H=12.18, n=30, $g.l.$=2, p<0.01). Los sitios monoespecíficos de *C. paspaloides* y mixtos registraron mayor profundidad y un grano de mayor tamaño a diferencia del sitio monoespecífico de *T. testudinum* (Tabla 2).

Tabla 2. Datos fisicoquímicos obtenidos para los tres sitios de estudio

	Sitio 3	**Sitio 2**	***Sitio 1***	***p***
Profundidad (m)	3.23±0.16	2.81±0.18	**1.50±0.24**	**<0.01**
Temperatura (C°)	26,77±0.66	27,29±0.74	25,93±0.58	>0.05
pH	8,07±0.05	8,07±0.06	8,05±0.07	>0.05
Salinidad	36,14±0.80	36,34±0.74	36,32±0.78	>0.05
Oxígeno disuelto	6,15±0.21	6,25±0.23	5,74±0.29	>0.05
Conductibilidad	54,49±1.19	54,71±1.25	54,29±1.35	>0.05
NID (mg/l)	15,24±1.65	6,66±1.64	7,89±1.75	>0.05
Fósforo total (PT) (mg/l)	2,77±0.43	1,33±0.42	1,87±0.41	>0.05
Sílice (mg/l)	8,55±0.85	5,48±0.83	5,75±0.81	>0.05
Amonio sed (mg/l)	895,59±136.11	593,97±123.6	751,78±0.145	>0.05
PT en sedimentos (mg/l)	13,97±5.09	13,44±6.09	18,51±5.98	>0.05
Carbono orgánico	4,45±0.42	4,45±0.43	4,24±2.03	>0.05
Materia orgánica	7,66±4.56	7,65±4.98	7,30±0.48	>0.05
Tamaño del grano (Mz)	1,88±0.23	0,73±0.28	**2,75±0.23**	**<0.05**

En cuanto a los parámetros fisicoquímicos por temporada se encontraron diferencias significativas en temperatura en las temporadas climáticas (*H*=14.48, *g.l.*=2, *n*=30, *p*<0.01), sílice (*H*= 6.85, *g.l.*=2, *n*=30, *p*=0.032) y NID (Nitrógeno inorgánico disuelto) (*H*= 17.73, *g.l.*=2, *n*=30, *p*=0.01). La salinidad fue mayor en la temporada de secas (*H*= 6.7, *g.l.*=2, *n*=30, *p=0.034*) (Tabla 3).

Tabla 3. Datos fisicoquímicos obtenidos para las temporadas nortes, secas y lluvias

	Secas	**Lluvias**	**Nortes**	***p***
Profundidad (m)	2,43±0.15	2,51±0.18	2,60±0.17	>0.05
Temperatura (C°)	25,27±0.53	**29,71±0.32**	25,33±0.45	**<0.01**
pH	8,22±0.07	7,93±0.08	8,06±0.09	>0.05
Salinidad	**37,87±8.79**	35,82±8.46	34,73±8.95	**0.034**
Oxígeno disuelto	6,09±0.22	5,91±0.32	6,45±0.48	>0.05
Conductibilidad	56,15±1.15	55,75±1.16	51,58±1.18	>0.05
Nitrógeno inorgánico disuelto (mg/l)	3,51±1.62	**16,81±4.53**	9,47±3.23	**0.01**
Fósforo total (PT) (mg/l)	1,40±0.42	1,68±0.52	2,80±0.85	>0.05
Sílice (mg/l)	5,28±0.85	**8,98±0.78**	5,52±0.83	**0.032**
Amonio sed (mg/l)	728,05±136.56	836,89±135.23	676,39±123.5	>0.05
PT sed (mg/l)	29,47±5.23	9,93±4.56	6,52±3.56	>0.05
Carbono orgánico	3,38±0.42	5,68±0.58	4,07±0.69	>0.05
Materia orgánica	5,83±0.75	9,77±0.89	7,02±0.98	>0.05
Tamaño de grano Mz	1,92±0.25	1,94±0.29	1,50±0.36	>0.05

4.3 Demografía de *T. testudinum*

Hubo diferencias significativas en los sitios y en los años en las estructuras morfológicas de *T. testudinum*. En el año 2018, hubo mayor número de internodos (18±9) y en el diámetro del rizoma (5.22±0.11) (Tabla 4). En el Sitio 2 (pradera mixta) se registró un mayor tamaño de hojas promedio en el año 2017 (24.34±1.89), mayor distancia entre cicatrices de hoja a hoja (1.28±0.46) y en ambos años un mayor número de cicatrices de hojas (2017-37, 2018-45). En el Sitio 1 (pradera monoespecífica de *T. testudinum*) los individuos presentaron mayor número de hojas (3±1) y tamaño del rizoma (9.43±0.70).

El registro de las características demográficas (Tabla 5) se obtuvo que fueran mayores en el sitio 1 en el año 2018. Sin embargo, el sitio 1 en el año 2017 registro el mayor número de hojas al año (30) y la mayor tasa de reclutamiento de haces (0.90) y el sitio 2 en el año 2018 registro el mayor porcentaje de biomasa aérea (59.94%) y el mayor crecimiento vertical (5.02 cm/año).

Tabla 4. Variables morfológicas de *T. testudinum* (número de hojas, número de cicatrices de hojas, internodos, número de hojas, número de cicatrices de hojas e internodos)

Variable morfológica	**Sitio 1-2017**	**Sitio 1-2018**	**Sitio 2-2017**	**Sitio 2-2018**	***F/p***		
					Sitios	Años	Interacción
Número de hojas	**3±1**	**3±1**	2±1	2±1	**6.83/ <0.01**	0.12/ 0.06	0.72/ 0.13
Número de cicatrices de hoja	35±22	32±27	**37±28**	**45±31**	**7.64/ <0.01**	0.003/ 0.95	2.84/ 0.06
Distancia entre cicatriz de hoja a hoja (cm)	0.77±0.26	0.91±0.28	**1.28±0.46**	1.10±0.30	**801.68/ <0.01**	**14.84/ <0.01**	**187.57/ <0.01**
Número de internodos	14 ±6	**18±9**	12.5 ±6	**15.53 ±8**	3.22/ 0.07	**13.37/ <0.01**	0.42/ 0.51
Tamaño de haces (cm)	4.51 ±0.27	4.35±0.26	4.36 ±0.53	5.14 ±0.43	0.33/ 0.56	1.02/ 0.31	0.92/ 0.33
Tamaño de hojas (cm)	18.64±1.32	19.90±1.20	**24.34±1.89**	18.6 ±0.95	2.56/ 0.11	2.62/ 0.10	**6.46/ 0.01**
Ancho de la hoja (cm)	0.72±0.02	0.77±0.03	0.71±0.03	0.84 ±0.21	0.05/ 0.81	0.24/ 0.62	0.02/ 0.87
Tamaño del rizoma (cm)	**8.35±0.49**	**9.43±0.70**	6.55±0.49	6.37 ±0.45	**8.32/ <0.01**	0.28/ 0.59	0.56/ 0.45
Diámetro del rizoma (cm)	5.19±0.08	**5.22±0.11**	4.93±0.12	**4.87±0.09**	0.27/ 0.59	**4.68/ 0.03**	0.05/ 0.81

Tabla 5. Parámetros demográficos para las praderas de *T. testudinum* en los años 2017 y 2018

Parámetro demográfico	Sitio 2 2017	Sitio 1 2017	Sitio 2 2018	Sitio 1 2018
Biomasa aérea (g/m^2)	687,74	1368,42	846,30	**1543,13**
Biomasa subterránea(g/m^2)	535,25	1923,87	565,55	**2147,06**
Biomasa total (g/m^2)	1222,99	3292,29	1411,85	**3690,19**
% Biomasa aérea	56,23	41,56	**59,94**	41,82
% Biomasa subterránea	43,77	58,44	40,06	**58,18**
Densidad poblacional (ind/m^2)	757,43	1545,00	1030,10	**1787,53**
Número de hojas por año	31	**33**	31	**33**
Número de cicatrices de hojas entre cicatriz de flor	23	**34**	23	**34**
Densidad floral (ind con flor/m^2)	30	151	333	**1060**
% Floral	4	32	11	59
Crecimiento vertical (cm/año)	3,38	3,79	**5,02**	4,26
Tasa de reclutamiento de haces	0,81	**0,90**	0,84	0,42
Crecimiento horizontal (cm/año)	34.56	36.46	40.90	**67.34**

La regresión lineal general entre el número de hojas y el tamaño de cada haz para calcular los parámetros demográficos de *T. testudinum* fue de y = 0.0988x + 0.7564 R^2 = 0.7767, y la prueba de residuales nos indica que los datos se ajustan al modelo lineal (F=587.46, $g.l.$= 1 p<0.01) (Fig. 3). El crecimiento horizontal obtuvo una regresión lineal de y = 0.3274x + 2.8563 R^2 = 0.5253 (Fig. 4).

En términos generales, el Sitio 1 presenta mayores características demográficas. Sin embargo, el Sitio 2 presenta mayor porcentaje de biomasa aérea y mayor crecimiento vertical.

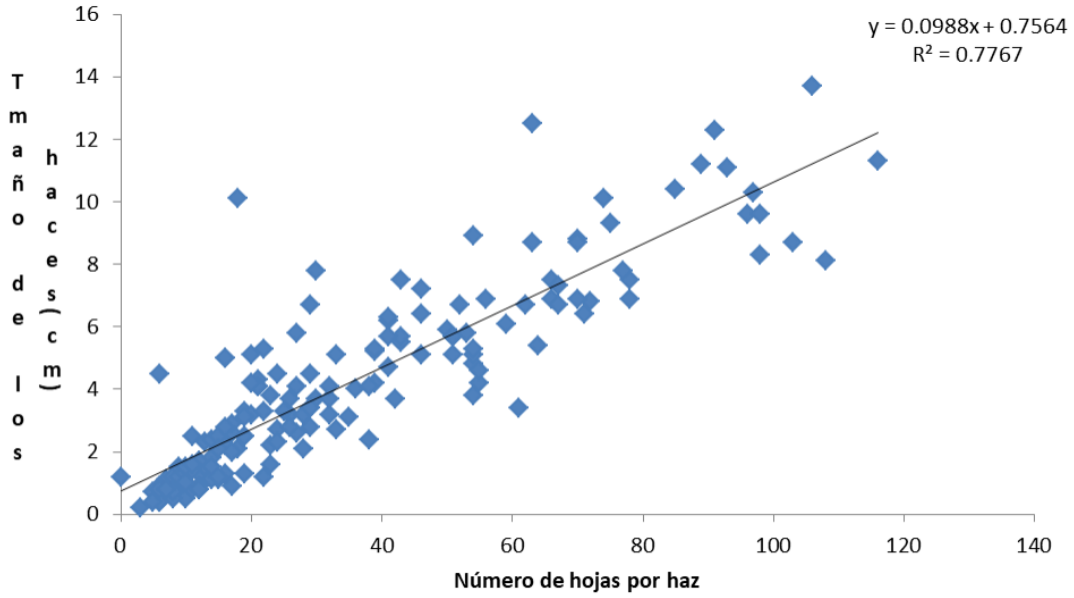


Figura 3-. Regresión obtenida con el número de hojas por haz y por el tamaño de haces verticales.

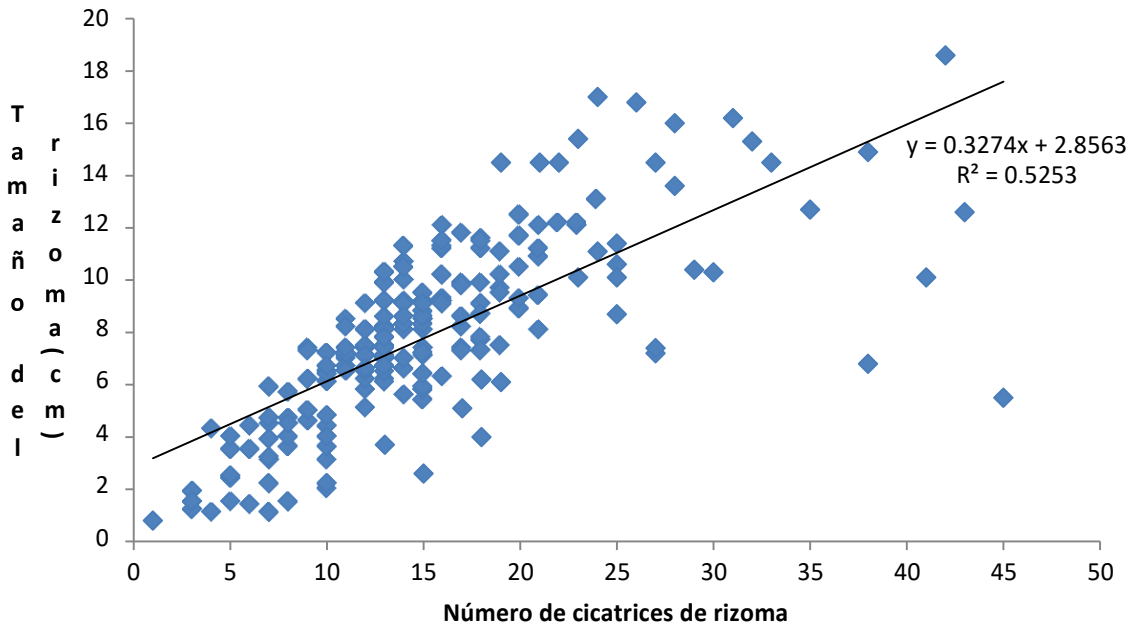


Figura 4-. Crecimiento horizontal calculado a partir del número de cicatrices de rizoma y el tamaño de rizoma.

El número de hojas producido en un año se calculó para el sitio 1 de 33 para ambos años y en el sitio 2 de 31 en ambos años y a partir de las cicatrices florales fue de 34 en el sitio 1 y 23 en el sitio 2 (Tabla 5).

La longitud internodal muestra ciclos en el crecimiento vertical y se calculó para el Sitio 1, 33 hojas en 2017 y 34 hojas en 2018 y Sitio 2, 26 hojas en ambos años. Por lo tanto, se llegó a la conclusión que los haces del Sitio 1 tienen 34 IP por año y el Sitio 2, 30 IP por año.

El Sitio 1 (N = 150 individuos) presentó un máximo de edad de 4 años (160 IP) y el Sitio 2 registró (N = 107 individuos) un máximo de edad de 5 años (165 IP) (Fig. 5). Las estructuras de edades por año fueron diferentes (χ^2= 187.26, *g.l.*=3, p<0.01) la prueba de residuales registró mayor número de haces verticales menores de un año en el Sitio 1 que los esperados (Fig. 5).

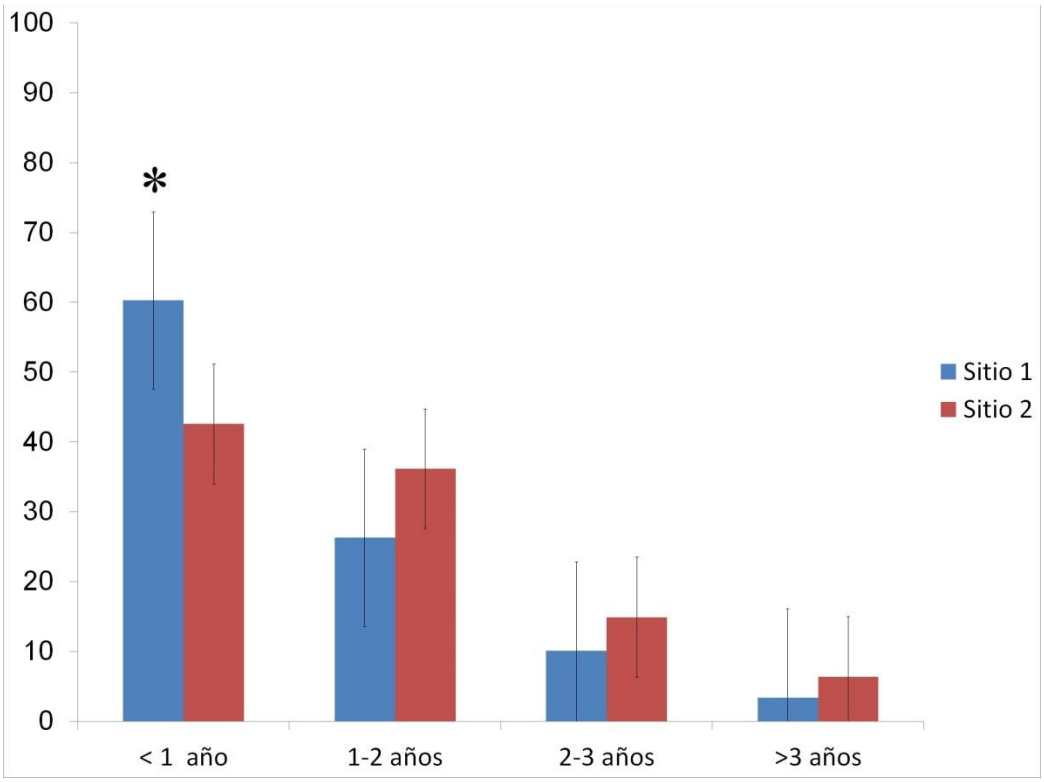


Figura 5-. Estructura de edades de *T. testudinum* en la pradera monoespecífica y la mixta. * Señala la categoría que es diferente entre las dos estructuras.

Se obtuvieron diferencias significativas en el crecimiento de hojas por día. La prueba *post-hoc*, indicó que los sitios tienen un mayor crecimiento de hojas en ambos sitios (sitio 1- 0.25±0.10, sitio 2- 0.21± 0.10) en la temporada de lluvias y el menor crecimiento en la temporada de nortes en el sitio 1 (0.15±0.08) (Tabla 6).

Tabla 6. Registro de crecimiento de hojas por día en el Sitio 1 y el Sitio 2 *testudinum* en las tres temporadas climáticas

Pradera (cm)	**Secas**	**Lluvias**	**Nortes**		**Valor de *p/F***	
				Praderas	Temporadas	P×T
Sitio 1	**0.25±0.10**	0.19±0.08	0.15±0.08	0.32 /	**<0.01/**	**<0.01/**
				0.96	**11.06**	**5.93**
Sitio 2	**0.21±0.11**	0.16±0.05	0.19±0.08			

Los registros de λ poblacional señalan que ambas poblaciones crecen en el año ya que son mayores a 1 en todas las praderas (Tabla 7).

Tabla 7. Registros de *λ* para las poblaciones de *T. testudinum*

	Sitio 2	**Sitio 1**
Individual λ	1.16	1.36
Aérea λ	1.22 ± 0.19	1.14 ± 0.27
Subterránea λ	1.07 ± 0.22	1.14 ± 0.17
Total λ	1.12 ± 0.03	1.15 ± 0.03

4.4 Demografía de *C. paspaloides*

Se obtuvieron diferencias significativas en los sitios y en las temporadas (Tabla 8), en todas las variables morfológicas en el sitio 3 (sitio monoespecífico de *C. paspaloides*) fue mayor que en el Sitio 2 (mixto) y la temporada de secas es donde hay menor registro de las variables morfológicas (Tabla 8) (Fig. 6).

Tabla 8. Parámetros morfológicos para *Caulerpa paspaloides*. Variables significativas están marcadas en negras en las praderas, temporadas y la interacción en los análisis ANOVA.

Variable Morfológica	**Sitio 3**	**Sitio 2**	**Valor de *F/p***		
			Sitios	Temporadas	S×T
Número de estolones	**36±8.81**	19 ±10.59	**136.107/<0.01**	**7.363/<0.01**	2.92/0.06
Número de frondas completas	**171±51.20**	75±43.21	**181.186/<0.01**	**5.765/<0.01**	0.285/0.75
Número de frondas incompletas	**108±47**	45±40	**89.32/<0.01**	**7.88/<0.01**	**3.13/0.04**
Biomasa (g/m^2)	**10.64±4.78**	3.7±2.3	**156.81/<0.01**	**7.81/<0.01**	2.21/0.11
Longitud de la fronda (cm)	**5.65±4.78**	3.67±1.56	**91.31/<0.01**	2.76/0.06	0.358/0.69
Diámetro del estolón (mm)	**2.46±0.21**	1.83±0.64	**84.61/<0.01**	**15.86/<0.01**	**9.59/<0.01**

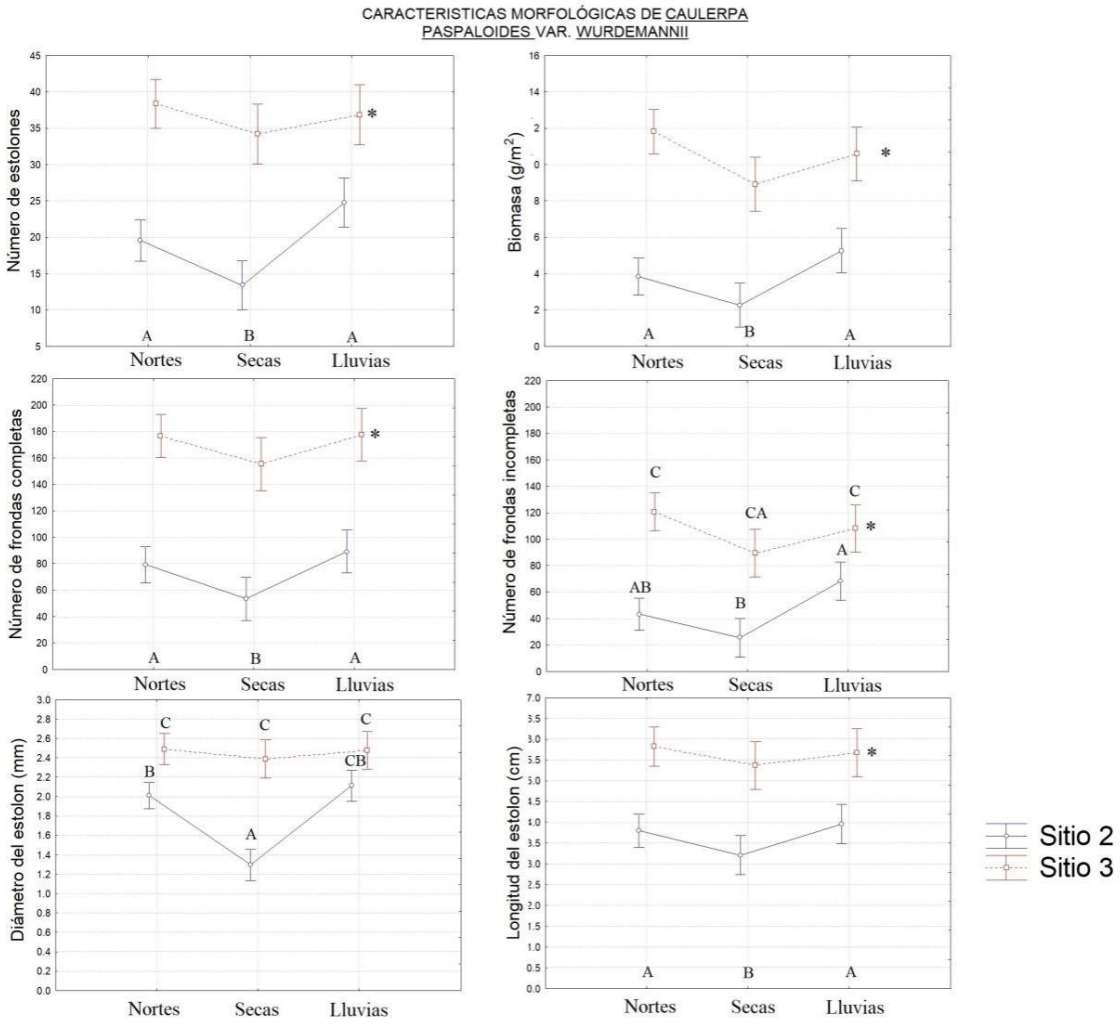


Figura 6-. Medias de frondas completas, frondas incompletas, diámetro del estolón, longitud del estolón, número de estolones y biomasa de *C. paspaloides*, en las praderas monoespecíficas y mixtas durante las tres temporadas. Las letras señalan los grupos de la prueba post-hoc y los asteriscos los sitios con mayores conteos.

Se obtuvieron diferencias significativas entre temporadas en el crecimiento de frondas por día (cm) (Temporada *p*=0.01). La prueba *post-hoc* indicó dos grupos: el primero, en la temporada de secas donde tiene el mayor crecimiento y el segundo, en la temporada de nortes que tiene el menor crecimiento (Fig. 7).

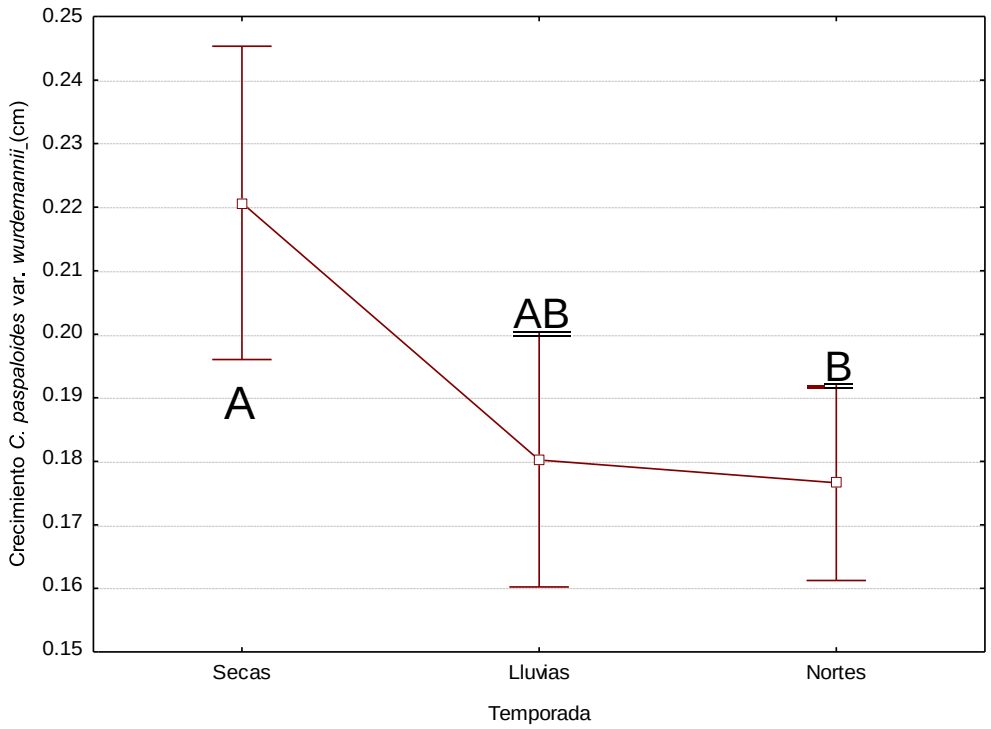


Figura 7-. Registro de crecimiento de frondas por día en *C. paspaloides* durante las tres temporadas climáticas. Las letras señalan los grupos que se formaron por la prueba *post-hoc*.

Las tasas finitas de crecimiento de *C. paspaloides* (λ) indican que en general crecen mayores a 1. El Sitio 3 registró crecimiento de nortes a secas, en cambio el Sitio 2 registró crecimiento de nortes a secas y de secas a lluvias (Tabla 9) (Fig. 8).

Tabla 9. Tasas finitas de crecimiento (*λ*) de *C. paspaloides* en las diferentes temporadas.

C. paspaloides	**Sitio 3**	**Sitio 2**
nortes-secas	**2.79±0.52**	**1.45±0.51**
secas-lluvias	0.68±0.26	**1.59±0.27**
lluvias-nortes	0.82±0.08	0.90±0.15
Total	1.44±0.36	1.29±0.24

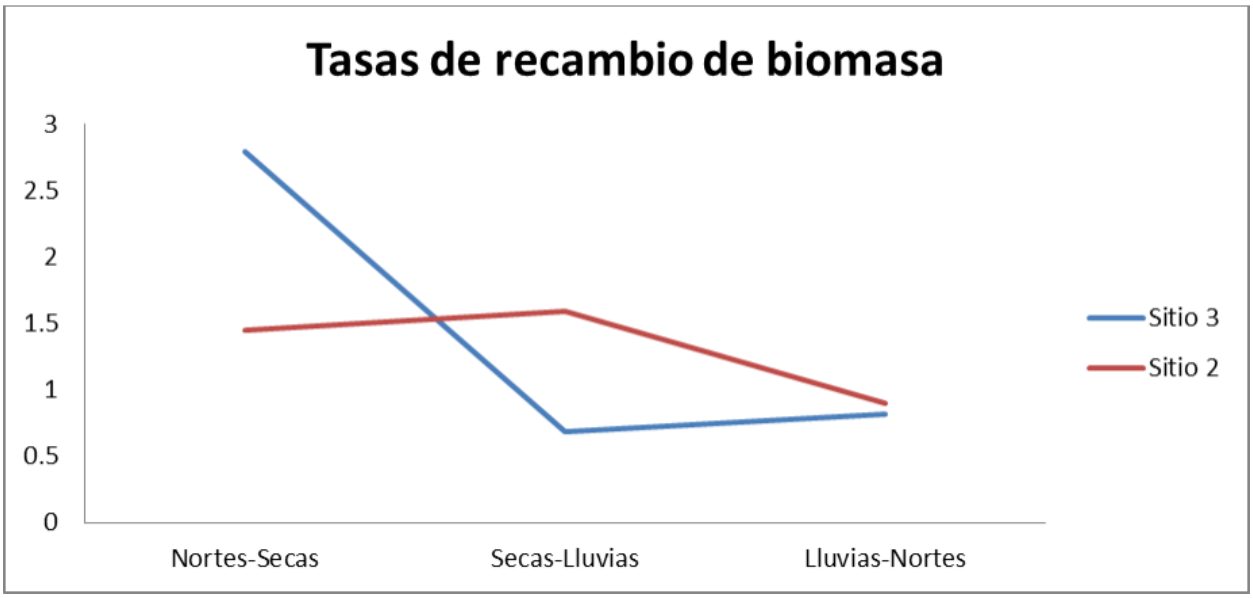


Figura 8-. Tasas de recambio de biomasas para *C. paspaloides* en las diferentes temporadas y sitios.

4.5 Caracterización de luz entre las praderas

Los porcentajes de luz en el fondo para el sitio 1 fueron desde 16.9% al 31.39%, el sitio 2 de 2.46% al 0.50% y el sitio 3 de 0.15% al 0.005% (Tabla 10).

Solo se pudo obtener información de HOBOS para el año 2018 en la temporada de secas (junio), lluvias (agosto) y nortes (octubre). Se obtuvo que la mayor intensidad de luz fue en el día 30 de septiembre del 2018 (14466.8 lux) en el Sitio 2 y la mínima fue de (10.8 lux) en los demás días (Tabla 11). Se obtuvieron diferencias significativas en los sitios 2 y 3 en la temporada de lluvias. El Sitio 2 tuvo mayor intensidad de luz que el Sitio 3 ($Z=24.48$, $p>0.01$).

Tabla 10. Coeficiente de pérdida de luz y máximo porcentaje de luz para cada uno de los sitios (profundidades máximas entre paréntesis), en las temporadas de secas, lluvias y nortes

Coeficiente de atenuación de luz/Máximo porcentaje de luz en el fondo (%)	**Secas**	**Lluvias**	**Nortes**
Sitio 1 (2m)	-0,721/23.64	**-0,604/29.87**	-0,957/14.74
Sitio 2 (3.2m)	-0,535/18.05	-0,873/6.12	-1,175/2.32
Sitio 3(4m)	-0,716/5.70	-1,087/1.29	-0,651/7.39

Tabla 11. Intensidad de luz (len los diferentes sitios obtenidos por los hobos

Sitio	Mínima intensidad de luz (lux)	Máxima intensidad de luz (lux)
1	10.80	3272.20 (secas)
2	10.80	14466.80 (lluvias)
3	10.80	13089.00(lluvias)

4.6 Eficiencia fotosintética de *T. testudinum* y *C. paspaloides*

Con todos los registros de *Fv/Fm* para *T. testudinum* se registró una media de 0.725 (0.63-0.84) Fig. 9 A) y para *C. paspaloides* de 0.50 (0.15- 0.88 Fig. 9 B).

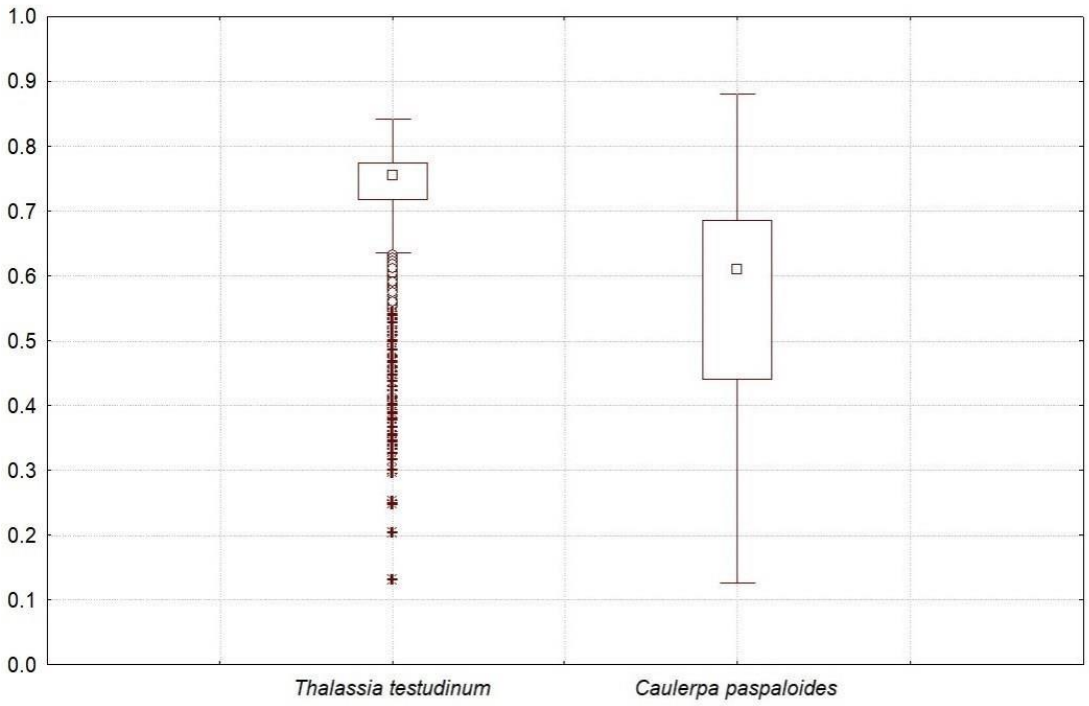


Figura 9-. Medias de eficiencia cuántica para *T. testudinum* y *C. paspaloides*.

Se encontraron diferencias significativas en la *Fv*/*Fm* de *C. paspaloides*. La prueba *post-hoc* indica que la temporada de lluvias en sitios mixtos presenta menor *Fv*/*Fm*. *T. testudinum* presentó diferencias significativas en la *Fv*/*Fm* en la temporada de lluvias en ambas praderas (Tabla 12).

Tabla 12. Valores de *Fv/Fm* para las especies *T. testudinum* y *C. paspaloides* en los tres sitios

Sitio/ especie	**Nortes**	**Secas**	**Lluvias**	**Promedio**	**Valor de *F/p***		
					Pradera	Temporada	P×A
Sitio 1 *T. testudinum*	0.74 ±0.03	0.74 ±0.05	**0.69±0.09**	0.72± 0.06	1.49/ 0.22	**20.81/ >0.01**	0.38/ 0.68
Sitio 2 *T. testudinum*	0.76 ±0.02	0.75±0.03	**0.69 ±0.07**	0.73± 0.05			
Sitio 3 *C. paspaloides*	0.59 ±0.19	**0.69±0.10**	0.58 ±0.17	0.61± 0.16	**7.97/ >0.01**	**25.08/ >0.01**	**15.58/ >0.01**
Sitio 2 *C. paspaloides*	0.68 ±0.57	0.60±0.13	**0.36 ±0.16**	0.55± 0.18			

Se encontraron diferencias significativas en la proporción de pigmentos de *C. paspaloides*. La presencia de zeaxantina solamente existe en el Sitio 1 en la temporada de secas y la violaxantina es alta en el Sitio 2 en la temporada de nortes (χ^2= 543.34, *g.l.* 15, p< 0.01) (Fig. 10), y la clorofila b es mayor en el Sitio 3 en la temporada de secas y la clorofila a es más baja (χ^2= 2235.87, *g.l.* 5, p< 0.01). En cambio, en *T. testudinum* no se encontraron diferencias significativas (χ^2= 12.34, *g.l.* 15, p> 0.05) (χ^2= 5.87, *g.l.* 5, p>0.05), los pigmentos más abundantes son la anteraxantina y la clorofila "a" para la especie (Fig. 11).

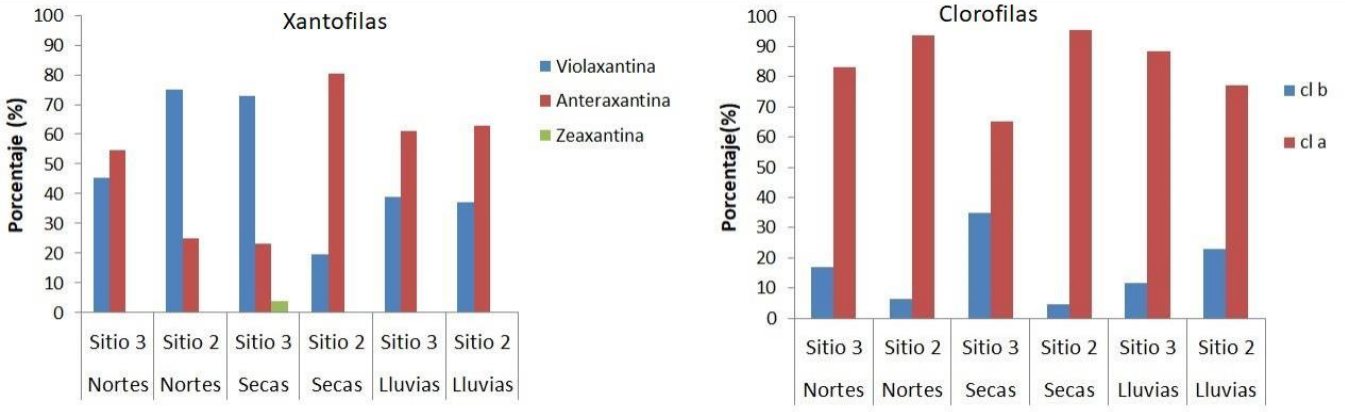


Figura 10-. Pigmentos accesorios de la especie *C. paspaloides* en las temporadas climáticas (Nortes, Secas y Lluvias) en el sitio 3 y Sitio 2.

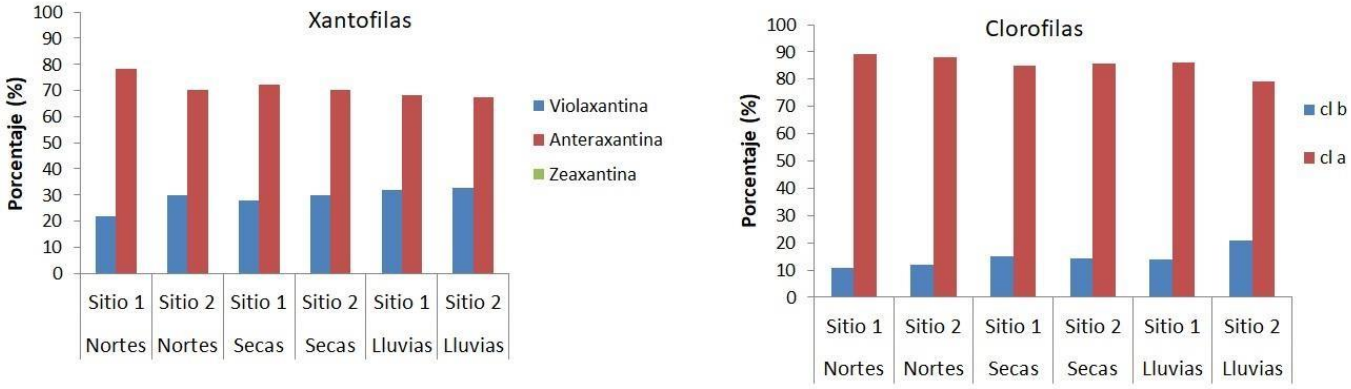


Figura 11-. Pigmentos accesorios de la especie *T. testudinum* en las temporadas climáticas (nortes, secas y lluvias) en el Sitio 1 y en el Sitio 3.

No se encontraron diferencias significativas entre sitios (*d.f.* 2, χ^2= 6.86, *p*> 0.05). Sin embargo, sí se encontraron diferencias significativas para ambas especies en las temporadas (*T. testudinum*, *d.f.* 2, χ^2= 26.70, *p*> 0.05) (*C. paspaloides*, *d.f.* 2, χ^2= 26.70, *p*> 0.05). La prueba *post-hoc* de residuales indica que los eventos de estrés son mayores en la temporada de lluvias en *T. testudinum* y en *C. paspaloides)*. En la temporada de secas hay menores registros de estrés (Fig. 12).

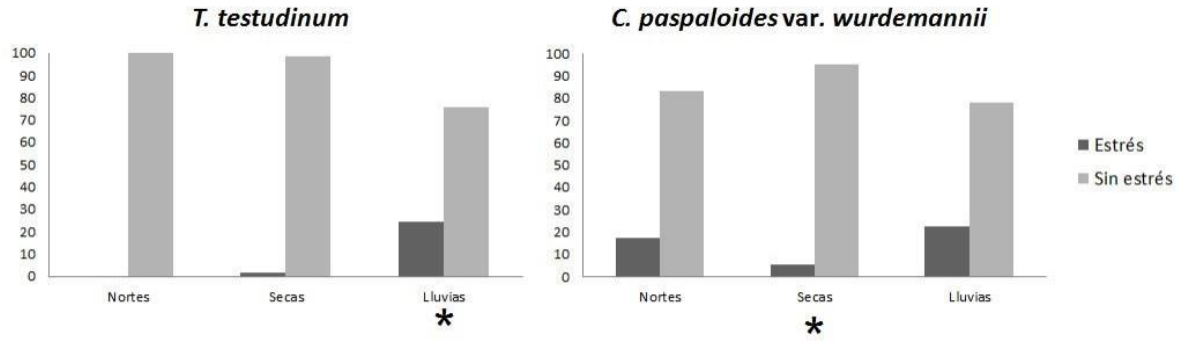


Figura 12-. Frecuencia de eventos de estrés para *T. testudinum* y *C. paspaloides* en las temporadas climáticas. El asterisco marca las temporada con más eventos de estrés en *T. testudinum* y con menor estrés en *C. paspaloides.*

4.7 Análisis de componentes principales y relación de la eficiencia fotosintética con factores fisicoquímicos

El PCA mostró que tres factores abarcaron el 75.90% de la variación en los datos. Las variables más importantes en el factor 1 fueron *Fv/Fm* de *T. testudinum* (-0.746), *Fv/Fm* de *C. paspaloides* (0.876), la profundidad (0.934) y el porcentaje de luz en el fondo (-0.813). El factor 2 fue integrado por el NID (0.858) y la temperatura (0.802) (Fig. 13).

El PCA señala que los mayores registros de *Fv/Fm* de *T. testudinum* estan asociados a mayores registros de luz en el fondo, así como de forma negativa con los altos registros de *Fv/Fm* de *C. paspaloides*. Los factores abióticos (temperatura, profundidad y NID) y está asociado a sitios con mayores registros de *Fv/Fm* de *C. paspaloides* (Fig. 14).

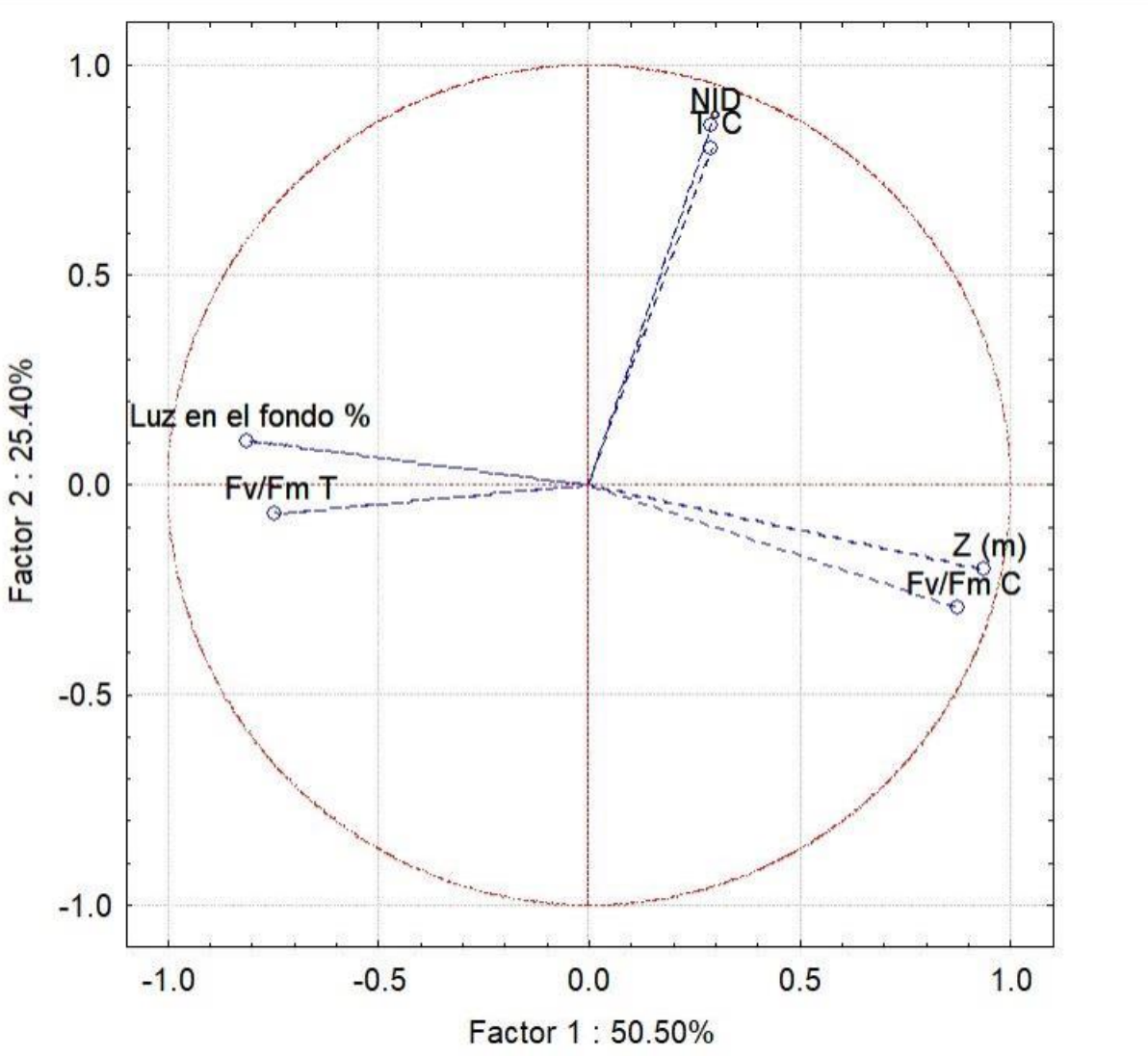


Figura 13-. En el factor 1 y 2, el porcentaje de luz, la eficiencia fotosintética de *T. testudinum*, nitrógeno inorgánico disuelto, temperatura y eficiencia fotosintética de *C. paspaloides*.

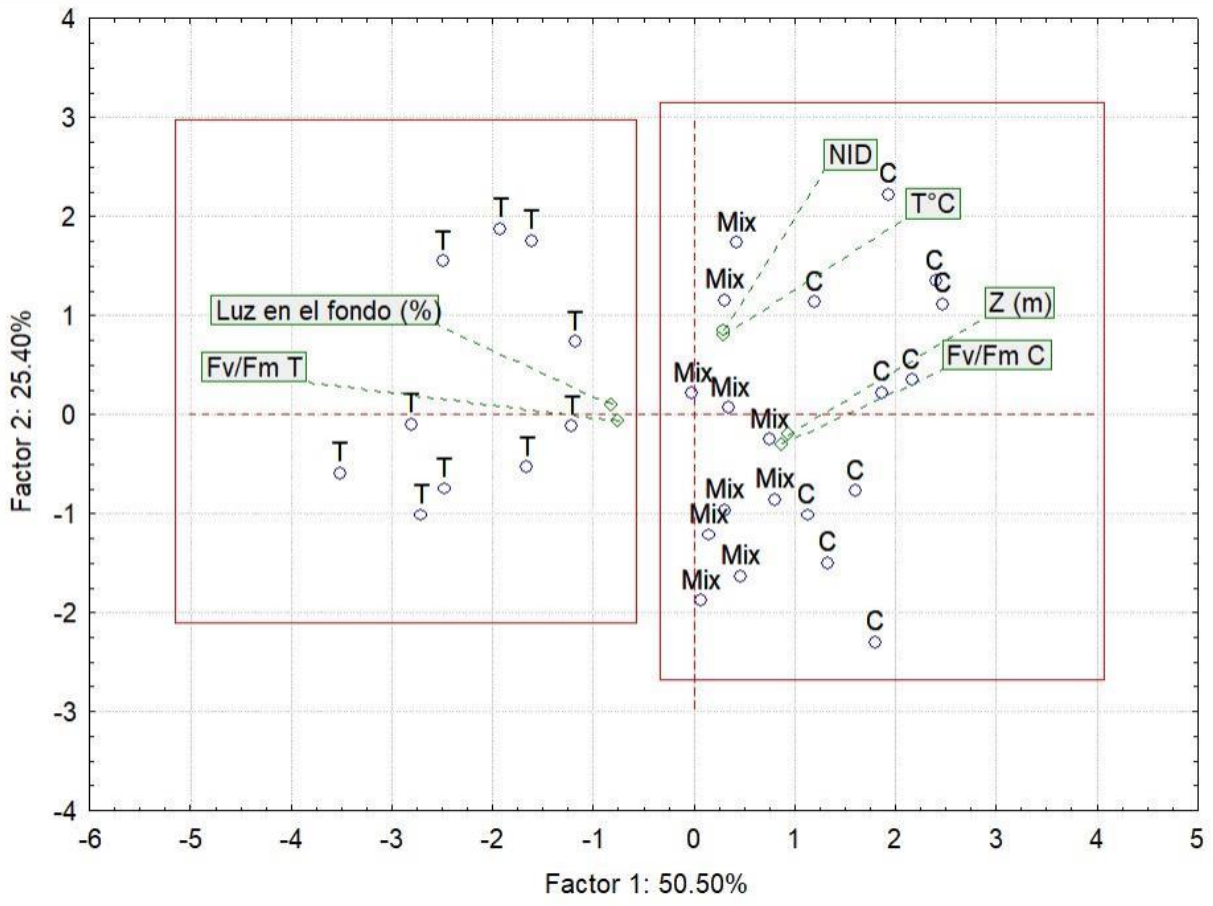


Figura 14-. Análisis de componentes principales que asocia la *eficiencia fotosintética* de *T. testudinum*, señala que los mayores registros de *Fv/Fm* de *T. testudinum* se asocian a los mayores registros de porcentaje de luz en el fondo y las praderas monoespecíficas de *T. testudinum*. Registros altos de *Fv/Fm* de *C. paspaloides* se localizan en praderas monoespecíficas de *C. paspaloides*, así como con las variables fisicoquímicas (profundidad, nitrógeno inorgánico disuelto y temperatura).

4.8 Análisis de componentes principales para *T. testudinum* y *C. paspaloides*

Se encontró que el 72.3% de la variación acumulada se explica por los tres primeros factores. El factor 1 se caracterizó por la profundidad (0.923), el porcentaje de luz en el fondo (-0.773), biomasa de *T. testudinum* (-0.900), *Fv/Fm* de *T. testudinum* (-0.772), biomasa de *C. paspaloides* (0.793) y su respectiva *Fv/Fm* (0.866) El factor 2 se integró por la temperatura (0.780), y NID (0.860), mientras que el factor 3 por el fósforo total intersticial (0.756) (Fig. 16).

El PCA señala que las mayores biomasas de *T. testudinum* están asociadas a la *Fv/Fm* de *T. testudinum* y negativamente con la biomasa de *C. paspaloides*. Altas biomasas de *C. paspaloides* están asociadas a la profundidad altas y hay una asociación entre el NID y el fósforo en agua intersticial y la temperatura (Fig. 15).

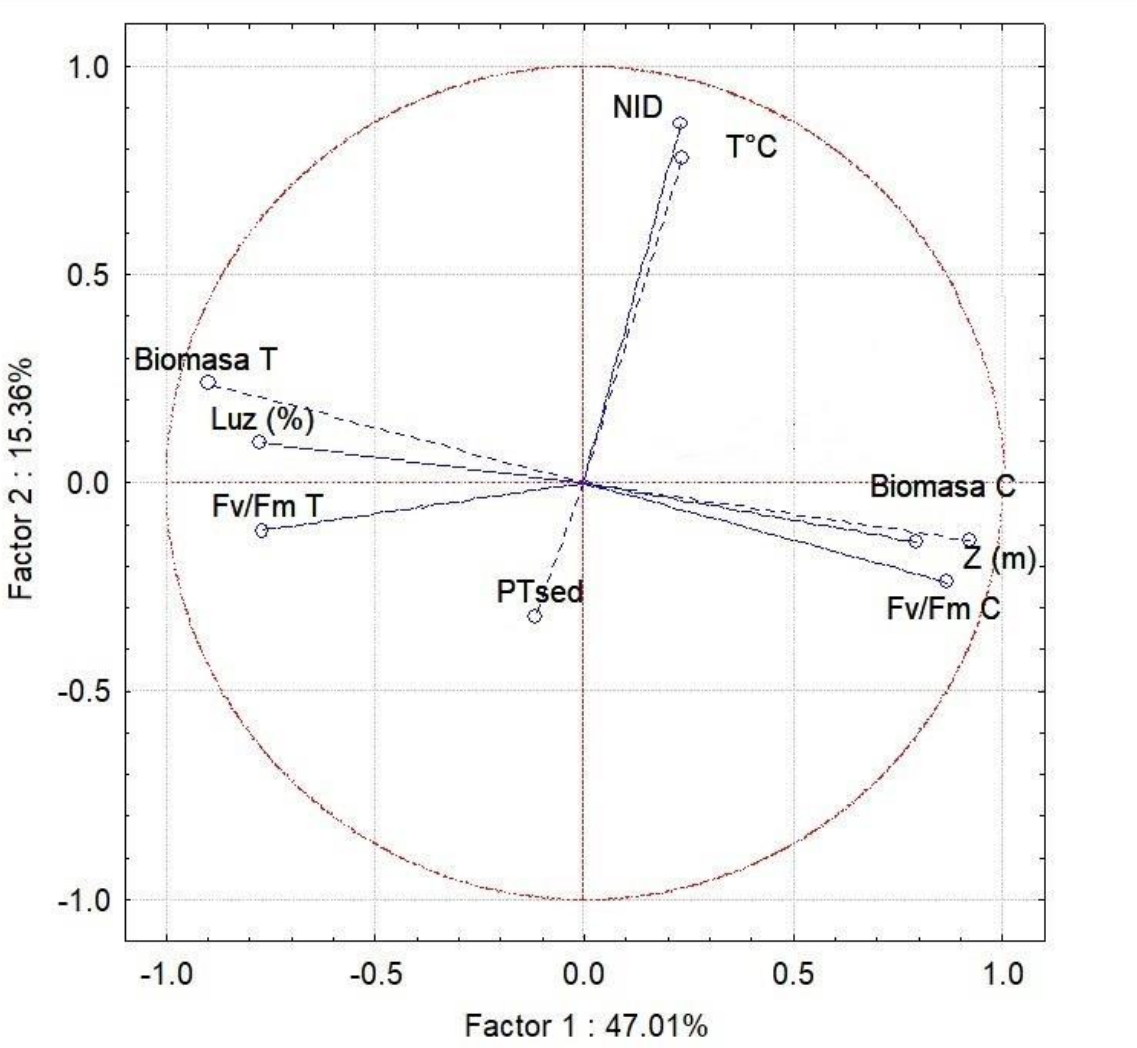


Figura 15-. Las variables importantes en el factor 1 y 2: la biomasa y eficiencia fotosintética de *T. testudinum*, la luz en el fondo, nitrógeno inorgánico disuelto, la temperatura, la profundidad, la biomasa y la eficiencia fotosintética de *C. paspaloides*.

El PCA sugiere dos grupos: el primero está compuesto por los sitios monoespecíficos de *T. testudinum* que tuvieron las mayores biomasas, mayores registros de *Fv/Fm* y menor profundidad y a mayor luz en el fondo. El segundo grupo son los sitios monoespecíficos de *C. paspaloides* y las praderas mixtas que están asociados a las mayores biomasas de *C. paspaloides,* sus respectivas eficiencias fotosintéticas y a

los factores abióticos (mayores profundidades, la temperatura, NID y fosforo intersticial (Fig. 17).

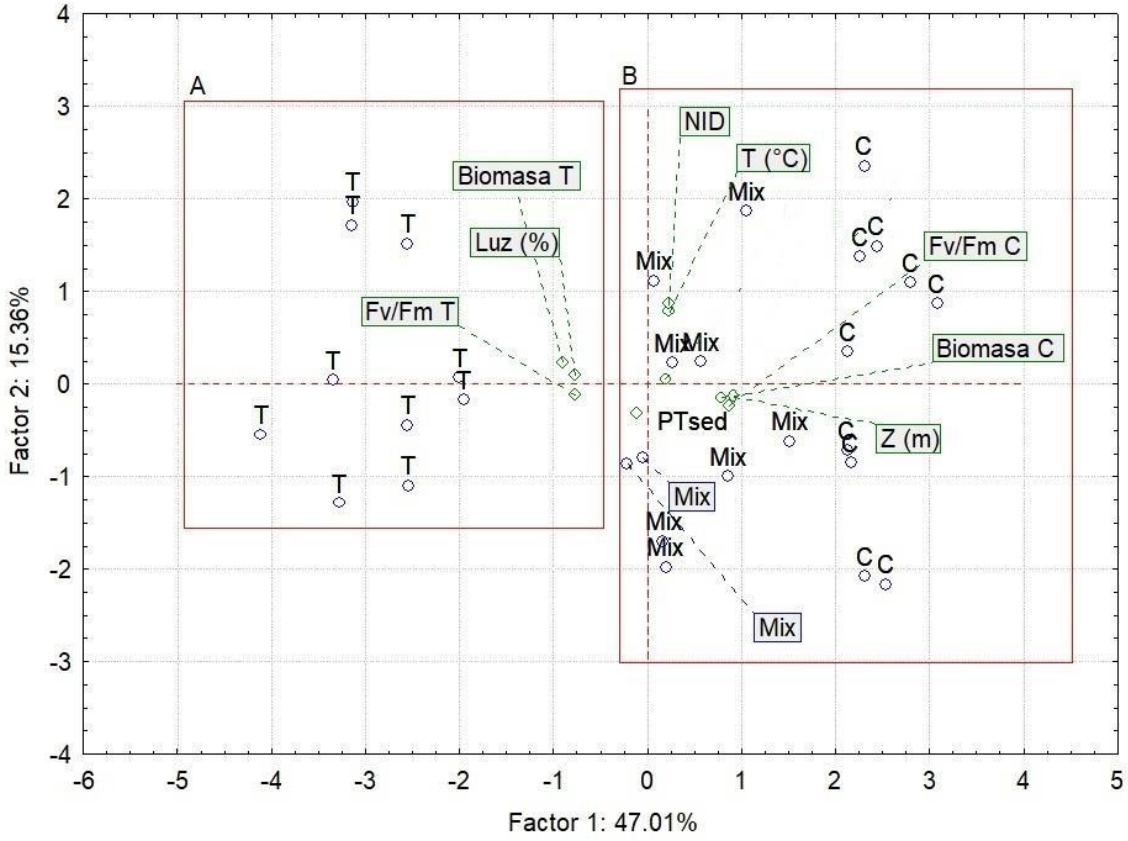


Figura 16-. Análisis de componentes principales que asocia la biomasa de *T. testudinum* con la *Fv/Fm* de *T. testudinum* y la luz en el fondo, señalando que las mayores biomasas se localizan en las praderas monoespecíficas de *T. testudinum*. La biomasa de *C. paspaloides* está relacionada con su eficiencia fotosintética, las mayores biomasas se ubican en las praderas monoespecíficas de *C. paspaloides*. Las variables abióticas como el nitrógeno inorgánico disuelto, la profundidad, nutrientes intersticiales y la temperatura están asociadas a las praderas mixtas.

4.9 Gráficas de comportamiento de las variables más representativas

Las gráficas indican que el comportamiento de las biomasas de las especies *T. testudinum* y en *C. paspaloides* son similares en todo el estudio. Sin embargo, en el mes de noviembre de 2017 y febrero de 2018 se detecta un comportamiento antagónico en ambas especies: un pico de crecimiento en *C. paspaloides* en el mes de junio de 2017 y una reducción en los meses de noviembre de 2017 y febrero de 2018. Las eficiencias fotosintéticas también se encontraron relacionadas con las biomasas (Fig. 17). El comportamiento de la profundidad está más asociado al de *C. paspaloides* y la luz en el fondo al comportamiento de *T. testudinum*. En cuanto a la temperatura se observa aumento en los meses de precipitaciones altas (junio y agosto) (Fig. 18). En junio de 2018 hay un aumento del NID, estos aumentos coinciden con el aumento de biomasa de *C. paspaloides* y en febrero de 2018 hay aumentos de los nutrientes intersticiales, esto coincide con el aumento de biomasa de *T. testudinum* (Fig. 19).

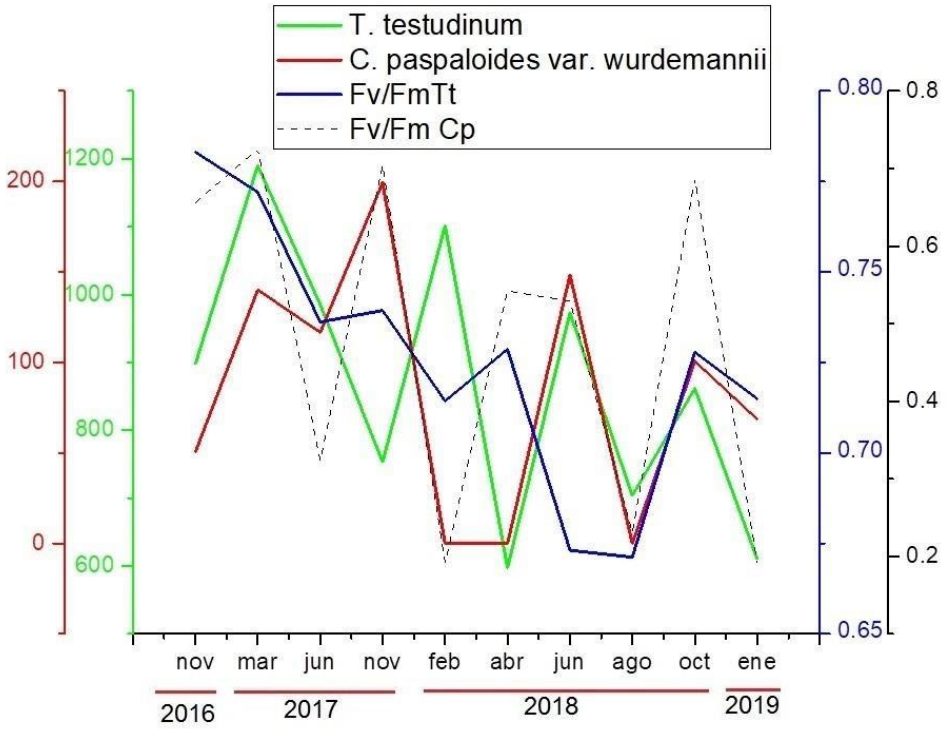


Figura 17-. Gráficas de comportamiento de las biomasas de *T. testudinum* y en *C. paspaloides*, y sus respectivas eficiencias fotosintéticas.

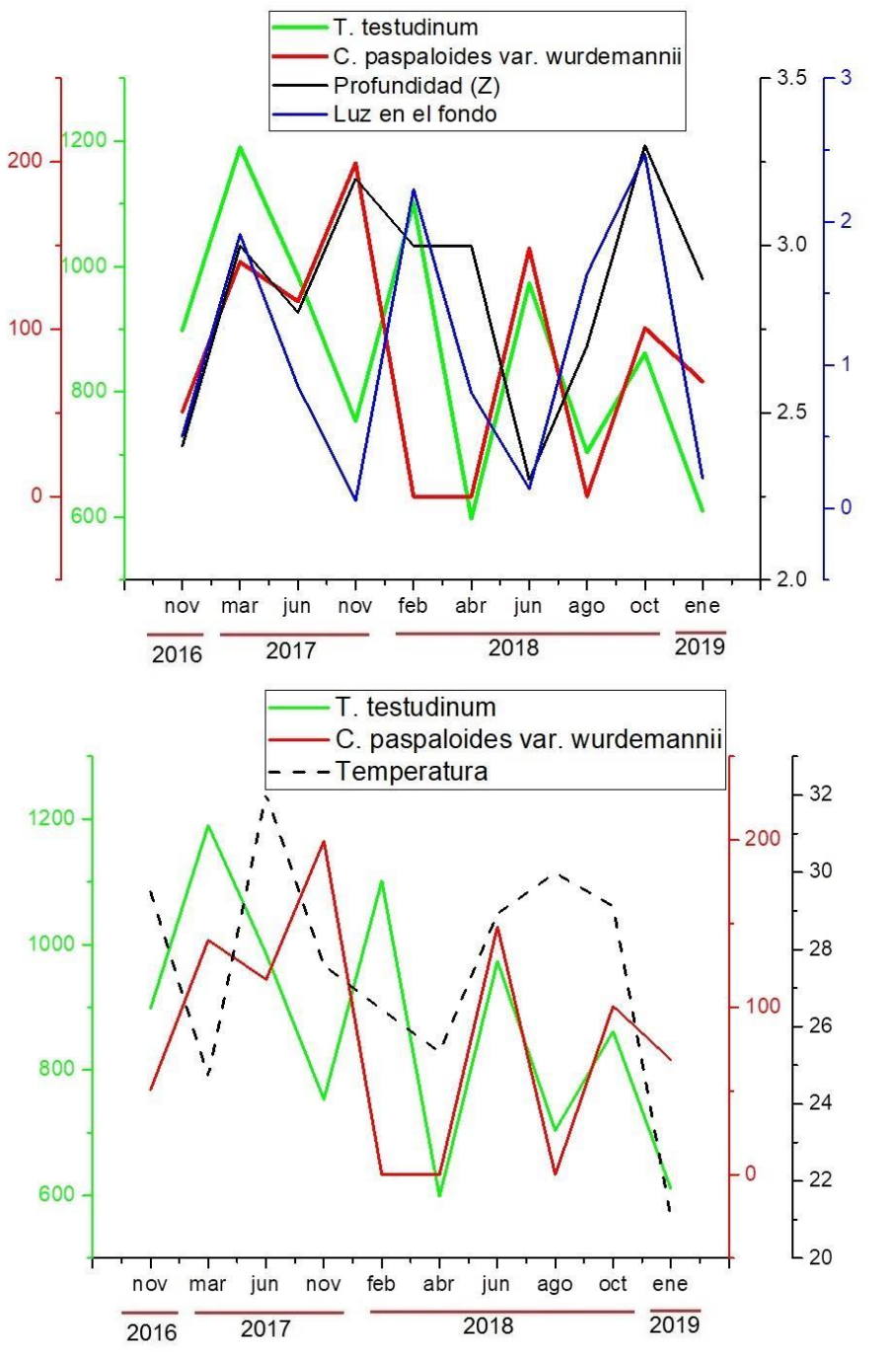


Figura 18-. Gráficas de comportamiento de las biomasas de *T. testudinum* y en *C. paspaloides* asociado a la temperatura, profundidad y luz.

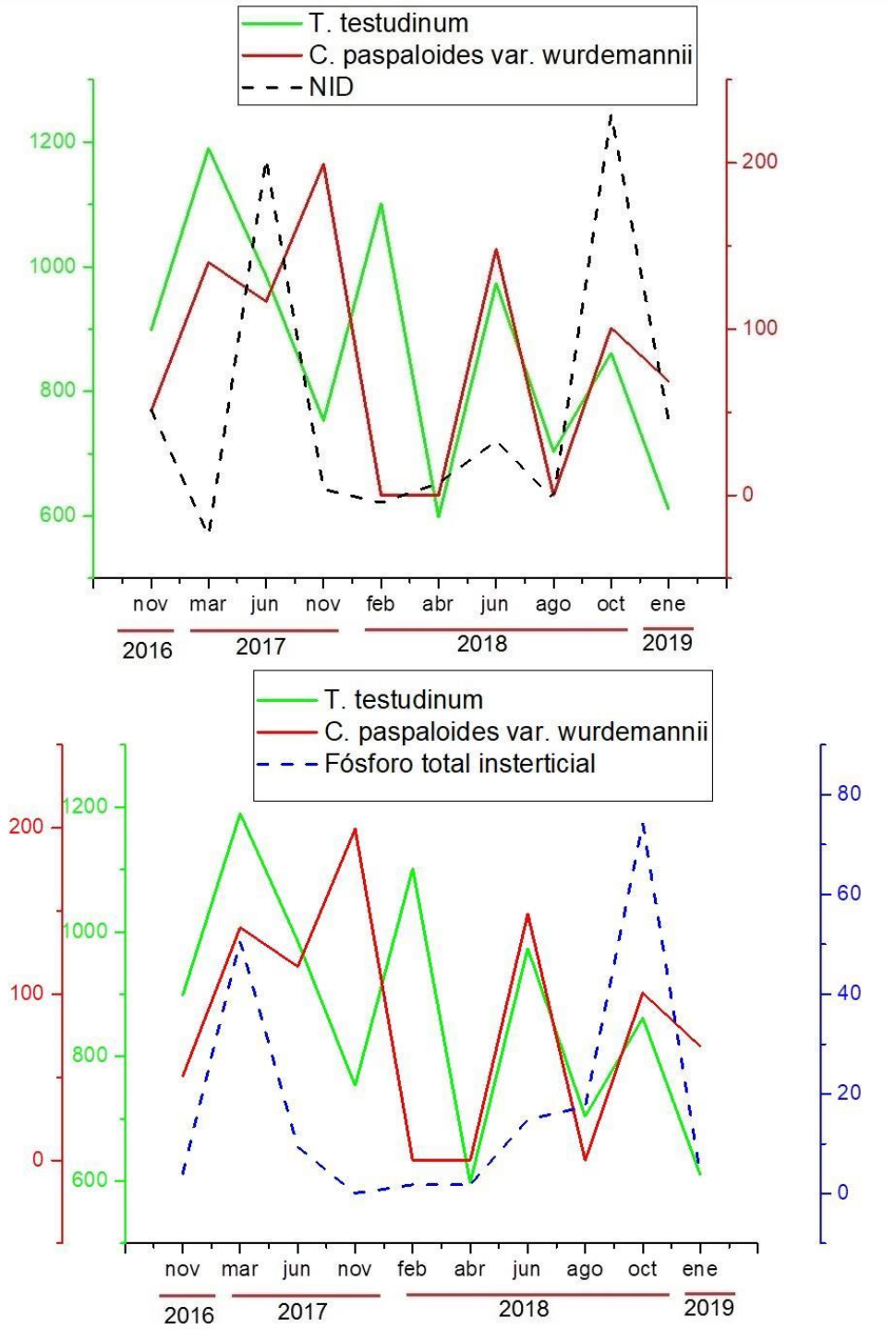


Figura 19-. Gráficas de comportamiento de las biomasas de *T. testudinum* y en *C. paspaloides*, asociado al nitrógeno inorgánico disuelto y a fósforo total intersticial.

5-. DISCUSIÓN

El Sitio 1 presentó profundidades de 1 a 2m. En promedio, el sedimento estuvo compuesto por arenas finas, fue asimétrico hacia grueso y platicúrtico. La única especie presente en el área en todas las fechas fue *T. testudinum* (Fig. 2), por lo tanto, se le pudo considerar una pradera monoespecífica de *T. testudinum*.

El Sitio 2 presentó profundidades de 2.3-3.3m. En promedio, el sedimento fue arena muy gruesa, asimétrico hacia fino y mesocúrtico. La VAS del sitio estuvo compuesta por *T. testudinum*, *C. paspaloides* y otras macroalgas. En la temporada de nortes-17 hubo la presencia de macroalgas y espacios en blanco, fue hasta lluvias-18 donde ya no hay espacios en blanco y aumenta la presencia de *T. testudinum*. Por lo tanto, se pudo considerar una pradera mixta con especies predominantes *T. testudinum* y *C. paspaloides* (Fig. 2).

El sitio 3 presento profundidades de 2.6 a 4m. En promedio, el sedimento fue arena gruesa, simétrico y mesocúrtico. El sitio presentó mayor cobertura de *C. paspaloides*. Desde lluvias-17 presento presencia de otras macroalgas y espacios en blanco y en nortes-18 hubo presencia de *T. testudinum* (5%).

Fuentes et al. (2014) reporto que las praderas mixtas de *T. testudinum* con *C. paspaloides* en las zonas de Rio verde en los Petenes, se encontraron en profundidades menores a 2m y el sedimento tenia de composition 83% de arcillas, 7% de limos y 10% de arena. En toda la zona de Petenes, Pérez et al. (2019) reportaron que las praderas monoespecíficas de *T. testudinum* se encuentran entre profundidades de 0.9 m y 2.13 m y las praderas mixtas con otras macroalgas de 0.9 m y 2.7 m. Estas características son importantes para el establecimiento de la VAS; por ejemplo, en sitios más profundos habrá una dominancia de especies algales (Pacheco et al., 2008) y en sitios menos profundos será de pastos marinos como *T. testudinum* (Van Tussenbroek et al., 2010).

Borum et al. (2005) señala que los pastos marinos a diferencia de las macroalgas, se verán limitadas por la cantidad de oxigeno que hay en el medio. Los pastos marinos obtienen oxigeno de dos formas, de forma activa por medio de la fotosíntesis y de

forma pasiva por medio de sus hojas y los rizomas por el parénquima. Ambientes con baja disponibilidad de Oxigeno dificultara el crecimiento y establecimiento de los pastos marinos a diferencia de las macroalgas. Sin embargo, en los registros de oxígeno disuelto, no hubo diferencias entre sitios. Lo que podría sugerir que en la zona de “Los Petenes” no hay limitación de oxígeno en cualquier profundidad. En ambientes más someros la disponibilidad de luz es mayor y en ambientes profundos será menor. Por lo tanto se puede sugerir que lugares más profundos la presencia de *T. testudinum* es menor que en sitios someros. En el caso de las macroalgas, estas pueden tener menor disponibilidad de luz por tener diversas estrategias fotosintéticas para compensar la menor disponibilidad de luz y habitar en zonas con mayor profundidad.

El tamaño del sedimento está asociado a ciertas características físicas y geoquímicas en el suelo acuático, los sedimentos de grano grueso son el resultado de altas velocidades en la dinámica del agua y alta fuerza del oleaje en el agua (Fonseca, 1996). En las comunidades de pastos marinos el sedimento es más fino que en zonas donde escasea la vegetación (Hemminga et al., 1991), pues los rizomas de los pastos marinos atrapan el sedimento y lo desintegran en pequeñas partículas, y de este modo, las comunidades bacteriológicas podrán establecerse y ayudarán a la asimilación de nutrientes y a la descomposición de la materia orgánica.

A pesar de que en el resto de los parámetros no se encontraron diferencias significativas entre los sitios, cabe destacar que las concentraciones de nutrientes intersticiales en La Reserva de la Biosfera de los Petenes”, son mayores a los registrados en la literatura (Tabla 3). Esto sugiere que hay una mayor disponibilidad de nutrientes en toda la reserva de “Los Petenes” y las diferencias biológicas que existen en los sitios, se deben a las diferentes profundidades y a la composición del sedimento fisicoquímicamente hablando.

Sin embargo, en este estudio se obtuvieron diferencias significativas en el NID y la temperatura; estos parámetros son más altos en la temporada de lluvias. Mijangos (2018) describió que en la zona de “Los Petenes” se encontraron diferencias

fisicoquímicas como baja salinidad y alta temperatura en la temporada de lluvias. Estos cambios tuvieron un efecto en las poblaciones de *T. testudinum* en la zona.

Fuentes (2015) encontró cambios en las poblaciones de *C. paspaloides*: antes de los nortes las poblaciones eran abundantes, pero después de los nortes las poblaciones disminuían. En este estudio la cobertura de *C. paspaloides* en los sitios 2 y 3 se redujo en la temporada de nortes 2017 y 2018, habiendo la presencia de espacios en blanco y macroalgas y en el sitio 3 la incorporación de *T. testudinum* en el medio. Esto sugiere que la estacionalidad tiene un efecto en *C. paspaloides* y no en *T. testudinum*, ya que como se discutió anteriormente la disponibilidad de oxígeno es homogénea en los tres sitios, por lo tanto los tres sitios son aptos para el crecimiento y el establecimiento de *T. testudinum*. Aunque en el sitio 3 estará limitado por la disponibilidad de luz principalmente y la presencia de macroalgas en el medio. En el caso de *C. paspaloides* se puede suponer que los cambios que hay en cobertura de la especie se debe a factores físicos como son la presencia de huracanes en esa temporada que desprenden a la especie mecánicamente.

Los resultados sugieren que hay una homogeneidad ambiental en términos generales. Las diferencias que se presentan en los sitios (profundidad y tamaño de grano) y en la temporalidad (temperatura, sílice, NID y salinidad) son relevantes para la composición de la VAS y la abundancia de especies que habrá en cada área de Petenes y los cambios que se presentan en el tiempo.

Tablas 13. Valores de nutrientes intersticiales en zonas del Golfo de México

Nutrientes en agua Intersticial	Amonio (µM)	Fosforo total (µM)	Referencia
Bahía de Florida	90-400	No registrado	Powell et al. 1989
Parque Nacional Biscayne	45±52	4±1	Szmant y Forrester 1993
Cayos Largos	69±42	3±0.9	Szmant y Forrester 1993
Cayo Largo	72±54	3±1	Szmant y Forrester 1993
Looe	27±23	3±1	Szmant y Forrester 1993
Laguna Río Indio	81	10	Short et al. 1993
Petenes	853.37±569.47	15.88±20.56	Este estudio

T. testudinum se describe como una especie persistente (Kilminster, et al. 2015); es decir, la permanencia será la característica demográfica más importante. En términos generales ambas poblaciones tienen valores altos de crecimiento horizontal, comparándolos con las poblaciones del Caribe (35 cm y 69 cm al año Marba et al. 1998) y los de la reserva de “Los Petenes” (23.35 a 66.84 cm al año, Mijangos 2018); así mismo, ambas praderas tuvieron diferencias mínimas en la tasa de crecimiento (λ) que es mayor a 1, sugiriendo que ambas poblaciones crecen y se establecen óptimamente en la reserva de “Los Petenes”. Aunque se encontraron diferencias morfológicas y de crecimiento, hubo más indicadores reproductivos en praderas

monoespecíficas y crecimiento vertical y de hojas en praderas mixtas. Esto indica que las condiciones bióticas se encuentran correlacionadas con cambios en los atributos demográficos. Bricker (et al., 2018). En el Golfo de México se obtuvo que el crecimiento clonal de *T. testudinum* era más frecuente en praderas con un índice de perturbación alto y la presencia de macroalgas. Esto sugiere que, en praderas mixtas, *T. testudinum* invierte los recursos en la formación de hojas y el crecimiento vertical por la presencia de competidores, y en praderas monoespecíficas invertirá más en el crecimiento horizontal y la formación de estructuras reproductivas.

C. paspaloides registró valores de λ mayores a 2 en ambas praderas, por lo tanto, esto sugiere que las poblaciones duplican su tamaño en la temporada de lluvias a lo largo de la reserva. A pesar de que Kilminster et al. (2015) no clasificaron macroalgas, el haber registrado que en ambas praderas *C. paspaloides* tiene un crecimiento alto y hay temporadas donde se reducen sus poblaciones, ésta se podría definir como una especie colonialista. Biber et al. (2004) describen que las macroalgas tienen un papel principal en las comunidades de pastos marinos, que es estabilizar y dar las condiciones apropiadas para la colonización de especies complejas de pastos marinos como *T. testudinum*, algo similar a las etapas tempranas de una sucesión ecológica,

Sin embargo, en este estudio se registró que después de los nortes (baja precipitación) las poblaciones de *C. paspaloides* redujeron su tamaño en la temporada de nortes. Fuentes et al. (2014) confirmó esto con poblaciones de *C. paspaloides* a más de 15 km de distancia hacia el manglar. Fechas después de los nortes (diciembre y febrero), las poblaciones redujeron sus números drásticamente, a diferencia de las poblaciones que estaban a 6 o 3 km de distancia hacia el manglar. Una de las posibles explicaciones fue el efecto de una dinámica más fuerte de la columna de aguay un efecto amortiguador del manglar. A pesar de las pérdidas durante la época de nortes, en los meses de mayo y junio las poblaciones se recuperaron volviendo a tener los mismos valores de biomasa y de individuos. Por lo tanto, *C. paspaloides*, gracias a su crecimiento rápido es capaz de recuperarse de

eventos de disturbio y mantener poblaciones viables a través de las diferentes temporadas.

En la pradera monoespecífica *C. paspaloides* tiene dos periodos de baja poblacional (nortes-secas y secas-lluvias) y una de crecimiento (lluvias-nortes), en cambio en praderas mixtas hay dos temporadas de crecimiento (secas-lluvias y lluvias y nortes), y una de reducción de la población (nortes-secas). A pesar de que hay aumento de nutrientes en lluvias y que la disponibilidad de nutrientes en ambas praderas es la misma, se podría pensar que en ausencia de competidores *C. paspaloides* tendría más periodos de crecimiento que en la pradera mixta.

La existencia de un competidor tiende a reducir el espacio disponible, así como la disponibilidad de recursos (Van Tussenbroek et al., 2006). El éxito de establecimiento de una especie dependerá de cómo puede conseguir y aprovechar recursos y colonizar lo más rápido posible. *T. testudinum*, al tener un mayor crecimiento clonal en las praderas mixtas, sugiere que en presencia de competidores la especie invertirá los recursos y la energía disponible en el crecimiento y establecimiento, en cambio sin competidores invertirá más en la reproducción sexual y la permanencia. En cambio, la temporada de secas *afecta de manera negativa a C. paspaloides*. Como registra Phillips (2006), la reproducción sexual es rara en las especies de *Caulerpa*, pero cuando hay un evento que reduzca la adecuación de otros competidores como son otras especies de macroalgas, su capacidad de crecer rápido y producir clones aumentará su población al l doble y ocupará el espacio disponible que dejaron estas especies en la temporada de secas. Su presencia es el resultado de esta sucesión, una vez que *T. testudinum* se establece, la diversidad de macroalgas será menor. Pero los lugares con colonización temprana tendrán una mayor diversidad de macroalgas.

En la temporada de lluvias hay aumento de los nutrientes en columna de agua como el NID, esto puede sugerir que aumenta la disponibilidad de éstos y aumenta el tamaño poblacional de *C. paspaloides*. Fuentes et al. (2014) sugieren que la temporada de nortes es un control natural de las poblaciones de *C. paspaloides*, abriendo espacios colonizables para *T. testudinum* u otros competidores. El haber

registrado bajas λ en ciertas temporadas lo confirma y es un comportamiento consistente entre años. Se encuentra que pesar de que en ambas praderas se registran mayores biomasas en lluvias, estos valores bajan en la temporada de nortes y en la temporada de secas. Otro factor que ayuda a *T. testudinum* a su permanencia es la producción de rizoma. En las praderas monoespecíficas de *T. testudinum* se registró mayor producción de rizoma y mayor tamaño. Esto sugiere que estas praderas resisten mejor que las macroalgas, y cuando ocurren los nortes la remoción solo afectará a las macroalgas por su pequeño tamaño en los rizoides. Biber et al. (2004) también describió que el éxito en la permanencia de macroalgas rizofílicas es la producción de sustancias toxicas y dañinas a depredadores formadas por silicatos y carbonatos en la zona. Aunque en este estudio no se analizó la depredación de las especies, se puede argumentar que la aparición y desaparición de *C. paspaloides*, gracias a la temporalidad, afectará la composición y el establecimiento de otros elementos bióticos de las praderas.

Uno de los efectos que tienen especies del género *Caulerpa* en el Mediterráneo es cambiar el pH del sedimento por medio de la incorporación del CO_2, esto permite el surgimiento de una microcomunidad de bacterias que son capaces de alterar el sedimento y las condiciones de colonización que hay en el ambiente (Roth-Schulze et al. 2017). Los registros de biomasa *T. testudinum* sugieren que la presencia de macroalgas es mínima en praderas monoespecíficas de *T. testudinum*, ya que no existirá espacio de colonización para las macroalgas y, por lo tanto, habrá menos competencia para *T. testudinum*. Esto puede sugerir que hay una sucesión ecológica en las praderas, las praderas primarias serán las que tienen praderas monoespecíficas de macroalgas, las intermedias las mixtas y las más complejas las monoespecíficas de *T. testudinum*.

Uno de los factores que afecta la composición y el desarrollo en la VAS es la disponibilidad de luz. Se obtuvo que los sitios tienen diferencias en la profundidad, esto indica que la disponibilidad de luz será diferente entre los tres sitios y, por lo tanto, en la composición de la VAS, esto lo confirman los coeficientes de atenuación de luz, la luz en el fondo (%) y los registros de HOBO. La pradera monoespecífica de

T. testudinum (sitio 1), registraron los valores más altos de luz en el fondo (31.39%-16.9%), en cambio los menores registros en la pradera monospecífica de *C. paspaloides* (Sitio 3, 0.005%-0.10%). Los registros que indican mayor pérdida de luz son el Sitio 3 (lluvias) y el Sitio 2 (nortes).

Ralph et al. (2007) señala que a menor disponibilidad de luz las especies oportunistas como las macroalgas o especies de pastos marinos pequeñas, aparecen en la VAS en lugar de especies longevas y grandes como seria *T. testudinum*, esto y los datos de luz, *Fv/Fm* así como sugiriendo que el sitio 3 tiene las condiciones idóneas de luz para que se establezca *C. paspaloides* y el sitio 1 para que se establezca adecuadamente *T. testudinum*.

Para que los pastos marinos puedan vivir adecuadamente se reportan valores de luz en el fondo de 10% a 25% (Markager y Sand-Jensen, 1992, 1996; Agusti et al., 1994, Carruthers et al., 2001), sin embargo en nuestro estudio reporta un mínimo de 0.005% de luz en el fondo y se registró la presencia de *T. testudinum* en los últimos muestreos en el sitio 3 (Fig. 2). Este dato, que los valores de *Fv/Fm* no cambiaron y que los porcentajes de pigmentos fotosintéticos para *T. testudinum* no cambiaron, sugiere que *T. testudinum* en “Los Petenes” tiene una adaptación a profundidades altas y a menor disponibilidad de luz.

Cayabyab y Enríquez (2007) reportan que el daño fotosintético en las hojas de *T. testudinum* ocurre cuando la eficiencia fotosintética baja a 0.7. En ambas praderas los valores de *Fv/Fm* para *T. testudinum* es menor a estos valores en la temporada de lluvias. Esto junto con los datos de luz se esperaría que en la temporada de lluvias las praderas mixtas tengan condiciones altas de estrés fotosintético. Los pigmentos accesorios son un mecanismo que usan las plantas para resistir factores estresantes como serían el aumento y la diminución de la luz en el medio. No se encontraron diferencias significativas en las especies de *T. testudinum* los porcentajes de pigmentos fotosintéticos para ambas praderas. Esto y el hecho de que el sitio 2 (mixto) se registró valores menores al 10% de luz, valor mínimo para que los pastos marinos se puedan establecer (Carruthers et al., 2001), puede sugerir que los valores mínimos de *Fv/Fm* pueden ser menores a los que plantea la literatura

y *T. testudinum* en “Los Petenes” tendrá una resistencia mayor que las especies que habitan en el Caribe u otras áreas. Los datos de máximos y mínimos señalan que el mínimo valor de eficiencia fotosintética fue de 0.63 (Fig. 10 A), por lo tanto, los resultados sugieren que en “Los Petenes” el estrés fotosintético de *T. testudinum* se presentó en valores menores al 0.63. Los bajos valores de *Fv/Fm* en lluvias, podrían sugerir que hay factores que afectan la salud de *T. testudinum* ya que éstos ocuparán un mayor espacio en las hojas y disminuirá la capacidad del fotosistema II en las hojas de *T. testudinum* lo que trae como consecuencia la necrosis de hojas. Aunque, gracias a la estrategia de *self-shading* y a la disminución de la temperatura, los nutrientes en la columna de agua y la luz en la temporada de nortes, permitirán la recuperación fisiológica de *T. testudinum*. A pesar de que *T. testudinum* tiene la capacidad de protegerse eficientemente, existen ciertos factores que provocan estrés; como, por ejemplo, la presencia de organismos fitoplanctónicos y epífitos en las hojas. Fong y Harwell (1994) establecieron que el aumento de la biomasa de organismos epífitos, está asociado con el aumento en la luz, en la temperatura y en la concentración de nutrientes en la columna de agua. Se ha demostrado que en la temporada de lluvias hay un aumento de estos parámetros. A pesar que este estudio no tomo encuentra estos factores, se puede sugerir que esto también ocurría en los sitios de estudio.

Para las macroalgas los valores menores a 0.5 son señal que hay estrés fotosintético (Biber et al., 2004). En este estudio, *C. paspaloides* presentó valores de *Fv/Fm* menores a ese dato en el sitio 2 en lluvias. *C. paspaloides* presentó más estrés fotosintético en las praderas mixtas que en las monoespecíficas.

Las frondas de *C. paspaloides* en praderas mixtas no presenta la zeaxantina en secas y presenta un valor de 0.6 en la misma, pero se encontró que hubo una reducción de eficiencia fotosintética en la temporada de lluvias (0.36). Esto puede sugerir que el daño fotosintético se produjo en la temporada de secas y la consecuencia se reflejó en la temporada de lluvias. Una de las causas de estrés fotosintético es el exceso de luz, ya que las macroalgas se registra que pueden estar en condiciones de luz entre 0-1% (Markager y Sand-Jensen, 1992), en el estudio

está claro que el sitio 3 (monoespecífico de *C. paspaloides*) presenta esos valores de luz. Sin embargo, el sitio 2 presenta valores más altos, por lo cual se puede sugerir que el aumento de luz que se da en la temporada de secas provoca daño fotosintético y reduce el desempeño de las poblaciones de *C. paspaloides*. Gómez et al. (2004) y Guo et al. (2015) reportan que varias macroalgas clorófitas llegan a presentar fotoinhibición a valores menores al 0.5, lo que confirma esta idea de que las macroalgas en general de “Los Petenes” pueden soportar profundidades altas y bajas cantidades de luz.

En la temporada de secas hay presencia de zeaxantina en el sitio monoespecifico de *C. paspaloides* y en el sitio mixto no. La zeaxantina es un pigmento que se encarga bajo condiciones de luz excesiva, se encarga de depoxidar la violaxantina a través de la monoepoxidación de la anteraxantina a través de la activación de la violaxantina de-epoxidasa que es una enzima en los tilacoides. (Lambers, 2008). Esto puede sugerir que la competencia tendrá un efecto en el desempeño fotosintético de *C. paspaloides*, no solo afectará la *Fv/Fm* en la temporada de lluvias, sino que el ciclo de las xantofilas se afectará en la temporada de secas, donde hay mayor irradiación solar, ya que no hay suficiente zeaxantina, a pesar que los pigmentos se estabilizan en la temporada de lluvias. En cambio *T. testudinum* no será afectado fotosintéticamente hablando.

Se ha estudiado que, a pesar de que las macroalgas son especies de crecimiento rápido, su ciclo de vida es corto y sus poblaciones pueden cambiar con facilidad. Con condiciones apropiadas crecen y colonizan de manera rápida. Como estas características son similares a los organismos fitoplanctónicos y a los epífitos, se puede sugerir que compiten por los mismos recursos. Esto sugiere que *C. paspaloides* será afectada por la competencia con estos organismos.

El PCA sugiere que el NID y la temperatura están relacionados con la eficiencia fotosintética de ambas especies, además de que están ambas variables relacionadas. Sin embargo, esto solo puede sugerir que estos parámetros están asociados a la temporalidad más que a la eficiencia fotosintética.

Las características abióticas en las tres praderas son diferentes (profundidad, luz disponible en el fondo y características del sedimento), por lo tanto las características bióticas (composición de la VAS, características fisiológicas y poblacionales) son diferentes (Tabla 13).

Los factores fisicoquímicos que reducen el crecimiento y establecimiento de los pastos marinos son la reducción de la disponibilidad de luz, el aumento de los nutrientes en columna de agua (que como consecuencia tiene el aumento de fitoplancton y macroalgas) y los aumentos en la temperatura del agua (Duarko y Moffler, 1987 y Powell et al., 1989).

Tabla 14-. Características bióticas y abióticas de los tres sitios

Características	Sitio 1 (Monoespecífico de *T. Testudinum*)	Sitio 2 (*Mixto*)	Sitio 3 (Monoespecífico de *C. paspaloides*)
Profundidad	1.2m a 2m	2.3m a 3.2m	2.6m a 4.0m
Sedimento	Arenas finas	Arenas gruesas	Arenas medias
Floración de *T. testudinum*	59%	11%	-
Número de individuos de *T. testudinum*	156	89	-
Biomasa Subterránea	59%	44%	-
Biomasa Aérea	41%	56%	-
Crecimiento vertical	4.26±0.02	5.02±0.02	-
Crecimiento horizontal	8.74±0.06	8.43±0.06	-
λ de *T. testudinum*	1.15	1.12	-
Medidas de *C. paspaloides* (estolones, frondas, diámetro de estolon y biomasa)	-	Menores	Mayores
λ de *C. paspaloides*	-	1.29	1.44
Eventos de λ menores a 1		1	2
Crecimiento de hojas de *T. tesudinum*	0.23cm/día	19cm/día	-
Crecimiento de frondas de *C. paspaloides*	-	0.19	0.25
Fv/Fm *T. testudinum*	0.72	0.73	
Fv/Fm *C. paspaloides*		0.55	0.61
Luz en el fondo	de 14.74% a 29.87	de 2.32 a 18.05	de 1.29 a 7.39
Atenuación de luz	de -0.604 a -0.957	de -0.532 a -1.175	de -0.651 a -1.087
Pigmentos de Xantofilas y Clorofila en *T. testudinum*	Igual	Igual	-
Pigmentos de Xantofilas en *C. paspaloides*	-	Aumento de Violaxantina en Nortes	Aumento de Zeaxantina en Secas
Pigmentos de Clorofila en *C. paspaloides*	-	Aumento de Clorofila B en Lluvias	Aumento de Clorofila B en Secas

La luz es uno de los factores que limita el crecimiento, composición y establecimiento de la VAS, a pesar de que los pastos marinos y las macroalgas son organismos fotosintéticos, tienen características diferentes para ocupar nichos diferentes en el agua. Pérez et al. (2019) a pesar de que registró gradientes de VAS a diferentes profundidades en la Reserva de “Los Petenes”, registró comunidades de macroalgas en bajas profundidades (0-3m)

Considerando que la disponibilidad de luz en el fondo del sitio 1 es la más alta (29.87% - 14.74%), la actividad fotosintética y la productividad primaria es mayor. A pesar de que si hay mayor biomasa en el sitio 1 y el sitio 2 tiene menor disponibilidad de luz en el fondo (18.05% - 2.32%), no se encontraron diferencias significativas en las *Fv/Fm T. testudinum* para ambos sitios. Desde la temporada de nortes del 2018, se registró la presencia de *T. testudinum* en el sitio 3 (monoespecifico *C. paspaloides*). A pesar que la literatura sugiere que los pastos requieren un mínimo de 10% de luz en el fondo (Carruthers et al., 2001), los datos obtenidos pueden sugerir que *T. testudinum* se puede adaptar a condiciones bajas de luz, aunque puede ser que estos eventos de poca luz no sean frecuentes en el medio en especial al medio día donde la irradiación de luz sea alta.

Como se ha discutido anteriormente *T. testudinum* es una especie permanente, teniendo como características principales la supervivencia en el tiempo y la resistencia fisiológica (Kilminster, et al. 2015). El estudio demostró que *T. testudinum* en ambos sitios tienen la misma adecuación, aunque hay ciertas características demográficas que son diferentes, en el sitio 1 (monoespecífico de *T. testudinum*), el crecimiento de rizomas (biomasa subterránea) y porcentaje floral es mayor y en el sitio 2 (Mixto) el crecimiento de hojas y los haces son mayores. Este hecho y el no haber encontrado diferencias significativas en los pigmentos fotosintéticos de *T. testudinum*, sugiere que la actividad fotosintética de esta especie es la misma en ambas praderas. Sin embargo, en el sitio 1 los recursos se utilizara para la reproducción sexual (producción de flores) y el crecimiento horizontal (rizomas) y en el sitio 2 se invertirá más en la formación de hojas y el crecimiento vertical (haces). Esta característica de crecimiento vertical es importante para *T. testudinum* ya que

convive con especies de crecimiento alto (macroalgas y *C. paspaloides*) y será una característica que le dará ventaja en el sitio 2.

Los factores bióticos juegan un papel importante en la composición y el tamaño del sedimento. En el sitio 1 ya que hay mayor crecimiento de rizomas, el sedimento está compuesto por arenas finas principalmente y por lo tanto será de menor tamaño. En cambio en el sitio 2, *T. testudinum* presenta menor producción de rizoma y hay mayor producción de haces verticales y hojas, sugiriendo que los sedimentos serán de mayor tamaño ya que la desintegración de parte del rizoma será menor como es el caso de las macroalgas y las macroalgas por su sistema de rizoides.

Las macroalgas al ser organismos más primitivos pueden colonizar varios gradientes de profundidad donde la disponibilidad de luz es diferente e incluso menor (Markager y Sand-Jensen, 1992, 1996). A pesar de que puedan colonizar los 3 sitios, al no haber espacio disponible para su colonización no se podrán establecer en los sitios como es en el sitio 1, ya que *T. testudinum* acapara con su sistema de rizomas, por lo del espacio disponible y las estrategias que usen para colonizarlo será importante, zonas poco profundas que permitan una gran cantidad de luz podrían ser viables para *C. paspaloides* siempre y cuando exista espacio disponible.

Fong y Harwell (1994) han estudiado que la disponibilidad, así como la ausencia de nutrientes en la VAS tienen un efecto en la aparición y desaparición de las plantas. También describieron que las macroalgas, epifitas y fitoplancton asimilan los nutrientes en columna de agua; en cambio, los pastos marinos en praderas de *T. testudinum* en el Golfo de México usan también los nutrientes intersticiales. Davis y Fourqueran (2001) describieron que los pastos marinos obtienen el nitrógeno a partir del amonio (NH_4) de forma subterránea, pero en algunos casos las hojas pueden asimilar las formas nitrogenadas (NO_3 y NO_2) en la columna de agua y el fósforo en forma subterránea (Davis y Fourqueran, 2001). Archer et al. (2018) observaron que el crecimiento de *T. testudinum* no cambia a pesar de haber presencia de un competidor (*Halichondria melanadocia*). Aunque, al aumentar los nitratos en el sitio donde había un competidor, se redujo la biomasa y la tasa de crecimiento de *T. testudinum*, sugiriendo que la interacción cambiaba de un comensalismo a un

amensalismo o, incluso, a un parasitismo si la dinámica de los nutrientes se alteraba. Además, el aumento de macroalgas en las praderas está asociado al aumento del NID en la columna de agua (Davis y Fourqueran, 2001). Cole et al. (2017) encontraron que el fósforo tiende a ser tóxico para los pastos marinos y su aumento puede incrementar el crecimiento explosivo de las macroalgas, confirmando el papel que tienen éstas como modificadoras del medio.

No haber encontrado diferencias significativas en los sitios y los registros de nutrientes (columna de agua e intersticiales) que superan a los reportados en la literatura para *T. testudinum* y macroalgas (Tabla 4) (Fong y Harwell, 1994), (Davis y Fourqueran, 2001), (Biber et al., 2004) y (Hoffman et al., 2019), puede sugerir que, en general, las especies no están sujetas a limitaciones en los nutrientes y tienen las mismas condiciones abióticas para desarrollarse.

Los resultados de λ de ambas especies, la fotosíntesis de *T. testudinum* y el no haber encontrado diferencias significativas en los nutrientes, fitoplancton y temperatura en los tres sitios, sugiere que los sitios tienen las mismas condiciones de salud y hay baja perturbación en las praderas de pastos marinos. Puesto que la zona de “Los Petenes” es un área natural protegida, se puede hacer la suposición de que las perturbaciones son bajas. Lo que confirmaría que las condiciones abióticas no tienen un efecto en la presencia y ausencia de estas dos especies en “Los Petenes”.

En la Reserva de la Biosfera de los Petenes se han reportado cambios en la composición de la VAS (CONANP, 2023) durante sus tres temporadas climáticas . Fuentes et al. (2014) registraron que la cobertura y las biomasas de *C. paspaloides* cambian después de la temporada de nortes, sugiriendo que hay una reducción de sus poblaciones. Las tasas de crecimiento (λ) de *C. paspaloides* durante las temporadas confirman esto, así como la aparición de otros elementos (Cuales?) en las praderas monoespecíficas de esta especie.

Los registros de la temperatura y el NID de columna de agua fueron mayores en la temporada de lluvias en los tres sitios de manera consistente. Una de las características que tiene la temporada de lluvias es el aumento del aporte de agua de

origen epicontinental ya que esta bordeado por manglares. Se puede sugerir que el agua que se incorpora aporta nutrientes en su mayoría NID. El PCA sugiere que hay una fuerte asociación con los nutrientes, el sitio mixto y la temporalidad, lo que sugiere que la temporada de lluvias tiene un efecto sobre los nutrientes que, a su vez, tiene efectos en la VAS de estos sitios con un aumento importante de producción primaria.

El PCA también sugiere que hay una fuerte asociación con el amonio intersticial, aunque dependiente del sitio y no del tiempo. El amonio intersticial es el que se produce por la descomposición de la materia orgánica por las bacterias del sedimento. El hecho de que hay una diversidad de macroalgas mayor sugiere que hay procesos para que este nutriente esté disponible en el medio y pueda persistir *T. testudinum* en la zona. Según la literatura, los nutrientes intersticiales son importantes para el establecimiento y crecimiento de *T. testudinum*, y claramente se correlaciona con nuestros resultados.

5.1 Posibles escenarios para *T. testudinum* y *C. paspaloides*

Las gráficas señalan que los aumentos de biomasa de *T. testudinum* y los nutrientes intersticiales coinciden. Esto puede sugerir que el aumento que hubo en ambas praderas (λ poblacional), crecimiento de hojas, haces verticales y número de haces verticales, así como flores pudo deberse a que aumentaron los nutrientes intersticiales en el año.

También se observa que hay aumentos de biomasa de *C. paspaloides* cuando hay aumentos en la temperatura y los nutrientes de columna de agua. Esto junto con los datos del PCA, λ y eficiencia fotosintética de *C. paspaloides* sugiere que la temporalidad afectara el crecimiento de la especie, así como la ausencia de los nutrientes en columna de agua que se da cuando bajan las precipitaciones en el año.

Se ha registrado que en el año 2016 hubo un fenómeno de Mega Niño (altas temperaturas en el agua). Este fenómeno persiste en las zonas tropicales por más tiempo y a finales de 2017 empezó el fenómeno de la Niña (bajas temperaturas en agua) (Pinheiro et al. 2020). Al principio del estudio se registró un crecimiento

explosivo de las poblaciones de *C. paspaloides* y en principios del año 2018 la población desapareció en poblaciones mixtas y en las monoespecíficas se redujo su cobertura al 50%. Esto puede sugerir que cuando hay fenómenos que aumentan la temperatura del agua éstos permiten altas tasas de crecimiento en *C. paspaloides*, con efectos negativos por las altas temperaturas. En el caso de *T. testudinum* se ha registrado que es una especie fisiológicamente tolerante, por lo tanto, las condiciones ambientales que se presentan en el año no producen un estrés fotosintético foliar. Sin embargo, el que no haya una alta mortalidad en macroalgas, puede sugerir que se disminuirá la disponibilidad de espacio colonizable, así como de los nutrientes en columna de agua. A pesar de que las macroalgas usan más los nutrientes de columna de agua que los intersticiales, se ha estudiado que el amonio es el producto de la descomposición de la materia orgánica en el sedimento por las bacterias y otros organismos microscópicos. Encontrar amonio intersticial está asociado a los muestreos de bajas precipitaciones (nortes y secas) con una disminución en las poblaciones de *C. paspaloides*. Esto puede sugerir que la mortalidad de macroalgas y otros productores primarios tendrá un efecto en el aumento de los nutrientes intersticiales y dará las condiciones apropiadas para el crecimiento y expansión de *T. testudinum*. Esto puede sugerir que el fenómeno de la Niña, a pesar de tener disminuciones en la temperatura, va a tener como consecuencia la alta mortalidad de macroalgas y otros productores primarios, produciendo materia orgánica procesada por organismos microscópicos, convirtiéndola en nutrientes intersticiales que permitirán el crecimiento y la expansión de los pastos marinos. No haber encontrado diferencias significativas en la materia orgánica en los sitios y en las temporadas, sugiere que la descomposición es constante y depende de eventos de mayor periodo de tiempo y a escalas geográficas más grandes como con los fenómenos de El Niño y La Niña. Para confirmar esta idea serían necesarios estudios dirigidos de bacterias y organismos descomponedores en las praderas de pastos marinos, así como de su asimilación de la materia orgánica.

Hay factores biológicos que no se consideraron en este estudio como la presencia y ausencia de epifitas en las frondas de *C. paspaloides* y hojas de *T. testudinum*. Fong y Harwell (1994) describen a las epifitas como un elemento que afecta a *T.*

testudinum, ya que su aumento en las hojas disminuirá su actividad fotosintética de y habrá un desgaste energético en la especie. Aunque, por la estrategia de auto sombreado (*self-shading*) que ya se abordó anteriormente, *T. testudinum* desecha las hojas viejas y protege a las hojas nuevas para aumentar la supervivencia y generar aportes de nutrientes intersticiales. Biber et al. (2004) también argumentó que las epifitas en las frondas de macroalgas rizofílicas afecta el desempeño de la especie, esto podría explicar las altas mortalidades que se dan desde la temporada de nortes en *C. paspaloides*. Aunque se puede hipotetizar que no afectaría la adecuación de la especie, ya que en la temporada de precipitaciones altas se recuperan y crecen al doble de su tamaño poblacional.

También no se consideró los herbívoros respectivos que hay para las dos especies, su efecto en las poblaciones y eficiencia fotosintética. En el caso de *T. testudinum* se ha documentado que las tortugas marinas (*Chelonia mydas*) son su principal herbívoro, aunque también se ha reportado que los erizos de mar como *Tripneustes ventricosus* y *Lytechinus variegatus* y ciertas especies de peces como *Sparisoma radians* (Zieman et al., 1984). A pesar que se ha reportado que las tortugas y los peces no tienen un efecto negativo en los pastos marinos, si llegan a aumentar los números de tortugas residentes en el medio, este reducirá la cobertura de la VAS significativamente, aunque si existe una alta diversidad en las especies que conforman la VAS *T. testudinum* no se verá afectadas por la herbívora (Roth, 2023).

Otra aspecto ambiental que no se tomó en cuenta es el sulfuro en agua, ya que se ha reportado en el Mediterráneo (Najdek-Dragić et al., 2020) y en el Golfo de México (Borum et al., 2005) que el sulfuro en praderas sanas y altamente productivas fue menor que en praderas con poca vegetación o con la presencia de *Caulerpa*, el sulfuro en el medio acuático hasta valores mayores de 10µM haciendo que sea mortal para las especies de pastos marinos. Se sugiere que en futuras investigaciones se incorpore el análisis de sulfuro en “Los Petenes”.

6-. CONCLUSIÓN

Existe una competencia entre *T. testudinum y C. paspaloides* por el espacio y la luz principalmente.

T. testudinum podrá establecerse en lugares con y sin competidores, siempre y cuando estén disponibles los nutrientes intersticiales en el sistema. En praderas monoespecíficas las estrategias de vida óptimas son el crecimiento de rizoma y la reproducción sexual. En cambio, en praderas mixtas lo óptimo es el crecimiento clonal por crecimiento de haces verticales y la formación acelerada de hojas. Por lo tanto, *T. testudinum* en todo "Los Petenes" podrá incrementar su cobertura y abundancia, gracias a sus diferentes estrategias demográficas, como poder asignar recursos necesarios a sus diferentes rasgos en su ciclo de vida.

C. paspaloides dependerá de la temporalidad de la zona; en la temporada de bajas precipitaciones y nortes la supervivencia de individuos será importante para el establecimiento de la especie. En cambio, en altas precipitaciones será más frecuente el crecimiento rápido, a causa del aumento de la temperatura y NID en el medio.

La composición de la VAS de macroalgas es fluctuante en el tiempo y dependiente de factores ambientales con ciclos de crecimiento positivo mezclado con ciclos de crecimiento negativo. Las especies más perenes de la VAS utilizan una estrategia demográfica ante los factores de presión ambientales de tal manera que asignan diferencialmente recursos a rasgos del ciclo de vida diferentes.

Este estudio recomienda lo siguiente:

- Estudiar y aplicar estas herramientas a otros elementos de la VAS que interaccionan con *T. testudinum* y *C. paspaloides*, como son *Syringodium filiforme*, *Halodulle wrightii* y *Penicillus dumetosus*.
- Hacer experimento in-situ en ambas especies para determinar, teniendo de partida los elementos que fueron relevantes en este estudio para manipular y

conocer en específico los factores que influencias en su crecimiento y desarrollo.

- Hacer en el mismo experimento in-situ, experimentos de presencia y ausencia de las dos especies para confirmar las hipótesis generadas en este estudio.
- Analizar otros elementos que no se midieron como son la diversidad bacteriana de los sedimentos y su rol en las VAS como serán los aportes importantes a la producción y a la fijación de nutrientes.
- Analizar la comunidad de epifitas para cada especie que se estudió en este estudio y su posible impacto en la fotosíntesis.
- Analizar los organismos bentónicos que hay en las praderas y si son iguales o diferentes dependiendo de la pradera en la que estén, así como su abundancia y diversidad.

7-. ANEXO

Thalassia: es un género de plantas acuáticas de la familia Hydrocharitaceae. Son plantas perennes, enraizadas sumergidas, dioicas. Tallos rizomatosos, escariosos, con 1 raíz en cada nudo. Flores unisexuales. Espata de las flores estaminadas difila, lisa, pedunculada, con 1 flor pedicelada; brácteas connatas basalmente; tépalos 3, reflexos; estambres 8-13, sésiles o subsésiles; las anteras 4-loculares. Espata de las flores pistiladas difila, lisa, persistente, pedunculada, con 1 flor cortamente pedicelada, con el hipanto alargado; brácteas connatas basalmente; tépalos 3, reflexos; ovario 1-locular con varios lobos placentarios dirigidos hacia el centro; estilos 6-8; estigmas 12-16, papilosos. Fruto globoso, equinado, de dehiscencia irregular; semillas coniformes, con la parte basal engrosada, la testa glabra (Van Tussenbroek et al., 2010).

Comprende 7 especies descritas y de estas, solo 2 aceptadas:

Thalassia hemprichii (Ehrenb. ex Solms) Asch., Petermanns Geogr. Mitt. 17: 242 (1871).

Thalassia testudinum Banks & Sol. ex K.D.Koenig, Ann. Bot. (König & Sims) 2: 96 (1805).

Las dos especies pertenecientes al género *Thalassia* (Familia: Hydrocharitaceae), *T. testudinum* Banks ex König y *T. hemprichii (*Ehrenberg) Ascherson están ampliamente distribuidas en zonas costeras poco profundas de los trópicos y subtrópicos del Atlántico occidental (*T. testudinum*) y del Indo-Pacífico *(T. hemprichii)*. (Phillips y Meñez, 1988; Spalding et al., 2003), y se las considera 'especies gemelas'. Teniendo en cuenta los tipos de hábitat donde se encuentran las dos especies de *Thalassia*, sus lechos podrían extenderse potencialmente sobre áreas enormes (cientos de miles de kilómetros cuadrados).

Caulerpa: El género está ubicado en el Reino *Plantae, Phylum Chlorophyta,* Clase *Bryopsidophyceae,* Orden *Bryopsidales y* Familia *Caulerpaceae.*

Según Jacobs (1994) este género tiene la peculiaridad tener un nivel de organización cenocítico, donde hay una rápida división nuclear con respecto de la división celular dando lugar a células multinucleadas. Para identificarlas se divide en tres partes principalmente:

Partes principales de un alga del género Caulerpa. Está compuesto por la fronda, el estolón y el rizoide.

Las especies de Caulerpa presentan reproducción sexual y fragmentación de cualquier parte (Phillips, 2009). La sexual se da por la unión de dos gametos de diferente sexualidad, producidos en las frondas, formando un cigoto, el cual se divide meioticamente formando esporas las cuales forman un estolón nuevo.

*Muchas de las especies llegan a tener estolones de más de 3 m y con 200 frondas. Se han identificado 347 especies en este género (*Guiry y Guiry*, 2023).*

A nivel mundial *Caulerpa* se localiza en zona pantropical (Meñez y Calumpong, 1982). Existe como especie exótica invasora en El Mediterráneo (Phillips y Price, 2002), partes de Australia (Wrigth, 2005) y en E.U.A. California (Williams y Grosholz, 2002).

En México, Pedroche et al*.* (2005) ubica el género *Caulerpa* en el Pacífico y Ortega et al*.* (2001) en el Caribe, en Islas Alacranes y en Islas Mujeres. Sin embargo, hay registros recientes que ubican a la especie en el estado de Campeche (Pacheco et al*.*, 2009). Garduño-Solórzano et al*.* (2005) ubica a este género como el segundo en mayor riqueza específica en las costas mexicanas del Golfo de México y el Caribe.

Las especies de *Caulerpa paspaloides* ubicadas en el Atlántico mexicano (Pedroche y Sentíes, 2020):

Caulerpa paspaloides f. *flabellata* Weber Bosse X -

Caulerpa paspaloides f. *phleoides* (Bory) Weber Bosse X -

Caulerpa paspaloides f. *phyllaphlaston* (G. Murray) Weber Bosse X -

Caulerpa paspaloides var. *compressa* (Weber Bosse) M. Howe X -

Caulerpa paspaloides var. *laxa* Weber Bosse X -

Caulerpa paspaloides var. *wurdemanii* Weber Bosse

8-. BIBLIOGRAFÍA

Archer, S. K., Hensel, E., y Layman, C. A. 2018. Ambient nutrient availability drives the outcome of an interaction between a sponge (Halichondria melanadocia) and seagrass (Thalassia testudinum). *Journal of Experimental Marine Biology and Ecology*, *503*, 86-91.

Adhitya, A., Folkard, A. M., Govers, L. L., van Katwijk, M. M., de Iongh, H. H., Herman, P. M. J., y Bouma, T. J. 2016. The exchange of dissolved nutrients between the water column and substrate pore-water due to hydrodynamic adjustment at seagrass meadow edges: A flume study. *Limnology and Oceanography*, *61*(6), 2286-2295.

Aschehoug ET, Brooker R, Atwater DZ, Maron JL, Callaway RM. 2016. The mechanisms and consequences of interspecific competition among plants*. Annual Review of Ecology Evolution y Systematics* 47: 263–81.

Agusti, S., Enriquez, S., Frost-Christensen, H., Sand-Jensen, K., y Duarte, C. M. 1994. Light harvesting among photosynthetic organisms. *Functional Ecology*, 6; 5(3): 273-279.

Bell S.S. y Hall M.O. 1995 Drift macroalgal abundance in seagrass beds: Investigating large-scale associations with physical and biotic attributes. *Marine Ecology Progress Series* 147: 277–283.

Biber, PD, Harwell, MA y Cropper Jr, WP, 2004. Modeling the dynamics of three functional groups of macroalgae in tropical seagrass habitats. Ecological Modelling, 175(1): 25-54.

Borum, J., Pedersen, O., Greve, T. M., Frankovich, T. A., Zieman, J. C., Fourqurean, J. W., y Madden, C. J. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, Thalassia testudinum. *Journal of Ecology*, *93*(1): 148-158.

Bulleri, F., Benedetti-Cecchi, L., y Cinelli, F. 1999. Grazing by the sea urchins Arbacia lixula L. and Paracentrotus lividus Lam. in the Northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, *241*(1): 81-95.

Camargo, J. A., y Alonso, A. 2007. Contaminación por nitrógeno inorgánico en los ecosistemas acuáticos: problemas medioambientales, criterios de calidad del agua, e implicaciones del cambio climático. *Ecosistemas*, *16*(2):113

Carruthers, T. J., Longstaff, B. J., Dennison, W. C., Abal, E. G., y Aioi, K. 2001. Measurement of light penetration in relation to seagrass. Global seagrass research methods, 370-392.

Caswell, H. 2001. Matrix population models. Sinauer, Nueva York, EE.UU.

Cayabyab, N.M. y Enríquez, S. 2007. Leaf photoacclimatory responses of the tropical seagrass *Thalassia testudinum* under mesocosm conditions. A mechanistic scaling-up study. *New Phytologist* 176:108-123.

Ceccherelli, G. y Cinelli F. 1997. Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. *Journal of Experimental Marine Biology and Ecology* 217, 165–177.

CONABIO www.conabio.gob.mx Fecha de consulta: 12/12/2023.

CONAGUA https://smn.conagua.gob.mx/es/ Fecha de consulta: 12/12/2023.

CONANP www.conanp.gob.mx/ Fecha de consulta: 12/12/2023.

Davis, B.C. y J.W. Fourqurean. 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. *Aquatic Botany* 71(3):217-232.

Dean Jr, W. E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. Journal of Sedimentary Research 44: (1): 242–248.

De los Santos, Carmen, Olivé I, Moreira M, Silva A, Freitas C, Luna RA, Quental-Ferreira H, Martins M, Costa MM, Silva J, y Cunha M.E. 2022. Seagrass meadows improve inflowing water quality in aquaculture ponds. *Aquaculture*, 528: 1-22.

Duarte, C. M. 1990. Seagrass nutrient content. *Marine ecology progress series. Oldendorf*, *6*(2): 201-207.

Duarte, C. M., Marbá, N., Agawin, N., Cebrián, J., Enríques, S., Fortes, M. D., Gallegos, M. E., Merino, M., Olesen, B., Sand-Jensen, K., Uri, J., y Vermaat, J. 1994. Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series*, 107: 211-222.

Duarte, C.M., y Cebrián, J., 1996, The fate of marine autotrophic production, *Limnology and Oceanography*, 41: 1758-1766.

Enríquez, S., Merino, M. y Iglesias-Prieto, R. 2002. Variations in the photosynthetic performance along the leaves of the tropical seagrass Thalassia testudinum. Marine Biology, 140(5): 891–900.

Falkowski, P. G., y Raven, J. A. (2013). *Aquatic photosynthesis*. Princeton University Press.

Folk, R. L. 1974. The natural history of crystalline calcium carbonate: effect of magnesium content and salinity. *Journal of Sedimentary Research,* 44(1): 40–53.

Fong, P. y Harwell, M.A., 1994. Modeling seagrass communities in tropical and subtropical bays and estuaries: a mathematical model synthesis of current hypotheses. *Bulletin of Marine Science*, *54*(3): 757-781.

Fonseca, M. S. (1996). The role of seagrasses in nearshore sedimentary processes: a review. In *Estuarine Shores: Evolution, Environments and Human Alterations* (eds Nordstrom, K. F. and Roman, C. T.), Wiley.

Fuentes, S. A., Gallegos, M. E., y Mandujano, M. C. 2014. Demografía de *Caulerpa paspaloides var. wurdemanniii* (*Bryopsidales: Caulerpaceae*) en la zona costera de Campeche, México. *Revista de Biología Tropical*, 62(2): 729-741.

Fuentes-Agueda, S.A. 2015. Demografía de *Caulerpa paspaloides* var. *wurdemannii* en tres poblaciones de la zona costera de Campeche. Tesis de Maestría. Instituto de Ecología, Universidad Nacional Autónoma de México. 46 pp.

Gallegos, M. (2010). Pastos Marinos.. En Villalobos-Zapata, G. J. y Mendoza, J. (Coord.). 2010. *La biodiversidad de Campeche*. Comisión Nacional para el conocimiento y uso de la biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur. México, 204-209

Garduño-Solórzano, M., Godínez, J.L. y Ortega, M.M. 2005. Distribución geográfica y afinidad por el sustrato de las algas verdes (CHLOROPHYCEAE) bénticas de las costas mexicanas del Golfo de México y Mar Caribe. Boletín de la Sociedad Botánica de México, 76: 61-78.

Gaudette, H. E., Flight, W. R., Toner, L., y Folger, D. W. 1974. An inexpensive titration method for the determination of organic carbon in recent sediments. *Journal of Sedimentary Research*, *44*(1): 249-253.

Glardon C., Walters L., Olsen J., Stam W. y Quintana-Ascencio ,P., 2008 Predicting risks of invasion of *Caulerpa* species in Florida. *Biological Invasions* 10:1147–1157.

Gómez, I., López-Figueroa, F., Ulloa, N., Morales, V., Lovengreen, C., Huovinen, P., y Hess, S., 2004. Patterns of photosynthesis in 18 species of intertidal macroalgae from southern Chile. *Marine Ecology Progress Series*, *270*: 103-116.

Guiry, M.D. y Guiry, G.M. 2023. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; consultado el 9 de mayo 2023.

Guo, L. P., Kang, H. J., Ouyang, Z., Zhuang, W., y Yu, Q., 2015. Photosynthetic parameter estimations by considering interactive effects of light, temperature and CO2 concentration. *International Journal of Plant Production*, *9*(3), 321-346.

Hacker, S. y S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology*, 78:1990-2003.

HACH http://latam.hach.com/global Fecha de consulta: 15/3/2023.

Harper, J.L. 1977 *Population Biology of Plants*. Academic press, London England.

Hemminga, M. A., Harrison, P. G., y Van Lent, F., 1991. The balance of nutrient losses and gains in seagrass meadows. *Marine Ecology Progress Series*, 71: 85-96.

Hixon, M.A y M. H. Carr.1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science.* 277: 946-949.

Hixon, M.A., S. W. Pacala y S. A. Sandin. 2002. Population regulation: Historical context and contemporary challenges of open vs. closed systems. *Ecology* 83: 1490-1508.

Hoffman, D.K., McCarthy, M.J., Newell, S.E., Gardner, W.S., Niewinski, D.N., Gao, J. y Mutchler, T.R., 2019. Relative Contributions of DNRA and Denitrification to Nitrate Reduction in Thalassia testudinum Seagrass Beds in Coastal Florida (USA). *Estuaries and Coasts*, *42*(4): 1001-1014.

Kalaji, H.M., Schansker, G., Ladle, R.J., Goltsev, V., Bosa, K., Allakhverdiev, S.I., Brestic, M., Bussotti, F., Calatayud, A., Dąbrowski, P. y Elsheery, N.I., 2014. Frequently asked questions about in vivo chlorophyll fluorescence: practical issues. *Photosynthesis research*, *122*(2): 121-158.

Kilminster, K., McMahon, K., Waycott, M., Kendrick, G.A., Scanes, P., McKenzie, L., O'Brien, K.R., Lyons, M., Ferguson, A., Maxwell, P. and Glasby, T., 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, *534*: 97-109.

Lambers, H., Chapin III, F.S. y Pons, T.L., 2008. *Plant physiological ecology*. Springer Science & Business Media.

Levinton, J. S. 2009. *Marine Biology: function, biodiversity, ecology.* Oxford University Press. N.Y.

Libes, S., 2011. *Introduction to marine biogeochemistry*. Academic Press.

Mandujano, M. C., Montaña, C., Franco, M., Golubov, J., y Flores-Martínez, A. 2001. Integration of demographic annual variability in a clonal desert cactus. *Ecology, 82*: 344-359.

Mandujano, M.C. 2007 La clonalidad y sus efectos en la biología de poblaciones. En: Eguiarte, L., Souza, V., Aguirre, X. (eds.), Ecología molecular. Instituto Nacional de Ecología, 215-250

Markager, S., y Sand-Jensen, K. 1992. Light requirements and depth zonation of marine macroalgae. *Marine Ecology - Progress Series*, (88): 83-92.

Markager, S., y Sand-Jensen, K. 1996. Implications of thallus thickness for growth-irradiance relationships of marine macroalgae. *European Journal of Phycology*, *31*(1), 79-87.

Marbà, N., Gallegos, M. E., Merino, M., y Duarte, C. M. 1994. Vertical growth of Thalassia testudinum: seasonal and interannual variability. *Aquatic Botany*, *47*(1): 1-11.

Marbà, N., Holmer, M., Gacia, E. y Barron, C., 2007. Seagrass beds and coastal biogeochemistry. En *Seagrasses: biology, ecology and conservation* Springer, Dordrecht, 135-157.

Meñez, E.G y Calumpong, H.P. 1982. The genus *Caulerpa* from the central Visayas, Philippines, Smithsonian Contributions in Marine Science, 17: 1-21.

Mijangos-Hernández, A. I. 2018. Análisis de la productividad de *Thalassia testudinum* Banks ex Köenig y su relación con los factores ambientales de la Reserva de la Biósfera Los Petenes, Campeche. CDMX, Tesis de Maestría, México: Universidad Autónoma Metropolitana, Unidad Iztapalapa, 73 pp.

Moosmann, L., Gächter, R., Müller, B. y Wüest, A., 2006. Is phosphorus retention in autochthonous lake sediments controlled by oxygen or phosphorus? *Limnology and Oceanography*, *51*: 763-771.

Moreno-Marín, F., Vergara, J. J., Pérez-Llorens, J. L., Pedersen, M. F., y Brun, F. G., 2016. Interaction between Ammonium Toxicity and Green Tide Development Over Seagrass Meadows: A Laboratory Study. *PLOS ONE*, *11*(4): 1-12

Najdek-Dragić, M., Korlević, M., Paliaga, P., Markovski, M., Ivančić, I., Iveša, L., Felja y Herndl, G. 2020. Effects of the invasion of Caulerpa cylindracea in a Cymodocea nodosa meadow in the northern Adriatic Sea, Frontiers, 7: 1-16

Nowicki, B. L., y Nixon, S. W., 1985. Benthic nutrient remineralization in a coastal lagoon ecosystem. *Estuaries*, *8*: 182-190.

Ortega, M., Godínez-Ortega, J. y Garduño, G. 2001. Catálogo de algas bénticas de las costas mexicanas del Golfo de México y Mar Caribe. Cuadernos del IBUNAM No. 34. UNAM, CONABIO.

Orth, R. J., Carruthers, T. I. M. J. B., Dennison, W. C., Duarte, C. M., James, W., Jr, K. L. H. y Williams, S. L., 2006. *A Global Crisis for Seagrass Ecosystems*, *56*(12): 987–996.

Pacheco M.C., Pacheco-Ruíz, I., Ramos, J., Cetz-Navarro, N. P. y Soto J. L. 2009. Presencia del género *Caulerpa* en Bahía de San Francisco de Campeche, Cam. *Hidrobiológica,* 19 (3): 57-69.

Páez-Osuna, F., Fong-Lee, M. L. y Fernández, H.1984. Comparación de tres técnicas para analizar materia orgánica en sedimentos: nota científica. *Anales del Instituto de Ciencias del Mar y Limnología*. Universidad Nacional. Autónoma de México, 11(1): 233-239.

Pérez, Espinosa, I., Gallegos Martínez, M. E., Ressl, R. A., Valderrama Landeros, L. H., y Hernández Cárdenas, G., 2019. Distribución espacial de los pastos marinos y la vegetación acuática sumergida en los Petenes, Campeche/Spatial distribution of

seagrasses and submerged aquatic vegetation of los Petenes, Campeche. *Terra Digitalis*, *3*(2): 1-37.

Pedroche, F.F., Silva P.C., Aguilar–Rosas, L.E., Dreckmann, K.M. y Aguilar–Rosas, R. 2005. Catálogo de las algas marinas bentónicas del Pacífico de México. I. Chlorophycota. Universidad Autónoma Metropolitana/ Universidad Autónoma de Baja California/ University of California, México, D.F.

Pedroche, F. F., y Sentíes, A. (2020). Diversidad de macroalgas marinas en México. Una actualización florística y nomenclatural. *Cymbella*, *6*(1): 4-55.

Pinheiro, E., da Rocha, R.P. y Drumond, A., 2020. Assessment of 20th-century reanalysis circulation patterns associated with El Niño–Southern Oscillation impacts on the tropical Atlantic and northeastern Brazil rainy season. *International Journal of Climatology*, 41(7): 3824-3840.

Phillips, Ronald C. y Meñez, Ernani G. 1988. "Seagrasses." *Smithsonian Contributions to the Marine Sciences*. 34(1): 104.

Phillips, J.A. y Price, I.R. 2002. How different is Mediterranean *Caulerpa taxifolia* (Caulerpales: Chlorophyta) to other populations of the species? Marine Ecology Progress Series, 238: 61–71.

Phillips, A.J. 2009. Reproductive ecology of *Caulerpa taxifolia* (Caulerpaceae, Briopsidales) in subtropical eastern Australia. European Journal of Phycology 44(1): 81-88.

Powell, G.V.; Kenworthy, J.W. y Fourqurean, J.W., 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. Bulletin of Marine Science, 44(1), 324-340.

Pugnaire, F. I. y M. T. Luque. 2001. Changes in plant interaction along a gradient of environmental stress. *Oikos*, 93:42-49.

Raz-Guzmán, A. y A. Sánchez-Martínez. 2001. La biodiversidad de los ambientes estuarinos y marinos de México. *Revista Ciencia Nicolaita,* 26: 125-146.

Reece, Jane B., y Neil A. Campbell. *Campbell Biology*. Boston: Benjamin Cummings / Pearson, 2011.

Roth-Schulze, A. J., Thomas, T., Steinberg, P., Deveney, M. R., Tanner, J. E., Wiltshire, K. H. y Gurgel, C. F. D., 2018. The effects of warming and ocean acidification on growth, photosynthesis, and bacterial communities for the marine invasive macroalga Caulerpa taxifolia. *Limnology and Oceanography*, *63*(1): 459-471.

Sandoval-Gil, J., Alexandre, A., Santos, R., y Camacho-Ibar, V. F. 2016. Nitrogen Uptake and Internal Recycling in Zostera marina Exposed to Oyster Farming: Eelgrass Potential as a Natural Biofilter. *Estuaries and Coasts*, *39*(6): 1694-1708.

Short, F. T., Montgomery, J., Zimmermann, C. F., y Short, C. A. 1993. Production and nutrient dynamics of a Syringodium filiforme Kütz. seagrass bed in Indian River Lagoon, Florida. *Estuaries*, *16*: 323-334.

Silvertown, J. 1987. *Introduction to Plant Population* Ecology. 2a. Edición. Longman, New York.

Spalding, M., Taylor, M, Ravilious, C., Short, F, y Green, E., 2003. The distribution and status of seagrasses. World Atlas of Seagrasses. 5-26.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Szmant, A.M. y Forrester, A., 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs*, *15*(1): 21-41.

Tabachnick, B.G. y Fidell L.S. 2019. Using multivariate statistics. New York, USA. Pearson press.

Terrados, J. y Williams, S.L., 1997. Leaf versus root nitrogen uptake by the surfgrass Phyllospadix torreyi. *Marine Ecology Progress Series,* 149: 267–277.

Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.

Thomas, J.E. 2003. *Caulerpa taxifolia* in Moreton Bay—distribution and seagrass interactions. Honours Thesis, The University of Queensland, 60 pp.

Van Tussenbroek, B.I.; Vonk, J.A., Stapel, J., Erftemeijer, P.L., Middelburg, J.J. y Zieman, J.C., 2007. The biology of Thalassia: paradigms and recent advances in research. In Larkum, A.W., Orth, R.J. y Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Dordrecht, The Netherlands, Springer, 409–439.

Van Tussenbroek, B. I.; Barba-Santos, M. G., Wong, J. G. R., van Dijk, J. K. y Waycott, M., 2010. Guía de los pastos marinos tropicales del Atlántico oeste. México D.F., Universidad Nacional Autónoma de México Press.

Waycott, M., Procaccini, G., Les, D.H. y Reusch, T.B., 2007. Seagrass evolution, ecology and conservation: Nutrient Dynamics in Seagrass Ecosystems. En *Seagrasses: biology, ecology and conservation*, Springer, Dordrecht, 25-50.

Williams, S. y Groscholtz, E.D. 2002. Preliminary reports from the *Caulerpa taxifolia* invasion in southern California. *Marine Ecology Progress Series*, 233: 307–310.

Wright, J.T. 2005. Differences between native and invasive *Caulerpa taxifolia*: a link between asexual fragmentation and abundance in invasive populations. Marine Biology, 147: 559-569.

Yoshioka, P.M. y Yoshioka, B.B., 1991. A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. *Marine Ecology Progress Series, 69:* 253-260.

Zamora-Crescencio, P., Mas, J.F., Rico-Gray, V., Domínguez-Carrasco, M.D.R., Villegas, P., Gutiérrez-Báez, C. y Barrientos-Medina, R.C., 2015. Composición y estructura arbórea de petenes en la Reserva de la Biosfera de “Los Petenes”, Campeche, México. *Polibotánica*, 39: 1-19

Zieman, J. C., Iverson, R. L., y Ogden, J. C., 1984. Herbivory effects on Thalassia testudinum leaf growth and nitrogen content. *Marine Ecology Progress Series*, 15: 151-158.

Zimmerman, R.C., Cabello-Pasini, A. y Alberte, R.S. 1994. Modelling daily production of aquatic macrophytes from irradiance measurements: a comparative analysis. *Marine Ecology Progress Series.* 114: 185-196.

Zimmerman, R.C., 2007. Light and photosynthesis in seagrass meadows. En *Seagrasses: Biology, Ecology and Conservation*, Springer, Dordrecht., 303-321.

9-. Publicación aceptada

Journal of Coastal Research	00	0	000–000	Charlotte, North Carolina	Month 0000

Contrasting Growth and Establishment of *Thalassia testudinum* along a Cover Gradient in the Gulf of Mexico

Sergio A. Fuentes-Agueda[†]*, Margarita E. Gallegos[‡], María C. Mandujano[§], and Jordan Golubov[††]

[†]Doctorado en Ciencias Biológicas y de la Salud
Universidad Autónoma Metropolitana
Ciudad de México 14387, México

[‡]Área de ecosistemas costeros Laboratorio de pastos marinos
Universidad Autónoma Metropolitana–Iztapalapa
Ciudad de México 09340, México

[§]Laboratorio de Genética y Ecología
Instituto de Ecología
Universidad Nacional Autónoma de México
Ciudad de México 04510, México

[††]Laboratorio de Ecología y Taxonomía Vegetal
Departamento El Hombre y su Ambiente
Universidad Autónoma Metropolitana–Xochimilco
Ciudad de México 04960, México

www.cerf-jcr.org

www.JCRonline.org

ABSTRACT

Fuentes-Agueda, S.A.; Gallegos, M.E.; Mandujano, M.C., and Golubov, J., 0000. Contrasting growth and establishment of *Thalassia testudinum* along a cover gradient in the Gulf of Mexico. *Journal of Coastal Research*, 00(0), 000–000. Charlotte (North Carolina), ISSN 0749-0208.

Seagrasses are important for coastal ecosystem health and have significant economic benefits; however, they are undergoing important negative changes worldwide. The seagrass *Thalassia testudinum* comprises one of the main elements in submerged aquatic vegetation (SAV) habitats, and it grows in monospecific and mixed meadows along the continental shelf of the Gulf of Mexico. In this study, *T. testudinum* monospecific and mixed meadows were monitored over a 2 year period to identify the abiotic and biotic conditions that may correlate with population parameters through the plastochron index (PI). Plants found in monospecific meadows had larger rhizomes and more flowers in comparison to those in mixed meadows, while the latter produced more leaves and larger shoots. The annual rate of change in biomass (Br) of *T. testudinum* in the monospecific meadow was 1.15 ± 0.03, which was slightly higher than that in the mixed meadow, with a value of 1.12 ± 0.03. *T. testudinum* in monospecific meadows tended to exhibit increased sexual reproduction, while vegetative growth and clonal reproduction were more common in mixed meadows. The results highlight that *T. testudinum* life-history strategies and establishment are affected by both biotic and abiotic factors like depth, temperature, and water nutrients.

ADDITIONAL INDEX WORDS: *Mexico, life-history traits, physicochemical variables, population dynamics, seagrasses.*

INTRODUCTION

Seagrasses are significant organisms in marine ecosystems (Gallegos, 2010) and have an important positive economic effects on fisheries (Tuya, Haroun, and Espino, 2014). However, external pressure and impacts on seagrass populations have increased around the world through overexploitation, physical modification, nutrient and sediment pollution, the introduction of nonnative species, and global climate change (Orth *et al.*, 2006; Waycott *et al.*, 2009). Of those that have been studied, the encroachment of macroalgae into seagrass meadows has been shown to be significant (Phillips and Durako, 2000). In some parts of the world (Mediterranean Sea, Suez Canal, and areas south of Australia), species such as *Caulerpa taxifolia*, *Caulerpa racemosa* var. *cylindracea*, and *Caulerpa prolifera* have outcompeted native seagrasses by reducing individual growth, colonization, and fitness (Dumay, Fernandez, and Pergent, 2002; Smith and Walters, 1999; Thomas, 2003; Wiltshire and Deveney, 2017). Accordingly, among the reasons behind the invasive spread of these species are the lack of natural herbivores and the high clonality (Boumediene and Lotfi, 2019; Maidanou *et al.*, 2017), which reduces colonization space for native seagrasses (Fourqurean *et al.*, 1995).

Demographic studies on seagrasses are useful tools for studying and describing seagrass meadow health. These studies are based on the reconstruction of the age distribution of living shoots, or plastochron index (PI), which is a measure of the growth and the number of flower scars on each shoot, as a measure of reproductive output in the population (Duarte *et al.*, 1994; Powell, Kenworthy, and Fourqurean, 1989). Seagrass populations are characterized by large numbers of young shoots (<1 year old), which exponentially decline with increasing shoot age (Duarte *et al.*, 1994). Healthy meadows are expected to have the following characteristics: a horizontal growth rate (which increases expansion), the establishment of shoots, the accumulation of sediment, and a high scar flower ratio (an indicator of sexual reproduction; Gallegos *et al.*, 1992; Van Tussenbroek *et al.*, 2006).

Several abiotic factors affect the growth, establishment, and distribution of seagrasses; for example, low temperatures (<20°C) and high salinity (>35) will kill tropical seagrass shoots, and light availability will limit their occurrence at lower depths (<10 m; Van Tussenbroek *et al.*, 2006). High amounts of nutrients will increase leaf and rhizome growth, whereas low

DOI: 10.2112/JCOASTRES-D-22-00025.1 received 17 March 2022; accepted in revision 6 November 2022; corrected proofs received 9 January 2022.
*Corresponding author: kamahl2004@gmail.com

Figure 1. A meadow of *Thalassia testudinum* with the short shoots and exposed rhizomes in "Los Petenes" Biosphere Reserve.

nutrient availability will affect leaf senescence and result in low establishment (Powell, Kenworthy, and Fourqurean, 1989). However, high amounts of nutrients are not always beneficial; in some cases, they can increase the presence of other seagrass species or macroalgae in monospecific meadows (Williams, 1987). For example, the presence and high growth rates of macroalgae reduced the establishment of *Thalassia testudinum* in Florida (Van Tussenbroek *et al.*, 2006).

Thalassia testudinum (Banks ex (König)) is an underwater angiosperm formed by horizontal rhizomes with vertical shoots, 30-cm-long leaves, and green or pink flowers, which grow once a year (Gallegos *et al.*, 1992; Van Tussenbroek *et al.*, 2010), having fruits and seeds commonly dispersed by waves. Populations can be found in monospecific and mixed meadows with other seagrasses throughout the Caribbean Sea and the Gulf of Mexico (*e.g.*, associated with *Halodule wrightii*, *Syringodium filiforme*, and *Halophila decipiens*; Gallegos, 2010) (Figure 1).

The aim of this study was to evaluate the growth, reproduction, and establishment of *T. testudinum* in "Los Petenes" Biosphere Reserve at three sites that differed in abundance. The main biotic and abiotic factors that affect the establishment of *T. testudinum* located in monospecific and mixed meadows were described. The hypothesis assumed that *T. testudinum* development and growth would be higher in monospecific meadows than in mixed meadows, because other submerged aquatic vegetation (SAV) species would use water nutrients and colonize space and negatively affect *T. testudinum* growth and establishment.

METHODS

Surveys were done in Los Petenes Biosphere Reserve, a protected area located in the Gulf of Mexico off the coast of southeastern Mexico, which possesses the largest area of SAV in Mexico (1817.64 km^2, 20°51′30″ N 90°20′00″ W). In Los Petenes, *T. testudinum* can be found in monospecific and in mixed stands with macroalgae across the reserve, and it is the most abundant and common species, followed by *S. filiforme*, *H. wrightii*, and a diversity of macroalgae (Espinosa *et al.*, 2019). Within the macroalgae, *Caulerpa paspaloides* var. *wurdemannii* (Weber Bosse) is the most frequent, and it grows sympatrically with *T. testudinum* (Fuentes, Gallegos, and Mandujano, 2014). During 2012–16, three sampling sites were chosen for their accessibility and SAV relative cover: 100% *T. testudinum* (T100), 50% *T. testudinum* (T50), and one site with no cover of *T. testudinum* (T0). The sites were separated from each other by at least 15 km (Figure 2). Field measurements were obtained in 2017 and 2018.

Environmental variables were measured in the water column as well as in sediment ($n = 4$ samples per site per year). Water depth was obtained with a Secchi disk, and water samples (250 mL) were collected in the field at half depth with a Van Dorn bottle, from which salinity, temperature, pH, and dissolved oxygen (DO) were measured with a multiparametric sensor (YSI 556 MPS) *in situ*. Water-column nutrients (including dissolved inorganic nitrogen [DIN], NO_2^-, NO_3^-, ammonium [NH_4^+], and total phosphorus [TP]) and pore-water nutrients (ammonium and phosphorus) were obtained and analyzed with a HACH 3900 spectrophotometer at the Seagrass Laboratory of Universidad Autónoma Metropolitana–Iztapalapa.

Paired sediment cores (5 cm diameter × 30 cm length) were collected by divers (4 samples per site per year). One core was used to obtain soil pore water, and the other was used for sediment analysis. The soil pore-water samples were extracted in an anoxic chamber and separated with a centrifuge (Eppendorf centrifuge 5702) to measure ammonium and TP with standard methods (Strickland and Parsons, 1972). The sediment core samples were oven-dried to constant weight at 60°C for 2 days and separated with a sieving tower shaker (including sieves of 0.074 mm, 0.125 mm, 0.25 mm, 0.5 mm, 1 mm, and 2 mm). Mean grain size (Mz) was calculated by the mean weight of each sieve, sediment type, and diameter (mm) and assigned following the Wentworth class size (Erftemeijer and Koch, 2001; Folk, 1974). Data were resampled ($n = 75$) with an add-on in Excel 2010 in order to work directly with the actual distribution of the data (Good, 2000). Differences in each environmental variable between sites were tested with an analysis of variance (ANOVA; STATISTICA 9.0; Larose, 2016).

SAV Cover

SAV cover was quantified in each site with a 0.25 cm^2 grid (0.5 × 0.5 cm plot), with 10 replicated measurements at each site during eight surveys. The SAV categories were split into species, including *T. testudinum* and *C. paspaloides* var. *wurdemannii*, as well as cover by other macroalgae and spaces with no vegetation.

Data were resampled ($n = 75$) with an add-on in Excel 2010 in order to work directly with the actual distribution of the data (Good, 2000). For each SAV cover type (*T. testudinum*, *C. paspaloides* var. *wurdemannii*, other macroalgae, and no vegetation), a t test was used to find differences between years (Y; 2017 and 2018) for each site (STATISTICA 9.0; Larose, 2016).

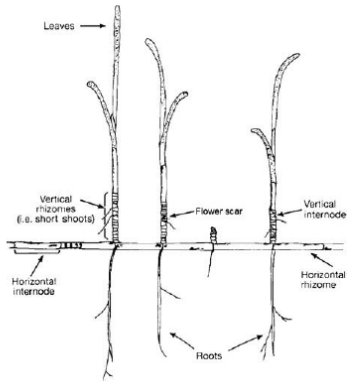


Figure 3. Modules and structures of *Thalassia testudinum* (Duarte *et al.*, 1994).

The PI was calculated using the number of leaf scars and leaves on each shoot found in samples from cores for each site (Duarte *et al.*, 1994). The vertical growth rate of shoots was then calculated through linear regression of PI and shoot length. *Thalassia testudinum* shoots have flowers once a year, so shoot age was calculated using the number of leaves formed between successive flower scars, and age structures were constructed and analyzed for each site (Gallegos *et al.*, 1992). An analysis of covariance was used to compare the growth rate slopes between sites, and a χ^2 test for the number of shoots was used to assess differences in the age structures between the sites and within years, followed by *post hoc* standardized adjusted residuals (STATISTICA 9.0; Tabachnick and Fidell, 2019).

Individual density was calculated from the total number of shoots in the core (0.3 m^2), and flowering percentage was calculated by the number of flower scars and total shoots at each site (Duarte *et al.*, 1994). The horizontal growth rate was calculated by multiplying the average length of the rhizome by the rate of horizontal internode formation (*i.e.* multiplying the ratio of average internodes and PI by the number of days a leaf is produced; Duarte *et al.*, 1994).

Samples were subsequently oven dried at 60°C for 2 days and weighed to the nearest 0.001 g to estimate the annual rate of change in biomass (Br, g m^{-2}):

$$Br = B_{t+1}/B_t \quad (1)$$

where, B_t = biomass at time t (2017), and B_{t+1} = biomass at time t+1 (2018).

Principal Component Analysis for Biotic and Abiotic Variables

A principal component analysis (PCA; STATISTICA 9.0; Tabachnick and Fidell, 2019) was conducted with the factors (T100, T50, and T0) and response variables (depth, temperature, salinity, pH, DO, DIN, TP, pore-water ammonium, and pore-water phosphorus). A biotic component of biomass was included in each factor, for which *T. testudinum* biomass was extracted with a 10-cm-diameter metal core ($n = 12$ cores per site per year). Cores were stored in plastic bags and transported, cleaned of debris, sediment, and organisms, and oven-dried for 2 days at 60°C. Factor loadings with values above 0.40 were considered to be important variables (Tabachnick and Fidell, 2019).

RESULTS

T100 was shallower (1.2–2 m) and had significantly higher Mz than T50 and T0; the latter sites did not differ between themselves (2.4–3.2 m). T100 sediment was classified as medium and fine sands with a diameter of 0.125–0.5 mm. On the other hand, T50 and T0 sediments were medium and coarse sands with a diameter of 0.25–1 mm. The other environmental variables (temperature, pH, salinity, and DO), water-column nutrients (TP and DIN), and pore-water nutrients (phosphorus and ammonium) were not different between sites (Table 1).

SAV Cover

At T100, *T. testudinum* had 0.25 m^2 cover that remained stable during the study period. However, at T50 ($t_1 = -4.98$, $p < 0.05$; Figure 4) and T0 ($t_1 = -10.98$, $p < 0.05$; Figure 4), cover was higher in 2018. Although *T. testudinum* was not present at T0 in 2017, a small mean cover of 0.02 ± 0.003 m^2 was found in 2018 (Figure 4). *C. paspaloides* var. *wurdemannii* cover decreased between the years at both sites where it was present (T50, $t_1 = 11.74$, $p < 0.05$; Figure 4) (T0, $t_1 = 11.96$, $p < 0.05$; Figure 4). At both sites, other macroalgae (*Derbesia marina* [Lyngbye] Solier, *Batophora oerstedii* J. Agardh, *Penicillus dumetosus* [J.V. Lamouroux] Blainville, *Avrainvillea levis* M. Howe, *Caulerpa prolifera* [Forsskål] J.V. Lamouroux, and *Halimeda monile* [J. Ellis & Solander] J.V. Lamouroux; Guiry

Table 1. *Summary (mean ± SE) of environmental variables and the results of comparisons between sites with ANOVA tests. Significant differences are highlighted in bold (df = 2).*

Environmental Variables	T100	T50	T0	*F*	*p*
Depth (m)	**1.57 ± 0.03**	2.97 ± 0.01	3.15 ± 0.03	**839.07**	**<0.01**
Temperature (°C)	27.02 ± 0.23	27.80 ± 0.27	27.20 ± 0.22	2.73	0.06
pH	**7.91 ± 0.03**	8.04 ± 0.02	8.23 ± 0.03	24.3	**<0.01**
Salinity	34.97 ± 0.31	34.47 ± 0.47	35.32 ± 0.51	0.91	0.40
Dissolve oxygen, DO (μM)	**5.74 ± 0.12**	6.33 ± 0.03	6.33 ± 0.12	10.73	**<0.01**
Total phosphorus, TP (μM)	1.07 ± 0.08	0.99 ± 0.06	**1.52 ± 0.12**	8.88	**<0.01**
Dissolved inorganic nitrogen, DIN (μM)	9.19 ± 0.64	6.04 ± 0.54	**15.64 ± 1.04**	39.71	**<0.01**
Pore-water ammonium (μM)	962.51 ± 43.87	909.05 ± 69.54	976.18 ± 70.71	0.32	0.72
Pore-water total phosphorus (μM)	22.59 ± 2.69	21.94 ± 3.28	**13.73 ± 1.98**	3.32	**0.03**
Mean grain size (Mz)	**2.67 ± 0.11**	1.02 ± 0.06	1.81 ± 0.05	**101.61**	**<0.01**

Allen Press, Inc. ■ 6 February 2023 ■ 11:22 am
//titan/Production/c/coas/live jobs/coas-39/coas-39-02/coas-39-02-13/layouts/coas-39-02-13.3d

Table 2. *Morphological variables of* T. testudinum *(number of leaves, number of leaf scars, number of internodes, length of shoots, length of leaves, width of leaves, rhizome size, and rhizome diameter; mean ± SE) in 2017 and 2018. Significance levels are denoted by bold in the sites (S), years (Y), and (S×Y) columns from the ANOVA/GML tests.*

					F/*p*		
Morphological Variable	T100 2017	T100 2018	T50 2017	T50 2018	Sites	Years	S×Y
Number of leaves	**3 ± 1**	**3 ± 1**	2 ± 1	2 ± 1	**6.83**	0.12	0.72
					<0.01	0.06	0.13
Number of leave scars	35 ± 22	32 ± 27	**37 ± 28**	**45 ± 31**	**7.64**	0.003	2.84
					<0.01	0.95	0.06
Number of internodes	14 ± 6	**18 ± 9**	12.5 ± 6	**15.53 ± 8**	3.22	**13.37**	0.42
					0.07	**<0.01**	0.51
Length of shoots (cm)	4.51 ± 0.27	4.35 ± 0.26	4.36 ± 0.53	5.14 ± 0.43	0.33	1.02	0.92
					0.56	0.31	0.33
Length of leaves (cm)	18.64 ± 1.32	19.90 ± 1.20	**24.34 ± 1.89**	18.6 ± 0.95	2.56	2.62	**6.46**
					0.11	0.10	**0.01**
Width of leaves (cm)	0.72 ± 0.02	0.77 ± 0.03	0.71 ± 0.03	0.84 ± 0.21	0.05	0.24	0.02
					0.81	0.62	0.87
Rhizome size (cm)	**8.35 ± 0.49**	**9.43 ± 0.70**	6.55 ± 0.49	6.37 ± 0.45	**8.32**	0.28	0.56
					<0.01	0.59	0.45
Rhizome diameter (mm)	5.19 ± 0.08	**5.22 ± 0.11**	4.93 ± 0.12	**4.87 ± 0.09**	0.27	**4.68**	0.05
					0.59	**0.03**	0.81

and Guiry, 2019) and spaces without vegetation increased their cover during the years at both sites (T50 macroalgae, $t_1 = -2.39$, $p < 0.05$; Figure 4) (T0 macroalgae, $t_1 = -4.59$, $p < 0.05$; Figure 4) (T50 no vegetation, $t_1 = -7.07$, $p < 0.05$; Figure 4) (T0 no vegetation, $t_1 = -5.29$, $p < 0.05$; Figure 4).

Morphological Variables of *Thalassia testudinum*

Leaf number and rhizome size were higher at T100 (3 leaves and 9.45 cm) than in T50 (2 leaves and 6.37 cm), and leaf scars were higher at T50 (45 scars). However, the number of internodes and rhizome diameter were higher in 2018 for both sites (T100, 18 internodes, 5.22 cm; T50, 15.53 internodes, 4.87 cm) (Table 2). T100 had the highest horizontal growth rate (67.34 cm y^{-1}), biomass (3292.29 g m^{-2}), and flowering percentage (59%) in 2018, while T50 had the highest vertical growth rate in 2018 (5.02 cm y^{-1}) (Table 3).

PI and Population Structure

Vertical growth rate was higher at T100 ($R^2 = 0.7212$, $y = 0.109x + 0.8575$) than at T50 ($R^2 = 0.6654$, $y = 0.0883x + 1.0757$; $F = 928$, df = 1, $p < 0.01$; Figure 5). Differences between age categories were found between sites ($\chi^2 = 187.26$, df = 3, $p < 0.01$; Figure 6), with more frequent individuals in all categories at T100.

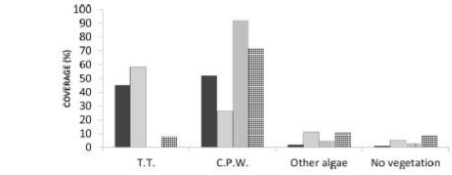


Figure 4. SAV cover (%) in T50 (colors) and T0 (lines and points). Black bars and lines represent coverage in 2017; gray bars and points represent cover in 2018 (T.T. = *Thalassia testudinum* and C.P.W. = *Caulerpa paspaloides* var. *wurdemannii*).

Biomass Accumulation

The T100 site accumulated more biomass in all analyzed size categories, with positive annual rates of change in belowground biomass (1.14 ± 0.16) and total biomass (1.15 ± 0.03). T50 biomass was also positive but at smaller rates ($Br_{belowground}$ = 1.07 ± 0.26 and Br_{total} = 1.12 ± 0.03). In contrast, the aboveground biomass accumulation at T50 (1.22 ± 0.18) was slightly higher than that at T100 (1.14 ± 0.26). This suggests that *T. testudinum* biomass accumulation increased at both sites; however, the relative aboveground to belowground accumulation differed between sites (Table 4).

PCA Analysis in *Thalassia testudinum*

The first principal component of the PCA (C1), composed of depth, sediment size, and dissolved oxygen, explained 33.20% of the data variability (Table 5). The second component (C2), composed of temperature and DIN, explained 22.30% of total variation, while C3 represented soil pore-water nutrients, and it explained 16.61% of total variation. The distribution of sites could clearly be linked to the variables associated with monospecific meadows (Figure 7A) and mixed meadows (Figure 7B).

DISCUSSION

Depth and sediment size were abiotic factors that influenced the cover of *T. testudinum* distributions in Los Petenes. Other factors were also associated with differences in *T. testudinum* cover, such as DO, water nutrients (DIN, pore-water phosphorus and ammonium), and temperature. Generally, *T. testudi-*

Table 3. *Comparative variables of* T. testudinum *(Tt) (biomass, population density, flowerage percentage, vertical and horizontal growth rate) in 2017 and 2018.*

Year	2017		2018	
Site	T100	T50	T100	T50
Total biomass, Tt (g m^{-2})	3292.29	1222.99	**3690.19**	1411.85
Flowering percentage (%)	32	4	**59**	11
Vertical growth rate (cm y^{-1})	3.79	3.38	4.26	**5.02**
Horizontal growth rate (cm y^{-1})	36.46	34.56	**67.34**	40.90

Allen Press, Inc. ■ 6 February 2023 ■ 11:22 am
//titan/Production/c/coas/live_jobs/coas-39/coas-39-02/coas-39-02-13/layouts/coas-39-02-13.3d

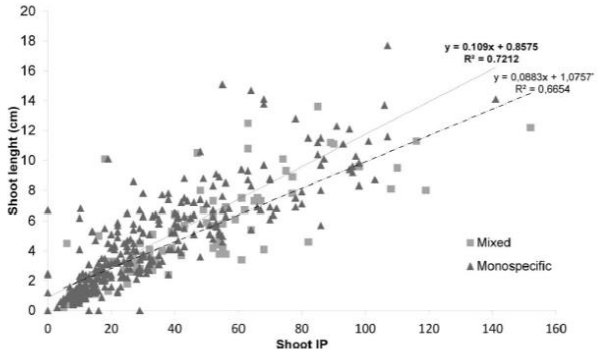


Figure 5. Vertical growth rate of monospecific (triangle) and mixed (square) meadows of *T. testudinum* in Los Petenes. Dashed line and bold letter show monospecific population (T100), and straight line shows mixed population (T50).

num can establish populations in water depths that are less than 10 m (Van Tussenbroek *et al.*, 2010), while macroalgae tend to establish in areas deeper than 10 m (Pachecho *et al.*, 2008). In Los Petenes Biosphere Reserve, Espinosa *et al.* (2019) reported that monospecific meadows of *T. testudinum* are located between 0.9 m and 2.13 m, while they are mixed with macroalgae between 0.9 m and 2.7 m. Fuentes, Gallegos, and Mandujano (2014) reported mixed meadows of *T. testudinum* and *C. paspaloides* var. *wurdemannii* in areas between 1.3 m and 2 m deep and monospecific meadows of *C. paspaloides* var. *wurdemannii* between 2.5 m and 3 m deep. A possible explanation for differences in SAV composition is light availability, because deeper areas will have higher light attenuation than shallow areas (Ramírez *et al.*, 2015). Light is an important factor for the establishment and growth of SAV species (Fong and Harwell, 1994); therefore, monospecific meadows of *T. testudinum* in shallow water could mean more available light than in mixed meadows. As a result, there could be a higher growth and establishment of *T. testudinum* in shallow waters, and macroalgae could have higher development in deep water.

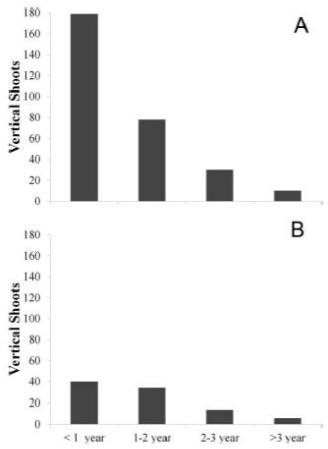


Figure 6. Age distribution of *T. testudinum* in T100 (A) and T50 (B) represented in percentages. Asterisk represents the categories that are statistically different (T100 categories are higher than T50 categories).

Dissolved oxygen in the water column is an indirect measurement of photosynthetic activity (Wetzel, 2001). The PCA suggests that mixed meadows were related to high DO; in addition, T50 and T0 presented high diversity in SAV cover, and higher DO values were registered in T50 and T0. This means that mixed meadows may have a high diversity of autotrophs (seagrasses, macroalgae, phytoplankton, and cyanobacteria) and thus have high photosynthetic activity. Although shallow water is expected to have high photosynthetic activity, during high photosynthesis and active plant growth, the respiratory oxygen consumption is much lower than oxygen release to the external media (Borum *et al.*, 2007). This could suggest that *T. testudinum* in mixed meadows will invest the resources in growth and reduce the consumption of oxygen, allowing the establishment of other elements in the SAV such as macrolagae.

Sediment size is an indication of a variety of physical and geochemical characteristics in seagrass meadows, and coarse grains are usually related to high wave energy and current velocities (Fonseca, 1996). Hemminga, Harrison, and Van Lent (1991) reported that grain size and sediments will be finer in vegetative areas than in unvegetated areas, because seagrass

Table 4. *Annual rate of change of* T. testudinum *at T100 and T50, calculated with the aboveground, belowground, and total ground biomass of* T. testudinum *in the years 2017 and 2018.*

Type of biomass accumulation	T100	T50
Aboveground	1.14 ± 0.26	1.22 ± 0.18
Belowground	1.14 ± 0.16	1.07 ± 0.26
Total	1.15 ± 0.03	1.12 ± 0.03

Allen Press, Inc. ■ 6 February 2023 ■ 11:22 am
//titan/Production/c/coas/live_jobs/coas-39/coas-39-02/coas-39-02-13/layouts/coas-39-02-13.3d

Table 5. *Percentage of variance explained and PCA loadings of the variables that were the most representative in the study. C1, C2, and C3 were the main components, and high contributions of each variable in each factor are in bold numbers.*

	C1	C2	C3
Explained variance (%)	33.21	22.30	16.61
Depth (m)	**0.913**	0.104	−0.032
Temperature (°C)	0.403	**−0.737**	0.026
DO (μM)	**0.632**	0.194	0.267
DIN (μM)	0.229	**−0.906**	−0.091
Pore-water ammonium (μM)	0.055	−0.355	**−0.718**
Pore-water total phosphorus (μM)	−0.162	0.349	**−0.822**
Sediment size (φ)	**−0.665**	−0.277	0.212
Biomass, Tt (g m^{-2})	**−0.857**	−0.208	0.096

rhizomes act as a sediment trap and disintegrate the sediment into smaller pieces, so bacterial communities are able to establish and help with the assimilation of water nutrients in the system. The PCA did find sediment size as an important variable in the establishment of *T. testudinum*. This could suggest that wave energy and water currents not only have an effect on abiotic components like the quality of sediments, but they also have an effect also on biotic factors such as species composition.

Column water nutrients were higher in sites without *T. testudinum* (T0). Rose and Dawes (1999) found that monospecific meadows of *T. testudinum* had lower column water nutrients than mixed meadows coformed with macroalgae in Florida. The PCA suggests that the DIN and soil pore-water nutrients were relevant variables in the establishment and growth of *T. testudinum*, consistent with previous findings in which increased water nutrients affected growth and establishment of seagrasses and macroalgae. For example, Fourqurean *et al.* (1995) found that higher water-column nitrogen tended to increase growth and presence of macroalgae and, thus, reduce the establishment of *T. testudinum*, and Williams (1987) found that competitors (*S. filiforme*) increased their growth and establishment with a rise in pore-water nutrients, which could turn into a decrease in *T. testudinum* populations. Water nutrients values in this study were higher than those previously reported for SAV in the Gulf of Mexico (Table 6), meaning high nutrient availability throughout Los Petenes, which favors establishment and growth of both species. Some of the reasons could be the high supply of inorganic and organic nutrients by the terrestrial continent. Although it has been suggested that higher values of water nutrients in SAV communities (phosphate ranges from 0.1 to 1.7 μM in the water column and from 0.3 to 20 μM in sediment pore water and ammonium ranges from 0 to 3.2 μM in the water column and from 1 to 180 μM NH_4^+ in sediment pore water; Burkholder, Tomasko, and Touchette, 2007) are detrimental for seagrasses,

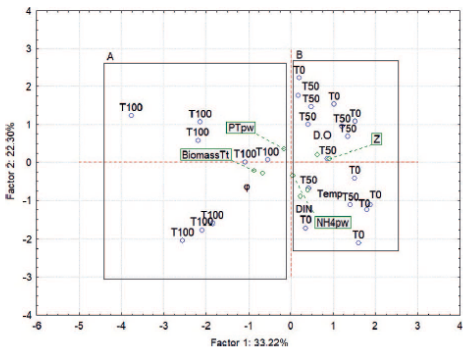


Figure 7. Factor loading represented in the PCA with the significant variables: depth (*Z*), dissolved oxygen (DO), dissolved inorganic nitrogen (DIN), temperature (Temp), pore-water nutrients (phosphorus [TPpw] and ammonium [NH4pw]), sediment size (φ), biomass of *T. testudinum* (Biomass, Tt), and relative position of the sites. Squares represent the important variables in *T. testudinum* monospecific meadows (A) and mixed meadows (B).

the results of this study could suggest that *T. testudinum* in Los Petenes is adapted to oligotrophic habitats or has an adaptive response to changing nutrient regimes (Burkholder, Tomasko, and Touchette, 2007).

Although there were no differences in temperature between sites, the PCA associated temperature as an important variable for mixed meadows. Phytoplankton and frequent macroalgae are related to high temperatures and high concentrations of water-column nutrients (Medellu, Suriani, and Komansilan, 2019; Thomas, 2003). Although there were no changes in temperature between sites, different abiotic conditions in Los Petenes may be found during the three seasons ("norte," dry, and rainy). For example, Mijangos-Hernández (2018) reported an increase in water-column nutrients and temperature in Los Petenes during the rainy season. Fuentes, Gallegos, and Mandujano (2014) suggested that the rainy season affects growth and reproduction of *C. paspaloides* var. *wurdemannii*, which decreased during the colder seasons ("nortes"). *Caulerpa paspaloides* var. *wurdemannii* in T50 and T0 reduced its cover, which could be associated with environmental changes that have a high impact, and which could open spaces for other colonizing SAV species like *T. testudinum*. The T50 and T0 sites were associated with high DO, DIN, and temperature. The data suggest that these variables could be important for other SAV like macroalgae. Also, Borum *et al.* (2007) addressed the relative importance of respiration, which increased

Table 6. *Column and pore-water nutrients in seagrass meadows of the Gulf of Mexico.*

Places	NH_4 (μM)	TP (μM)	Pore-water NH_4 (μM)	Pore-water TP (μM)	Source
Florida Bay	NA	NA	6.3–240	>0.05	Fourqurean, Zieman, and Powell (1992)
Florida (Key Largo)	NA	NA	69 ± 42	3 ± 0.9	Szmant and Forrester (1996)
Florida (St. Joseph Bay vegetated)	1.51 ± 1.82	0.10 ± 0.01	NA	NA	Hoffman *et al.* (2019)
Florida (St. Joseph Bay unvegetated)	2.21 ± 0.66	0.10 ± 0.02	NA	NA	Hoffman *et al.* (2019)
Campeche (Los Petenes)	6.76 ± 0.87	9.77 ± 2.66	853.37 ± 111.91	20.18 ± 4.7	This study

Allen Press, Inc. ■ 6 February 2023 ■ 11:22 am
//titan/Production/c/coas/live_jobs/coas-39/coas-39-02/coas-39-02-13/layouts/coas-39-02-13.3d

markedly with increasing temperature or at times of low photosynthetic rates in seagrasses; this suggests that high temperatures could reduce *T. testudinum* establishment and increase macroalgae presence.

Macroalgae have high growth rates and low establishment, which can be classified as a colonizing species (Kilminster *et al.*, 2015). Fast growth and high clonality are traits that are reported for *C. paspaloides* var. *wurdemannii* (Fuentes, Gallegos, and Mandujano, 2014), because of high vegetative growth due to simple structures and coenocyte growth (Phillips, 2009) that favor spread. In addition, species of *Caulerpa* are reported to have the ability to alter the seabed (*e.g.*, by altering the pH of the substrate due to the increase of CO_2 from algae metabolism), which leads to changes in the marine community, and particularly in the benthos community and substrate bacteria (Gribben *et al.*, 2017).

Studies in Mexico have shown that *T. testudinum* has a horizontal growth rate of 35 cm y^{-1}, reported as an indicator of good health and establishment for *T. testudinum* (Van Tussenbroek *et al.*, 2006). This study found that *T. testudinum* had a higher horizontal growth rate (51.9 cm y^{-1} at T100 and 37.73 cm y^{-1} at T50) in Los Petenes, which suggests healthy meadows, even in areas where a reduced growth rate was expected by the presence of macroalgae (T50).

Enduring meadows of a persistent species usually have small variations in their abundance and population dynamics over time (Kilminster *et al.*, 2015). Differences in resource allocation (belowground and aboveground structures) showed that *T. testudinum* allocated resources towards rhizomes and sexual reproduction in T100 and toward vertical growth in T50. Hemminga, Harrison, and Van Lent (1991) described that seagrasses will present leaf senescence in a chaotic environment (presence of other SAV species and reduced water nutrients). In these conditions, plants will invest more in vertical growth than in horizontal growth, because as older leaves die, nutrients will be integrated *via* translocation, and energy will be distributed in shoots. This process has been reported in mixed meadows of *T. testudinum* in Florida (Bricker *et al.*, 2018), which showed high mortality and clonality of younger shoots. This could mean that, although the meadows have the same quantity of nutrients, competition with other SAV species like macroalgae triggers a process of differential allocation in *T. testudinum* in order to have high availability of nutrients for the shoots.

The hypothesis that *T. testudinum* growth, flowering, and establishment should be higher in monospecific meadows (T100) holds for most demographic estimates. However, mixed meadows showed higher aboveground biomass accumulation and vertical growth rates; this could mean that SAV composition could affect the components of life history and development of *T. testudinum* in Los Petenes. A trade-off was potentially created by *T. testudinum* exchanging high sexual reproduction and high production of rhizomes for fast shoot growth and leaf production in T50 (which had the highest aboveground biomass accumulation estimate). This would help *T. testudinum* cover more space, have more available light, and avoid being displaced by other elements of the SAV. *Thalassia testudinum* in harsh conditions, like having minimal amounts of nutrients or competition with other species, will recycle older leaves to strengthen younger leaves and develop vertical growth. Higher values of DO in T50 could reflect higher photosynthetic activity, as a consequence of high production of leaves and shoot growth. In addition, colonizing space is one of the resources used by species in the SAV habitat (Fong and Harwell, 1994), in which growth and establishment are important traits that help them to occupy space, traits commonly found in clonal species (Bricker *et al.*, 2018). If the marine environment undergoes permanent changes, the establishment of persistent species like *T. testudinum* will be reduced (Roth-Schulze *et al.*, 2018), followed by more persistent species of macroalgae.

CONCLUSIONS

Seagrass cover is in healthy stage at Los Petenes Biosphere Reserve, as the *T. testudinum* population was found to be growing along the cover gradient. *Thalassia testudinum* will have changes in its life-history strategies in different meadows; sexual reproduction and increased longevity will be common in monospecific meadows, while clonal and vegetative growth will be common in mixed meadows. Key abiotic factors that enhance *T. testudinum* growth and establishment are pore-water total phosphorus and shallow depth. High DO, temperature, DIN, and pore-water ammonium and deeper water are relevant in mixed meadows and represent conditions that allow macroalgae to grow and establish.

ACKNOWLEDGMENTS

This study was part of the Doctorado en Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana, México by Fuentes-Agueda. It was also of the project "Estado de salud, conservación y vulnerabilidad de los ecosistemas de pastos marinos del Litoral del Golfo de México," with the support and funding of the Secretariat of Energy, Consejo Nacional de Ciencia y Tecnología (Centro de Investigación Científica y de Educación Superior de Ensenada, The Gulf of Mexico Research Consortium). This study was possible with the help of the laboratory of seagrasses Universidad Autónoma Metropolitana–Iztapalapa crew (Gaby, Paco, Fer, Omar, Lalo, Ivanhoe, Itai, Iliana, Martin, and Guille), whom we thank for their camaraderie and support. We also thank Alma and Gil for the creation of the study area map and Juan Chay for his support, friendship, and guidance in Campeche and across "Los Petenes." Thanks to Dr. Kurt M. Dreckmann and Dr. Abel Sentíes for the identification of the macroalgae in this study.

LITERATURE CITED

Borum, J.; Sand-Jensen, K.; Binzer, T.; Pedersen, O., and Greve, T.M., 2007. Oxygen movement in seagrasses. *In:* Larkum A.W.D.; Orth, R.J., and Duarte C.M. (eds.), *Seagrasses: Biology, Ecology and Conservation*. Dordrecht, The Netherlands: Springer, pp. 255–270.

Boumediene, H.K. and Lotfi, B.T., 2019. First record of invasive green algae *Caulerpa racemosa* var. *cylindracea* in Oran Bay (western Algeria). *Indian Journal of Geo-Marine Sciences*, 48(3), 335–342.

Bricker, E.; Calladine, A.; Virnstein, R., and Waycott, M., 2018. Mega clonality in an aquatic plant—A potential survival strategy in a changing environment. *Frontiers in Plant Science*, 9, 435–444.

Burkholder, J.M.; Tomasko, D.A., and Touchette, B.W., 2007. Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology*, 350(1–2), 46–72.

Duarte, C.M.; Marbá, N.; Agawin, N.; Cebrián, J.; Enriquez, S.; Fortes, M.D.; Gallegos, M.E.; Merino, M.; Olesen, B.; Sand-Jensen, K.; Uri, J., and Vermaat, J., 1994. Reconstruction of seagrass dynamics: Age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series*, 107, 211–222.

Dumay, O.; Fernandez, C., and Pergent, G., 2002. Primary production and vegetative cycle in *Posidonia oceanica* when in competition with the green algae *Caulerpa taxifolia* and *Caulerpa racemosa*. *Journal of the Marine Biological Association of the United Kingdom*, 82(3), 379–387.

Erftemeijer, P.L. and Koch, E.W., 2001. Sediment geology methods for seagrass habitat. *In:* Short, F.T. and Coles, R.G. (eds.), *Global Seagrass Research Method, Volume 33*. Amsterdam, the Netherlands: Elsevier, pp. 345–367.

Espinosa, I.P.; Martínez, M.E.G.; Ressl, R.A.; Landeros, L.H.V., and Cárdenas, G.H., 2019. Distribución espacial de la vegetación acuática sumergida en los Petenes, Campeche. *Terra Digitalis*, 3(2), 1–11.

Folk, R.L., 1974. The natural history of crystalline calcium carbonate; effect of magnesium content and salinity. *Journal of Sedimentary Research*, 44(1), 40–53.

Fong, P. and Harwell, M.A., 1994. Modeling seagrass communities in tropical and subtropical bays and estuaries: A mathematical model synthesis of current hypotheses. *Bulletin of Marine Science*, 54(3), 757–781.

Fonseca, M.S., 1996. The role of seagrasses in nearshore sedimentary processes: A review. *Estuarine Shores: Evolution, Environments and Human Alterations*, 35(6), 565–576.

Fourqurean, J.W.; Powell, G.V.; Kenworthy, W.J., and Zieman, J.C., 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos*, 72(3), 349–358.

Fourqurean, J.W.; Zieman, J.C., and Powell, G.V.N., 1992. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology*, 114(1), 57–65.

Fuentes, S.A.; Gallegos, M.E., and Mandujano, M.C., 2014. Demografía de *Caulerpa paspaloides* var. *wudermannii* (Bryopsidales: Caulerpaceae) en la zona costera de Campeche, México. *Revista de Biología Tropical*, 62(2), 729–741.

Gallegos, M. 2010. Pastos marinos. *In:* Villalobos-Zapata, G.J. and Mendoza, J. (eds.), *La biodiversidad de Campeche*. Campeche, México: Comisión Nacional para el conocimiento y uso de la biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur, pp. 204–209.

Gallegos, M.E.; Merino, M.; Marba, N., and Duarte, C.M., 1992. Flowering of *Thalassia testudinum* Banks ex König in the Mexican Caribbean: Age-dependence and interannual variability. *Aquatic Botany*, 43(3), 249–255.

Good, P. 2000. *A Practical Guide to Resampling Methods for Testing Hypotheses*. New York: Springer-Verlag, 228p.

Gribben, P.E.; Nielsen, S.; Seymour, J.R.; Bradley, D.J.; West, M.N., and Thomas, T., 2017. Microbial communities in marine sediments modify success of an invasive macrophyte. *Scientific Reports*, 7(1), 1–8.

Guiry, M.D. and Guiry, G.M. 2019. *AlgaeBase*. Galway, Ireland: National University of Ireland. https://www.algaebase.org

Hemminga, M.A.; Harrison, P.G., and Van Lent, F., 1991. The balance of nutrient losses and gains in seagrass meadows. *Marine Ecology Progress Series*, 71(1), 85–96.

Hoffman, D.K.; McCarthy, M.J.; Newell, S.E.; Gardner, W.S.; Niewinski, D.N.; Gao, J., and Mutchler, T.R., 2019. Relative contributions of DNRA and denitrification to nitrate reduction in *Thalassia testudinum* seagrass beds in coastal Florida (USA). *Estuaries and Coasts*, 42(4), 1001–1014.

Kilminster, K.; McMahon, K.; Waycott, M.; Kendrick, G.A.; Scanes, P.; McKenzie, L.; O'Brien, K.R.; Lyons, M.; Ferguson, A.; Maxwell, P., and Glasby, T., 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, 534, 97–109.

Larose, D., 2016. *Discovering Statistics*. New York: W.H. Freeman and Company, 910p.

Maidanou, M.; Koulouri, P.; Arvanitidis, C.; Koutsoubas, D., and Dounas, C., 2017. Macrobenthic assemblage structure associated with a *Caulerpa prolifera* meadow in the eastern Mediterranean Sea (Elounda Bay, Crete Island). *Regional Studies in Marine Science*, 14, 1–14.

Medellu, C.S.; Suriani, N.W., and Komansilan, A., 2019. Physical and chemical water condition in and around the area of seaweed "Lahe" (*Caulerpa* sp.) growth. *Journal of Physics: Conference Series*, 317, 012048.

Mijangos-Hernández, A.I., 2018. Análisis de la productividad de *Thalassia testudinum* Banks ex Köenig y su relación con los factores ambientales de la Reserva de la Biósfera Los Petenes, Campeche. Mexico City, México: Universidad Autónoma Metropolitana, Unidad Iztapalapa, Master's thesis, 73p.

Orth, R.J.; Carruthers, T.J.; Dennison, W.C.; Duarte, C.M.; Fourqurean, J.W.; Heck, K.L.; Hughes, A.R.; Kendrick, G.A.; Kenworthy, W.J.; Olyarnik, S., and Short, F.T., 2006. A global crisis for seagrass ecosystems. *Bioscience*, 56(12), 987–996.

Pacheco, M.C.; Pacheco-Ruíz, I.; Ramos, J.; Cetz-Navarro, N.P., and Soto, J.L., 2009. Presencia del género *Caulerpa* en Bahía de San Francisco de Campeche, Cam. *Hidrobiológica*, 19(3), 57–69.

Phillips, J.A., 2009. Reproductive ecology of *Caulerpa taxifolia* (Caulerpaceae, Bryopsidales) in subtropical eastern Australia. *European Journal of Phycology*, 44(1), 81–88.

Phillips, R.C. and Durako M.J., 2000. Global status of seagrasses. *In:* Sheppard, C. (ed.), *Seas at the Millennium: An Environmental Evaluation, Volume 3*. Amsterdam: Elsevier Science, pp. 1–16.

Powell, G.V.; Kenworthy, J.W., and Fourqurean, J.W., 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Science*, 44(1), 324–340.

Ramírez, R.; Jairo, J.; Arcila, L.; Cristina, M.; Sepúlveda, A., and Catalina, S., 2015. Quantification of components affecting the vertical attenuation coefficient for downward irradiance in Ríogrande II reservoir (Colombia). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 39(151), 228–238.

Rose, C.D. and Dawes, C.J., 1999. Effects of community structure on the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series*, 184, 83–95.

Roth-Schulze, A.J.; Thomas, T.; Steinberg, P.; Deveney, M.R.; Tanner, J.E.; Wiltshire, K.H.; Papantoniou, S.; Runcie, J.W., and Gurgel, C.F.D., 2018. The effects of warming and ocean acidification on growth, photosynthesis, and bacterial communities for the marine invasive macroalga *Caulerpa taxifolia*. *Limnology and Oceanography*, 63(1), 459–471.

Smith, C.M. and Walters, L.J., 1999. Fragmentation as a strategy for *Caulerpa* species: Fates of fragments and implications for management of an invasive weed. *Marine Ecology*, 20(3–4), 307–319.

Strickland, J.D. and Parsons, T.R., 1972. *A Practical Handbook of Seawater Analysis*. Ottawa, Canada, Fisheries Research Board of Canada, 310p.

Szmant, A.M. and Forrester, A., 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs*, 15(1), 21–41.

Tabachnick, B.G. and Fidell, L.S., 2019. *Using Multivariate Statistics*. New York: Pearson Press, 815p.

Thomas, J.E., 2003. *Caulerpa taxifolia* in Moreton Bay—Distribution and Seagrass Interactions. Queensland, Australia: The University of Queensland, Bachelor's thesis, 58p.

Tuya, F.; Haroun, R., and Espino, F., 2014. Economic assessment of ecosystem services: Monetary value of seagrass meadows for coastal fisheries. *Ocean and Coastal Management*, 96, 181–187.

Van Tussenbroek, B.I.; Barba-Santos, M.G.; Wong, J.G.R.; van Dijk, J.K., and Waycott, M., 2010. *Guía de los pastos marinos tropicales del Atlántico oeste*. México D.F.: Universidad Nacional Autónoma de México Press, 79p.

Van Tussenbroek, B.I.; Vonk, J.A.; Stapel, J.; Erftemeijer, P.L.; Middelburg, J.J., and Zieman, J.C., 2006. The biology of *Thalassia*: Paradigms and recent advances in research. *In:* Larkum, A.W.; Orth, R.J., and Duarte, C.M. (eds.), *Seagrasses: Biology, Ecology*

and Conservation. Dordrecht, The Netherlands, Springer, pp. 409–439.

Waycott, M.; Procaccini, G.; Les, D.H., and Reusch, T.B., 2007. Seagrass evolution, ecology and conservation: Nutrient dynamics in seagrass ecosystems. *In:* larkum, A.W.D.; Orth, R.J., and Duarte, C. (eds.), *Seagrasses: Biology, Ecology and Conservation*. Dordrecht, The Netherlands: Springer, pp. 25–50.

Wetzel, R.G., 2001. *Limnology: Lake and River Ecosystems*. San Diego, California: Academic Press, 985p.

Williams, S.L., 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Marine Ecology Progress Series*, 35, 91–98.

Wiltshire, K.H. and Deveney, M.R., 2017. *The Introduced Alga* Caulerpa taxifolia *in South Australia: Infestation Boundary Surveys and Feasibility of Control for Populations Outside the Containment Area*. Adelaide, Australia: South Australian Research and Development Institute (SARDI), *Research Report Series No. 946*, 16p.

Casa abierta al tiempo
UNIVERSIDAD AUTÓNOMA METROPOLITANA

Doctorado en Ciencias Biológicas y de la Salud

IZTAPALAPA
BIOLOGICAL AND HEALTH SCIENCES
DOCTORATE IN BIOLOGICAL AND HEALTH SCIENCES

THESIS

"STUDY OF THE INTERACTION BETWEEN *THALASSIA TESTUDINUM* AND *CAULERPA PASPALOIDES* IN THE LOS PETENES BIOSPHERE RESERVE, CAMPECHE, MEXICO"

TO OBTAIN THE DEGREE OF

DOCTOR IN BIOLOGICAL AND HEALTH SCIENCES

PRESENTS

M. IN B. C. SERGIO ARMANDO FUENTES AGUEDA
Register: 2163802437
kamahl2004@gmail.com/ sfagueda87@xanum.uam.mx

ORCID: 0000-0003-3297-5104

DIRECTORA: MARGARITA ELIZABETH GALLEGOS MARTÍNEZ

JURY
PRESIDENT: DR. MARGARITA ELIZABETH GALLEGOS MARTÍNEZ
SECRETARY: DR. JORDAN KYRIL GOLUBOV FIGUEROA
VOCAL 1: DR. MARÍA DEL CARMEN MANDUJANO SÁNCHEZ
VOCAL 2: DR. THOMAS A. FRANKOVICH
VOCAL 3: DR. ABEL SENTÍES GRANADOS

IZTAPALAPA, MEXICO CITY, 24TH OF MAY, 2025

This project was carried out:

In The Seagrass Laboratory of the Universidad Autónoma Metropolitana, Iztapalapa, Department of Hydrobiology, under the direction of Dr. Margarita Elizabeth Gallegos Martínez.

In The Ecology and Evolution Laboratory at the Institute of Ecology of the National Autonomous University of Mexico under the advice of Dr. María del Carmen Mandujano Sánchez.

In The Laboratory of Plant Ecology and Taxonomy of the Universidad Autónoma Metropolitana Xochimilco under the advice of Dr. Jordan K. Golubov Figueroa

The author thanks the National Council of Science and Technology (CONACyT) for the scholarship granted for his doctoral studies, with registration number 288716, which covered the period from September 1, 2016, to August 31, 2020. Also, the UAM Postgraduate Extraordinary Support Committee for the extraordinary support it has given since September 2020.

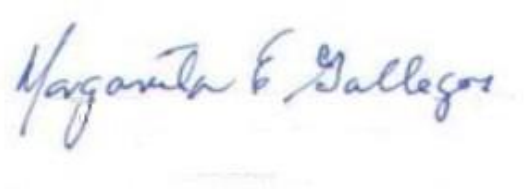
The Doctorate of Biological and Health Sciences of the Universidad Autónoma Metropolitana belong to the CONACyT Register of Excellence Postgraduates and, in addition, have the support of the same Council with the agreement PFP-20-93.

The Academic Commission assigned the jury for the Doctorate in Biological and Health Sciences of the Universidad Autónoma Metropolitana approved the thesis presented:

Sergio Armando Fuentes Agueda

Thesis approval date: May 24th, 2024

JURY:



President: Dr. Margarita Elizabeth Gallegos Martínez

Secretary: Dr. Jordan Kyril Golubov Figueroa

Member 1: Dr. María del Carmen Mandujano

Member 2: Dr. Thomas A. Frankovich

Member 3: Dr. Abel Sentíes Granados

ACKNOWLEDGMENTS:

This thesis was thanks to:

- Dr. Margarita Elizabeth Gallegos Martínez for directing this thesis.

- Dr. María del Carmen Mandujano Sánchez for advising this thesis.

- Dr. Jordan K. Golubov Figueroa for advising this thesis.

- The Tutoring Committee was formed by Dr. Margarita Elizabeth Gallegos, Dr. María del Carmen Mandujano Sánchez Martínez, and Jordan K. Golubov Figueroa for their advice, development, support, and reviews they gave during this project.

- The Jury formed by Dr. Carlos Manuel Duarte Quesada, Dr. Margarita Elizabeth Gallegos, Dr. María del Carmen Mandujano Sánchez, Dr. Thomas A. Frankovich, Dr. Jordan Kiril Golubov Figueroa and Dr. Abel Sentíes Granados.

- Dr. Noé Manuel Montaño Arias for reviewing this thesis and being The Representative of the Academic Commission of the pre-doctorate exam process.

- The Ph.D. Program in Biological and Health Sciences at the Universidad Autónoma Metropolitana for their support and reviews in the process.

- The Universidad Autónoma Metropolitana for its support in the facilities and services provided in the Ph.D. process.

- The project "State of Health, conservation and Vulnerability of the seagrass ecosystems of the Coast of the Gulf of Mexico" was sponsored by the Secretary of Energy, CONACYT (CISESE, CIGOM).

- The members of the UAM-I seagrass laboratory, which support and friendship was given during this critical period of my life:

  Hydrobiologist Gabriela Márquez Labastida for the logistics in the field trips, laboratory work, and support in the SAV biomass data.

  Hydrobiologist Francisco Javier Ordoñez Gasca for his support in the logistics of the field trips, and complementation of the light and nutrient data and laboratory work.

  Hydrobiologist Ivanhoe Ricardo Herrera Moro Chao for his advice and support in the area of physicochemical parameters associated with seagrass and statistical analysis, physicochemical data, laboratory work, as well as for his help in the field work.

  Hydrobiologist Omar López for his support in the logistics of the field trips, and nutrient data and laboratory work.

  Hydrobiologist Eduardo Hernández Elizalde for his support in the field, the organic matter data, and for the laboratory work.

  Hydrobiologist Yolanda Gabriela Valencia Vilchis for her support in the field, for complementing the data on photosynthetic pigments, and for the laboratory work.

  Hydrobiologist Alfredo Alcántara León for his support in the field and his work in the laboratory.

  Environmental Engineer Martín for his support in the field and his work in the laboratory.

Biologist Guillermina Avelino for her advice on the demographics of seagrasses, as well as for advised on the data and for the laboratory work.

M.C. Gilberto Hernández Cárdenas for supporting the spatial data and preparing the area map.

M.C. Fernando Valdez Cruz for his advice on sediments and organic matter related to the SAV, as well as for the support in the field, for the complementation of sediment data, and the laboratory work.

M.C. Angélica Itai Mijangos Hernández for her advice on the health conditions of the seagrasses, as well as for the support in the field and the laboratory work.

M.C. Alma Delia Toledo Guzmán for her support in the spatial data of the species and the preparation of maps associated with photosynthetic efficiency.

M.C. Iliana Pérez Espinosa for her support in the spatial data of the species, in the field work, advised and work in the laboratory.

- The Biologist José Alfredo Arévalo Ramírez of the UAM-X for advice, review, corrections, and suggestions in the photosynthetic efficiency.

- Dr. Abel Sentíes and Dr. Kurt M. Dreckmann from the Macroalgae Laboratory of the Universidad Autónoma Metropolitana Iztapalapa for identifying the algae species.

- Dr. Carlos Canto of the Physics Institute of the UNAM for advice on the creation of behavior models and the use of the Origin program.

- Dr. Mariana Rojas Aréchiga for the support and logistics in the Ecology and Evolution laboratory at UNAM.

- The members of the Article Workshop of the Institute of Ecology, UNAM, Joanne Peel, Donaji López, Omar Díaz Segura, Gabriel Urschid, Héctor Tapia, Juan Carlos Flores, Vania Olmos, Jessica Reyes, Sandra, Rosa, Cristina Ramírez, Omar Durán, Jerry, Linda Mariana, Esteban, Saldino, Isabel, Manuel, Mapa, Tania, Jazz, Pactli, Andrés, Pepillo and other students for the suggestions and corrections of the project.

- Juan Chay and company not only for guiding us to the study areas, but also for their help in the field, their attention during the sampling, and the friendship they gave us during the project.

- The EBC (Science Diving Team) for the knowledge and preparation they taught me to dive, since without it, it would not have been possible to carry out this thesis.
- The Kalohi Kamahine Polynesian cultural center, directed by Alejandro Ocejo and Corina Ocejo and their members, for helping me through a difficult part in my life and teaching me that dance and life have a lot in common.
- Lic. Adolfo Ruiz for helping me with the mental health and mindfulness.
- Dr. Alexis Lodigiani for helping me with my physical health and reminding me that one sets limits and decides to exceed them or not.
- My family for the support they gave me during my Ph.D.
- Life itself for being my teacher in blood and flesh.

ABSTRACT

Interactions between seagrasses and macroalgae have been defined as competitive relationships since they use nutrients, sunlight, and colonization space as limiting resources in marine environments. It is not known whether *Thalassia testudinum* is affected explicitly by its interaction with *Caulerpa paspaloides***.**

The research aims to determine and analyze the type of interaction between of *T. testudinum* and *C. paspaloides* using population, physicochemical, and photosynthetic efficiency indicators. Monitoring was done in the Petenes Biosphere in three meadows (monospecific of *T. testudinum*, monospecific of *C. paspaloides,* and a mix of both species) in three seasons that differ climatically: dry, rains and “nortes” from 2016 to the year 2019. Biomass samples of *T. testudinum* and *C. paspaloides* were collected to estimate the effects of species interactions on growth, and the finite growth rate of both species and their growth per day in leaves were determined. The physicochemical factors at the three sites, the relative amount of nutrients in the water and interstitial column, and the quantum efficiency of both species were measured. For these parameters, PCA tests were performed to establish the most representative variables that have a direct relationship in the study. The fitness in monospecific meadows and mixed meadows for both species was the same, and the growing and abiotic variables that were different in the fields were depth and grain size. Temperature, nitrates, nitrites, and DIN were different during the seasons. Photosynthetic efficiency was lower in the mixed meadows of *C. paspaloides* during the rainy season, and *T. testudinum* was significatively lower in the rainy season in both meadows. The PCA indicates that the most important factors were water depth, biomass of both species, the *Fv/Fm* of both species, the presence of macroalgae, and the other factors were composed of temperature and NID. The presence of *T. testudinum* and *C. paspaloides* is mainly due to biological factors. In monospecific populations, due to the absence of competitors, the fitness of both species will be increased. However, the mortality of *C. paspaloides* was higher than the mortality of *T. testudinum* and allowed for the colonization of macroalgae. In shallow sites, *T. testudinum* grew favorably, and *C. paspaloides*, in deep places**.** Biomass samples with high temperatures and NID were associated with an increase in macroalgae and

the growth of *C. paspaloides* in mixed populations. Increase in nutrients and temperature could have a significative increase in *C. paspaloides* populations during the rainy season.

Keywords: Interactions, submerged aquatic vegetation, competition, demography, photosynthetic efficiency, abiotic factors.

RESUMEN

En todo el mundo se han estudiado los factores abióticos que establecen la distribución y abundancia de los pastos marinos en zonas tropicales; éstos son: la temperatura, la salinidad, la atenuación de luz, la composición del sedimento y la profundidad. Las interacciones entre pastos marinos y macroalgas se han definido como relaciones de competencia, ya que usan los nutrientes, la luz solar y el espacio de colonización como recursos comunes en los ambientes marinos. La parte biótica como las interacciones con otros elementos de la vegetación acuática sumergida no se ha abordado debido a su complejidad. El objetivo de este trabajo fue determinar y analizar el tipo de interacción que hay entre las especies de *T. testudinum* y *Caulerpa paspaloides* usando indicadores poblacionales, fisicoquímicos y de eficiencia fotosintética. Los monitoreos se hicieron en la Biosfera de los Petenes en tres praderas de Vegetación Acuática Sumergida (VAS) (monoespecífica de *T. testudinum,* una monoespecífica de *C. paspaloides* y mixta de ambas especies) en las temporadas de nortes, lluvias y secas desde 2016 a 2019. Se cuantificaron los factores fisicoquímicos en los tres sitios, la cantidad relativa de nutrientes en columna de agua e intersticiales y la eficiencia fotosintética que tienen ambas especies. Para estimar los efectos en el crecimiento de las interacciones entre especies se colectaron muestras de biomasa de *T. testudinum* y *C. paspaloides*, se determinó la tasa finita de crecimiento de ambas especies, así como su crecimiento por días. Se realizó un PCA para encontrar los factores más representativos que pueden tener una relación directa con el establecimiento y la abundancia de las dos especies. Se encontró que los factores fisicoquímicos que difieren en las praderas son la profundidad y el tamaño del grano. Sin embargo, las variables fisicoquímicas de temperatura y del Nitrógeno Inorgánico Disuelto (NID) eran diferentes a lo largo de las tres temporadas, siendo mayores en la temporada de lluvias. A pesar de esto, el crecimiento y establecimiento de ambas especies fue el mismo en praderas monoespecíficas, pero la eficiencia fotosintética de *C. paspaloides* fue menor en la temporada de lluvias y en las praderas mixtas. El PCA nos indica que los factores más importantes son la profundidad, las biomasas de ambas especies, las *Fv/Fm* de ambas especies y la presencia de otras macroalgas que conforman el factor 1 y la

temperatura, y el NID que conforma el factor 2. La presencia de *T. testudinum* y *C. paspaloides* se da principalmente por factores biológicos. Debido a que existe mínima competencia en praderas monoespecíficas, *T. testudinum* invierte los recursos en reproducción sexual y crecimiento horizontal; en cambio, en praderas mixtas los invierte en crecimiento vertical y formación de hojas. Sin embargo, *C. paspaloides* en praderas mixtas presenta dos temporadas de crecimiento, sugiriendo que la presencia de *T. testudinum* reduce los competidores y permite un mayor establecimiento de las especies. A pesar de que la mortalidad de *C. paspaloides* ocurre en la temporada de nortes esto permite el establecimiento de *T. testudinum*. Se sugiere que la adecuación de *T. testudinum* tiene una relación inversa a la de *C. paspaloides*, y que los aumentos en la temperatura y NID se asocian al aumento de macroalgas y al crecimiento.

Palabras clave: Interacciones, vegetación acuática sumergida, competencia, demografía, eficiencia fotosintética, pastos marinos, macroalgas.

1-. INTRODUCTION

Biological interactions are the relationships between organisms in an ecosystem. We can divide them into two, the intraspecific ones that occur mainly between individuals of the same species and the interspecific ones that occur between individuals of different species (Aschehoug et al., 2016). Biological interactions can be classified from the relationship that individuals have; if both individuals benefit each other, it is called mutualism or commensalism (Hacker and Gaines, 1997); when one individual harms the other and the other benefits, it is called parasitism and, finally, if both individuals need a shared resource for their vital functions and one of them suffers a drop in fitness, it is called competition (Tilman, 1994).

"The capture of essential resources in a limited and commonplace by nearby individuals" is defined as Competition for resources (Aschehoug et al., 2016). There are two criteria for the capture of resources in a competition: whether the plants can capture and use resources before their neighbors or that they can invest in structures that help them capture and use resources efficiently and, as a result, generate a trade-off in the allocation of energy to different parts of the plant; for example, developing large leaves and as a consequence having few rhizomes.

When there is competition for one resource, other resources are affected; For example, if an individual can better assimilate sunlight, which is a resource that plants use for the formation and growth of structures that incorporate nutrients such as roots, they will be able to absorb water and nutrients in the soil better. (Pugnaire and Luque, 2001). If the resources are sufficient in the environment, coexistence between the two individuals is possible, and they can interact without affecting their growth, reproduction, or survival (Tilman, 1984).

For a population to persist, some demographic parameters must behave in a density-dependent manner, at least at some time or place (Hixon and Carr 1997). Sale and Tolimieri (2000) have called this PEDDTOP ("persistence equals density dependence at some time or place") because the conditions in which the populations develop do not remain constant over time, which affects the rates of demographics causing fluctuations in population size. Hixon et al. (2002) mention that regulation is essential

for the persistence of populations and that density dependence is the only possible mechanism through competition and predation.

To find out if there is competition or coexistence is consider the population growth (dN/dt), the number of individuals (N), and the carrying capacity (K) of both are considered species (Roughgarden,1983). Although the model only indicates the logistic growth of a population, it can be integrated with another variable which is how another population affects this population, called "α" for population one and "β" for population 2, and thus have a coupled model for both populations:

$$\frac{dN}{dt} = rN\frac{(K - \alpha N)}{K}$$

$$\frac{dN}{dt} = rN\frac{(K - \beta N)}{K}$$

Therefore, to know the interaction between two species, it is necessary to understand the population dynamics of the competing populations and the dynamics of the resources that these populations use for their adaptation (Roughgarden, 1983).

1.1 Seagrasses

Seagrasses are angiosperms that carry out their life cycle submerged in the seabed. There are a total of 58 species worldwide (Orth et al., 2006). Despite being a small group of plants, seagrass meadows have significant ecological and biological importance since, in addition to coral reefs and mangroves, they are systems that register high primary productivity (500- 4000 g carbon/m^2/year) (Duarte and Cebrian, 1996). They also provide shelter, food, and protection and are mating, spawning, and growth sites for numerous species of marine invertebrates of economic and ecological importance, such as bivalves and crustaceans (Raz-Guzmán and Sánchez-Martínez, 2001).

In Mexico, there are 11 species of seagrasses. In the Gulf of Mexico and the Caribbean region, *Thalassia testudinum* (Banks ex König), *Syringodium filiforme* (Kützing), and *Halodule wrightii* (Ascherson) are the main dominant species (Gallegos, 2010). Seagrasses grow in monospecific populations and mixed populations with other species of seagrass and with macroalgae. Of these, the macroalgae that have been most studied in terms of their relationship with seagrass meadows are those belonging to the genus Caulerpa (Levinton, 2009).

1.2 Biotic and abiotic factors

The composition of seagrass meadows and the marine fauna that live in these systems depends on the abiotic conditions that surround it, such as temperature, salinity, water movement, and the essential elements (carbon, hydrogen, oxygen, and

nitrogen; Davis and Fourqurean, 2001) and (Reece, 2011). Plants acquire these essential elements (CHON) directly from the water column and interstitial water in the form of nutrients such as ammonium, nitrates, and phosphorus and by the decomposition of organic matter by bacteria and other organisms (Duarte, 1990).

Ammonium is produced directly from animal waste and/or animal carcasses which constitutes an essential source of nitrogen and hydrogen for seagrasses (Sandoval-Gil, 2016). Therefore, seagrasses act as biofilters in the environment, absorbing ammonia and breaking it down for their metabolic functions. Since seagrasses are mostly long-lived compared to macroalgae, this makes them effective biofilters (de los Santos et al. 2020). Nowicki and Nixon (1985) found that in muddy sediments, ammonia tends to be higher, thanks to the fact that there is a positive relation with the amount of organic matter and the size of the grain that traps ammonium. Therefore, sandy sediments have a lower amount of ammonium since the grain is more prominent and releases ammonia into the water column. Nowicki and Nixon (1985) also found that ammonium is higher in deep areas than in shallow regions; basically due to the lack of light leading to lower synthesis by plant organisms that do not metabolize it properly.

Nitrates can be found naturally in the rain and the nitrification of organic compounds (Moreno-Marín, 2016). However, excess fertilizers and chemicals of agricultural or livestock origin can also be significant source. In this case, ammonium is consumed more than nitrates. Still, seagrass can use nitrates in the water column, especially in areas with high CO_2 levels, where nitrates are consumed at a higher assimilation rates than ammonium (Alexandre et al., 2016). Even though Nowicki and Nixon (1985) did not find a relationship between temperature or light with the amount of nitrates in the medium, they observed that the interstitial nitrates were higher in sandy sediments than in muddy ones. Nitrates can be classified into two, high nitrates, which are the nitrogen produced by organic matter produced by living beings (organic waste, plant parts, and dead animals), used by plant organisms, and low nitrates, which are residual nitrogen resulting from the consumption of organic matter by

microbes. *Nitrates* in large quantities can be toxic to marine flora and fauna (Camargo et al., 2005).

Seagrass leaves can absorb nitrates and can therefore be a significant loss of nitrogen when there is a high foliar loss. However, when the leaves reach the sediment, they can be reabsorbed in the roots (Terrados and Williams, 1997) as low nitrates. The residual nitrogen resulting from the consumption of organic matter by microbes is deposited in the sediment and reabsorbs through the root system. However, excess nitrates also produced by litter fall in large quantities can be toxic to marine flora and fauna (Camargo et al., 2005).

Phosphorus is a nutrient associated with organic and agricultural waste processed by photosynthetic organisms to generate high vegetative growth and reproduction, however, high amounts of this nutrient will result in eutrophication (Moosman et al., 2006). Libes (2009) points out that phosphorus is a nutrient that, in excess, is associated with anoxic environments. The use of phosphorous is also sediment dependent: muddy environments use less than in sandy sediments, probably associated to grain size as phosphorus to travel more efficiently with increased pore size. Additionally, Nowicki and Nixon (1985) found that in muddy sediments, phosphorus is higher than in sandy sediments. Also, there is more phosphorus in the deposits at higher temperatures.

The interest in studying the nutrients related to the SAV is first to detect the areas that suffer from nutrient limitation and, therefore, the establishment of the elements of the SAV. For example, the increase in nutrients increases the growth of macroalgae (Waycott et al., 2007) and can be used as an indicator of environmental deterioration or anthropic influence.

The composition of the sediment, as well as its size, is a determinant of seagrass meadows. Seagrasses such as several species of *Thalassia* not only cover part of the water column, but their rhizomes, depending on the species, can cover varying depths (centimeters to meters deep). The availability, storage, and loss of pore-water nutrients will depend on the sediment's physical characteristics and composition. For

example, t the permeability in sandy sediments is higher leading to different physicochemical characteristics species distribution and composition (Adhitya et al., 2016).

Therefore, in simple SAV communities (composed of colonizing seagrass species and macroalgae), the sediment composition will be loosely compact and coarse-grained since they do not have rhizoid systems that decompose the sediment or organic matter for the establishment of microbiota, in addition to the loss of interstitial nutrients such as nitrogen and phosphorus, so it will tend to have colonizing seagrass species and macroalgae. On the contrary, permanent species such as *T. testudinum* can be found in fine sediments that are irregular in composition and more stratified. Populations of this species will tend to have a more extensive rhizoid system, a more developed microbiota in the sediment, and, therefore, higher sediment decomposition (Marbá et al. 2007).

In the area of the Yucatan Peninsula, unlike other regions of the world, there are three marked seasons during the year, one of the heavy rains from May to August (rains), another of cold and strong winds that come from the north (locally known as “nortes”) from September to November and another when there is no rain (dry), from December to April (CONAGUA, 2015). The climatic seasons have clear ecological consequences in the area, the “nortes” season negatively affects the SAV composition and distribution, causing the disappearance of plant species, of both algae and some species of seagrass (Fuentes et al., 2014).

1.3 Demography in seagrasses and macroalgae

By definition, demography describes the numerical changes that occur, either due to biotic or abiotic factors. The changes are represented through the evaluation of the natality and mortality of the individuals that comprise them based on the differences in age and the stage of development in which they are found (Stearns, 1999). In addition, it is also responsible for describing and hypothesizing how populations are affected by changes in the environment. Therefore, population ecology studies make it possible to assess and investigate whether populations are increasing, decreasing,

or are in numerical equilibrium (Caswell, 2001) and to point out what biological or anthropogenic phenomena could alter the demographic behavior of populations (Glardon et al., 2008).

Population ecology aims to understand how a population is formed, how it is affected by environmental alterations, what needs it has, and how it works (Harper, 1977). Cyclical fluctuation trends can be seen for specific populations, such as specific dynamic trends related to environmental changes, but not entirely controlled by the environment (Arango, 2008).

There are two fundamental types of demographic studies: dynamic studies, which consist of monitoring a cohort of individuals over one or several years, and static studies (several cohorts), in which only the age structure and fertility at a given time is known (Harper, 1977; Silvertown, 1987).

The vital fertility and survival rates obtained from the follow-up of each individual can be summarized and represented in different ways, such as in life tables, which allow us to redive the age of first reproduction, mortality birth and growth rates, reproductive value, and population structure (Harper, 1977; Silvertown, 1987).

In the case of clonal organisms (those that produce similar sections (ramets) that act as an independent and separate organism from the organism (Harper, 1977)), it is not easy to establish the age of individuals, and this is not always the variable that determines their demographic behavior, as happens with corals, plants, algae or insects with variable development phases. Often, age is a less reliable indicator due to the variability of growth and development. For example, in *Pseudopterogorgia americana* corals, the established age for 100 cm individuals is 14 to 60 years (Yoshioka and Yoshioka, 1991). Therefore, for these corals, it is more meaningful to use classification by stages rather than age, as in the case of many plant species (Mandujano et al., 2001).

In seagrasses and algae, recording biomass per square meter has been a helpful tool for monitoring the survival and establishment of individuals in a population (Phillips and Price, 2002, Van Tussenbroek et al., 2010). However, demographic methods

have been designed to measure and identify the status of the populations of these species in a more direct and precise way, considering that they are species with modular growth. *T. testudinum* to quantify the age of each shoot is used the plastochrone index (PI), which consists of the number of leaves produced by a shoot per year, it is essential to establish the ages of the vertical shoots of *T. testudinum* (Duarte et al. 1994). Since *C. paspaloides* is a highly clonal organism due to its coenocytic growth, stolons, and fronds can be considered demographic units to analyze the populations of this species (Fuentes et al. 2014). Since both species have different life histories and are taxonomically different, it can be challenging to compare the growth and establishment of both species. However, there are adequacy estimators that summarize whether a species grows, is maintained, or decreases over time, and that can be standardized for any biological species, as is the case of the finite growth rate (λ) (Mandujano et al., 2001), which is a ratio of the number of individuals or biomass change over time.

1.4 Photosynthesis in seagrasses and macroalgae

The CHON elements (Carbon, Hydrogen, Oxygen, and Nitrogen) are essential in photosynthesis (Reece, 2011). A large proportion (40%) of planetary photosynthesis takes place in aquatic-marine systems; therefore, along with phytoplankton, seagrasses are important as O_2 generators and carbon sinks (Falkowski and Raven, 2013).

In seagrass meadows, photosynthesis can be altered by abiotic factors; for example, at greater depths and turbidity in the water, lower production of oxygen has been recorded as a consequence of reduced seagrass photosynthesis (Zimmerman, 2007).

Photosynthesis can be recorded by direct measurement of oxygen production in an enclosed environment or by recording photosynthetic efficiency (*Fv/Fm*). Indirect methods of chloroplast fluorescence (in photosystem II) are used, saturating with light and recording the saturation curve (Kalaji et al., 2014). Changes and decreases in photosynthetic efficiency are used as indicators of stress and environmental disturbances that affect photosynthesis (turbidity, temperature, pH, contamination,

etc.), indicating the state of physiological health of the plants. Furthermore, it has been found that *Fv/Fm* is positively correlated with the rate of CO_2 assimilation and the rate of O_2 production (Lamberts, 2008). Therefore, photosynthetic efficiency tells us which species are stressed and predicts areas of high environmental impact. The established norm assumes those values less than 0.8 are a sign of photosynthetic stress and, therefore, there is damage to photosystem II (Lamberts, 2008). Underwater plants had to adapt to a decrease in available light, so naturally, their light requirements are lower (0.7 for *T. testudinum* Maxwell, 2003 and 0.6 for macroalgae Biber et al., 2004).

Since plants live in variable systems and are subject to factors that affect their fitness, there are regulatory mechanisms that allow them to adapt to these adverse conditions. In the case of increased or decreased sunlight, certain accessory pigments in chloroplasts regulate the arrival of light through photosystem II and prevent overheating and denaturation of chloroplast proteins in the event of increased radiation (Lamberts, 2008). One of these processes, the xanthophyll cycle, generates a conversion of antheraxanthin to zeaxanthin in the absence of light and antheraxanthin production in leaves with excess light. The accessory pigments are also tools to establish the quality of life of the SAV in the aquatic environment.

1.5 Interaction of seagrases and macroalgae

The interactions that seagrasses and macroalgae have in native environments are competition for nutrients, space in substrate and sunlight. Some of the strategies used by seagrass are the growth of leaves to capture light better and the assimilation of nutrients in the water column. However, if there are macroalgae in the community, they will have better absorption of nutrients from the water column since they compete with epiphytic organisms and phytoplankton (Fong and Harwell, 1994).

Fong and Harwell (1994) also deduced that under high conditions of solar irradiation and interstitial nutrients, they could have a greater establishment and abundance in the system and this is shared with macroalgae and other seagrass species such as *S. filiforme* and *H. wrightii*. However, Biber et al. (2004) saw that for macroalgae in

mixed environments, the limiting resource would be the nutrients of the water column, which is why they are more relevant in seagrass systems.

2-. LITERATURE REVIEW

Studies that have associated competition between seagrass with macroalgae have explored the availability of light, space, and nutrients in the environment (Carbon and Nitrogen; Van Tussenbroek et al., 2010).

Ceccherelli and Cinelli (1997) described the competition between *C. taxifolia* and the seagrass *Cymodocea nodosa* in the Mediterranean, where they observed that there is a direct interaction between the two species, negatively affecting the cover of *C. nodosa* and indicating two competition processes: the successful acquisition of nutrients and their practical use when they are absent.

Thomas (2003) observed that in Australia, *Caulerpa taxifolia* presented allelopathic strategies by releasing toxic substances, which suggests that there is competition between these two species. He identified sunlight as the limiting resource since he observed that in habitats covered with *C. taxifolia*, eutrophication levels were high.

Fong and Harwel (1994) described the SAV community that exists in Florida, USA, defining biological and physicochemical factors that affect the survival and establishment of the species that comprise it, such as *T. testudinum*. Water with intermediate temperatures (25-32°C), intermediate salinities (less than 40), low concentrations of nutrients in the water column (less than 1.5 mg), and high concentrations of interstitial nutrients (greater than 2mg) were suitable conditions for growth and establishment of *T. testudinum*. Instead, the factors that benefit the growth and establishment of macroalgae, in general, were high temperatures (greater than 32°C), intermediate salinity (less than 40), and high concentration of nutrients in the water column (greater than 2mg).

Other studies, such as those by Davis and Fourqurean (2001), have given greater importance to nutrients in water and sediments, with Nitrogen and Phosphorus being the most significant for establishing abundant SAV elements. However, in tropical areas, it has been seen that these interactions are not always harmful, such as in pantropical regions, as reported by Meñez and Calumpong (1982), where algae consume heavy metals and other nutrients that seagrasses cannot naturally

assimilate or even have contributions to the benthic community such as providing nutrients.

In “Los Petenes,” *Thalassia testudinum* can be found in monospecific or mixed meadows with macroalgae across the reserve and is the most abundant and common species, followed by *S. filiforme, H. wrightii* and a diversity of macroalgae (Pérez *et al.*, 2019). Within the macroalgae, *Caulerpa paspaloides* (Weber Bosse) is the most frequent and grows sympatrically with *T. testudinum* (Fuentes *et al.*, 2014). However, in Campeche Mexico, it is more likely found forming monospecific meadows in ports and around a hydroelectric power plant (Pacheco, 2009). Fuentes (2015) suggested that in the “nortes” season, there is a negative effect on the suitability of *C. paspaloides* since there are increases in water dynamics and a reduction in nutrients in the water column. For this reason, *C. pasapaloides* var *wurdermannii* grows and develops in the rainy season, survives during the “nortes”, and its recruitment and development begin in the dry season.

Studies of the interactions between seagrass and algae are scarce, and no updated information allows us to understand the mechanisms that determine them, so this proyect aims to answer the following questions:

- What factors (biological and abiotic) have a significant influence over the interaction and the establishment of each species?
- What kind of interaction characterizes *T. testudinum* and *C. paspaloides* when found in mixed meadows?

The general objective was to determine and analyze the type of interaction between Caulerpa and seagrass species using population indicators, in this particular case of *Thalassia testudinum* and *Caulerpa paspaloides* in the Petenes Biosphere. Through the analysis of biotic factors (demography, photosynthesis, and species) and abiotic factors (nutrients, sediment, and environmental characteristics).The particular objectives were:

- Describe the biological composition of monospecific and mixed meadows of *T. testudinum* and *C. paspaloides*.
- Describe the physicochemical characteristics of monospecific and mixed meadows of *T. testudinum* and *C. paspaloides*.
- To evaluate the population dynamics and growth of *T. testudinum* and *C. paspaloides* in monospecific or mixed populations.
- To evaluate the health status of *T. testudinum* and *C. paspaloides* with photosynthetic efficiency and pigment content parameters.
- To evaluate which physicochemical factors can affect the health status of *T. testudinum* and *C. paspaloides*.
- Describe the main biotic and abiotic factors that affect the growth and establishment of *T. testudinum* and *C. paspaloides*.
- Describe the interaction of *T. testudinum* and *C. paspaloides*.

The hypothesis is that there is a competition between *T. testudinum* and *C. paspaloides*, where *T. testudinum* has the advantage for its strategies of permanence and photosynthetic efficiency.

3-. METHODS

3.1 Description of the area

Surveys were done in “Los Petenes” marine preserve, a protected area located in the Gulf of Mexico located in southeastern Mexico which possesses the largest region in Mexico of Submerged Aquatic Vegetation (SAV, 1,817.64 km^2, 20°51′30″N 90°20′00″W). In “Los Petenes,” *Thalassia testudinum* can be found in monospecific or mixed stands with macroalgae across the reserve and is the most abundant and common species, followed by *S. filiforme, H. wrightii* and a diversity of macroalgae (Pérez et al., 2019). Within the macroalgae, *Caulerpa paspaloides* (Weber Bosse) is the most frequent and grows sympatrically with *T. testudinum* (Fuentes et al., 2014).

This area is distinguished by the presence of islands of wooded vegetation known as “Peten.” These vegetation formations are located in bodies of water commonly formed by the groundwater table that drains into the Gulf of Mexico, and their predominant vegetation is mangrove and low deciduous forest. The most common tree species in The Petenes are*: Rhizophora mangle* (L.), *Avicennia germinans* (L.), *Laguncularia racemosa* (L.) Gaertn., *Manilkara zapota* (P. Royen), *Ficus continifolia* (Kunth), *Swietenia macrophylla* (King), *Tabebuia rosea* (a (Bertol.) DC), *Sabal yapa* (C. Wright. ex Becc.), *Bravaisia berlandieriana* ((Nees) TF Daniel), Metopium brownei ((Jacq.) Urb.), *Bursera simaruba* (L.) Sarg., *Annona glabra* (L.), *Pisonia aculeata* (L.) and *Acrostichum aureumen* (L.) (Zamora-Crescencio, 2015) (CONABIO, 2016).

In 2014 and 2015, a pilot monitoring phase was carried out where the relative coverage of "Los Petenes" was recorded and evaluated. Based on these observations, three zones were chosen, one zone with comparable cover of 100% of *C. paspaloides*, one with 100% relative cover of *T. testudinum*, and one with 50% relative cover of the two species (Fig. 1). Once established all the cover analyses and physicochemical characterization of the sites were carried out during 2016 (November), 2017 (March, July, November), 2018 (February, April, June, August, October), and 2019 (January).

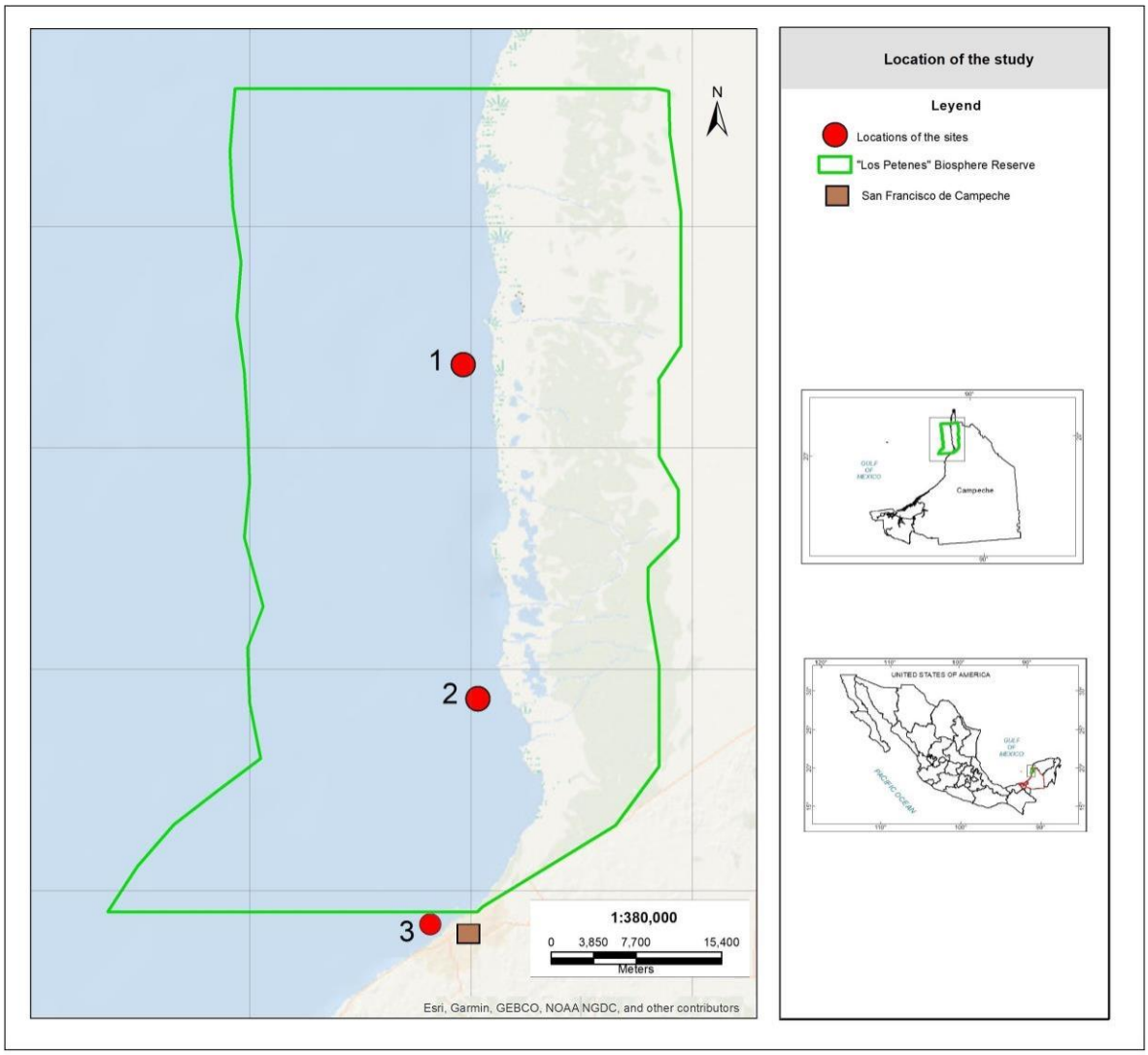


Figure 1 Study areas for the characterization of the submerged aquatic vegetation and physicochemistry for the sampling sites (1-. 100% *T. testudinum*, 2-. 50% *T. testudinum*, and 50% *C. paspaloides* and 3-. 50% *C. paspaloides*).

3.2 Submerged aquatic vegetation register

SAV cover was quantified in each site with a 0.25 cm^2 grid (0.5 × 0.5 cm plot), with 10 replicated measurements per 3 sites per 8 surveys. The SAV categories were split into species *T, testudinum*, *C. paspaloides*, as well as cover by other macroalgae and spaces with no vegetation. Random 10cm diameter cores were collected at the three sites in 2016 (November), 2017 (March, July, November), 2018 (February, April, June, August, October) and 2019 (January). Each core collected was separated into

T. testudinum biomass and other SAV elements like macroalgae, dried at 55°C for three days, and weighed. The relative record of biomass of macroalgae and *T. testudinum* was obtained.

3.3 Phytoplankton biomass

The phytoplankton biomass was obtained from a water sample (500ml), filtered through 5-micron-thick filters, and stored in cold aluminum foil in a dry environment. In the laboratory, the samples were disintegrated with acetone in plastic test tubes and centrifuged at 5000 rpm to separate the phytoplankton mass from the filter. A HACH 3900 spectrometer (HACH, 2015) was used to analyze the amount of representative phytoplankton mass in the water column.

3.4 Characterization of macroalgae species

Macroalgae samples were collected, fixed in 80% alcohol, and analyzed and identified in the UAM-I Marine and Brackish Macroalgae laboratory.

3.5 Physicochemical characterization of the meadows

Environmental variables were measured in the water column as well as in sediment (n = 4 samples per site per year). Water depth was obtained with a Secchi disk, and water samples (250 ml) were collected in the field at half depth with a Van Dorn bottle in which salinity, temperature, pH, and dissolved oxygen (D.O.) were measured with a Multiparametric sensor (YSI 556 MPS) *in situ*.

3.6 Colum water and pore water nutrients

Water column nutrients (Dissolved Inorganic Nitrogen (DIN NO_2-+NO_3- + NH_4+) and total phosphorus TP) and pore water nutrients (ammonium and total phosphorus) were obtained and analyzed with a HACH 3900 spectrophotometer at the Seagrass Laboratory of UAM Iztapalapa.

Paired sediment cores (5cm diameter × 30 cm long) were collected by divers (4 samples per site per year). One core was used to obtain soil pore water, and the other for sediment analysis. The soil pore water samples were extracted in an anoxic

chamber and separated with a centrifuge (Eppendorf centrifuge 5702) to measure ammonium and total phosphorous with the following methods (Strickland and Parsons, 1974):

For ammonium, 2ml of phenol-ethanol, 2ml of solution, sodium nitroprusside, and 5ml of alkaline solution (trisodium citrate and sodium hydroxide) were used for 50ml of water. The spectrophotometric reading was done at 640nm.

Nitrites were quantified with 1ml of a sulphanilamide solution for 50ml of water and 0.1 naphthyl-ethylenediamine dihydrochloride solutions after 6 min of rest. The spectrophotometric reading was done at 543nm.

For nitrates, 1 ml of dilute ammonium chloride solution was added to 50 ml of water through a solution column. The spectrophotometric reading was done at 543nm.

For total phosphorus, 5ml of the solution made up of ammonium molybdate (100ml), sulfuric acid (250ml), ascorbic acid (100ml), and antimony tartrate (50ml) were added to a quantity of 5ml of water. The spectrophotometric reading was done at 885nm.

For silica, 1.0 ml of ammonium molybdate solution was added to plastic cups, 200µl of 1:1 hydrochloric acid, and 10 minutes later, 300µl of oxalic acid. The spectrophotometric reading was done at 410nm.

The sediment core samples were oven-dried to constant weight at 60°C for two days and separated with a sieving tower shaker (including sieves of 0.074 mm, 0.125 mm, 0.25 mm, 0.5 mm, 1 mm, and 2 mm). Mean grain size (Mz) was calculated by the mean weight of each sieve, sediment type, and diameter (mm) and assigned following the Wentworth class size classification (Erftemeijer and Koch, 2001; Folk, 1974).

The quantification of the organic matter in the sediment was carried out according to the technique of Dean (1974), Paez-Osuna et al. (1984), and Gaudette et al. (1974). The percentage of losses on ignition was obtained after calcinating the sediment in crucibles in a muffle at a temperature of 55°C for one hour. The difference in weights

before and after calcination is attributed to the transformation of the organic matter of the sample into CO^2 and H_2O.

3.7 Demographic methods of *Thalassia testudinum*

For age and reproductive event estimations, *T. testudinum* cores were collected with a 21cm diameter metal core in July 2017 and August 2018 (*n* = 3 sampled cores per site per year) as changes in *T. testudinum* populations can only be observed in a period of >1 year. Cores were stored in plastic bags and cleaned of debris, sediment, and organisms. The number of leaves, leaf scars, internodes, flower scars, as well as average shoot length (cm), leaf length (cm), leaf width (cm), rhizome length (cm), and rhizome diameter (cm), were taken for each sampled core. In addition, core contents were divided into below-ground biomass (rhizome and subterranean shoots) and above-ground biomass (vertical shoots and leaves). The plastochrone index (PI) was calculated using the number of leaf scars and leaves in each shoot found in samples cores for each site (Duarte et al., 1994). The vertical growth rate of shoots was then calculated through linear regression of PI and shoot length. *Thalassia testudinum* shoots have flowers once a year, so shoot age was calculated with the number of leaves formed between successive flower scars and age structures were constructed and analyzed for each site (Gallegos et al. 1992). Individual density was calculated by the total number of shoots in the core (0.3 m^2). The flowering percentage was calculated by the number of flower scars and total shoots in each site (Duarte et al., 1994). The horizontal growth rate was calculated by multiplying the rhizome's average length with the horizontal internode formation rate (multiplying the ratio of average internodes and PI by the number of days a leaf is produced; Duarte et al., 1994). The distance between leaf scars for each flowering shoot, was measured to verify the age in years of a shoot (Marba et al. 1994). With this, a relationship was made with the PI and it was determined in how many years a shoot grows (Duarte et al., 1994).

After the individual quantification of the structures, they were classified into aerial biomass (leaves, vertical shoot) and underground biomass (rhizomes, roots, horizontal shoot). Samples were subsequently oven dried at 60°C for two days and

weighed to the nearest 0.001 g to estimate the rate of change in biomass (population λ) (Caswell, 2001):

$\lambda=N_{t+1}/N_t$. Where:

λ= finite rate of biomass growth

N_t=*biomass at time t*

N_{t+1}= *the biomass at time t+1*

These demography methodologies are used by Duarte et al. (1994) to calculate the plastochron interval, and Fuentes et al. (2014) to evaluate the growth rate.

To estimate the modular growth of *T. testudinum*, 50 vertical shoots of *T. testudinum* were marked in monospecific and mixed meadows. A perforation was made in the *T. testudinum* leaf with a needle, and the vertical shoot was marked with a shiny wire. After 90 days, the marked shoots were collected, and how much they grew from the scar left by the needle was measure, according to the method described by Zimmerman (1994).

To calculate the modular *λ*, the formula ($\lambda=N_{t+1}/N_t$) where:

λ= finite rate of modular growth

N_t= the length of the leaf at time *t*

N_{t+1}= the length of the leaf at time *t+1*

In this case, the length after the mark was N_t since it indicates the length on the first day, and the total length was (N_{t+1}), representing the length reached 30 days later. This methodology was adapted to that used by Duarte et al. (1994) to calculate the plastochron interval and Mandujano et al. (2001) for module marking and evaluation of the modular growth rate.

3.8 Demographic methods of *Caulerpa paspaloides*

Samples were selected (Fig. 1 (2 and 3)) with 100% coverage of *C. paspaloides* within the 0.25 cm^2 grid (0.5 × 0.5 cm plot) (ten samples per site). The samples obtained were stored in sealed plastic bags, and the number of stolons, complete and incomplete fronds, and each stolon's diameter were registered.

Samples were subsequently oven dried at 60°C for two days and weighed to the nearest 0.001 g to estimate the rate of change in biomass (population λ) (Caswell, 2001):

$\lambda = N_{t+1}/N_t$. Where:

λ= *finite rate of biomass growth*

N_t=*biomass at time t*

N_{t+1}= *the biomass at time t+1*

Fuentes et al. (2014) established this algal demography methodology for *Caulerpa paspaloides*.

Fifty fronds were marked in each of the monospecific and mixed meadows *C. paspaloides*. The fronds marked with these wires were collected 90 days later. The same formula was applied ($\lambda = N_{t+1}/N_t$); the length before the tag was N_t since it indicates its length on the first day, and the total length was (N_{t+1}), representing the length it reached at 90 days. In this case, the length of the fronds of *C. paspaloides* represents the status of each module. To calculate the modular λ, the formula ($\lambda = N_{t+1}/N_t$) where:

λ= finite rate of modular growth

N_t= the length of the leaf at time *t*

N_{t+1}= the length of the leaf at time *t+1*

In this case, the length after the mark was N_t since it indicates the length on the first day, and the total length was (N_{t+1}), representing the length reached 90 days later. In this case, the length of the fronds of *C. paspaloides* represented the status of each module. This methodology was adapted to that used by Fuentes et al. (2014) and Mandujano et al. (2001) for module marking and evaluation of the modular growth rate.

Random 10cm diameter cores were collected at the three sites from 2016 (November), 2017 (March, July, November), 2018 (February, April, June, August, October), and 2019 (January). Each *T. testudinum* biomass core collected was separated from the macroalgae found, dried at 55°C for three days, and weighed. Thus, the relative record of macroalgae biomass and *T. testudinum* was obtained.

3.9 Characterization of light at each site and each temperature

Photosynthetically active radiation (PAR) was recorded at each study site (µmol/m^2/s) in the water column with LY-COR LI-193 from the surface (before touching the water), covering the water, and every meter after that to the bottom. With this record, the light loss was calculated for each site through the relationship between depth and PAR.

With the maximum and minimum PAR and a rearrangement with the Lambert-Beer equation was made in order to calculate the percent light at the bottom for each site and each season:

$$I_z / I_0 = e^{(-K_d * z)}$$

I z= minimum PAR

I 0= maximum PAR

$$\text{Percent light at bottom (\%)} = e^{(-K_d * z)} * 100$$

e = base of the natural logarithm

K_d *= light attenuation coefficient*

z = depth

Also a HOBO UA-002-64 device was placed on the seabed at each site to record light each hour; each device was collected and changed every three month.

3.10 Photosynthetic efficiency of *T. testudinum* and *C. paspaloides*

At each site, 10 vertical shoots of *T. testudinum* and 10 fronds of *C. paspaloides* were sampled. Each sample was placed under darkness with constant air for a minimum of 30 min. In a dark room, the photosynthetic response for each vertical beam and each frond was recorded using a fluorometer (mini-PAM, Heinz Walz, Effeltrich, Germany). This technique allowed the description of the spatiotemporal variability of the photochemical efficiency of PSII (Fv/Fm).

3.11 Photosynthetic pigments of *T. testudinum* and *C. paspaloides*

The samples of the leaves and fronds used to measure photosynthetic efficiency were kept in aluminum foil and a container with liquid nitrogen. The samples were macerated with a glass rod inside the Eppendorf with 2% ammonium acetate 0.5M and volumetric to 2ml. They were kept in the dark for 24 hours at -20°C. The tubes were allowed to stand at room temperature and sonicated for 3 min. They were subjected to an ultracentrifuge at 70,000rpm for 20min, the supernatant was extracted, and the filtrate was placed in labeled vials stored at a temperature of -20°C. The samples were processed in HPLC using a mobile phase (30% ammonium acetate and 70% methanol) and 0.5 M ammonium acetate.

3.12 Statistical analysis

Percentage cover of the SAV was analyzed with a chi-square test to find differences in the relative coverage of each species in each meadow. Standardized residuals were used to test for further significant differences.

For the physicochemical variables (physicochemical, nutrients, sediment size, and organic matter) and phytoplankton biomass, a non-parametric test (Wruskall-Wallis) was performed since the number of data is limited (10 per site) to find significant differences in the places and the seasons (“nortes”, rainy, and dry).

The morphological data of *T. testudinum* (length of shoots (cm), length of leaves (cm), number of internodes, length (cm), diameter (cm) and number of rhizomes and number of flowers and floral scars) were analyzed with a two-way ANCOVA to evaluate if there were changes in the morphological data during the years 2017 and 2018. The other morphological data of *T. testudinum* (number of leaves, leaf scars, internodes, and flowers), as they are discrete numerical variables, were analyzed with a generalized linear model (GML) to find significant differences in grasslands (monospecific and mixed) and years (2017 and 2018). A *post-hoc* Student test was used for each parameter in which significant differences were found.

The morphological data of *C. paspaloides* (the number of stolons, complete and incomplete fronds, stolon diameter, and weight in g/m^2) were analyzed with analysis of variance (ANCOVA) to identify significant differences in the meadows (monospecific and mixed), during the years 2017 and 2018, and the seasons (rainy, dry, and nortes).

A multifactorial ANCOVA test was carried out to evaluate if there were changes in the Fv/Fm in both species in the sites and the seasons.

The data were recorded in percentage of xanthophyll pigments (zeaxanthin, antheraxanthin, and violaxanthin) and chlorophylls (a and b) and were analyzed in a Chi-square test to find differences in the number of pigments in the seasons and the sites, and their corresponding analysis of residuals.

A principal component analysis (PCA; Tabachnick and Fidell, 2019, STATISTICA 9.0) was done with the factors (Sites 1, 2, and 3) and the response variables (depth, % light at bottom, temperature, salinity, pH, dissolved oxygen, dissolved inorganic nitrogen, Total phosphorus, ammonium and phosphorus in interstitial water and the *Fv/Fm*). Factors with values above 0.63 were considered very good values (Tabachnick and Fidell, 2019).

A principal component analysis (PCA; Tabachnick and Fidell, 2019, STATISTICA 9.0, StatSoft USA) was performed with the factors (Site 1, 2, and 3) and the response variables (Biomass of *C. paspaloides*, depth, temperature, salinity, pH, dissolved

oxygen, dissolved inorganic nitrogen, total phosphorus, ammonium and phosphorus in interstitial water and *Fv/Fm*). Factors above 0.63 were considered very good (Tabachnick and Fidell, 2019).

Once the most representative variables of the study were known, a behavior analysis of the most relevant variables was made with the Originpro 2016 program (Multion, USA) to find out if the variables have patterns in common or behave randomly at different times throughout the sampling dates.

4-. RESULTS

4.1 Characterization of the submerged aquatic vegetation and biological elements in the three sites

Site 1 registered 100% *T. testudinum*; Site 2 recorded a relative coverage of 52% *T. testudinum*, 38% *C. paspaloides*, 5% macroalgae, and 5% open spaces; and site 3 registered 5% *T. testudinum*, 81% *C. paspaloides*, 8% macroalgae and 6% open spaces, on average. Significant differences were found between sites 2 and 3 (χ^2= 19.02, *d.f.*=3, *p*<0. 01) (Table 1). In the analysis of residuals, the cover of *T. testudinum* is significantly higher in Site 1, and the cover of *C. paspaloides* is significative higher at site 3 as expected (Figure 2).

No significant differences were found in the amount of phytoplankton biomass in the meadows or between the seasons (*H*= 2.27, *n*=30, *d.f.*=2, *p*=0.32). In general, there is an average of 1.59 ±0.26 mg/m^3 in the area.

The macroalgae species recorded at sites 2 and 3 were the following: *Derbesia marina* ((Lyngbye) Solier), *Avrainvillea levis* (M. Howe), *Caulerpa prolifera* ((Forsskål) JV Lamouroux), *Halimeda monile* ((J. Ellis and Solander) JV Lamouroux)), *Batophora oerstedii* (J. Agardh) and *Penicillus dumetosus* (JV Lamouroux) Blainville.

Table 1 Submerged aquatic vegetation coverage for each site

Site	***T. testudinum***	***C. paspaloides***	**Macroalgae**	**Open spaces**	**p>0.01**
1	100%	NA	NA	NA	0.10
2	**52%**	38%	5 %	5 %	<0.01
3	5 %	**81%**	8%	6%	<0.01

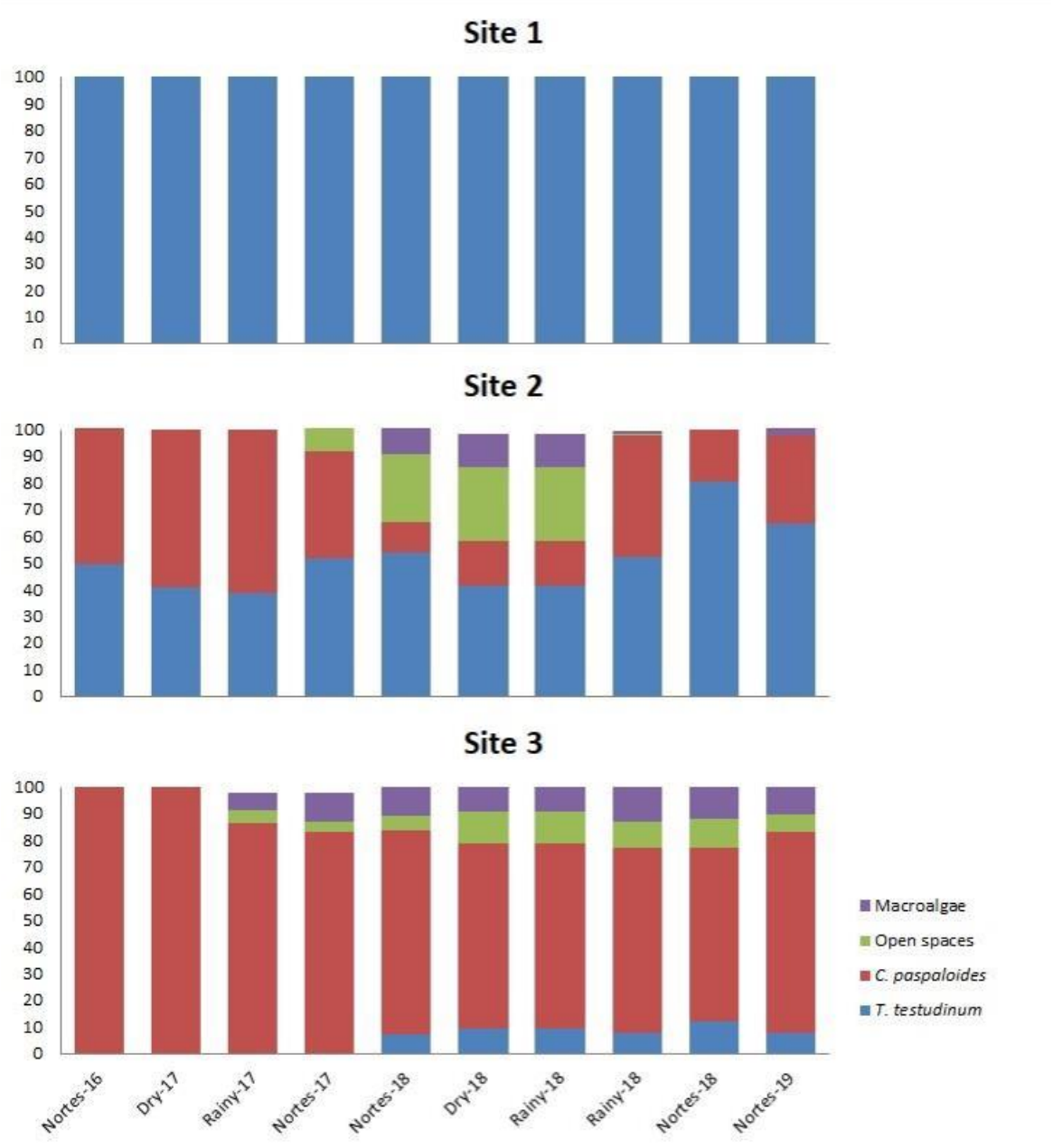


Figure 2 Coverage of the submerged aquatic vegetation in the three sites, along the sampling dates.

4.2 Physicochemical differences between sites

Significant differences were found in depth (H=21.84, n=30, $d.f.$=2, p<0.01) and grain size (Mz) (H=12.18, n=30, $d.f.$=2, p<0.01). . The monospecific sites of *C. paspaloides* (site 3) and mixed recorded greater depth and a larger grain, unlike the monospecific site of *T. testudinum* (site 1) (Table 2).

Table 2 Physicochemical data obtained for the three study sites

	Site 3	**Site 2**	***Site 1***	***p***
Depth (m)	3.23±0.16	2.81±0.18	**1.50±0.24**	**<0.01**
Temperature (C°)	26.77±0.66	27.29±0.74	25.93±0.58	>0.05
pH	8.07±0.05	8.07±0.06	8.05±0.07	>0.05
Salinity	36.14±0.80	36.34±0.74	36.32±0.78	>0.05
Dissolved oxygen	6.15±0.21	6.25±0.23	5.74±0.29	>0.05
Conductivity	54.49±1.19	54.71±1.25	54.29±1.35	>0.05
Dissolved Inorganic Nitrogen (mg/l)	15.24±1.65	6.66±1.64	7.89±1.75	>0.05
Total Phosphorus (TP) (mg/l)	2.77±0.43	1.33±0.42	1.87±0.41	>0.05
Silica (mg/l)	8.55±0.85	5.48±0.83	5.75±0.81	>0.05
Pore-water Ammonium (mg/l)	895.59±136.11	593.97±123.6	751.78±0.145	>0.05
Pore-water PT (mg/l)	13.97±5.09	13.44±6.09	18.51±5.98	>0.05
Organic carbon	4.45±0.42	4.45±0.43	4.24±2.03	>0.05
Organic matter	7.66±4.56	7.65±4.98	7.30±0.48	>0.05
Grain size (Mz)	1.88±0.23	0.73±0.28	**2.75±0.23**	**<0.05**

Regarding the physicochemical parameters by season, significant differences were found in temperature between seasons (H=14.48, $d.f.$=2, n=30, p<0.01), silica (H= 6.85, $d.f.$=2, n=30, p=0.032) and DIN (Dissolved inorganic nitrogen) (H= 17.73, $d.f.$=2, n=30, p=0.01). Salinity was higher in the dry season (H= 6.7, $d.f.$=2, n=30, p=0.034) (Table 3).

Table 3 Physicochemical data for the norte, dry, and rainy seasons.

	Dry	**Rainy**	**Norte**	***p***
Depth (m)	2.43±0.15	2.51±0.18	2.60±0.17	>0.05
Temperature (C°)	25.27±0.53	**29.71±0.32**	25.33±0.45	**<0.01**
pH	8.22±0.07	7.93±0.08	8.06±0.09	>0.05
Salinity	**37.87±8.79**	35.82±8.46	34.73±8.95	**0.034**
Dissolved oxygen	6.09±0.22	5.91±0.32	6.45±0.48	>0.05
conductivity	56.15±1.15	55.75±1.16	51.58±1.18	>0.05
Dissolved inorganic nitrogen (mg/l)	3.51±1.62	**16.81±4.53**	9.47±3.23	**0.01**
Total Phosphorus (TP) (mg/l)	1.40±0.42	1.68±0.52	2.80±0.85	>0.05
Silicate (mg/l)	5.28±0.85	**8.98±0.78**	5.52±0.83	**0.032**
Pore-water Ammonium (mg/l)	728.05±136.56	836.89±135.23	676.39±123.5	>0.05
Pore-Water PT (mg/l)	29.47±5.23	9.93±4.56	6.52±3.56	>0.05
Organic carbon	3.38±0.42	5.68±0.58	4.07±0.69	>0.05
Organic matter	5.83±0.75	9.77±0.89	7.02±0.98	>0.05
Grain size (Mz)	1.92±0.25	1.94±0.29	1.50±0.36	>0.05

4.3 *T. testudinum* demography

There were significant differences in the sites and the years in the morphological structures of *T. testudinum*. In 2018 registered a higher number of internodes (18±9) and the diameter of the rhizome (5.22±0.11) were found (Table 5). At Site 2 (mixed meadow), a larger average leaf size (24.34±1.89) was recorded in 2017, Internodal length (cm) (1.28±0.46) and a high number of leaf scars in both years (2017-37, 2018-45). At Site 1 (monospecific *T. testudinum* meadow), the individuals presented more leaves (3±1) and bigger rhizome size (9.43±0.70).

The record of demographic characteristics (Table 6) was found to be higher at site 1 in 2018. However, site 1 in 2017 recorded the highest number of sheets per year (30) and the highest rate of bundle recruitment (0.90) and site 2 in 2018 recorded the highest percentage of aerial biomass (59.94%) and the highest vertical growth (5.02 cm/year) (Table 6).

Table 5 Morphological variables of *T. testudinum* (number of leaves, number of leaf scars, internodes, number of leaves, leaf scars, and internodes)

Morphological variable	**Site 1-2017**	**Site 1-2018**	**Site 2-2017**	**Site 2-2018**	***f/p***		
					sites	Years	Interaction
Number of leaves	**3±1**	**3±1**	2±1	2±1	**6.83/ <0.01**	0.12/ 0.06	0.72/ 0.13
Number of leave scars	35±22	32±27	**37±28**	**45±31**	**7.64/ <0.01**	0.003/ 0.95	2.84/ 0.06
Number of internodes	14 ±6	**18±9**	12.5 ±6	**15.53 ±8**	3.22/ 0.07	**13.37/ <0.01**	0.42/ 0.51
Internodal length(cm)	0.77±0.26	0.91±0.28	**1.28±0.46**	1.10±0.30	**801.68/ <0.01**	**14.84/ <0.01**	**187.57/ <0.01**
Shoot size (cm)	4.51 ±0.27	4.35±0.26	4.36 ±0.53	5.14 ±0.43	0.33/ 0.56	1.02/ 0.31	0.92/ 0.33
Leaf size (cm)	18.64±1.32	19.90±1.20	**24.34±1.89**	18.6 ±0.95	2.56/ 0.11	2.62/ 0.10	**6.46/ 0.01**
Leaf width (cm)	0.72±0.02	0.77±0.03	0.71±0.03	0.84 ±0.21	0.05/ 0.81	0.24/ 0.62	0.02/ 0.87
Rhizome size (cm)	**8.35±0.49**	**9.43±0.70**	6.55±0.49	6.37 ±0.45	**8.32/ <0.01**	0.28/ 0.59	0.56/ 0.45
Rhizome diameter (cm)	5.19±0.08	**5.22±0.11**	4.93±0.12	**4.87±0.09**	0.27/ 0.59	**4.68/ 0.03**	0.05/ 0.81

Table 6 Demographic parameters for *T. testudinum* meadows in the years 2017 and 2018

Demographic parameter	Site 2 2017	Site 1 2017	Site 2 2018	Site 1 2018
Aboveground biomass (g/m²)	687.74	1368.42	846.30	**1543.13**
Belowground biomass(g/m²)	535.25	1923.87	565.55	**2147.06**
Total biomass (g/m²)	1222.99	3292.29	1411.85	**3690.19**
% Aboveground biomass	56.23	41.56	**59.94**	41.82
% Belowground biomass	43.77	58.44	40.06	**58.18**
Population density (ind/m²)	757.43	1545.00	1030.10	**1787.53**
Number of leaves per year	23	**30**	23	**30**
Floral density (ind with flower/m²)	30	151	333	**1060**
% Floral	4	32	eleven	59
Vertical growth (cm/year)	3.38	3.79	**5.02**	4.26
Shoot Recruitment Rate	0.81	**0.90**	0.84	0.42
Horizontal growth (cm/year)	34.56	36.46	40.90	**67.34**

The general linear regression between the number of leaves and the size of each shoot to calculate the demographic parameters of *T. testudinum* was y = 0.0988x + 0.7564 R^2 = 0.7767, and the residual test indicates that the data fit the model linear (F=587.46, *d.f.*= 1 p<0.01) (Fig. 3). Horizontal growth obtained a linear regression of y = 0.3274x + 2.8563R^2 = 0.5253 (Fig. 4).

In general terms, Site 1 presents the highest changed in the demographic parameters measured. However, Site 2 presents a higher percentage of above-ground biomass and higher vertical growth.

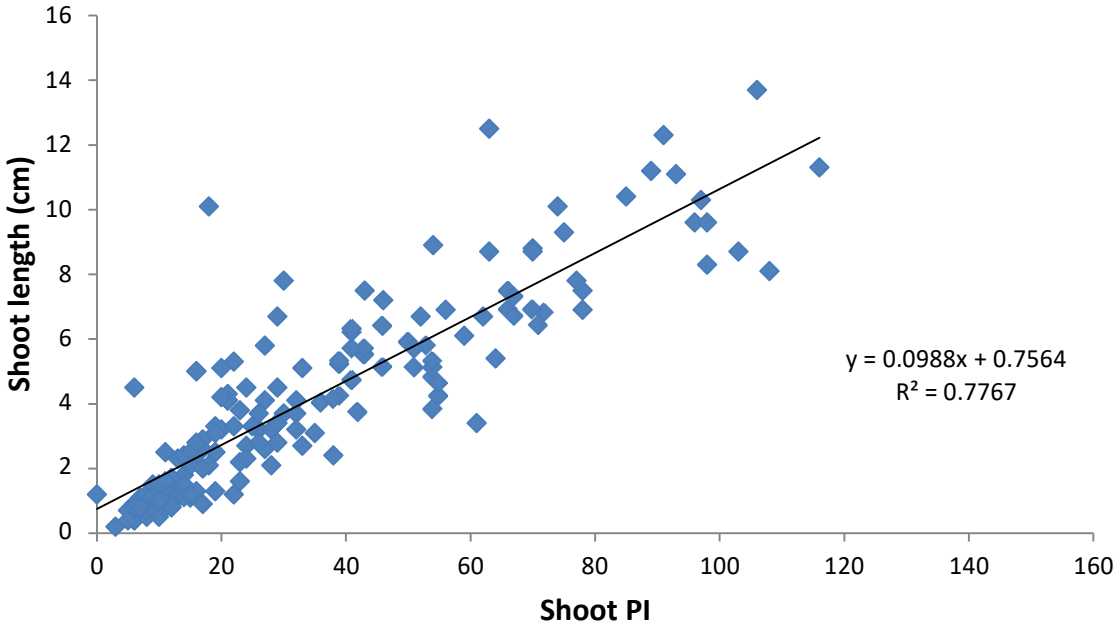


Figure 3 Regression obtained with the number of leaves per shoot and by the size of vertical shoots.

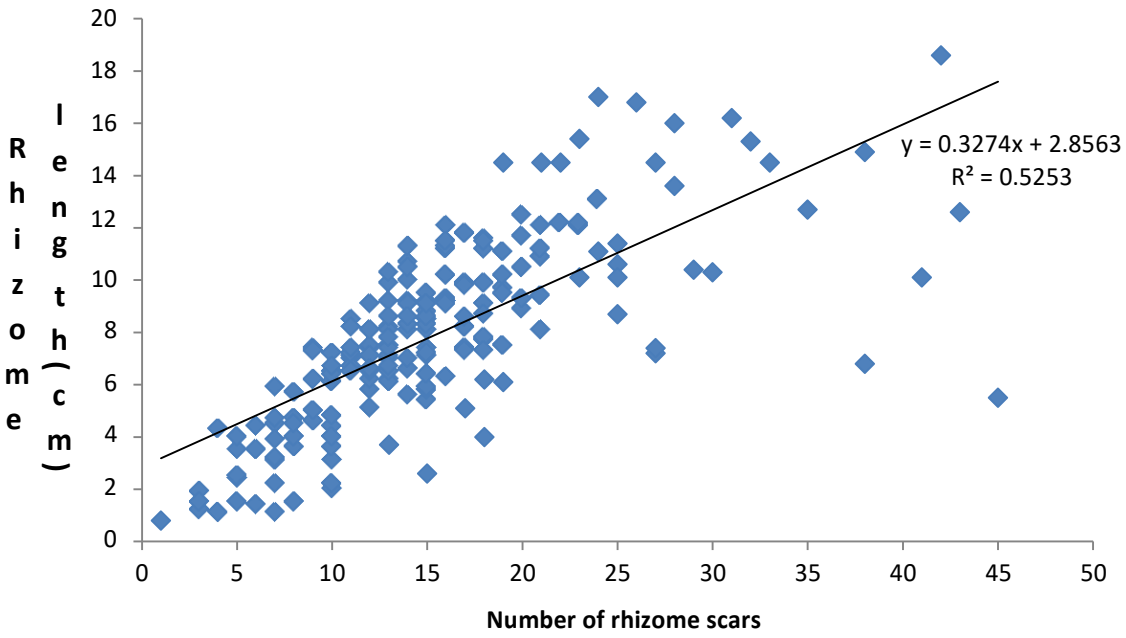


Figure 4 Horizontal growth calculated from the number of rhizome scars and the rhizome size

The number of leaves produced in one year was calculated for site 1 out of 33 for both years and at site 2 out of 31 in both years and from the floral scars it was 34 at site 1 and 23 at site 2 (Table 5).

The intermodal length shows cycles in vertical growth and was calculated for Site 1, 33 leaves in 2017 and 34 leaves in 2018 and Site 2, 26 leaves in both years. Therefore, it was concluded that the Site 1 beams have 34 IPs per year and Site 2, 30 IPs per year.

Site 1 had an average shoot growth of 35 PIs per year, and Site 2, 30 PIs per year. Site 1 (N = 150 individuals) had a maximum age of 3 years (160 PI) while Site 2 (N = 107 individuals) presented a maximum age of 4 years (165 PI) (Fig. 5). The age structures per year were different (χ^2= 187.26, *d.f.*=3, p<0.01), the residual tests registered the most number of vertical shoots under one year old at Site 1.

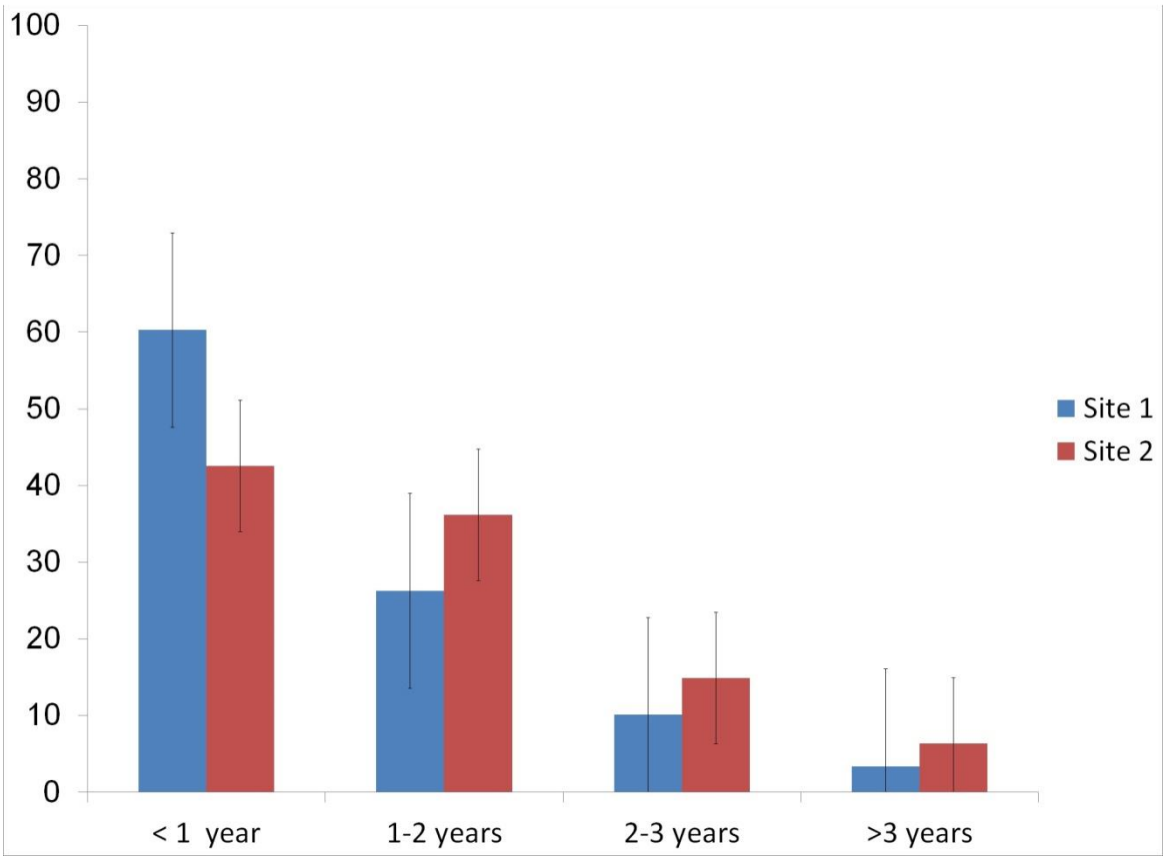


Figure 5 The age structure of *T. testudinum* in the monospecific and mixed meadows.

* Indicates the category that is different between the two structures.

Significant differences in leaf growth per day were obtained. The p*ost-hoc* indicated that both sites registered higher growth in the rainy season (0.25±0.10) and the site 1 register lower growth in the norte season (0.15±0.08) (Table 6).

Table 6 Record of leaf growth per day at Site 1 and Site 2 *T. testudinum* in the three climatic seasons

Leaf growth (cm)	**Dry**	**Rainy**	**Norte**		**p/F value**	
				meadows	seasons	P×T
site 1	**0.25±0.10**	0.19±0.08	**0.15±0.08**	0.32 / 0.96	**<0.01/ 11.06**	**<0.01/ 5.93**
site 2	**0.21±0.11**	0.16±0.05	0.19±0.08			

The records of population λ indicate that both populations grew during the study period (Table 7).

Table 7 Records of *λ* for *T. testudinum* populations

	site 2	**site 1**
Individual λ	1.16	1.36
Aboveground λ	1.22 ± 0.19	1.14 ± 0.27
Belowground λ	1.07 ± 0.22	1.14 ± 0.17
Total λ	1.12 ± 0.03	1.15 ± 0.03

4.4 *C. paspaloides* demography

Significant differences were obtained between sites and seasons (Table 8). All morphological variables in site 3 (monospecific site of *C. paspaloides*) were consistently higher than in site 2 (mixed): The dry season meant slower growth rates for all variables (Table 8) (Fig. 6).

Table 8. Morphological parameters for *C. paspaloides*

Morphological Variable (cm)	**site 3**	**site 2**	**F/p value**		
			sites	seasons	S×T
Number of stolons	**36±8.81**	19 ±10.59	**136.107/<0.01**	**7.363/<0.01**	2.92/0.06
Number of complete fronds	**171±51.20**	75±43.21	**181.186/<0.01**	**5.765/<0.01**	0.285/0.75
Number of incomplete fronds	**108±47**	45±40	**89.32/<0.01**	**7.88/<0.01**	**3.13/0.04**
Biomass (g/m2)	**10.64±4.78**	3.7±2.3	**156.81/<0.01**	**7.81/<0.01**	2.21/0.11
Frond length (cm)	**5.65±4.78**	3.67±1.56	**91.31/<0.01**	2.76/0.06	0.358/0.69
Stolon diameter (mm)	**2.46±0.21**	1.83±0.64	**84.61/<0.01**	**15.86/<0.01**	**9.59/<0.01**

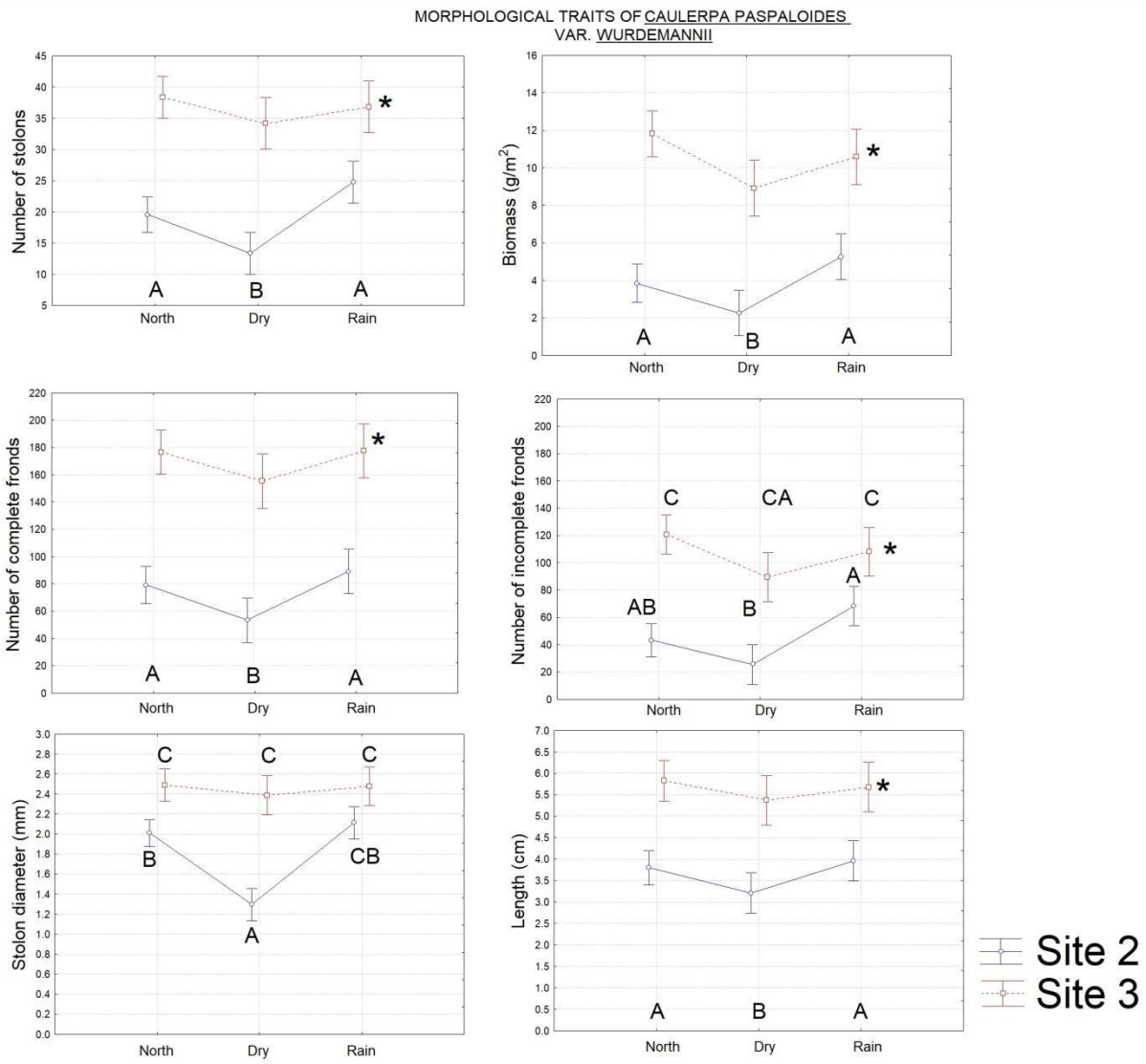


Figure 6 Means of complete fronds, incomplete fronds, stolon diameter, stolon length, number of stolons, and biomass (g/m^2) of *C. paspaloides* in the monospecific and mixed meadows during the three seasons. The letters indicate the groups of the post-hoc test and the asterisks are the sites with the highest counts.

Significant differences were obtained between seasons in frond growth per day (cm) (Season p=0.01). The test separated two groups: the first, in the dry season, where it has the highest growth and the second, in the season north that has the least growth (Fig. 7).

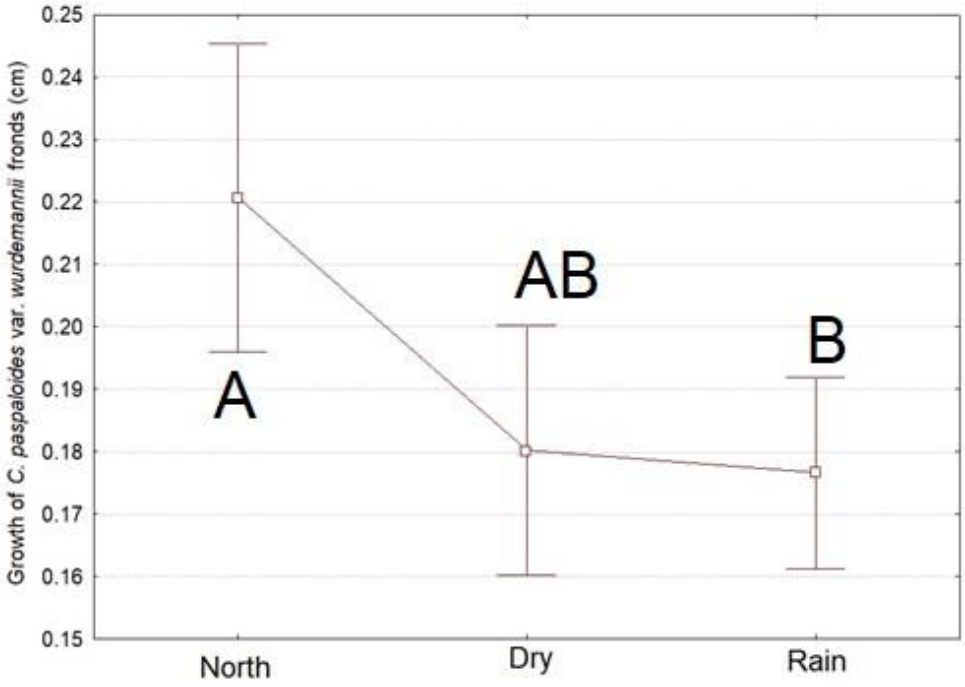


Figure 7 Record of leaf growth per day in *C. paspaloides* during the climatic seasons. The letters indicate the groups that were formed by the test *post hoc*.

The finite growth rates of *C. paspaloides* (λ) indicate that they generally grow greater than 1. Site 3 registered growth from north to dry, while Site 2 reported growth from north to rain (Table 9) (Fig. 8).

Table 9 Finite growth rates (*λ*) of *C. paspaloides* in different seasons

C. paspaloides	**Site 3**	**Site 2**
north-dry	**2.79±0.52**	**1.45±0.51**
dry-rain	0.68±0.26	**1.59±0.27**
rain-north	0.82±0.08	0.90±0.15
Total	1.44±0.36	1.29±0.24

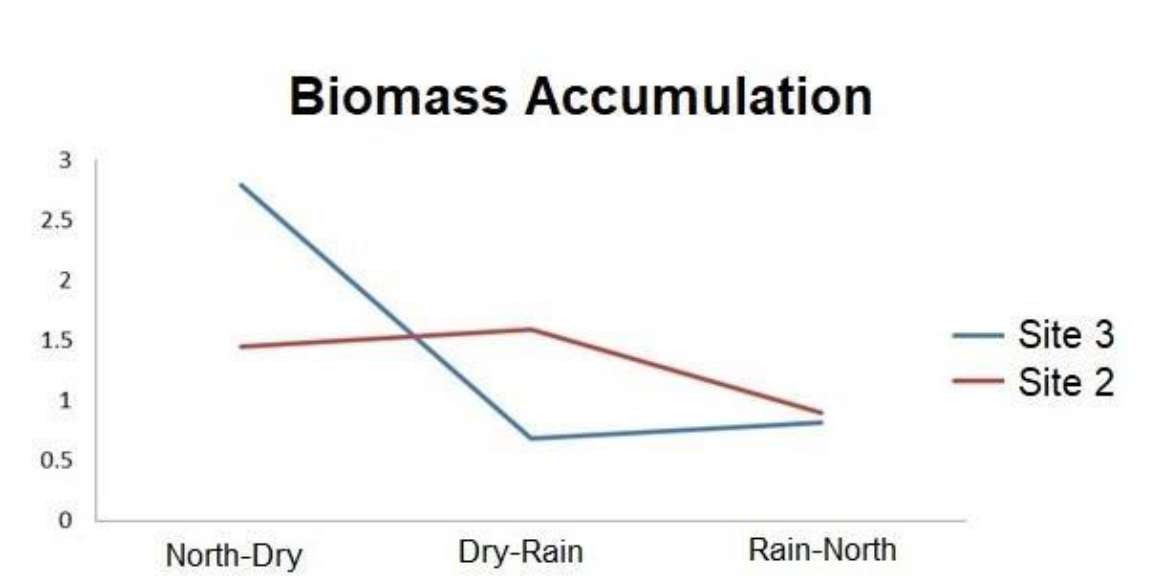


Figure 8 Biomass rates for *C. paspaloides* in different seasons and sites.

The percentages of bottom light for site 1 were from 16.9% to 31.39%, site 2 from 2.46% to 0.50%, and site 3 from 0.15% to 0.005% (Table 10).

4.5 Light analysis between the meadows

It was only possible to obtain HOBOS information during the year 2018, in May (Dry), August (Rainy), and October (Nortes). The highest light intensity was on September 30th, 2018 (14466.8 lux) at Site 2, and the minimum was (10.8 lux) on several days (Table 11). Significant differences were obtained in sites 2 and 3 in the rainy season. Site 2 had higher light intensity than Site 3 (Z = 24.48, p<0.01).

Table 10 Light loss coefficient and Maximum percentage of bottom light for each site (parenthesis maximum depth) at the dry, rainy, and norte seasons

Light loss coefficient /Maximum percentage of bottom light (%)	**Dry**	**Rainy**	**Norths**
Site 1 (2m)	-0,721/23.64	**-0,604/29.87**	-0,957/14.74
Site 2 (3.2m)	**-0,535/18.05**	-0,873/6.12	-1,175/2.32
Site 3 (4m)	-0,716/5.70	-1,087/1.29	-0,651/7.39

Table 11 Light intensity (lux) at different sites

Site	Minimum light intensity (lux)	Maximum light intensity (lux)
1	10.80	3272.20 (dry)
2	10.80	14466.80 (rain)
3	10.80	13089.00 (rain)

4.6 Photosynthetic efficiency of *T. testudinum* and *C. paspaloides*

With all the records of *Fv/Fm* for *T. testudinum,* an average of 0.725 (0.63-0.84) Fig. 9 A) was recorded, and for *C. paspaloides* of 0.50 (0.15- 0.88 Fig. 9 B).

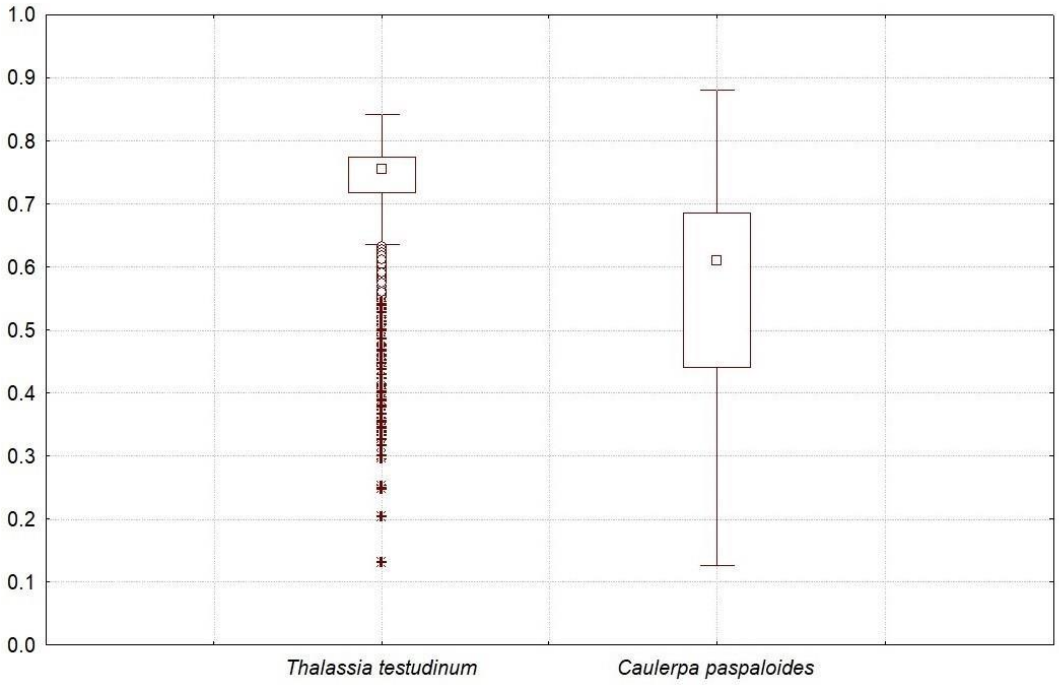


Figure 9 Average quantum efficiency for *T. testudinum* and *C. paspaloides*.

Significant differences were found in the *Fv/Fm* of *C. paspaloides*. The proof *post hoc* indicates that the rainy season in mixed sites presents lower *Fv/Fm*. *T. testudinum* presented significant differences in *Fv/Fm* in the rainy season in both meadows (Table 12).

Table 12 *Fv/Fm* values for *T. testudinum* y *C. paspaloides* at the three sites (site 1 (1.50m±0.24), site 2 (2.81m±0.18) y site 3 (3.23m±0.16) and in the climatic seasons (Nortes, Dry and Rainy). ANOVA test indicates differences in photosynthetic efficiency (*Fv /Fm*) by season and site. F/P indicates F value (ANOVA)/ P value (statistical significance). Main effects = Season, Site, Interaction = Site X Season.

Site/species	**Norte**	**Dry**	**Rainy**	**Average**	**F/p value**		
					Site	Season	P×H
Site 1 *T. testudinum*	0.74 ±0.03	0.74 ±0.05	**0.69±0.09**	0.72± 0.06	1.49/ 0.22	**20.81/ >0.01**	0.38/ 0.68
Site 2 *T. testudinum* (mixed)	0.76 ±0.02	0.75±0.03	**0.69 ±0.07**	0.73±0.05			
Site 3 *C. paspaloides*	0.59 ±0.19	**0.69±0.10**	0.58 ±0.17	0.61± 0.16	**7.97/ >0.01**	**25.08/ >0.01**	**15.58/ >0.01**
***Site 2 C. paspaloides* (mixed)**	0.68 ±0.57	0.60±0.13	**0.36 ±0.16**	0.55±0.18			

Significant differences were found in the proportion of pigments of *C. paspaloides*. The presence of zeaxanthin only exists at Site 1 in the dry season and violaxanthin is high at Site 2 in the norte season (χ^2= 543.34, *d.f.*= 15, $p < 0.01$) (Fig. 10), and chlorophyll b is higher at Site 3 in the dry season and chlorophyll a is lower (χ^2= 2235.87, *d.f.* 5, $p< 0.01$). In contrast, in *T. testudinum* no significant differences were found (χ^2= 12.34, *d.f.* 15, $p> 0.05$) (χ^2= 5.87, *df*= 5, $p> 0.05$), the most abundant pigments are antheraxanthin and chlorophyll "a" for the species (Fig. 11).

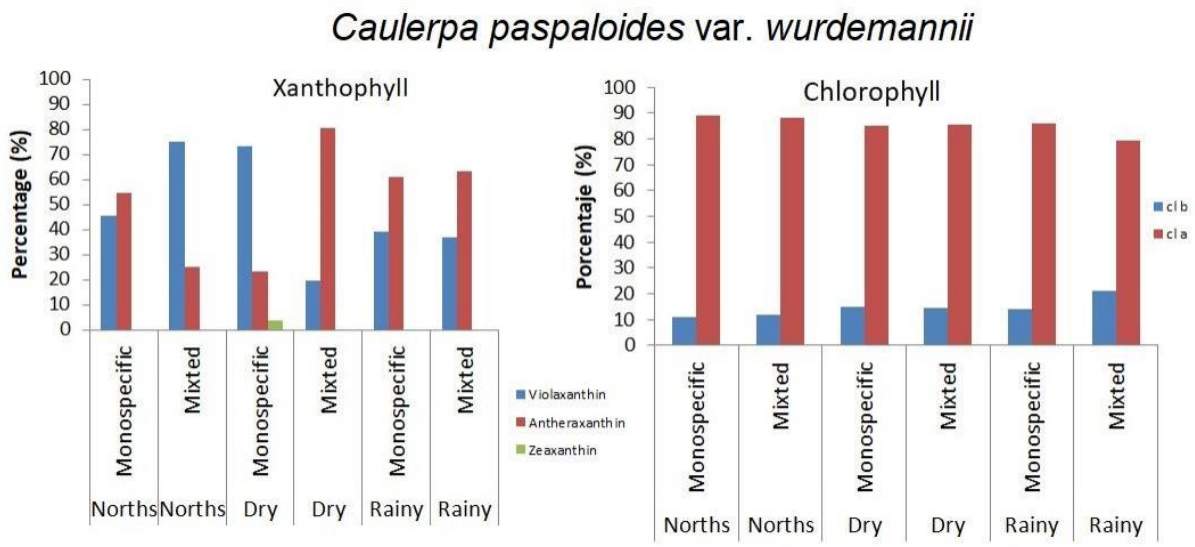


Figure 10 Accessory pigments of *C. paspaloides* in the climatic seasons (Norte, Dry, and Rain) at Site 3 and Site 2.

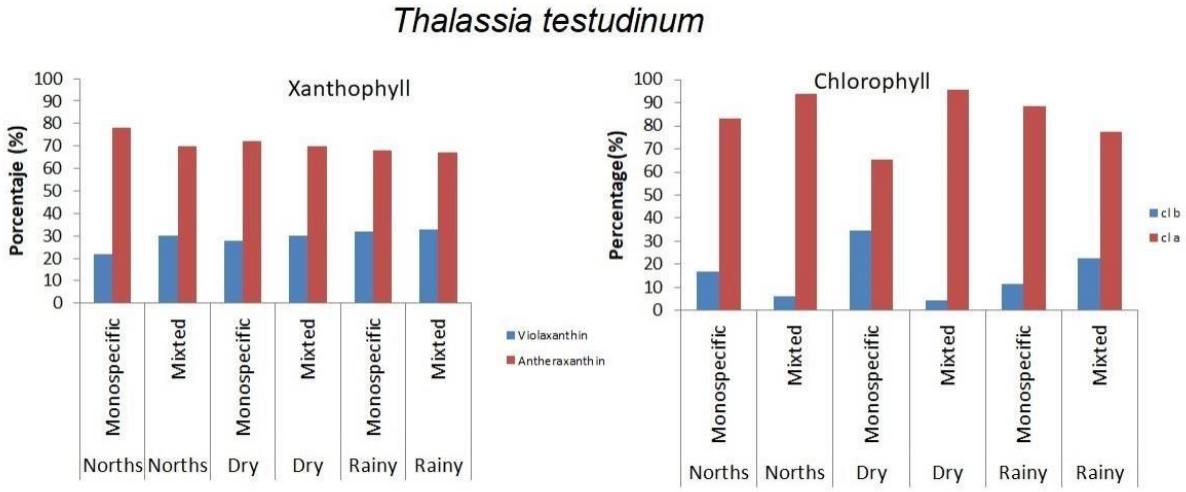


Figure 11 Accessory pigments of *T. testudinum* in the climatic seasons (Norte, Dry, and Rain) at Site 1 and Site 2.

No significant differences were found between sites (χ^2= 6.86, *df* = 2, *p* > 0.05). However, significant differences were found for both species in the seasons (*T. testudinum*, χ^2= 26.70, *df*= 2, *p*< 0.05) (*C. paspaloides*, χ^2= 26.70, *df* = 2, *p* < 0.05). The *post hoc* test indicated that stress events are greater in the rainy season in *T. testudinum* and *C. paspaloides*. In the dry season, there are fewer stress records (Fig. 12).

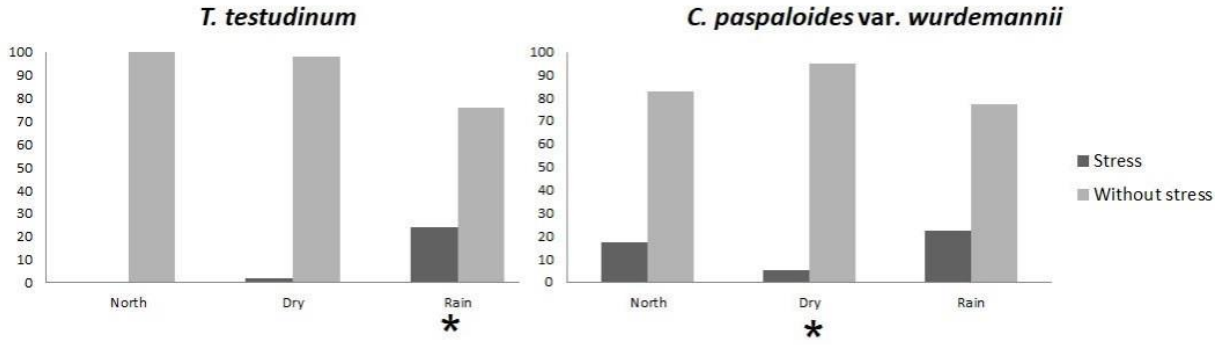


Figure 12 Frequency of stress events for *T. testudinum* and *C. paspaloides* in the climatic seasons. Asterisks point the seasons which has higher stress in *T. testudinum* and less stress in *C. paspaloides.*

4.7 Principal component analysis and relationship of photosynthetic efficiency with physicochemical factors

The PCA showed that three factors accounted for 75.90% of the variation in the data. The most critical variables in factor 1 were *Fv/Fm* of *T. testudinum (-0.746)*, *Fv/Fm* of *C. paspaloides* (0.876), depth (0.934) y light at bottom (-0.813). Factor 2 was integrated by DIN (0.858) y temperature (0.802) (Fig. 13).

The PCA points out that the highest *Fv/Fm* records of *T. testudinum* are associated by highest light at bottom (%) and negatively with the high *Fv/Fm* records of *C. paspaloides.* Abiotic factors (depth, temperature and DIN) are associated with sites with higher *Fv/Fm* records of *C. paspaloides* (Fig. 14).

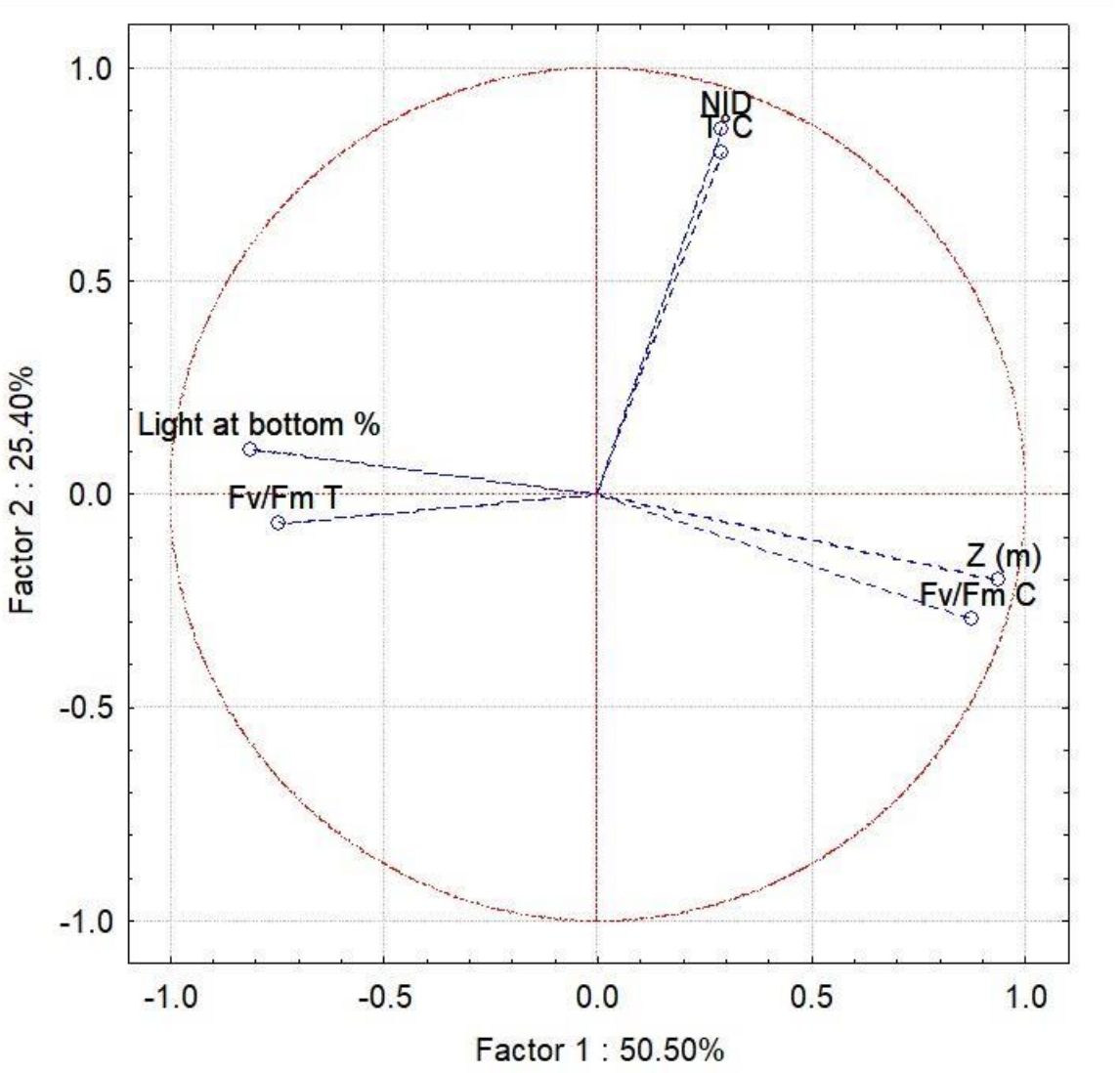


Figure 13 The important variables in factors 1 and 2: the photosynthetic efficiency of *T. testudinum*, dissolved inorganic oxygen, temperature, depth, light at bottom and photosynthetic efficiency of *C. paspaloides*.

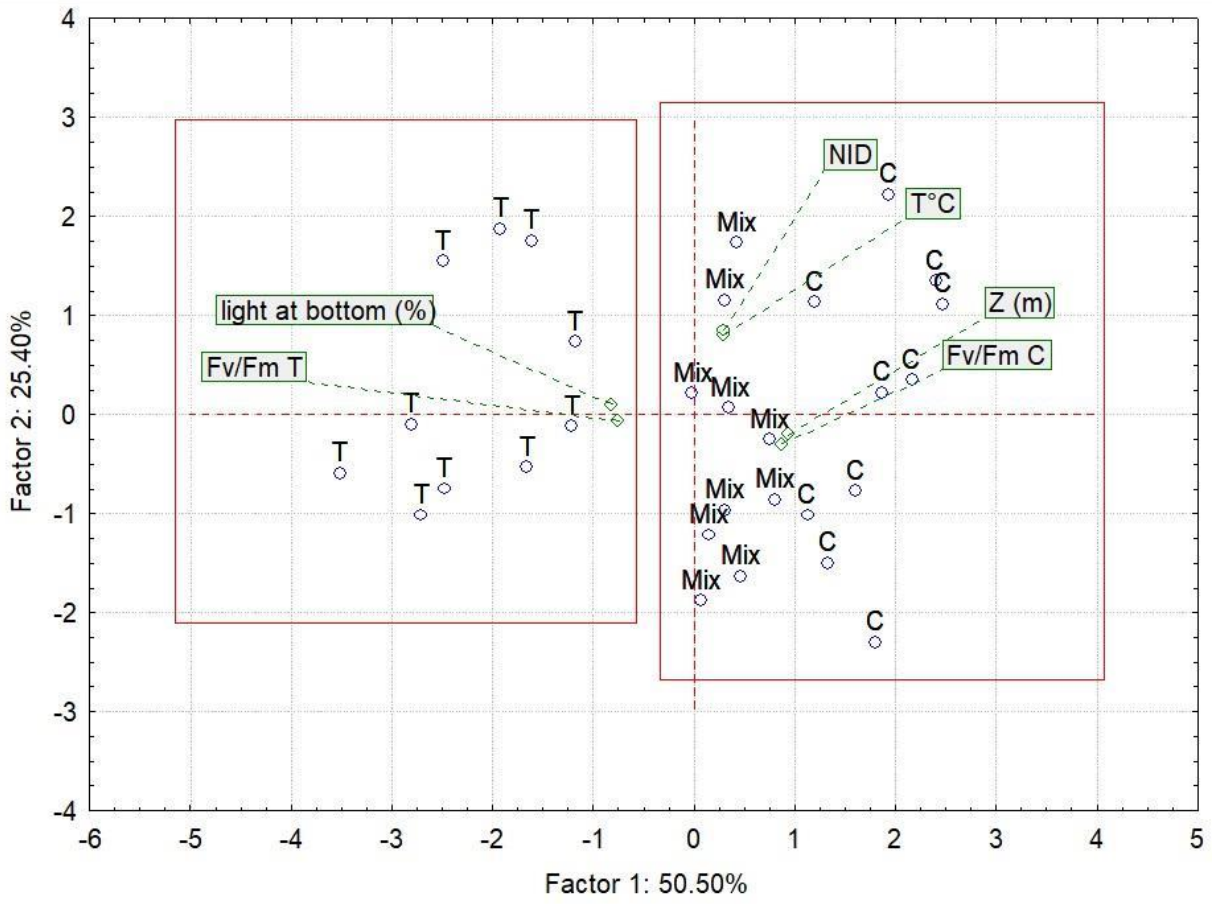


Figure 14 Principal component analysis associates the *Fv/Fm* of *T. testudinum* indicates that the highest records of Fv/Fm of *T. testudinum* are associated with highest records of light at bottom and are located in the monospecific meadows of *T. testudinum*. High *Fv/Fm* records of *C. paspaloides* are found in monospecific *C. paspaloides* and mixed meadows, as well as with the physicochemical variables (depth, dissolved inorganic oxygen and temperature).

4.8 Principal component analysis for *T. testudinum* and *C. paspaloides*

It was found that the first three factors explain 72.3% of the accumulated variation. Factor 1 was characterized by depth (0.923), light at bottom (-0.773), the biomass of *T. testudinum* (-0.900), *Fv/Fm* of *T. testudinum* (-0.772), the biomass of *C. paspaloides* (-0.793), *Fv/Fm* of *C. paspaloides* (0.866). Factor 2 was integrated by temperature (0.780) and DIN (0.860), while factor 3 was pore-water phosphorus (0.756).

The PCA indicates that the highest biomasses of *T. testudinum* are associated with higher light at the bottom, higher values of *Fv/Fm* of *T. testudinum* and negatively with the biomass of *C. paspaloides* and macroalgae. High biomasses of *C. paspaloides* are associated with at high depths. Temperature, DIN and pore-water phosphorous are associated (Fig. 15).

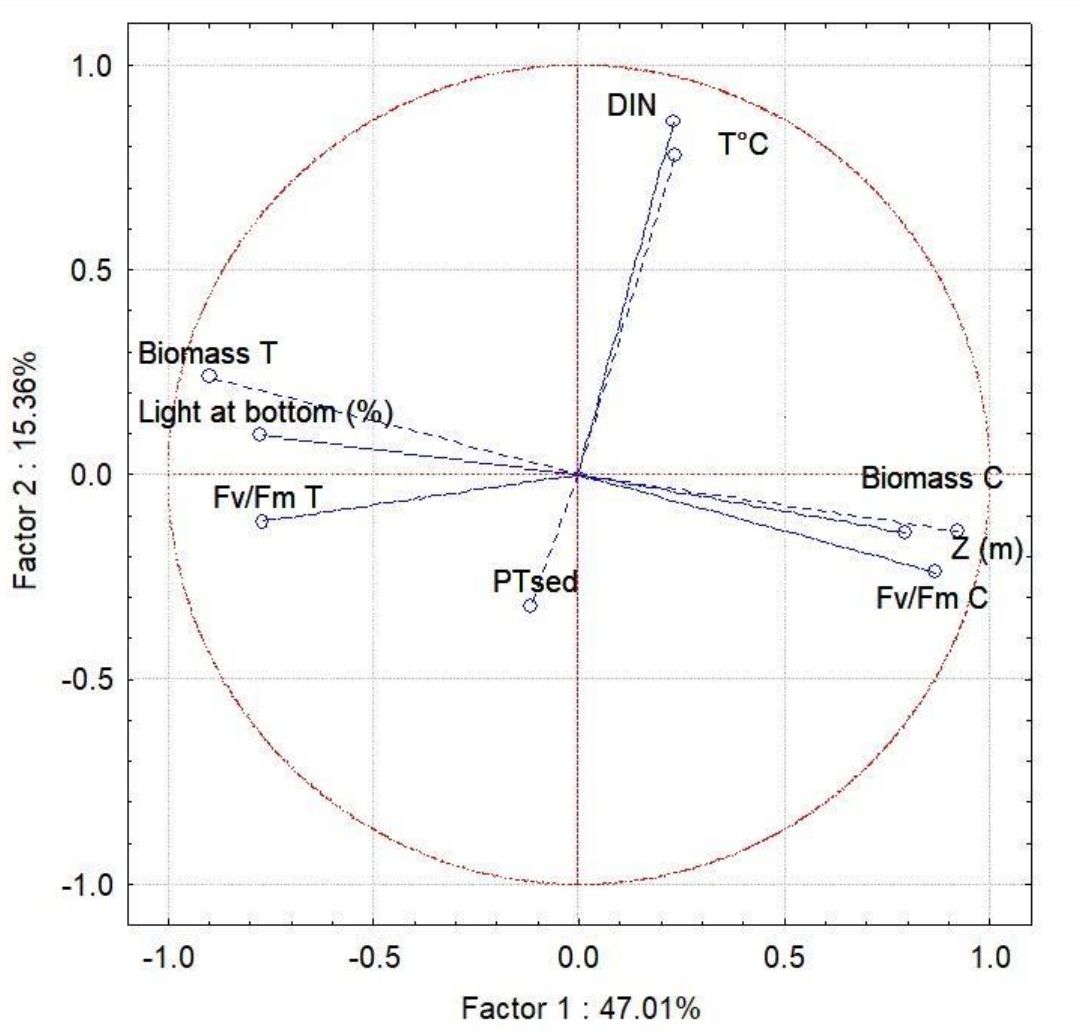


Figure 15 The important variables in factors 1 and 2: biomass and photosynthetic efficiency of *T. testudinum*, light at bottom, dissolved inorganic oxygen, temperature, depth, biomass, and photosynthetic efficiency of *C. paspaloides*.

The PCA suggests two groups: the first is composed of the *T. testudinum* monospecific sites with the highest biomasses, *Fv/Fm* records, and high light at bottom (%). The second group is the monospecific sites of *C. paspaloides* that are associated with the highest biomasses of *C. paspaloides*, photosynthetic efficiency and at greater depths. Mixed meadows were more related to abiotic factors, temperature, DIN, and pore-water phosphorous (Fig. 16).

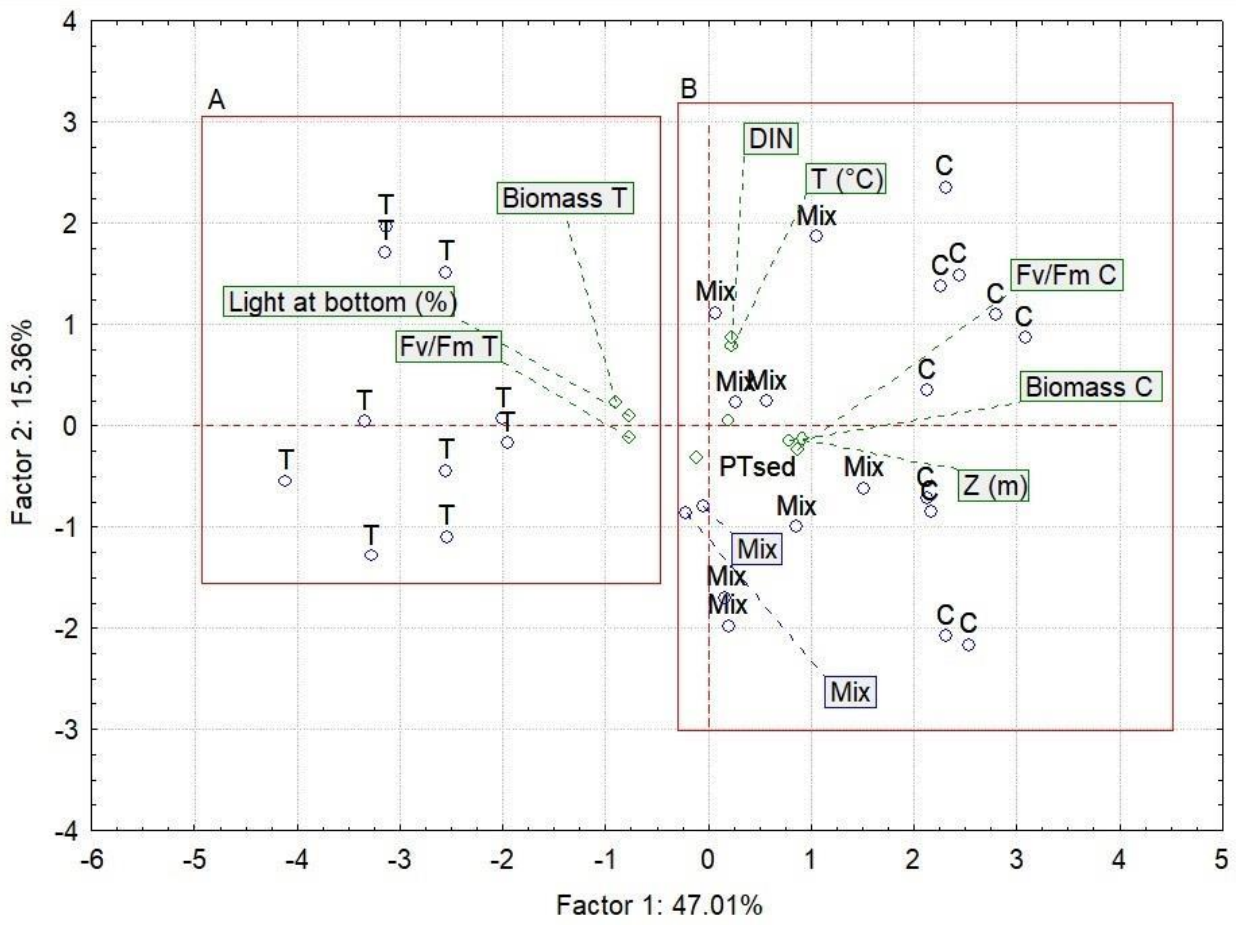


Figure 16 Principal component analisys associates the biomass of *T. testudinum* with the *Fv/Fm* of *T. testudinum*, and light at bottom, indicating that the highest biomasses are located in the monospecific meadows of *T. testudinum*. The biomass of *C. paspaloides* is related to its photosynthetic efficiency and macroalgae biomass. The highest biomasses are located in the monospecific meadows of *C. paspaloides*. Abiotic variables such as dissolved inorganic nitrogen, depth, pore-water nutrients total phosphorus, and temperature are associated with mixed meadows.

4.9 Behavior graphs of the most representative variables

The graphs indicate that the behavior of the biomass of the species *T. testudinum* and *C. paspaloides* are similar throughout the study. However, in November 2017 and February 2018, antagonistic behavior was detected in both species: a growth peak in macroalgae in June 2017 and a reduction in November 2017 and February 2018. Photosynthetic efficiencies were also found to be related to biomasses (Fig. 17). Depth behavior is more associated with the biomass of *C. paspaloides* and light at bottom with *T. testudinum* biomass. As for the temperature; an increase is observed in the months of high rainfall (June and August) (Fig. 18). In June 2018, there is an increase in the DIN, these increases coincide with the increase in biomass of *C. paspaloides* and in February 2018 there are increases in interstitial phosphorous (Fig. 19).

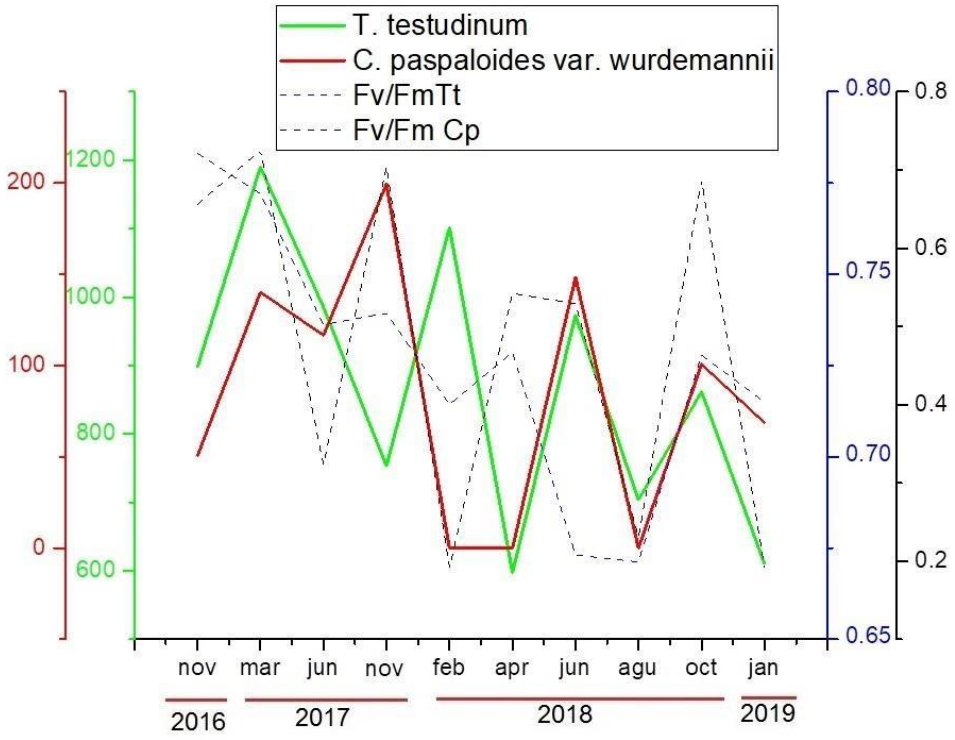


Figure 17 Graphs of the behavior of *T. testudinum* and *C. paspaloides* are associated with the biomass of macroalgae and their respective photosynthetic efficiencies.

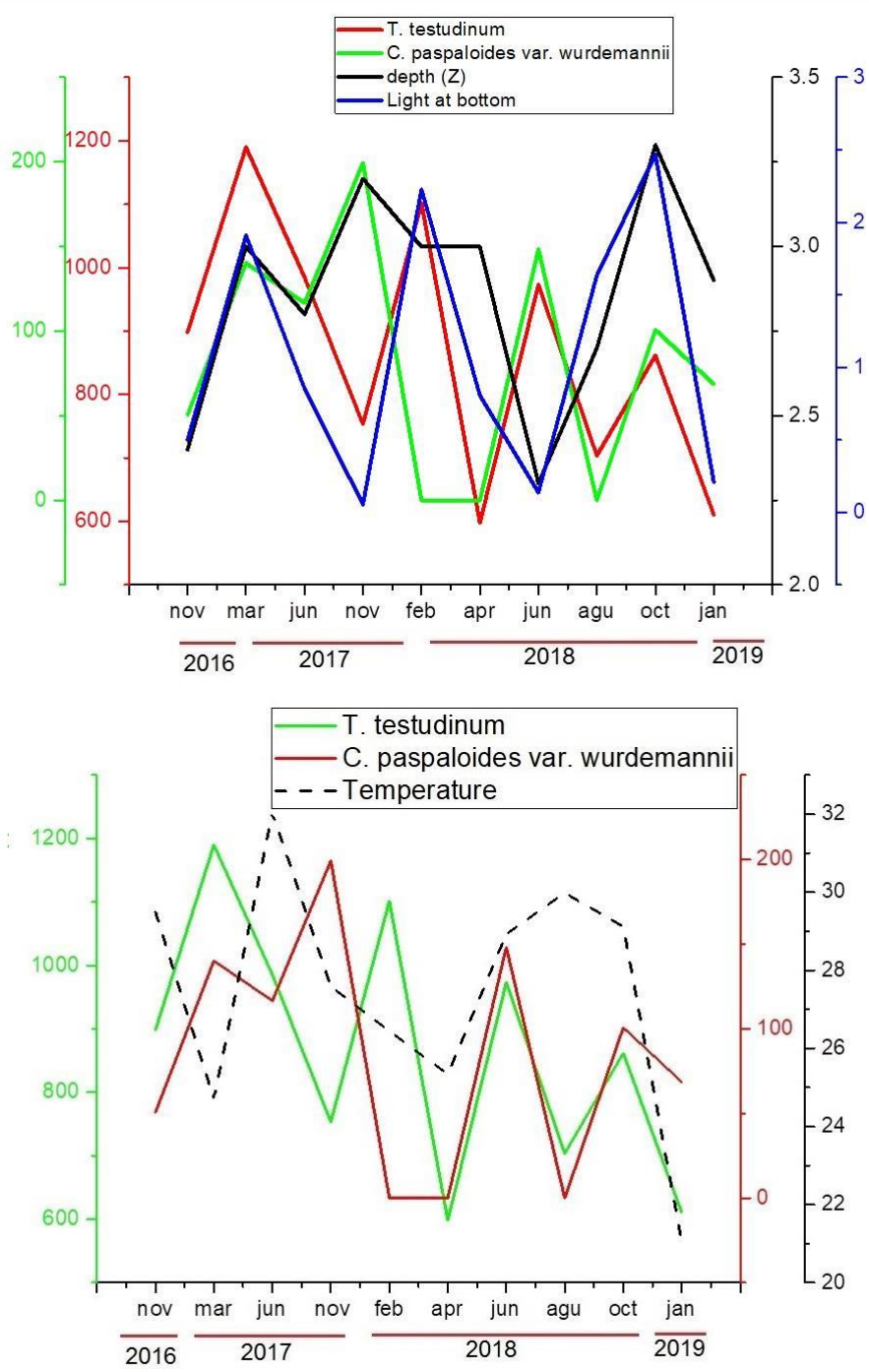


Figure 18 Graphs of the behavior of the biomass of *T. testudinum* and *C. paspaloides* associated with temperature, depth and light at bottom.

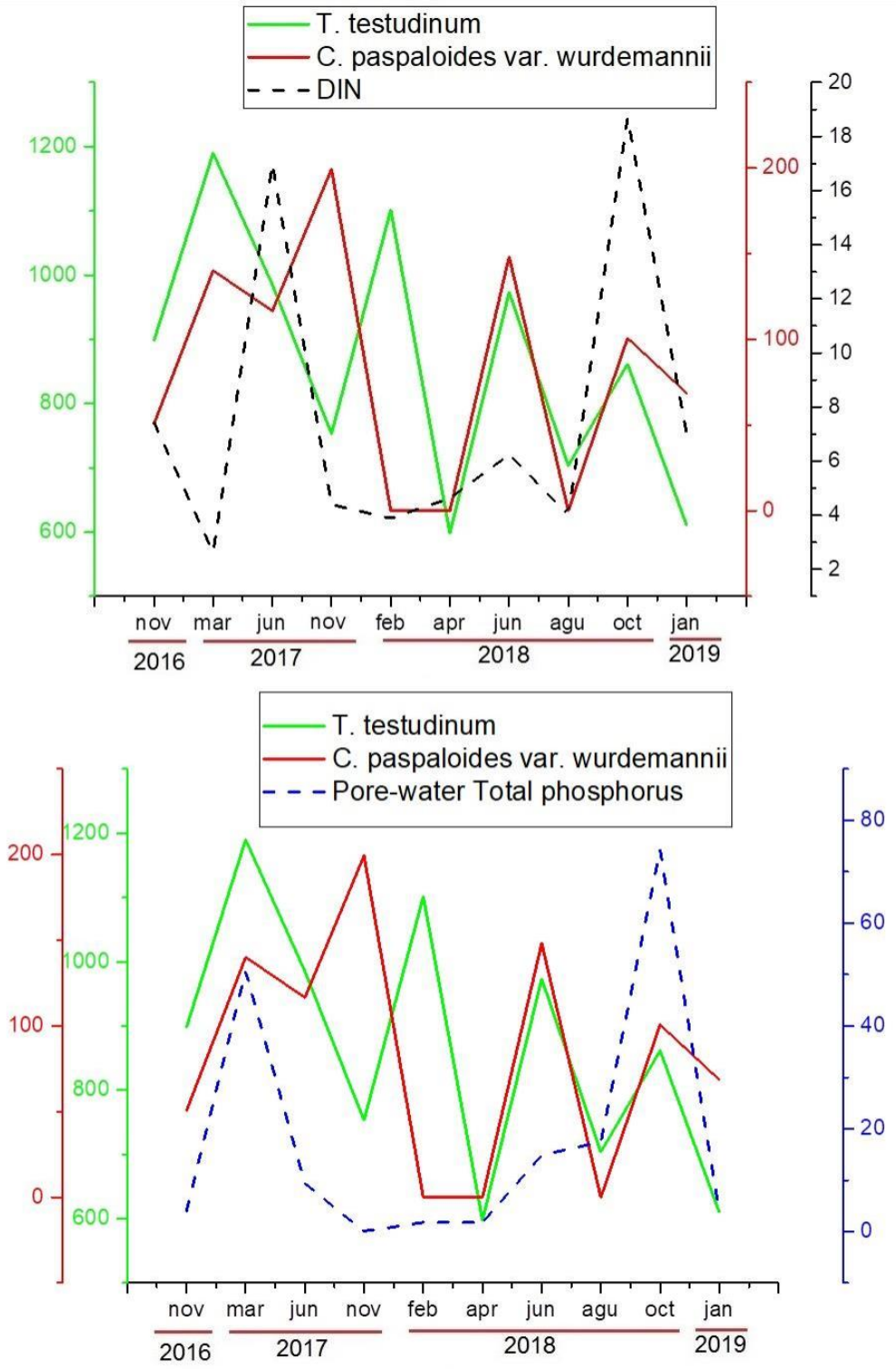


Figure 19 Graphs of the behavior of the biomass of *T. testudinum* and *C. paspaloides*, associated with DIN and pore-water total phosphorus.

5-. DISCUSSION

Site 1 presented depths of 1 to 2m and on average, the sediment was composed of fine sand, asymmetric towards coarse and platicurtic. The only species present in the sampling dates was *T. testudinum*. Therefore, it could be considered a monospecific meadow of *T. testudinum*.

Site 2 presented depths of 2.3-3.3m. On average, the sediment was very coarse sand, asymmetric towards fine and mesokurtic. The SAV of the site was composed of *T. testudinum*, *C. paspaloides.* However, in nortes-17 it was present other macroalgae and open spaces, until rainy-18 that coverage of *T. testudinum* increases. Thus, it was possible to consider a mixed meadow with *T. testudinum* and *C. paspaloides* as the predominant species.

Site 3 presented depths of 2.6 to 4m. On average, the sediment was coarse sand, symmetrical, and mesokurtic. The site presented high coverage of *C. paspaloides.* However, in rainy-17 there were presence of other species of macroalgae and in nortes-18 a minimal presence of *T. testudinum* (5%) was register (Fig. 2).

Fuentes et al. (2014) reported that the mixed meadows of *T. testudinum* with *C. paspaloides* in the Petenes zone in the Río Verde area were found in water that was less than 2m deep, and the sediment had a variable composition, 83% clay, 7% silt, and 10% sand. Throughout the Petenes area, Pérez et al. (2019) reported that the monospecific meadows of *T. testudinum* were found between depths of 0.9 m and 2.13 m, and the mixed meadows with other macroalgae from 0.9 m and 2.7 m. These characteristics are essential for the establishment of the SAV; for example, in deeper sites, algal species will be dominant (Pacheco et al., 2008), and in shallower areas, it will be seagrass such as *T. testudinum* (Van Tussenbroek et al., 2010).

Borum et. al (2006) points out that seagrasses, unlike macroalgae, will be limited by the amount of oxygen in the environment. Seagrasses obtained oxygen in two ways, actively through photosynthesis and passively through their leaves and by the aerenchyma. Environments with low oxygen availability will hinder the growth and establishment of seagrass unlike macroalgae. However, in dissolved oxygen records,

there were no differences between sites. This suggests that in the "Los Petenes" area there is no oxygen limitation at any depth. In shallower environments the availability of light is greater and in deep environments it will be less. Therefore it can be suggested that the presence of *T. testudinum* is lower in deeper places than in shallower sites. In the case of macroalgae, they may have less light availability because they have different photosynthetic strategies to compensate for less light availability and inhabit deeper areas.

The size of the sediment associated with specific physical and geochemical characteristics in the aquatic soil; coarse-grained sediments result from high speeds in the dynamics of the water and the increased force of the waves in the water (Fonseca, 1996). In seagrass communities, the sediment is finer than in areas where vegetation is scarce (Hemminga et al., 1991), as the seagrass rhizomes trap the sediment and break it down into small particles. In this way, the bacteriological communities can be established and will help the assimilation of nutrients and the decomposition of organic matter.

Although no significant differences were found between the sites in the rest of the parameters, it should be noted that the concentrations of interstitial nutrients in The “Petenes Biosphere Reserve” are higher than those reported in the literature (Table 4). As a result, there is a greater availability of nutrients in the entire reserve of "Los Petenes," the biological differences in the sites are due to the different depths and the sediment composition.

However, in this study, significant differences were obtained in NID and temperature; these parameters are higher in the rainy season. Mijangos (2018) described that physicochemical differences were found in the area of "Los Petenes" such as low salinity and high temperature in the rainy season. These changes affected the *T. testudinum* populations in the area. Fuentes (2015) found differences in *C. paspaloides* populations: before “norte”, the populations were abundant but decreased after this “norte” period. In this study the coverage of *C. paspaloides* at sites 2 and 3 was reduced in the 2017 and 2018 season, with the presence of white spaces and macroalgae and at site 3 the incorporation of *T. testudinum* in the

medium. This suggests that seasonality has an effect on *C. paspaloides*, since as previously discussed the availability of oxygen is homogeneous in the three sites; therefore the three sites are suitable for the growth and establishment of *T. testudinum*. Although in site 3 it will be limited mainly by the availability of light and the presence of macroalgae in the middle. In the case of *C. paspaloides* it can be assumed that the changes in the species cover are due to physical factors such as the presence of hurricanes in that season that mechanically detach the species.

The results suggest that there is an environmental homogeneity in general terms. The differences that occur in the sites (depth and grain size) and in the temporality (temperature, silica, DIN, and salinity) are relevant to the composition of the SAV and the abundance of species in each area of Petenes.

Table 12 Values of pore-water nutrients in areas of the Gulf of Mexico

Pore-water Nutrients	Ammonium (µM)	Total Phosphorus (µM)	Reference
Florida Bay	90-400	Not registered	Powell et al. 1989
Byscayne National Park	45±52	4±1	Szmant and Forrester 1993
Long keys	69±42	3±0.9	Szmant and Forrester 1993
Long key	72±54	3±1	Szmant and Forrester 1993
Looe	27±23	3±1	Szmant and Forrester 1993
Indian River Lagoon	81	10	Short et al. 1993
Petenes	853.37±569.47	15.88±20.56	This study

T. testudinum is described as a persistent species (Kilminster et al. 2015); with survival as the most important demographic characteristic. In general terms, both populations have high values of horizontal growth compared to those of the Caribbean populations (35 cm to 69 cm in the year, Marba et al. 1998) and those in “Los Petenes” (23.35cm to 66.84 cm in the year, Mijangos 2018); also, both meadows had minimal differences in growth rate (λ), suggesting that both populations grow and establish themselves optimally in "Los Petenes". Although morphological and growth

differences were found, there were more reproductive indicators in monospecific meadows and vertical and leaf growth in mixed meadows. Biotic conditions were correlated with changes in demographic attributes. Bricker et al. (2018) found that clonal growth of *T. testudinum* was more frequent in meadows with a high disturbance index and the presence of macroalgae. This suggests that, in mixed grasslands, *T. testudinum* invests resources in leaf formation and vertical growth due to the presence of competitors.

C. paspaloides recorded values of λ greater than 2 in both meadows. Therefore, this suggests that the populations double their size in the rainy season throughout the reserve. Although Kilminster et al. (2015) did not classify macroalgae, having recorded that in both meadows, *C. paspaloides* have high growth, and there are seasons where its populations are reduced, this could be defined as a pioneer species. Biber et al. (2004) describe that macroalgae have a primary role in seagrass communities, which is to stabilize and provide the appropriate conditions to follow for the colonization of complex species of seagrass such as *T. testudinum*, something similar to the early stages of ecological succession.

However, this study recorded that after the “nortes” (low rainfall); the populations of *C. paspaloides* reduced their size. Fuentes et al. (2015) confirmed this with populations of *C. paspaloides* more than 15 km away from the mangrove. After the “nortes” season (December and February), the populations drastically reduced their numbers, unlike the populations that were 6 or 3 km away from the mangrove. One of the possible explanations was the effect of stronger water column dynamics and a buffering effect of the mangrove. Despite the losses during the north season, in May and June, the populations recovered, returning to the same values of biomass and individuals.

In the monospecific meadow, *C. paspaloides* has two periods of low population (nortes-dry and dry-rain) and one of growth (rain-nortes). In contrast, in mixed meadows, there are two growing seasons (dry-rainy and rainy-norte) and one of reduction of the population (norte-dry). Even though there is an increase in nutrients in the rains and the availability of nutrients in both meadows is the same, it could be

thought that in the absence of competitors, *C. paspaloides* would have more growth periods than in the mixed meadow.

The existence of a competitor tends to reduce the space available, as well as the availability of resources (Van Tussenbroek et al., 2006). The establishment success of a species will depend on how it can obtain and use resources and colonize as quickly as possible. *T. testudinum,* by having higher clonal growth in mixed grasslands, suggests that in the presence of competitors, the species will invest the resources and available energy in growth and establishment. In contrast, without competitors, it will invest more in sexual reproduction and permanence. In contrast, the dry season negatively affects *C. paspaloides*. Phillips (2006) reported that sexual reproduction is rare in *Caulerpa* species. Still, when an event reduces the fitness of competitors such as other species of macroalgae, their ability to grow fast and produce clones will increase their population size and occupy the space left by these species in the dry season. Once *T. testudinum* is established, the diversity of macroalgae will be lower. But places with early colonization will have a wider variety of macroalgae.

In the rainy season, nutrients increase in the water column, such as the DIN; this may suggest that their availability is increased and thus, the population size of *C. paspaloides*. Fuentes et al. (2014) indicate that the “nortes” season is a natural control of *C. paspaloides* populations, opening colonizable spaces for *T. testudinum* or other competitors. Having registered lower λ in certain seasons is a consistent behavior between years. Although higher biomasses are recorded in both meadows in rainy seasons, these values drop in the “nortes” and dry seasons. Another factor that helps *T. testudinum* survival is the production of the rhizome. In the monospecific meadows of *T. testudinum*, higher rhizome production and larger sizes were recorded. This suggests that these meadows are more resistant than macroalgae, and when the “nortes” season occurs, the removal will only affect the macroalgae due to their small size. Biber et al. (2004) also described that the success in the permanence of rhizophilic macroalgae is the production of toxic and harmful substances to predators formed by silicates and carbonates. Although predation on

the species was not analyzed in this study, it can be argued that the appearance and disappearance of *C. paspaloides*, thanks to the temporality, will affect the composition and the establishment of other biotic elements of the meadows.

One of the effects that species of the genus *Caulerpa* have in the Mediterranean is to change sediment pH through the incorporation of CO_2; this allows the emergence of bacteria communities that are capable of altering the sediment and the colonization conditions that exist in the environment (Roth-Schulze et al. 2017). Biomass occurrence of *T. testudinum* suggests that the presence of macroalgae is minimal in monospecific *T. testudinum* meadows as potentially there will be no colonization space for macroalgae and, therefore, there will be less competition for *T. testudinum*. Ecological succession in the meadows can be through the primary colonization with monospecific meadows of macroalgae, followed by intermediate mixed ones, and finally the most complex monospecific stands of *T. testudinum*.

One factor affecting the composition and development of the SAV is the availability of light. In Chapter 4 sites had differences in depth leading to an effect on light availability and in the composition of the SAV. The records in this study (light at bottom, HOBO data and Light loss coefficient) confirm this idea. The monospecific meadow of *T. testudinum* (site 1) recorded the highest light values at bottom (31.39%-16.9%), while the lowest records were recorded in the monospecific meadow of *C. paspaloides (*Site 3, 0.005%-0.10%). The records that indicate the highest light loss coefficient are Site 3 (rain) and Site 2 (norte).

Ralph et al. (2007) indicated that with less light availability, opportunistic species such as macroalgae or small seagrass species are more frequent than long-lived and large species such as the *T. testudinum* series. Light availability and light loss data indicate that Site 3 has the lowest light availability compared to the other sites, and it is the site where *C. paspaloides* is monospecific.

In order for seagrasses to live adequately, light values at the bottom of 15% to 25% are reported to be optimal (Markager and Sand-Jensen, 1992, 1996; Agusti et al., 1994, Carruthers et al., 2001), however in our study a minimum of 0.005% light was

register and in Chapter 4 the presence of *T. testudinum* was recorded in the coverage at site 3 (Fig. 2). Having not changes in the *Fv/Fm* values and the percentages of photosynthetic pigments for *T. testudinum*, suggests that *T. testudinum* in “Los Petenes” has an adaptation to high depths and less light availability.

Cayabyab and Enríquez (2007) reports photosynthetic damage in *T. testudinum* leaves occurs when photosynthetic efficiency drops below 0.7. In both meadows, the *Fv/Fm* values for *T. testudinum* are lower than those in the rainy season, in monospecific meadows and in mixed meadows the rainy season, *Fv/Fm* and the light data suggest that, for both species, the mixed meadows will have high photosynthetic stress conditions in the rainy season. Plants use accessory pigments to resist stressors such as increased and decreased light in the environment. The results indicate no significant differences in the accessory pigments *T. testudinum* species for both meadows (Figure 11). This and the fact that site 2 (mixed) registered values lower than 10% light (Carruthers et al., 2001) (2.40%-0.50%) may suggest that the minimum values of *Fv/Fm* may be lower than those suggested by the literature and *T. testudinum* in "Los Petenes" will have a greater resistance than the species that inhabit the Caribbean or other areas. *Fv/Fm* maximum and minimum indicates that the minimum value of photosynthetic efficiency was 0.63 (Fig. 10 A). Therefore, the results suggest that in "Los Petenes," the photosynthetic stress of *T. testudinum* occurred in values lower than 0.63.

Even though *T. testudinum* can protect itself efficiently, certain factors cause stress, such as, for example, the presence of phytoplanktonic organisms and epiphytes on the leaves. Fong and Harwell (1994) established that the increase in the biomass of epiphytic microorganisms is associated with the increase in light, temperature, and nutrient concentration in the water column. Also, Ralph (1999) established that increased epiphytic organisms are a seagrasses stress factor. Although it was not measured the amount of epiphytes on the leaves, it has been shown low values of *Fv/Fm* in the rainy seasons and an increase in physicochemical parameters in the rainy season, it can suggested that this also occurred in the study sites. As epiphytic organisms will occupy leaf space the capacity of photosystem II in *T. testudinum*

leaves will decrease, resulting in leaf necrosis. However, thanks to the strategy of *self-shading* and the decrease in temperature, the nutrients in the water column and the light in the “nortes” season will allow the physiological recovery of *T. testudinum*.

Biber et al*.* (2004) report that for macroalgae*, Fv/Fm* it is less than 0.5 (2004). The fronds of *C. paspaloides* in mixed meadows do not present zeaxanthin in dry conditions and present a value of 0.6. Still, it was found that there was a reduction in photosynthetic efficiency in the rainy season (0.36). One of the causes of photosynthetic stress is excess light, since macroalgae are recorded to be in light conditions between 0-1% (Markager and Sand-Jensen, 1992), in the study it is clear that site 3 (monospecific of *C. paspaloides*) presents these light values. However, site 2 presents higher values, so it can be suggested that the increase in light that occurs in the dry season causes photosynthetic damage and reduces the performance of the *C. paspaloides*. Gomez et al. (2004) and Gou et al. (2015) report that several chlorophyte macroalgae present photo inhibition at values less than 0.5. This suggests that macroalgae in “Los Petenes” could have higher tolerance in light gradients.

In the dry season there is presence of zeaxanthin in the monospecific site of *C. paspaloides* (site 1) but not in the mixed site (site 2). *C. paspaloides* presented more photosynthetic stress in the mixed meadows than in the monospecific ones. Zeaxanthin in a pigment which is involved in high amount of light, violaxanthin is de-epoxidized to zeaxanthin via the monoepoxide antheraxanthin due to the activation of violaxanthin de-epoxidase, a thylakoid lumen enzyme Lamberts, 2008). In the dry season, there are fewer fronds recorded without photosynthetic stress. This suggests that the excess dry light will significantly affect photosynthetic efficiency. Still, due to competition, the resources obtained are used in growth and *Fv/Fm*, but not zeaxanthin formation. This may suggest that competition will affect the photosynthetic performance of *C. paspaloides*, which will affect not only the *Fv/Fm* in the rainy season but the xanthophyll cycle will be involved in the dry season, which has higher solar irradiance, there is no enough production of zeaxanthin, although the pigments are balance in the rainy season. In contrast, although the *Fv/Fm* of *T. testudinum*

decreases in the rainy season, there are no changes in the accessory pigments, as a consequence there is no stress in *T. testudinum.*

Macroalgae are fast-growing species, their life cycle is short, and their populations can overgrow other species under appropriate conditions. This may suggest that *C. paspaloides* will be affected by competition with other fast-growing species phytoplanktonic organisms and epiphytes organisms.

The PCA suggests that the DIN and the temperature are related to the photosynthetic efficiency of both species, in addition to the fact that both variables are related. However, this can only suggest that these parameters are associated with temporality rather than photosynthetic efficiency.

Both species are in good health in the study sites but in the particular case of *C. paspaloides* in mixed meadows in the dry season, its health decreases. Available light is an important factor for the photosynthetic efficiency, higher light *T. testudinum* will have higher photosynthetic efficiency and lower light *C. paspaloides* will have higher photosynthetic efficiency. Also there is an antagonistic effect in both species; being *C. paspaloides* was negatively affected.

The abiotic (depth, available light at the bottom and sediment characteristics), and biotic characteristics (composition of the VAS, physiological and population characteristics) were different in the sites (Table 13).

Physicochemical factors that reduce the growth and establishment of seagrasses are reduced light availability, increased nutrients in the water column (which, as a consequence, increases phytoplankton and macroalgae), and increases in sea temperature water (Duarko and Moffler, 1987 Powell et al., 1989).

Table 13 Biotic and abiotic characteristics of the three meadows

Characteristics	**Site 1 (Monospecific of *T. Testudinum*)**	**Sitio 2 (Mixed)**	**Sitio 3 (Monospecific of *C. paspaloides*)**
Depth	1.2m a 2m	2.3m a 3.2m	2.6m a 4.0m
Sediment	Fine sand	Rough sand	Medium sand
Flowering in *T. testudinum*	59%	11%	-----
Number of shoots in *T. testudinum*	156	89	-----
Biomass Aboveground	59%	44%	-----
Biomass Belowground	41%	56%	-----
Vertical growth	4.26±0.02	5.02±0.02	-----
Horizontal growth	8.74±0.06	8.43±0.06	-----
λ of *T. testudinum*	1.15	1.12	-----
***C. paspaloides* measurements (stolons, fronds, diameter of stolon y biomass)**	-----	Lower	Higher
λ of *C. paspaloides*	-----	1.29	1.44
λ lower than 1 events	-----	1	2
Growth of leaves of *T. tesudinum*	0.23cm/day	19cm/day	-----
Growth of fronds of *C. paspaloides*	-	0.19	0.25
Fv/Fm* of *T. testudinum	0.72	0.73	
Fv/Fm* of *C. paspaloides		0.55	0.61
Percentage of light bottom	de 14.74% to 29.87	de 2.32 a 18.05	de 1.29 a 7.39
Light loss coefficient	Between **-0.604** and **-0.957**	Between **-0.532** and **-1.175**	Between **-0.651** and **-1.087**
Pigments of Xanthophyll and Chlorophyll in *T. testudinum*	Same	Same	----
Pigments of Xanthophyll in *C. paspaloides*	-----	Increase of Violaxanthin on Nortes season	Increase of Zeaxanthin on Dry season
Pigments of Chlorophyll in *C. paspaloides*	-----	Increase of Chlorophyll B on Rainy season	Increase of Chlorophyll B on Dry season

Light is one of the factors that limit the growth, composition, and establishment of the SAV. Although seagrasses and macroalgae are photosynthetic organisms, they have different characteristics to occupy different niches in the water. Pérez et al. (2019) observed SAV depth gradients throughout “Los Petenes” Reserve, macroalgae communities can be seen at low depths.

Considering that the availability of light at the bottom is greater at site 1 (29.87% - 14.74%), this suggests that the photosynthetic activity will be higher. Although there is greater biomass in site 1 and site 2 which have lower light availability at the bottom (18.05% - 2.32%), no significant differences were found in their *Fv/Fm* in both sites. From the north in 2018, the presence of *T. testudinum* was recorded at site 3 (monospecific *C. paspaloides*). Although the literature suggests that seagrasses require a minimum of 10% background light (Carruthers et al., 2001), the data obtained may suggest that *T. testudinum* can adapt to low-light conditions.

As previously discussed, *T. testudinum* is a permanent species, with survival over time and physiological resistance as its main characteristics (Kilminster, et al. 2015). The study showed that *T. testudinum* in both sites have the same fitness (equal population and modular λ) there are certain demographic characteristics that are different, in site 1 (monospecific of *T. testudinum*) flowering and rhizome growth is more present (below-ground biomass) and in site 2 (Mixed) vegetative growth and the growth of leaves and bundles will be more frequent (above-biomass) and greater leaf growth throughout the year. The fact that significant differences in photosynthetic pigments in both sites were not found, suggest that photosynthetic activity is the same in both meadows and thus resources assimilation are equal. In site 1 the resources were used for sexual reproduction (production of flowers and fruits) and horizontal growth (rhizomes) and site 2 will invest in vertical growth. Since site 2 is light limited at the bottom, growth of vertical bundles as well as leaves will be important for *T. testudinum* and for other species (macroalgae and *C . paspaloides*), therefore the investment of resources will focus on the growth of leaves and vertical bundles. In site 1, since there is greater growth of rhizomes, the sediment is mainly composed of fine sand and therefore will be smaller in size, but in site 2 and 3 apart

from the fact that *T. testudinum* is dedicated to the production of vertical bundles and leaves, the sites have the presence of macroalgae and their rhizoid systems do not present structures that help the disintegration of sediment and only its fixation. Thus, the composition of the sediment as well as its size is established by biotic factors.

Macroalgae, being more primitive organisms, can colonize various depth gradients where light availability is different and even low (Markager and Sand-Jensen, 1992, 1996). This may suggest that they could colonize all the sites, but in some site like site 1, there is no space available for their colonization, as a result *T. testudinum* monopolizes it with its rhizome system. Depending on the available space, shallow areas that allow a large amount of light could be viable for the species as long as there is available space.

The availability and absence of nutrients in the meadows affect the appearance and disappearance of the plants that form the SAV (Fong and Harwell, 1999). Also, they described that macroalgae, epiphytes, and phytoplankton assimilates nutrients in the water column. In contrast, *T. testudinum* meadows in the Gulf of Mexico use interstitial nutrients to a greater extent. Davis and Fourqueran (2001) described that seagrasses obtain nitrogen from ammonium (NH4) underground, but in some cases, the leaves can assimilate nitrogenous forms (NO_3 and NO_2) in the water column and phosphorus in underground form (Davis and Fourqueran, 2001). Archer et al. (2018) observed that the growth of *T. testudinum* does not change despite the presence of a competitor (*Halichondria melanadocia*). Although, increasing nitrates at the site where there was a competitor reduced the biomass and growth rate of *T. testudinum*, suggesting that the interaction changed from commensalism to amensalism if nutrient dynamics were altered. In addition, the increase of macroalgae in the meadows is associated with increased DIN in the water column (Davis and Fourqueran, 2001). Cole et al. (2017) found that phosphorus tends to be toxic to seagrasses, and its increase can increase the explosive growth of macroalgae, confirming the role that these have as modifiers of the environment.

Not having found significant differences in the sites and nutrient records (column and pore-water) and these records exceed those reported in the literature for *T.*

testudinum and macroalgae (Table 2 and 3) (Fong and Harwell, 1994; Davis and Fourqueran, 2001; Biber et al., 2004; Hoffman et al., 2019), may suggest that, in general, the species are not subject to nutrient limitations and have the same abiotic conditions to develop.

The results in λ for both species, the photosynthesis of *T. testudinum* and not having found significant differences in nutrients, phytoplankton, and temperature in the three sites, suggests that the sites have the same health conditions and there is little disturbance in the seagrass meadows. Since the "Los Petenes" zone is a protected natural area, it can be assumed that disturbances are low. This would confirm that abiotic conditions do not affect the presence and absence of these two species in "Los Petenes".

The Petenes Biosphere Reserve, during its three seasons, has reported changes in the composition of the SAV (CONAMP, 2018). Fuentes et al. (2014) recorded that the cover and biomasses of *C. paspaloides* change after the “norte” season, suggesting a reduction in their populations during this period. The growth rates (λ) of *C. paspaloides* during the seasons confirm this, as well as the appearance of other elements in the monospecific meadows of this species.

The temperature and DIN records of the water column were consistently higher in the rainy season in the three sites. One of the characteristics of the rainy season is the increase in precipitation and water supply through epicontinental origin. It can be suggested that the incorporated water contributes nutrients, mostly DIN. The PCA suggests that there is a strong association with nutrients, the mixed site, and seasonality, implying that the rainy season affects nutrients, which, in turn, affects the SAV of these sites with an increase in higher primary production.

The PCA also suggests a strong association with interstitial ammonium, but dependent on site rather than time. Interstitial ammonium is produced by the decomposition of organic matter by sediment bacteria. The fact that there is a greater diversity of macroalgae suggests that there are processes for this nutrient to be available in the environment and for *T. testudinum* to persist in the area. According to

the literature, interstitial nutrients are essential for the establishment and growth of *T. testudinum*, and this correlates with our results.

5.1 Possible scenarios for *T. testudinum* and *C. paspaloides*

The graphs indicate that the increases in *T. testudinum* biomass and interstitial nutrients coincide. This may suggest that the rise in both meadows (population λ), growth of leaves, vertical shoots, and the number of vertical shoots and flowers could be due to increased pore-water nutrients in the year.

It is also observed that there are increases in the biomass of *C. paspaloides* when there are increases in water column temperature and nutrients. This, together with the PCA data, *λ* and photosynthetic efficiency of *C. paspaloides,* suggests that seasonality will affect the growth of the species, as well as the absence of nutrients in the water column that occurs when rainfall decreases throughout the year.

It has been recorded that 2016 there was a Mega Niño phenomenon (high temperatures in the water). This phenomenon persists in tropical areas for longer, and at the end of 2017, “La Niña” phenomenon began (low water temperatures) (Pinheiro et al. 2020). At the beginning of the study, explosive growth in *C. paspaloides*, and early 2018, the population disappeared in mixed populations, and in monospecific populations, its coverage was reduced to 50%. This may suggest that phenomena that increase the water's temperature allow high growth rates in *C. paspaloides*, with adverse effects due to high temperatures. In the case of *T. testudinum*, it has been recorded that it is a physiologically tolerant species. Therefore, the environmental conditions throughout the year do not produce foliar photosynthetic stress. However, the fact that there is no high mortality in macroalgae may suggest that the availability of colonizable space and the nutrients in the water column will decrease. Although macroalgae use more water column nutrients than interstitial ones, it has been studied that ammonium is the product of the decomposition of organic matter in the sediment by bacteria and other microscopic organisms. Finding interstitial ammonium is associated with low rainfall sampling (north and dry) with a decrease in the populations of *C. paspaloides*. This may

suggest that the mortality of macroalgae and other primary producers will increase interstitial nutrients and provide the appropriate conditions for the growth and expansion of *T. testudinum*. This may suggest that the La Niña phenomenon will result in the high mortality of macroalgae and other primary producers, producing organic matter processed by microscopic organisms and converting it into interstitial nutrients that will allow growth and the expansion of seagrasses. Not having found significant differences in organic matter in the sites and the seasons suggests that the decomposition is constant and depends on events over a longer time and larger geographic scales such as El Niño and La Niña phenomena. To confirm this idea, directed studies of bacteria and decomposer organisms in seagrass beds and their assimilation of organic matter would be necessary.

This study did not consider some biological factors, such as the presence and absence of epiphytes in the fronds of *C. paspaloides* and leaves of *T. testudinum*. Fong and Harwell (1994) describe the epiphytes as an element that affects *T. testudinum* since their increase in the leaves will decrease the photosynthetic activity of the species and there will be an energetic waste in the species. Although, by the self-shadowing strategy (*self-shading*) previously discussed, *T. testudinum* sheds old leaves and protects new leaves to increase survival and generate interstitial nutrient inputs. Biber et al. (2004) also argued that the epiphytes in the fronds of rhizophilic macroalgae affect the performance of the species; this could explain the high mortalities that occur since the north season in *C. paspaloides*. Although it can be hypothesized that it would not affect the adequacy of the species, since in the high rainfall season, they recover and grow twice their population size.

Also the respective herbivores that exist for the two species, their effect on the populations and photosynthetic efficiency was not consider in this study. In the case of *T. testudinum*, it is documented that sea turtles (*Chelonia mydas*) are its main herbivore. However, it has been reported that sea urchins such as *Tripneustes ventricosus* and *Lytechinus variegatus* and certain fish species such as *Sparisoma radians* are important herbivores for SAV (Zieman et al., 1984). Although it has been reported that turtles and fish do not have a negative effect on seagrasses generally, if

the numbers of resident turtles in the environment is increased, this will reduce the coverage of the SAV significantly. Although if there is high diversity in the SAV, species such as *T. testudinum* will not be affected by herbivory (Roth, 2023), this and the reduced coverage of *C. paspaloides* could suggest that *C. paspaloides* is more affected by herbivory than *T. testudinum*, especially by sea urchins which are present in “Los Petenes”.

Another environmental aspect which was not consider is the sulfur in water, it has been reported in the Mediterranean (Najdek-Dragić et al., 2020) and in the Gulf of Mexico (Borum et al., 2005) that sulfur in healthy and highly productive meadows was lower than in meadows with little vegetation or with the presence of *Caulerpa*, the sulfur in the aquatic environment up to values greater than 10μM is dangerous for seagrass species. Suggesting that in “Los Petenes” sulfur in water is not a problem. However it is suggested that analysis of sulfur could be done in the area.

6-. CONCLUSION

There is competition between *T. testudinum* and *C. paspaloides* for space and available light.

T. testudinum may be established in places with and without competitors as long as interstitial nutrients are available in the system. The optimal life strategies in monospecific meadows are rhizome growth and sexual reproduction. On the other hand, in mixed meadows, the optimal is clonal growth by the development of vertical shoots and the accelerated formation of leaves. Therefore, *T. testudinum* throughout "Los Petenes" will be able to increase its coverage and abundance, thanks to its different demographic strategies, such as allocating necessary resources to its other traits in its life cycle.

C. paspaloides will depend on the seasonality of the area; in the dry and norte seasons, the survival of individuals will be necessary to establish the species. On the other hand, rapid growth will be more frequent in high rainfall due to the increased DIN in the environment and the seasonal temperature increase.

The composition of the SAV of macroalgae fluctuates over time and depends on environmental factors with positive growth cycles mixed with negative growth cycles. The more perennial species of the SAV use a demographic strategy in the face of ecological pressure factors in such a way that they differentially allocate resources to different life history traits.

This study recommends the following:

• Study and apply these tools to other elements of the SAV that interact with *T. testudinum* and *C. paspaloides* in “Los Petenes”, such as *Syringodium filiforme*, *Halodulle wrightii,* and *Penicillus dumetosus*.

• Applying in-situ experiments on both species to determine, starting with the elements that were relevant in this study, to manipulate and find out specifically the factors that influence their growth and development.

• In the same in-situ experiment, experiments of the presence and absence of the two species confirm the hypotheses generated in this study.

• Analyze other elements that were not measured, such as the bacterial diversity of the sediments and their role in the SAV, such as the important contributions to the production and fixation of nutrients.

• Analyze the epiphyte community for each species studied in this study and its possible impact on photosynthesis.

• Analyze the benthic organisms found in the meadows and whether they are the same or different depending on the meadow they are in, as well as their abundance and diversity.

7-. ANNEX

Thalassia: is a genus of aquatic plants in the Hydrocharitaceae family. They are perennial plants, rooted submerged, dioecious. Rhizomatous, scarious stems, with 1 root at each node. Unisexual flowers. Spathe of the staminate flowers diphyle, smooth, pedunculated, with 1 pediceled flower; bracts connate basally; tepals 3, reflexive; stamens 8-13, sessile or subsessile; the 4-locular anthers. Spathe of the pistillate flowers diphyle, smooth, persistent, pedunculated, with 1 flower shortly pediceled, with an elongated hypanthium; bracts connate basally; tepals 3, reflexive; 1-locular ovary with several placental lobes directed towards the center; styles 6-8; stigmas 12-16, papillose. Globose, equina fruit, with irregular dehiscence; seeds coniform, with the basal part thickened and the testa glabra.

It includes 7 described species and of these, only 2 accepted:

Thalassia hemprichii (Ehrenb. ex Solms) Asch., Petermanns Geogr. Mitt. 17: 242 (1871).

Thalassia testudinum Banks & Sol. former K.D.Koenig, Ann. Bot. (König & Sims) 2: 96 (1805).

The two species belonging to the genus *Thalassia* (Family: Hydrocharitaceae), *T. testudinum* Banks ex König and *T. hemprichii* (Ehrenberg) Ascherson, are widely distributed in shallow coastal areas of the tropics and subtropics of the western Atlantic (*T. testudinum*) and the Indo-Pacific (*T. hemprichii*) (den Hartog, 1970; Phillips and Meñez, 1988; Spalding et al., 2003), and they are considered 'twin species'. Considering the habitat types where the two species of *Thalassia* occur, their beds could potentially extend over huge areas (hundreds of thousands of square km).

Caulerpa: The genus is located in the Kingdom Plantae, Phylum Chlorophyta, Class Bryopsidophyceae, Order Bryopsidales and Family Caulerpaceae.

According to Jacobs (1994), this genus has the peculiarity of having a coenocytic level of organization, where there is a rapid nuclear division with respect to cell

division, giving rise to multinucleated cells. To identify them, it is divided into three main parts:

Main parts of algae of the genus *Caulerpa*. It is composed of the frond, the stolon and the rhizoid.

Caulerpa species exhibit sexual reproduction and fragmentation of any part (Phillips, 2009). The sexual one occurs by the union of two gametes of different sexuality, produced in the fronds, forming a zygote, which divides meiotically forming spores which form a new stolon.

Many of the species have stolons of more than 3 m and 200 fronds. 347 species have been identified in this genus (Guiry and Guiry, 2012).

At the global level, *Caulerpa* is located in the pantropical zone (Meñez and Calumpong, 1982). It exists as an invasive alien species in the Mediterranean (Phillips and Price, 2002), parts of Australia (Wrigth, 2005) and in the USA, California (Williams and Grosholz, 2002).

In Mexico, Pedroche et al. (2005) places the genus *Caulerpa* in the Pacific and Ortega et al. (2001) in the Caribbean, on the Alacranes Islands and on the Islas Mujeres. However, there are recent records that place the species in the state of Campeche (Pacheco et al., 2009). Garduño-Solórzano et al. (2005) places this genus as the second in greatest specific richness on the Mexican coasts of the Gulf of Mexico and the Caribbean.

Of the species of *Caulerpa paspaloides* located in the Mexican Atlantic (Pedroche and Sentíes, 2020):

Caulerpa paspaloides f. *flabellata* Weber Bosse

Caulerpa paspaloides f. *phleoides* (Bory) Weber Bosse

Caulerpa paspaloides f. *phyllaphlaston* (G. Murray) Weber Bosse

Caulerpa paspaloides var. *compressa* (Weber Bosse) M. Howe X -

Caulerpa paspaloides var. *lax* Weber Bosse

Caulerpa paspaloides var. *wurdemanii* Weber Bosse

8-. LITERATURE CITED

Archer, S. K., Hensel, E., and Layman, C. A. 2018. Ambient nutrient availability drives the outcome of an interaction between a sponge (Halichondria melanadocia) and seagrass (Thalassia testudinum). *Journal of Experimental Marine Biology and Ecology*, *503*, 86-91.

Adhitya, A., Folkard, A. M., Govers, L. L., van Katwijk, M. M., de Iongh, H. H., Herman, P. M. J., and Bouma, T. J. 2016. The exchange of dissolved nutrients between the water column and substrate pore-water due to hydrodynamic adjustment at seagrass meadow edges: A flume study. *Limnology and Oceanography*, *61*(6), 2286-2295.

Aschehoug ET, Brooker R, Atwater DZ, Maron JL, Callaway RM. 2016. The mechanisms and consequences of interspecific competition among plants*. Annual Review of Ecology Evolution y Systematics* 47: 263–81.

Agusti, S., Enriquez, S., Frost-Christensen, H., Sand-Jensen, K., and Duarte, C. M. 1994. Light harvesting among photosynthetic organisms. *Functional Ecology*, 6; 5(3): 273-279.

Bell S.S. and Hall M.O. 1995 Drift macroalgal abundance in seagrass beds: Investigating large-scale associations with physical and biotic attributes. *Marine Ecology Progress Series* 147: 277–283.

Biber, PD, Harwell, MA and Cropper Jr, WP, 2004. Modeling the dynamics of three functional groups of macroalgae in tropical seagrass habitats. Ecological Modelling, 175(1): 25-54.

Borum, J., Pedersen, O., Greve, T. M., Frankovich, T. A., Zieman, J. C., Fourqurean, J. W., and Madden, C. J. 2005. The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, Thalassia testudinum. *Journal of Ecology*, *93*(1): 148-158.

Bulleri, F., Benedetti-Cecchi, L., and Cinelli, F. 1999. Grazing by the sea urchins Arbacia lixula L. and Paracentrotus lividus Lam. in the Northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, *241*(1): 81-95.

Camargo, J. A., and Alonso, A. 2007. Contaminación por nitrógeno inorgánico en los ecosistemas acuáticos: problemas medioambientales, criterios de calidad del agua, e implicaciones del cambio climático. *Ecosistemas*, *16*(2):113

Carruthers, T. J., Longstaff, B. J., Dennison, W. C., Abal, E. G., and Aioi, K. 2001. Measurement of light penetration in relation to seagrass. Global seagrass research methods, 370-392.

Caswell, H. 2001. Matrix population models. Sinauer, Nueva York, EE.UU.

Cayabyab, N.M. and Enríquez, S. 2007. Leaf photoacclimatory responses of the tropical seagrass *Thalassia testudinum* under mesocosm conditions. A mechanistic scaling-up study. *New Phytologist* 176:108-123.

Ceccherelli, G. and Cinelli F. 1997. Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. *Journal of Experimental Marine Biology and Ecology* 217, 165–177.

CONABIO www.conabio.gob.mx Fecha de consulta: 12/12/2023.

CONAGUA https://smn.conagua.gob.mx/es/ Fecha de consulta: 12/12/2023.

CONANP www.conanp.gob.mx/ Fecha de consulta: 12/12/2023.

Davis, B.C. and J.W. Fourqurean. 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. *Aquatic Botany* 71(3):217-232.

Dean Jr, W. E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. Journal of Sedimentary Research 44: (1): 242–248.

De los Santos, Carmen, Olivé I, Moreira M, Silva A, Freitas C, Luna RA, Quental-Ferreira H, Martins M, Costa MM, Silva J and Cunha M.E. 2022. Seagrass meadows improve inflowing water quality in aquaculture ponds. *Aquaculture*, 528: 1-22.

Duarte, C. M. 1990. Seagrass nutrient content. *Marine ecology progress series. Oldendorf*, *6*(2): 201-207.

Duarte, C. M., Marbá, N., Agawin, N., Cebrián, J., Enríques, S., Fortes, M. D., Gallegos, M. E., Merino, M., Olesen, B., Sand-Jensen, K., Uri, J., and Vermaat, J. 1994. Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series*, 107: 211-222.

Duarte, C. M. and Cebrián, J., 1996, The fate of marine autotrophic production, *Limnology and Oceanography*, 41: 1758-1766.

Enríquez, S., Merino, M. and Iglesias-Prieto, R. 2002. Variations in the photosynthetic performance along the leaves of the tropical seagrass Thalassia testudinum. Marine Biology, 140(5): 891–900.

Falkowski, P. G., and Raven, J. A. (2013). *Aquatic photosynthesis*. Princeton University Press.

Folk, R. L. 1974. The natural history of crystalline calcium carbonate: effect of magnesium content and salinity. *Journal of Sedimentary Research,* 44(1): 40–53.

Fong, P. and Harwell, M.A., 1994. Modeling seagrass communities in tropical and subtropical bays and estuaries: a mathematical model synthesis of current hypotheses. *Bulletin of Marine Science*, *54*(3): 757-781.

Fonseca, M. S. (1996). The role of seagrasses in nearshore sedimentary processes: a review. In *Estuarine Shores: Evolution, Environments and Human Alterations* (eds Nordstrom, K. F. and Roman, C. T.), Wiley.

Fuentes, S. A., Gallegos, M. E., and Mandujano, M. C. 2014. Demografía de *Caulerpa paspaloides var. wurdemanniii* (*Bryopsidales: Caulerpaceae*) en la zona costera de Campeche, México. *Revista de Biología Tropical*, 62(2): 729-741.

Fuentes-Agueda, S.A. 2015. Demografía de *Caulerpa paspaloides* var. *wurdemannii* en tres poblaciones de la zona costera de Campeche. Tesis de Maestría. Instituto de Ecología, Universidad Nacional Autónoma de México. 46 pp.

Gallegos, M. (2010). Pastos Marinos.. En Villalobos-Zapata, G. J. y Mendoza, J. (Coord.). 2010. *La biodiversidad de Campeche*. Comisión Nacional para el conocimiento y uso de la biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur. México, 204-209

Garduño-Solórzano, M., Godínez, J.L. and Ortega, M.M. 2005. Distribución geográfica y afinidad por el sustrato de las algas verdes (CHLOROPHYCEAE) bénticas de las costas mexicanas del Golfo de México y Mar Caribe. Boletín de la Sociedad Botánica de México, 76: 61-78.

Gaudette, H. E., Flight, W. R., Toner, L., and y Folger, D. W. 1974. An inexpensive titration method for the determination of organic carbon in recent sediments. *Journal of Sedimentary Research*, *44*(1): 249-253.

Glardon C., Walters L., Olsen J., Stam W. and Quintana-Ascencio ,P., 2008 Predicting risks of invasion of *Caulerpa* species in Florida. *Biological Invasions* 10:1147–1157.

Gómez, I., López-Figueroa, F., Ulloa, N., Morales, V., Lovengreen, C., Huovinen, P., and Hess, S., 2004. Patterns of photosynthesis in 18 species of intertidal macroalgae from southern Chile. *Marine Ecology Progress Series*, *270*: 103-116.

Guiry, M.D. and Guiry, G.M. 2023. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; consultado el 9 de mayo 2023.

Guo, L. P., Kang, H. J., Ouyang, Z., Zhuang, W., and Yu, Q., 2015. Photosynthetic parameter estimations by considering interactive effects of light, temperature and CO2 concentration. *International Journal of Plant Production*, *9*(3), 321-346.

Hacker, S. and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology*, 78:1990-2003.

HACH http://latam.hach.com/global Fecha de consulta: 15/3/2023.

Harper, J.L. 1977 *Population Biology of Plants*. Academic press, London England.

Hemminga, M. A., Harrison, P. G., and Van Lent, F., 1991. The balance of nutrient losses and gains in seagrass meadows. *Marine Ecology Progress Series*, 71: 85-96.

Hixon, M.A and M. H. Carr.1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science.* 277: 946-949.

Hixon, M.A., S. W. Pacala and S. A. Sandin. 2002. Population regulation: Historical context and contemporary challenges of open vs. closed systems. *Ecology* 83: 1490-1508.

Hoffman, D.K., McCarthy, M.J., Newell, S.E., Gardner, W.S., Niewinski, D.N., Gao, J. and Mutchler, T.R., 2019. Relative Contributions of DNRA and Denitrification to Nitrate Reduction in Thalassia testudinum Seagrass Beds in Coastal Florida (USA). *Estuaries and Coasts*, *42*(4): 1001-1014.

Kalaji, H.M., Schansker, G., Ladle, R.J., Goltsev, V., Bosa, K., Allakhverdiev, S.I., Brestic, M., Bussotti, F., Calatayud, A., Dąbrowski, P. and Elsheery, N.I., 2014. Frequently asked questions about in vivo chlorophyll fluorescence: practical issues. *Photosynthesis research*, *122*(2): 121-158.

Kilminster, K., McMahon, K., Waycott, M., Kendrick, G.A., Scanes, P., McKenzie, L., O'Brien, K.R., Lyons, M., Ferguson, A., Maxwell, P. and Glasby, T., 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, *534*: 97-109.

Lambers, H., Chapin III, F.S. and Pons, T.L., 2008. *Plant physiological ecology*. Springer Science & Business Media.

Levinton, J. S. 2009. *Marine Biology: function, biodiversity, ecology.* Oxford University Press. N.Y.

Libes, S., 2011. *Introduction to marine biogeochemistry*. Academic Press.

Mandujano, M. C., Montaña, C., Franco, M., Golubov, J., and Flores-Martínez, A. 2001. Integration of demographic annual variability in a clonal desert cactus. *Ecology, 82*: 344-359.

Mandujano, M.C. 2007 La clonalidad y sus efectos en la biología de poblaciones. En: Eguiarte, L., Souza, V., Aguirre, X. (eds.), Ecología molecular. Instituto Nacional de Ecología, 215-250

Markager, S., and Sand-Jensen, K. 1992. Light requirements and depth zonation of marine macroalgae. *Marine Ecology - Progress Series*, (88): 83-92.

Markager, S., and Sand-Jensen, K. 1996. Implications of thallus thickness for growth-irradiance relationships of marine macroalgae. *European Journal of Phycology*, *31*(1), 79-87.

Marbà, N., Gallegos, M. E., Merino, M., and Duarte, C. M. 1994. Vertical growth of Thalassia testudinum: seasonal and interannual variability. *Aquatic Botany*, *47*(1): 1-11.

Marbà, N., Holmer, M., Gacia, E. and Barron, C., 2007. Seagrass beds and coastal biogeochemistry. En *Seagrasses: biology, ecology and conservation* Springer, Dordrecht, 135-157.

Meñez, E.G and Calumpong, H.P. 1982. The genus *Caulerpa* from the central Visayas, Philippines, Smithsonian Contributions in Marine Science, 17: 1-21.

Mijangos-Hernández, A. I. 2018. Análisis de la productividad de *Thalassia testudinum* Banks ex Köenig y su relación con los factores ambientales de la Reserva de la Biósfera Los Petenes, Campeche. CDMX, Tesis de Maestría, México: Universidad Autónoma Metropolitana, Unidad Iztapalapa, 73 pp.

Moosmann, L., Gächter, R., Müller, B. and Wüest, A., 2006. Is phosphorus retention in autochthonous lake sediments controlled by oxygen or phosphorus? *Limnology and Oceanography*, *51*: 763-771.

Moreno-Marín, F., Vergara, J. J., Pérez-Llorens, J. L., Pedersen, M. F., and Brun, F. G., 2016. Interaction between Ammonium Toxicity and Green Tide Development Over Seagrass Meadows: A Laboratory Study. *PLOS ONE*, *11*(4): 1-12

Najdek-Dragić, M., Korlević, M., Paliaga, P., Markovski, M., Ivančić, I., Iveša, L., Felja and Herndl, G. 2020. Effects of the invasion of Caulerpa cylindracea in a Cymodocea nodosa meadow in the northern Adriatic Sea, Frontiers, 7: 1-16

Nowicki, B. L., and Nixon, S. W., 1985. Benthic nutrient remineralization in a coastal lagoon ecosystem. *Estuaries*, *8*: 182-190.

Ortega, M., Godínez-Ortega, J. and Garduño, G. 2001. Catálogo de algas bénticas de las costas mexicanas del Golfo de México y Mar Caribe. Cuadernos del IBUNAM No. 34. UNAM, CONABIO.

Orth, R. J., Carruthers, T. I. M. J. B., Dennison, W. C., Duarte, C. M., James, W., Jr, K. L. H. and Williams, S. L., 2006. *A Global Crisis for Seagrass Ecosystems*, *56*(12): 987–996.

Pacheco M.C., Pacheco-Ruíz, I., Ramos, J., Cetz-Navarro, N. P. and Soto J. L. 2009. Presencia del género *Caulerpa* en Bahía de San Francisco de Campeche, Cam. *Hidrobiológica,* 19 (3): 57-69.

Páez-Osuna, F., Fong-Lee, M. L. and Fernández, H.1984. Comparación de tres técnicas para analizar materia orgánica en sedimentos: nota científica. *Anales del Instituto de Ciencias del Mar y Limnología*. Universidad Nacional. Autónoma de México, 11(1): 233-239.

Pérez, Espinosa, I., Gallegos Martínez, M. E., Ressl, R. A., Valderrama Landeros, L. H., and Hernández Cárdenas, G., 2019. Distribución espacial de los pastos marinos y la vegetación acuática sumergida en los Petenes, Campeche/Spatial distribution of

seagrasses and submerged aquatic vegetation of los Petenes, Campeche. *Terra Digitalis*, *3*(2): 1-37.

Pedroche, F.F., Silva P.C., Aguilar–Rosas, L.E., Dreckmann, K.M. and Aguilar–Rosas, R. 2005. Catálogo de las algas marinas bentónicas del Pacífico de México. I. Chlorophycota. Universidad Autónoma Metropolitana/ Universidad Autónoma de Baja California/ University of California, México, D.F.

Pedroche, F. F., and Sentíes, A. (2020). Diversidad de macroalgas marinas en México. Una actualización florística y nomenclatural. *Cymbella*, *6*(1): 4-55.

Pinheiro, E., da Rocha, R.P. and Drumond, A., 2020. Assessment of 20th-century reanalysis circulation patterns associated with El Niño–Southern Oscillation impacts on the tropical Atlantic and northeastern Brazil rainy season. *International Journal of Climatology*, 41(7): 3824-3840.

Phillips, Ronald C. and Meñez, Ernani G. 1988. "Seagrasses." *Smithsonian Contributions to the Marine Sciences*. 34(1): 104.

Phillips, J.A. and Price, I.R. 2002. How different is Mediterranean *Caulerpa taxifolia* (Caulerpales: Chlorophyta) to other populations of the species? Marine Ecology Progress Series, 238: 61–71.

Phillips, A.J. 2009. Reproductive ecology of *Caulerpa taxifolia* (Caulerpaceae, Briopsidales) in subtropical eastern Australia. European Journal of Phycology 44(1): 81-88.

Powell, G.V.; Kenworthy, J.W. and Fourqurean, J.W., 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. Bulletin of Marine Science, 44(1), 324-340.

Pugnaire, F. I. and M. T. Luque. 2001. Changes in plant interaction along a gradient of environmental stress. *Oikos*, 93:42-49.

Raz-Guzmán, A. and A. Sánchez-Martínez. 2001. La biodiversidad de los ambientes estuarinos y marinos de México. *Revista Ciencia Nicolaita,* 26: 125-146.

Reece, Jane B., and Neil A. Campbell. *Campbell Biology*. Boston: Benjamin Cummings / Pearson, 2011.

Roth-Schulze, A. J., Thomas, T., Steinberg, P., Deveney, M. R., Tanner, J. E., Wiltshire, K. H. and Gurgel, C. F. D., 2018. The effects of warming and ocean acidification on growth, photosynthesis, and bacterial communities for the marine invasive macroalga Caulerpa taxifolia. *Limnology and Oceanography*, *63*(1): 459-471.

Sandoval-Gil, J., Alexandre, A., Santos, R., and Camacho-Ibar, V. F. 2016. Nitrogen Uptake and Internal Recycling in Zostera marina Exposed to Oyster Farming: Eelgrass Potential as a Natural Biofilter. *Estuaries and Coasts*, *39*(6): 1694-1708.

Short, F. T., Montgomery, J., Zimmermann, C. F., and Short, C. A. 1993. Production and nutrient dynamics of a Syringodium filiforme Kütz. seagrass bed in Indian River Lagoon, Florida. *Estuaries*, *16*: 323-334.

Silvertown, J. 1987. *Introduction to Plant Population* Ecology. 2a. Edición. Longman, New York.

Spalding, M., Taylor, M, Ravilious, C., Short, F, and Green, E., 2003. The distribution and status of seagrasses. World Atlas of Seagrasses. 5-26.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Szmant, A.M. and Forrester, A., 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs*, *15*(1): 21-41.

Tabachnick, B.G. and Fidell L.S. 2019. Using multivariate statistics. New York, USA. Pearson press.

Terrados, J. and Williams, S.L., 1997. Leaf versus root nitrogen uptake by the surfgrass Phyllospadix torreyi. *Marine Ecology Progress Series,* 149: 267–277.

Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.

Thomas, J.E. 2003. *Caulerpa taxifolia* in Moreton Bay—distribution and seagrass interactions. Honours Thesis, The University of Queensland, 60 pp.

Van Tussenbroek, B.I.; Vonk, J.A., Stapel, J., Erftemeijer, P.L., Middelburg, J.J. and Zieman, J.C., 2007. The biology of Thalassia: paradigms and recent advances in research. In Larkum, A.W., Orth, R.J. y Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Dordrecht, The Netherlands, Springer, 409–439.

Van Tussenbroek, B. I.; Barba-Santos, M. G., Wong, J. G. R., van Dijk, J. K. and Waycott, M., 2010. Guía de los pastos marinos tropicales del Atlántico oeste. México D.F., Universidad Nacional Autónoma de México Press.

Waycott, M., Procaccini, G., Les, D.H. and Reusch, T.B., 2007. Seagrass evolution, ecology and conservation: Nutrient Dynamics in Seagrass Ecosystems. En *Seagrasses: biology, ecology and conservation*, Springer, Dordrecht, 25-50.

Williams, S. and Groscholtz, E.D. 2002. Preliminary reports from the *Caulerpa taxifolia* invasion in southern California. *Marine Ecology Progress Series*, 233: 307–310.

Wright, J.T. 2005. Differences between native and invasive *Caulerpa taxifolia*: a link between asexual fragmentation and abundance in invasive populations. Marine Biology, 147: 559-569.

Yoshioka, P.M. and Yoshioka, B.B., 1991. A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. *Marine Ecology Progress Series, 69:* 253-260.

Zamora-Crescencio, P., Mas, J.F., Rico-Gray, V., Domínguez-Carrasco, M.D.R., Villegas, P., Gutiérrez-Báez, C. and Barrientos-Medina, R.C., 2015. Composición y estructura arbórea de petenes en la Reserva de la Biosfera de “Los Petenes”, Campeche, México. *Polibotánica*, 39: 1-19

Zieman, J. C., Iverson, R. L., and Ogden, J. C., 1984. Herbivory effects on Thalassia testudinum leaf growth and nitrogen content. *Marine Ecology Progress Series*, 15: 151-158.

Zimmerman, R.C., Cabello-Pasini, A. and Alberte, R.S. 1994. Modelling daily production of aquatic macrophytes from irradiance measurements: a comparative analysis. *Marine Ecology Progress Series.* 114: 185-196.

Zimmerman, R.C., 2007. Light and photosynthesis in seagrass meadows. En *Seagrasses: Biology, Ecology and Conservation*, Springer, Dordrecht., 303-321.

9-. PUBLISHED ARTICLE

Journal of Coastal Research	00	0	000–000	Charlotte, North Carolina	Month 0000

Contrasting Growth and Establishment of *Thalassia testudinum* along a Cover Gradient in the Gulf of Mexico

Sergio A. Fuentes-Agueda[†]*, Margarita E. Gallegos[‡], María C. Mandujano[§], and Jordan Golubov[††]

[†]Doctorado en Ciencias Biológicas y de la Salud
Universidad Autónoma Metropolitana
Ciudad de México 14387, México

[‡]Área de ecosistemas costeros Laboratorio de pastos marinos
Universidad Autónoma Metropolitana–Iztapalapa
Ciudad de México 09340, México

[§]Laboratorio de Genética y Ecología
Instituto de Ecología
Universidad Nacional Autónoma de México
Ciudad de México 04510, México

[††]Laboratorio de Ecología y Taxonomía Vegetal
Departamento El Hombre y su Ambiente
Universidad Autónoma Metropolitana–Xochimilco
Ciudad de México 04960, México

www.cerf-jcr.org

www.JCRonline.org

ABSTRACT

Fuentes-Agueda, S.A.; Gallegos, M.E.; Mandujano, M.C., and Golubov, J., 0000. Contrasting growth and establishment of *Thalassia testudinum* along a cover gradient in the Gulf of Mexico. *Journal of Coastal Research,* 00(0), 000–000. Charlotte (North Carolina), ISSN 0749-0208.

Seagrasses are important for coastal ecosystem health and have significant economic benefits; however, they are undergoing important negative changes worldwide. The seagrass *Thalassia testudinum* comprises one of the main elements in submerged aquatic vegetation (SAV) habitats, and it grows in monospecific and mixed meadows along the continental shelf of the Gulf of Mexico. In this study, *T. testudinum* monospecific and mixed meadows were monitored over a 2 year period to identify the abiotic and biotic conditions that may correlate with population parameters through the plastochron index (PI). Plants found in monospecific meadows had larger rhizomes and more flowers in comparison to those in mixed meadows, while the latter produced more leaves and larger shoots. The annual rate of change in biomass (Br) of *T. testudinum* in the monospecific meadow was 1.15 ± 0.03, which was slightly higher than that in the mixed meadow, with a value of 1.12 ± 0.03. *T. testudinum* in monospecific meadows tended to exhibit increased sexual reproduction, while vegetative growth and clonal reproduction were more common in mixed meadows. The results highlight that *T. testudinum* life-history strategies and establishment are affected by both biotic and abiotic factors like depth, temperature, and water nutrients.

ADDITIONAL INDEX WORDS: *Mexico, life-history traits, physicochemical variables, population dynamics, seagrasses.*

INTRODUCTION

Seagrasses are significant organisms in marine ecosystems (Gallegos, 2010) and have an important positive economic effects on fisheries (Tuya, Haroun, and Espino, 2014). However, external pressure and impacts on seagrass populations have increased around the world through overexploitation, physical modification, nutrient and sediment pollution, the introduction of nonnative species, and global climate change (Orth *et al.*, 2006; Waycott *et al.*, 2009). Of those that have been studied, the encroachment of macroalgae into seagrass meadows has been shown to be significant (Phillips and Durako, 2000). In some parts of the world (Mediterranean Sea, Suez Canal, and areas south of Australia), species such as *Caulerpa taxifolia*, *Caulerpa racemosa* var. *cylindracea*, and *Caulerpa prolifera* have outcompeted native seagrasses by reducing individual growth, colonization, and fitness (Dumay, Fernandez, and Pergent, 2002; Smith and Walters, 1999; Thomas, 2003; Wiltshire and Deveney, 2017). Accordingly, among the reasons behind the invasive spread of these species are the lack of natural herbivores and the high clonality (Boumediene and Lotfi, 2019; Maidanou *et al.*, 2017), which reduces colonization space for native seagrasses (Fourqurean *et al.*, 1995).

Demographic studies on seagrasses are useful tools for studying and describing seagrass meadow health. These studies are based on the reconstruction of the age distribution of living shoots, or plastochron index (PI), which is a measure of the growth and the number of flower scars on each shoot, as a measure of reproductive output in the population (Duarte *et al.*, 1994; Powell, Kenworthy, and Fourqurean, 1989). Seagrass populations are characterized by large numbers of young shoots (<1 year old), which exponentially decline with increasing shoot age (Duarte *et al.*, 1994). Healthy meadows are expected to have the following characteristics: a horizontal growth rate (which increases expansion), the establishment of shoots, the accumulation of sediment, and a high scar flower ratio (an indicator of sexual reproduction; Gallegos *et al.*, 1992; Van Tussenbroek *et al.*, 2006).

Several abiotic factors affect the growth, establishment, and distribution of seagrasses; for example, low temperatures (<20°C) and high salinity (>35) will kill tropical seagrass shoots, and light availability will limit their occurrence at lower depths (<10 m; Van Tussenbroek *et al.*, 2006). High amounts of nutrients will increase leaf and rhizome growth, whereas low

DOI: 10.2112/JCOASTRES-D-22-00025.1 received 17 March 2022; accepted in revision 6 November 2022; corrected proofs received 9 January 2022.

*Corresponding author: kamahl2004@gmail.com

Figure 1. A meadow of *Thalassia testudinum* with the short shoots and exposed rhizomes in "Los Petenes" Biosphere Reserve.

nutrient availability will affect leaf senescence and result in low establishment (Powell, Kenworthy, and Fourqurean, 1989). However, high amounts of nutrients are not always beneficial; in some cases, they can increase the presence of other seagrass species or macroalgae in monospecific meadows (Williams, 1987). For example, the presence and high growth rates of macroalgae reduced the establishment of *Thalassia testudinum* in Florida (Van Tussenbroek *et al.*, 2006).

Thalassia testudinum (Banks ex (König)) is an underwater angiosperm formed by horizontal rhizomes with vertical shoots, 30-cm-long leaves, and green or pink flowers, which grow once a year (Gallegos *et al.*, 1992; Van Tussenbroek *et al.*, 2010), having fruits and seeds commonly dispersed by waves. Populations can be found in monospecific and mixed meadows with other seagrasses throughout the Caribbean Sea and the Gulf of Mexico (*e.g.*, associated with *Halodule wrightii*, *Syringodium filiforme*, and *Halophila decipiens*; Gallegos, 2010) (Figure 1).

The aim of this study was to evaluate the growth, reproduction, and establishment of *T. testudinum* in "Los Petenes" Biosphere Reserve at three sites that differed in abundance. The main biotic and abiotic factors that affect the establishment of *T. testudinum* located in monospecific and mixed meadows were described. The hypothesis assumed that *T. testudinum* development and growth would be higher in monospecific meadows than in mixed meadows, because other submerged aquatic vegetation (SAV) species would use water nutrients and colonize space and negatively affect *T. testudinum* growth and establishment.

METHODS

Surveys were done in Los Petenes Biosphere Reserve, a protected area located in the Gulf of Mexico off the coast of southeastern Mexico, which possesses the largest area of SAV in Mexico (1817.64 km^2, 20°51′30″ N 90°20′00″ W). In Los Petenes, *T. testudinum* can be found in monospecific and in mixed stands with macroalgae across the reserve, and it is the most abundant and common species, followed by *S. filiforme*, *H. wrightii*, and a diversity of macroalgae (Espinosa *et al.*, 2019). Within the macroalgae, *Caulerpa paspaloides* var. *wurdemannii* (Weber Bosse) is the most frequent, and it grows sympatrically with *T. testudinum* (Fuentes, Gallegos, and Mandujano, 2014). During 2012–16, three sampling sites were chosen for their accessibility and SAV relative cover: 100% *T. testudinum* (T100), 50% *T. testudinum* (T50), and one site with no cover of *T. testudinum* (T0). The sites were separated from each other by at least 15 km (Figure 2). Field measurements were obtained in 2017 and 2018.

Environmental variables were measured in the water column as well as in sediment ($n = 4$ samples per site per year). Water depth was obtained with a Secchi disk, and water samples (250 mL) were collected in the field at half depth with a Van Dorn bottle, from which salinity, temperature, pH, and dissolved oxygen (DO) were measured with a multiparametric sensor (YSI 556 MPS) *in situ*. Water-column nutrients (including dissolved inorganic nitrogen [DIN], NO_2^-, NO_3^-, ammonium [NH_4^+], and total phosphorus [TP]) and pore-water nutrients (ammonium and phosphorus) were obtained and analyzed with a HACH 3900 spectrophotometer at the Seagrass Laboratory of Universidad Autónoma Metropolitana–Iztapalapa.

Paired sediment cores (5 cm diameter × 30 cm length) were collected by divers (4 samples per site per year). One core was used to obtain soil pore water, and the other was used for sediment analysis. The soil pore-water samples were extracted in an anoxic chamber and separated with a centrifuge (Eppendorf centrifuge 5702) to measure ammonium and TP with standard methods (Strickland and Parsons, 1972). The sediment core samples were oven-dried to constant weight at 60°C for 2 days and separated with a sieving tower shaker (including sieves of 0.074 mm, 0.125 mm, 0.25 mm, 0.5 mm, 1 mm, and 2 mm). Mean grain size (Mz) was calculated by the mean weight of each sieve, sediment type, and diameter (mm) and assigned following the Wentworth class size (Erftemeijer and Koch, 2001; Folk, 1974). Data were resampled ($n = 75$) with an add-on in Excel 2010 in order to work directly with the actual distribution of the data (Good, 2000). Differences in each environmental variable between sites were tested with an analysis of variance (ANOVA; STATISTICA 9.0; Larose, 2016).

SAV Cover

SAV cover was quantified in each site with a 0.25 cm^2 grid (0.5 × 0.5 cm plot), with 10 replicated measurements at each site during eight surveys. The SAV categories were split into species, including *T. testudinum* and *C. paspaloides* var. *wurdemannii*, as well as cover by other macroalgae and spaces with no vegetation.

Data were resampled ($n = 75$) with an add-on in Excel 2010 in order to work directly with the actual distribution of the data (Good, 2000). For each SAV cover type (*T. testudinum*, *C. paspaloides* var. *wurdemannii*, other macroalgae, and no vegetation), a t test was used to find differences between years (Y; 2017 and 2018) for each site (STATISTICA 9.0; Larose, 2016).

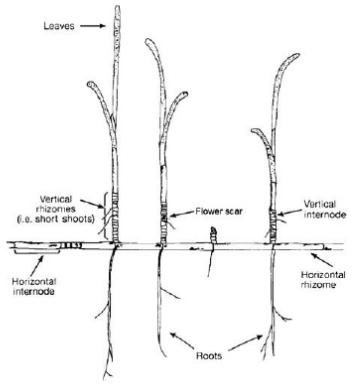


Figure 3. Modules and structures of *Thalassia testudinum* (Duarte *et al.*, 1994).

The PI was calculated using the number of leaf scars and leaves on each shoot found in samples from cores for each site (Duarte *et al.*, 1994). The vertical growth rate of shoots was then calculated through linear regression of PI and shoot length. *Thalassia testudinum* shoots have flowers once a year, so shoot age was calculated using the number of leaves formed between successive flower scars, and age structures were constructed and analyzed for each site (Gallegos *et al.*, 1992). An analysis of covariance was used to compare the growth rate slopes between sites, and a χ^2 test for the number of shoots was used to assess differences in the age structures between the sites and within years, followed by *post hoc* standardized adjusted residuals (STATISTICA 9.0; Tabachnick and Fidell, 2019).

Individual density was calculated from the total number of shoots in the core (0.3 m^2), and flowering percentage was calculated by the number of flower scars and total shoots at each site (Duarte *et al.*, 1994). The horizontal growth rate was calculated by multiplying the average length of the rhizome by the rate of horizontal internode formation (*i.e.* multiplying the ratio of average internodes and PI by the number of days a leaf is produced; Duarte *et al.*, 1994).

Samples were subsequently oven dried at 60°C for 2 days and weighed to the nearest 0.001 g to estimate the annual rate of change in biomass (Br, g m^{-2}):

$$Br = B_{t+1}/B_t \quad (1)$$

where, B_t = biomass at time t (2017), and B_{t+1} = biomass at time t+1 (2018).

Principal Component Analysis for Biotic and Abiotic Variables

A principal component analysis (PCA; STATISTICA 9.0; Tabachnick and Fidell, 2019) was conducted with the factors (T100, T50, and T0) and response variables (depth, temperature, salinity, pH, DO, DIN, TP, pore-water ammonium, and pore-water phosphorus). A biotic component of biomass was included in each factor, for which *T. testudinum* biomass was extracted with a 10-cm-diameter metal core ($n = 12$ cores per site per year). Cores were stored in plastic bags and transported, cleaned of debris, sediment, and organisms, and oven-dried for 2 days at 60°C. Factor loadings with values above 0.40 were considered to be important variables (Tabachnick and Fidell, 2019).

RESULTS

T100 was shallower (1.2–2 m) and had significantly higher Mz than T50 and T0; the latter sites did not differ between themselves (2.4–3.2 m). T100 sediment was classified as medium and fine sands with a diameter of 0.125–0.5 mm. On the other hand, T50 and T0 sediments were medium and coarse sands with a diameter of 0.25–1 mm. The other environmental variables (temperature, pH, salinity, and DO), water-column nutrients (TP and DIN), and pore-water nutrients (phosphorus and ammonium) were not different between sites (Table 1).

SAV Cover

At T100, *T. testudinum* had 0.25 m^2 cover that remained stable during the study period. However, at T50 ($t_1 = -4.98$, $p < 0.05$; Figure 4) and T0 ($t_1 = -10.98$, $p < 0.05$; Figure 4), cover was higher in 2018. Although *T. testudinum* was not present at T0 in 2017, a small mean cover of 0.02 ± 0.003 m^2 was found in 2018 (Figure 4). *C. paspaloides* var. *wurdemannii* cover decreased between the years at both sites where it was present (T50, $t_1 = 11.74$, $p < 0.05$; Figure 4) (T0, $t_1 = 11.96$, $p < 0.05$; Figure 4). At both sites, other macroalgae (*Derbesia marina* [Lyngbye] Solier, *Batophora oerstedii* J. Agardh, *Penicillus dumetosus* [J.V. Lamouroux] Blainville, *Avrainvillea levis* M. Howe, *Caulerpa prolifera* [Forsskål] J.V. Lamouroux, and *Halimeda monile* [J. Ellis & Solander] J.V. Lamouroux; Guiry

Table 1. *Summary (mean ± SE) of environmental variables and the results of comparisons between sites with ANOVA tests. Significant differences are highlighted in bold (df = 2).*

Environmental Variables	T100	T50	T0	*F*	*p*
Depth (m)	**1.57 ± 0.03**	2.97 ± 0.01	3.15 ± 0.03	**839.07**	**<0.01**
Temperature (°C)	27.02 ± 0.23	27.80 ± 0.27	27.20 ± 0.22	2.73	0.06
pH	**7.91 ± 0.03**	8.04 ± 0.02	8.23 ± 0.03	24.3	**<0.01**
Salinity	34.97 ± 0.31	34.47 ± 0.47	35.32 ± 0.51	0.91	0.40
Dissolve oxygen, DO (μM)	**5.74 ± 0.12**	6.33 ± 0.03	6.33 ± 0.12	10.73	**<0.01**
Total phosphorus, TP (μM)	1.07 ± 0.08	0.99 ± 0.06	**1.52 ± 0.12**	8.88	**<0.01**
Dissolved inorganic nitrogen, DIN (μM)	9.19 ± 0.64	6.04 ± 0.54	**15.64 ± 1.04**	39.71	**<0.01**
Pore-water ammonium (μM)	962.51 ± 43.87	909.05 ± 69.54	976.18 ± 70.71	0.32	0.72
Pore-water total phosphorus (μM)	22.59 ± 2.69	21.94 ± 3.28	**13.73 ± 1.98**	3.32	**0.03**
Mean grain size (Mz)	**2.67 ± 0.11**	1.02 ± 0.06	1.81 ± 0.05	**101.61**	**<0.01**

Allen Press, Inc. ■ 6 February 2023 ■ 11:22 am
//titan/Production/c/coas/live jobs/coas-39/coas-39-02/coas-39-02-13/layouts/coas-39-02-13.3d

Table 2. *Morphological variables of* T. testudinum *(number of leaves, number of leaf scars, number of internodes, length of shoots, length of leaves, width of leaves, rhizome size, and rhizome diameter; mean ± SE) in 2017 and 2018. Significance levels are denoted by bold in the sites (S), years (Y), and (S×Y) columns from the ANOVA/GML tests.*

					F/*p*		
Morphological Variable	T100 2017	T100 2018	T50 2017	T50 2018	Sites	Years	S×Y
Number of leaves	**3 ± 1**	**3 ± 1**	2 ± 1	2 ± 1	**6.83**	0.12	0.72
					<0.01	0.06	0.13
Number of leave scars	35 ± 22	32 ± 27	**37 ± 28**	**45 ± 31**	**7.64**	0.003	2.84
					<0.01	0.95	0.06
Number of internodes	14 ± 6	**18 ± 9**	12.5 ± 6	**15.53 ± 8**	3.22	**13.37**	0.42
					0.07	**<0.01**	0.51
Length of shoots (cm)	4.51 ± 0.27	4.35 ± 0.26	4.36 ± 0.53	5.14 ± 0.43	0.33	1.02	0.92
					0.56	0.31	0.33
Length of leaves (cm)	18.64 ± 1.32	19.90 ± 1.20	**24.34 ± 1.89**	18.6 ± 0.95	2.56	2.62	**6.46**
					0.11	0.10	**0.01**
Width of leaves (cm)	0.72 ± 0.02	0.77 ± 0.03	0.71 ± 0.03	0.84 ± 0.21	0.05	0.24	0.02
					0.81	0.62	0.87
Rhizome size (cm)	**8.35 ± 0.49**	**9.43 ± 0.70**	6.55 ± 0.49	6.37 ± 0.45	**8.32**	0.28	0.56
					<0.01	0.59	0.45
Rhizome diameter (mm)	5.19 ± 0.08	**5.22 ± 0.11**	4.93 ± 0.12	**4.87 ± 0.09**	0.27	**4.68**	0.05
					0.59	**0.03**	0.81

and Guiry, 2019) and spaces without vegetation increased their cover during the years at both sites (T50 macroalgae, $t_1 = -2.39$, $p < 0.05$; Figure 4) (T0 macroalgae, $t_1 = -4.59$, $p < 0.05$; Figure 4) (T50 no vegetation, $t_1 = -7.07$, $p < 0.05$; Figure 4) (T0 no vegetation, $t_1 = -5.29$, $p < 0.05$; Figure 4).

Morphological Variables of *Thalassia testudinum*

Leaf number and rhizome size were higher at T100 (3 leaves and 9.45 cm) than in T50 (2 leaves and 6.37 cm), and leaf scars were higher at T50 (45 scars). However, the number of internodes and rhizome diameter were higher in 2018 for both sites (T100, 18 internodes, 5.22 cm; T50, 15.53 internodes, 4.87 cm) (Table 2). T100 had the highest horizontal growth rate (67.34 cm y^{-1}), biomass (3292.29 g m^{-2}), and flowering percentage (59%) in 2018, while T50 had the highest vertical growth rate in 2018 (5.02 cm y^{-1}) (Table 3).

PI and Population Structure

Vertical growth rate was higher at T100 ($R^2 = 0.7212$, $y = 0.109x + 0.8575$) than at T50 ($R^2 = 0.6654$, $y = 0.0883x + 1.0757$; $F = 928$, df = 1, $p < 0.01$; Figure 5). Differences between age categories were found between sites ($\chi^2 = 187.26$, df = 3, $p < 0.01$; Figure 6), with more frequent individuals in all categories at T100.

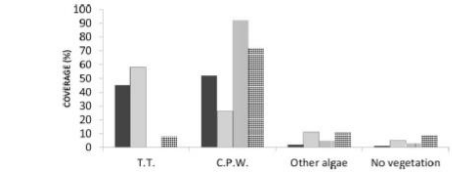


Figure 4. SAV cover (%) in T50 (colors) and T0 (lines and points). Black bars and lines represent coverage in 2017; gray bars and points represent cover in 2018 (T.T. = *Thalassia testudinum* and C.P.W. = *Caulerpa paspaloides* var. *wurdemannii*).

Biomass Accumulation

The T100 site accumulated more biomass in all analyzed size categories, with positive annual rates of change in belowground biomass (1.14 ± 0.16) and total biomass (1.15 ± 0.03). T50 biomass was also positive but at smaller rates ($Br_{belowground}$ = 1.07 ± 0.26 and Br_{total} = 1.12 ± 0.03). In contrast, the aboveground biomass accumulation at T50 (1.22 ± 0.18) was slightly higher than that at T100 (1.14 ± 0.26). This suggests that *T. testudinum* biomass accumulation increased at both sites; however, the relative aboveground to belowground accumulation differed between sites (Table 4).

PCA Analysis in *Thalassia testudinum*

The first principal component of the PCA (C1), composed of depth, sediment size, and dissolved oxygen, explained 33.20% of the data variability (Table 5). The second component (C2), composed of temperature and DIN, explained 22.30% of total variation, while C3 represented soil pore-water nutrients, and it explained 16.61% of total variation. The distribution of sites could clearly be linked to the variables associated with monospecific meadows (Figure 7A) and mixed meadows (Figure 7B).

DISCUSSION

Depth and sediment size were abiotic factors that influenced the cover of *T. testudinum* distributions in Los Petenes. Other factors were also associated with differences in *T. testudinum* cover, such as DO, water nutrients (DIN, pore-water phosphorus and ammonium), and temperature. Generally, *T. testudi-*

Table 3. *Comparative variables of* T. testudinum *(Tt) (biomass, population density, flowerage percentage, vertical and horizontal growth rate) in 2017 and 2018.*

Year	2017		2018	
Site	T100	T50	T100	T50
Total biomass, Tt (g m^{-2})	3292.29	1222.99	**3690.19**	1411.85
Flowering percentage (%)	32	4	**59**	11
Vertical growth rate (cm y^{-1})	3.79	3.38	4.26	**5.02**
Horizontal growth rate (cm y^{-1})	36.46	34.56	**67.34**	40.90

Allen Press, Inc. ■ 6 February 2023 ■ 11:22 am
//titan/Production/c/coas/live_jobs/coas-39/coas-39-02/coas-39-02-13/layouts/coas-39-02-13.3d

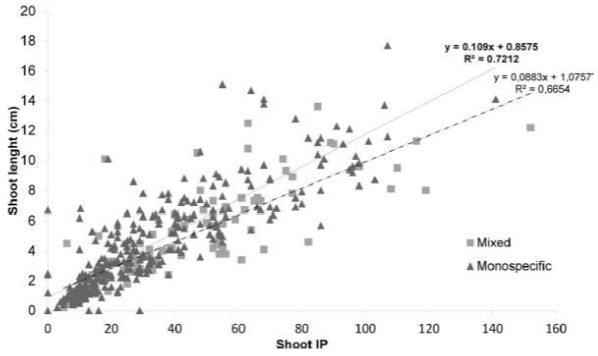


Figure 5. Vertical growth rate of monospecific (triangle) and mixed (square) meadows of *T. testudinum* in Los Petenes. Dashed line and bold letter show monospecific population (T100), and straight line shows mixed population (T50).

num can establish populations in water depths that are less than 10 m (Van Tussenbroek *et al.*, 2010), while macroalgae tend to establish in areas deeper than 10 m (Pachecho *et al.*, 2008). In Los Petenes Biosphere Reserve, Espinosa *et al.* (2019) reported that monospecific meadows of *T. testudinum* are located between 0.9 m and 2.13 m, while they are mixed with macroalgae between 0.9 m and 2.7 m. Fuentes, Gallegos, and Mandujano (2014) reported mixed meadows of *T. testudinum* and *C. paspaloides* var. *wurdemannii* in areas between 1.3 m and 2 m deep and monospecific meadows of *C. paspaloides* var. *wurdemannii* between 2.5 m and 3 m deep. A possible explanation for differences in SAV composition is light availability, because deeper areas will have higher light attenuation than shallow areas (Ramírez *et al.*, 2015). Light is an important factor for the establishment and growth of SAV species (Fong and Harwell, 1994); therefore, monospecific meadows of *T. testudinum* in shallow water could mean more available light than in mixed meadows. As a result, there could be a higher growth and establishment of *T. testudinum* in shallow waters, and macroalgae could have higher development in deep water.

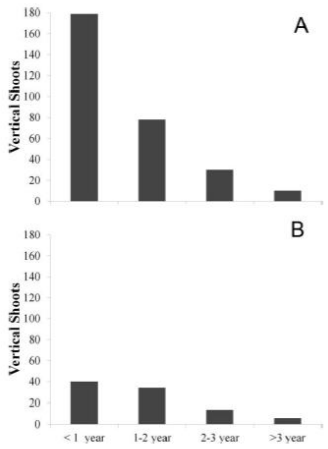


Figure 6. Age distribution of *T. testudinum* in T100 (A) and T50 (B) represented in percentages. Asterisk represents the categories that are statistically different (T100 categories are higher than T50 categories).

Dissolved oxygen in the water column is an indirect measurement of photosynthetic activity (Wetzel, 2001). The PCA suggests that mixed meadows were related to high DO; in addition, T50 and T0 presented high diversity in SAV cover, and higher DO values were registered in T50 and T0. This means that mixed meadows may have a high diversity of autotrophs (seagrasses, macroalgae, phytoplankton, and cyanobacteria) and thus have high photosynthetic activity. Although shallow water is expected to have high photosynthetic activity, during high photosynthesis and active plant growth, the respiratory oxygen consumption is much lower than oxygen release to the external media (Borum *et al.*, 2007). This could suggest that *T. testudinum* in mixed meadows will invest the resources in growth and reduce the consumption of oxygen, allowing the establishment of other elements in the SAV such as macrolagae.

Sediment size is an indication of a variety of physical and geochemical characteristics in seagrass meadows, and coarse grains are usually related to high wave energy and current velocities (Fonseca, 1996). Hemminga, Harrison, and Van Lent (1991) reported that grain size and sediments will be finer in vegetative areas than in unvegetated areas, because seagrass

Table 4. *Annual rate of change of* T. testudinum *at T100 and T50, calculated with the aboveground, belowground, and total ground biomass of* T. testudinum *in the years 2017 and 2018.*

Type of biomass accumulation	T100	T50
Aboveground	1.14 ± 0.26	1.22 ± 0.18
Belowground	1.14 ± 0.16	1.07 ± 0.26
Total	1.15 ± 0.03	1.12 ± 0.03

Table 5. *Percentage of variance explained and PCA loadings of the variables that were the most representative in the study. C1, C2, and C3 were the main components, and high contributions of each variable in each factor are in bold numbers.*

	C1	C2	C3
Explained variance (%)	33.21	22.30	16.61
Depth (m)	**0.913**	0.104	−0.032
Temperature (°C)	0.403	**−0.737**	0.026
DO (μM)	**0.632**	0.194	0.267
DIN (μM)	0.229	**−0.906**	−0.091
Pore-water ammonium (μM)	0.055	−0.355	**−0.718**
Pore-water total phosphorus (μM)	−0.162	0.349	**−0.822**
Sediment size (φ)	**−0.665**	−0.277	0.212
Biomass, Tt (g m^{-2})	**−0.857**	−0.208	0.096

rhizomes act as a sediment trap and disintegrate the sediment into smaller pieces, so bacterial communities are able to establish and help with the assimilation of water nutrients in the system. The PCA did find sediment size as an important variable in the establishment of *T. testudinum*. This could suggest that wave energy and water currents not only have an effect on abiotic components like the quality of sediments, but they also have an effect also on biotic factors such as species composition.

Column water nutrients were higher in sites without *T. testudinum* (T0). Rose and Dawes (1999) found that monospecific meadows of *T. testudinum* had lower column water nutrients than mixed meadows coformed with macroalgae in Florida. The PCA suggests that the DIN and soil pore-water nutrients were relevant variables in the establishment and growth of *T. testudinum*, consistent with previous findings in which increased water nutrients affected growth and establishment of seagrasses and macroalgae. For example, Fourqurean *et al.* (1995) found that higher water-column nitrogen tended to increase growth and presence of macroalgae and, thus, reduce the establishment of *T. testudinum*, and Williams (1987) found that competitors (*S. filiforme*) increased their growth and establishment with a rise in pore-water nutrients, which could turn into a decrease in *T. testudinum* populations. Water nutrients values in this study were higher than those previously reported for SAV in the Gulf of Mexico (Table 6), meaning high nutrient availability throughout Los Petenes, which favors establishment and growth of both species. Some of the reasons could be the high supply of inorganic and organic nutrients by the terrestrial continent. Although it has been suggested that higher values of water nutrients in SAV communities (phosphate ranges from 0.1 to 1.7 μM in the water column and from 0.3 to 20 μM in sediment pore water and ammonium ranges from 0 to 3.2 μM in the water column and from 1 to 180 μM NH_4^+ in sediment pore water; Burkholder, Tomasko, and Touchette, 2007) are detrimental for seagrasses,

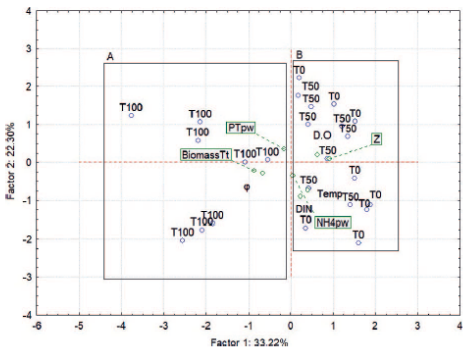


Figure 7. Factor loading represented in the PCA with the significant variables: depth (*Z*), dissolved oxygen (DO), dissolved inorganic nitrogen (DIN), temperature (Temp), pore-water nutrients (phosphorus [TPpw] and ammonium [NH4pw]), sediment size (φ), biomass of *T. testudinum* (Biomass, Tt), and relative position of the sites. Squares represent the important variables in *T. testudinum* monospecific meadows (A) and mixed meadows (B).

the results of this study could suggest that *T. testudinum* in Los Petenes is adapted to oligotrophic habitats or has an adaptive response to changing nutrient regimes (Burkholder, Tomasko, and Touchette, 2007).

Although there were no differences in temperature between sites, the PCA associated temperature as an important variable for mixed meadows. Phytoplankton and frequent macroalgae are related to high temperatures and high concentrations of water-column nutrients (Medellu, Suriani, and Komansilan, 2019; Thomas, 2003). Although there were no changes in temperature between sites, different abiotic conditions in Los Petenes may be found during the three seasons ("norte," dry, and rainy). For example, Mijangos-Hernández (2018) reported an increase in water-column nutrients and temperature in Los Petenes during the rainy season. Fuentes, Gallegos, and Mandujano (2014) suggested that the rainy season affects growth and reproduction of *C. paspaloides* var. *wurdemannii*, which decreased during the colder seasons ("nortes"). *Caulerpa paspaloides* var. *wurdemannii* in T50 and T0 reduced its cover, which could be associated with environmental changes that have a high impact, and which could open spaces for other colonizing SAV species like *T. testudinum*. The T50 and T0 sites were associated with high DO, DIN, and temperature. The data suggest that these variables could be important for other SAV like macroalgae. Also, Borum *et al.* (2007) addressed the relative importance of respiration, which increased

Table 6. *Column and pore-water nutrients in seagrass meadows of the Gulf of Mexico.*

Places	NH_4 (μM)	TP (μM)	Pore-water NH_4 (μM)	Pore-water TP (μM)	Source
Florida Bay	NA	NA	6.3–240	>0.05	Fourqurean, Zieman, and Powell (1992)
Florida (Key Largo)	NA	NA	69 ± 42	3 ± 0.9	Szmant and Forrester (1996)
Florida (St. Joseph Bay vegetated)	1.51 ± 1.82	0.10 ± 0.01	NA	NA	Hoffman *et al.* (2019)
Florida (St. Joseph Bay unvegetated)	2.21 ± 0.66	0.10 ± 0.02	NA	NA	Hoffman *et al.* (2019)
Campeche (Los Petenes)	6.76 ± 0.87	9.77 ± 2.66	853.37 ± 111.91	20.18 ± 4.7	This study

Allen Press, Inc. ■ 6 February 2023 ■ 11:22 am
//titan/Production/c/coas/live_jobs/coas-39/coas-39-02/coas-39-02-13/layouts/coas-39-02-13.3d

markedly with increasing temperature or at times of low photosynthetic rates in seagrasses; this suggests that high temperatures could reduce *T. testudinum* establishment and increase macroalgae presence.

Macroalgae have high growth rates and low establishment, which can be classified as a colonizing species (Kilminster *et al.*, 2015). Fast growth and high clonality are traits that are reported for *C. paspaloides* var. *wurdemannii* (Fuentes, Gallegos, and Mandujano, 2014), because of high vegetative growth due to simple structures and coenocyte growth (Phillips, 2009) that favor spread. In addition, species of *Caulerpa* are reported to have the ability to alter the seabed (*e.g.*, by altering the pH of the substrate due to the increase of CO_2 from algae metabolism), which leads to changes in the marine community, and particularly in the benthos community and substrate bacteria (Gribben *et al.*, 2017).

Studies in Mexico have shown that *T. testudinum* has a horizontal growth rate of 35 cm y^{-1}, reported as an indicator of good health and establishment for *T. testudinum* (Van Tussenbroek *et al.*, 2006). This study found that *T. testudinum* had a higher horizontal growth rate (51.9 cm y^{-1} at T100 and 37.73 cm y^{-1} at T50) in Los Petenes, which suggests healthy meadows, even in areas where a reduced growth rate was expected by the presence of macroalgae (T50).

Enduring meadows of a persistent species usually have small variations in their abundance and population dynamics over time (Kilminster *et al.*, 2015). Differences in resource allocation (belowground and aboveground structures) showed that *T. testudinum* allocated resources towards rhizomes and sexual reproduction in T100 and toward vertical growth in T50. Hemminga, Harrison, and Van Lent (1991) described that seagrasses will present leaf senescence in a chaotic environment (presence of other SAV species and reduced water nutrients). In these conditions, plants will invest more in vertical growth than in horizontal growth, because as older leaves die, nutrients will be integrated *via* translocation, and energy will be distributed in shoots. This process has been reported in mixed meadows of *T. testudinum* in Florida (Bricker *et al.*, 2018), which showed high mortality and clonality of younger shoots. This could mean that, although the meadows have the same quantity of nutrients, competition with other SAV species like macroalgae triggers a process of differential allocation in *T. testudinum* in order to have high availability of nutrients for the shoots.

The hypothesis that *T. testudinum* growth, flowering, and establishment should be higher in monospecific meadows (T100) holds for most demographic estimates. However, mixed meadows showed higher aboveground biomass accumulation and vertical growth rates; this could mean that SAV composition could affect the components of life history and development of *T. testudinum* in Los Petenes. A trade-off was potentially created by *T. testudinum* exchanging high sexual reproduction and high production of rhizomes for fast shoot growth and leaf production in T50 (which had the highest aboveground biomass accumulation estimate). This would help *T. testudinum* cover more space, have more available light, and avoid being displaced by other elements of the SAV. *Thalassia testudinum* in harsh conditions, like having minimal amounts of nutrients or competition with other species, will recycle older leaves to strengthen younger leaves and develop vertical growth. Higher values of DO in T50 could reflect higher photosynthetic activity, as a consequence of high production of leaves and shoot growth. In addition, colonizing space is one of the resources used by species in the SAV habitat (Fong and Harwell, 1994), in which growth and establishment are important traits that help them to occupy space, traits commonly found in clonal species (Bricker *et al.*, 2018). If the marine environment undergoes permanent changes, the establishment of persistent species like *T. testudinum* will be reduced (Roth-Schulze *et al.*, 2018), followed by more persistent species of macroalgae.

CONCLUSIONS

Seagrass cover is in healthy stage at Los Petenes Biosphere Reserve, as the *T. testudinum* population was found to be growing along the cover gradient. *Thalassia testudinum* will have changes in its life-history strategies in different meadows; sexual reproduction and increased longevity will be common in monospecific meadows, while clonal and vegetative growth will be common in mixed meadows. Key abiotic factors that enhance *T. testudinum* growth and establishment are pore-water total phosphorus and shallow depth. High DO, temperature, DIN, and pore-water ammonium and deeper water are relevant in mixed meadows and represent conditions that allow macroalgae to grow and establish.

ACKNOWLEDGMENTS

This study was part of the Doctorado en Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana, México by Fuentes-Agueda. It was also of the project "Estado de salud, conservación y vulnerabilidad de los ecosistemas de pastos marinos del Litoral del Golfo de México," with the support and funding of the Secretariat of Energy, Consejo Nacional de Ciencia y Tecnología (Centro de Investigación Científica y de Educación Superior de Ensenada, The Gulf of Mexico Research Consortium). This study was possible with the help of the laboratory of seagrasses Universidad Autónoma Metropolitana–Iztapalapa crew (Gaby, Paco, Fer, Omar, Lalo, Ivanhoe, Itai, Iliana, Martin, and Guille), whom we thank for their camaraderie and support. We also thank Alma and Gil for the creation of the study area map and Juan Chay for his support, friendship, and guidance in Campeche and across "Los Petenes." Thanks to Dr. Kurt M. Dreckmann and Dr. Abel Sentíes for the identification of the macroalgae in this study.

LITERATURE CITED

Borum, J.; Sand-Jensen, K.; Binzer, T.; Pedersen, O., and Greve, T.M., 2007. Oxygen movement in seagrasses. *In:* Larkum A.W.D.; Orth, R.J., and Duarte C.M. (eds.), *Seagrasses: Biology, Ecology and Conservation*. Dordrecht, The Netherlands: Springer, pp. 255–270.

Boumediene, H.K. and Lotfi, B.T., 2019. First record of invasive green algae *Caulerpa racemosa* var. *cylindracea* in Oran Bay (western Algeria). *Indian Journal of Geo-Marine Sciences*, 48(3), 335–342.

Bricker, E.; Calladine, A.; Virnstein, R., and Waycott, M., 2018. Mega clonality in an aquatic plant—A potential survival strategy in a changing environment. *Frontiers in Plant Science*, 9, 435–444.

Burkholder, J.M.; Tomasko, D.A., and Touchette, B.W., 2007. Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology*, 350(1–2), 46–72.

Duarte, C.M.; Marbá, N.; Agawin, N.; Cebrián, J.; Enriquez, S.; Fortes, M.D.; Gallegos, M.E.; Merino, M.; Olesen, B.; Sand-Jensen, K.; Uri, J., and Vermaat, J., 1994. Reconstruction of seagrass dynamics: Age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series*, 107, 211–222.

Dumay, O.; Fernandez, C., and Pergent, G., 2002. Primary production and vegetative cycle in *Posidonia oceanica* when in competition with the green algae *Caulerpa taxifolia* and *Caulerpa racemosa*. *Journal of the Marine Biological Association of the United Kingdom*, 82(3), 379–387.

Erftemeijer, P.L. and Koch, E.W., 2001. Sediment geology methods for seagrass habitat. *In:* Short, F.T. and Coles, R.G. (eds.), *Global Seagrass Research Method, Volume 33*. Amsterdam, the Netherlands: Elsevier, pp. 345–367.

Espinosa, I.P.; Martínez, M.E.G.; Ressl, R.A.; Landeros, L.H.V., and Cárdenas, G.H., 2019. Distribución espacial de la vegetación acuática sumergida en los Petenes, Campeche. *Terra Digitalis*, 3(2), 1–11.

Folk, R.L., 1974. The natural history of crystalline calcium carbonate; effect of magnesium content and salinity. *Journal of Sedimentary Research*, 44(1), 40–53.

Fong, P. and Harwell, M.A., 1994. Modeling seagrass communities in tropical and subtropical bays and estuaries: A mathematical model synthesis of current hypotheses. *Bulletin of Marine Science*, 54(3), 757–781.

Fonseca, M.S., 1996. The role of seagrasses in nearshore sedimentary processes: A review. *Estuarine Shores: Evolution, Environments and Human Alterations*, 35(6), 565–576.

Fourqurean, J.W.; Powell, G.V.; Kenworthy, W.J., and Zieman, J.C., 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos*, 72(3), 349–358.

Fourqurean, J.W.; Zieman, J.C., and Powell, G.V.N., 1992. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology*, 114(1), 57–65.

Fuentes, S.A.; Gallegos, M.E., and Mandujano, M.C., 2014. Demografía de *Caulerpa paspaloides* var. *wudermannii* (Bryopsidales: Caulerpaceae) en la zona costera de Campeche, México. *Revista de Biología Tropical*, 62(2), 729–741.

Gallegos, M. 2010. Pastos marinos. *In:* Villalobos-Zapata, G.J. and Mendoza, J. (eds.), *La biodiversidad de Campeche*. Campeche, México: Comisión Nacional para el conocimiento y uso de la biodiversidad (CONABIO), Gobierno del Estado de Campeche, Universidad Autónoma de Campeche, El Colegio de la Frontera Sur, pp. 204–209.

Gallegos, M.E.; Merino, M.; Marba, N., and Duarte, C.M., 1992. Flowering of *Thalassia testudinum* Banks ex König in the Mexican Caribbean: Age-dependence and interannual variability. *Aquatic Botany*, 43(3), 249–255.

Good, P. 2000. *A Practical Guide to Resampling Methods for Testing Hypotheses*. New York: Springer-Verlag, 228p.

Gribben, P.E.; Nielsen, S.; Seymour, J.R.; Bradley, D.J.; West, M.N., and Thomas, T., 2017. Microbial communities in marine sediments modify success of an invasive macrophyte. *Scientific Reports*, 7(1), 1–8.

Guiry, M.D. and Guiry, G.M. 2019. *AlgaeBase*. Galway, Ireland: National University of Ireland. https://www.algaebase.org

Hemminga, M.A.; Harrison, P.G., and Van Lent, F., 1991. The balance of nutrient losses and gains in seagrass meadows. *Marine Ecology Progress Series*, 71(1), 85–96.

Hoffman, D.K.; McCarthy, M.J.; Newell, S.E.; Gardner, W.S.; Niewinski, D.N.; Gao, J., and Mutchler, T.R., 2019. Relative contributions of DNRA and denitrification to nitrate reduction in *Thalassia testudinum* seagrass beds in coastal Florida (USA). *Estuaries and Coasts*, 42(4), 1001–1014.

Kilminster, K.; McMahon, K.; Waycott, M.; Kendrick, G.A.; Scanes, P.; McKenzie, L.; O'Brien, K.R.; Lyons, M.; Ferguson, A.; Maxwell, P., and Glasby, T., 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, 534, 97–109.

Larose, D., 2016. *Discovering Statistics*. New York: W.H. Freeman and Company, 910p.

Maidanou, M.; Koulouri, P.; Arvanitidis, C.; Koutsoubas, D., and Dounas, C., 2017. Macrobenthic assemblage structure associated with a *Caulerpa prolifera* meadow in the eastern Mediterranean Sea (Elounda Bay, Crete Island). *Regional Studies in Marine Science*, 14, 1–14.

Medellu, C.S.; Suriani, N.W., and Komansilan, A., 2019. Physical and chemical water condition in and around the area of seaweed "Lahe" (*Caulerpa* sp.) growth. *Journal of Physics: Conference Series*, 317, 012048.

Mijangos-Hernández, A.I., 2018. Análisis de la productividad de *Thalassia testudinum* Banks ex Köenig y su relación con los factores ambientales de la Reserva de la Biósfera Los Petenes, Campeche. Mexico City, México: Universidad Autónoma Metropolitana, Unidad Iztapalapa, Master's thesis, 73p.

Orth, R.J.; Carruthers, T.J.; Dennison, W.C.; Duarte, C.M.; Fourqurean, J.W.; Heck, K.L.; Hughes, A.R.; Kendrick, G.A.; Kenworthy, W.J.; Olyarnik, S., and Short, F.T., 2006. A global crisis for seagrass ecosystems. *Bioscience*, 56(12), 987–996.

Pacheco, M.C.; Pacheco-Ruíz, I.; Ramos, J.; Cetz-Navarro, N.P., and Soto, J.L., 2009. Presencia del género *Caulerpa* en Bahía de San Francisco de Campeche, Cam. *Hidrobiológica*, 19(3), 57–69.

Phillips, J.A., 2009. Reproductive ecology of *Caulerpa taxifolia* (Caulerpaceae, Bryopsidales) in subtropical eastern Australia. *European Journal of Phycology*, 44(1), 81–88.

Phillips, R.C. and Durako M.J., 2000. Global status of seagrasses. *In:* Sheppard, C. (ed.), *Seas at the Millennium: An Environmental Evaluation, Volume 3*. Amsterdam: Elsevier Science, pp. 1–16.

Powell, G.V.; Kenworthy, J.W., and Fourqurean, J.W., 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Science*, 44(1), 324–340.

Ramírez, R.; Jairo, J.; Arcila, L.; Cristina, M.; Sepúlveda, A., and Catalina, S., 2015. Quantification of components affecting the vertical attenuation coefficient for downward irradiance in Ríogrande II reservoir (Colombia). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 39(151), 228–238.

Rose, C.D. and Dawes, C.J., 1999. Effects of community structure on the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series*, 184, 83–95.

Roth-Schulze, A.J.; Thomas, T.; Steinberg, P.; Deveney, M.R.; Tanner, J.E.; Wiltshire, K.H.; Papantoniou, S.; Runcie, J.W., and Gurgel, C.F.D., 2018. The effects of warming and ocean acidification on growth, photosynthesis, and bacterial communities for the marine invasive macroalga *Caulerpa taxifolia*. *Limnology and Oceanography*, 63(1), 459–471.

Smith, C.M. and Walters, L.J., 1999. Fragmentation as a strategy for *Caulerpa* species: Fates of fragments and implications for management of an invasive weed. *Marine Ecology*, 20(3–4), 307–319.

Strickland, J.D. and Parsons, T.R., 1972. *A Practical Handbook of Seawater Analysis*. Ottawa, Canada, Fisheries Research Board of Canada, 310p.

Szmant, A.M. and Forrester, A., 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs*, 15(1), 21–41.

Tabachnick, B.G. and Fidell, L.S., 2019. *Using Multivariate Statistics*. New York: Pearson Press, 815p.

Thomas, J.E., 2003. *Caulerpa taxifolia* in Moreton Bay—Distribution and Seagrass Interactions. Queensland, Australia: The University of Queensland, Bachelor's thesis, 58p.

Tuya, F.; Haroun, R., and Espino, F., 2014. Economic assessment of ecosystem services: Monetary value of seagrass meadows for coastal fisheries. *Ocean and Coastal Management*, 96, 181–187.

Van Tussenbroek, B.I.; Barba-Santos, M.G.; Wong, J.G.R.; van Dijk, J.K., and Waycott, M., 2010. *Guía de los pastos marinos tropicales del Atlántico oeste*. México D.F.: Universidad Nacional Autónoma de México Press, 79p.

Van Tussenbroek, B.I.; Vonk, J.A.; Stapel, J.; Erftemeijer, P.L.; Middelburg, J.J., and Zieman, J.C., 2006. The biology of *Thalassia*: Paradigms and recent advances in research. *In:* Larkum, A.W.; Orth, R.J., and Duarte, C.M. (eds.), *Seagrasses: Biology, Ecology*

and Conservation. Dordrecht, The Netherlands, Springer, pp. 409–439.

Waycott, M.; Procaccini, G.; Les, D.H., and Reusch, T.B., 2007. Seagrass evolution, ecology and conservation: Nutrient dynamics in seagrass ecosystems. *In:* larkum, A.W.D.; Orth, R.J., and Duarte, C. (eds.), *Seagrasses: Biology, Ecology and Conservation*. Dordrecht, The Netherlands: Springer, pp. 25–50.

Wetzel, R.G., 2001. *Limnology: Lake and River Ecosystems*. San Diego, California: Academic Press, 985p.

Williams, S.L., 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Marine Ecology Progress Series*, 35, 91–98.

Wiltshire, K.H. and Deveney, M.R., 2017. *The Introduced Alga* Caulerpa taxifolia *in South Australia: Infestation Boundary Surveys and Feasibility of Control for Populations Outside the Containment Area*. Adelaide, Australia: South Australian Research and Development Institute (SARDI), *Research Report Series No. 946*, 16p.

Casa abierta al tiempo
UNIVERSIDAD AUTÓNOMA METROPOLITANA

ACTA DE DISERTACIÓN PÚBLICA

No. 00149
Matrícula: 2163802437

Estudio de la interacción entre Thalassia testudinum y Caulerpa paspaloides en la Reserva de la Biosfera de los Petenes, Campeche, México.

SERGIO ARMANDO FUENTES AGUEDA
ALUMNO

En la Ciudad de México, se presentaron a las 9:00 horas del día 24 del mes de mayo del año 2024 en la Unidad Iztapalapa de la Universidad Autónoma Metropolitana, los suscritos miembros del jurado:

DRA. MARGARITA ELIZABETH GALLEGOS MARTINEZ
DRA. MARIA DEL CARMEN MANDUJANO SANCHEZ
DR. ABEL SENTIES GRANADOS
DR. THOMAS A. FRANKOVICH
DR. JORDAN KYRIL GOLUBOV FIGUEROA

Bajo la Presidencia de la primera y con carácter de Secretario el último, se reunieron a la presentación de la Disertación Pública cuya denominación aparece al margen, para la obtención del grado de:

DOCTOR EN CIENCIAS BIOLÓGICAS Y DE LA SALUD

DE: SERGIO ARMANDO FUENTES AGUEDA

y de acuerdo con el artículo 78 fracción IV del Reglamento de Estudios Superiores de la Universidad Autónoma Metropolitana, los miembros del jurado resolvieron:

Aprobar

Acto continuo, la presidenta del jurado comunicó al interesado el resultado de la evaluación y, en caso aprobatorio, le fue tomada la protesta.

REVISÓ

MTRA. ROSALIA SERRANO DE LA PAZ
DIRECTORA DE SISTEMAS ESCOLARES

DIRECTOR DE LA DIVISIÓN DE CBS

DR. JOSE LUIS GOMEZ OLIVARES

PRESIDENTA

DRA. MARGARITA ELIZABETH GALLEGOS MARTINEZ

VOCAL

DRA. MARIA DEL CARMEN MANDUJANO SANCHEZ

VOCAL

DR. ABEL SENTIES GRANADOS

VOCAL

DR. THOMAS A. FRANKOVICH

SECRETARIO

DR. JORDAN KYRIL GOLUBOV FIGUEROA